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Natural History, Biogeography and Evolution of the Iberian white oak syngameon (*Quercus* L. Sect. *Quercus*)

Carlos Martins Vila-Viçosa

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Natural History, Biogeography and Evolution of the Iberian white oak syngameon (*Quercus* L. Sect. *Quercus*)

Carlos Magno Martins Vila-Viçosa

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Natural History, Biogeography and Evolution of the Iberian white oak syngameon (*Quercus* L. Sect. *Quercus*)

Carlos Magno Martins Vila-Viçosa
Doutoramento em Biodiversidade, Genética e Evolução
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Orientador
Rubim Almeida, Professor Auxiliar e Investigador, Faculdade de Ciências da Universidade do Porto

Coorientador
Cristina García Professor, Investigador, The Royal Holloway, University of London

Coorientador
Herlander Azevedo Investigador-Principal, BIOPOLIS-CIBIO/InBIO, Universidade do Porto

Dedicated to my daughter

Sworn Statement

I, Carlos Magno Martins Vila-Viçosa, enrolled in the Doctor's Degree Biodiversity Genetics and Evolution at the Faculty of Sciences of the University of Porto hereby declare, in accordance with the provisions of paragraph a) of Article 14 of the Code of Ethical Conduct of the University of Porto, that the content of this thesis reflects perspectives, research work and my own interpretations at the time of its submission.

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Foreword

According to the General Regulation of Doctoral Programs of the University of Porto (number 2, 4th Article) and the Decree Law 74/2006 (Article 31, 24 of March) revised under the Decree law 230/2009 (14th of September), this thesis includes manuscripts published or in consideration for publication in peer-reviewed scientific journals. These manuscripts are the result of collaborations with several co-authors. The candidate declares that he actively contributed to the ideas and the development of the research work, including the compilation, analysis, results, discussion and writing as in its current publication form. Additionally, the candidate was co-author in two other featured research paper co-related with the Thesis theme. These articles were not included as thesis chapters but are mentioned in final *Annex*. The candidate was supported by national funds through FCT – Fundação para a Ciência e a Tecnologia with a PhD Grant (PD/BD/52607/2014), within the Doctoral Program in Biodiversity, Genetics & Evolution (BIODIV) from the Faculty of Sciences of the University of Porto and Portuguese I.P. /MCTES, through national fundings (PIDDAC) and the Project PLANTSHIFTS (PTDC/BIA-BIC/5223/2014), through Fundo Europeu de Desenvolvimento Regional (FEDER). The thesis was developed in CIBIO-InBIO (BIOPOLIS) under the supervision of Professor Rubim Almeida from the Faculty of Sciences of the University of Porto, the co-supervisor Cristina Garcia, from the Department of Biological Sciences of the Royal Holloway University of London (RHUL), and the co-supervisor Herlander Azevedo, principal researcher from BIOPOLIS-CIBIO/InBIO, University of Porto.

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Index of published names

Quercus subsect. *Hartwissianae* (Maleev) Vila-Viçosa, Capelo, P.Alves, R.Almeida & F.M.Vázquez, Medit. Bot. 44: 9 (2022).

Quercus ×*almeidae* Vila-Viçosa, Capelo, P.Alves & F.M.Vázquez, Medit. Bot. 44: 18 (2022).

Quercus ×*alvesii* Vila-Viçosa, Capelo, R.Almeida & F.M.Vázquez, Medit. Bot. 44: 19 (2022).

Quercus ×*capeloana* Vila-Viçosa, P.Alves, P.Lemos, R.Almeida & F.M.Vázquez, Medit. Bot. 44: 22 (2022).

Quercus ×*duriensis* (Franco & Vasc.) Vila-Viçosa, Capelo, P.Alves, R.Almeida & F.M.Vázquez, Medit. Bot. 44: 24 (2022).

Quercus ×*eborense* Vila-Viçosa, Capelo, P.Alves, J.Junqueira, R.Almeida & F.M.Vázquez, Medit. Bot. 44: 24 (2022).

Quercus pseudococcifera subsp. *rivasmartinezii* (Capelo & J.C.Costa) Capelo, Vila-Viçosa & F.M.Vázquez, Medit. Bot. 44: 7 (2022).

Quercus ×*sampaioana* Vila-Viçosa, Capelo, P.Alves, R.Almeida & F.M.Vázquez, Medit. Bot. 44: 27 (2022).

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Resumo

O género *Quercus* L. é um dos géneros mais diversos e importante das plantas lenhosas, especialmente quando consideramos que são as árvores que dominam as florestas do Hemisfério Norte. A sua biogeografia intricada atravessa diversos gradientes climáticos e edáficos, contendo uma grande ambiguidade no que à delimitação das suas espécies diz respeito. Frequentemente, as propostas taxonómicas trazidas pelos trabalhos tradicionais da botânica Lineana inflacionam o número de espécies e de nomes atribuídas às mesmas, que por sua vez se dissolvem por categorias taxonómicas discordantes e indefinidas, variando da espécie à subespécie ou mesmo variedade. A preponderância dada a caracteres morfológicos naturalmente frágeis e plásticos, dispersos ao longo das áreas de distribuição de diferentes linhagens, podem gerar ambiguidade na identificação e correta delimitação das diferentes espécies. Entre os carvalhos distribuídos pela Região Paleártica Ocidental, os de folha caduca ou marcescente são dos que apresentam uma maior ambiguidade em termos do número de espécies e da sua delimitação. Esta ambiguidade é especialmente significativa na região circum-mediterrânica e nas áreas de transição entre duas importantes regiões biogeográficas, a Euro-Siberiana e a Mediterrânica. Este grau de incerteza, que se intensifica em direção ao sul da Europa, é ainda aumentado pela facilidade com que as diferentes espécies do género *Quercus* têm em hibridar entre si.

O presente trabalho tem por base uma moldura holística que abrange múltiplas áreas, do estudo taxonómico e evolutivo deste género, até à biogeografia e caracterização molecular. Este trabalho teve como objectivo principal resolver a delimitação das espécies de carvalhos caduco-marcescentes da Península Ibérica e a sua putativa introgressão, aumentado o conhecimento sobre a diversidade de espécies, tendo em vista a conservação destas espécies e das suas florestas. Um dos objectivos específicos consistiu em cruzar a revisão da história natural dos táxones dominantes e os diferentes tratamentos realizados por diferentes autores, com observações pessoais. Estes dados foram incorporados em ferramentas de modelação ecológica e caracterização molecular, resultando numa nova proposta taxonómica. Na Secção A obtiveram-se resultados de um extenso trabalho de campo, revisão de literatura e análise de colecções museológicas (herbário), atualizando a nomenclatura dos carvalhos Portugueses e mediterrânicos ocidentais. A secção B foi sustentada pela revisão aprofundada da Secção A, e promoveu a elaboração de modelos de distribuição de espécies mais detalhados, que alimentaram exercícios de projeções a períodos

passados (*ca.* 20 Ma) e futuros (2070-2100), de estudo das dinâmicas das alterações de distribuição de espécies de carvalhos mediterrânicos. O estudo de alterações na dinâmica de distribuição das espécies, projetados tanto no passado como no futuro, levaram à resolução de perguntas biogeográficas importantes, em particular as relacionadas com dinâmicas passadas. Estas permitiram melhorar o nosso conhecimento sobre as respostas das espécies a mudanças nos regimes climáticos, permitindo antecipar futuras respostas a cenários de alteração climática. A Secção C compreendeu a caracterização molecular dos carvalhos caduco-marcescentes ibéricos e dos seus híbridos, cuja delimitação é normalmente dúbia quando se pretende inferir o estatuto de uma espécie ou hipotética participação de um táxone parental em enxames de híbridos naturais. Este trabalho permitiu desvendar a filogenia dos carvalhos deste grupo presentes na região Paleártica Ocidental, sugerindo uma segregação marcada dos carvalhos-pedunculados ibéricos e revelando duas subsecções dentro da Secção *Quercus*. Estas subsecções estão biogeograficamente bem segregadas e apresentam elevados níveis de introgressão entre espécies. Os resultados obtidos demonstraram a eficiência da tecnologia de RADSeq para a reconstrução da filogenia reticulada destes carvalhos no continente Euroasiático, evidenciando a Península Ibérica como *hotspot* para a diversidade do género.

Implementámos uma abordagem circular destes métodos, em que todos se retroalimentam em termos da geração de conhecimento, como estratégia eficiente para conseguir resolver a história evolutiva deste difícil grupo de plantas. Estimamos que a biogeografia histórica reticulada destes carvalhos do Paleártico ocidental necessita de maior escrutínio, nomeadamente através da inclusão das populações vicariantes destes carvalhos oriundas do Norte de África, Próximo Oriente e Penínsulas do Sul da Europa. Os métodos a aplicar devem seguir este processo sequencial de associar uma profunda revisão da História Natural e extenso trabalho de campo, desenvolvido nas populações-tipo, com pesquisa molecular envolvento estudos de nível genómico, por forma a resolver este grupo de plantas. Com o presente trabalho contribuímos significativamente para a delimitação da unidade base de trabalho em biodiversidade (a Espécie), no complexo género *Quercus.* Providenciamos ainda ferramentas que contribuirão para a conservação das florestas mediterrânicas de carvalhos, que dominam um dos Biomas mais importantes (e um dos mais ameaçados) para a conservação de plantas a nível mundial.

Palavras-chave: alterações climáticas, conservação da biodiversidade, evolução, delimitação de espécies, herbários, florestas mediterrânicas, genómica, modelação ecológica, nomenclatura botânica, modelação ecológica, RADSeq, taxonomia

Abstract

The genus *Quercus* L. is one of the most diverse and important group of woody plants, particularly when considering that they are the trees that rule the Northern Hemisphere forests. Oaks have an intricate Biogeography that criss-crosses diverse climatic and edaphic gradients, encompassing a huge ambiguity in terms of species delimitation. Frequently, the taxonomic proposals brought by traditional Linnaean Botany are either insufficient or rather inflate the number of species and nomenclatural assignments, which are further diluted into inconsistent taxonomic ranks, varying from species to subspecies and varieties. The supremacy given to morphological characters that are inherently fragile and plastic, spread across the distribution areas of distinct lineages, may carry ambiguity on the identification and proper species delimitation. From the oaks that are distributed across the Western Palearctic region, the ones that are deciduous or brevi-deciduous present higher levels of ambiguity in terms of species number and their delimitation. This ambiguity is particularly strong in the circummediterranean region and in the transitional areas between the two major biogeographic Regions of the western Palearctic region, the Euro-Siberian and Mediterranean. This degree of uncertainty, which increases towards the Southern European Peninsulas, is amplified by the ease that the different species of oaks tend to hybridize among them.

The present work provides a holistic framework that covers multiple areas, from the taxonomic and evolutive study of this genus, to biogeography and molecular characterization. Its major objective was to resolve the species delimitation of the Iberian deciduous and marcescent oaks and putative introgression among them, enhancing the available knowledge about species diversity, which can foster suitable species and forest conservation. A specific objective was to cross-reference the natural history revision and the different taxonomic treatments brought by distinct authors, with personal observations. These data were then incorporated into ecological modelling and molecular characterization, which in the end fed a newly updated taxonomic proposal. In Section A we obtained results from extensive field, herbaria, and literature review, updating the nomenclature of the Portuguese and western Mediterranean oaks. Section B was supported by Section A's in-depth review and enabled finer species distribution models, nurturing both hindcast (since *ca.* 20 Kyr) and forecast (2070-2100) exercises of the range dynamics of Mediterranean oaks species. The study of past and future range shifts solved important pending biogeographic questions, especially related to past range-shifts. Such past-range shifts improved our knowledge on species responses to

climate dynamics and allowed a better anticipation of future responses of range shifts driven by climate change. Section C encompassed the molecular characterization of Iberian white oak species and their hybrids, whose delimitation is often faltering when one intends to infer about species rank, or hypothesize about the participation of parent taxon in natural hybrid swarms. This work allowed us to solve the phylogenetic backbone of western Palearctic white oaks, suggesting a significant segregation of the Iberian pedunculate oaks and unveiling two subsections inside Section *Quercus*. These subsections are biogeographically well-segregated and present diverse levels of introgression among species. Results demonstrated the efficiency of RADSeq for rebuilding the reticulate phylogeny of the Eurasian white oaks, showcasing the significance of the Iberian Peninsula as a major hotspot for oak diversity.

We implemented a circular approach to these methods, which retro-fed themselves in terms of insight generation, enabling a powerful strategy to solve the evolutionary history of this difficult groups of plants. We estimate that the reticulate historical biogeography of the western Palearctic white oaks deserves further scrutiny by adding vicariant oak populations from northern Africa, the Near East and southern European Peninsulas. Methods should again follow this similar additive and sequential process of adjoining deep Natural History examination, with extensive fieldwork in type populations and genome-wide molecular surveys, in order to solve this group of plants. With the present work, we were able to significantly improve on the depiction of the basic unit of Biodiversity (the Species), in the complex *Quercus* genus. We provided tools to enable further efforts for the conservation of the Mediterranean oak forests, which overwhelm one of the most important (and one of the most threatened) Biomes for plant conservation at the global scale.

Keywords: biodiversity conservation, botanical nomenclature, climate change, ecological modelling, evolution, herbaria, genomics, Mediterranean forests, RadSeq, species delimitation, taxonomy

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List of Abbreviations

A.S.L.	ABOVE SEA LEVEL
ANN	ARTIFICIAL NEURAL NETWORKS
AUC	AREA UNDER THE RECEIVER-OPERATING CURVE
BA	BØLLING-ALLERØD
CA.	CIRCA (AROUND)
CMIP-6	COUPLED MODEL INTERCOMPARISON PROJECT PHASE 6
CTA	CLASSIFICATION TREE ANALYSIS
DDRAD	DOUBLE-DIGEST RAD SEQUENCING
E	EAST
EBVS	ESSENTIAL BIODIVERSITY VARIABLES
EFA	ECOSYSTEM FUNCTIONAL ATTRIBUTES
EH	EARLY-HOLOCENE
EQN.	EQUATION
EVI	ENHANCED VEGETATION INDEX
FDA	FLEXIBLE DISCRIMINANT ANALYSIS
G	GAIN
GAM	GENERALIZED ADDITIVE MODELS
GBM(S)	GENERALIZED BOOSTED MODELS
GCMS	GENERAL CIRCULATION MODELS
GEDI	GLOBAL ECOSYSTEM DYNAMICS INVESTIGATION
GEE	GOOGLE'S EARTH ENGINE
GLM	GENERALIZED LINEAR MODELS
HS	HEINRICH-STADIAL
IP	IBERIAN PENINSULA
KAPPA	COHEN'S KAPPA
KM	KILOMETER
KM^2	SQUARE KILOMETER
KYR	THOUSAND YEARS
L	LOSS
LGM	LATE GLACIAL MAXIMUM
LH	LATE-HOLOCENE
LIDAR	LIGHT DETECTION AND RANGING
M	METER
MARS	MULTIVARIATE ADAPTIVE REGRESSION SPLINES

MAXENT	MAXIMUM ENTROPY MODEL
MH	MID-HOLOCENE
MODIS	MODERATE RESOLUTION IMAGING SPECTROMETER
N	NORTH
NDE	NARROW DISTRIBUTED AND ENDEMIC
NDWI	NORMALIZED DIFFERENCE WATER INDEX
NW	NORTHWEST
PA(S)	PSEUDOABSENCES
PP	SPECIES PREVALENCE
R^2	COEFFICIENT OF DETERMINATION
RF	RANDOM FORESTS
ROC	RECEIVER-OPERATING CURVE
SDMS	SPECIES DISTRIBUTION MODELS
SD	SORENSEN DISTANCE
SRS	SATELLITE REMOTE SENSING
SRTM	SHUTTLE RADAR TOPOGRAPHY MISSION
SS	STABLE SUITABLE
SSPS	SHARED SOCIOECONOMIC PATHWAYS SCENARIOS
SU	STABLE UNSUITABLE
TLS	TERRESTRIAL LASER SCANNING
TRI_AVG	TOPOGRAPHIC RUGGEDNESS INDEX AVERAGE
TSS	TRUE-SKILL STATISTIC
TWI_STD	TOPOGRAPHIC WETNESS INDEX STANDARD-DEVIATION
W	WEST
Y	YEAR
YDS	YOUNGER-DRYAS

Chapter 1.

General Introduction

1.1. The genus *Quercus*, a primer

Oaks species *Quercus* Linnaeus (1753: 994) belong to the family Fagaceae Dumort (1829: 12), and are one of the most important genus of woody plants, considering that they are a key component in ecosystem dynamics, majorly comprising the top climax stages of several forest topologies across the Northern hemisphere (Manos & Stanford, 2001; Nixon, 2006; Aldrich & Cavender-Bares, 2011; Carrero *et al.*, 2020). The genus is one of the most speciose tree genera, alongside *Salix*, and one of the most important in terms of biomass, at least in the Americas (Cavender-Bares, 2016; Cavender-Bares, 2019). Oaks served mankind throughout the Pleistocene and Holocene and became loaded with symbolism, as their forests provided crucial ecosystem services and impacted strongly on human well-being (Marañón *et al.*, 2012; Chassé, 2016; Van der Plas *et al.*, 2016; Da Ponte *et al.*, 2017; Aznar-Sánchez *et al.*, 2018; Acharya *et al.*, 2019; Leroy *et al.*, 2020b). Benefits included the production of consumable goods like food and shelter, climate regulation, medicine, fuelwood, charcoal, dyes, cork, bark, and art (Anderson, 2007; Eastwood & Oldfield, 2007; Kroeger *et al.*, 2014). Consumption of oak acorns played a major role in the socioeconomic development of mankind, and is registered in several archaeobotanical and review-essays (Aurenche, 1997; Brodie, 2006; Abrams & Nowacki, 2008; Deforce *et al.*, 2009; Antolín & Jacomet, 2015; Chassé, 2016). Acorn consumption habits are even related with taxonomic species discrimination, as is the case of the round-leaf Oak (*Q. rotundifolia* Lam.), which is traditionally segregated from *Q. ilex* L. by its allegedly sweeter acorns (Desfontaines, 1791; Desfontaines, 1799; Sampaio, 1909; Franco, 1990; Vázquez *et al.*, 2004; Vázquez & Coombes, 2017). This character is essentially associated with a lower concentration of tannins, as a by-product of ecological conditions, with no taxonomic or phylogenetic correspondence (Pignone & Laghetti, 2010; López-Hidalgo *et al.*, 2021; Montserrat, 2021). Apart from the human-plant dimension, oak forests regulate the environment, functioning as an important source of carbon storage, and provide habitat for wildlife, thus functioning as keystone species and adhesive elements that aggregate all the biodiversity underneath (Paine, 1969; Mills *et al.*, 1993; Nixon, 2006; Piao *et al.*, 2009; Aldrich & Cavender-Bares, 2011; Lin *et al.*, 2012; McGarvey *et al.*, 2015).

The paramount importance of oaks spans several components of global biodiversity conservation, crisscrossing from the oak species level to the oak forests habitat *per se*, whose conservation value is recognized in Europe through the European Union habitats directive, North America and Asia (Evans, 2006; Kappelle, 2006; Zhang, 2007; Torres-

Miranda *et al.*, 2011; Dey, 2014; Cavender-Bares, 2016; Committee, 2018; Deng *et al.*, 2018; Carrero *et al.*, 2020). This value is amplified by the importance of old-growth forests that are dominated or co-dominated by oak species (Burrascano *et al.*, 2009; Burrascano *et al.*, 2013; Sabatini *et al.*, 2018). These are known to hold high levels of biodiversity across several spectra, like insects, birds, but especially organisms with low dispersal abilities (Gering & Crist, 2000; Jeffries *et al.*, 2006; Flensted *et al.*, 2016; Roleček & Řepka, 2020; Benedetti *et al.*, 2021; Gonçalves *et al.*, 2021; Holuša *et al.*, 2021). The latter can include key groups like lichens and bryophytes, nemoral herbs that are shade-dependent, and especially mutualistic mycorrhizal fungi (White, 2003; Matlack, 2005; Richard *et al.*, 2005; Brunet, 2007; Ranius *et al.*, 2008; Brunialti *et al.*, 2010; Winter *et al.*, 2015; Nguyen *et al.*, 2016; Olchowik *et al.*, 2019). Even isolated old-growth oak trees are, on their own, incredible ecosystems and holders of a huge diversity, related with a wealth of microhabitats and particular conditions, which are crucial for the establishment and conservation of a growing number of organisms that span from fungi to beetles, namely xylophagous and saproxylic species (Skarpaas *et al.*, 2017; Eckelt *et al.*, 2018; Percel *et al.*, 2018; Cárdenas *et al.*, 2020; Martin *et al.*, 2022).

In addition to the remarkable role for mankind and biodiversity conservation, oaks also stand as a model clade for studies that intersect the realms of Ecology and Biogeography with Evolution (Cavender-Bares, 2019). Oak lineages tend to occupy similar ranges of habitats in different biogeographical contexts, which are intrinsically co-related with environmental drivers like climate and substrate, therefore oaks are the object of continued ecological and adaptation studies among phylogenetic and biogeographically related species (Koenig *et al.*, 2016; Meng *et al.*, 2017; Cavender-Bares *et al.*, 2018; Oney-Birol *et al.*, 2018; Alonso-Forn *et al.*, 2020; Aranda *et al.*, 2021; Pinto-Ledezma & Cavender-Bares, 2021; Sancho-Knapik *et al.*, 2021; Skelton *et al.*, 2021; Fontes *et al.*, 2022; Limousin *et al.*, 2022). At the same time, similar biogeographic patterns seem to emulate species relationships at both the macro and microevolutionary levels (Cavender-Bares *et al.*, 2015; Deng *et al.*, 2018; Hipp *et al.*, 2018; Jiang *et al.*, 2019; Cannon & Petit, 2020). This appeal is inflated by the known low barriers to introgression among oak species, which allow in-depth studies on how adaptation and persistence occurred in long-lived plant species in face of selection and past abrupt changes (Andrews, 1998; Raymo *et al.*, 1998; Petit *et al.*, 2005; Shuman *et al.*, 2009; Fletcher *et al.*, 2010; Popescu *et al.*, 2010; Eaton *et al.*, 2015; Hipp, 2015; Kremer, 2016; Firmat *et al.*, 2017; McVay *et al.*, 2017b; Li *et al.*, 2019; Leroy *et al.*, 2020a; Lazic *et al.*, 2021).

In this sense, oaks are a suitable clade to investigate speciation patterns and mechanisms, which are related with major environmental changes, linking both ecological and evolutionary perspectives (Cavender-Bares, 2019). Foremost, oaks are quite reliably considered to be among the worst models to address the biological species concept, since these species present low-barriers to gene exchange and partial reproductive isolation, with widespread interspecific gene flow in natural populations (Belahbib *et al.*, 2001; Craft *et al.*, 2002; Coyne & Orr, 2004; Petit *et al.*, 2004; Arnold & Arnold, 2006; Lepais *et al.*, 2013; Hauser *et al.*, 2017). Here, in spite of extensive introgression being common among plants, oaks tend to keep their phylogenetic and morphological coherence when in sympatry, persisting as interfertile species with well-defined boundaries (Lotsy, 1925; Van Valen, 1976; Grant, 1981; Suarez-Gonzalez *et al.*, 2018). This intricate and extant evolutionary and taxonomic complexity is reflected at the genome level, as showcased by powerful genomics studies of oak biology (Plomion & Martin, 2020; Backs & Ashley, 2021). These include the implementation of genome-wide methods that have already helped to reconstruct the evolutionary history of several main groups and flag-species such as *Q. robur*, *Q. lobata* and *Q. suber* (Plomion *et al.*, 2016; Sork *et al.*, 2016a; Ramos *et al.*, 2018). As further genomic tools become implemented, oaks stand as a major model-clade to characterize important functional genes, which will be crucial to address selection and adaptation in the face of environmental changes (Sork *et al.*, 2016b; Gil-Pelegrín *et al.*, 2017; Ramírez-Valiente *et al.*, 2017). This is fundamental also for studying population-level processes and adaptation, including introgression and the role of gene flow on the adaptation and persistence of long-lived organisms, which had to face highly variable environments and abrupt changes across their lifetime when compared to short-lived plants (Cavender-Bares, 2019). Hence, the well-known introgression in oaks and the implicit increase in genetic diversity encompasses important ecological and evolutionary consequences, especially by shaping community structure and assemblages that were established across biogeographic gradients (Lepais *et al.*, 2009; Guichoux *et al.*, 2013; Valencia-Cuevas *et al.*, 2014). This process is then essential for the adaptation of populations to new environments, avoiding local extinction in some cases, and providing selective advantages (Schwarz, 1936c; Villar, 1958; Cannon & Lerdau, 2015; Ottenburghs, 2021). Despite the fact that these hybrid interactions may be seen as evolutionary dead-ends, with adverse consequences for the interbreeding populations like extinction or genetic swamping, hybridization can also provide ecological and evolutionary opportunities, like the increase of genetic diversity by facilitating the exchange of adaptive loci trough ecological adaptation and the creation of new hybrid species (Rhymer & Simberloff,

1996; Mallet, 2007; Ruhsam *et al.*, 2011; Hedrick, 2013; Todesco *et al.*, 2016; Arnold & Kunte, 2017; Ottenburghs, 2018). These new hybrid species are generally formed by backcrossing with parental lineages, often inside hybrid swarms (where normally two sympatric populations of different species produce viable and fertile descendance) (Carney *et al.*, 2000). This may lead to extinction of parent species in a given area, especially due to an induced environmental stress (e.g. increasing drought), or on the other hand, it might give the opportunity for adaptive radiation (Schwarz, 1936c; Seehausen, 2004; Marques *et al.*, 2019; Zhang *et al.*, 2019).

Distinct edaphoclimatic envelopes have determined the evolution of oak lineages and ensuing biogeographic histories, and as such, these envelopes have played a major role on the evolutionary history of oak species and their forests (Cavender-Bares, 2019). Their past demographic processes of contraction and expansion and persistence in climatically suitable areas, or migration from refugia are reflected in ecological drivers (Svenning & Skov, 2007; Svenning *et al.*, 2015). Here, it is important to acknowledge microevolutionary (bellow the species level) and macroevolutionary (at the clade level) processes (Kremer & Hipp, 2020). Working within smaller evolutionary scales (species and geographic ranges) has the benefit of enabling better depictions of the genetic and ecological mechanisms beyond adaptation. The identification of those mechanisms (e.g. populational adaptive differentiation or persistence facing environmental change) are of utmost importance for conservation (Sork *et al.*, 2016b; Sáenz-Romero *et al.*, 2017; Ramírez-Valiente *et al.*, 2018; Cavender-Bares, 2019; Leroy *et al.*, 2020a). This biogeographic and ecological awareness is important for phylogenetic backbone resolution at both the macro and microevolutionary scales, especially when intended to solve species or infrasectional delimitation in groups with fast rates of diversification like the Eurasian roburoid oaks endured in the Late Miocene (Rundell & Price, 2009; Hipp *et al.*, 2020). Eurasian roburoid oaks deserve an in-depth analysis, addressed by new genomic tools (Kremer *et al.*, 2010; Lesur *et al.*, 2015; Plomion *et al.*, 2018).

Traditional studies on oaks have been based on compartmentalized approaches, that single out different aspects of oak biology like natural history and nomenclatural assignments, biogeography, niche modelling, and molecular-based evolutionary insights. Such somehow isolated approaches lack an integrative strategy or background. Here, we advocate that new hypothesis-generation on oak phylogeny and biology should be approached through multidisciplinary frameworks that emerge from the interface of complementary cornerstones. These encompasses the thorough review of natural history, complemented with the modelling of the environmental drivers that shaped

current or past biogeographic patterns of the previously studied taxa, that can be revisited under the light of high-resolution genomic data. This will provide solid foundations for solving or bring new insights into the evolutionary history and phylogenetic backbone resolution of distinct oak species, groups, or lineages.

1.2. Mediterranean oaks as keystone species for forest conservation, a biogeographic and modelling overview

Forest ecosystems are dominant across the globe, playing a considerable role on biosphere's primary production (Yuan *et al.*, 2010). The Mediterranean Forest and Scrubs Biome is one of the most important worldwide, by entailing the highest floristic diversity in the extratropical areas, and accumulating almost 20% of the global plant diversity, in spite of its small area (0,5% of the Earth's surface) (Cody, 1986; Medail & Quezel, 1997; Myers *et al.*, 2000; Cramer *et al.*, 2018). The wealth of woody species diversity that includes both trees and diverse nanerophytes, when in comparison with European Forests, emerges as result of a plethora of diverse ecological, geologic and climatic gradients that shaped its paleogeography (Quézel, 1976; Quézel, 1985; Verlaque *et al.*, 1997). The Mediterranean forests have *ca.* 200 more species than Europe (Médail *et al.*, 2019), encompassing 154 exclusive trees and 34 genera, in contrast to the seven genera that are exclusive of Central European forests (Quézel *et al.*, 1999). Oaks (*Quercus* L.) are one of the most important woody angiosperm genus, and are the endpoint to the ecosystem succession of most of the potential natural vegetation in the Mediterranean Basin (Zohary, 1973; Blasi *et al.*, 2004; Loidi *et al.*, 2010; Rivas-Martínez, Salvador *et al.*, 2011; Meddour *et al.*, 2017; Taleb & Fennane, 2019). When excluding infraspecific variation, the genus holds between 20 to 30 species in Europe, which can be extrapolated to 31 in the Mediterranean Basin if we consider *Quercus afares* Pomel (1875: 391), the African endemic from Section Cerris (Schwarz, 1964; Denk *et al.*, 2017; Kremer & Hipp, 2020; Coombes & Vázquez, 2021; El Mokni, 2022).

Even though ca. 30 species in the Mediterranean Basin can be considered a small amount when considering the global number of 430 oak species , the Iberian Peninsula by itself hosts nearly half the European *Quercus* taxa (Schwarz, 1964; Franco, 1990; Rivas-Martínez & Saénz, 1991; Carrero *et al.*, 2020). The Iberian Peninsula is thus rightly considered a hot-spot and refugia, especially concerning the white oaks (Olalde *et al.*, 2002). The Iberian oaks span the two unique subgenera *Cerris* and *Quercus* (Table 1).

Each subgenera broadly relates to one type of leaf behaviour, by opposing evergreen sclerophyll oaks (Subgenus *Cerris*), distributed between Sections *Cerris* and *Ilex,* to deciduous or marcescent oaks included in a unique Section (*Quercus*) (Denk *et al.*, 2017). Biogeographically, the distinctiveness of both subgenera is mostly ascribed to the transition between two main biogeographic subregions: the Eurosiberian subregion with a temperate climate and cold and rainy winters, versus the Mediterranean subregion with expressive hot and dry summers (Rivas-Martínez, S. *et al.*, 2011; Rivas Martínez *et al.*, 2011).

Section *Cerris* encompasses the cork oaks, while Section *Ilex* encompasses the holm and kermes oaks (Denk *et al.*, 2017; Hipp *et al.*, 2020). Conversely, Section *Quercus* broadly encompasses the deciduous and brevi-deciduous or marcescent oaks. They include the most emblematic pair of temperate distributed oaks, the pedunculate oak and the sessile oak, but also a subset of brevi-deciduous or marcescent oaks, adapted to transitional zones towards the Southern Mediterranean areas (De Dios *et al.*, 2009; García-Mijangos *et al.*, 2015). Brevi-deciduous or marcescent oaks include dry-adapted species that were traditionally ascribed to different sections within the *Lepidobalanus* subgenus, as proposed by Schwarz (1936a). The subset of marcescent oaks included in this former subgenus were distributed across Sections *Galliferae* and *Dascia* (Spach, 1842; Gürke, 1897; Schwarz, 1936a; Tschan & Denk, 2012). The species here included span the Algerian oak, the Portuguese oak, the Lusitanian dwarf-oak and the Pyrenean oak, as western Mediterranean representatives, and the downy oak with a wider distribution across Europe, bridging both East and West Mediterranean sub-basins (Schwarz, 1964; Franco, 1990; Pasta *et al.*, 2016).

Table 1 - Taxonomic scheme of the Iberian white oak species, following Flora Iberica (Franco, 1990). Leaf imagery was adapted from the Oak Names Database (http://www.oaknames.org/search/index.asp).

Species	Biogeography	References
Subgenus* Cerris *Oerst., Section* Cerris *Dumortier		
Q. suber L. cork oak 	Western Mediterranean Region silicate-derived and acidic soils, seldom on leached limestone- or marble-derived soils. Oceanic areas, being commonly excluded by low winter temperatures in continental areas and cold bioclimatic areas above 1000 m.	(Linnaeus, 1753; Dumortier, 1829; Oersted, 1873; Blanco-Castro *et al.*, 2005; Denk *et al.*, 2017)
Subgenus* Cerris *Oerst., Section* Ilex *Loudon		
Q. rotundifolia Lam. round-leaf oak 	Western Mediterranean Region (Iberian Peninsula, Morocco and Algeria). Edaphic indifferent from extremely dry Mediterranean areas to humid temperate woodlands as secondary evergreen forest in xerophytic outrcrops, standing with extreme low and high temperatures.	(Lamarck, 1785; Loudon, 1838; Oersted, 1873; Blanco-Castro *et al.*, 2005; Vázquez & Coombes, 2017; Vazquez *et al.*, 2020)
Q. ilex L. holm oak 	Mediterranean Region with temperate climate distribution, dependent on high annual rainfall and diminishing of precipitation seasonality, above eutrophic and mesotrophic soils.	(Linnaeus, 1753; Loudon, 1838; Oersted, 1873; Blanco-Castro *et al.*, 2005; Vázquez & Coombes, 2017)
Q. coccifera L. kermes oak 	Mediterranean Region, essentially on xerophytic outcrops and indifferent for lithology.	(Linnaeus, 1753; Loudon, 1838; Oersted, 1873; Blanco-Castro *et al.*, 2005; Iamonico & Peruzzi, 2013)
Subgenus* Quercus *Hickel & Camus, Section* Quercus *Nixon & Muller		
Quercus faginea Lam. Portuguese oak	Western Mediterranean Region, basophile taxon, it endures the lowest annual precipitation of all Iberian white oaks, being present in submediterranean areas.	(Lamarck, 1785; Sampaio, 1910b; Villar, 1935; Vasconcellos & Franco, 1954; Villar, 1958; Saénz de Rivas, 1969; Nixon, 1993; Nixon &

		Muller, 1997; Blanco-Castro *et al.*, 2005; Vazquez *et al.*, 2020)
Quercus lusitanica Lam. Lusitanian dwarf oak 	Iberian Peninsula and Morocco. Exclusive to siliceous bedrock, with an Atlantic distribution, and high intolerance to low winter minimal temperatures.	(Lamarck, 1785; Sampaio, 1910b; Nixon, 1993; Nixon & Muller, 1997; Nixon *et al.*, 1997; Vazquez *et al.*, 2020)
Quercus pyrenaica Willd. Pyrenean Oak 	Western Mediterranean Region. Mesophytic species and edaphic indifferent, although preferring siliceous bedrock in transitional submediterranean areas.	(Willdenow, 1805; Nixon, 1993; Nixon & Muller, 1997; Blanco-Castro *et al.*, 2005; Vilches *et al.*, 2016)
Quercus pubescens Willd. pubescent oak 	European Region, being distributed from Iberian Peninsula to the Middle East, up to the Danube River. It's the white oak with wider distribution range, crisscrossing from temperate to mediterranean areas. Basophile species, that stands thermophilic areas.	(Willdenow, 1796; Schwarz, 1936c; Loidi & Herrera, 1990; Nixon, 1993; Nixon & Muller, 1997; Govaerts & Avishai, 2000; Pasta *et al.*, 2016)
Quercus robur L. pedunculate oak 	Western Palearctic Distribution. Temperate species, dependent on higher annual rainfall and low precipitation Temperate-oceanic climates. Its edaphic indifferent but prefers siliceous bedrock in Iberian Peninsula.	(Linnaeus, 1753; Schwarz, 1935; Schwarz, 1936c; Schwarz, 1937; Vicioso, 1950; Nixon, 1993; Nixon & Muller, 1997; Blanco-Castro *et al.*, 2005; Eaton *et al.*, 2016; Amigo *et al.*, 2017)
Quercus petraea (Matt.) Liebl. sessile oak 	European distribution. Temperate species, dependent on higher annual rainfall, and coping with continental climates, when in comparison with *Q. robur*. Edaphic indifferent.	(Linnaeus, 1753; Lieblein, 1784; Schwarz, 1936c; Schwarz, 1936a; Nixon, 1993; Nixon & Muller, 1997; Eaton *et al.*, 2016)

At the microevolutionary scale (bellow the species level), most of the Iberian white oaks have a history of poorly solved or inherently inflated nomenclature, with the proposal and description of several independent taxa, which includes nothotaxa being randomly

proposed as independent species, subspecies or hybrids (Schwarz, 1935; Vicioso, 1950; Villar, 1958; Franco & González, 1987; Rivas-Martínez & Saénz, 1991; Penas *et al.*, 1997; Rivas-Martínez *et al.*, 2002; Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018). The complex taxonomic diversity and growing ambiguity in species delimitation inside Section *Quercus* grows towards the southern European Peninsulas, North Africa and Near East, and is intricately related with its paleogeography and the ecological diversity across the Mediterranean Basin (Kotschy, 1862; Schwarz, 1934; Schwarz, 1935; Schwarz, 1936c; Schwarz, 1936b; Schwarz, 1936a; Schwarz, 1937; Menitsky, 1984; Verlaque *et al.*, 1997; Barbero *et al.*, 2001; Manos & Stanford, 2001; Fortini *et al.*, 2015; Di Pietro *et al.*, 2020). The wealth of nomenclatural and taxonomic uncertainty at the species level emerges as major point of concern. It hampers all downstream works that envisages biodiversity conservation and the understanding of the patterns, which are related with the environmental drivers that shaped species historical biogeography, a crucial issue for contemporary ecological research and forest conservation (Hoban *et al.*, 2019; Brunialti & Frati, 2021).

Many studies on historical biogeography call for integrative approaches that bind several lines of evidence, with distinct datatypes originated from different disciplines, like phylogenetic information, fossil descriptions or hindcasted species niche modelling (Wiens & Donoghue, 2004; Hoban *et al.*, 2019). All these lines of evidence are intrinsically co-dependent, and the success of the final analysis is mandatorily influenced by the quality of each one of them. For instance, using niche conservatism to capture the fundamental niche of a given species, which is preserved across long evolutionary scales, is an indisputable task (Hutchinson, 1957; Wiens *et al.*, 2010). Therefore, to depict the oak species' niche, it is paramount to predict how climate change will affect the forest or community assemblages in a given area where its realized niche can be fully captured, i.e. without niche truncations and avoiding projections limited by environmental restrictions (Chevalier *et al.*, 2021; Chevalier *et al.*, 2022). The knowledge gap about the species, or the accurate identification of a given register (geographic reference) related with taxonomic uncertainty or inaccurate species delimitation, will result in erroneous conclusions. This is especially notorious when the major bulk of available information is accessible via online databases like www.gbif.org, which are mostly dependent or rely on ancient herbaria collections, lacking thorough taxonomic and nomenclatural revisions and updates. The error related with taxonomic misidentification is one of the main caveats related with the information that is stemming from natural history collections, followed by the geographic and environmental biases

from *ad hoc* data, collected in an unsystematic manner, and then all this is hampered by a presence-only register (Graham *et al.*, 2004; Marcer *et al.*, 2022). Phylogenetic essays can also be misled, considering that they may involuntarily incorporate misidentified samples, especially at the microevolutionary level (though also at the clade/macroevolutionary level) (Ahrends *et al.*, 2011; Ely *et al.*, 2017; Coleman & Radulovici, 2020). Picturing the environmental limits or tolerance of a given species or clade emerges as a crucial factor to understand or explain the separation of an ancestral species into a novel or separate lineage (Wiens, 2004). Environmental predictors measure a species' suitability and how it changed across both space and time geographic scales. Properly depicting those predictors can help to advance the understanding of macro and microevolutionary processes, and help to infer on how species persistence or migration have shaped actual biogeographic contexts of vicariance (Kremer, 2016; Humphries *et al.*, 2017; Jablonski, 2017; Hembry & Weber, 2020; Kremer & Hipp, 2020).

In recent years we have witnessed significant progress in the use of modelling approaches based on computational algorithms that calculate the environmental and geographic species' niches (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Sillero, 2011; Sillero *et al.*, 2021). Through Species Distribution Models (SDMs) (aka Ecological Niche Models, Climate Envelope Models, or Habitat Suitability Models) are nowadays the most widely used tools to assess species habitat suitability, normally employed to measure the impact of global change on biodiversity, and to inform policy makers (Guisan *et al.*, 2013; Ferraz *et al.*, 2021). Also, recent approaches have been used to provide insights on the past biogeographic trajectories of a species, which can feed evolutionary or demographic range-shift questioning, and a wide plethora of applications in forest-conservation research (Rodríguez-Sánchez *et al.*, 2010; Svenning *et al.*, 2011; Forester *et al.*, 2013; Maguire *et al.*, 2015; Guisan *et al.*, 2017; Brunialti & Frati, 2021; Chakraborty *et al.*, 2021; Blair *et al.*, 2022; Sanz-Arnal *et al.*, 2022). In this sense, oaks are known to have stable realized niches, where the models for this genus tend to have high predictive accuracy (Veloz *et al.*, 2012). This characteristic supports the usefulness of oaks as excellent models to study range-shift dynamics and vicariance biogeography. They may also serve as a source to investigate further biodiversity losses driven by shifts in climate suitability of oak species or community assemblages (Svenning *et al.*, 2011; Fordham *et al.*, 2014; Fordham *et al.*, 2016; Saltré *et al.*, 2016). The largest hampering factor when trying to predict the distribution of a species across the geographic space, is the constrain of the misidentification or misinformation given by the

distinct data sources, which is deeply related with the species concept and delimitation of a given taxon. Thus, the aforementioned problems associated with oak misidentification become especially relevant when using modelling approaches to address oak diversity, distribution and its intricate biogeography.

1.3. The *species* concept within the context of oaks

Species are the fundamental unit of biodiversity (Mayr, 1982; De Queiroz, 2005; Hohenegger, 2014). They are particularly critical for advancing the study of historical biogeography (Ackerly, 2003; Wiens & Donoghue, 2004), which merges the scientific disciplines of ecology, evolution and biodiversity conservation (Brown *et al.*, 1996; Sites & Crandall, 1997; Blackburn & Gaston, 1998; Peterson & Navarro-Sigüenza, 1999; Barraclough & Nee, 2001; Avise, 2007). Ultimately, this demands that systematists envisage ways to objectively or accurately delimit species units in nature (Sites Jr & Marshall, 2003). Broadly, there are 26 distinct species concepts, which amplifies the confusion and controversy on conservation and decision making (Wilkins, 2009; Hausdorf, 2011). It also obliges taxonomists and conservationists to work together towards establishing consensus on what constitutes a species (Mace, 2004; Frankham *et al.*, 2012).

In plants, the biological species concept based on reproductive isolation is still the most widely applied and accepted (Aguiar, 2021). However, the concept is not impermeable to discrepancies, like the fact that expected reproductive barriers are often permissive to gene flow (Hey & Pinho, 2012). Interestingly, species can be maintained as cohesive units, despite the presence of inter-breeding that often leads to new species formation, or the presence of parallel adaptation due to polyploidization (Papadopulos *et al.*, 2011; Rice *et al.*, 2019). The former, related with inter-specific gene-flow when in sympatry, is particularly notable in oaks (Burger, 1975). Therefore, oaks are seen as a species syngameon, where species can extensively exchange genetic information through hybridization, but at the same time keep their major and well-defined morphological and molecular barriers (Lotsy, 1925; Grant, 1981; Cannon & Petit, 2020).

The known pervasive hybridization among oaks along with the species-syngameon concept have been fairly reported in classic natural history (Brotero, 1805; Coutinho, 1888; Sampaio, 1910a; Trelease, 1917; Schwarz, 1935; Schwarz, 1937; Camus, 1938; Camus, 1939), and validated by molecular analysis and the more recent genomic studies

(De Dios *et al.*, 2006; Burgarella *et al.*, 2009; Lepais *et al.*, 2009; Guichoux *et al.*, 2013; Eaton *et al.*, 2015; Fortini *et al.*, 2015; Hipp, 2015; An *et al.*, 2017; McVay *et al.*, 2017b; Hipp *et al.*, 2019a; Hipp *et al.*, 2019b; Cannon & Petit, 2020; Hipp *et al.*, 2020; Leroy *et al.*, 2020a; Plomion & Martin, 2020; Backs & Ashley, 2021; Chen *et al.*, 2021; Lazic *et al.*, 2021; Li *et al.*, 2022; Zhou *et al.*, 2022).

The delimiting of species is important towards understanding basic evolutionary processes (Sites Jr & Marshall, 2003). As such, the over- or under-resolving of species is a source of confusion when studying population or species-level processes. This bottleneck obliges researchers to accurately define each species units, and establish which ones are to be tested in molecular frameworks. These species units should be solidly substantiated by combining morphological characters and ecological awareness, that will enable biogeographically informed phylogenies, which are intrinsically and deeply related with the genus natural history (Manos & Stanford, 2001).

1.4. Natural history of oaks

1.4.1. The broad European overview

The natural history of oaks began with the first European Botanical work of the French naturalist Charles de l'Ecluse (Clusius, 1576), where eight oaks were mentioned. These included six current species: *Quercus lusitanica* Lam., *Q. petraea* (Matt.) Liebl and *Q. pyrenaica* Willd. in the deciduous and marcescent oaks; *Q. coccifera* L., *Q. rotundifolia* Lam. and *Q. suber* L. as the evergreen species. Linnaeus (1753) added *Q. aegilops* L., *Q. alba* L., *Q. cerris* L., *Q. ilex* L., *Q. nigra* L., *Q. prinus* L. *Q. robur* L., *Q. phellos* L., and *Q. rubra* L. to the list, later supplemented by Lamarck (1785) with *Q.* ×*crenata* Lam., *Q. faginea* Lam., *Q. pubescens* Willd. and *Q. velutina* Lam. Still in the 18th century, Desfontaines (1799) added *Q. pseudococcifera* to the kermes oaks list. In the 19th century, Willdenow (1801, 1805, 1809) described *Q. bicolor* Willd, *Q. canariensis* Willd., *Q. prinoides* Willd. *Q. montana* Willd. and *Q. myrtifolia* Willd.

Portuguese naturalist Brotero (1805) became the first botanist to talk about hybridization gradients in oaks, when describing *Q. hybrida* Brot.. He referred to the Portuguese oak (*Q. faginea* Lam.), highlighting the geographic areas that were known to generate hybrid swarms between this species and the pedunculate oak (*Q. robur)* in central-western Portugal (Figure 1). These hybrid swarms were later recognized by Coutinho (1888) and

posteriorly described as *Q.* ×*coutinhoi* Samp. by Sampaio (1910a). At this stage, the first infrageneric and sectional proposals started to emerge, such as the ones provided by Loudon (1838); Spach (1842); Endlicher (1847), and the one from Ørsted (1871) which ultimately became the major infrageneric reference. In the 20th century, the works of Trelease (1924); Maleev (1935); Schwarz (1936a); Camus (1938;1939); Menitsky (1984) and Nixon (1993) became the major taxonomic references up until the most contemporary work of Denk *et al.* (2017). All the pre-molecular era works are complementary of each other. Conversely, the proposal of Denk *et al.* (2017) linking morphology with molecular data led to a reorganization of the previous proposals.



Figure 1 - Climax forest of *Quercus faginea* Lam. (Alcolombal, Mafra, Lisbon, Portugal).

The genus *Quercus* has as Type-species the pedunculate oak (*Q. robur* L.) (Britton & Brown, 1913; Sprague, 1929). Recent molecular works have brought consistency to the two historically established subgenera, *Cerris* and *Quercus*. The former incorporates Sections *Cyclobalanopsis, Cerris* and *Ilex*, while the latter incorporates Sections *Lobatae*, *Protobalanus*, *Quercus, Ponticae* and *Virentes* (Denk *et al.*, 2017). Sections *Ponticae, Protobalanus* and *Virentes* have a small number of species (2,4 and 7 respectively), with *Ponticae* displaying a peculiar biogeographic disjunction between the Caucasus in Europe (*Q. pontica* K. Koch) and north California/south Oregon in the United States (*Q. sadleriana* R.Br.ter) (Denk *et al.*, 2017; Carrero *et al.*, 2020). The cycle cup oaks (section *Cyclobalanopsis*) are only found in Asia with 112 species, while Section

Cerris (15 species) and *Ilex* (39 species) extended into the western Palearctic Region (Deng *et al.*, 2018; Simeone *et al.*, 2018; Jiang *et al.*, 2019; Carrero *et al.*, 2020). In the American continent, the red oaks (Section *Lobatae*) are the most speciose with 113 species, ranging from North America to the solitary *Q. humboldtii* Bonpl. in Colombia (Torres-Miranda *et al.*, 2011; Hauser *et al.*, 2017; Carrero *et al.*, 2020). The white oaks (Section *Quercus*) have 128 species, distributed across both the Eurasian and the American Continents (Camus, 1939; Schwarz, 1964; Nixon *et al.*, 1997; Petit *et al.*, 2002; Carrero *et al.*, 2020).

1.4.2. The European white oaks

Inside the Eurasian white oaks, the Roburoids clade evidenced unique rates of diversification across the Late Miocene (Hipp *et al.*, 2020). In the past, this group received distinct treatments by different taxonomists. Almost simultaneously, Camus (1934) and Maleev (1935), provided infrasectional discrimination to the Eurasian Roburoid oaks, proposing a subsection *Macrantherae* (Stef.) A. Camus, coupled with two other subsections (*Macrolepides* and *Ponticae*), inside Section Mesobalanus (Camus, 1934). The former subsection (*Macrantherae*) was based on the previous independent Section proposal of Stefanoff (1930) and included *Q. frainetto* Ten., *Q. macranthera* Fisch. & C.A.Mey. ex Hohen. and *Q. pyrenaica* Willd. This proposal from Camus (1934) is reiterated and validly published by Maleev (1935), who included in a Section *Cerridolepis*, the same subsection *Macrantherae*. The same author incorporated Subsection *Galliferae* in Section *Eulepidobalanus* (Ørsted, 1871), where he included *Q. boissieri* Reut. and *Q. dshorochensis* K.Koch. Another Subsection referenced by Maleev (1935) is *Robur* (Reichenbach, 1832), to which he subdues Series *Hartwissianae* (*Q. hartiwissiana* Steven)*, Euroburi* (the broad European *Q. robur* L.), *Eusessiles (broad European Q. petraea*)*, Haas* and *Ibericae.* These last two broadly include related infraspecific taxa that are mostly southeastern distributed and were described by Steven (1857) and Kotschy (1862). Examples in Section *Haas* included *Q. erucifolia* Steven, *Q. haas* Kotschy, *Q. imeretina* Steven ex Woronow, *Q. longipes* Steven, and *Q. pedunculiflora* K.Koch, and were related to the broad *Q. robur* group. Species in Section *Ibericae* included *Q. iberica* Steven, *Q. hypochrysa* Steven, *Q. kozlowskyi* Woronow ex Grossh., while *Q. pubescens* Willd. was included in the broad *Q. petraea* group.

Soon after, Schwarz (1936a) kept the subgenus *Lepidobalanus* Ørsted (1871), establishing six Sections (*Dascia, Galliferae, Prinopsis, Prinus, Robur* and *Roburoides*). The Eurasian Roburoids were distributed among four of them (*Dascia, Galliferae, Robur* and *Roburoides*). The subsections inside the former sections *Robur* and *Roburoides* contained the European broad *Q. robur* (*Robur*) and *Q. petraea* (*Roburoides*), respectively. According to the author, subsection *Roburiformis* inside Section *Roburoides* included two series (*Lamprophyllae* and *Sessiliflorae*) belonging to the broad *Q. petraea* group. Series *Lamprophyllae* incorporated a pool of relict taxa that are mostly distributed in the southern European peninsulas "*Q. iberica* Steven*, Q. huguetiana* (Franco & G.López) Rivas Mart.*, Q. dshorochensis* K.K ch. and *Q. mannifera* Lindl.". Series *Sessiliflorae* incorporated the Central European and temperate distributed taxa like *Q. polycarpa* Schur, *Q. petraea* (Matt.) Liebl, *Q. dalechampii* Ten., *Q. pinnatiloba* K. Koch, *Q. cedrorum* Kotschy, and *Q. longifolia* K. Koch. In the broad *Q. robur* group (Sect Robur), Schwarz (1936a) used a similar dichotomy as for the broad *Q. petraea* species, by indicating a primitive group (Series *Primitivae*) and a Series *Pedunculatae.* Series *Primitivae* included *Q. hartwissiana* Steven and his recently described *Q. estremadurensis* O. Schwarz. These are grouped due to the fact that they share particularly related sets of characters, like pubescent twigs and peduncles, but especially the presence of a leaf margin with numerous, straight/rectilinear and even lobes, with total absence of sinual nerves, and cup-scales that are more numerous and smaller towards the base of the cup (Schwarz, 1935). Series *Pedunculatae* incorporates the temperate distributed *Q. robur* L., *Q. haas* Kotschy, *Q. erucifolia* Steven and *Q. pedunculiflora* K. Koch.

As stated, the Eurasian Roburoids included sections *Dascia* and *Galliferae* in addition to Sections *Robur* and *Roburoides*. Section *Dascia* included three subsections (*Daimio*, *Esculus*, *Pseudoprinus*), with the first two incorporating the Eurosiberian white oaks. Subsection *Daimio* included the Asian distributed *Q. dentata* Thunb., subsection *Esculus* incorporated a set of western Paleartic white oaks (Schwarz, 1936a), distributed across three relevant Series. Series *Confertae* includes a foursome of oak species that contain morphologically related oaks, distributed across the circummediterranean area. In a clear west-to-east gradient, these are *Q. pyrenaica* Willd., *Q. frainetto* Ten., *Q. vulcanica* Boiss. et Heldr. and *Q. kotschyana* O. Schwarz. Secondly, Series *Esculiformes* incorporates taxa related with *Q. macranthera* Fisch. & C.A.Mey. ex Hohen.*,* like *Q. syspyrensis* K.Koch, *Q. bornmuelleriana* O.Schwarz, *Q. esculiformis* O.Schwarz and *Q. sicula* Borzí. Finally, Series *Lanuginosae* incorporates all taxa related with broad *Q.*

pubescens, like *Q. congesta* Presl., *Q. brachyphylla* Kotschy and *Q. virgiliana* Ten. As to Section *Galliferae*, it incorporated the Eurasian subsection *Chimonophyllum*, that was divided into three Series. Series *Orientales* included *Q. canariensis* Willd. and *Q. boisseri* Reut.; Series *Occidentales* included *Q. faginea*; Series *Humiles* included *Q. lusitanica* Lam. and *Q. infectoria* G.Olivier.

Later, both Camus (1939) and (Menitsky, 1972) endorsed similar sectional and infrasectional circumscriptions, with small nuances. Camus (1939) recognized subsections *Hartwissianae*, *Pedunculatae, Sessiliflorae*, *Galliferae* and *Lanuginosae,* with a similar approach to the same subsets of taxa. Notwithstanding, she kept the taxa from Series *Confertae* and *Esculiformis* "Section *Dascia sensu* Schwarz (1936a)" in their own section (*Mesobalanus*). She also shifted some taxa between subsections *Lanuginosae* and *Sessiliflorae*, like the pubescent petraeoid oaks *Q. dalechampii* Ten. and *Q. cedrorum* Kotschy. Menitsky (1972) proposed the contemporary Section *Quercus* for the occidental Asian-distributed white oaks, and assumed three subsections that covered subsection *Robur* (Endlicher, 1847)*,* with *Q. hartwissiana* Steven and several subspecies included in broad *Q. robur* (*Q. robur* L. *s.s.* and *Q. pedunculiflora* K.Koch) and broad *Q. petraea* (*Q. iberica* Steven, *Q. dshorochensis* K.Koch, and *Q. pinnatiloba* K. Koch). The subsection *Galliferae* (Gürke, 1897), included two taxa as subspecies of *Q. infectoria* (*Q. infectoria* G. Oliver and *Q. boissieri* Reut.). Subsection *Macrantherae* (Camus, 1934) also has two subspecies inside *Q. macranthera* (*Q. macranthera* Fisch. & C.A.Mey. ex Hohen.*,* and *Q. syspyrensis* K.Koch), plus *Q. frainetto* Ten.*.* Notably, the author (Menitsky, 1972) assumed *Q. pubescens* Willd. and related subspecies (*Q. anatolica* O.Schwarz) as *species insertae sedis* (species of uncertain placement), since traditionally this species group were positioned in subsection *Robur* by (Endlicher, 1847), due to the convergence of characters with the sessile oaks (broad *Q. petraea*). This questioning by the author is of significance, since Menitsky (1972) recognizes closeness to subsections *Macrantherae,* similar to Schwarz (1936a) who inserted it in the same Section (*Dascia*).

1.4.3. The Iberian white oaks

As to the Iberian Peninsula's white oaks, the most prominent and recent work by Franco (1990) suggests the presence of seven native species (Franco, 1990): *Q. robur* L., *Q. petraea* (Matt.) Liebl., *Q. faginea* Lam., *Q. canariensis* Willd., *Q. lusitanica* Lam., *Q.*

pyrenaica Willd. and *Q. pubescens* Willd (Figure 2). Franco (1990) recognizes subspecies inside *Q. faginea* and *Q. petraea*. These include taxa that other authors assume as independent species, like *Quercus broteroi* (Cout.) Rivas Mart. & Sáenz de Rivas as former subspecies of *Q. faginea* Lam., and *Q. huguetiana* (Franco & G.López) Rivas Mart. as former subspecies of *Q. petraea* (Matt.) Liebl. (Rivas-Martínez & Saénz, 1991; Saéz & Aymerich, 2021).

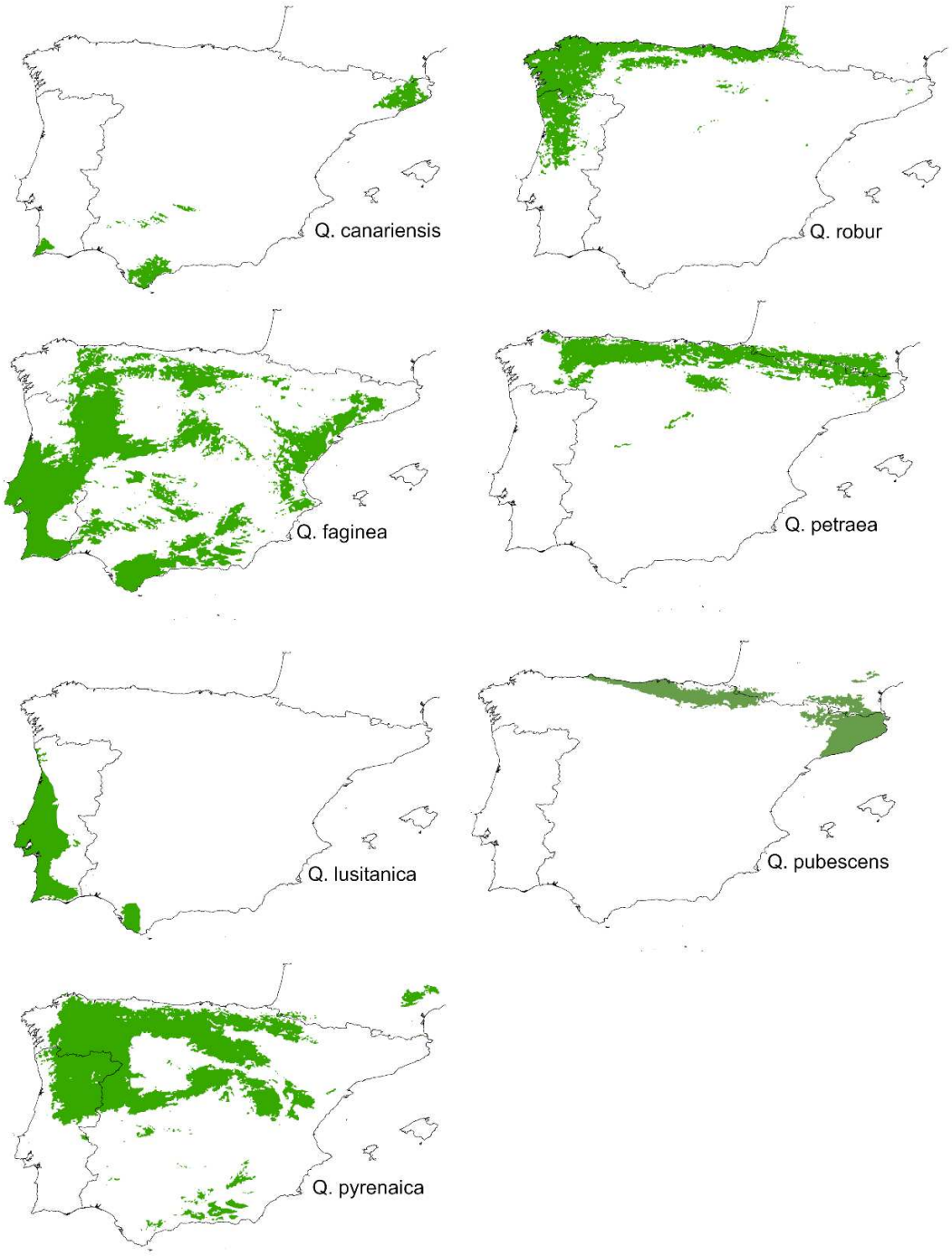


Figure 2 – Broad distribution of the Iberian white oaks (Section *Quercus*). Adapted from Vila-Viçosa *et al.* (2019).

Previous essays on Iberian white oaks entail the works of Brotero (1805), who recognized five species in Portugal. He acknowledged *Q. robur* L., *Q. pyrenaica* Willd., *Q. faginea* Lam. and *Q. lusitanica* Lam., and insightfully recognized a dichotomy inside *Q. robur* L., thus adding *Q. racemosa* Lam. to the list, as determined by specimens from Center-West Portugal with larger peduncles. Afterwards, Willkomm and Lange (1861) recognized the same white oak species, but included *Q.* ×*cerrioides* Willk. & Costa as a variety of *Q. petraea* (Matt.) Liebl., designating the populations of the littoral mountains of Catalonia. The later work of Coutinho (1888) is an extensive review of all Portuguese species, forms, varieties and hybrids among oaks. It has the particularity of already adding *Q. canariensis* Willd. to the Iberian list of white oaks, albeit reported as a variety of *Q. faginea* Lam. "*Q. lusitanica* var. *mirbeckii* (Durieu) Cout". In the early 20th century, Sampaio (1910b) disambiguated nomenclatural issues between the names *Q. lusitanica* Lam. and *Q. faginea* Lam.. Still, these issues remained pervasive amongst botanists that kept using *Q. lusitanica* to name the Mediterranean trees inside Section *Galliferae,* namely *Q. faginea* Lam. (Webb, 1838; Candolle, 1864; Schwarz, 1936c; Schwarz, 1936a; Schwarz, 1937; Vicioso, 1950). In the same year, Sampaio (1910a) assigned names to Iberian hybrid oaks, where he included *Q.* ×*coutinhoi* Samp. (Figure 3), *Q.* ×*welwitschii* Samp. and *Q.* ×*tavaresii* Samp., related to the hybrids between *Q. robur* L. and *Q. faginea* Lam., *Q. pyrenaica* Willd. and *Q. faginea* Lam. and *Q. robur* L. and *Q. pyrenaica* Willd, respectively. This last hybrid was published previously as *Q.* ×*andegavensis* Hy (1895).



Figure 3 - *Quercus* ×*coutinhoi* Samp. from Caldas da Rainha, Portugal.

After describing a new species inside Section *Robur* (*Q. estremadurensis* O. Schwarz) (Schwarz, 1935), Schwarz (1936c) produced a global review of the Subgenus *Lepidobalanus* in Catalonia, adding an Iberian subspecies of *Q. pubescens* Willd. (*Q. pubescens* subsp. *palensis* (Palassou) O.Schwarz). This work is quite important, since the author started to evoke hybridogenous branches (nothotaxa) that biogeographically occupied or outweighed one of their parents. He articulated that by possessing broader ecological limits, these nothotaxa may have led to the extinction of one of the parents under contexts of climatic shifts. Schwarz frequently gave to this nothotaxa the rank of subspecies, on their way to become new species. The author mentioned relevant nothotaxa, namely *Q.* ×*subpyrenaica* Villar previously described by Villar (1935), *Q* ×*cerrioides* Willk. & Costa, *Q.* ×*anselmi* auct. ex O.Schwarz, *Q.* ×*fontqueri* O.Schwarz, *Q.* ×*calvescens* Vukot., *Q.* ×*viveri* Sennen and *Q. lusitanica* subsp. *navarrana* as a transitional hybridization area of *Q. faginea* Lam. and *Q. robur* L in the Basque Country (Schwarz, 1936c). Remarkably, the author already mentioned the morphological plasticity as a hampering factor for species delimitation when in the presence of hybrid swarms, considering that tools were restricted, at that time, to distinctive morphological characters. One example refers to places where Section *Galliferae*'s oaks contact with species of Section *Dascia*, like the sympatric *Q. faginea* Lam., *Q. pyrenaica* Willd. and *Q. pubescens* Willd. in the Northeast Iberian Peninsula. The author mentions that it is virtually impossible to distinguish between different hybrids, either of *Q. faginea* with *Q. pyrenaica* or *Q.* ×*subpyrenaica* Villar, and between them and the parents, due to the overlap of trichome types and leaf shapes (Schwarz, 1936c).

Later on, Schwarz (1937) dismissed his previous proposal on *Q. estremadurensis* O. Schwarz, assuming it as a "lost" lineage that was probably heavily hybridized with *Q. faginea* Lam. or *Q. lusitanica* Lam.. He then described a subspecies of *Q. robur* as *Q. robur* subsp. *broteroana* O. Schwarz for the Northwest Iberian Peninsula, which putatively resulted from the transitional hybridization gradient between his previously described *Q. estremadurensis* (Figure 4) and the European *Q. robur* L. (Figure 5). Later, for the European Flora (Schwarz, 1964), the author erased his Iberian infraspecific and specific considerations, synonymizing both taxa to the European *Q. robur*. Extraordinarily, he kept the remaining southern European taxa that were related within the pedunculate Oak. Examples included *Q. robur* subsp. *brutia* (Ten.) O.Schwarz in Italy and *Q. pedunculiflora* K.Koch in the eastern Mediterranean basin.



Figure 4 - *Quercus estremadurensis* (Sintra, Portugal).



Figure 5 - *Quercus robur* subsp. *broteroana* O. Schwarz (left) and *Q. estremadurensis* O. Schwarz (right), (Sintra, Portugal).

The global review of Camus (1939) recognized the specificity of the Iberian subspecies of *Q. robur* L., by downgrading *Q. estremadurensis* from Schwarz (1935) to the subspecies rank (*Q. robur* subsp. *estremadurensis* (O.Schwarz) A.Camus). She also reestablished *Q. faginea* Lam. as the legitimate name for the Portuguese oak, and she described a big set of hybrids between almost all Iberian white oaks. She went as far as to give different names to the cross between subspecies and some backcrosses between already stablished hybrids and their parents. Some of these hybrids are described upon the same materials studied by Coutinho (1888) and Sampaio (1910a), creating an overflow of names. Some examples include *Q.* ×*subandegavensis* A.Camus, *Q.* ×*subalpestris* A. Camus, *Q.*×*pseudofaginea* A.Camus, *Q.* ×*mairei* A.Camus, *Q.* ×*neomairei* A.Camus, *Q.* ×*ferreirae* A.Camus, *Q.*× *carrissoana* A.Camus, *Q.* ×*allorgeana* A.Camus, *Q.* ×*molleri* A.Camus and *Q.* ×*jahandiezii* A.Camus., which overlap each other in terms of participating taxa and nomenclatural assignments.

The biggest collective of information about the Genus *Quercus* in the Iberian Peninsula was summarized by Vicioso (1950). Here, the author compiled all the information from the previous authors (Coutinho, 1888; Coutinho, 1930; Schwarz, 1935; Schwarz, 1936c; Schwarz, 1936b; Schwarz, 1936a; Schwarz, 1937; Camus, 1938; Camus, 1939; Coutinho, 1939). He followed the sectional proposal of Schwarz (1936a) and added to the list of the already mentioned oaks the three subspecies inside *Q. robur* (*Q. broteroana, Q. estremadurensis* and *Q. pedunculata*), the subspecies inside *Q. petraea* (*Q. huguetiana*), *Q. pyrenaica, Q. pubescens* with one subspecies (*Q. palensis*), and *Q.* ×*cerrioides* Willk. & Costa as independent species inside Section *Dascia*. He incorporated inside section *Galliferae* the *Q. canariensis*, *Q. lusitanica* and two subspecies inside *Q. faginea* (*Q. broteroi* and *Q. valentina*). Vicioso (1950) added new nothotaxa on his own, i.e. *Q.* ×*secalliana* C.Vicioso, *Q.* ×*salcedoi* C.Vicioso, *Q.* ×*marianica* C.Vicioso, *Q.* ×*legionensis* C.Vicioso, *Q.* ×*costae* C.Vicioso, and *Q.* ×*aruciensis* C.Vicioso.

Four years afterwards, Vasconcellos and Franco (1954) produced a new review of the Portuguese Oaks that incorporated interesting insights. Foremost, they recovered the name *Q. faginea* Lam. as the legitim designation for the Portuguese oak, after reviewing the P-Lam herbarium in Paris. They relegated alleged subspecies to the variety rank (*Q. faginea* var. *salicifolia* (Cout.) Franco & Vasc.). The authors also disregarded any infraspecific variation inside broad *Q. robur,* yet they made important contributions to the recognition and description of some Portuguese nothotaxa, with emphasis on the tomentose kermes oak that lives in karstic limestones of the western Mediterranean

Basin, described as a putative hybrid between *Q. rotundifolia* and *Q. coccifera* (*Q. ×airensis* Franco & Vasconcellos).

An important review about the western Mediterranean oaks was performed by Villar (1958), bringing a valuable perspective from a physical geographer that was mostly based in the analysis of climax vegetation and forest associations (Tuxen, 1956; Loidi & Fernández-González, 2012; Somodi *et al.*, 2021) (Figure 6). His contribution is also important considering that the author surveyed North African herbaria oak collections (Villar, 1938; Villar, 1943; Villar, 1949), which are of vital importance for the Western Mediterranean biogeography. Villar (1958) disregarded the nomenclatural rules but brought important insights to the taxonomic ranks and species of the Iberian white oaks. He was averse to the contributions of Otto Schwarz and rejected *Q. estremadurensis* O. Schwarz as a valid species, attributing its leaf variation to the plasticity of vernal twigs (he remarkably related the leaf morphology of *Q. estremadurensis* to *Q. huguetiana*, a broad *petraea* oak). Furthermore, he redesigned the distribution at the varietal level of the alleged subspecies inside *Q. faginea*. He hypothesized that the south- and western-distributed original concept of *Q. faginea* Lam. had an amplified area across the Douro thermophilic Basin (up to Burgos), contrasting with the previous (Coutinho, 1888; Vicioso, 1950) and actual assumptions (Franco, 1990; Rivas-Martínez & Saénz, 1991) that place this border in the Northeast of Portugal.

The most recent advances on Iberian oaks, from the end of the 20th century and start of the 21st century, were conducted by Prof. Salvador Rivas-Martinez who lead the geobotanical Iberian school of Phytosociology. Soon after Flora Iberica (Franco, 1990), Rivas-Martínez and Saénz (1991) produced an enumeration of the Iberian oaks, establishing new independent taxa and updating the nomenclature of a large set of nothotaxa. Rivas-Martínez and collaborators established narrow endemic species inside broad *Q. robur* group, like *Q. orocantabrica* Rivas Mart. & al. (Rivas-Martínez *et al.*, 2002), and inside broad *Q. petraea* group like *Q. pauciradiata* Penas & al. (Penas *et al.*, 1997). This was based on distinctive morphological characters that included leaf shape, petiole length and cup-scale structure in *Q. orocantabrica*, and trichome type morphology and leaf phenology in *Q. pauciradata*. More recently, other works expanded their geographical distribution within the Iberian Peninsula and addressed these taxa's hybridization with other oaks (del Río *et al.*, 2014; Martínez & Llamas, 2022b; Martínez & Llamas, 2022a).



Figure 6 - *Arisaro shimorrhini-Quercetum fagineae* forest association established at mid-slope (Serras de Loures, Lisbon, Portugal).

Globally, we are in the presence of notorious contributions and a wealth of thorough revisions and insights across the realms of Linnaean taxonomy, plant morphology, vegetation ecology and natural history, done by expert-based naturalists and taxonomists. Most of these proposals agree between each other, across both macro and microevolutionary processes-scales. Interestingly, a minority entail different aspects that deserves scrutiny, considering that they are based upon accurate observations from the leading experts in the field. Such proposals are particularly meaningful when addressing infrasectional and specific inferences that force-feedback towards evolutionary relationships. They urge novel molecular-level insights to better depict the historical biogeography of this genus, define the basic units to work with (species), and integrate phylogeny with species circumscription towards better suited ecological modelling. All this insight ultimately targets knowledge-based establishment of decision-making frameworks towards oak and forest conservation.

1.5. Molecular insights on oak biodiversity

The most standard morphological features used to distinguish oak species are foliar and cup characters (Wrońska-Pilarek *et al.*, 2016). Since these are highly plastic, fragile and may transcend the interspecific rank, the demand for the use of molecular tools to solve

species delimitation is indisputable. This is particularly vital in close species' groups that experienced rapid and recent explosions, like the European Roburoids (Hipp *et al.*, 2020). For the last three decades, the use of molecular tools has been crucial to address biodiversity, speciation, and conservation (Barraclough & Nee, 2001; Rull, 2008; Whitham et al., 2008). Advances in this field have greatly helped to discern the genetic basis of the inherent barriers to panmixia, which cause structuring and drift, and ultimately lead to taxonomic differentiation (Noor & Feder, 2006). This differentiation is often due to demography but can also be caused by natural selection. The signatures left in the genome by these two phenomena can be hard to distinguish when genome-wide inference is not employed. The latter can identify genomic blocks, single markers and genes related with adaptation or fitness, while simultaneously identifying genomic regions that display neutral variation and are more apt to estimate genetic diversity parameters (Luikart et al., 2003).

The *Quercus* genus is phylogenetically challenging due to multiple features, including the ability to accumulate large reservoirs of diversity within populations and species, their ecological proficiency for rapid migration, the high intraspecific genetic variation coupled with low interspecific differentiation, and the frequent interspecific gene flow (Denk & Grimm, 2010; Kremer *et al.*, 2012; Hipp, 2015; Kremer & Hipp, 2020). The genus is particularly problematic with regards to species delimitation, where frequent species hybridization can generate a complex history of past introgressions within the same taxonomic group. This gives to the oak genome the characteristics of a mosaic (Hipp *et al.*, 2020) that is shaped by ecology, biogeography and hybridization.

1.5.1. Use of low-resolution molecular DNA markers

Up until recently, the study of the evolutionary history of oaks was conditioned by the presence of an incomplete fossil register and limitations in molecular-based techniques, which were often based on a limited number of polymorphic loci. These limitations resulted from small number of available plastid and nuclear ribosomal markers, which do not contain sufficient information for resolving challenging nodes in the presence of processes regarding hybridization or incomplete lineage sorting (Zimmer & Wen, 2015) . None withstanding, a variety of molecular DNA markers enabled the characterization of forest resources among oaks (Soto *et al.*, 2003; Petit *et al.*, 2004; Guichoux *et al.*, 2013; Lind & Gailing, 2013; Hipp *et al.*, 2019a). For instance, the use of low resolution

molecular markers allowed to unveil already the five-to-six major sections (*Cerris*, *Cyclobalanopsis*, *Ilex*, *Protobalanus* and *Quercus*) (Manos *et al.*, 1999; Manos & Stanford, 2001; Denk & Grimm, 2010; Hubert *et al.*, 2014). Other examples include, for instance, the work of Scotti-Saintagne *et al.* (2004) who addressed the differentiation among the two most common European white oaks (*Q. robur and* Q. petraea). Coelho *et al.* (2006) used AFLP to infer genetic diversity among *Q. suber* and *Q. rotundifolia*. SSRs (microsatellites) were used to study several aspects of oak genetics, from genetic diversity and differentiation (Degen *et al.*, 1999; Gugerli *et al.*, 2007; Herrera-Arroyo *et al.*, 2013; Zhang *et al.*, 2013; Cao *et al.*, 2021) to population structure (Ainsworth *et al.*, 2003; Ramírez-Valiente *et al.*, 2019; Di Pietro *et al.*, 2021; Guo *et al.*, 2021; Tamaki *et al.*, 2021) and hybridization analysis (Lepais *et al.*, 2009; Ortego & Bonal, 2010; Peñaloza-Ramírez *et al.*, 2010; Lepais *et al.*, 2013; Beatty *et al.*, 2016; Sullivan *et al.*, 2016; Lopez De Heredia *et al.*, 2018; Pérez-Pedraza *et al.*, 2021). Furthermore, the oaks' plastidial information was commonly used along with nuclear DNA (Fineschi *et al.*, 2002; Fernández i Marti *et al.*, 2018; Li *et al.*, 2019; Degen *et al.*, 2021; Li *et al.*, 2022), though results suggest that it may be poorly suited to fine-scale DNA barcoding and phylogenetic approaches (Simeone *et al.*, 2013; Pham *et al.*, 2017). Broadly, the characterization of a reduced number of loci cannot accurately translate the evolutionary history of a species or genus, thus requesting for the higher resolution associated with genome-level approaches (de la Harpe *et al.*, 2017; Cavender-Bares, 2019).

1.5.2. Reduced representation strategies (RADSeq, GBS, HYBSeq)

Recent years have witnessed significant progress in the capacity to analyse species diversity at the molecular level, with the advent of platforms that progressively bring genome-level resolution to the fore. Such progress has been mostly leveraged by next generation sequencing (NGS) technologies (Faure & Joly, 2015), which are based on the massive parallelization of DNA sequencing. The entrance into the genomic era has allowed a boost in our knowledge on the life history of oaks and Fagaceae (Petit *et al.*, 2013; Plomion & Martin, 2020). Recently, Leroy *et al.* (2020b) have revisited the symbolism of longevity, cohesiveness, and robustness associated with oaks, through the lens of genomics, emphasising how the evolutionary history of the Holocene has strengthened the relationships between mankind and oaks. Backs and Ashley (2021) highlight the need to increase the number of focal species, targeting rare and threatened oaks that are underrepresented in most genomic studies.

Broadly, NGS-enabled strategies can be divided between reduced representation strategies, whole genome resequencing (WGS), and de novo assembled genomes. Reduced representation strategies comprise techniques that cost-effectively subsample regions of the genome (e.g. RADSeq, GBS, HYBSeq, AHE) or pool individuals into a single genome resequencing effort (PoolSeq). Restriction site-associated DNA sequencing (RADSeq) generates a reduced representation of the genome by using a set of enzymes (one or more) to cut the genome at specific restriction sites. These are selected and ligated to Illumina specific adaptors for high-throughput sequencing (HTS) of the genomic regions adjacent to the restriction sites, also called RADloci. The recovery of thousands of RADloci can be used to search for single nucleotide polymorphisms (SNPs) and other nucleotide sequence variants, in order to investigate species phylogeographic patterns (Miller *et al.*, 2007). It enables the low-cost discovery and genotyping of numerous genetic markers without requiring a reference genome, as is the case of most non-model organisms (Andrews *et al.*, 2016). By unveiling thousands of polymorphic genetic markers across the genome, it offers robust sampling by targeting a subset of the genome with major depth of coverage per locus (Mastretta-Yanes *et al.*, 2015; Shafer *et al.*, 2017). Genotyping by sequencing (GBS) is akin to RADSeq, and uses enzyme-based complexity reduction to target a small portion of the genome, which is coupled with DNA barcoded adapters followed by simultaneous marker detection and genotyping (Poland & Rife, 2012). GBS has been used to address introgression and adaptation in oaks (Gugger *et al.*, 2021; O'Donnell *et al.*, 2021). Finally, HybSeq combines target enrichment of nuclear genes with the use of low-coverage shotgun sequencing to assemble high-copy genomic targets. This efficiently generates copious data from both the low-copy nuclear genome and high-copy elements (e.g. organellar genomes), suitable for phylogenomic analyses in plants (Weitemier *et al.*, 2014). Anchored Hybrid Enrichment (AHE) is a method that was designed to recover hundreds of unique orthologous and conservative loci, allowing the resolution of both shallow and deep evolutionary relationships. Specifically, it uses probes designed for target enrichment of these hundreds of loci in highly conserved anchor regions, which are flanked by less conserved regions within reference genomes. This methodology allows to recover a large number of unlinked loci that are useful at varying phylogenetic timescales (Lemmon *et al.*, 2012). By using targeted enrichment of nuclear loci, AHE provides similar insights to RADSeq albeit allowing for longer loci to be sequenced, which generates more complete datasets, as demonstrated for white oaks evolution (Crowl *et al.*, 2020).

Recent works tend to favour HybSeq as the most appropriate high-throughput sequencing technology for plant systematics (Dodsworth *et al.*, 2019). Still, HybSeq, AHE and RADSeq are both powerful in solving phylogenies (Crowl *et al.*, 2020; Zhou & Xiang, 2022), with RADSeq being considered more appropriate inside genus or species with reduced phylogenetic divergences, and HybSeq within multiple taxonomic scales (Arnold *et al.*, 2013; Eaton & Ree, 2013). Zhou and Xiang (2022) working with *Castanea* (Fagaceae) indicate that RADSeq better suits work with limited funding and time, whilst advising caution on the building of species trees that use short RADSeq loci, and suggesting the avoidance of trees of individual loci. Interestingly, to the best of our knowledge HybSeq has not been used in oaks, though it has been largely used to solve the systematics of challenging groups of plants (Giaretta *et al.*, 2021). Conversely, oak diversity and speciation have been strongly addressed using RADSeq approaches, including the variant ddRAD. These studies have targeted multiple aspects of the oaks genomic landscape (Jiang *et al.*, 2019; Hipp *et al.*, 2020; Tóth *et al.*, 2021). Of note, RADSeq contributed to solve the backbone of the American and Asian oak clades (Hipp *et al.*, 2014; Cavender-Bares *et al.*, 2015; Fitz-Gibbon *et al.*, 2017; Hauser *et al.*, 2017; Deng *et al.*, 2018; Kim *et al.*, 2018). McVay and co-workers (2017a; 2017b) have unveiled the obscure legacy of extensive hybridisation within the Eurasian *Roburoid* and disjunct *Ponticae* lineages, also by applying RADSeq. Recently, Hipp et al. (2020) published the most coherent and complete approach to the landscape genomics of the global oaks' phylogeny, establishing the subgenera *Quercus* (with sections *Quercus*, *Lobatae*, *Virentes*, *Protobalanus*, and *Ponticae*) and *Cerris* (with sections *Cyclobalanopsis*, *Cerris* and *Ilex*). Yet with all these advances, the phylogenetic relationships within the main groups of Quercus are yet to be unveiled, especially at the infrasectional level, which entails a major challenge and questioning in Oak evolution (Denk et al., 2017). This is particularly true within the Eurasian Roburoid clade, which displays outstanding rates of diversification through the Late Miocene (Hipp et al., 2020). Considering that the use of RADSeq data offers technical limitations to the study of hybridization, Crowl and co-workers (2020) recently employed a separate reduced representation strategy: anchored hybrid enrichment (AHE). Here, they used a genomic dataset of 493 nuclear loci to evaluate the reticulate history of white oaks and the consequences of historical introgression. Ultimately, they detected signatures of historical gene flow between an ancestor of the Eurasian Roburoid lineage and the now-allopatric *Quercus pontica*, and between two allopatric North American lineages, *Dumosae* and *Prinoideae* (Crowl *et al.*, 2020).

1.5.3. Genome-levels approaches (WGS and de novo genomes)

Reduced representation strategies are very useful and have a high potential for approaching close species complexes, by enabling the incorporation of many samples (de la Harpe *et al.*, 2017; McKain *et al.*, 2018; Johnson *et al.*, 2019). However, the decrease in per-base DNA sequencing costs may increasingly favour the use of whole genome resequencing. WGS is characterized by the shotgun sequencing of genomic DNA, which is then mapped onto a reference de novo genome. Since it incorporates information from the whole genome rather than subsampling a given number of loci, WGS has emerged as the most powerful approach to connect the micro- an macroevolutionary scales. In oaks, WGS have been used mostly in landscape and population genomics (Zhou *et al.*, 2021; Fu *et al.*, 2022; Liang *et al.*, 2022), especially focused on the genetic variation enrolled in species local adaptation, adaptive divergence, the impact of introgression, and the importance of selection in shaping genetic variation. Such studies can cover the prediction of the dynamics of climate change scenarios and depict the features underlying the evolutionary success history of oaks on conquering the northern hemisphere forests (Sork *et al.*, 2022). On the phylogenomic front, WGS has been specifically used to tackle major macroevolutionary events and ancient genome-wide signatures of hybridization across Fagaceae, with an emphasis on *Quercus* genus species (Zhou *et al.*, 2022). It is reasonable to expect a surge in studies that incorporate whole genome sequence information to tackle multiple aspects of oak genetic variation. The cornerstone for any genomics progress in each species or genus is the existence of quality de novo assembled reference genomes. In oaks, reference genomes have been generated and made publicly available for at least 10 species (NCBI; accessed 18 October 2022). Most significant sequencing projects incorporate *Q. robur* (Plomion *et al.*, 2016; Plomion *et al.*, 2018), *Q. lobata* (Sork *et al.*, 2016a), *Q. suber* (Ramos et al., 2018), *Q. mongolica* (Ai et al., 2022), *Q. rotundifolia* (Rey *et al.*, 2022) and *Q. acutissima* (Fu et al., 2022). The high quality reference genome of *Q. robur* L. provided by Plomion *et al.* (2016) and used to tackle longevity in tree species, is already an indisputable tool to develop downstream works, either for forest trees adaption or for species delimitation, where NGS-based tools can leverage stronger phylogenetic backbone resolution (de la Harpe *et al.*, 2017). These initiatives are of paramount importance to assess the genomic basis of perennial and longevous organisms like trees and especially oaks, which benefited from direct fitness advantages across the evolutionary timeline, facilitating adaptability to changing environments (Deng *et al.*, 2018; Plomion *et al.*, 2018; Sork *et al.*, 2022).

1.6. Objectives and thesis outline

1.6.1. Objectives

The present thesis summarizes a collective effort to address the taxonomy, distribution, and phylogenetic backbone of the Iberian white oak syngameon. This is accomplished through an integrative approach that combines natural history, ecological modelling, biogeography, and evolutionary molecular analysis. Initially, we intended to specifically address the phylogenetic positioning of submediterranean marcescent oaks, traditionally ascribed to subsection *Galliferae*. However, the work was subsequently enlarged to all Section Quercus, due the tendency that these species have to hybridize with other sympatric white oaks. Thus, the main objective was to resolve the phylogenetic backbone of this interesting subset of white oaks, targeting the many problems associated with nomenclatural and taxonomic inflation that are exponentiated by hybridization. Work entailed the readdressing of the syngameon inside the Iberian Peninsula, relocating it in the evolutionary context of the Eurasian white oaks. It also addressed the potential contribution of the Iberian Peninsula as biogeographic landmark to understand the evolutionary history of the paramount *Quercus* genus in the western Palearctic Region. Specific objectives encompassed the combination of three major components (natural history, ecological modelling, and evolution), and can be summarized as:

- an effort to provide a thorough review of oak species nomenclature and the study of the type specimen available in referenced herbaria;

- the application of species distribution models based on previous suitably circumscribed taxa, in order to infer on their demographic history, ranging from past to future climate scenarios;

- an inference on both demographic history and evolutionary questioning, towards developing future frameworks for the conservation of vulnerable taxa;

- an effort to merge taxonomic and biogeographic data with newly generated molecular insights, to solve phylogenetic backbones and species delimitation;

- a focal analysis and testing of the position of submediterranean oaks (mostly from Subsection *Galliferae*) inside Section Quercus, inferring on the importance of the

Iberian Peninsula as a biogeographic landmark for understanding the western Palearctic white oaks;

- a targeting of the introgression issue inside the Iberian white oaks, which are widely known for a history of taxonomic inflation, putative hybridization, and nomenclatural inconsistency.

1.6.2. Thesis outline

The present thesis is divided into **eight chapters**. Additionally, results have been organized around three sections, which thematically group the four published papers and the two chapters currently in preparation for publication.

Chapter 1 (Introduction) contextualizes the Genus *Quercus* detailing its broad importance for mankind, as well as its significance as a model to combine ecology and biogeography with plant evolution. Afterwards, it provides a broad overview on the relevance of Mediterranean Forests to the conservation of this genus, which suffers with inconsistencies around species delimitation. This brings downstream problematics when one intends to reach the final unit for conservation (the species), which is then examined with more detail within the Iberian subset of white oaks (Section *Quercus*), by providing a chronological overview of past natural history contextualization efforts. On a more forward look, Chapter 1 then reflects upon the emerging status of molecular tools to solve the phylogenetic backbone and species delimitation of this peculiar group of plants.

Section A (Natural History and Oak Taxonomy) addresses the western Mediterranean oaks natural history, taxonomy and nomenclature and contains two chapters. **Chapter 2** develops a new annotated checklist of the Portuguese Oaks, with a full nomenclatural update of the oaks' taxa and nothotaxa. It was feasible through the accumulation of more than a decade of fieldwork across the Iberian Peninsula, and the thorough examination of 15 herbaria plus all the available historical literature. It enlarges the traditional number of eight oaks' species to eleven and re-stablishes a new record of 23 hybrids, spread across the continent. These taxa include four yet unreported to science, and one in need of nomenclatural assignment. **Chapter 3** contains a review of the type oaks' specimens described by René Louiche Desfontaines in the Paris herbarium (P-Desf). This work scrutinizes three names largely used and traditionally synonymized to other taxa, and

provides a chorological and nomenclatural update to the biogeography of western Mediterranean oaks forests (i.e. *Q. faginea, Q. ilex* and *Q. pseudococcifera*).

Section B (Biogeography and Conservation of southern European white oaks) encompasses three chapters related to Oak biogeography and conservation through the lens of ecological modelling. **Chapter 4** intends to elucidate the late-Quaternary dynamics of the Temperate-Mediterranean transition area since the Last Glacial Maximum, using eight oak taxa in the Iberian Peninsula. It applies correlative species distribution models to hindcast the demographic evolution of the marcescent forest ecotone and depicts the relation of past transiently co-occurring oaks with the present occurrence of hybrids. **Chapter 5** developed hindcasts of past distributional shifts for eight submediterranean white oaks to infer their capability to unveil future range shifts. This work targets vulnerable oaks, ranging an east-to-west gradient across the Mediterranean Basin. Finally, **Chapter 6** also uses distribution models and intends to measure the influence of remotely-sensed Ecosystem Functioning Attributes (EFAs) and climatic variables (either separately or combined) to depict adequate areas for Iberian white oaks' conservation. It also provides spatially explicit information about the ecological suitability of each oak species or subset of species, which is relevant for developing biogeographic conservation frameworks.

Section C (Molecular phylogeny and Evolution of Iberian white-oaks) encompasses the single **Chapter 7**, which entails the molecular characterization using RADSeq, geared towards resolving the phylogenetic backbone of the Iberian white oaks. Here, we developed a combination of phylogenetic and complexity reduction methods that solves pending taxonomic issues about speciation and hybridization in Iberian white oak species. We also enlarged the current understanding of the phylogeography of the Eurasian white oaks by adding a considerable number of Iberian oaks to the world phylogenetic tree.

Finally, **Chapter 8** (General discussion, concluding remarks and future perspectives) provides a summarizing exercise, offering an integrative discussion of the different chapters, followed by the general conclusions of the work and a set of future questions in need of addressing upon the results presented in the present thesis.

Disclaimer: The thesis outline does not follow a chronological sequence of publications. Instead, it follows the narrative the three sections and their chapters, stablished by the author and supervising team. In this sense, species nomenclature adopted the official

nomenclature assignable at the moment of the data treatment of each chapter, or updated as ongoing data became available.

1.7. References

Abrams MD, Nowacki GJ. 2008. Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *The Holocene* **18**(7): 1123-1137.

Acharya RP, Maraseni T, Cockfield G. 2019. Global trend of forest ecosystem services valuation–An analysis of publications. *Ecosystem Services* **39**: 100979.

Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* **164**(S3): S165-S184.

Aguiar C. 2021. *Evolução das Plantas*. Lisbon: Imprensa Nacional - Casa da Moeda, S. A.

Ahrends A, Rahbek C, Bulling MT, Burgess ND, Platts PJ, Lovett JC, Kindemba VW, Owen N, Sallu AN, Marshall AR. 2011. Conservation and the botanist effect. *Biological Conservation* **144**(1): 131-140.

Ai W, Liu Y, Mei M, Zhang X, Tan E, Liu H, Han X, Zhan H, Lu X. 2022. A chromosome-scale genome assembly of the Mongolian oak (Quercus mongolica). *Molecular ecology resources* **22**(6): 2396-2410.

Ainsworth E, Tranel P, Drake BG, Long S. 2003. The clonal structure of Quercus geminata revealed by conserved microsatellite loci. *Molecular Ecology* **12**(2): 527-532.

Aldrich PR, Cavender-Bares J 2011. Quercus. *Wild crop relatives: Genomic and breeding resources*: Springer, 89-129.

Alonso-Forn D, Sancho-Knapik D, Ferrio JP, Peguero-Pina JJ, Bueno A, Onoda Y, Cavender-Bares J, Niinemets Ü, Jansen S, Riederer M, et al. 2020. Revisiting the Functional Basis of Sclerophylly Within the Leaf Economics Spectrum of Oaks: Different Roads to Rome. *Current Forestry Reports* **6**(4): 260-281.

Amigo J, Rodríguez-Guitián MA, Honrado J, Alves P 2017. The lowlands and midlands of Northwestern Atlantic Iberia. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 191-250.

An M, Deng M, Zheng S-S, Jiang X-L, Song Y-G. 2017. Introgression threatens the genetic diversity of Quercus austrocochinchinensis (Fagaceae), an endangered oak: a case inferred by molecular markers. *Frontiers in Plant Science* **8**: 229.

Anderson MK. 2007. Indigenous uses, management, and restoration of oaks of the far western United States. *Technical Note, United States Department of Agriculture Natural Resources Conservation Service, Washington DC, USA*.

Andrews JT. 1998. Abrupt changes (Heinrich events) in late Quaternary North Atlantic marine environments: a history and review of data and concepts. *Journal of Quaternary Science: Published for the Quaternary Research Association* **13**(1): 3-16.

Andrews KR, Good JM, Miller MR, Luikart G, Hohenlohe PA. 2016. Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics* **17**(2): 81-92.

Antolín F, Jacomet S. 2015. Wild fruit use among early farmers in the Neolithic (5400–2300 cal bc) in the north-east of the Iberian Peninsula: an intensive practice? *Vegetation History and Archaeobotany* **24**(1): 19-33.

Aranda I, Cadahía E, Fernández De Simón B. 2021. Specific leaf metabolic changes that underlie adjustment of osmotic potential in response to drought by four Quercus species. *Tree Physiology* **41**(5): 728-743.

Arnold B, Corbett-Detig RB, Hartl D, Bomblies K. 2013. RAD seq underestimates diversity and introduces genealogical biases due to nonrandom haplotype sampling. *Molecular Ecology* **22**(11): 3179-3190.

Arnold ML, Arnold ML. 2006. *Evolution through genetic exchange*: Oxford University Press.

Arnold ML, Kunte K. 2017. Adaptive genetic exchange: a tangled history of admixture and evolutionary innovation. *Trends in ecology & evolution* **32**(8): 601-611.

Aurenche O. 1997. Balanophagie: mythe ou réalité? *Paléorient*: 75-85.

Avise JC 2007. Twenty-five key evolutionary insights from the phylogeographic revolution in population genetics. *Phylogeography of southern European refugia*: Springer, 7-21.

Aznar-Sánchez JA, Belmonte-Ureña LJ, López-Serrano MJ, Velasco-Muñoz JF. 2018. Forest ecosystem services: An analysis of worldwide research. *Forests* **9**(8): 453.

Backs JR, Ashley MV. 2021. Quercus conservation genetics and genomics: past, present, and future. *Forests* **12**(7): 882.

Barbero M, Loisel R, Médail F, Quézel P. 2001. Signification biogéographique et biodiversité des forêts du bassin méditerranéen. *Bocconea* **13**: 11-25.

Barraclough TG, Nee S. 2001. Phylogenetics and speciation. *Trends in ecology & evolution* **16**(7): 391-399.

Beatty GE, Montgomery WI, Spaans F, Tosh DG, Provan J. 2016. Pure species in a continuum of genetic and morphological variation: sympatric oaks at the edge of their range. *Annals of Botany* **117**(4): 541-549.

Belahbib N, Pemonge MH, Ouassou A, Sbay H, Kremer A, Petit R. 2001. Frequent cytoplasmic exchanges between oak species that are not closely related: Quercus suber and Q. ilex in Morocco. *Molecular Ecology* **10**(8): 2003-2012.

Benedetti Y, Kapsalis E, Morelli F, Kati V. 2021. Sacred oak woods increase bird diversity and specialization: Links with the European Biodiversity Strategy for 2030. *Journal of Environmental Management* **294**: 112982.

Blackburn TM, Gaston KJ. 1998. Some methodological issues in macroecology. *The American Naturalist* **151**(1): 68-83.

Blair ME, Le MD, Xu M. 2022. Species distribution modeling to inform transboundary species conservation and management under climate change: promise and pitfalls. *Frontiers of Biogeography* **14**(1): 1-11.

Blanco-Castro E, Casado-Gonzáles M, Costa-Tenorio M, Escribano R, García-Antón M, Génova-Fuster M, Gómez-Mazaneque Á, Gómez-Mazaneque F, Moreno-Saiz JC, Juaristi CM, et al. 2005. *Los bosques ibéricos. Una interpretación geobotánica*. Barcelona: Editorial Planeta, Barcelona, Spain.

Blasi C, Filibeck G, Frondoni R, Rosati L, Smiraglia D. 2004. The map of the vegetation series of Italy. *Fitosociologia* **41**(1): 21-26.

Britton NL, Brown A. 1913. *An Illustrated Flora of the Northern United States: Canada and the British Possessions from Newfoundland to the Parallel of the Southern Boundary of Virginia, and from the Atlantic Ocean Westward to the 102d Meridian*: C. Scribner's sons.

Brodie C. 2006. Oak: The Frame of Civilization. *American Scientist* **94**(2): 188-189.

Brotero FA. 1805. *Flora Lusitanica, seu plantarum, quae in Lusitania vel sponte crescunt, velfrequentius coluntur, ex florum praesertim sexubus systematice distributarum, synopsis.* Lisboa: Typographia regia.

Brown JH, Stevens GC, Kaufman DM. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual review of Ecology and Systematics*: 597-623.

Brunet J. 2007. Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology* **44**(3): 563-572.

Brunialti G, Frati L. 2021. Modeling of Species Distribution and Biodiversity in Forests. *Forests* **12**(3): 319.

Brunialti G, Frati L, Aleffi M, Marignani M, Rosati L, Burrascano S, Ravera S. 2010. Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. *Plant Biosystems* **144**(1): 221-233.

Burgarella C, Lorenzo Z, Jabbour-Zahab R, Lumaret R, Guichoux E, Petit R, Soto A, Gil L. 2009. Detection of hybrids in nature: application to oaks (Quercus suber and Q. ilex). *Heredity* **102**(5): 442-452.

Burger WC. 1975. The species concept in Quercus. *Taxon* **24**(1): 45-50.

Burrascano S, Keeton WS, Sabatini FM, Blasi C. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest ecology and management* **291**: 458-479.

Burrascano S, Rosati L, Blasi C. 2009. Plant species diversity in Mediterranean old-growth forests: a case study from central Italy. *Plant Biosystems* **143**(1): 190-200.

Camus A 1934. Quelques diagnoses de Fagacées. In: France Stbd ed. *Bulletin de la Société Botanique de France*. Paris: La Société, 814-818.

Camus A. 1938. *Les chênes. Monographie du genre Quercus. Genre Quercus, sous-genre Cyclobalanopsis, sous-genre Euquercus (sections Cerris et Mesobalanus).* . Paris: Lechevalier.

Camus A. 1939. *Les Chênes. Monographie du genre Quercus. Genre Quercus, sous-genre Euquercus (sections Lepidobalanus et Macrobalanus).* Paris: Lechevalier.

Candolle AD. 1864. *Prodromus systematis naturalis regni vegetabilis sive enumeratio contracta ordinum, generum specierumque plantarum huc usque cognitarum, juxta methodi naturalis normas digesta sumptibus sociorum*. Paris: Treuttel et Würtz.

Cannon CH, Lerdau M. 2015. Variable mating behaviors and the maintenance of tropical biodiversity. *Frontiers in Genetics* **6**: 183.

Cannon CH, Petit RJ. 2020. The oak syngameon: more than the sum of its parts. *New Phytologist* **226**(4): 978-983.

Cao Y, Zhang D-Y, Zeng Y-F, Bai W-N. 2021. Recent demographic histories of temperate deciduous trees inferred from microsatellite markers. *BMC ecology and evolution* **21**(1): 1-9.

Cárdenas AM, Gallardo P, Salido Á, Márquez J. 2020. Effects of Environmental Traits and Landscape Management on the Biodiversity of Saproxylic Beetles in Mediterranean Oak Forests. *Diversity* **12**(12): 451.

Carney SE, Gardner KA, Rieseberg LH. 2000. Evolutionary changes over the fifty-year history of a hybrid population of sunflowers (Helianthus). *Evolution* **54**(2): 462-474.

Carrero C, Jerome D, Beckman E, Byrne A, Coombes A, Deng M, González-Rodríguez A, Hoang V, Khoo E, Nguyen N. 2020. The red list of oaks 2020. *The Morton Arboretum: Lisle, IL, USA*: 11-12.

Cavender-Bares J. 2016. Diversity, distribution and ecosystem services of the North American oaks. *International Oaks* **27**: 37-48.

Cavender-Bares J. 2019. Diversification, adaptation, and community assembly of the American oaks (Quercus), a model clade for integrating ecology and evolution. *New Phytologist* **221**(2): 669-692.

Cavender-Bares J, González-Rodríguez A, Eaton DA, Hipp AA, Beulke A, Manos PS. 2015. Phylogeny and biogeography of the American live oaks (Quercus

subsection Virentes): a genomic and population genetics approach. *Molecular Ecology* **24**(14): 3668-3687.

Cavender-Bares J, Kothari S, Meireles JE, Kaproth MA, Manos PS, Hipp AL. 2018. The role of diversification in community assembly of the oaks (Quercus L.) across the continental U.S. *American Journal of Botany* **105**(3): 565-586.

Chakraborty D, Móricz N, Rasztovits E, Dobor L, Schueler S. 2021. Provisioning forest and conservation science with high-resolution maps of potential distribution of major European tree species under climate change. *Annals of Forest Science* **78**(2).

Chassé B. 2016. Eating acorns: what story do the distant, far and near past tell us, and why. *Int. Oaks* **27**: 107-135.

Chen J, Zeng Y-F, Zhang D-Y. 2021. Dispersal as a result of asymmetrical hybridization between two closely related oak species in China. *Molecular phylogenetics and evolution* **154**: 106964.

Chevalier M, Broennimann O, Cornuault J, Guisan A. 2021. Data integration methods to account for spatial niche truncation effects in regional projections of species distribution. *Ecological Applications* **31**(7): e02427.

Chevalier M, Zarzo-Arias A, Guélat J, Mateo RG, Guisan A. 2022. Accounting for niche truncation to improve spatial and temporal predictions of species distributions. *Frontiers in Ecology and Evolution* **10**: 944116.

Clusius C. 1576. *Rariorum aliquot stirpium per Hispanias observatarum historia*. Antwerpen: Ex officina Christophori Plantin.

Cody ML 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. In: Soule ME ed. *Conservation biology : the science of scarcity and diversity*. Sunderland, Mass. (USA): Sinauer Associates.

Coelho AC, Lima M, Neves D, Cravador A. 2006. Genetic diversity of two evergreen oaks [Quercus suber (L.) and Quercus ilex subsp rotundifolia (Lam.)] in Portugal using AFLP markers. *Silvae Genetica* **55**(3): 105-118.

Coleman CO, Radulovici AE. 2020. Challenges for the future of taxonomy: talents, databases and knowledge growth. *Megataxa* **1**(1): 28–34-28–34.

Committee FoCE. 2018. Flora of China. *Flora of China.*

Coombes AJ, Vázquez FM. 2021. Correct citation and lectotypification of Quercus× kabylica and Q.× numidica (Fagaceae). *Phytotaxa* **478**(2): 275–280-275–280.

Coutinho AXP. 1888. Os Quercus de Portugal. *Boletim da Sociedade Broteriana* **6**: 47-116.

Coutinho AXP. 1930. *Notas da Flora de Portugal*. Paris: Aillaud, Albes & Cia.

Coutinho AXP. 1939. *Flora de Portugal (Plantas Vasculares)*. Lisbon.

Coyne JA, Orr HA. 2004. *Speciation*: Sinauer associates Sunderland, MA.

Craft KJ, Ashley MV, Koenig WD. 2002. Limited hybridization between Quercus lobata and Quercus douglasii (Fagaceae) in a mixed stand in central coastal California. *American Journal of Botany* **89**(11): 1792-1798.

Cramer W, Guiot J, Fader M, Garrabou J, Gattuso J-P, Iglesias A, Lange MA, Lionello P, Llasat MC, Paz S, et al. 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change* **8**(11): 972-980.

Crowl AA, Manos PS, McVay JD, Lemmon AR, Lemmon EM, Hipp AL. 2020. Uncovering the genomic signature of ancient introgression between white oak lineages (Quercus). *New Phytologist* **226**(4): 1158-1170.

Da Ponte E, Kuenzer C, Parker A, Rodas O, Oppelt N, Fleckenstein M. 2017. Forest cover loss in Paraguay and perception of ecosystem services: A case study of the Upper Parana Forest. *Ecosystem Services* **24**: 200-212.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2006. Hybrid zones between two European oaks: a plant community approach. *Plant Ecology* **187**(1): 109-125.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology* **204**(2): 189-205.

de la Harpe M, Paris M, Karger DN, Rolland J, Kessler M, Salamin N, Lexer C. 2017. Molecular ecology studies of species radiations: current research gaps, opportunities and challenges. *Molecular Ecology* **26**(10): 2608-2622.

De Queiroz K. 2005. Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences* **102**(suppl_1): 6600-6607.

Deforce K, Bastiaens J, Van Calster H, Vanhoutte S. 2009. Iron Age acorns from Boezinge (Belgium): the role of acorn consumption in prehistory. *Archaologisches Korrespondenzblatt* **12**(3): 381.

Degen B, Streiff R, Ziegenhagen B. 1999. Comparative study of genetic variation and differentiation of two pedunculate oak (Quercus robur) stands using microsatellite and allozyme loci. *Heredity* **83**(5): 597-603.

Degen B, Yanbaev Y, Mader M, Ianbaev R, Bakhtina S, Schroeder H, Blanc-Jolivet C. 2021. Impact of Gene Flow and Introgression on the Range Wide Genetic Structure of Quercus robur (L.) in Europe. *Forests* **12**(10): 1425.

del Río S, Álvarez Nogal R, Candelas A, González-Sierra S, Herrero L, Penas A. 2014. Preliminary study on taxonomic review using histological sections of some Iberian species from the genus Quercus L.(Fagaceae). *American Journal of Plant Sciences* **5**: 2773-2784.

Deng M, Jiang X-L, Hipp AL, Manos PS, Hahn M. 2018. Phylogeny and biogeography of East Asian evergreen oaks (Quercus section Cyclobalanopsis; Fagaceae): insights into the Cenozoic history of evergreen broad-leaved forests in subtropical Asia. *Molecular phylogenetics and evolution* **119**: 170-181.

Denk T, Grimm GW. 2010. The oaks of western Eurasia: traditional classifications and evidence from two nuclear markers. *Taxon* **59**(2): 351-366.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Desfontaines R 1791. Observations sur le chêne Ballota ou à glands doux du Mont-Atlas. In: (France) Ards ed. *Histoire de l'Académie royale des sciences, avec les mémoires de mathématique et de physique*. Paris: Du Pont, 394-399

Desfontaines R. 1799. *Flora Atlantica, sive Historia Plantarum, quae in Atlante, Agro tunetano et algeriensi crescunt*: Panckouckes.

Dey DC. 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *Forest Science* **60**(5): 926-942.

Di Pietro R, Conte AL, Di Marzio P, Fortini P, Farris E, Gianguzzi L, Müller M, Rosati L, Spampinato G, Gailing O. 2021. Does the genetic diversity among pubescent white oaks in southern Italy, Sicily and Sardinia islands support the current taxonomic classification? *European Journal of Forest Research* **140**(2): 355-371.

Di Pietro R, Conte AL, Di Marzio P, Gianguzzi L, Spampinato G, Caldarella O, Fortini P. 2020. A multivariate morphometric analysis of diagnostic traits in southern Italy and Sicily pubescent oaks. *Folia Geobotanica* **55**(3): 163-183.

Dodsworth S, Pokorny L, Johnson MG, Kim JT, Maurin O, Wickett NJ, Forest F, Baker WJ. 2019. Hyb-Seq for flowering plant systematics. *Trends in Plant Science* **24**(10): 887-891.

Dumortier B-C. 1829. *Analyse des familles des plantes: avec l'indication des principaux genres qui s'y rattachent*. Tournay: J. Casterman, Ainé.

Eastwood A, Oldfield S. 2007. *Red list of oaks*: Fauna & Flora International.

Eaton DA, Hipp AL, González-Rodríguez A, Cavender-Bares J. 2015. Historical introgression among the American live oaks and the comparative nature of tests for introgression. *Evolution* **69**(10): 2587-2601.

Eaton DA, Ree RH. 2013. Inferring phylogeny and introgression using RADseq data: an example from flowering plants (Pedicularis: Orobanchaceae). *Systematic biology* **62**(5): 689-706.

Eaton E, Caudullo G, Oliveira S, De Rigo D 2016. Quercus robur and Quercus petraea in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A eds. *European Atlas of Forest Tree Species*: Off. EU, Luxembourg, 160-163.

Eckelt A, Müller J, Bense U, Brustel H, Bußler H, Chittaro Y, Cizek L, Frei A, Holzer E, Kadej M. 2018. "Primeval forest relict beetles" of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. *Journal of Insect Conservation* **22**(1): 15-28.

El Mokni R. 2022. Quercus× numidica Trabut (Fagaceae, Quercoideae) and Cynosuro peltierii-Quercetum afaredis Laribi 2000 new taxon and syntaxon to Kroumirian oak forests of Tunisia with remarks on their ecology and conservation. *Hacquetia* **21**(1): 153-162.

Ely CV, de Loreto Bordignon SA, Trevisan R, Boldrini II. 2017. Implications of poor taxonomy in conservation. *Journal for Nature Conservation* **36**: 10-13.

Endlicher S. 1847. *Generum plantarum supplementum quartum*. Vienna: Fr. Beck.

Evans D 2006. The habitats of the European Union habitats directive. *Biology and Environment: Proceedings of the Royal Irish Academy*: JSTOR. 167-173.

Faure D, Joly D. 2015. Next-generation sequencing as a powerful motor for advances in the biological and environmental sciences. *Genetica* **143**(2): 129-132.

Fernández i Marti A, Romero-Rodríguez C, Navarro-Cerrillo RM, Abril N, Jorrín-Novo JV, Dodd RS. 2018. Population genetic diversity of Quercus ilex subsp. ballota (Desf.) Samp. reveals divergence in recent and evolutionary migration rates in the Spanish dehesas. *Forests* **9**(6): 337.

Ferraz KMPMdB, Morato RG, Bovo AAA, da Costa COR, Ribeiro YGG, de Paula RC, Desbiez ALJ, Angelieri CSC, Traylor-Holzer K. 2021. Bridging the gap between researchers, conservation planners, and decision makers to improve species conservation decision-making. *Conservation Science and Practice* **3**(2): e330.

Fineschi S, Taurchini D, Grossoni P, Petit RJ, Vendramin GG. 2002. Chloroplast DNA variation of white oaks in Italy. *Forest ecology and management* **156**(1-3): 103-114.

Firmat C, Delzon S, Louvet JM, Parmentier J, Kremer A. 2017. Evolutionary dynamics of the leaf phenological cycle in an oak metapopulation along an elevation gradient. *Journal of Evolutionary Biology* **30**(12): 2116-2131.

Fitz-Gibbon S, Hipp AL, Pham KK, Manos PS, Sork VL. 2017. Phylogenomic inferences from reference-mapped and de novo assembled short-read sequence data using RADseq sequencing of California white oaks (Quercus section Quercus). *Genome* **60**(9): 743-755.

Flensted KK, Bruun HH, Ejrnæs R, Eskildsen A, Thomsen PF, Heilmann-Clausen J. 2016. Red-listed species and forest continuity–A multi-taxon approach to conservation in temperate forests. *Forest ecology and management* **378**: 144-159.

Fletcher WJ, Sánchez-Goñi M, Peyron O, Dormoy I. 2010. Abrupt climate changes of the last deglaciation detected in a Western Mediterranean forest record. *Climate of the Past* **6**(2): 245-264.

Fontes CG, Pinto-Ledezma J, Jacobsen AL, Pratt RB, Cavender-Bares J. 2022. Adaptive variation among oaks in wood anatomical properties is shaped by

climate of origin and shows limited plasticity across environments. *Functional Ecology* **36**(2): 326-340.

Fordham DA, Akçakaya HR, Alroy J, Saltré F, Wigley TM, Brook BW. 2016. Predicting and mitigating future biodiversity loss using long-term ecological proxies. *Nature Climate Change* **6**(10): 909-916.

Fordham DA, Brook BW, Moritz C, Nogués-Bravo D. 2014. Better forecasts of range dynamics using genetic data. *Trends in ecology & evolution* **29**(8): 436-443.

Forester BR, DeChaine EG, Bunn AG. 2013. Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions* **19**(12): 1480-1495.

Fortini P, Di Marzio P, Di Pietro R. 2015. Differentiation and hybridization of Quercus frainetto, Q. petraea, and Q. pubescens (Fagaceae): insights from macro-morphological leaf traits and molecular data. *Plant systematics and evolution* **301**(1): 375-385.

Franco J, González GL 1987. Notas referentes al género" Quercus". *Anales del Jardín Botânico De Madrid*: Real Jardín Botánico. 555-558.

Franco JA 1990. Quercus L. In: S. C, al. e eds. *Flora Iberica, (Plantanaceae-Plumbaginaceae [Partim])*. Madrid: Real Jardín Botánico, CSIC, pp. 15-36.

Frankham R, Ballou JD, Dudash MR, Eldridge MD, Fenster CB, Lacy RC, Mendelson III JR, Porton IJ, Ralls K, Ryder OA. 2012. Implications of different species concepts for conserving biodiversity. *Biological Conservation* **153**: 25-31.

Fu R, Zhu Y, Liu Y, Feng Y, Lu R-S, Li Y, Li P, Kremer A, Lascoux M, Chen J. 2022. Genome-wide analyses of introgression between two sympatric Asian oak species. *Nature Ecology & Evolution*: 1-12.

García-Mijangos I, Campos JA, Biurrun I, Herrera M, Loidi J 2015. Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: Box EO, Fujiwara K eds. *Warm-temperate deciduous forests around the Northern hemisphere*. London: Springer, 119-138.

Gering JC, Crist TO. 2000. Patterns of beetle (Coleoptera) diversity in crowns of representative tree species in an old-growth temperate deciduous forest. *Selbyana* **21**(1/2): 38-47.

Giaretta A, Murphy B, Maurin O, Mazine FF, Sano P, Lucas E. 2021. Phylogenetic relationships within the hyper-diverse genus Eugenia (Myrtaceae: Myrteae) based on target enrichment sequencing. *Frontiers in Plant Science* **12**: 759460.

Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D. 2017. Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.

Gonçalves AR, Vila-Viçosa C, Gonçalves J. 2021. The Ant-like Tachydromia Complex in the Iberian Peninsula—Insights from Habitat Suitability Modelling for the Conservation of an Endemism (Diptera: Hybotidae). *Insects* **12**(12): 1068.

Govaerts RH, Avishai M. 2000. The conserved type of the name Quercus pubescens Willd.(Fagaceae). *Taxon* **49**(3): 537.

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT. 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in ecology & evolution* **19**(9): 497-503.

Grant V 1981. The Syngameon. *Plant speciation*: Columbia University Press, 234-241.

Gugerli F, Walser J-C, Dounavi K, Holderegger R, Finkeldey R. 2007. Coincidence of small-scale spatial discontinuities in leaf morphology and nuclear microsatellite variation of Quercus petraea and Q. robur in a mixed forest. *Annals of Botany* **99**(4): 713-722.

Gugger PF, Fitz-Gibbon ST, Albarrán-Lara A, Wright JW, Sork VL. 2021. Landscape genomics of Quercus lobata reveals genes involved in local climate adaptation at multiple spatial scales. *Molecular Ecology* **30**(2): 406-423.

Guichoux E, Garnier-Géré P, Lagache L, Lang T, Boury C, Petit R. 2013. Outlier loci highlight the direction of introgression in oaks. *Molecular Ecology* **22**(2): 450-462.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology letters* **8**(9): 993-1009.

Guisan A, Thuiller W, Zimmermann NE. 2017. *Habitat suitability and distribution models: with applications in R*: Cambridge University Press.

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C. 2013. Predicting species distributions for conservation decisions. *Ecology letters* **16**(12): 1424-1435.

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological modelling* **135**(2-3): 147-186.

Guo B, Hao X, Han L, Zhai Y, Zhou S, Chen S, Ren D, An X. 2021. Unraveling the genetic diversity and structure of Quercus liaotungensis population through analysis of microsatellite markers. *PeerJ* **9**: e10922.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hausdorf B. 2011. Progress toward a general species concept. *Evolution: International Journal of Organic Evolution* **65**(4): 923-931.

Hauser DA, Keuter A, McVay JD, Hipp AL, Manos PS. 2017. The evolution and diversification of the red oaks of the California Floristic Province (Quercus section Lobatae, series Agrifoliae). *American Journal of Botany* **104**(10): 1581-1595.

Hedrick PW. 2013. Adaptive introgression in animals: examples and comparison to new mutation and standing variation as sources of adaptive variation. *Molecular Ecology* **22**(18): 4606-4618.

Hembry DH, Weber MG. 2020. Ecological interactions and macroevolution: a new field with old roots. *Annual Review of Ecology, Evolution, and Systematics* **51**(1).

Herrera-Arroyo ML, Sork VL, González-Rodríguez A, Rocha-Ramírez V, Vega E, Oyama K. 2013. Seed-mediated connectivity among fragmented populations of Quercus castanea (Fagaceae) in a Mexican landscape. *American Journal of Botany* **100**(8): 1663-1671.

Hey J, Pinho C. 2012. Population genetics and objectivity in species diagnosis. *Evolution: International Journal of Organic Evolution* **66**(5): 1413-1429.

Hipp AL. 2015. Should hybridization make us skeptical of the oak phylogeny. *International Oak Journal* **26**: 9-18.

Hipp AL, Eaton DA, Cavender-Bares J, Fitzek E, Nipper R, Manos PS. 2014. A framework phylogeny of the American oak clade based on sequenced RAD data. *PloS one* **9**(4): e93975.

Hipp AL, Manos PS, González-Rodríguez A, Hahn M, Kaproth M, McVay JD, Avalos SV, Cavender-Bares J. 2018. Sympatric parallel diversification of major oak clades in the Americas and the origins of Mexican species diversity. *New Phytologist* **217**(1): 439-452.

Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl A, Deng M, Denk T, Fitz-Gibbon S. 2020. Genomic landscape of the global oak phylogeny. *New Phytologist* **226**(4): 1198-1212.

Hipp AL, Whittemore AT, Garner M, Hahn M, Fitzek E, Guichoux E, Cavender-Bares J, Gugger PF, Manos PS, Pearse IS. 2019a. Conserved DNA

polymorphisms distinguish species in the eastern North American white oak syngameon: Insights from an 80-SNP oak DNA genotyping toolkit. *bioRxiv*: 602573.

Hipp AL, Whittemore AT, Garner M, Hahn M, Fitzek E, Guichoux E, Cavender-Bares J, Gugger PF, Manos PS, Pearse IS. 2019b. Genomic Identity of White Oak Species in an Eastern North American Syngameon1. *Annals of the Missouri Botanical Garden* **104**(3): 455-477.

Hoban S, Dawson A, Robinson JD, Smith AB, Strand AE. 2019. Inference of biogeographic history by formally integrating distinct lines of evidence: genetic, environmental niche and fossil. *Ecography* **42**(12): 1991-2011.

Hohenegger J. 2014. Species as the basic units in evolution and biodiversity: Recognition of species in the Recent and geological past as exemplified by larger foraminifera. *Gondwana Research* **25**(2): 707-728.

Holuša J, Fiala T, Foit J. 2021. Ambrosia beetles prefer closed canopies: A case study in oak forests in Central Europe. *Forests* **12**(9): 1223.

Hubert F, Grimm GW, Jousselin E, Berry V, Franc A, Kremer A. 2014. Multiple nuclear genes stabilize the phylogenetic backbone of the genus Quercus. *Systematics and Biodiversity* **12**(4): 405-423.

Humphries CJ, Escudero M, Martín-Bravo S 2017. Vicariance biogeography. In: Roitberg B ed. *Reference Module in Life Sciences*. Cambridge, UK: Elsevier, 1-13.

Hutchinson GE 1957. The multivariate niche. *Cold Spring Harbor Symposia on Quantitative Biology*. 415-421.

Hy MlaF. 1895. Sur quelques chenes hybrides observés aux environs D'Angers. *Bulletin de la Société Botanique de France* **42**(6): 552-560.

Iamonico D, Peruzzi L. 2013. Lectotypification of Linnaean names in the genus Quercus (Fagaceae). *Taxon* **62**(5): 1041-1045.

Jablonski D. 2017. Approaches to macroevolution: 2. Sorting of variation, some overarching issues, and general conclusions. *Evolutionary Biology* **44**(4): 451-475.

Jeffries JM, Marquis RJ, Forkner RE. 2006. Forest age influences oak insect herbivore community structure, richness, and density. *Ecological Applications* **16**(3): 901-912.

Jiang X-L, Hipp AL, Deng M, Su T, Zhou Z-K, Yan M-X. 2019. East Asian origins of European holly oaks (Quercus section Ilex Loudon) via the Tibet-Himalaya. *Journal of Biogeography* **46**(10): 2203-2214.

Johnson MG, Pokorny L, Dodsworth S, Botigue LR, Cowan RS, Devault A, Eiserhardt WL, Epitawalage N, Forest F, Kim JT. 2019. A universal probe set for targeted sequencing of 353 nuclear genes from any flowering plant designed using k-medoids clustering. *Systematic biology* **68**(4): 594-606.

Kappelle M. 2006. *Ecology and conservation of neotropical montane oak forests*: Springer Science & Business Media.

Kim BY, Wei X, Fitz-Gibbon S, Lohmueller KE, Ortego J, Gugger PF, Sork VL. 2018. RADseq data reveal ancient, but not pervasive, introgression between Californian tree and scrub oak species (Quercus sect. Quercus: Fagaceae). *Molecular Ecology* **27**(22): 4556-4571.

Koenig WD, Alejano R, Carbonero MD, Fernández-Rebollo P, Knops JMH, Marañón T, Padilla-Díaz CM, Pearse IS, Pérez-Ramos IM, Vázquez-Piqué J, et al. 2016. Is the relationship between mast-seeding and weather in oaks related to their life-history or phylogeny? *Ecology* **97**(10): 2603-2615.

Kotschy T. 1862. *Die Eichen Europa‘s und des Orient‘s*. Wien und Olmütz: E. Hölzel.

Kremer A. 2016. Microevolution of European temperate oaks in response to environmental changes. *Comptes rendus biologies* **339**(7-8): 263-267.

Kremer A, Abbott AG, Carlson JE, Manos PS, Plomion C, Sisco P, Staton ME, Ueno S, Vendramin GG. 2012. Genomics of Fagaceae. *Tree Genetics & Genomes* **8**(3): 583-610.

Kremer A, Hipp AL. 2020. Oaks: an evolutionary success story. *New Phytologist* **226**(4): 987-1011.

Kremer A, Le Corre V, Petit RJ, Ducousso A. 2010. Historical and contemporary dynamics of adaptive differentiation in European oaks. *Molecular approaches in natural resource conservation*: 101-122.

Kroeger T, Escobedo FJ, Hernandez JL, Varela S, Delphin S, Fisher JRB, Waldron J. 2014. Reforestation as a novel abatement and compliance measure for ground-level ozone. *Proceedings of the National Academy of Sciences* **111**(40): E4204-E4213.

Lamarck JB. 1785. *Encyclopédie méthodique. Botanique*. Paris: Panckoucke.

Lazic D, Hipp AL, Carlson JE, Gailing O. 2021. Use of genomic resources to assess adaptive divergence and introgression in oaks. *Forests* **12**(6): 690.

Lemmon AR, Emme SA, Lemmon EM. 2012. Anchored hybrid enrichment for massively high-throughput phylogenomics. *Systematic biology* **61**(5): 727-744.

Lepais O, Petit R, Guichoux E, Lavabre J, Alberto F, Kremer A, Gerber S. 2009. Species relative abundance and direction of introgression in oaks. *Molecular Ecology* **18**(10): 2228-2242.

Lepais O, Roussel G, Hubert F, Kremer A, Gerber S. 2013. Strength and variability of postmating reproductive isolating barriers between four European white oak species. *Tree Genetics & Genomes* **9**(3): 841-853.

Leroy T, Louvet JM, Lalanne C, Le Provost G, Labadie K, Aury JM, Delzon S, Plomion C, Kremer A. 2020a. Adaptive introgression as a driver of local adaptation to climate in European white oaks. *New Phytologist* **226**(4): 1171-1182.

Leroy T, Plomion C, Kremer A. 2020b. Oak symbolism in the light of genomics. *New Phytologist* **226**(4): 1012-1017.

Lesur I, Le Provost G, Bento P, Da Silva C, Leplé J-C, Murat F, Ueno S, Bartholomé J, Lalanne C, Ehrenmann F. 2015. The oak gene expression atlas: insights into Fagaceae genome evolution and the discovery of genes regulated during bud dormancy release. *BMC genomics* **16**(1): 1-23.

Li Y, Zhang X, Fang Y. 2019. Landscape features and climatic forces shape the genetic structure and evolutionary history of an oak species (Quercus chenii) in East China. *Frontiers in Plant Science* **10**: 1060.

Li Y, Zhang X, Wang L, Sork VL, Mao L, Fang Y. 2022. Influence of Pliocene and Pleistocene climates on hybridization patterns between two closely related oak species in China. *Annals of Botany* **129**(2): 231-245.

Liang YY, Shi Y, Yuan S, Zhou BF, Chen XY, An QQ, Ingvarsson PK, Plomion C, Wang B. 2022. Linked selection shapes the landscape of genomic variation in three oak species. *New Phytologist* **233**(1): 555-568.

Lieblein FK. 1784. *Flora fuldensis oder Verzeichniss der in dem Fürstenthume Fuld wildwachsenden Bäume*. Frankfurt: Sträucher und Pflanzen.

Limousin JM, Roussel A, Rodríguez-Calcerrada J, Torres-Ruiz JM, Moreno M, Garcia de Jalon L, Ourcival JM, Simioni G, Cochard H, Martin-StPaul N. 2022. Drought acclimation of Quercus ilex leaves improves tolerance to moderate drought but not resistance to severe water stress. *Plant, Cell & Environment* **45**(7): 1967-1984.

Lin D, Lai J, Muller-Landau HC, Mi X, Ma K. 2012. Topographic variation in aboveground biomass in a subtropical evergreen broad-leaved forest in China. *PloS one* **7**(10): e48244.

Lind JF, Gailing O. 2013. Genetic structure of Quercus rubra L. and Quercus ellipsoidalis E. J. Hill populations at gene-based EST-SSR and nuclear SSR markers. *Tree Genetics & Genomes* **9**(3): 707-722.

Linnaeus C. 1753. *Species Plantarum*. Stockholm: Impensis Laurentii Salvii.

Loidi J, Del Arco M, Pérez de Paz PL, Asensi A, Díez Garretas B, Costa M, Díaz González T, Fernández-González F, Izco J, Penas Á. 2010. Understanding properly the potential natural vegetation'concept. *Journal of Biogeography* **37**(11): 2209-2211.

Loidi J, Fernández-González F. 2012. Potential natural vegetation: reburying or reboring? *Journal of vegetation Science* **23**(3): 596-604.

Loidi J, Herrera M. 1990. The Quercus pubescens and Quercus faginea forests in the Basque Country (Spain): distribution and typology in relation to climatic factors. *Plant Ecology* **90**(1): 81-92.

López-Hidalgo C, Menéndez M, Jorrin-Novo JV. 2021. Phytochemical composition and variability in Quercus ilex acorn morphotypes as determined by NIRS and MS-based approaches. *Food Chemistry* **338**: 127803.

Lopez De Heredia U, Sanchez H, Soto A. 2018. Molecular evidence of bidirectional introgression between Quercus suber and Quercus ilex. *iForest-Biogeosciences and Forestry* **11**(2): 338.

Lotsy J. 1925. Species or linneon. *Genetica* **7**(5): 487-506.

Loudon JC. 1838. *Arboretum et fruticetum britannicum*. London: Longman, Orme, Brown, Green, and Longmans.

Luikart G, England PR, Tallmon D, Jordan S, Taberlet P. 2003. The power and promise of population genomics: from genotyping to genome typing. *Nature Reviews Genetics* **4**(12): 981-994.

Mace GM. 2004. The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**(1444): 711-719.

Maguire KC, Nieto-Lugilde D, Fitzpatrick MC, Williams JW, Blois JL. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. *Annual Review of Ecology, Evolution, and Systematics* **46**: 343-368.

Maleev VP. 1935. A Review of Oak Trees in Caucasus through theirs Taxonomical and geographical relations and concerning to evolution of group Robur. *Bot. Zhur.* **20**(2): 156-172.

Mallet J. 2007. Hybrid speciation. *Nature* **446**(7133): 279-283.

Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). *Molecular phylogenetics and evolution* **12**(3): 333-349.

Manos PS, Stanford AM. 2001. The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. *International Journal of Plant Sciences* **162**(S6): S77-S93.

Marañón T, Ibáñez B, Anaya-Romero M, Muñoz-Rojas M, Pérez-Ramos I. 2012. Oak trees and woodlands providing ecosystem services in Southern Spain. *Trees beyond the wood: An exploration of concepts of woods, forests and trees. Wildtrack Publishing, Sheffield*: 291-299.

Marcer A, Chapman AD, Wieczorek JR, Xavier Picó F, Uribe F, Waller J, Ariño AH. 2022. Uncertainty matters: ascertaining where specimens in natural history collections come from and its implications for predicting species distributions. *Ecography* **2022**(9): e06025.

Marques DA, Meier JI, Seehausen O. 2019. A combinatorial view on speciation and adaptive radiation. *Trends in ecology & evolution* **34**(6): 531-544.

Martin M, Paillet Y, Larrieu L, Kern CC, Raymond P, Drapeau P, Fenton NJ. 2022. Tree-Related Microhabitats Are Promising Yet Underused Tools for Biodiversity

and Nature Conservation: A Systematic Review for International Perspectives. *Frontiers in Forests and Global Change* **5**: 818474.

Martínez AC, Llamas F. 2022a. Quercus orocantabrica Rivas Mart., Penas, TE Díaz & Llamas (Fagaceae) en el Sistema Ibérico septentrional y áreas adyacentes española. *Flora Montiberica* **83**: 58-60.

Martínez AC, Llamas F. 2022b. Quercus petraea (Matt.) Liebl. y otros robles del Sistema Ibérico septentrional. *Flora Montiberica* **84**: 15-17.

Mastretta-Yanes A, Arrigo N, Alvarez N, Jorgensen TH, Piñero D, Emerson BC. 2015. Restriction site-associated DNA sequencing, genotyping error estimation and de novo assembly optimization for population genetic inference. *Molecular ecology resources* **15**(1): 28-41.

Matlack GR. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology* **93**(1): 50-59.

Mayr E. 1982. *The growth of biological thought: Diversity, evolution, and inheritance*: Harvard University Press.

McGarvey JC, Thompson JR, Epstein HE, Shugart Jr HH. 2015. Carbon storage in old-growth forests of the Mid-Atlantic: toward better understanding the eastern forest carbon sink. *Ecology* **96**(2): 311-317.

McKain MR, Johnson MG, Uribe-Convers S, Eaton D, Yang Y. 2018. Practical considerations for plant phylogenomics. *Applications in plant sciences* **6**(3): e1038.

McVay JD, Hauser D, Hipp AL, Manos PS. 2017a. Phylogenomics reveals a complex evolutionary history of lobed-leaf white oaks in western North America. *Genome* **60**(9): 733-742.

McVay JD, Hipp AL, Manos PS. 2017b. A genetic legacy of introgression confounds phylogeny and biogeography in oaks. *Proc. R. Soc. B* **284**(1854): 20170300.

Médail F, Monnet A-C, Pavon D, Nikolic T, Dimopoulos P, Bacchetta G, Arroyo J, Barina Z, Albassatneh MC, Domina G. 2019. What is a tree in the Mediterranean Basin hotspot? A critical analysis. *Forest Ecosystems* **6**(1): 1-19.

Medail F, Quezel P. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden*: 112-127.

Meddour R, Meddour-Sahar O, Zeraia L, Mucina L. 2017. Syntaxonomic synopsis of the forest and tall scrub vegetation of Northern Algeria. *Lazaroa* **38**(2): 127-163.

Meng HH, Su T, Gao XY, Li J, Jiang XL, Sun H, Zhou ZK. 2017. Warm–cold colonization: response of oaks to uplift of the Himalaya–Hengduan Mountains. *Molecular Ecology* **26**(12): 3276-3294.

Menitsky G. 1972. *Generis Quercus L. species asiae austro-occidentalis*.

Menitsky YL. 1984. Duby Azii. *Leningrad [English ed.: 2005, Plymouth]*.

Miller MR, Dunham JP, Amores A, Cresko WA, Johnson EA. 2007. Rapid and cost-effective polymorphism identification and genotyping using restriction site associated DNA (RAD) markers. *Genome research* **17**(2): 240-248.

Mills LS, Soulé ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. *BioScience* **43**(4): 219-224.

Montserrat J. 2021. As Sweet As it Gets. *International Oaks*(32).

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**(6772): 853-858.

Nguyen NH, Williams LJ, Vincent JB, Stefanski A, Cavender-Bares J, Messier C, Paquette A, Gravel D, Reich PB, Kennedy PG. 2016. Ectomycorrhizal fungal diversity and saprotrophic fungal diversity are linked to different tree community attributes in a field-based tree experiment. *Molecular Ecology* **25**(16): 4032-4046.

Nixon K, Muller C 1997. Quercus Sect. Quercus Linneus. In: Committee FoNAE ed. *Flora of North America North of Mexico*.

Nixon K, Muller C, Committee FoNAE. 1997. Quercus Sect. Quercus Linneus. *Flora of North America North of Mexico* **3**.

Nixon KC. 1993. Infrageneric classification of Quercus (Fagaceae) and typification of sectional names. *Annales des sciences forestières* **50**: 25-34.

Nixon KC 2006. Global and neotropical distribution and diversity of oak (genus Quercus) and oak forests. *Ecology and Conservation of Neotropical Montane Oak Forests*: Springer, 3-13.

Noor MAF, Feder JL. 2006. Speciation genetics: evolving approaches. *Nature Reviews Genetics* **7**(11): 851-861.

O'Donnell ST, Fitz-Gibbon ST, Sork VL. 2021. Ancient introgression between distantly related White Oaks (Quercus sect. Quercus) shows evidence of climate-associated asymmetric gene exchange. *Journal of Heredity* **112**(7): 663-670.

Oersted AS. 1873. *Bidrag til Kundskab om Egefamilien i nutid og fortid Det Kongelige Danske videnskabernes selskabs skrifter*. Kjøbenhavn: Bianco Lunos.

Olalde M, Herrán A, Espinel S, Goicoechea PG. 2002. White oaks phylogeography in the Iberian Peninsula. *Forest ecology and management* **156**(1-3): 89-102.

Olchowik J, Hilszczańska D, Bzdyk RM, Studnicki M, Malewski T, Borowski Z. 2019. Effect of deadwood on ectomycorrhizal colonisation of old-growth oak forests. *Forests* **10**(6): 480.

Oney-Birol S, Fitz-Gibbon S, Chen J-M, Gugger PF, Sork VL. 2018. Assessment of shared alleles in drought-associated candidate genes among southern California white oak species (Quercus sect. Quercus). *BMC genetics* **19**(1): 1-12.

Ørsted AS. 1871. *Bidrag til kundskab om Egefamilien i Nutid og Fortid*: Bianco Lunos Bogtrykkeri ved FS Muhle.

Ortego J, Bonal R. 2010. Natural hybridisation between kermes (Quercus coccifera L.) and holm oaks (Q. ilex L.) revealed by microsatellite markers. *Plant Biology* **12**(1): 234-238.

Ottenburghs J. 2018. Exploring the hybrid speciation continuum in birds. *Ecology and Evolution* **8**(24): 13027-13034.

Ottenburghs J. 2021. The genic view of hybridization in the Anthropocene. *Evolutionary Applications* **14**(10): 2342-2360.

Paine RT. 1969. A note on trophic complexity and community stability. *The American Naturalist* **103**(929): 91-93.

Papadopulos AS, Baker WJ, Crayn D, Butlin RK, Kynast RG, Hutton I, Savolainen V. 2011. Speciation with gene flow on Lord Howe Island. *Proceedings of the National Academy of Sciences* **108**(32): 13188-13193.

Pasta S, de Rigo D, Caudullo G 2016. Quercus pubescens in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A eds. *European atlas of forest tree species*. Luxembourg: Publications Office of the European Union, 156-157.

Peñaloza-Ramírez JM, González-Rodríguez A, Mendoza-Cuenca L, Caron H, Kremer A, Oyama K. 2010. Interspecific gene flow in a multispecies oak hybrid zone in the Sierra Tarahumara of Mexico. *Annals of Botany* **105**(3): 389-399.

Penas A, Llamas F, Perez-Morales C, Acedo C. 1997. A new species of Quercus L. (Fagaceae) from NW Spain. *Botanica Helvetica* **107**: 75-82.

Percel G, Parmain G, Laroche F, Bouget C. 2018. The larger, the better? Effects of delayed diameter-limit cutting on old-growth attributes and saproxylic beetle diversity in temperate oak forests. *European Journal of Forest Research* **137**(2): 237-249.

Pérez-Pedraza A, Rodríguez-Correa H, Valencia-Ávalos S, Torres-Miranda CA, Arenas-Navarro M, Oyama K. 2021. Effect of hybridization on the

morphological differentiation of the red oaks Quercus acutifolia and Quercus grahamii (Fagaceae). *Plant systematics and evolution* **307**(3): 37.

Peterson AT, Navarro-Sigüenza AG. 1999. Alternate species concepts as bases for determining priority conservation areas. *Conservation Biology* **13**(2): 427-431.

Petit RJ, Bodénès C, Ducousso A, Roussel G, Kremer A. 2004. Hybridization as a mechanism of invasion in oaks. *New Phytologist* **161**(1): 151-164.

Petit RJ, Brewer S, Bordács S, Burg K, Cheddadi R, Coart E, Cottrell J, Csaikl UM, van Dam B, Deans JD. 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest ecology and management* **156**(1): 49-74.

Petit RJ, Carlson J, Curtu AL, Loustau M-L, Plomion C, González-Rodríguez A, Sork V, Ducousso A. 2013. Fagaceae trees as models to integrate ecology, evolution and genomics. *New Phytologist* **197**(2): 369-371.

Petit RJ, Hampe A, Cheddadi R. 2005. Climate changes and tree phylogeography in the Mediterranean. *Taxon* **54**(4): 877-885.

Pham KK, Hipp AL, Manos PS, Cronn RC. 2017. A time and a place for everything: phylogenetic history and geography as joint predictors of oak plastome phylogeny. *Genome* **60**(9): 720-732.

Piao S, Fang J, Ciais P, Peylin P, Huang Y, Sitch S, Wang T. 2009. The carbon balance of terrestrial ecosystems in China. *Nature* **458**(7241): 1009-1013.

Pignone D, Laghetti G. 2010. On sweet acorn (Quercus spp.) cake tradition in Italian cultural and ethnic islands. *Genetic Resources and Crop Evolution* **57**(8): 1261-1266.

Pinto-Ledezma JN, Cavender-Bares J. 2021. Predicting species distributions and community composition using satellite remote sensing predictors. *Scientific reports* **11**(1).

Plomion C, Aury J-M, Amselem J, Leroy T, Murat F, Duplessis S, Faye S, Francillonne N, Labadie K, Le Provost G, et al. 2018. Oak genome reveals facets of long lifespan. *Nature Plants* **4**(7): 440-452.

Plomion C, Aury JM, Amselem J, Alaeitabar T, Barbe V, Belser C, Bergès H, Bodénès C, Boudet N, Boury C. 2016. Decoding the oak genome: public release of sequence data, assembly, annotation and publication strategies. *Molecular ecology resources* **16**(1): 254-265.

Plomion C, Martin F. 2020. Oak genomics is proving its worth. *New Phytologist* **226**(4): 943-946.

Poland JA, Rife TW. 2012. Genotyping-by-sequencing for plant breeding and genetics. *The plant genome* **5**(3): 92-102.

Pomel AN. 1875. *Nouveaux matériaux pour la flore atlantique*. Paris: Savy.

Popescu S-M, Biltekin D, Winter H, Suc J-P, Melinte-Dobrinescu MC, Klotz S, Rabineau M, Combourieu-Nebout N, Clauzon G, Deaconu F. 2010. Pliocene and Lower Pleistocene vegetation and climate changes at the European scale: Long pollen records and climatostratigraphy. *Quaternary international* **219**(1-2): 152-167.

Quézel P. 1976. Les forêts du pourtour méditerranéen. *Forêts et maquis méditerranéens: écologie, conservation et aménagement*: 9-33.

Quézel P. 1985. Definition of the Mediterranean region and the origin of its flora. *Geobotany*.

Quézel P, Médail F, Loisel R, Barbero M. 1999. Biodiversity and conservation of forest species in the Mediterranean basin. *UNASYLVA-FAO-*: 21-28.

Ramírez-Valiente JA, Center A, Sparks JP, Sparks KL, Etterson JR, Longwell T, Pilz G, Cavender-Bares J. 2017. Population-Level Differentiation in Growth Rates and Leaf Traits in Seedlings of the Neotropical Live Oak Quercus oleoides Grown under Natural and Manipulated Precipitation Regimes. *Frontiers in Plant Science* **8**: 585.

Ramírez-Valiente JA, Etterson JR, Deacon NJ, Cavender-Bares J. 2019. Evolutionary potential varies across populations and traits in the neotropical oak Quercus oleoides. *Tree Physiology* **39**(3): 427-439.

Ramírez-Valiente JA, Deacon NJ, Etterson J, Center A, Sparks JP, Sparks KL, Longwell T, Pilz G, Cavender-Bares J. 2018. Natural selection and neutral evolutionary processes contribute to genetic divergence in leaf traits across a precipitation gradient in the tropical oak Quercus oleoides. *Molecular Ecology* **27**(9): 2176-2192.

Ramos AM, Usié A, Barbosa P, Barros PM, Capote T, Chaves I, Simões F, Abreu I, Carrasquinho I, Faro C. 2018. The draft genome sequence of cork oak. *Scientific data* **5**(1): 1-12.

Ranius T, Eliasson P, Johansson P. 2008. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. *Biodiversity and Conservation* **17**(10): 2371-2381.

Raymo M, Ganley K, Carter S, Oppo D, McManus J. 1998. Millennial-scale climate instability during the early Pleistocene epoch. *Nature* **392**(6677): 699-702.

Reichenbach HGL. 1832. *Flora Germanica excursoria ex affinitate regni vegetabilis naturali disposita, sive principia synopseos plantarum in Germania terrisque in Europa media adiacentibus sponte nascentium cultarumque frequentius*: Carolum Cnobloch.

Rey M-D, Labella-Ortega M, Guerrero-Sanchez VM, Carleial R, Castillejo M-A, Rodriguez-Franco A, Buggs R, Ruggieri V, Jorrin-Novo JV. 2022. A first draft genome of Holm oak (Quercus ilex L.), the most representative species of the Mediterranean forest and the Spanish agrosilvopastoral ecosystem dehesa. *bioRxiv*.

Rhymer JM, Simberloff D. 1996. Extinction by hybridization and introgression. *Annual review of Ecology and Systematics*: 83-109.

Rice A, Šmarda P, Novosolov M, Drori M, Glick L, Sabath N, Meiri S, Belmaker J, Mayrose I. 2019. The global biogeography of polyploid plants. *Nature Ecology & Evolution* **3**(2): 265-273.

Richard F, Millot S, Gardes M, Selosse MA. 2005. Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth Mediterranean forest dominated by Quercus ilex. *New Phytologist* **166**(3): 1011-1023.

Rivas-Martínez S, Aguiar C, Aguilella A, Alonso R, Alvarez M, Amich F, Arnaiz C, Baccheta G, Barbero M, Barbour M. 2011. Map of series, geoseries and geopermaseries of vegetation in Spain [MEMORY OF MAP OF POTENTIAL VEGETATION OF SPAIN, 2011] PART II. *Itinera Geobotanica* **18**(II): 1-764.

Rivas-Martínez S, González-Días TE, González FF, Loidi JJ, Lousã MF, Merino ÁP. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica*(15): 433-922.

Rivas-Martínez S, Rivas-Sáenz S, Penas A, Alcaraz F, Amigo J, Asensi A. 2011. World bioclimatic classification system. *Global Geobotany* **1**: 1–634.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rivas Martínez S, Rivas Sáenz S, Penas Á, del Río S 2011. Biogeographic map of Europe. Second concise advance. *1st International Symposium of the FIP - Global Strategy for plant conservation*. Valencia: Società Italiana Scienza della Vegetazione.

Rodríguez-Sánchez F, Hampe A, Jordano P, Arroyo J. 2010. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Review of Palaeobotany and Palynology* **162**(3): 507-521.

Roleček J, Řepka R. 2020. Formerly coppiced old growth stands act as refugia of threatened biodiversity in a managed steppic oak forest. *Forest ecology and management* **472**: 118245.

Ruhsam M, Hollingsworth PM, Ennos R. 2011. Early evolution in a hybrid swarm between outcrossing and selfing lineages in Geum. *Heredity* **107**(3): 246-255.

Rull V. 2008. Speciation timing and neotropical biodiversity: the Tertiary–Quaternary debate in the light of molecular phylogenetic evidence. *Molecular Ecology* **17**(11): 2722-2729.

Rundell RJ, Price TD. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in ecology & evolution* **24**(7): 394-399.

Sabatini FM, Burrascano S, Keeton WS, Levers C, Lindner M, Pötzschner F, Verkerk PJ, Bauhus J, Buchwald E, Chaskovsky O. 2018. Where are Europe's last primary forests? *Diversity and Distributions* **24**(10): 1426-1439.

Sáenz-Romero C, Lamy J-B, Ducousso A, Musch B, Ehrenmann F, Delzon S, Cavers S, Chałupka W, Dağdaş S, Hansen JK, et al. 2017. Adaptive and plastic responses of Quercus petraea populations to climate across Europe. *Global Change Biology* **23**(7): 2831-2847.

Saénz de Rivas C 1969. Estudios biométrico-taxonómicos sobre Quercus faginea Lamk.In Sevilla Ud. *V Simposio de Flora Europaea*. Sevilla: Universidad de Sevilla. 335-350.

Saéz L, Aymerich P. 2021. *An annotated Checklist of the Vascular Plants of Catalonia (northeastern Iberian Peninsula)*. Barcelona: Kit-book Serveis Editorials.

Saltré F, Rodríguez-Rey M, Brook BW, Johnson CN, Turney CS, Alroy J, Cooper A, Beeton N, Bird MI, Fordham DA. 2016. Climate change not to blame for late Quaternary megafauna extinctions in Australia. *Nature communications* **7**(1): 1-7.

Sampaio G. 1909. Flora vascular de Odemira. *Boletim da Sociedade Broteriana* **24**: 7-132.

Sampaio G. 1910a. *Manual da Flora Portugueza*. Porto: Universidade do Porto.

Sampaio G. 1910b. Nota a propósito dos Quercus lusitanica Lamk., Q. humilis Lamk e Quercus faginea, Lamk. . *Annaes Scientificos da Academia Polytechnica do Porto* **5**(3): 161-165.

Sancho-Knapik D, Escudero A, Mediavilla S, Scoffoni C, Zailaa J, Cavender-Bares J, Álvarez-Arenas TG, Molins A, Alonso-Forn D, Ferrio JP, et al. 2021. Deciduous and evergreen oaks show contrasting adaptive responses in leaf mass per area across environments. *New Phytologist* **230**(2): 521-534.

Sanz-Arnal M, Benítez-Benítez C, Miguez M, Jiménez-Mejías P, Martín-Bravo S. 2022. Are Cenozoic relict species also climatic relicts? Insights from the macroecological evolution of the giant sedges of Carex sect. Rhynchocystis (Cyperaceae). *American Journal of Botany* **109**(1): 115-129.

Schwarz O. 1934. Die in der Türkei vorkommenden Bäume und Sträucher: Quercus L. (Beiträge zur Flora Klein-Asien). *Repert. Spec. Nov. Regni Veg* **33**: 321–338.

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O. 1936a. Entwurf zu einem natürlichen System der Cupuliferen und der Gattung Quercus L. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*: 1-22.

Schwarz O. 1936b. *Monographie der Eichen Europas und des Mittelmeergebietes*: Selbstverlag.

Schwarz O. 1936c. Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* **8**: 65–100.

Schwarz O. 1937. Monographie der Eichen Europas und des Mittelmeergebietes. *Repertorium novarum speciarum regni vegetabilis* **1**: 1-200.

Schwarz O 1964. Quercus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, DA. W eds. *Flora Europaea*. Cambridge: Cambridge University Press, 61-64.

Scotti-Saintagne C, Mariette S, Porth I, Goicoechea PG, Barreneche T, Bodénes C, Burg K, Kremer A. 2004. Genome scanning for interspecific differentiation between two closely related oak species [Quercus robur L. and Q. petraea (Matt.) Liebl.]. *Genetics* **168**(3): 1615-1626.

Seehausen O. 2004. Hybridization and adaptive radiation. *Trends in ecology & evolution* **19**(4): 198-207.

Shafer AB, Peart CR, Tusso S, Maayan I, Brelsford A, Wheat CW, Wolf JB. 2017. Bioinformatic processing of RAD-seq data dramatically impacts downstream population genetic inference. *Methods in Ecology and Evolution* **8**(8): 907-917.

Shuman BN, Newby P, Donnelly JP. 2009. Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quaternary Science Reviews* **28**(17-18): 1693-1709.

Sillero N. 2011. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecological modelling* **222**(8): 1343-1346.

Sillero N, Arenas-Castro S, Enriquez-Urzelai U, Vale CG, Sousa-Guedes D, Martínez-Freiría F, Real R, Barbosa AM. 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. *Ecological modelling* **456**: 109671.

Simeone MC, Cardoni S, Piredda R, Imperatori F, Avishai M, Grimm GW, Denk T. 2018. Comparative systematics and phylogeography ofQuercusSectionCerrisin western Eurasia: inferences from plastid and nuclear DNA variation. *PeerJ* **6**: e5793.

Simeone MC, Piredda R, Papini A, Vessella F, Schirone B. 2013. Application of plastid and nuclear markers to DNA barcoding of Euro-Mediterranean oaks (Quercus, Fagaceae): problems, prospects and phylogenetic implications. *Botanical Journal of the Linnean Society* **172**(4): 478-499.

Sites Jr JW, Marshall JC. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in ecology & evolution* **18**(9): 462-470.

Sites JW, Crandall KA. 1997. Testing species boundaries in biodiversity studies. *Conservation Biology* **11**(6): 1289-1297.

Skarpaas O, Blumentrath S, Evju M, Sverdrup-Thygeson A. 2017. Prediction of biodiversity hotspots in the Anthropocene: The case of veteran oaks. *Ecology and Evolution* **7**(19): 7987-7997.

Skelton RP, Anderegg LD, Diaz J, Kling MM, Papper P, Lamarque LJ, Delzon S, Dawson TE, Ackerly DD. 2021. Evolutionary relationships between drought-related traits and climate shape large hydraulic safety margins in western North American oaks. *Proceedings of the National Academy of Sciences* **118**(10): e2008987118.

Somodi I, Ewald J, Bede-Fazekas Á, Molnár Z. 2021. The relevance of the concept of potential natural vegetation in the Anthropocene. *Plant Ecology & Diversity* **14**(1-2): 13-22.

Sork VL, Cokus SJ, Fitz-Gibbon ST, Zimin AV, Puiu D, Garcia JA, Gugger PF, Henriquez CL, Zhen Y, Lohmueller KE. 2022. High-quality genome and methylomes illustrate features underlying evolutionary success of oaks. *Nature communications* **13**(1): 1-15.

Sork VL, Fitz-Gibbon ST, Puiu D, Crepeau M, Gugger PF, Sherman R, Stevens K, Langley CH, Pellegrini M, Salzberg SL. 2016a. First draft assembly and

annotation of the genome of a California endemic oak Quercus lobata Née (Fagaceae). *G3: Genes, Genomes, Genetics* **6**(11): 3485-3495.

Sork VL, Squire K, Gugger PF, Steele SE, Levy ED, Eckert AJ. 2016b. Landscape genomic analysis of candidate genes for climate adaptation in a California endemic oak, Quercus lobata. *American Journal of Botany* **103**(1): 33-46.

Soto A, Lorenzo Z, Gil L. 2003. Nuclear microsatellite markers for the identification of Quercus ilex L. and Q. suber L. hybrids. *Silvae Genetica* **52**(2): 63-66.

Spach É. 1842. *Histoire naturelle des végétaux: Phanérogames. Vol. 11. Librairie encyclopédique de Roret, Paris*. Paris.

Sprague T. 1929. International Botanical Congress Cambridge (England), 1930. *Nomenclature Proposals by British Botanists. Wyman & Sons, London*.

Stefanoff B. 1930. Sur les relations systématiques des chênes de la Section Robur (Spach) Loudon par B. Stefanoff. *Annuaire Univ. Sofia, Fac. Agron. et Sylvicult.* **8**(53-63).

Steven C 1857. Verzeichnis der auf der taurischen Halbinsel wildwachsenden Pflanzen. Buchdruckerei der Kaiserlichen Universität. In: prirody Mol ed. *Bulletin de la Société impériale des naturalistes de Moscou*. Moscou: Société impériale des naturalistes de Moscou, 325-398.

Suarez-Gonzalez A, Lexer C, Cronk QC. 2018. Adaptive introgression: a plant perspective. *Biology letters* **14**(3): 20170688.

Sullivan AR, Owusu SA, Weber JA, Hipp AL, Gailing O. 2016. Hybridization and divergence in multi-species oak (Quercus) communities. *Botanical Journal of the Linnean Society* **181**(1): 99-114.

Svenning J-C, Eiserhardt WL, Normand S, Ordonez A, Sandel B. 2015. The Influence of Paleoclimate on Present-Day Patterns in Biodiversity and Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **46**(1): 551-572.

Svenning J-C, Fløjgaard C, Marske KA, Nógues-Bravo D, Normand S. 2011. Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* **30**(21-22): 2930-2947.

Svenning JC, Skov F. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography* **16**(2): 234-245.

Taleb MS, Fennane M. 2019. *Vascular plant communities of Morocco*: Springer.

Tamaki I, Obora T, Ohsawa T, Matsumoto A, Saito Y, Ide Y. 2021. Different population size change and migration histories created genetic diversity of three oaks in Tokai region, central Japan. *Journal of plant research* **134**(5): 933-946.

Todesco M, Pascual MA, Owens GL, Ostevik KL, Moyers BT, Hübner S, Heredia SM, Hahn MA, Caseys C, Bock DG. 2016. Hybridization and extinction. *Evolutionary Applications* **9**(7): 892-908.

Torres-Miranda A, Luna-Vega I, Oyama K. 2011. Conservation biogeography of red oaks (Quercus, section Lobatae) in Mexico and Central America. *American Journal of Botany* **98**(2): 290-305.

Tóth EG, Köbölkuti ZA, Cseke K, Kámpel JD, Takács R, Tomov VT, Ábrán P, Stojnic S, Vastag E, Mataruga M. 2021. A genomic dataset of single-nucleotide polymorphisms generated by ddRAD tag sequencing in Q. petraea (Matt.) Liebl. populations from Central-Eastern Europe and Balkan Peninsula. *Annals of Forest Science* **78**(2): 1-13.

Trelease W. 1917. Naming American hybrid oaks. *Proceedings of the American Philosophical Society* **56**(1): 44-52.

Trelease W. 1924. *The American oaks*. New York: Plant Monograph Reprints.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

Tuxen R. 1956. Die huetige potentielle naturliche Vegetation als Gegestand der Vegetationskarierung. *Angewandte Pflanzensozioligie* **13**: 5-42.

Valencia-Cuevas L, Piñero D, Mussali-Galante P, Valencia-Ávalos S, Tovar-Sánchez E. 2014. Effect of a red oak species gradient on genetic structure and diversity of Quercus castanea (Fagaceae) in Mexico. *Tree Genetics & Genomes* **10**(3): 641-652.

Van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L. 2016. Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature communications* **7**(1): 1-11.

Van Valen L. 1976. Ecological species, multispecies, and oaks. *Taxon*: 233-239.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vazquez FM, Coombes A, Almeida R, Garcia-Alonso D, Marquez-Garcia F, Vila-Vicosa C. 2020. Lectotypification of names of Quercus spp.(Fagaceae) described by Lamarck from the Iberian Peninsula. *Phytotaxa* **455**(3): 205–213-205–213.

Vázquez FM, Coombes AJ. 2017. (2569) Proposal to conserve the name Quercus ilex (Fagaceae) with a conserved type. *Taxon* **66**(6): 1473-1475.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Vázquez FM, Ramos S, Garcia S. 2004. Diversity of Iberian oaks. *International Oaks Journal* **15**: 31-43.

Veloz SD, Williams JW, Blois JL, He F, Otto-Bliesner B, Liu Z. 2012. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology* **18**(5): 1698-1713.

Verlaque R, Médail F, Quézel P, Babinot J-F. 1997. Endémisme végétal et paléogéographie dans le bassin méditerranéen. *Geobios* **30**: 159-166.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C, Marcos B, Garcia C, Gonçalves J 2019. Biogeography from space—A new tool to disentangle Iberian Forests Ecology and Distribution. *Proceedings of the SIBECOL. 1st Meeting of the Iberian Ecological Society & XIV AEET Meeting, Barcelona, Spain*. 4-17.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vilches B, Sánchez-Mata D, Gavilán RG 2016. Marcescent Quercus pyrenaica Forest on the Iberian Peninsula. *Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales*: Springer, 257-283.

Villar E 1949. Les Quercus de la section galliferae de L'Afrique du Nord. *Mem. Soc. Hist. Nat: Afr. N.* Alger, 165-171.

Villar EH. 1935. Sur le nom de quelques Quercus et la systématique du faginea. *Cavanillesia* **7**: 57-70.

Villar EH 1938. Les Quercus de L`Herbier d´Alger. In: d'Alger SFdS ed. *Bulletin de la Société d'histoire naturelle de l'Afrique du nord*. Argel: Minerva, 432-478.

Villar EH 1943. Nouvelle note sur les Quercus de l'Afrique du Nord. In: Maroc SdSNd ed. *Bulletin de la Société des sciences naturelles du Maroc.* . Rabat: L'Institut Scientifique Chérifien, 2-3.

Villar EH. 1958. Estudios sobre los Quercus del Oeste mediterráneo. *Anales del Instituto Botanico de A.J. Cavanilles* **15**: 3-114.

Webb P. 1838. *Iter Hispaniense.* Paris: Béthune and Plon.

Weitemier K, Straub SC, Cronn RC, Fishbein M, Schmickl R, McDonnell A, Liston A. 2014. Hyb-Seq: Combining target enrichment and genome skimming for plant phylogenomics. *Applications in plant sciences* **2**(9): 1400042.

White NA. 2003. The importance of wood-decay fungi in forest ecosystems. *Fungal biotechnology in agriculture, food and environmental applications. New York: Marcel Dekker*: 375-392.

Whitham TG, DiFazio SP, Schweitzer JA, Shuster SM, Allan GJ, Bailey JK, Woolbright SA. 2008. Extending genomics to natural communities and ecosystems. *Science* **320**(5875): 492-495.

Wiens JJ. 2004. Speciation and Ecology Revisited: Phylogenetic Niche Conservatism And the Origin of Species. *Evolution* **58**(1): 193-197.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes JA, Harrison SP. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters* **13**(10): 1310-1324.

Wiens JJ, Donoghue MJ. 2004. Historical biogeography, ecology and species richness. *Trends in ecology & evolution* **19**(12): 639-644.

Wilkins JS 2009. Species. *Species*: University of California Press.

Willdenow CL. 1796. *Berlinische Baumzucht oder Beschreibung der in den Gärten um Berlin im Freien ausdauernden Bäume und Sträucher für Gartenliebhaber und Freunde der Botanik*. Berlin: Nauck.

Willdenow CL. 1805. *Species plantarum exhibentes plantas rite cognitas ad genera relatas cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis naturalibus secundum systema sexuale digestas*. Berlin: Nauck.

Willdenow CL. 1809. *Enumeratio plantarum Horti Regii Berolinensis*. Berlin: Taberna libraria Scholae Realis.

Willdenow Cv 1801. Der Gesellschaft naturforschender Freunde zu Berlin, Neue Schriften: Auf Hosten der Gesellschaft, Berlin.

Willkomm M, Lange J. 1861. *Prodromus florae Hispanicae. I.*: Stuttgart.

Winter S, Lüderitz M, Rzanny M. 2015. Unterirdische Kontinuität und Pilzvielfalt alter Waldstandorte. *Schweizerische Zeitschrift fur Forstwesen* **166**(2): 83-90.

Wrońska-Pilarek D, Danielewicz W, Bocianowski J, Maliński T, Janyszek M. 2016. Comparative pollen morphological analysis and Its systematic implications on three european Oak (Quercus L., Fagaceae) species and their spontaneous hybrids. *PloS one* **11**(8): e0161762.

Yuan W, Liu S, Yu G, Bonnefond J-M, Chen J, Davis K, Desai AR, Goldstein AH, Gianelle D, Rossi F. 2010. Global estimates of evapotranspiration and gross primary production based on MODIS and global meteorology data. *Remote sensing of environment* **114**(7): 1416-1431.

Zhang L, Thibert-Plante X, Ripa J, Svanbäck R, Brännström Å. 2019. Biodiversity loss through speciation collapse: mechanisms, warning signals, and possible rescue. *Evolution* **73**(8): 1504-1516.

Zhang X. 2007. Vegetation of China and its geographic patterns. *China Geology Publ. House, Beijing*.

Zhang YY, Fang YM, Yu MK, Li XX, Xia T. 2013. Molecular characterization and genetic structure of Quercus acutissima germplasm in China using microsatellites. *Molecular Biology Reports* **40**(6): 4083-4090.

Zhou BF, Shi Y, Chen XY, Yuan S, Liang YY, Wang B. 2021. Linked selection, ancient polymorphism, and ecological adaptation shape the genomic landscape of divergence in Quercus dentata. *Journal of Systematics and Evolution* **60**(6): 1344–1357.

Zhou BF, Yuan S, Crowl AA, Liang Y-Y, Shi Y, Chen X-Y, An Q-Q, Kang M, Manos PS, Wang B. 2022. Phylogenomic analyses highlight innovation and

introgression in the continental radiations of Fagaceae across the Northern Hemisphere. *Nature communications* **13**(1).

Zhou W, Xiang Q-YJ. 2022. Phylogenomics and Biogeography of Castanea (Chestnut) and Hamamelis (Witch-hazel)-Choosing between RAD-seq and Hyb-Seq Approaches. *Molecular phylogenetics and evolution*: 107592.

Zimmer EA, Wen J. 2015. Using nuclear gene data for plant phylogenetics: Progress and prospects II. Next-gen approaches. *Journal of Systematics and Evolution* **53**(5): 371-379.

Zohary M. 1973. *Geobotanical foundations of the Middle East*: Fischer.

SECTION A

Natural History and Oak Taxonomy

Chapter 2.

New annotated checklist of the Portuguese oaks (*Quercus*, Fagaceae)

Carlos Vila-Viçosa[1,2,3,4,*], Jorge Capelo[2,4,5] , Paulo Alves[1,6], Rubim Almeida[1,2,3,4], Francisco M. Vázquez[7] (2023). Mediterranean Botany. 44. 1-46.
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[1] MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto – Herbário PO, Universidade do Porto. Praça Gomes Teixeira, 4099-002, Porto, Portugal.
[2] CIBIO (Research Center in Biodiversity and Genetic Resources) - InBIO (Research Network in Biodiversity and Evolutionary Biology), University of Porto. Campus Agrário de Vairão; Rua Padre Armando Quintas; 4485-661 Vairão; Portugal.
[3] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal.
[4] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO. Campus de Vairão, 4485-661 Vairão, Portugal
[5] Instituto Nacional de Investigação Agrária e Veterinária, I. P. (INIAV), Quinta do Marquês, 2780-159 Oeiras, Portugal.
[6] Floradata – Biodiversidade, Ambiente e Recursos Naturais. Lda. Rua do Campinho, 32 3.º Frente, 4000-151, Porto. Portugal.
[7] HSS Herbarium. Dep. Forest Production and Biodiversity. CICYTEX. 06187. Guadajira, Badajoz, Spain.

2.1. Abstract

We present a comprehensive taxonomic and nomenclatural review of the Portuguese oaks (*Quercus*), issuing from thorough biogeographical, historical, bibliographic, field and herbarium data. We propose a new annotated checklist for all taxa and nothotaxa belonging to *Quercus* genus in the Portuguese national territory, extending the analysis to the broader biogeographical context of the Western Mediterranean subregion. Fifteen herbaria collections were exhaustively studied and complemented by information retrieved from digital collections, resulting in the recognition of eleven native oaks. Further treatment at infraspecific level includes one subspecies and additional 23 nothotaxa. We designate lectotypes for 27 names and add a preliminary list of 148 cultivated taxa, resulting in a total of 183 oaks found in Portugal.

Moreover, we clarify the taxonomical status and reinstate *Q. pseudococcifera* and *Q. airensis* as native to the western Mediterranean subregion. We recover the concept of *Q. faginea*, as the widespread gall oak in Portugal and update its synonym list. We propose *Q. orocantabrica* and *Q. estremadurensis* as autonomous species within the broad European *Q. robur s.l.* group, alongside two newly circumscribed subsections within Section *Quercus.* We describe five new nothotaxa, including four unreported to nature and one with missing suitable names (*Q.* ×*almeidae, Q.* ×*alvesii, Q.* ×*capeloana, Q.* ×*eborense* and *Q.* ×*sampaioana*) and we approach the nomenclatural resolution of the remaining natural hybrids. Lastly, we provide an identification key, intelligible for non-specialists, including both native taxa and most frequent nothotaxa.

We emphasise the importance of historical and literature review, combined with accurate biogeographical information, as paramount to coherent taxonomical resolution. Both specimens and their associated records were found of crucial significance to a taxonomical model that is, in the end, useful for biodiversity conservation.

2.2. Introduction

As one of the most important genera of woody plants in northern hemisphere, *Quercus* Linnaeus (1753: 994) possesses circa 435 species, spanning across Temperate, Mediterranean, and Tropical biomes. Oaks are key components of mature woodlands and tall scrubland vegetation in the Iberian Peninsula (Axelrod, 1983; Manos *et al.*, 1999; Rivas-Martínez, Salvador *et al.*, 2011; Costa *et al.*, 2012; Carrero *et al.*, 2020).

In Portugal, eight oak species have been considered native (Franco, 1971; Pereira *et al.*, 2016). These were: Mirbeck's oak (*Quercus canariensis* Willdenow (1809: 975)), kermes oak (*Q. coccifera* Linnaeus (1753: 995)), Portuguese oak (*Q. faginea* Lamarck (1785: 725)), Lusitanian dwarf oak (*Q. lusitanica* Lamarck (1785: 725)), Pyrenean oak (*Q. pyrenaica* Willdenow (1805: 451)), pedunculate oak (*Q. robur* Linnaeus (1753: 996)), round-leaf oak (*Q. rotundifolia* Lamarck (1785: 723)) and cork oak (*Q. suber* Linnaeus (1753: 995)).

Several botanists have produced standard reviews of oak taxonomic diversity in the Iberian Peninsula (Coutinho, 1888; Schwarz, 1936b; Vicioso, 1950; Vasconcellos & Franco, 1954; Franco & González, 1987; Franco, 1990). Nevertheless, recent updates to the Portuguese and western Mediterranean scenario asks for a new synthesis (Vázquez *et al.*, 2003; Vázquez *et al.*, 2004; Capelo & Costa, 2005; Vila-Viçosa, 2012; Vila-Viçosa *et al.*, 2014; Vinagre, 2014; Vázquez *et al.*, 2015; Vila-Viçosa *et al.*, 2015; Vázquez & Coombes, 2016; Vázquez *et al.*, 2018; Vazquez *et al.*, 2020; Vila-Viçosa *et al.*, 2022b).

Moreover, we should be aware that the current image of oak taxonomy is that of a 'never-ending story', with an entangled nomenclature, that is inflated by intrinsic natural variation. Downstream, due to natural history artifacts, this drains in a wealth of names that are given to different subsets of taxonomic entities, creating manifold artificial species, instead of valid taxa with 'real' biological meaning. First, many simplistic descriptions lacked further typification and created dubious or phantom names. Second, a wealth of atypical heterogeneous herbarium material, that are not necessarily representative of natural variation, led authors to produce an inflation of species, by endorsing many several artificial 'herbarium taxa' (Vila-Viçosa *et al.*, 2022b). In addition, the known low interspecific barriers to gene flow and proliferation of several nothotaxa, enhanced by anthropogenic action, shuffles the potential combinations of shared characters (Vila-Viçosa *et al.*, 2014; Vila-Viçosa *et al.*, 2015; Vázquez *et al.*, 2018). This led to more taxonomic misperceptions and the ongoing profusion of names (Vila-Viçosa *et al.*, 2022b). However, modern access to online collections and biodiversity libraries leverages the detailed resolution of such cryptic information. An example is that is easier to find elusive type material in original collections.

Thus, our primary objective is to provide a resolved overview of the Portuguese oaks names with a direct taxonomic update and species delimitation, based on the current available information. We also note the biogeographic and synecological characteristics

of the recognized taxa and provide straightforward diagnoses and an identification key, accessible to non-specialists.

2.3. Material and methods

This work relies on the combined observations of authors, along with extensive fieldwork in Portugal and Spain since 2006. We performed a full in-situ review of Iberian *Quercus* L. collections in fifteen Herbaria, ten Portuguese (AVE, BRESA, COI, HVR, LISE, LISFA, LISI, LISU, PO and UEVH); three Spanish (BCN; HSS and MA); one in the Netherlands (L); and one French (P). Furthermore, we consulted eight online collections (B, FI, G-BOIS, K, LINN, MAIA, S and MPU) (Thiers, 2022), covering a few thousand specimens. A SYNTHESIS grant (FR-TAF-280), targeting Iberian oaks, at P-Lam, P-Desf, P-Juss and the general collection in the Herbarium of the Paris Muséum National d'Histoire Naturelle (P) was crucial for the presented results (Paris Herbarium Review – Digital Annex).

We complement new name propositions or taxa circumscription with drawings, type images, ecological and chorological features. We provide morphological descriptions in Latin and English. For all taxa, we supply the most relevant synonyms, including many names often misplaced in taxonomic literature. For unambiguous, but already well-documented names, we add updated descriptions, focusing mainly on combinations of diagnostic-characters, presented in the final key.

Taxa and nothotaxa circumscription follows the proposals of Brotero (1805); Coutinho (1888; 1913; 1930; 1935); Schwarz (1935; 1936b; 1936a); Camus (1935; 1936; 1938; 1939); Villar (1935; 1938; 1943; 1949; 1958); Vicioso (1942; 1950); Vasconcellos and Franco (1954); Saénz de Rivas (1967; 1969; 1975); Saénz de Rivas and Rivas-Martínez (1971); Rivas-Martínez and Saénz (1991); Penas *et al.* (1994); Llamas *et al.* (2003); Vázquez (1995); Vázquez *et al.* (2003); Vázquez *et al.* (2004); Vázquez *et al.* (2015); Vázquez and Coombes (2016); Vázquez *et al.* (2018); Vazquez *et al.* (2020); Capelo and Costa (2005);Vila-Viçosa *et al.* (2014).

Taxonomy was adapted from the infrageneric review of Denk *et al.* (2017) and the world oaks' phylogenetic backbone of Hipp *et al.* (2020) (Supplementary Information S1). Furthermore, we account for recent and ongoing molecular studies dealing with infrageneric classification (Manos & Hipp, 2021; Vila-Viçosa *et al.*, 2021).

For cultivated specimens we used Cullen and Maxwell (1989), Nixon and Muller (1997) and Cullen & Maxwell (1989), Nixon (1997) and Huang *et al.* (1999), altogether supported by the original protologues, subsequent authors comments and combined with the previously mentioned works.

Trichome analysis was made using a binocular magnifier (SZX16), coupled with a digital camera (OlympusSC-30) and a scanning microscope (Carl Zeiss EQ – 01784).

Authorship orthography follows the International Plant Names Index: http://www.ipni.org [accessed in December 2020].

Bioclimatic and biogeographic typology follows, respectively, Rivas-Martínez, S. *et al.* (2011); Rivas-Martínez *et al.* (2017) and the update of Vila-Viçosa *et al.* (2017). Syntaxonomic references followed Costa *et al.* (2012).

We collected information about exotic cultivated species, either cultivated in gardens or used as ornamentals, herbarium records, the nursery of the Botanical Garden of the University of Porto (Vila-Viçosa *et al.*, 2022a) and personal communication by experts.

2.4. Results

We present a full list of 183 oaks recognized in Portugal, 35 native and 148 cultivated. The list of native taxa includes eleven species, one subspecies and 23 nothotaxa with 287 heterotypic (=) and 57 homotypic synonyms (≡), that were revisited and updated, with substantial exchanges across taxa. We provide the annotated checklist of native oaks, ordered by sub-genus, section, subsection and species (Supplementary Information S1). We also provide the list of cultivated taxa (Supplementary Information S2- Digital Annex). Finally, we provide a synthetic key for native taxa and nothotaxa, based in differential characters inside groups.

We update from eight to eleven the list of native oaks, previously published by Franco (1990). The list of nothotaxa includes three yet unreported hybrids and two missing nomenclatural reassignments. We designate the lectotypes of 27 names, mentioning three important isolectotypes, seventeen holotypes, eighteen syntypes, four paratypes and twelve explicit references to previously designated lectotypes, in a total of eighty-one significant herbarium type-specimens.

We propose that the Iberian white oaks, together with the western Palearctic Section *Quercus*, to be distributed in two subsections, in agreement with previous proposals (Camus, 1934; Maleev, 1935) that are being supported by ongoing molecular analysis, based in next-generation sequencing (RADSeq) (Vila-Viçosa *et al.*, 2021).

2.4.1. Taxonomy

Quercus L. (1753: 994)

I. *Quercus* subgen. *Cerris* Oerst. (1866: 74)

Section *Cerris* Dumortier (1829: 15)

cork oak

1. *Quercus suber* L. (1753: 995) =*Quercus suberosa* Salisbury (1796: 392) =*Quercus occidentalis* Gay (1857: 243) ≡*Quercus suber* L. subsp. *occidentalis* (Gay) A. Camus (1938: 510) =*Quercus cintrana* Welw. ex Nyman (1881: 662)

Lectotype (designated by Iamonico and Peruzzi (2013): 1044)**:** (LINN - 1128.11 [digital image]!: Available at: http://linnean-online.org/11701/)

Ecology: Found mostly on silicate-derived and acidic soils, seldom on leached limestone- or marble-derived soils. Dominant in zonal woodlands in oceanic climates, from upper dry to hyper-humid ombrotypes. Occurs also as azonal (edaphoxerophile) or secondary forest, in the context of zonal deciduous forests; or as edaphohygrophile in lower dry ombrotypes. It is commonly excluded by low winter temperatures (absolute minimum below -10º C), in continental areas, supramediterranean and supratemperate belts.

Biogeography: Entire Portuguese mainland, excluding areas above 1000 m.

Syntaxonomy: *Quercetalia ilicis*

Section *Ilex* Loudon (1838: 1899)

Subsection *Ilex* Oerst (1866: 69)

round-leaf oak

2. *Quercus rotundifolia* Lam. (1785: 723) ≡*Quercus ilex* L. var. *rotundifolia* (Lam.) Trabut (Battandier & Trabut 1905: 309) ≡*Quercus ilex* L. subsp. *rotundifolia* (Lam.) O. Schwarz ex Taborda de Morais (1940: 122) =*Quercus ballota* Desfontaines (1791: 395) ≡*Quercus ilex* L. var. *ballota* (Desf.) Candolle (1864: 39) ≡*Quercus ballota* (Desf.) Nyman (1881: 662) ≡*Quercus ilex* subsp. *ballota* (Desf.) Sampaio (1909: 102) =*Quercus calycina* Poiret (Lamarck & Poiret, 1811: 216) =*Quercus ilex* L. subf. *coutinhoi* Villar Lectotype (designated here): MPU010434! [digital image!] https://science.mnhn.fr/institution/um/collection/mpu/item/mpu010434 =*Quercus ilex* var. *dolichocalyx* C. Vicioso (1950: 170) =*Quercus rotundifolia* L. var. *macrocarpa* (Cout.) F.M. Vázquez, S. Ramos & S. García (2004: 31).

Lectotype (designated by Vazquez *et al.* (2020)): (P-Lam - P00382458! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00382458)

Ecology: Edaphic indifferent, either in ultramafic, limestone or poor acidic soils, without waterlogging. Found under a large range of continental climate in lower-dry Mediterranean areas but reaching supratemperate and hyper-humid bioclimatic belts in Northwest Portugal as edaphoxerophile woods Pinto-Gomes *et al.* (2010).

Notes: Widely distributed taxon, frequently considered as a distinct species from *Quercus ilex* by ecological and biogeographic segregation and morphological distinctive characters (Franco, (1971; 1990); Schwarz (1964); Rivas-Martínez and Saénz (1991) Vila-Viçosa *et al.* (2022b)). Phylogeographic assessments sustain the latter hypothesis (Lumaret *et al.*, 2002).

Biogeography: All Portuguese mainland.

Syntaxonomy: *Quercetalia ilicis*

holm-oak

2.1 *Quercus ilex* L. (1753: 995) =*Quercus smilax* Linnaeus (1753: 994) =*Quercus sempervirens* Miller (1768: 508) ≡*Quercus ilicifolia* Salisbury (1796: 392) =*Quercus ilex* var. *angustifolia* Lamarck =*Quercus ilex* L. var. *oblongifolia* Lamarck (1805: 313) =*Quercus prasina* Persoon (1807: 568) =*Quercus expansa* Poiret (Lamarck & Poiret, 1811: 217) =*Quercus integrifolia* Steudel (1821: 673) =*Quercus variifolia* Sweet (1830: 465) =*Quercus ilex* L. subvar. *dehnhardtii* Tenore =*Quercus ilex* L. var. *macrophylla* Ten. =*Quercus ilex* L. var. *undulata* Ten. (1831: 472) =*Quercus ilex* L. var. *intermedia* Ten. =*Quercus ilex* L. var. *oleifolia* Ten. =*Quercus ilex* L. var. *operculata* Ten. =*Quercus ilex* L. var. *polycarpa* Ten. (1831: 473) =*Quercus ilex* L. var. *strangulata* Ten. (1831: 474)

=*Quercus cookii* Loudon (1838: 1926) ==*Quercus ilex* L. var. *fordii* Loudon (1843: 35) =*Quercus alpina* Endlicher (1847: 25) =*Quercus fordii* (Loudon) Carr (1861: 114) =*Quercus ilex* L. var. *lanceolata* Kotschy (*Exsicc.* 1855: 204) =*Quercus gracilis* Lange (1862: 36) =*Quercus ilex* L. var. *revoluta* Martrin-Donos & Timb.-Lagr. =*Quercus sinuata* Martrin-Donos & Timb.-Lagr. (1864:11) =*Quercus ilex* L. subvar. *micracylos* Martrin-Donos & Timb.-Lagr. (1864:12) =*Quercus ilex* L. var. *aperta* Martrin-Donos & Timb.-Lagr. (1864:13) =*Quercus ilex* L. var. *rostrata* Martrin-Donos & Timb.-Lagr.=*Quercus ilex* L. var. *argentata* Martrin-Donos & Timb.-Lagr. (1864:14) =*Quercus ilex* L. subvar. *capreifolia* Martrin-Donos & Timb.-Lagr. (1864:15) =*Quercus ilex* L. var. *glaucocaesia* Martrin-Donos & Timb.-Lagr. =*Quercus glauca* Martrin-Donos & Timb.-Lagr. (1864: 16) =*Quercus pseudoilex* Chatin (1869: 22) =*Quercus crispa* K. Koch (1873: 56) =*Quercus fagifolia* K. Koch =*Quercus oblonga* K.Koch, (1873: 56) =*Quercus ilex* L. var. *angustifolia* Gillot (1877: 48) =*Quercus ilex* L. var. *salicifolia* Borzí =*Quercus ilex* L. var. *parvifolia* Borzí (1880: 169); =*Quercus cyclophylla* Welw. ex Nyman (1881: 662) =*Quercus ilex* var. *laurifolia* Laguna (1883: 254) =*Quercus ilex* L. var. *gracilis* (Lange) Laguna (1883: 255) =*Quercus ilex* L. subvar. *oleoides* Trabut (Battandier & Trabut 1890: 824) Lectotype (designated here): MPU007892 [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007892 =*Quercus ilex* L. var. *diversifolia* G.Nicholson (1896: 189) =*Quercus ilex* L. var. *phillyreoides* (A.Gray) Franch. (1899: 152) =*Quercus ilex* L. var. *rufescens* Franch. (1899:151) =*Quercus ilex* L. var. spinosa (David) Franch =*Quercus ilex* L. var. *bullata* (Seemen) Franch. (1899: 152) =*Quercus ilex* L. var. *acrodonta* (Seemen) Skan (1902: 516) =*Quercus mixta* Reyn. (1903: 129) =*Quercus smilax* L. var. *fordii* (Loudon) Halácsy (1904: 132) =*Quercus ilex* L. var. *eucalyptoides* Lojac. (1907: 384) =*Quercus ilex* L. var. *oosperma* Albert (1908: 439) (Albert & Jahandiez, 1908) =*Quercus ilex* L. subvar. *brevicalyx* Albert =*Quercus ilex* L. var. *depressa* Albert =*Quercus ilex* L. var. *elegans* Albert =*Quercus ilex* L. var. *ovatiacutifolia* Albert =*Quercus ilex* L. var. *myrtifolia* Albert =*Quercus* ilex L. var. *ovifolia* Albert =*Quercus ilex* L. subvar. *parvifolia* (Borzí) Albert =*Quercus ilex* L. var. *sinuosifolia* Albert =*Quercus ilex* L. var. *undulata* Albert (1908: 440) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *cerasifolia* Albert =*Quercus ilex* L. var. *mirabilis* Albert =*Quercus ilex* L. var. *revoluta* Albert =*Quercus ilex* L. var. *cordifolia* Albert (1908: 441) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *reducta* Albert =*Quercus ilex* L. var. *spinulosa* Albert (1908: 442) (Albert & Jahandiez , 1908) =*Quercus ilex* L. var. *ellipticifolia* Albert =*Quercus ilex* L. var. *pisiformis* Albert =*Quercus ilex* L. var. *serratifolia* Albert (1908: 443) (Albert & Jahandiez, 1908) =*Quercus ilex* L. subvar. *laurifolia* (Laguna) Albert =*Quercus ilex* L. var. *ambigua* =*Quercus ilex* L. var. *crispata* Albert (1908: 444) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *fagifolia* Sprenger (1908: 154) =*Quercus marcetii* Pau (1909: 95) =*Quercus ilex* L. subvar. *marginata* Rouy =*Quercus ilex* L. subvar. *plicata* Rouy (1910: 321) =*Quercus ilex* L. var. *smilax* (L.) Asch. & Graebn. (1911: 472) =*Quercus ilex* L. var. *genabii* Bean (1914: 312) =*Quercus laurei* Coutange (1928: 157) =*Quercus ilex* var. *genuina* Cout. f. *laurifolia* Laguna (Coutinho 1930: 5) Lectotype (designated here): LISU P-10617! =*Quercus ilex* L. var. *plicata* (Rouy) A.Camus (1935: 8) =*Quercus murbeckii* Sennen (1936: 29) Lectotype (designated here): MA-01-00467547! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00467547) =*Quercus ilex* L. subvar. *brevicalyx* Trab. ex A.Camus (1939: 88) =*Quercus ilex* L. subvar. *cordifolia* (Albert) A.Camus (1939: 54) =*Quercus ilex* L. subvar. *caduca* A.Camus (1939: 54) =*Quercus ilex* L. subvar. *reducta* (Albert) A.Camus (1939: 54) =*Quercus ilex*

L. var. *gracilis* (Lange) A.Camus (1939: 64); =*Quercus ilex* L. var. *subrevoluta* A.Camus (1939: 57) =*Quercus ilex* L. subsp. *montserratensis* Svent. & Marcet (Marcet 1945: 37) ≡*Quercus montserratensis* (Svent. & Marcet) Sventenius & Marcet (1952: 335) Marcet (1952) =*Quercus ilex* L. var. *subsphaerocarpa* Albert (1946: 104) =*Quercus ilex* L. subsp. *genuina* (Cout.) C.Vicioso =*Quercus ilex* L. var. *vulgaris* (Cout.) C.Vicioso (1950: 161) =*Quercus ilex* L. f. *ambigua* (Albert) C. Vicioso (1950: 163) =*Quercus ilex* L. subsp. *genuina* (Cout.) C. Vicioso var. *gracilis* (Lange) C.Vicioso (1950: 164); =*Quercus ilex* L. var. *marcetii* (Pau) C.Vicioso (1950: 166) =*Quercus ilex* L. subsp. *refugiorum* Radic (1983: 18) =*Quercus ilex* L. f. *conoidea* Radic =*Quercus ilex* L. f. *lingulata* Radic =*Quercus ilex* L. f. *patula* Radic =*Quercus ilex* L. f. *rubella* =*Quercus ilex L. var. gymnobalanus Radic* (1983: 22) =*Quercus ilex* L. f. *pallida* Radic =*Quercus ilex* L. f. *tristigmata* Radic (1983: 23) =*Quercus ilex* L. f. *almissana* Radic =*Quercus ilex* L. f. *bistonensis* Radic =*Quercus ilex* L. f. *subtillima* Radic (1983: 24) =*Quercus ilex* L. f. *introversa* Radic (1983: 25) =*Quercus ilex* L. f. *glauca* Radic =*Quercus ilex* L. f. *mucurensis* Radic =*Quercus ilex* L. var. *glauca* Radic (1983 : 26) =*Quercus ilex* L. subsp. *gracilis* Rivas Mart. & Sáenz de Rivas (2002: 705).

Lectotype (designated by Vázquez and Coombes (2017): 1473–1475): (LINN 1128.4 [digital image]!: http://linnean-online.org/11694/).

Ecology: Thermo to meso-temperate bioclimatic belts, normally in mesotrophic soils.

Biogeography: Potential native distribution in Northeastern Portugal (Luso-Duriense Sector).

Syntaxonomy: *Quercetalia ilicis* | *Quercenion ilicis*

Notes: Despite not being usually considered a Portuguese native species, Coutinho (1930) names a specimen from Vimioso in northeast Portugal (LISU P-10617!), *Quercus ilex* var. *genuina* f. *laurifolia* (=*Quercus ilex* var. *laurifolia* Laguna (1883: 254)). Given the biogeographic affinities with the northwest Iberian Peninsula (Saénz de Rivas, 1967), along with the recognition of *Q. ilex* hybrids with *Q. coccifera* (*Q.* ×*auzandri*) (LISI 10278/1999!) in the same biogeographic area (Luso-Duriense Sector), we cannot exclude the hypothetic survival of *Q. ilex* as rare relict in the Portuguese Douro Basin, despite *Q. ilex* not being found there so far.

Subsection *Cocciferae* (Spach) Gürke (1897: 70)

kermes oak

3. *Quercus coccifera* L. (1753: 995) =*Quercus coccifera* var. *vera* Candolle (1864: 52) non Cout. (1888: 101) =*Quercus coccifera* f. *exserta* Coutinho (1888: 101).

Lectotype (designated by Iamonico & Peruzzi 2013: 1042): UPS V-175683 (Herb. Burser): XXII: 113.

Description: Dense shrubs, up to 3 m high; branching from the base. Leaves: curled, concolorous, green, glabrous with 5-8 (9) pairs of secondary veins, shinny; petiolate, with spiny, serrate to dentate margins. Petiole and lower quarter of the midrib and secondary veins, sometimes with sparse fused-stellate trichomes; Cup: short (length/breadth ratio up to 0.5*) broad cupuliform (acetabuliform) to cylindrical. Cup-scales: elongated, partially connate, terete to irregular, trigonous, cuspidate, sometimes free, stinging, and erect.

Ecology: Essentially in xerophytic habitats (outcrops), being indifferent to lithology. Found in both subhumid oceanic and dry and continental bioclimate. In Portugal, it is mostly found in successional stages of *Quercus rotundifolia* dry woodlands.

Biogeography: Coastal Lusitanian and West Andalusia Province | West Iberian Mediterranean Province | Duriense Lusitanian Sector

Syntaxonomy: *Asparago albi-Rhamnion oleoidis*

Notes: *Quercus coccifera sensu stricto* was originally described by Linnaeus (1753) and recently lectotypified by Iamonico & Peruzzi (2013). The taxonomic reasoning about the western Mediterranean arboreal kermes oaks and related taxa, is discussed as follows.

Arboreal kermes oaks

Mediterranean arboreal kermes oaks are immersed in nomenclatural controversy. The widely used name *Quercus calliprinos* Webb (1838: 15) has been addressed to the eastern Mediterranean arboreal kermes oaks, while the original taxon was described from Northern Africa (Tétouan) by Webb (1838), referring to a tree with tomentose leaves (Vázquez *et al.*, 2018; Vila-Viçosa *et al.*, 2022b). This original concept of an '*arboreal Kermes oak*' with fully downy leaves was enlarged by the author, to include Near East (Lebanon) plants, earlier named as *Q. pseudococcifera* Labillardière (1812: 9) (Vila-Viçosa *et. al*. 2022a). The putative type-specimen for this Palestinian oak (FI 171706!) was labelled by Webb as "*Quercus calliprinos N*. / *pseudococcifera Labill. non Desf*." (Burdert, 1979). This specimen has sub-glabrous leaves and petioles, with erect to patent-flat and large cup scales and annual fructification. Subsequently, De Candolle

(1864) applied the name *Q. calliprinos* var. *eucalliprinos* Candolle (1864: 55) to the same Lebanese materials, that were later addressed by Zohary *in schedula*: "*To this specimen Webb is referring in his Iter Hispanicum! It is this specimen which is the Type of Q. calliprinos Webb"* (1970-05-24). As a result, this name (*Q. calliprinos*) was applied to the Palestinian oak until the present time. However, the latter tree has glabrous and oblong to lanceolate leaves, with few stellate and fused-stellate trichomes in the proximal half of the leaf-blade and midrib, with characteristically large and free cup scales. This set of characters enhances the proximity of this eastern Mediterranean representant of the arboreal kermes oaks, as vicarious taxon of the western distributed *Q. pseudococcifera* Desf. (1799: 349) (Vázquez *et al.*, 2018; Vila-Viçosa *et al.*, 2022b). The latter has also a cup with free scales, that are smaller, becoming sometimes retroflexed in maturity and commonly a sub-occult (hidden) fruit (more than 1/3 of the length) (Vila-Viçosa *et al.*, 2022b). The Portuguese arboreal kermes oak forests, first referenced by Webb (1838) and Boissier and Reuter (1842), were later studied by Capelo & Costa (2001; 2005) from Arrábida and Olissiponense District (Rivas-Martínez *et al.*, 2017) where *Quercus rivasmartinezii* (Capelo & J.C.Costa) Capelo & J.C. Costa (2005: 268), is a well-documented taxon, related to *Q. pseudococcifera* Desf. (Vila-Viçosa *et al.*, 2022b). *Q. rivasmartinezii* shares a set of taxonomic and ecological traits with the latter, namely broad linear, but conic scales (3.0-7.0 mm), appressed in the proximal half of the cup, then strongly curled upwards near the distal half. Both above-described trees co-occur in the western Mediterranean Basin, thus, the taxonomic treatment of the Portuguese arboreal kermes oaks is proposed as follows:

false-kermes Oak

4. *Quercus pseudococcifera* Desf. =*Quercus mesto* Boissier (1842: 579) (Lectotype: G00358092!; Syntype: G00358094!); =*Quercus coccifera* L. var. *imbricata* DC. (1864: 53) =*Quercus coccifera* L. var. *vera* DC. f. *laxispinosa* Coutinho (1888: 101) (LISU!) =*Quercus coccifera* f. *subintegrifolia* Coutinho. (1888: 101) (LISU!) =*Quercus coccifera* var. *vera* DC. f. *subinclusa* Coutinho (1888: 101) =*Quercus coccifera* var. *vera* DC. f. *densispinosa* Coutinho (1888: 101) =*Quercus coccifera* f. *lanceolata* Coutinho (1888: 101) (LISU!) =*Quercus coccifera* f. *latifolia* Trab. (Battandier & Trabut 1890: 825) Lectotype (designated here): (MPU007902 [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007902) =*Quercus* ×*battandieri* A. Camus (1939: 792) Lectotype (designated here): (MPU010410, [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu010410).

Lectotype (designated by Vázquez *et al.* (2018)): P00667225! [digital image] : http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667225

Description: Trees up to 18 m, with a clear single bole, including young individuals, reaching a diameter at breath height 0.6-0.7m; smooth grey bark with vertical cracks in maturity. Leaves: flat, oblong to elliptic-lanceolate or narrowly obovate (obovate-spathulate), normally sub-sessile to sessile; margins often sub-entire sometimes with spiny teeth, with 7-9(11) pairs of divaricate secondary veins, glabrous to sub-glabrous, sometimes with sparse, deciduous, fused-stellate trichomes in the leaf basis, near the midrib. Cup: dark brown, hemispheric to cylindrical (length/breadth ratio greater than 0.5). Cup with free scales, dense, elongated and slightly thicker, irregular and trigonous, 3,3-5,5 mm long, heavily retroflexed, acuminate or cuspidate in maturation; hidden acorn (1/2; >1/2), ovate to narrow obovate.

Ecology: Mesophytic species, living in oceanic areas, with higher ombrothermic features, normally as natural fringes of marcescent forests.

Biogeography: Coastal Lusitanian and West Andalusian Province

4.1. *Quercus pseudococcifera* Desf. subsp. ***rivasmartinezii*** (Capelo & J.C. Costa) Capelo, Vila-Viçosa & F.M. Vázquez ***comb. nov.***

Basyonym: *Quercus coccifera* L. subsp*. rivasmartinezii* Capelo & J.C. Costa (2001: 270) (Holotype: LISI!) ≡*Quercus rivasmartinezii* (Capelo & J.C. Costa) Capelo & J.C. Costa (2005: 268)

Diagnose: Leaves sometimes slightly spathulate**;** cups with obvious thick conic to terete, sometimes nearly cylindrical, and acuminate free scales, that become retroflexed in maturity. This subspecies is, for the most, circumscribed to the thermophilic forests above dolomitic limestone substrata from the Coastal Lusitanian Province, but especially in the Arrabida District (Rivas-Martínez *et al.*, 2017; Vila-Viçosa *et al.*, 2017) and punctual elsewhere, across the range of *Q. pseudococcifera*.

downy-kermes Oak

5. *Quercus airensis* Franco & Vasconcelos (1954: 119) **prop. hybr.** =*Quercus coccifera* var. *tomentosa* A.DC. (1864: 53) =*Quercus coccifera auct. pl.* non Linnaeus (1753:995) =*Quercus coccifera* f. *tomentosa* (A. DC.) Cout. (1888: 101) =*Quercus webbei* Amo (1861:351) *nom. nud*.

Holotype (Vasconcellos & Franco, 1954: 119): COI **–** 18715!; [digital image]!: http://coicatalogue.uc.pt/specimen/18715

Description: Trees to dendroid shrubs. Leaves: sclerophyllous, flat and spiny, 1,5-4 cm x 1-3 cm, ovate-oblong to semi-lanceolate, from sub-glabrous to fully tomentose in both adaxial and abaxial surfaces. Trichomes: multiradial and ramified, long rays with different lengths (300-400 (500) μm) and stipitate (stip up to 100 μm). Cups: hemispheric with free, erect slim, terete to irregular trigonous scales, arcuate in maturity, with half-hidden to hidden fruits.

Notes: The main distinctive character that led Webb (1838) to propose a new species (*Quercus calliprinos*), inside the Kermes oak complex, was its "downy" leaves from both faces. This fully tomentose and dendroid kermes oak, with typical *loci* from Tétouan (Morocco), occurs in the Atlantic coast of Portugal (Lisbon-Alenquer) where it was collected and recognized by Coutinho (1888; COI - 18906!) as *Q. coccifera* f. *tomentosa* (A.DC.) Cout. (1888: 101). This nomenclatural endorsement was based on the variety proposed by De Candolle (1864) (*Q. coccifera* L. var. *tomentosa* Candolle (1864: 53)), corresponding to the upper specimen in the same herbarium sheet that contains the first ascribed plant by Webb (1838) deposited in FI 011747! (Vázquez *et. al*. 2018). Furthermore, Candolle (1864) addresses a potential proximity of this taxon to its eastern Mediterranean vicariant taxon *Quercus aucheri* Jaub. & Spach (Jaubert, 1843: 113), which was also hypothesized as a putative hybrid between *Q. ilex* and *Q. calliprinos* by Kasapligil (1981), but possessing quite distinctive cups, if compared to those of the putative parents' species. Likewise, the Portuguese plant communities of *Q. coccifera (Quercetum coccifero-airensis*) from Montejunto and Aire and Candeeiros mountains were assumed to be co-dominated by a putative natural hybrid between *Q. coccifera* and *Q. rotundifolia*, named as *Quercus* ×*airensis* Franco & Vasc. (1954: 119) (Espírito-Santo, 1995). By analogy to *Q. aucheri, Q. airensis* also has fully tomentose leaves (Figure 1) and reveals comparable ecological features: karst limestones in hyperoceanic and coastal areas, protected from winter cold (Serteser, 2009). Therefore, we share the assumption made by Candolle (1864), relating the proximity between *Q. airensis* and *Q. aucheri* as vicariant taxa across the Mediterranean Basin. Both taxa deserve further molecular scrutiny, to be included in a global phylogeographic assessment of all kermes oak taxa from the Mediterranean Basin.

As stated above, the name *Q. calliprinos* was originally enlarged to the Near East arboreal kermes-oak (Webb, 1838; Vila-Viçosa *et al.*, 2022b), being in use for more than 50 years (Zohary, 1960). Thus, according to the Art. 14.9 of the ICN (Turland *et. al*. 2018) and to preserve the nomenclatural stability, we hereby recover the onward available name for the western Mediterranean tomentose kermes oak as *Q. airensis*, in

accordance with Vasconcellos and Franco (1954). The name *Q. calliprinos* Webb (1838: 15) should be properly preserved, with the respective elected type (FI-171706!) for the eastern Mediterranean arboreal Kermes oak (Palestinian oak) in future nomenclatural works (pro nom. cons. prop. nob.).

Biogeography: Coastal Lusitanian and West Andalusia Province

Syntaxonomy: *Quercion fagineae*

Ecology: Fringe-mantles of edaphoxerophile round-leaf oak (*Q. rotundifolia*) and Portuguese oak (*Q. faginea*) forests, normally in Cenozoic's karst limestone, marls or clay substrata.



Figure 1 - Fully tomentose abaxial leaf surface of *Q. airensis* Franco & Vasconcellos.

In Portugal, if the most common nothotaxa are also considered, four arboreal Kermes oaks can be found: i) the taxa *Q. pseudococcifera* and *Q. airensis* and ii) the nothotaxa *Quercus ×eborense nob.* and *Q. ×almeidae nob.,* further discussed in the hybrids section.

To address the taxonomy of tomentose kermes oaks and segregate autonomous taxa from the aforementioned hybrids, we rely on trichome analysis (see Figure 2). The nothospecies respectively inherit *Q. ilex* or *Q. rotundifolia* trichomes, which are exclusively fused stellate, subsessile and totally appressed (see Figure 2b and 2d), with

short rays (<150 µm in *Q. rotundifolia*; and slightly larger (<180 µm) in *Q. ilex* (Saénz de Rivas, 1967; Vila-Viçosa *et al.*, 2022b)) (see Figure 2a and 2b). In contrast, *Quercus airensis* (Figure 2e and 2f) possesses ramified multiradial trichomes, with large rays (>300-400 (500) µm) and a well-developed stipe (*ca.* 100 µm) (Figure 2e and 2f).

A synopsis of taxonomic criteria and nomenclature of the aforementioned Portuguese kermes oaks is presented in Table 1.

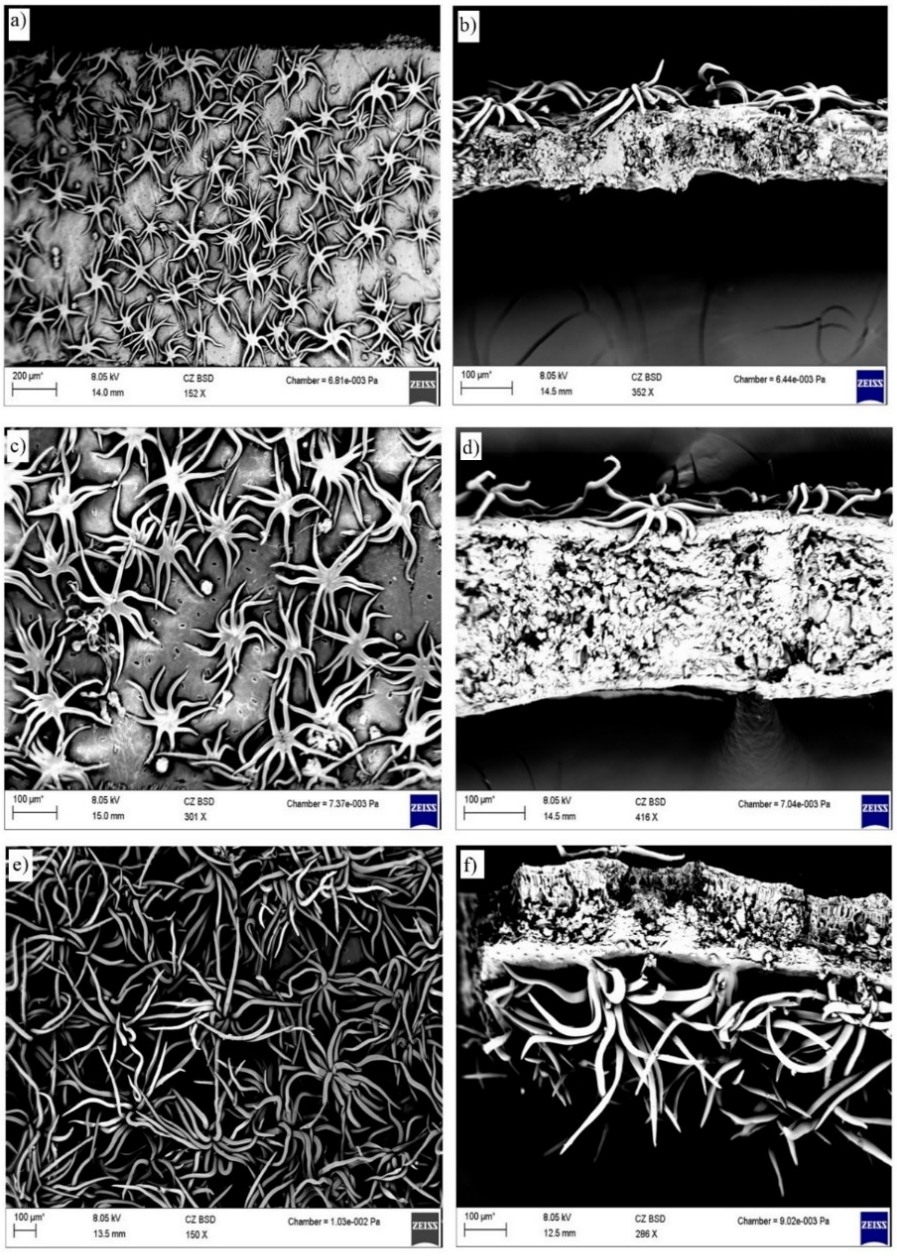


Figure 2 - Trichome analysis comparison (SEM) of Iberian hybrids between kermes oak and holm oak and *Quercus airensis* (a, b) - *Quercus* ×*eborense nob.*; (c, d) – *Q.* ×*auzandri;* (e, f) – *Q. airensis*); (a, c) – Detail of abaxial leaf surface with fused-stellate and stellate trichomes (152x magnifying in *Q.* ×*eborense nob.* and 301x in *Q.* ×*auzandri*); (b, d) – transversal overview and detail of appressed fused-stellate and stellate indumentum (abaxial leaf surface) (352x in *Q.* ×*eborense nob.* and 416x in *Q.* ×*auzandri*); (e, f) - Detail of multiradial and stipitate trichomes (e)-150x; f) - 286x) in *Q. airensis* with large rays (>300 µm).

Table 1 - Synthetic table of the differential characters for the western Mediterranean kermes oaks and related nothotaxa.

Q. airensis	***Q. coccifera***	***Q. ×eborense***	***Q. pseudococcifera***	***Q. pseudococcifera subsp. rivasmartinezii***	***Q. ×almeidae***
Leaf traits: Margin					
Irregular, Dentate, Flat	Irregular, Dentate, curly	Irregular, Dentate, curly	Sub-entire to serrate, Flat	Sub-entire to serrate, Flat	Irregular, Dentate, to sub-entire, flat
Leaf traits: Shape					
Ovate-oblong to semi-lanceolate	Ovate to obovate, sometimes semilanceolate, Petiolate	Ovate to obovate, sometimes semilanceolate, Petiolate	Lanceolate to ovate-oblong, Sub-sessile	Lanceolate to ovate-oblong, Sub-sessile	Ovate to obovate-oblong, Petiolate
Cup traits: Cup / Acorn					
Hemispheric cup Half hidden to hidden fruits	Short cupoliform (acetabuliform) to short cylindrical (length/breadth <0.5), large fruit not hidden	Hemispheric, large fruit not hidden,	Hemispheric to long cylindrical (length/breadth > 0.5) cup, dark brown, large to strait fruits, partially hidden	Hemispheric to long cylindrical (length/breadth > 0.5) cup, dark brown, large to strait fruits, partially hidden	Hemispheric cup, dark brown, large to straitfruits, partially hidden
Cup traits: Scales					
Large, retroflexed, thick and acute scales	Short, Thick, erect-patent to retroflexed in maturity	Short, half-free to imbricate, thick, erect-patent to slightly retroflexed in maturity	Free, large, flat and appressed in maturity, lax	Free, large, cylindrical and retroflexed in maturity, pungent	Plicate, appressed to slightly free
Trichome types: Presence/density					
Both adaxial and abaxial faces pubescent to heavily tomentose	Glabrous to glabrescent in petiole, lower part of midrib and branches	Pubescent to tomentose in abaxial face and pubescent to glabrescent in adaxial face	Glabrous to subglabrous, sometimes pubescent in abaxial leaf face (proximal edge) in the midrib, insertion of secondary nerves and petiole	Glabrous to subglabrous, sometimes pubescent in abaxial leaf face (proximal edge) in the midrib, insertion of secondary nerves and petiole	Pubescent in both abaxial and adaxial leaf faces

Trichome types: Bulbous					
-	-	+	-	-	-
Trichome types: Stellate					
++	-	+	+	+	+
Trichome types: Fused-Stellate					
++	++	+++	++	++	+++
Trichome types: Stipitate					
+++	-	-	-	-	-
Trichome types: Simple/uniseriate					
++	++	+	+	+	++
Trichome types: Multiradial					
+++	-	-	-	-	+

II. *Quercus* subgen. *Quercus* Hickel & Camus (1921: 379)

Section *Quercus* Menitsky (1972 : 107); Nixon & Muller (1997); Denk *et. al.* (2017: 13) ≡Section Robur Reichb. (1831 : 177) ≡Section Robur Loudon (1838: 1731))

Subsection *Hartwissianae* (Maleev) Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez ***comb. & stat. nov.***

Basionym: *Quercus* L. subgen. *Lepidobalanus* DC *emend*. Oerst.
Sect. *Eulepidobalanus* Oerst. subsect. *Robur* (Rchb.) Maleev
ser. *Hartwissianae* Maleev, *Bot. Zhur. URSS*, 20(2): 164. 1935.

Type species: *Quercus hartwissiana* Steven (1857: 387).

Includes: *Q. brutia* Ten., *Q. dalechampii* Ten., *Q. estremadurensis* O. Schwar, *Q. haas* Kotschy, *Q. huguetiana* (Franco & G. López) Rivas Mart. & Sáenz de Rivas, *Q. iberica* Steven ex M.Bieb., *Q. imeretina* Steven ex Woronow, *Quercus orocantabrica* Rivas-Martínez & al., *Q. pedunculiflora* K.Koch, *Q. petraea* (Matt.) Liebl, *Q. pinnatiloba* K. Koch, *Q. robur* L.

Description: Deciduous to brevi-deciduous trees, subsessile to long petiolate leaves with lobate to lobulate margins, and mostly irregular lobes. Less often regularly lobate to dentate, with or without vestigial intercalary nerves, seldom with tertiary ones that are subparallel to each other, coarsely and regularly reticulate. Glabrous to glabrescent or

pubescent leaves and twigs, with simple, bifurcate, stellate or more rarely fasciculate trichomes.

Estremadura Oak

6. *Quercus estremadurensis* O. Schwarz (1935: 463) ≡*Quercus robur* subsp. *estremadurensis* (O. Schwarz) A. Camus (1935a: 50) =*Quercus racemosa* Brotero (1804: 31) *non* Lamarck (1785: 715) =*Quercus pedunculata* f. *longipedunculata* Coutinho (1888: 58) =*Quercus robur* subsp. *broteroana auct. pl. non* Schwarz (1935: 463)

Lectotype (designated by Vázquez et al. (2018)): Portugal. Extremadura: Sintra, May, 1840, *Wellwitsch s.n.* (P06857436!); Syntype 1: Portugal. Beira Litoral: Coimbra, Arregaça, October 1904, *M. Ferreira s.n.* (P06857428!; Isosyntypes: LISU – 10353!, Fl. Lus. Exs. 1743; COI – 19267!; PO-V2073 G.S.!); Syntype 2: Portugal. Beira Litoral: Coimbra, Pinhaes da Fonte da Telha, April 1890, *A. Moller s.n.* (COI – 19268!, Fl. Lus. Exs. 876)

Ecology: Thermophilic species, found in oceanic humid and submediterranean areas, with short summer drought period. Preferring silicate-derived soils, but may be found in leached limestone soils, normally under slight temporary influence of the water table.

Notes: *Quercus estremadurensis* specimens have been commonly misidentified as putative hybrids between *Q. robur* and *Q. faginea* (*Q.* ×*coutinhoi* Samp.). This misconception comes from both trees being marcescent to evergreen and to the similar rhomboidal leathery leaf, with acute lobes. If compared to *Q. robur* L. or *Q. robur* subsp. *broteroana* (Schwarz, 1937), *Q. estremadurensis* tend to have lobes in a higher number (≥ (7)8) that are subequal, less deeply cut, with acute tips and sometimes mucronate. The petiole is normally larger (> 5 mm up to 15 mm) and the peduncle is often longer (> 8 cm). Leaf indumentum is composed of single/bifurcated trichomes throughout the midrib and ramified trichomes throughout the abaxial leaf surface, which varies from glabrescent to pubescent (Vázquez *et al.*, 2018) (Indumentum differences comparing *Q. estremadurensis* to *Q* ×*coutinhoi* will be discussed further on). The Portuguese herbaria review, performed by Schwarz (COI! and LISU!), that served as base for the original protologue of *Q. estremadurensis* (Schwarz, 1935), suggests an already frequent introgression with *Q. robur* (*Q. robur* subsp. *broteroana*). Such clinal variation led Vasconcellos & Franco (1954) to regard this taxon as mere phenotypic plasticity of *Q. robur s.l.*. The original protologue of Schwarz (1935) emphasizes differential characters,

like early leaf-development in spring shoots, leaves with a very regular structure, higher number of lobes and almost absence of sinual nerves. The higher number of cup-scales, larger towards the base and quickly becoming short towards the apex, is a character considered to belong to Ser. *Primitivae*, inside Section *Quercus* (Schwarz, 1936a). These are shared with other southern European roburoid oaks, like *Q. hartwissiana* Steven (1857: 387) (=*Quercus armeniaca* Kotschy (1860: 25)) (K000832028!; P06813011!; 06813013! 06861134!; L-1571371!; L-157376!). Accordingly, Camus (1939), Vicioso (1950) and Montserrat (1957) concur with recent essays (Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018; Vila-Viçosa *et al.*, 2020b) by reasoning that *Q. estremadurensis* can be a relict oak from the tertiary period (Schwarz, 1935). Such hypothesis is supported by the presence of this taxon in north Africa (P05622871!; P06860974!; P06857427!) (Paris Herbarium Review – Digital Annex), and southwest Iberian Peninsula, which enhances a biogeographic alliance to paleoclimatic thermophilic and subtropical relictual taxa with Tertiary affinity, like *Q. canariensis, Rhododendron ponticum* and *Prunus lusitanica* (Vila-Viçosa et al., 2020b).

Biogeography: Coastal Lusitanian and West Andalusia Province | West Iberian Province | Duriense Lusitanian Sector

Syntaxonomy: *Quercion fagineae* | *Quercenion pyrenaicae*

Galician Oak

7. *Quercus orocantabrica* Rivas Mart. & al. (2002: 706) =*Quercus robur* subsp. *broteroana* O. Schwarz (1937: 108) ≡*Quercus broteroana* (O. Schwarz) Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez, *alibi, nom. illegit.* Art. ICN 11.2 (Turland, 2018) Lectotype (designated here): Portugal. Minho. Serra do Soajo, Várzea, 600m, 9-VIII-1926, *A. Mendonça s.n.* (COI-19256!) [digital image]!: http://coicatalogue.uc.pt/specimen/19256; Syntype 1: Portugal. Extremadura: Sintra: Palácio da Pena, 12-V-1905- Kuegler s.n. (JE-28997!); Syntype 2: COI-19263!; Syntype 3: COI-19264!; Syntype 4: COI-91634!; Syntype 5: COI-19244!; Syntype 6: COI-19243!; Syntype 7: COI-19238!; Syntype 8: COI-19249!; Syntype 9: COI-19258!

Holotype (designated by Rivas-Martínez *et al.* (2002)): Spain. León: Puerto de las Señales, *in glareosibus,* ex. S.,30TUN1671, *ubi* Félix Llamas *legit*, 30-08-1998. LEB 65210, isotype: LEB65211, paratype: Torrestío (León) 28TQH47, robledal, 1255 m, leg. E. Puente & M.J. López Pacheco, LEB 53069.

Ecology: Silicate-derived soils, in humid to ultra-hiperhumid areas, or in temporihygrophile stations in areas with a short summer drought.

Notes: The Iberian pedunculate oaks have been studied by Schwarz (1935; 1937). The protologue of *Q. robur* subsp. *broteroana* O. Schwarz (1937: 108), addresses this taxon as the hybridization-front and transitional gradient between *Q. estremadurensis* and the European *Q. robur* L. Later, the author himself withdrew both his Iberian pedunculate oaks (Schwarz, 1964) since the observed differential characters can be found in non-Iberian populations. Despite the morphological plasticity across Europe, we found that Schwarz's perception of a higher frequency of distinctive character combination supporting *Q. robur* subsp. *broteroana* still holds and it's supported by molecular data (Vila-Viçosa *et al.*, 2021). This analysis reveals *Q. orocantabrica* to be conspecific with *Q. robur* subsp. *broteroana* and that this western Iberian pedunculate oak, to be a well-circumscribed sister-species of the European *Q. robur.* Further, the same molecular analysis also segregates *Q. estremadurensis* together with *Q. robur* subsp. *broteroana* from the European pedunculate oaks (*Q. robur* L. *s. str.*) (Vila-Viçosa *et. al*. 2021). Nevertheless, in the light of the ICN (Turland *et al.*, 2018), at the species rank, the headlong available name for the western Iberian pedunculate oak is *Q. orocantabrica* as priority according to the Article Art.11.2. When comparing with typical *Q. robur,* the diagnostic characters are related with leaf length, shape, and texture. Typically, *Q. orocantabrica* has a thicker and leathery blade, with oblong to oblong-transovate shape. Moreover, the leaves are wider and glossy with unequal lobes, more than 6(8) secondary nerves and larger cups, with brownish and acute not-fused scales. *Q. orocantabrica* often presents both longer petiole (up to 15 mm) and peduncle (up to 15 cm) in comparison with *Q. robur*. These characters are collectively distributed across all syntypes, that are cited by the authors (Schwarz, 1937; Rivas-Martínez *et al.*, 2002) in the protologues of both *Q. robur* subsp. *broteroana* and *Q. orocantabrica*. Some of these characters often overlap the description of *Q. estremadurensis* (Schwarz, 1935), which led to the indifferent use of both names (*Q. robur* subsp. *broteroana* and *Q. estremadurensis*) in several pedunculate oak herbaria specimens from center-west and northwest Portugal (LISI!; LISU!; HVR!).

Biogeography: Portuguese Divisorian Subprovince **|** Atlantic Oro-Lusitanian Subprovince | Toledanian-Taganian Sector

Syntaxonomy: *Querco-Fagetea sylvaticae*

Subsection *Macrantherae* (Stef.) Maleev (1935: 163)

Type species: *Quercus macranthera* Fisch. & C.A.Mey. ex Hohen (1838: 259).

Includes: *Q. boissieri* Reut., *Q. brachyphylla* Kotschy, *Q. canariensis* Willd., *Q. congesta* Presl., *Q. faginea* Lam., *Q. frainetto* Ten., *Q. ichnusae* Mossa, Bacch. & Brullo, *Q. infectoria* G.Olivier, *Q. kotschyana* O. Schwarz, *Quercus leptobalana* Guss., *Q. lusitanica* Lam., *Q. pubescens* Willd., *Q. pyrenaica* Willd., *Q. virgiliana* Ten., *Q. vulcanica* Boiss. et Heldr.

Description: Trees with brevi-deciduous or marcescent leaves. Crenate or ± deeply lobed to pinnatifid margins, coarsely toothed when crenate. Divaricate and irregular secondary nerves. Pubescent to tomentose abaxial leaf surfaces with simple, stellate, multistellate or fasciculate trichomes. Cups with small, flat to fat or gibbose scales, always appressed and never free or loosely imbricated and long. Commonly distributed across submediterranean areas from southern Europe, North Africa, and Near East to Transcaucasia and Iran.

Algerian oak

8. *Quercus canariensis* Willd. (1809: 975) =*Quercus lusitanica* Lam. var. *salzmanniana* Webb (1838: 12) =*Quercus mirbeckii* Durieu (Duchatre 1847: 426) Lectotype (designated here): P06860975! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06860975 ≡*Quercus lusitanica* Webb var. *mirbeckii* (Durieu) Candolle (1864: 19) ≡*Quercus infectoria* Boiss. subsp. *mirbeckii* (Durieu) Nyman (1881: 661) ≡*Quercus lusitanica* Webb subsp. *mirbeckii* (Durieu) Ball (1878: 666) ≡*Quercus lusitanica* Webb var. *mirbeckii* (Durieu) Coutinho (1888: 69) ≡*Quercus canariensis* Willd. var. *mirbeckii* (Durieu) C. Vicioso (1950: 94) =*Quercus esculenta* K. Koch (1873: 80) =*Quercus lusitanica* Lam. subsp. *mirbeckii* (Durieu) Ball, (1878: 666) =*Quercus corymbifolia* Ehrenb. ex Boiss. (1879: 1167) =*Quercus mirbeckii* Durieu var. *angustifolia* Trab. =*Quercus mirbeckii* Durieu var. *subpedunculata* (1890: 820) =*Quercus mirbeckii* Durieu var. *microphylla* =*Quercus mirbeckii* Durieu var. *brevipetiolata* Trab. =*Quercus mirbeckii* Durieu var. *fagifolia* Trab. (1890: 821) Battandier & Trabut (1890) =*Quercus faginea* Lam. var. *salzmanniana* (Webb) Sampaio (1910a: 164) ≡*Quercus lusitanica* Webb subsp. *salzmanniana* (Webb) Coutinho (1913: 165) ≡*Quercus salzmanniana* (Webb) Coutinho (1935: 36) Lectotype (designated here): (LISU – 10407!) ≡*Quercus canariensis* Willd. var. *salzmanniana* (Webb) C.Vicioso (1950: 94) =*Quercus lusitanica* var. *maroccana* Braun-Blanq. & Maire (1924: 155) ≡*Quercus faginea* Lam. var. *maroccana* (Braun-Blanq. & Maire) Jahand. & Maire (1932: 165) ≡*Quercus faginea* var. *maroccana* (Braun-Blanquet & Maire) A. Camus (1935a: 26) ≡*Quercus faginea* subsp. *maroccana* (Braun-Blanq. & Maire) F.M. Vázquez & Coombes (2016: 27) =*Quercus faginea* Lam. var. *spinosa* Maire & Trabut (Maire 1931b: 314)

Lectotype (designated here): (MPU002693, [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu002693) =*Quercus faginea* var. *fagifolia* Jahandiez. & Maire (1932: 165) =*Quercus faginea* var. *mirbeckii* (Durieu) Maire (1932: 178) =*Quercus carpinifolia* Sennen (1932: 807) ≡*Quercus canariensis* var. *carpinifolia* (Sennen) C. Vicioso (1950: 96) =*Quercus nordafricana* Villar (1938: 450) =*Quercus alpestris* f. *glabrescens* Villar (1938: 454) =*Quercus mirbeckii* var. *typica* A. Camus (1939: 156) =*Quercus faginea* var. *microphylla* (Trab.) Maire & Saccardy (1939: 364)

Lectotype (designated by Schwarz (1936a)): Spain, Teneriffa, *Brussounet s.n.* (B –W - 17608 -01 [digital image]!: http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=BW17608010).

Isolectotype: P06860905! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06860905

Ecology: Growing extensively on limestones in North Africa, the Iberian Peninsula subpopulations are exclusive from siliceous lithology. In Portugal occurs in the sienitic batholith of Monchique, in humid to hyper-humid ombrotypes, expanding through riverine forests in neighbouring areas, above schists. (Odemira and Aljezur). The main ecological feature associated to this species distribution is summer horizontal precipitation, originated either by advection fogs, either by thermic inversion in deep valleys or interior mountain areas (Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2020a; Vila-Viçosa *et al.*, 2020b; Vila-Viçosa & Arsénio, 2021).

Notes: A notable distinctive feature of *Quercus canariensis* is the indumentum type. The leaves are glabrescent only with a floccose indumentum of fasciculate, uniseriate single ramified trichomes concentrated near the midrib and secondary nerves. The absence of a stellate indumentum is a marked differential character of the species (*e.g.* compared to *Q. faginea* s.l.) as emphasized by Schwarz (1936b); whereas the presence of stellate trichomes indicates introgression with other *Galliferae* oaks (Gürke, 1897). In concrete, as discussed further on *Q. ×tlemcenensis*, that relates such introgression between *Q. canariensis* and *Q. faginea* in the western Mediterranean Basin.

Biogeography: Monchique County (Vila-Viçosa & Arsénio, 2021)

Syntaxonomy: *Euphorbio monchiquensis-Quercetum canariensis*

Portuguese oak

9. *Quercus faginea* Lam. (1785: 725) =*Quercus pseudosuber* Desfontaines (1799: 348) =*Quercus hybrida* Brotero (1805: 31) =*Quercus aegilopifolia* Persoon =*Quercus ovalifolia* Bosc *ex* Pers., (1807: 570) =*Quercus castellana* Bosc *ex* Pers. (1807: 571) =*Quercus castellana* Bosc (1808:24) **=***Quercus castellana* Bosc *ex* Poir., (Lamarck, 1811: 226) =*Quercus australis* Link *ex* Spreng (1826: 861) =*Quercus australis* Link, 1831: 466) =*Quercus cookii* Loudon (1838: 1926) =*Quercus lusitanica* var. *baetica* Webb (1838:12) Lectotype (designated here): P06857819! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06857819) ≡*Quercus lusitanica* subsp. *baetica* (Webb) A.DC. (1864: 19) ≡*Quercus faginea* var. *baetica* (Webb) Samp. (1910a: 123) ≡*Quercus faginea* Lam. subsp. *baetica* (Webb) Maire, (1931: 65) ≡*Quercus baetica* (Webb) Villar (1938: 455) =*Quercus alpestris* Boiss. (1838: 83) ≡*Quercus faginea* subsp. *alpestris* (Boiss.) Maire (1961: 100) ≡*Quercus lusitanica* subsp. *alpestris* (Boiss.) Nyman (1881: 661) ≡*Quercus lusitanica* var. *alpestris* (Boiss.) Cout. (1888: 68) ≡*Quercus lusitanica* subsp. *alpestris* (Boiss.) Mouill. (1897: 1161) =*Quercus quexigo* Cook *ex* Willk. & Lange (1862: 240) =*Quercus lusitanica* subsp. *faginea* (Lam.) A.DC. in A.P.de Candolle =*Quercus lusitanica* subsp. *faginea* (Lam.) A.DC. α *clusii* A.DC. (1864: 17) *nom. nud.*, *p.m.p.* ≡*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. =*Quercus lusitanica* subsp. *faginea* (Lam.) A.DC. (β) var. *brevipetiolata* A.DC. (1864: 17) =*Quercus lusitanica* subsp. *baetica* (Webb) A.DC. (β) var. *pedunculata* A.DC. (1864: 19) =*Quercus baetica* (Webb) H. Buek (De Candolle, 1874: 322) =*Quercus lusitanica* var. *broteroi* Coutinho (1888: 68) Lectotype (designated here): COI - 18933 [digital image]!: http://coicatalogue.uc.pt/specimen/18933 ≡*Quercus lusitanica* subsp. *broteroi* (Cout.) Mouillefert (1898: 1162) ≡*Quercus faginea* subsp. *broteroi* (Cout.) A. Camus (1939: 179) ≡*Quercus broteroi* (Cout.) Rivas-Martínez & C. Sáenz 1991: 104) =*Quercus lusitanica* Webb f. *salicifolia* Coutinho (1888: 68) ≡*Quercus alpestris* var. *salicifolia* (Cout.) A. Camus (1939: 166) =*Quercus lusitanica* Webb f. *ellipticifolia* Coutinho (1888: 68) ≡*Quercus alpestris* var. *ellipticifolia* (Cout.) A. Camus (1939: 166) =*Quercus lusitanica* var. *broter[o]i* Cout. f. *pedunculata* Cout. (1888: 69) =*Quercus lusitanica* Webb subsp. *faginea* (Lam.) Coutinho (1913: 165) ≡*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. f. *vulgaris* Cout. *nom. inval*. (Melbourne Code, Art. 23) ≡*Quercus faginea* subvar. *vulgaris* (Cout.) A. Camus, (1935: 113) *nom. inval.* (Melbourne Code, Art. 23); ≡*Quercus faginea* var. *vulgaris* A.Camus (1939: 177) *nom. inva*l. (Melbourne Code, Art. 23) ≡*Quercus faginea* subsp. *eufaginea* A.Camus (1939: 172) *nom. inval*. (Melbourne Code, Art. 23) =*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. f. *submembranacea* Cout. (1888: 67) =*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. f. *subsuberosa* Cout. (1888: 68) =*Quercus faginea* var. *submembranacea* (Cout.) A.Camus (1939: 177) ≡*Quercus lusitanica* var. *submembranacea* (Cout.) C. Vicioso (1950: 112) =*Quercus lusitanica* f. *obtusidens* C. Vicioso. (1950: 108); =*Quercus lusitanica* var. *submembranacea* (Cout.) C. Vicioso (1950: 112); =*Quercus lusitanica auct. pl*. non Lamarck (1875: 719) =*Quercus lusitanica* Lam. subsp. *faginea* (Lam.) Candolle (1864: 17) =*Quercus* ×*villariana* A. Camus (1939: 791) =*Quercus lusitanica* subsp. *broteroi* (Cout.) Muill. var. *lanceolata* C. Vicioso (1950: 112) Lectotype (designated here): [digital image]!: MA - 54728! http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00054728 =*Quercus* ×*clementei* C.Vicioso (1950: 140) Lectotype (designated here):

MA-01-00057382! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00057382 ≡*Quercus* ×*villariana* nothosubsp. *clementei* (C.Vicioso) F.M.Vázquez, S.Ramos & S.García (2004: 31) =*Quercus alpestris* f. *grandifolia* C. Vicioso, (1950: 102) Lectotype (designated here): MA-02-00054718! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-0054718 =*Quercus lusitanica* f. *obtusidens* C.Vicioso (1950: 108) =*Quercus gaditana* Vázquez *et. al*. (2014: 142) =*Quercus* ×*rosa-pintii* Vila-Viçosa, F.M. Vázquez, Meireles & C. Pinto-Gomes (2014: 146)

Lectotype (designated by Vázquez et al. (2018)): P-Lam P00382459!) [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00382459

Isolectotype: P-Juss P00320341!; Spain. Andalusia. XVIII century *Antoine Laurent de Jussieu s.n.* [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320341)

Ecology: Preferentially basophile taxon, but indifferent to lithology. From upper sub-humid to humid ombrotypes, or in temporihygrophile positions in drier stations.

Notes: This taxon has been enrolled in a wealth of unclear nomenclatural and taxonomic assignations since the study performed by Vasconcellos and Franco (1954), upon the original materials of Lamarck, kept in P-Lam (P00382459!) and P-Juss (P00320341!). Only the recent review elaborated by Vazquez *et al.* (2020) upon the historical herbarium of Antoine Laurent de Jussieu (JUSS) clarified the misinformation around this taxon name. Prior to that, Saénz de Rivas (1969) addressed as candidate type for this species, the material of *Q. faginea,* in Lamarck's herbarium (P-Lam - 000382459 – 2 (upper left exemplar)) (Saénz de Rivas, 1969). Nevertheless, the herbarium-sheet has four different small fragments referable to different taxa. Schwarz (1954) proposed that the upper right specimen corresponds to an epitype of *Q. faginea* Lam., but all remaining fragments, drawn from Jussieu's herbarium, correspond to other taxa (P-Lam – 000382460!), namely *Q. pubescens* subsp. *palensis* (Palassou) O.Schwarz (1936: 97). The fragment number "2" effectively has a short petiole and glabrescent leaves, that led to the subsequent nomenclatural change to what became later the broad *Q. faginea* concept, brought by Saénz de Rivas (1969) and adopted in Flora Iberica (Franco, 1990) as *Q. faginea* subsp. *faginea*. However, this fragment corresponds to a second specimen and herbarium sheet of *Q. faginea* beneath P-Juss (P00320341!), that presents such characters (glabrescent leaves, possessing stellate trichomes with shorter rays), but not the one elected and annotated by Lamarck (P00320341!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320341), which corresponds to a tomentose plant with stellate trichomes with large rays. Consequently, Franco (1990)

considered two subspecies of *Q. faginea,* based on the length of the rays of the stellate trichomes, thus segregating *Q. faginea* subsp. *faginea* by its glabrescent leaves and stellate trichomes with short rays (<150 μm), in accordance with Saénz de Rivas (1969), from *Q. faginea* subsp. *broteroi,* with tomentose leaves and a stellate indumentum with larger rays (> 180 μm). The originally claimed as typical subspecies (*Q. faginea* subsp. *faginea*) has shorter and curly leaves, small petioles and serrate to dentate leaf margins and is distributed mostly through the Northern and Eastern Iberian Peninsula. In turn, *Q. faginea* subsp*. broteroi* would have larger leaves and bigger petioles, plus a crenate margin. The latter is distributed through the southern and western halves of the Iberian Peninsula. As stated above, the name *Q. faginea* was mistakenly given to the first morphotype (fragment number "2" of P00382459!), while the lectotype of *Q. faginea* shows a fully tomentose abaxial leaf surface, with large petioles. This was previously diagnosed by Vasconcellos and Franco (1954) and recently reinstated by Vazquez *et al.* (2020) as the correct name to be addressed to this taxon. It distributes across the western Iberian Peninsula and north Africa, with a multistellate indumentum and denser trichomes and medium-sized rays ((7)8-14(16); (150)180-250(280) μm), also in accordance with *Q. faginea* subsp. *eufaginea* Maire (1931: 65).

Some botanists recognized individuality to a few Portuguese oaks from southwest Iberian Peninsula, with lanceolate and serrate leaves that are erroneously attributed to *Q.* ×*hispanica* Lam. (Brotero, 1805; Webb, 1838; Colmeiro & Boutelou, 1854; Candolle, 1864; Laguna, 1883), which are assignable to the morphological plasticity of *Q. faginea* (Vila-Viçosa *et al.*, 2022b). The original protologue of *Q. faginea* and *Q. hispanica* (Lamarck, 1785) states the morphological affinity of both taxa, due the lanceolate and dentate leaf blade. This also led to the later proposal of an independent species inside broad *Q. faginea*, as *Q. gaditana* Vázquez *et. al*. (Vila-Viçosa *et. al*. 2014: 142).

Biogeography: Coastal Lusitanian and West Andalusian Province | West Iberian Province | Carpetan Leonese Province

Syntaxonomy: *Quercion fagineae*

Lusitanian dwarf-Oak

10. *Quercus lusitanica* Lam. (1785: 719) =*Quercus humilis* Lam. (1785: 719) *nom. illegit.* =*Quercus fruticosa* Brot. (1805: 31) =*Quercus humilis* f. *prasina* (Bosc) Coutinho (1888: 79) ≡*Quercus humilis* var. *prasina* Sampaio (1910a: 123) ≡*Quercus*

faginea raç. *lusitanica* var. *prasina* (Bosc.) Sampaio (1947: 147) =*Quercus fruticosa* var. *pedunculata* (Cout.) A. Camus

Lectotype (designated by Vázquez et al. (2020)): (P00382467! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00382467).

Epitype: (P00938261!, [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00938261).

Ecology: Exclusive to siliceous lithology, in sub-humid to humid or hyperoceanic areas, mainly in the understory of semi-deciduous or evergreen woods. It has a high intolerance to low winter minimal temperature, so it is mostly found in the thermomediterranean to thermotemperate bioclimatic belts.

Notes: The name *Quercus lusitanica* Lam. (1785: 719) was proposed simultaneously to *Q. humilis* Lamarck (1785: 719). Both names belong to two taxa that are clearly conspecific and therefore one of the two is a superfluous name. This problem was solved, without a specific choice of any of the available two, when Sampaio (1910b) correctly addressed the name *Q. lusitanica* to the Lusitanian dwarf-oak, clarifying the interpretations provided by other botanists (Boissier, 1838; Webb, 1838; Candolle, 1864; Coutinho, 1888; Vicioso, 1950) that commonly linked the name *Q. lusitanica* to trees of *Q. faginea s.l.* were incorrect. The sheet corresponding to *Q. lusitanica* presents two varieties (α and β): the first (α - P00320340!; P-LAM – 00382467 (left exemplar)) was collected in the Portuguese Estremadura. This specimen refers *in schedulla*: "*cerqueiro-bravo*", which is the common name for the shrub that grows around Lisbon and below Tagus regions and was validated by Vasconcellos and Franco (1954). It presents a sessile, thick-sclerophyll and glabrescent blade, with an entire margin in the proximal third of the leaf. These characters, when in comparison to the protologue (Lamarck, 1785) and all studied specimens of *Q. lusitanica* (P-Lam and P-Juss) and respective synonyms (*Q. fruticosa*), allows us to agree with the proposal of Vasconcellos and Franco (1954), that addressed, without any doubt, the name *Q. lusitanica* to this taxon. These later authors analysed three locations mentioned in the original notes of Antoine de Jussieu, with comments on the origin of both *Q. lusitanica* Lam. and *Q. humilis* Lam. All references mention the Tagus and Sado Cenozoic Basin, where *Q. lusitanica* forms known scrublands (*Erico-Quercetum lusitanicae*), according to Costa *et al.* (2012), as follows: 1-between Vendas Novas and Montijo (Aldeia Galega), 2 - between Moita and Palmela and 3 - Alvalade do Sado. The second variety (β - P00320339!) shows a different set of characters that stands in the origin of the following nomenclatural

conundrum, around the name *Q. lusitanica*. Vasconcellos and Franco (1954) suggests this plant contains aestival leaves of the same taxon, but the studied specimen has no information beside that it was collected in Portugal. Additionally, the leaf shape links it to a roburoid oak, included in the broad plasticity of *Q. faginea,* or even to hybrids assignable to *Q.* ×*coutinhoi* Samp. or *Q.* ×*alentejana* Pinto-Gomes & Vázquez. This hybrid hypothesis is corroborated by Schwarz in his Lamarck herbarium review (1954), who regarded it as *Q. cerrioides* Willk. & Lange, which was his interpretation of the hybrid between *Q. faginea* and *Q. pubescens* subsp. *palensis* (Palassou) O. Schwarz (1936: 97) as *Quercus lusitanica* subsp. *cerrioides* (Willk. & Costa) O. Schwarz (1936: 72).

Biogeography: Coastal Lusitanian and West Andalusia Province | West Iberian Province | Galician-Portuguese Sector

Pyrenean Oak

11*. Quercus pyrenaica* Willd. (1805: 451) =*Quercus toza* Gillet ex Bosc (1792: 155) =*Quercus pubescens* Brotero (1805: 31) =*Quercus cerris* var. *tomentosa* DC. =*Quercus humilis* DC. (Lamarck & Candolle, 1805: 311) =*Quercus tauzin* Persoon (1807: 571) =*Quercus brossa* Bosc (1807: 319) =*Quercus toza* Bastard (1809: 346) =*Quercus stolonifera* Lapeyrouse (1813: 582) =*Quercus toza* Bosc var. *cœnomanensis* N.H.F.Desp. (Lamarck & Candolle, 1815: 352) =*Quercus castellana* Bosc ex Persoon (1807: 571) =*Quercus tauza* Desfontaines (1815: 245) =*Quercus cenomanensis* N.H.F.Desp. ex Endl. (1848: 24) =*Quercus camata* Petz. & G.Kirchn. (1864: 628) =*Quercus toza* Gillet ex Bosc var. *humilis* (A. DC.) Nyman =*Quercus toza* Gillet ex Bosc var. *pyrenaica* (Willd.) Wenz. (1886: 198) =*Quercus toza* Gillet ex Bosc var. *aurea* (Wierzb. ex Rochel) Nyman (1890: 279) =*Quercus toza* Gillet ex Bosc subsp. *conferta* (Kit.) Nyman (1890: 279) =*Quercus toza* Gillet ex Bosc var. *spectabilis* (Kit. ex Simonk.) (1891: 2) =*Quercus tauzinii* Bubani (1897: 67) =*Quercus toza* Gillet ex Bosc var. *spicata* Tourlet (1903: 423) =*Quercus toza* Gillet ex Bosc subsp. *conferta* Kit. (1908: 199) =*Quercus toza* Gillet ex Bosc var. *stenocarpa* Rouy (1910: 316) =*Quercus toza* Gillet ex Bosc var. *sphaerocarpa* Rouy (1910: 317) =*Quercus toza* Gillet ex Bosc var. *vulgaris* (Bastard) Cout. (1913: 164) =*Quercus toza* Gillet ex Bosc var. *normalis* Rouy (1913: 164) =*Quercus pyrenaica* Willd. f. *brachyloba* O. Schwarz =*Quercus pyrenaica* Willd. f. *laciniata* O. Schwarz =*Quercus pyrenaica* Willd. lus. pendula (Dippel) O. Schwarz =*Quercus pyrenaica* Willd. f. *pinnatifida* O. Schwarz (1937: 143); =*Quercus pyrenaica* Willd. f. *pinnatipartita* C. Vicioso (1950: 52) =*Quercus pyrenaica* Willd. var. *expansa* C. Vicioso (1950: 52) =*Quercus pyrenaica* Willd. f. *sphaerocarpa* (Rouy) F.M. Vázquez =*Quercus pyrenaica* Willd. f. *stenocarpa* (Rouy) F.M. Vázquez (1998: 82) =*Quercus pyrenaica* Willd. f. *normalis* (Rouy) F.M. Vázquez =*Quercus pyrenaica* Willd. f. *expansa* (C. Vicioso) F.M. Vázquez (1998: 82)

Lectotype (designated by Saénz de Rivas, 1975: 780): (B-W - 17651 – 03 [digital image]!: http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=BW17651030)

Ecology: Supports mesophytic conditions as edaphic indifferent, although preferring siliceous bedrock. From upper sub-humid to hyper-humid ombrotypes, coping with summer-drought, normally with marcescent behaviour in thermophilic areas.

Biogeography: All Portuguese mainland, except for *Baixo Alentejo-Andevalense* and *Promontório-Algarvio* Subsectors (Vila-Viçosa et. al. 2017).

Syntaxonomy: *Quercion pyrenaicae*

2.4.2. Hybrids

1. *Quercus ×alentejana* C. Pinto-Gomes & F.M. Vázquez (Vázquez *et al.* 2015: 49)

Parents: *Q. faginea* × *Q. pyrenaica*

Holotype Vázquez *et al.* (2015: 49): HSS **–** 49040!

Notes: Very polymorphic plant, normally having obovate leaves, with deep lobes and divaricate secondary nerves. Besides the stellate indumentum, it also has fasciculate trichomes with long rays belonging to *Q. pyrenaica*, especially across the midrib and secondary nerves.

Description: Tree up to 15 m, growing with the parents. Leathery leaves with pinnately lobed to crenate margins, lamina (7)10-15(20) × (4)5-8(10) cm. Adaxial lamina surface pubescent to tomentose. Abaxial leaf surface heavily tomentose, with the presence of a double indumentum with stellate trichomes with long rays (>180 μm) and large fasciculate trichomes.

Notes: This nothotaxon originally inherited the name *Q. ×neomairei* A. Camus (1938: 28; 1939: 408), from a specimen labelled by Coutinho (1988) as « *Quercus toza* × *Q. lusitanica* » (LISU 10402!). The latter specimen was collected by Welwitsch on the margin of the Mondego River (LISU!) and corresponds to a hybrid with the participation of different Parents species (see '*Q. ×welwitschii*'). Therefore, the natural hybrid between *Q. faginea* and *Q. pyrenaica* lacked an appropriate name.

2. *Quercus* ×*almeidae* Vila-Viçosa, Capelo, P. Alves & F.M. Vázquez **nothosp.nov.** (Figure 3)

Parents: *Q. pseudococcifera* × *Q. rotundifolia*

Holotype: HSS **-** 081083! (Figure 3) - Portugal. Alto-Alentejo: Évora, Herdade dos Padres, 342 m, 38.5885253; -8.1469238, 2014, *Carlos Vila-Viçosa s.n.* (Isotype: PO-V70053; LISE-96338)

Descriptio: *Arbor parva ad usque 6 m alta, inter parentibus incolente; foliis concoloribus atroviridibus 3-5(7) × 1-3(4) cm s ursum glabrescentibus deorsum pubescentibus indumento ex trichomatibus stellatis radiis parvis (160µm) ut illis Q. rotundifolia; obovatis oblongis vel lanceolatis dentatis spinosis. Maturatione fructus annua cupulae squamis imbricatis adpressis maturatione praecipue supernis liberis facientibus.*

Description: Tree up to 6 m, among parents, Dark green concolorous leaves 3-5(7) × 1-3(4) cm, obovate to oblong and sometimes lanceolate leaves, with dentate and spiny margins. Glabrescent adaxial leaf surface and pubescent abaxial leaf surface, with an indumentum of stellate trichomes with short rays (160 µm), like *Q. rotundifolia.* Annual fructification with cups possessing intricate and appressed scales that become free in maturity, especially the upper ones.

Dedicated: To the distinguished botanist and friend Rubim Almeida da Silva (1960).

Notes: Occurs among parents especially across the Coastal Lusitanian and West Andalusia Province in humid areas, where *Q. pseudococcifera* grows at the edge of marcescent thermophilic forests, contacting with *Q. rotundifolia* secondary forests in xerophytic outcrops or lithosols.

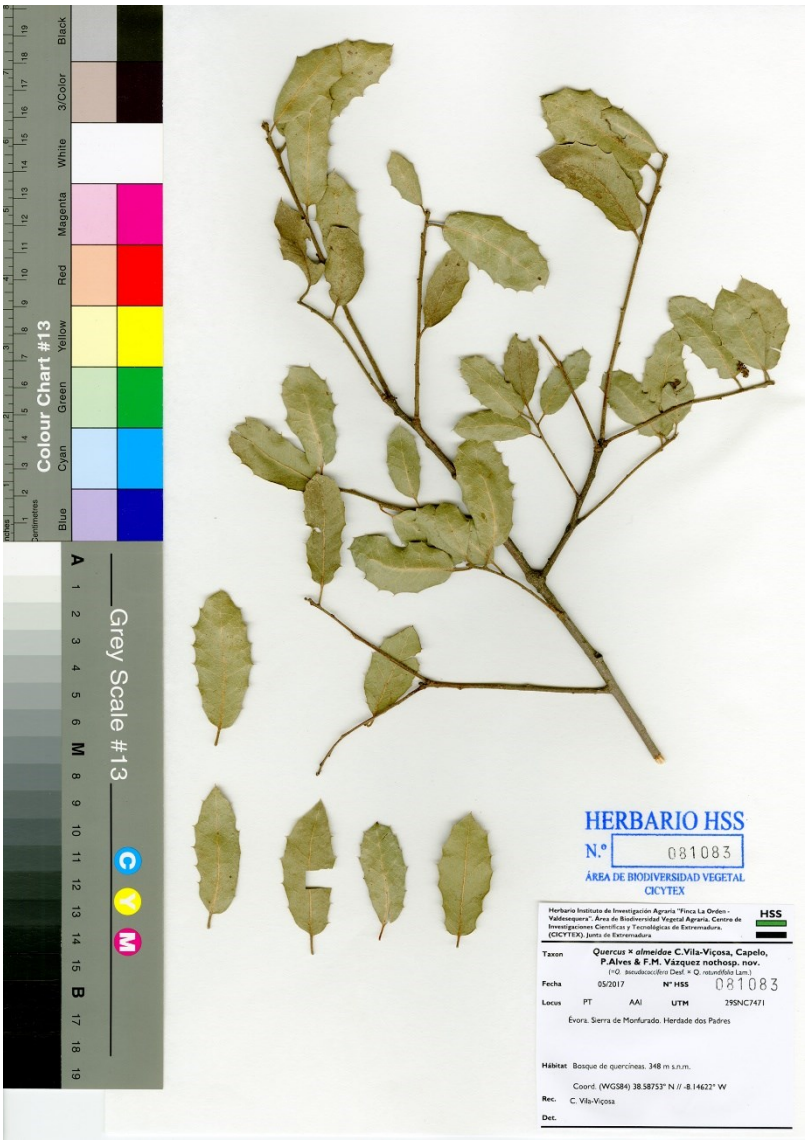


Figure 3 - Holotype of *Q.* ×*almeidae* Vila-Viçosa, Capelo, P.Alves & F.M. Vázquez nothosp.nov. HSS - 081083!.

3. *Quercus* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez **nothosp.nov.** (Figure 4)

Parents: *Q. lusitanica* × *Q. rotundifolia*

Holotype: PO **-** 62235! (Figure 5) - Portugal. Baixo-Alentejo: Almodôvar, São Barnabé, Carvais de Baixo, 447 m, 37º20'7.92'' N; -8º 6'8.82'' W, 09 November 2015, *Carlos Vila-Viçosa & Arlindo Rim s.n.* Isotype: HSS **-** 65657!.



Figure 4 - Illustration of *Quercus ×alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez nothosp.nov. Branch and leaf type morphologies (F.M. Vázquez)

Descriptio : *Frutex usque ad 100 cm altus, inter utrosque parentes intermedius, sed saepe Q. lusitanicae similior; folia ex ovato-obovatis ad lanceolata laminis (9)12-20(24) x (4)6-14(17)mm tertia parte infera marginibus integris autem secunda primaque sursum partibus ex serratis ad denticulatas, parvis mucronibus, supra glabrescentibus vel trichomatibus sparsis stellatis multistellatis simplicibus immo subtus tomentosis trichomatibus stellatis multistellatis fasciculatis radiatis simplicibusque, petiolo 2-7 mm pubescenti, nervis secundariis a base quam angulo maiore 45º abeuntibus prope marginibus saepe bifurcatis tamen eisdem supernis a Querco rotundifoliae similis sint.*

Description: Shrub up to 100 cm among Parents. Leaves ovate-obovate to lanceolate, blade with (9)1220(24) x (4)6-14(17) mm, entire margin in the first third (proximal), the second and distal thirds serrate to denticulate, with mutic mucrons and a 2-7 mm wide pubescent petiole (Figure 6). Adaxial leaf surface glabrescent, with stellate, multi-stellate, and simple trichomes. Abaxial leaf surface tomentose, with stellate, multi-stellate, radiate, single and fasciculate trichomes. Secondary veins bifurcated in the apex and forming almost rectilinear angles with the midrib in the proximal half of the leaf, like in *Quercus rotundifolia* Lam.

Dedicated: To the distinguished botanist and friend Paulo Jorge Mendes Alves (1975).

Notes: Grows with the parents, on sub-humid and thermophilic areas, namely on edaphoxerophile round-leaf-oak (*Q. rotundifolia*) forests. Also found in Serrano-Monchiquense district through fieldwork and herbarium review (COI) in Portuguese Divisorian Sector.



Figure 5 - Holotype of *Q.* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez nothosp.nov. PO-V62235! (Porto University, Natural History and Science Museum).



Figure 6 - Leaf detail of *Q.* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez nothosp.nov. PO-V62235! (Porto University, Natural History and Science Museum).

4. *Quercus* ×*aruciensis* C. Vicioso (1950: 139).

Parents: *Q. faginea* × *Quercus lusitanica*

Lectotype (designated here): Spain. Andalucia: Huelva, Los Marines, Sierra de Aracena, 21 June 1942, *C. Vicioso s.n.* (MA – 57386!). [Digital image]: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00057386

Notes: Detected in *Ulici welwitschianii-Quercetum fagineae* (Vila-Viçosa *et. al.* 2012), where sandy soil horizons overlap limestones, enabling the co-occurrence of *Q. lusitanica* and *Q. faginea*. It was not possible to locate the type materials of *Q.* ×*tingitana* A. Camus (1939) to study this putative prior name and we retain the name given by Vicioso (1950), corresponding to this hybrid, as we have directly studied its type.

5. *Quercus* ×*auzandrii* Gren. & Godr. (1855: 119) =*Quercus ilicococcifera* Saporta (1893: 206) =*Quercus* ×*reynieri* Albert (1902:129) =*Quercus* ×*comari* Albert (1902: 130) =*Quercus* ×*denudata* Albert (1902: 131) =*Quercus* ×*integrata* Albert (1902: 131) =*Quercus* ×*catalaunica* Sennen (1912: 243) Lecotype (designated here): (BCN-BC-Cadevall 823018!) =*Quercus* ×*rouxii* A. Camus (1935a: 54)

Parents: *Q. coccifera* × *Q. ilex*

Notes: The studied materials (LISI 10278/1999!) from Douro valley, contains hybrids of *Q. coccifera,* with the participation of *Quercus ilex* as a parent, apparent from the lauroid leaf shape and higher number of secondary nerves (>8). The label of the studied specimens also includes João do Amaral Franco's hand-notes, discussing the probable participation of *Q. ilex* instead of *Q. rotundifolia*.

6. *Quercus* ×*avellaniformis* Colmeiro & E. Boutelou (1854: 9) =*Quercus* ×*mixta* Villalobos ex Colmeiro (1888: 677) non Candolle (1864: 83) *nom. inval.* =*Quercus ilex* var. *avellaniformis* (Colmeiro & E. Boutelou) Cout. (1888: 95) =*Quercus ilex* f. *crassicupulata* Cout. (1888: 95) Lectotype (designated here): COI-19409! [Digital image]: http://coicatalogue.uc.pt/specimen/19409

Parents: *Q. rotundifolia* × *Q. suber*

Lectotype (designated by Vázquez et al. (2018)): Spain. Extremadura: Badajoz, Cabeza la Vaca, Dehesa de Murillo, *E. Boutelou s.n.*: MA-01-00026153! [Digital image]: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00026153)

Notes: Common among the parents, in bioclimatic areas where flowering and pollination periods of both parents often overlap, normally in neighbouring areas of cork oak and round-leaf oak vegetation series.

7. *Quercus* ×*capeloana* Vila-Viçosa; P. Alves, P.Lemos, R. Almeida & F.M. Vázquez **nothosp.nov.** (Figure 7)

Parents: *Q. pseudococcifera* × *Q. suber*

Holotype: PO V-70068! (Figure 7) - Portugal. Estremadura. Caldas da Rainha: Paúl da Tornada; Rua dos Bernardinos, 32 m, 39.444674 -9.145928, 28 October 2021, *Paulo Lemos s.n.* Isotypes: HSS-079482; LISE- 96336.



Figure 7 - Holotype of *Quercus* ×*capeloana* Vila-Viçosa, P. Alves, P. Lemos, R. Almeida & F.M. Vázquez nothosp.nov. (PO-V70068!) (Porto University, Natural History and Science Museum).

Descriptio: *Arbor ad 4 m alta apud parentibus inventa cortice tenuiter suberoso ad albescentem a aurantiaco. Foliae inter parentibus intermediis lanceolatas (3)4-7(8) ×(1)2-3(4) cm glabrescentibus vel pubescentibus margine denticulata petiolo pubescenti sursum atroviridibus glabrescentibus trichomatis stellatis sparsis deorsum pubescentibus trichomatis stellatis multistellatisque, nervis secundariis bifurcatis anastomosantibus praesertim a basi nervo medio recto inserto sed hoc paulatim accedentibus ab apice. Glans biennis cupulae squamis erectis longis teretibus crassis liberisque.*

Description: Tree up to 4 m, growing with the parents, with whitish to orangish corky bark. Glabrescent to pubescent and lanceolate leaves, (3)4-7(8) × (1)2-3(4) cm, denticulate margin and pubescent petiole. Dark-green and glabrescent adaxial surface, with scarce stellate trichomes. Pubescent abaxial surface, with stellate and multi-stellate, trichomes. Bifurcate (anastomosed) secondary veins, that are perpendicular with the midrib, especially at the base of the leave, normally forming progressively acute angles towards the apex. Leaf architecture between the parents. Biennial fruit maturation. Cups with large-free erect and thick cylindrical scales, retroflexed in maturity.

Dedicated: To the distinguished botanist and friend Jorge Henrique Capelo Gonçalves (1965).

Notes: Among the parents, in coastal hyperoceanic areas, of the Portuguese Divisorian Sector, above mixed Jurassic lime and sandstone derived soils. It is distinguished from *Q. coscojosuberiformis* by the totally free cup scales, compared to the slightly free to appressed-fused scales in the latter.

8. *Quercus* ×*celtica* F.M. Vázquez, Coombes, Rodr.-Coombes, Ramos & Doncel (2003: 52)

Parents: *Q. lusitanica* × *Q. suber*

Holotype: Vázquez *et al.* (2003): Portugal. Alto-Alentejo: Ponte-de-Sôr, Ervideira, 21 November 1999, *F.M. Vázquez s.n.* (HSS **–** 3718!)

Notes: Common taxon among the parents, in the understory of cork oak (*Q.* suber) forests, in Ribatagan-Sadense Sector.

9. *Quercus* ×*coscojosuberiformis* Baonza (2007: 365)

Parents: *Q. coccifera* × *Q. suber*

Holotype: Baonza (2007: 365): Spain. Madrid: Monte el Pardo, 3 March 2006, *J. Baonza Díaz s.n.* (MA-01-00737668!) [digital image]: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00737668

Notes: Not observed through fieldwork or in herbaria, but with high probability of existence in nature due to the extensive sympatric area of both parents.

10. *Quercus ×coutinhoi* Samp. (1910a: 123) ≡*Quercus faginea* var. *coutinhi* Samp. (1947: 147) =*Quercus lusitanica* var. *faginea* (Lam.) Boiss. ex Cout. f. *subpinnatifida* Cout. (1888: 67) ≡*Quercus faginea* var. *subpinnatifida* (Cout.) A. Camus (1939: 177) =*Quercus lusitanica* var. *faginea* (Lam.) Boiss. ex Cout. f. *bullata* Cout. =*Quercus lusitanica* var. *faginea* (Lam.) Boiss. ex Cout. f. *pedunculata* Cout. (1888: 68) Lectotype (designated here): COI: 18934! [digital image]!: http://coicatalogue.uc.pt/specimen/18934 ; Syntype 1: Portugal, Beira Litoral, Coimbra, Carapinheira do Campo, IX-1981 (COI: 18930!) ≡*Quercus faginea* var. *pedunculata* (Cout.) A. Camus (1939: 178) ≡*Quercus lusitanica* Lam. var. *pedunculata* (Cout.) C. Vicioso (1950: 110) =*Quercus lusitanica* var. *broter[o]i* Cout. f. *bullata* Cout. ≡*Quercus faginea* var. *bullata* (Cout.) A. Camus (1939: 178) =*Quercus lusitanica* var. *broter[o]i* Cout. f. *sublobata* (1888: 69) ≡*Quercus faginea* subvar. *sublobata* (Cout.) A. Camus (1939: 180) =*Quercus lusitanica* var. *broteroi* Cout. f. *subpinnatifida* Coutinho (1888: 67) ≡*Quercus faginea* var. *subpinnatifida* (Cout.) A. Camus (1938: 177) =*Quercus pedunculata* f. *brevipedunculata* Coutinho (1888: 58) =*Quercus ×molleri* A. Camus (1934: 44) Lectotype (designated here): LISU **–** 10358**!** (right specimen) **=***Quercus ×ferreirae* A. Camus (1934: 45) Camus (1938: 406): Lectotype (designated here): (COI: 19024!) [digital image]!: http://coicatalogue.uc.pt/specimen/19024 ≡*Quercus ×coutinhoi* A.Camus nothosubsp. *ferreirae* (A. Camus) F.M. Vázquez, S. Ramos & S. García. (2004: 31) =*Quercus ×subalpestris* A. Camus (1935a: 59) Lectotype (designated here): (LISU - P-10361!) ≡*Quercus ×coutinhoi* nothosubsp. *subalpestris* (A. Camus) F.M. Vázquez *et al.* (2004: 31) =*Quercus ×carrissoana* A. Camus (1935a: 59) =*Quercus ×coutinhoi* nothosubsp. *beturica* F.M. Vázquez *et.al.* (2003: 53) ≡*Quercus ×beturica* (F.M. Vázquez, *et al.*) F.M. Vázquez, *et al.* (Vila-Viçosa *et al.* 2014: 148): Holotype (Vázquez *et al.* 2014): (HSS: 22279!))

Parents: *Q. estremadurensis* × *Q. faginea*

Lectotype (designated here): Portugal. Beira Litoral: Coimbra. Fornos. Agri Conimbricense, August 1848, *Welwitsch s.n.* (LISU – 10364!)

Notes: All specimens determined by Coutinho (1888) (LISU!; COI!) as "*Quercus pedunculata* × *Q. lusitanica*", and posteriorly referenced by Sampaio (1910a) and Camus (1934), from Coimbra and Sintra, match the typical location from where *Q. estremadurensis* was described (Schwarz, 1935).

11. *Quercus ×diegoi* F.M.Vázquez, C. Pinto-Gomes, C. Vinagre & Vila-Viçosa (Vinagre *et al.* 2014: 95)

Parents: *Q. lusitanica* × *Q. pyrenaica*

Holotype: Vinagre *et al.* (2014): HSS **–** 62975!

Notes: Rare taxon, found among the parents, namely in thermophilic areas of *Arisaro simorrhini-Quercetum pyrenaicae* (Vila-Viçosa, 2012).

12. *Quercus ×duriensis* (Franco & Vasconcellos) Vila-Viçosa, Capelo, Alves, Almeida & Vázquez ***stat. nov***. ≡*Quercus* ×*coutinhoi* f. *duriensis* Franco & Vasconcellos [basion.] (Vasconcellos & Franco 1954: 33) ≡*Quercus* ×*coutinhoi* nothosubsp. *duriensis* (Franco & Vasc.) Monteiro-Henriques *et al.* (Costa *et al.* 2012: 122)

Parents: *Q. orocantabrica* × *Q. faginea*

Holotype: Vasconcellos and Franco (1954): LISI – 6046! -9702/1999-1! Portugal, Viseu, Lamego, entre Lamego e Várzea de Abrunhais, próximo de Alvéolos, 1943-06-12

Description: Tree, growing among parents, with intermediate leaf characters,: leaves oblong to obovate (80(8.7) x 45(52) mm), sub-sessile to short petiolate (<5(10) mm), auriculate; irregular margin lobate-sinuate to crenate, with 7 (8) blunt rounded and uneven lobes (resembling *Q. orocantabrica*); short or very few secondary nerves 7(8), often sinual; glabrescent to pubescent leaves on the abaxial leaf surface with scarce uniformly distributed stellate and multi-stellate trichomes; often pedunculate fruits (<6 cm).

Notes: These northern Portuguese (Douro Basin) hybrid swarms, generally correspond to the type-location of *Quercus* ×*coutinhoi* f. *duriensis* Franco & Vasconcellos. Field work, complemented by molecular analysis corroborates that the roburoid oak, sympatric with *Q. faginea* in those populations is *Q. orocantabrica* (Vila-Viçosa *et al.*, 2021). Accordingly, we propose to elevate the previous name given by Vasconcellos and Franco (1954) to nothospecies rank.

13. *Quercus ×eborense* Vila-Viçosa, Capelo, P. Alves, J. Junqueira, R. Almeida & F.M. Vázquez **nothosp.nov** (Figure 8).

Parents: *Q. coccifera* × *Q. rotundifolia*

Holotype: PO-V70054! (Figure 8) - Portugal. Alto-Alentejo, Évora: Alto de São Bento 367 m, 38.580084 -7.937871, 12, June, 2022, *João Junqueira s.n.* Isotypes: HSS-081136; LISE- 96337.



Figure 8 - Holotype of *Quercus* ×*eborense* Vila-Viçosa, Capelo, P. Alves, J. Junqueira, R. Almeida & F.M. Vázquez nothosp. nov. PO-V70054! (Porto University, Natural History and Science Museum).

Descriptio: *Frutex arborescens ad usque 3 m altum, inter parentibus incolente; foliis paene concoloribus sursum atroviridibus glabris sive glabrescentibus dum deorsum subviridibus sed cinerascentibus decentibus propter ipsis petiolisque pubescentibus vel sparso tomentosis in modo Querco rotundifolia hoc maxime iuvenibus sed tandem glabescentibus veteribus, orbicularibus a ovatis seu obovatis 2-4(5) × 1-3 (3,5) cm integris sive dentatis spinosis clare mucronatis a Q. coccifera similiter. Indumentum foliorum ex trichomatibus stellatis sive multistellatis foliis adpressis componuntur (Figure 2). Architectura formam foliorum ex Q. rotundifolia simili saepe venis secundariis bifurcatis anastomosantibus praesertim a basi nervo medio rectis insertis. Maturatione fructus annua sicut Quercus rotundifolia; glans ut Quercus rotundifolia cupulae squamis crassis adpressis nonnunquam ut Q. coccifera liberis facientibus.*

Description: Dendroid shrub up to 3 m high, growing among the parents. Green concolorous leaves, with a glabrous to glabrescent dark green adaxial leaf blade, while the abaxial leaf blade is light green, becoming greyish due to a pubescent indumentum and petiole, like *Q. rotundifolia*, that is notorious in younger leaves and branches, becoming glabrescent in older ones. Orbicular to ovate or obovate leaves, 2-4(5) × 1-3 (3,5) cm, with entire to dentate and spiny margins, with well-developed and non-mutic mucrons like *Q. coccifera*. Foliar indumentum composed by stellate and multistellate trichomes that are appressed to the leaf blade (Figure 2). *Q. rotundifolia* architectural leaf shape, with often bifurcate (anastomosed) secondary veins, that are perpendicular with the midrib, at the base of the leave. Annual fruit maturation like *Q. rotundifolia*. Cups with appressed and thick scales like *Q. rotundifolia*, but sometimes becoming free like in *Q. coccifera*, especially the upper ones.

Dedicated: To the city of Évora, the Capital of the Alentejo Region, where this hybrid is rather frequent across the typical Montado/Dehesa landscape.

Notes: Common hybrid in the Marianense and Portuguese Divisorian Sectors, as edaphic indifferent. It is distinguished from *Q. airensis* by the presence of stellate and multistellate appressed trichomes with rays <160 μm, that are inherited from *Q. rotundifolia* and the total absence of multiradial and stipitate trichomes with large rays (300-400 (500) μm) (Figure 2) that are typical from *Q. airensis*.

14. *Quercus ×fontquerii* O. Schwarz (1936b: 85).

Parents: *Q. canariensis* × *Q. pyrenaica*

Lectotype (designated here): Spain. Catalonia: Barcelona, Canyamas, Montalt, Font del Mal Pas, 1 September 1946, *P. Monserrat s.n.* (MA **-** 81789!).

Notes: Rare tree, present in *Euphorbio monchiquensis*-*Quercetum canariensis* forests in Southwest Portugal (Vila-Viçosa, 2012; Vila-Viçosa *et al.*, 2015).

15. *Quercus ×gallaecica* F. Llamas, Lence & C. Acedo (2003: 87)

Parents: *Q. orocantabrica* × *Q. lusitanica*

Holotype (Llamas *et al.*, 2003): LEB – 53647

Notes: Rare shrub, in Duriense Littoral District.

16. *Quercus ×lousae* Vila-Viçosa, F.M. Vázquez, Meireles & C. Pinto-Gomes (Vila-Viçosa *et al.* 2014: 145)

Parents: *Q. canariensis* × *Q. estremadurensis*

Holotype: Vila-Viçosa *et al.* (2014): HSS **–** 54488!

Notes: After an accurate analysis of all Welwitsch collected specimens, determined as *Q. mirbeckii* Durieu (LISU!; COI!)*,* we concluded that they correspond to broad-leafed *Q. faginea*. Thus, the hybrid between this former taxon and *Q. estremadurensis,* reiterated by Camus (1939) as *Q.* ×*carrissoana,* corresponds to *Q.* ***×****coutinhoi* Samp. In turn, the lectotype of *Q.* ×*lousae* was collected in a population where *Q. canariensis* was recently confirmed and the specimen exhibits intermediate features between the here established nothotaxon.

17. *Quercus ×pacensis* F.M. Vázquez (1996: 249)

Parents: *Q. faginea* × *Q. suber*

Holotype Vázquez (1995): HSS: 9092!. Isotype: MA-01-00526300! [digital image]: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00526300

Notes: The hybridization of *Q. faginea* and *Q. suber* has been assumed as being common and is often related with the concepts of *Q. ×hispanica* Lam. and *Q. pseudosuber* Desf. (Webb, 1838; Vicioso, 1950; Vázquez *et al.*, 2018). Nevertheless, many such individuals are pure *Q. faginea*, which occasionally develops a 'corky' bark, because of secondary growth, as stated by Coutinho (1888) when describing *Quercus lusitanica* α *faginea* f. *subsuberosa* Cout. Although this nothotaxon exists, it is rare in Southern Portugal (Ribatagan-Sadense sector and Alentejano District) in *Ulici-Quercetum fagineae* and *Pistacio-Quercetum fagineae* woodlands, demanding further molecular in-depth analysis to demonstrate genetic admixture.

18. *Quercus ×prasina* Bosc ex Endlicher (Bosc 1807: 330) Endlicher (1847: 25) =*Quercus ×angustifolia* Villar ex Gonz.Albo (1936: 1).

Parents: *Q. coccifera* × *Q. faginea*

Lectotype (designated by Vázquez et al. (2018)): P06847432! [digital image]: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06857698

Notes: Recognized through fieldwork and herbaria review (LISE **–** 45056!), in Portuguese Divisorian Sector.

19. *Quercus ×sampaioana* Vila-Viçosa, Capelo, P. Alves, R. Almeida, & F.M. Vázquez **nothosp. nov.** (Figure 9) =*Quercus humilis α genuina* f. *subcrenatolobata* Coutinho (1888: 79) Lectotype (designated here): COI-19014! [Digital image]!: http://coicatalogue.uc.pt/specimen/19014

Parents: *Q. estremadurensis* × *Q. lusitanica*

Holotype: Monserrate-Sintra, 26 August 1863, *Welwitsch s.n.* (LISU – 10359!). *Paratype 1: Serra de Sintra, entre o Alto do Monge e o Convento dos Capuchos, 26 August 1952, J. do Amaral Franco s.n* LISI - Nº 13 - 14395/1999!; Paratype 2: Portugal. Beira Litoral. Figueiró dos Vinhos, próximo ao Matadouro, 450 m.s.m., 9 October 1954, *A.R. Pinto da Silva s.n.* (LISI **-** 16741/1999!); Paratype 3: Portugal. Beira Litoral: Mealhada, Luso, Mata do Buçaco. October 1962, *Álvaro de Brito Pires s.n.* LISI - Nº 8 - 22038/1999!; Paratype

4: Portugal. Beira Litoral, C. de Montemor. 1888, *Bernardino A. de Barros Gomes s.n.* COI-19014.

Descriptio: *Frutex ad usque 150cm seu arbor, inter parentibus; folia paene sessilis petiolis brevis (<5mm) glabrisque; laminae foliorum obovatis seu rhomboidalis (5)813(15) x (2)4-5(8) cm, tertia parte infera marginibus integris autem secunda primaque sursum partibus ex crenatis ad dentatas lobulatasque, supra glabris immo subtus glabrescentibus trichomatibus stellatis multiradialisque 8-13 radiis brevibus (<15µm) praeterhac simplicibus petiolis nervis centralisque necnon sparsibus per laminam; pedunculi longi aliquando 9cm.*

Description: Shrub up to 150 cm or tree, growing with the parents. Leaves with obovate to rhomboidal lamina, (5)8-13(15) x (2)4-5(8) cm, with entire margin in the first third (proximal), the second and distal thirds crenate to dentate and lobulate, almost sessile with short (<5 mm) glabrous petiole. Lamina adaxial surface glabrous, abaxial surface glabrescent, with dispersed stellate and multiradial trichomes (8-13 rays), with short rays (<15µm) and simple trichomes in the midrib and scattered through the blade in the abaxial face. Large peduncle, up to 9 cm.

Dedicated: To distinguished botanist Gonçalo António da Silva Ferreira Sampaio (1865-1937).

Notes: Dispersed across the Coastal Lusitanian and West Andalusia Province, namely in the understory of *Asparago aphylli-Quercetum suberis*, *Arisaro simhorrini-Quercetum faginea* and *Avenello strictae-Quercetum faginea* (Vila-Viçosa *et al.*, 2012; Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2017).



Figure 9 - Holotype of *Quercus* ×*sampaioana* Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez nothosp. nov. (LISU – 10359!).

20. *Quercus* ×*tavaresii* Samp. (1910a: 123) ≡*Quercus* ×*subandegavensis* A. Camus (1935a: 60) ≡*Quercus* ×*andegavensis* nothosubsp. *subandegavensis* (A. Camus) Vila-Viçosa, F.M. Vázquez, Meireles & Pinto-Gomes (Vila-Viçosa 2012: 28)

Parents: *Q. orocantabrica* × *Q. pyrenaica*

Lectotype (designated here): Portugal. Beira Baixa: Soalheira, September 1902, *Joaquim da Silva Tavares s.n.*; LISU - P-10355!; Isolectotype: COI – 19233! [Digital image]!: http://coicatalogue.uc.pt/specimen/19233

Notes: Common among the parents, in Cantabrian Atlantic Subprovince. The lectotype, deposited in LISU (P-10355!) under *Quercus pyrenaica* and duplicated in *Q. robur* collection in COI (COI - 19233!), corresponds to the hybrid between *Q. orocantabrica* and *Q. pyrenaica*. It has large glabrescent leaves, with scarce fasciculate trichomes in the midrib and abaxial leaf surface, short petiole and auriculate leaf-base, plus a pinnately lobed to pinnatifid margin. It was later determined as *Q. pyrenaica* by Vasconcellos and Franco (1954) who argued the putative absence of *Q. orocantabrica* at the typical location, that is biogeographically ascribed to the potential forests of *Viburno tinii-Quercetum broteroanae* (Costa et. al. 2012).

21. *Quercus ×tentudaica* (F.M. Vázquez) F.M. Vázquez (Vázquez *et al.* 2015: 45) =*Quercus lusitanica* f. *microphylla* Coutinho (1888: 69) =*Quercus lusitanica* var. *broter[o]i* f. *microphylla* Cout. (1888: 69) ≡*Quercus faginea* subvar. *microphylla* (Cout.) A. Camus (1939: 180)

Parents: *Q. faginea* × *Q. rotundifolia*

Basionym: *Quercus* ×*senneniana* A. Camus nothosubsp. *tentudaicus* F.M. Vázquez. (1995: 250)

Holotype (Vázquez, 1995): HSS **–** 1314!

Notes: Rare taxon, among the parents.

22. *Quercus ×tlemcenensis* Trab. (1905: 308) ≡*Quercus mirbeckii* f. *tlemcenensis* (A.DC.) Trab. (1890: 821); ≡*Quercus faginea* var. *tlemcenensis* (A.DC.) Jahand. & Maire (1932: 165); ≡*Quercus broteroi* (Cout.) Rivas-Martínez & C. Saénz subsp. *tlemcenesis* (DC.) F.M. Vázquez & A. Coombes (2016: 29); =*Quercus lusitanica* Lam. var. *rhiphaea* Pau & Font Quer (1928: 132) =*Quercus faginea* subsp. *eufaginea* var. *tlemcenensis* Jahand & Maire (1932: 165) =*Quercus* ×*tlemcenensis* (A.DC.) Villar (1938: 452), *nom. inval. non* Trab. (Battandier & Trabut 1905: 308) ≡*Quercus faginea* subsp. *broteroi* (Cout.) var. *tlemcenensis* (A.DC.) A. Camus (1939: 180) =*Quercus* ×*maroccana* (Braun-Blanq. & Maire) Villar (1943: 3) ≡*Quercus tlemcenensis* (A.DC.) Villar f. *maro[ca]ccana* (Braun-Blanq. & Maire) Villar (1938: 453) =Quercus ×*fagineomirbeckii* Villar (1938 450) =*Quercus* ×*jahandiezii* A. Camus (1939: 791) =*Quercus* ×*pseudofaginea* A.Camus (1939: 792) =*Quercus* ×*marianica* C. Vicioso (1950: 129) =*Quercus faginea* subsp. *tlemcenensis* (A.DC.) Maire & Weiller var. *tlemcenensis* f. *villiramea* Maire & Weiller (Maire 1961: 101), *comb. inval.* =*Quercus*

faginea subsp. *tlemcenensis* (A.DC.) Maire & Weiller ex Greuter & Burdet. (Greuter & Raus 1982: 44)

Parents: *Q. canariensis* × *Q. faginea*

Lectotype (designated by Vázquez & Coombes, 2016): MPU007868! (right exemplar) [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007868)

Notes: This hybrid type material was extensively collected between Tlemcen and Bouira (Algeria), in mixed forests with *Q. canariensis,* and received the name *Quercus ×tlemcenensis* by Trabut (Battandier & Trabut, 1905). Here the author overlooked the presence of *Q. faginea* in the oak flora of Algeria, thus assuming the participation of *Q. ilex* in his nothospecies, due to the set of characters that combines both sclerophyll and spiny leaves with the presence of the floccose indumentum of *Q. canariensis* (=*Q. mirbeckii*) (Battandier &Trabut, 1905). Such set of characters is also verifiable in the proposed lectotype (MPU007868!) (Vázquez et al., 2018), as in the several syntypes collected in the typical *locus* "Bouira, Tlemcen" (P06861500!; P06861501!; P06861504!; P06861505! – Figure 10). This agrees with the original description, and the participation of *Q. canariensis* is indisputable, while *Q. faginea* characters are also evident by the leaf shape and co-dominance of a stellate indumentum (see Figure 10) in all type-specimens. Moreover, Schwarz states *in schedula* that the lectotype specimen correspond to *Q. faginea,* endorsing the participation of the Portuguese oak in the admixture. This morphotype, that matches *Q. faginea* leaf shape, and the floccose indumentum of *Q. canariensis,* also occurs in Southern Portugal. Conversely, the reverse morphotype, presents wide lanceolate leaves, like those of *Q. canariensis*, with more than eleven secondary nerves, becoming glabrescent with the presence of scattered stellate trichomes. This morphotype traditionally received the name given by Vicioso (1950) as *Q. ×marianica*, becoming the widespread name for this nothospecies while following several recent authors (Vasconcellos & Franco, 1954; Saénz de Rivas & Rivas-Martínez, 1971; Rivas-Martínez & Saénz, 1991; Vila-Viçosa, 2012; Vila-Viçosa *et al.*, 2014; Vila-Viçosa *et al.*, 2015). Nonetheless, the recent molecular analysis performed by Vila-Viçosa *et al.* (2021) reveals that both morphotypes broadly correspond to the introgression between *Q. canariensis* and *Q. faginea*, being *Q. ×tlemcenensis* the prior name for this nothotaxon in the western Mediterranean Basin. Several synonyms should be considered, as the most common ones are *Q. ×fagineomirbeckii* Villar (1938: 450), *Q. ×jahandiezii* A. Camus (1939: 791), *Q. ×maroccana* (Braun-Blanq. & Maire) Villar (1943: 3), *Q. ×pseudofaginea* A. Camus (1939: 792) and *Q. ×marianica* C. Vicioso (1950: 129).

Biogeography: Monchique County (Vila-Viçosa & Arsénio, 2021)

Syntaxonomy: *Quercenion rivasmartinezii-suberis*

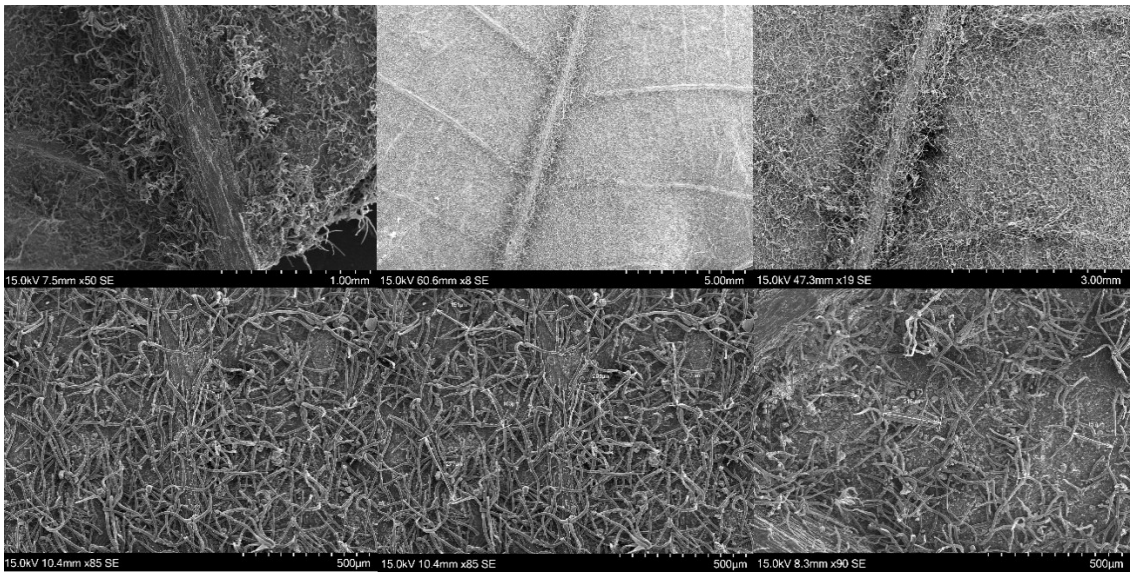


Figure 10 – SEM imagery of the abaxial leaf surface, retrieved from the syntype of *Q.* ×*tlemcenensis* Trab. from Bouira (Algeria) (P06861505!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06861505). Upper row showing both fuzzy fasciculate indumentum in the midrib, characteristic of *Q. canariensis* (*Q. mirbeckii*) and the stellate indumentum of *Q. faginea* on the leaf blade. Bottom row shows detailed images of *Q. faginea* stellate trichomes with rays up to *ca.* 280 µm long.

23. *Quercus* ×*welwitschii* Samp. (1910a: 123) *non* Gandoger *nom. illegit.* ≡*Quercus* ×*neomairei* A. Camus (1937: 28) Camus (1938: 408) =*Quercus* ×*henriquesii* Franco & Vasconcellos (Vasconcellos & Franco 1954: 25) ≡*Quercus* ×*andegavensis* Hy nothosubsp. *henriquesii* (Franco & Vasc.) Rivas-Martínez & Sáenz (1991: 104).

Parents: *Q. estremadurensis* × *Q. pyrenaica*

Lectotype (designated here): Portugal. Beira-Litoral: Coimbra, Mondego, 5 August 1848, *Welwitsch s.n.* (LISU **–** 10402!).

Notes: Type material (LISU: 10402!), collected by Welwitsch under *Quercus pubescens* Brot. was labelled as "*Q. toza* × *Q. lusitanica*" by Coutinho (1888), regarding the putative hybridization between *Q. pyrenaica* and *Quercus faginea*. Sampaio (1910a) named it for the first time as *Q.* ×*welwitschii,* dedicated to the collector. Later, the binomial *Q.*

×*neomairei* Camus (1937; 1938) was applied to the same specimen and was used by Vasconcellos & Franco (1954) and Franco (1990). The name *Q.* ×*welwitschii* Samp. was neglected by Govaerts and Frodin (1998), under the argument of an absent Latin description, but the same authors paradoxically accept the name *Q.* **×***coutinhoi* Samp. (1910a:123) described likewise, in the same work and page. Despite the alleged participation of *Q. faginea* and *Q. pyrenaica* in the type specimen (LISU: 10402!), Welwitsch refers *in schedulla* "…*frutex in sylvaticis…socialis c. Q. pedunculata et Q. lusitanica*" reporting the presence of a pedunculate oak in the population. Accordingly, the studied type material presents a pubescent to glabrescent abaxial leaf surface, with a single indumentum of fasciculate trichomes and total absence of stellate ones. In addition, the plant possesses a quite short petiole and a rhomboidal leaf shape, with acute lobes, which led us to infer that it has the participation of *Q. estremadurensis* and not *Q. faginea*, besides *Q. pyrenaica*. Furthermore, the studied types of *Q.* ×*henriquesii* Franco & Vasconcellos (LISI!) from Sintra, with the alleged introgression of *Q. broteroana* and *Q. pyrenaica* (Saénz de Rivas & Rivas-Martínez, 1991) also correspond to *Q. estremadurensis* as parent species, as it is observed in all type locations for *Q.* ×*welwitschii* and its synonyms.

2.4.3. Key for native and sub-spontaneous taxa

1. Evergreen trees or shrubs; sclerophyllous leaves, with entire, dentate or serrate margins……..……..…..2.

1' Marcescent, brevi-deciduous to deciduous trees or shrubs, with softened leaves, dentate, serrate, crenate to lobate or pinnately lobed, to pinnatifid margins……8.

2. Shrubs; sometimes trees, with concolour adult green leaves, varying from completely glabrous in both abaxial and adaxial leaf surface to pubescent and sometimes heavily tomentose……...….3.

2' Trees; discolour leaves, having a thick greyish indumentum of stellate and fused stellate indumentum on abaxial leaf surface ……..……..6.

3. Shrubs, sometimes trees with glabrous to sub-glabrous mature leaves, especial in abaxial leaf surface with free to weakly appressed (imbricate) cup scales, the median mostly patent or recurved in maturity, the upper ones soft, the lower sometimes acuminate and pungent……..…….4.

3' Shrubs, sometimes trees with mature pubescent to heavily tomentose leaves……..…….5.

4. Shrubs with glabrous, curled and green leaves, with spiny serrate to dentate margin; short broad cupoliform (acetabuliform) to short cylindrical cups (ratio length/breadth up to 0.5) with elongated partially connate scales, sometimes spiny and erect; petiolate leaves ……..……...***Q. coccifera***

4' Trees to dendroid shrubs reaching 17 m high, with a distinct bole; adult leaves glabrous to sub-glabrous, sometimes with fused-stellate indumentum in the limb base, near the midrib; normally sub-sessile to sessile and flat, or with short petiole (<3 mm); dark brown and thick hemispheric to long cylindrical cup (ratio length/breadth greater than 0.5), with elongated flat scales, free, sometimes acuminate, heavily retroflexed in maturation; partially hidden acorn (>1/2);……..……***Q. pseudococcifera***

a) As above (4') with thick nearly cylindrical trigonous and acuminate scales, often retroflexed in maturity…….……..***Q. pseudococcifera* subsp. *rivasmartinezii***

b) As above (4'), with corky orangish bark and lanceolate leaves, dark green on adaxial leaf surface and pubescent on abaxial leaf surface, large and totally free cup-scales, retroflex in maturity……***Q. ×capeloana***

c) As above (4'), with appressed-fused scales……..……..***Q. ×coscojosuberiformis***

5. Trees to dendroid shrubs; adult leaves pubescent to heavily tomentose (indumentum sometimes with light-brown rusty colour) on both abaxial and adaxial leaf faces; with multiradial, ramified and stipitate (stipe up to 100 µm) trichomes with large rays (> (250) 300 µm-400 (500) µm) on both abaxial and adaxial leaf faces; Hemispheric cups with free arcuate and thin scales and half-hidden to hidden acorns……***Q. airensis*** i. (Figures 1 and 2 e) f))

5' Shrubs with pubescent leaves, having a greyish indumentum of simple and fused-stellate trichomes with short rays (<150 µm) in both abaxial and adaxial faces; total absence of stipitate trichomes; either with appressed cup scales or free rigid and thick ones; proximal secondary veins perpendicular with the midrib, bifurcating heavily; leaf shape architecture like *Q. rotundifolia*……***Q. ×eborense*** ii. (Figures 1 a), b))

6. Presence of well-developed cork or corky bark (phellem) with discolour adult leaves, convex towards the adaxial face; pubescent with greyish indumentum of simple, stellate and fused-stellate trichomes; sinuous midrib; the secondary veins inserted with acute angles, (< 40-50º); never bifurcating in tertiary venation; free cup scales, frequently biennial fructification……***Q. suber***

a) Suberoid to fusiform bark, or with incipient cork; secondary veins inserted in > 45º angles, often bifurcating and turbinate cup……***Q. ×avellaniformis***

6' Absence of a corky bark (phellem); adult leaves with straight midrib; the secondary veins uncertain, forming in the proximal half angles higher than 50-80º, normally bifurcating in tertiary venation……..7.

7. Oblong-obovate to ovoid, or suborbicular leaves; with less than 7 pairs of secondary veins, petiole < 8 mm***……Q. rotundifolia***

a) As above, with greenish abaxial leaf surface, fully pubescent, greyish to dark brown cup, with plicate to slightly free and patent scales…….……***Q. ×almeidae***

7' Lanceolate to oblong-lanceolate leaves with entire to sub-entire margins, normally with more than (7) 8 pairs of secondary veins and petiole > 1cm ……..…… ***Q. ilex*** *

8. Trees or shrubs with glabrous to glabrescent mature leaves, sometimes with scarce indumentum in abaxial leaf surface, mainly in the midrib and secondary veins……9.

8' Trees or shrubs with mature pubescent to tomentose leaves…….…13.

9. Glabrous to glabrescent and cuneate leaves, with lobed to pinnately lobed margins, sometimes slightly pubescent with short simple (and bifurcated) trichomes in the abaxial leaf face and pedunculate fruits (> 5 cm).……10.

9' As above with glabrescent to pubescent abaxial leaf surface, with scarce stellate or fasciculate trichomes with lobed to crenate or pinnately lobed and dentate leaf margins……..12.

10. Regular rhomboidal and sclerophyllous leaves, with acute and equal lobes and (6)8-12(14) secondary nerves, rectilinear and parallel; without or rarely with sinual nerves in the base; glabrescent to pubescent, provided with single/bifurcate trichomes throughout the midrib and ramified trichomes throughout the abaxial leaf surface; with a developed petiole (5)8-15(18) mm; large peduncle (> 8 cm), sometimes with dark simple trichomes; with numerous scales that are large in the base of the cup, becoming smaller fast towards the apex……***Q. estremadurensis***

10' Irregular leaf shape, with sinuate-lobulate or pinnatilobate margins, with uneven and deep obtuse and round lobes, 4-8(9) secondary nerves; with glabrous to glabrescent branches; glabrescent peduncle and short petiole (<5 mm)……...11.

11. Thick and progressively obovate leaves (larger in the apical half); obtuse and uneven lobes (>6 (8)), with frequent sinual and intercalary veins; variable petiole ((2) 5-12(15) mm) sometimes marcescent; young branches and abaxial leaf surface, with scarce simple trichomes; big cups 18-25 mm, with brown scales, larger and free in the base becoming smaller and merged in the apex.……***Q. orocantabrica***

11' Young shoots glabrescent to pubescent, thick blade, matt in adaxial leaf surface; pubescent leaves with crenate to pinnatifid margins……..12.

12. As 10, with pinnatifid to pinnately lobed thick leaves, with acute lobes, glabrescent to pubescent, with scarce fasciculate and simple trichomes, mainly in the midrib or denser in the abaxial leaf surface often with pedunculate fruits……***Q. ×welwitschii***

a) As 10, with lobulate to crenate margins, glabrescent to pubescent with scarce stellate trichomes in the abaxial leaf surface, sympatric with *Q. estremadurensis* ..……..……***Q. ×coutinhoi***

12' As 11, with pinnatifid to pinnately lobed leaf margins and glabrescent to pubescent abaxial leaf surface, short petiole, and regularly pedunculate fruits, with

* cultivated

scarce indumentum of fasciculate trichomes with long rays (>0.5 mm), mainly in the midrib and secondary veins……***Q. ×tavaresii***

a) As 11, mostly shrubs, with serrate to sinuate-lobulated margins, sub-sessile leaves; sometimes with entire leaf margin in the proximal third, with scarce stellate and multistellate trichomes in abaxial leaf surface, sympatric with *Quercus orocantabrica* ……***Q. ×gallaecica***

b) As 11, with dentate to crenate leaves, with cuneate basis and scarce or homogeneously distributed stellate trichomes in the abaxial leaf surface, sympatric with *Q. orocantabrica*……***Q. ×duriensis***

13. Leaves with more than 10 pairs of secondary veins that are rectilinear (almost parallel), with obovate or progressively obovate towards the apex, crenate to serrate margins, usually glabrescent or slightly pubescent, with cotton-like deciduous indumentum of fasciculate-stipitate trichomes (sometimes reddish in drier stations and total absence of stellate trichomes) in the midrib and axils of the secondary veins, that becomes deciduous……***Q. canariensis***

a) As above, with single indumentum of stellate trichomes and absence of fuzzy fasciculate indumentum in the midrib and secondary nerves……***Q. ×tlemcenensis***

13’ Leaves with less than 10 pairs of secondary veins, with sinuate-lobulated to crenate-serrate or pinnately lobed to pinnatifid margins, from pubescent to tomentose abaxial leaf surface with fasciculate and/or stellate trichomes……14.

14. Trees with leathery leaves, velvety in both leaf surfaces, mostly with pinnatifid margins, but sometimes crenate to pinnately lobed, from pubescent to tomentose abaxial leaf surface, with dominance of fasciculate trichomes, with large rays (> (0.3)0.5 mm)……***Q. pyrenaica***

14’ Trees or shrubs with serrate, crenate, denticulate to lobulated margin, from glabrescent to tomentose abaxial leaf surface with dominance of stellate, multistellate and multiradial trichomes……15.

15. Shrubs up to 3 m high, with flat and almost sessile (petiole up to 3 mm) cuneate leaves, commonly with partial entire margin in the proximal third, serrate to dentate (occasionally lobulated) in 2/3 thirds of the leaf; glabrous to tomentose, with stellate and multistellate indumentum, sometimes pedunculated fruits……***Q. lusitanica***

a) As above (15), with crenate to serrate margin, with entire first third of the leaf margin and double thick indumentum of stellate and multistellate trichomes with long rays (>180 µm), sympatric with *Q. faginea*……***Q. ×aruciensis***

b) As above (15), with greyish indumentum, with ovate-obovate to lanceolate leaves; entire in the first third (proximal), the second and distal thirds serrate to denticulate, with mutic mucrons and pubescent petiole. Adaxial surface lamina glabrescent, abaxial surface lamina tomentose, with stellate, multistellate, radiate, and simple trichomes. Secondary veins bifurcate in the apex, perpendicular with the midrib in the proximal half of the leaf……***Q. ×alvesii***

c) As above (15), up to 2 m, with serrate and mucronated leaves and greyish indumentum, secondary veins forming acute angles with the midrib, with stellate, multistellate and simple trichomes in the midrib, leaf architecture like *Q. suber*……***Q. ×celtica***

d) As above (15), up to 3 m with serrate to pinnatifid margins, fully tomentose with both stellate and multistellate trichomes, plus fasciculate trichomes with long rays (>0.5 mm), sympatric with *Quercus pyrenaica*……..***Q. ×diegoi***

15’ Trees or shrubs with serrate-dentate to crenate margins, glabrescent to tomentose, with stellate, multistellate, multiradial, fasciculate or single trichomes……16.

16. Trees or shrubs with almost sessile leaves (petiole up to 0.5 cm), lobulate (acute lobes), to serrate-dentate margins, glabrescent, with stellate and multistellate trichomes below, and pedunculate fruits (Subsection *Hartwissianae* × Subsection *Macrantherae*)……17.

16’ Trees with flat or curly leaves, pubescent to tomentose abaxial leaf surface, crenate to serrate-dentate margin with single indumentum of stellate and multistellate trichomes……...20.

17. Shrubs, sometimes trees, with entire margin in the first third, lobed or lobulate (acute lobes), to serrate margins, glabrescent abaxial leaves, with stellate and multistellate trichomes, through the lamina and simple trichomes in the midrib, fruits with a well-developed peduncle……18.

17’ Trees with crenate-lobulate to dentate-serrate margins, normally with cordate leaf basis, glabrescent with single and scarce stellate indumentum, and pedunculate fruits……19.

18. Rhomboidal cuneate leaves, with entire margin in the first third, lobed or lobulate (acute lobes), to serrate margins, glabrescent abaxial leaves, with stellate and multistellate trichomes, through the lamina and simple trichomes in the midrib, fruits with a well-developed peduncle, sympatric with *Q. estremadurensis*…….***Q. ×sampaioana***

18’ Mostly shrubs, with cuneate and sub-sessile leaves, with serrate to sinuate-lobulate margins, with obtuse and uneven lobes, sometimes with entire leaf margin in the proximal third, having sinual and intercalary veins; with scarce stellate and multistellate trichomes on abaxial leaf surface, short petiole (< 3 mm), sympatric with *Quercus orocantabrica*……...……***Q. ×gallaecica***

19. Glabrescent leaves with dentate to serrate margins, or crenate to lobulate sometimes mucronate, with cordate base, short petiole (< 0.5 cm); scarce stellate indumentum with short rays (<150 µm) on abaxial leaf surface; simple trichomes mainly through the midrib, with pedunculate fruits, sympatric with *Q. estremadurensis*……...***Q. ×coutinhoi***

19’ As above, with uneven lobes and sinual nerves, sympatric with *Quercus orocantabrica*……***Q. ×duriensis***

20. Trees with long flat oblong to obovate and ovate leaves, pubescent to tomentose abaxial surface; crenate-lobulate to serrate or dentate margins; with stellate and multistellate indumentum……..***Q. faginea***a) As above with spiny leaves, greyish indumentum, of both stellate with large rays, with proximal secondary veins perpendicular with the midrib, bifurcating heavily……...***Q. ×tentudaica***

b) As above with crenate to pinnatilobed margin, fully tomentose with double indumentum of stellate and fasciculate trichomes with large rays (>0.5 mm), sympatric with *Q. pyrenaica*……***Q. ×alentejana***

20’ Trees with oblong to obovate and ovate leaves, with crenate to serrate margin, with a double indumentum formed of the same stellate and multiradiate trichomes, plus the fasciculate, fuzzy and cotton like indumentum on the midrib and leaf base, sympatric with *Q. canariensis*……***Q. ×tlemcenensis***

2.5. Discussion

The taxonomical model here proposed is found to be largely coherent with recent synchorological, syntaxonomical and with molecular analysis, concerning the white oaks (Vila-Viçosa et al., 2021). At the infrasectional level, our results are congruent with the segregation of two subsections (*Macrantherae* (Maleev, 1935) and *Hartwissianae* (Maleev, 1935)) inside section *Quercus*. These are supported by morphological trait combinations, that are transitional across both subgroups and is consistent with the southern European and circummediterranean biogeography and ongoing molecular surveys (Vila-Viçosa *et. al*. 2021). Submediterranean taxa (Subsection *Macrantherae*), usually found around the borders between Temperate and Mediterranean biomes - i.e. the transition of Euro-Siberian and Mediterranean subregions in southern Europe - share the same type of trichomes and similar edaphoclimatic envelopes. On the other hand, subsection *Hartwissianae* encompasses those taxa, in need of the increment of annual and summer precipitation, dominantly distributed across the Temperate bioclimatic belt, but preserved in Atlantic refugia inside the submediterranean ecotone across southern European Peninsulas (Vila-Viçosa *et. al.* 2020b). Therein, azonal conditions of soil water and horizontal precipitation compensate for summer aridity months, thus functioning as a proxy of temperate conditions by diminishing the effect of precipitation seasonality (Vila-Viçosa *et. al*. 2015; Vila-Viçosa *et. al*. 2020b). Subsection *Hartwissianae* incorporates broad *Q. petraea* and *Q. robur* species-syngameon, while subsection *Macrantherae* aggregate former Sections *Galliferae* and *Dascia* (Schwarz, 1936a) proposals, as the elected type-species better aggregates transversal morphological characters to the species inside their respective section.

Regarding the populations of the Iberian pedunculate oaks (*Q. gr. robur*), *Quercus estremadurensis* seems to be a consistent species, as the confusion with *Q. orocantabrica* (=*Quercus robur* subsp. *broteroana*) is clarified. Nomenclatural difficulties in sorting out subordinate taxa lead historical authors to the parsimonious solution of considering such taxa in the broad variation of *Q. robur*. Nevertheless, both *Q. orocantabrica* and *Q. estremadurensis,* possess high morphological plasticity and preserve high molecular divergence against the European *Q. robur* (Vila-Viçosa et al.,

2021). The latter analysis confirmed that the western Iberian pedunculate oak populations belong to *Q. orocantabrica*, and not the European *Q. robur,* as stated by past references (Schwarz, 1937; Rivas-Martínez *et al.*, 2002). The presence of substantial morphological and molecular divergence of the Iberian pedunculate oaks, enhances its important role in the evolutionary history of these lineage of temperate oaks, namely as tertiary relicts inside subsection *Hartwissianae*¸ as suggested by Schwarz (1935; 1936a) and Montserrat (1957).

We recover the name *Q. faginea* Lam. to stand for the whole of the southern and western Iberian populations of the Portuguese oak, as proposed by Vasconcellos and Franco (1954). The morphological and type material analysis (Vázquez *et. al*. 2020) complemented with the ongoing molecular studies (Vila-Viçosa *et. al*., 2021) cannot find coherent infraspecific differentiation inside *Q. faginea*, especially regarding to the western Iberian Peninsula. The latter molecular works fully corroborates the assumptions of Villar (1958), that amplifies the area of this taxon up to the Douro thermophilic Basin, incorporating the *Spiraeo obovatae-Quercetum faginea* (Bolòs & Montsserrat, 1984; Loidi & Herrera, 1990) forests, contrarily to the widely assumed northern-limit between its putative subspecies (Franco, 1990; Rivas-Martínez & Saénz, 1991) around the Salamanca Sector (Rivas-Martinez, 2017).

We should remark that forest fragmentation and land use changes after the Last Glacial Maximum contraction scenario, followed by periods of climatic amelioration, especially the Bølling–Allerød period, and the Early and Mid-Holocene, favoured interleaving expansions and contractions of oak forests (Lowe & Walker, 1984; Carrión *et al.*, 2010; Vila-Viçosa *et al.*, 2020b). This promoted genetic exchange between previously isolated populations and the establishment of hybrid swarms (Vila-Viçosa *et. al* 2020b). However, the recurrence of certain morphological characters as, for example, the conservative character of trichome-type, still observable in selective environments, provides insights on the hypothesis of putative phylogenetic relationship between existing species. This phenomenon most likely relies on the auto-ecological segregation of constant taxonomic character correlations, in response to environmental filtering. Likewise, the same phenomenon probably happened among both *Q. estremadurensis* and *Q. orocantabrica* with *Q. faginea* in Western Portugal and the Douro valley. During the Holocene, reduced seasonality and less severe summers and winters promoted bidirectional migrations of the roburoid oaks along a Northern-Southern and Western-Eastern gradients, leading to the formation of the known hybrid-swarms (*Q.* ×*coutinhoi* and *Q.* ×*duriensis*).

The western Mediterranean Kermes oak complex (*Quercus coccifera s.l.*) encompasses three taxa that are, in a way, coherently vicariant to the proposal of Kasapligil (1981) for eastern Mediterranean oaks. We here highlight the recovery of *Q. airensis* Franco & Vasconcellos*.,* related with the original concept of *Q. calliprinos* Webb, as a western species and so far, misunderstood with broad hybrids between *Q. coccifera* and *Q. rotundifolia*. This proposal is congruent with the vicariancy presented by *Q. aucheri* (Serteser *et. al*, 2009). *Q. airensis* is prominently distributed through northern Morocco and Portugal, with a Tingitan-Onubo-Algarvian distribution (Latorre *et al.*, 1996), and grows in Cenozoic karst and marly limestones in hyperoceanic areas, being however recognized by Laguna (1883: 266) in Montes de Toledo (Albarda, Spain). The recognition of a western Mediterranean arboreal kermes oak (*Q. pseudococcifera* Desf.) is in accordance with the original concepts of Desfontaines, 1799, Webb (1838) and Amo (1861), in which *Q. rivasmartinezii* is incorporated (Vila-Viçosa *et. al*. 2022a).

Nevertheless, an in-depth molecular work, preferably with next-generation sequencing tools, inside the western Mediterranean Section *Ilex* is a demanding task to solve, at the population and species level, all these inferences brought by the nomenclatural and morphological analysis.

2.6. Conclusions

We provided a full update of the Portuguese oak species and nomenclature, which was enrolled in a conundrum and lacked an in-depth approach to the type materials and literature, since the most recent reference-works. By combining herbaria and literature review, with fieldwork, and supported by ongoing molecular surveys, we disclosed ongoing taxonomic and nomenclatural uncertainties to a high number of taxa and nothotaxa.

The higher diversity of morphological traits observed among the white oaks species in the western and southern Iberian Peninsula, allows us to consider the western Iberian Peninsula as a likely candidate for a diversification centre for this group of oaks, when compared to European and circummediterranean counterparts. The notorious wealth of paleoclimatic relictual elements assumes an exceptional territorial cohesion, in Western Portuguese mainland, including southern mountains and seashore. Notably, we can highlight the occurrence-areas of *Quercus canariensis* and *Q. estremadurensis* as major

tertiary paleoclimatic relicts for this biogeographic enclosure, that is enhanced by *Q. orocantabrica* in the north-central quadrant of the Iberian Peninsula.

Accordingly, we supported the rearrangement of former infrasectional classifications (Subsections *Macrantherae* and *Hartwissianae*), based in consistent morphological and biogeographic transitional traits. Broadly, marcescent species are related to both tertiary paleoclimatic relictual areas and submediterranean ecotones and exhibit a disjunct amphimediterranean distribution. The forests they form have been biogeographical bridges between Eurosiberian and Mediterranean subregions, often hybridizing with other oaks inside Sections *Quercus*. Oaks in these sections are mesophytic, but simultaneously adapted to Mediterranean conditions. Examples of such drought-adapted traits are leaf scleromorphy and an often-persistent indumentum-type in the abaxial surface.

We expect our proposals to be compared with extensive phylogeographic and molecular analysis to validate morphological analysis and to evaluate any involuntary taxonomic inflation, especially among the evergreen oaks (Section *Ilex*).

Finally, we highlight the urgent necessity to rehabilitate the classic practice of taxonomy, linked with the exercise of biogeography and geobotany, as valuable sources for creating stronger taxonomic and evolutionary hypotheses. We think our work stresses the contributions of extensive fieldwork, museology, and historical botany as key cornerstones for taxonomic awareness, that can be perfected by molecular tools.

We contributed to the knowledge of the Iberian and western Mediterranean oak forest biogeography and plant diversity, updating the nomenclature and taxonomic delimitation of an important group of woody plants. This work better serves any conservation efforts and decision making in a paradigmatic Biome like the Mediterranean forests and scrubs.

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2.7. References

Albert A 1902. De quelques Quercus hybrides ou supposes tels, de Quercus ilex et coccifera. In: botanique Amidgo ed. *Bulletin de l'Académie internationale de géographie botanique*. Le Mans: Edmond Monnoyer, 129-131.

Albert A, Jahandiez É. 1908. Catalogue des plantes vasculaires qui croissent naturellement dans le Department du Var.

Amo M. 1861. *Memoria sobre la distribución geográfica de las familias de las plantas Crucíferas, Leguminosas, Rosáceas, Salsoláceas, Amentaceas, Coníferas y Gramíneas de la Peninsula Ibérica*. Madrid: Imprenta y librería de don Eusebio Aguado.

Axelrod DI. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden*: 629-657.

Bastard T. 1809. *Essai sur la flore du département de Maine et Loire*. Angers: Imprimerie de Ve. Pavie et Fils.

Battandier J, Trabut L. 1890. Flore de l'Algérie (Dicotyidones). *Alger & Paris*.

Battandier JA. 1888. *Flore de l'Algérie: Dicotylédones*: Adolphe Jourdan.

Battandier JA. 1890. *Flore de l'Algérie: contenant la description de toutes les plantes signalées jusqu'a ce jour comme spontanées en Algérie et catalogue des plantes du Maroc*: Typographie Adolphe Jourdan.

Battandier JA, Trabut LC. 1905. *Flore analytique et synoptique de l'Algérie et de la Tunisie.* . Argel: Vve Giralt, Imprimeur-Éditeur.

Bentham G, Hooker J. 1880. *Genera Plantarum.* London.

Blume CL 1850. Museum botanicum Lugduno-Batavum. sive, Stirpium exoticarum novarum vel minus cognitarum ex vivis aut siccis brevis expositio et descriptio, additis figuris. In: C.L. B ed. *Museum botanicum Lugduno-Batavum*. Leiden: E. J. Brill, 305-320.

Boissier E. 1838. *Elenchus plantarum novarum minusque cognitarum quas in itinere hispanico*: Typographia Lador et Ramboz.

Boissier E, Reuter GF. 1842. *Diagnoses plantarum novarum Hispanicarum*. Geneva: Typis Ferdinandi Ramboz.

Bolòs O, Montsserrat P. 1984. Datos sobre algunas comunidades vegetales, principalmente de los Pirineos de Aragón y de Navarra. *Lazaroa* **5**: 89-96.

Borzi A. 1881. L' Ilex-sughero (Quercus morisii Borzi), nuova Querce della Sardegna. *Nuovo Giornale botanico Italiano* **13**: 5-11.

Bosc LAG. 1792. Description du Cynips quercus-tozae. *Journal d'Histoire naturelle* **2**: 154-157.

Bosc LAG 1807. Mémoire sur les différentes espèces de chênes. In: (France) Ards ed. *Mémoires de l'Institut national des sciences et arts: sciences mathématiques et physiques*. Paris: Baudouin, 307-373.

Braun-Blanquet J, Maire R 1924. Études sur la végétation et la flore marocaines. . In: Maroc SdSNd ed. *Bulletin de la Société des sciences naturelles du Maroc*. Rabat: L'Institut Scientifique Chérifien, 1-244.

Brotero FA. 1805. *Flora Lusitanica, seu plantarum, quae in Lusitania vel sponte crescunt, velfrequentius coluntur, ex florum praesertim sexubus systematice distributarum, synopsis.* Lisboa: Typographia regia.

Bubani P. 1900. *Flora Pyrenaica per Ordines Naturales gradatim digesta*. Milan: Ulricus Hoeplius.

Buckley SB 1860. Description of several new species of plants. . In: Philadelphia AoNSo ed. *Proceedings of the Academy of Natural Sciences of Philadelphia*. Philadelphia: Academy of Natural Sciences of Philadelphia, 443-445.

Buckley SB 1881. Quercus rubra, L., var. texana. In: Philadelphia AoNSo ed. *Proceedings of the Academy of Natural Sciences of Philadelphia*. Philadelphia: Academy of Natural Sciences of Philadelphia, 123-125.

Camus A 1934. Quelques diagnoses de Fagacées. In: France Stbd ed. *Bulletin de la Société Botanique de France*. Paris: La Société, 814-818.

Camus A. 1935. *Les chênes: Monographie du genre Quercus. Atlas.* . Paris: Lechevalier.

Camus A. 1936. *Les chênes: monographie du genre Quercus. 1. Texte.-Sous-genre Cyclobalanopsis, sous-genre Euquercus,(sections Cerris et Mesobalanus)*: Lechevalier.

Camus A. 1938. *Les chênes. Monographie du genre Quercus. Genre Quercus, sous-genre Cyclobalanopsis, sous-genre Euquercus (sections Cerris et Mesobalanus).* . Paris: Lechevalier.

Camus A. 1939. *Les Chênes. Monographie du genre Quercus. Genre Quercus, sous-genre Euquercus (sections Lepidobalanus et Macrobalanus).* Paris: Lechevalier.

Candolle AD. 1864. *Prodromus systematis naturalis regni vegetabilis sive enumeratio contracta ordinum, generum specierumque plantarum huc usque cognitarum, juxta methodi naturalis normas digesta sumptibus sociorum*. Paris: Treuttel et Würtz.

Capelo J, Costa JC. 2001. Notícia acerca dos carrascais arbóreos da Serra da Arrábida. *Silva Lusitana* **9**(2): 269-271.

Capelo J, Costa JC. 2005. Quercus rivasmartinezii, uma espécie autónoma de carvalho, endémica de Portugal. *Silva Lusitana* **13**(2): 268-269.

Carrero C, Jerome D, Beckman E, Byrne A, Coombes A, Deng M, González-Rodríguez A, Hoang V, Khoo E, Nguyen N. 2020. The red list of oaks 2020. *The Morton Arboretum: Lisle, IL, USA*: 11-12.

Carrión JS, Fernández S, González-Sampériz P, Gil-Romera G, Badal E, Carrión-Marco Y, López-Merino L, López-Sáez JA, Fierro E, Burjachs F. 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Review of Palaeobotany and Palynology* **162**(3): 458-475.

Chatin MA. 1869. Sur Les Arbres Et Arbustes Truffiers. *Bulletin de la Société Botanique de France* **16**(1): 19-26.

Colmeiro M. 1888. *Enumeración y revision de las plantas de la Peninsula Hispano-Lusitana é Islas Baleares*. Madrid: Imprenta de la viuda é hija de Fuentenebro.

Colmeiro M, Boutelou E. 1854. Examen de las Encinas y demás arboles de la Peninsula Iberica que producen bellotas, con la designación de los que se llaman mestos. *Imprenta de D. Jose M, Geofrin*.

Costa JC, Neto C, Aguiar C, Capelo J, Espirito-Santo MD, Honrado J. 2012. Vascular plant communities in Portugal (Continental, the Azores and Madeira). *Global Geobotany* **2**: 1-180.

Coutinho AXP. 1888. Os Quercus de Portugal. *Boletim da Sociedade Broteriana* **6**: 47-116.

Coutinho AXP. 1913. *Flora de Portugal (plantas vasculares).* Paris: Aillaud Alves & Cia.

Coutinho AXP. 1930. *Notas da Flora de Portugal*. Paris: Aillaud, Albes & Cia.

Coutinho AXP. 1935. Suplemento da Flora de Portugal (Plantas Vasculares). . *Boletim da Sociedade Broteriana* **10**: 43-194.

Coutinho AXP. 1939. *Flora de Portugal (Plantas Vasculares)*. Lisbon.

Cullen J, Maxwell H. 1989. Quercus L. *The European Garden Flora* **3**.

Decaisne J 1835. Liste des plantes recueillies par M. Bové dans la Palestine et la Syrie. In: Guillemin BAD ed. *Annales des sciences naturelles. Botanique*. Paris: Paul Renouard, 343-360.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Desfontaines R 1791. Observations sur le chêne Ballota ou à glands doux du Mont-Atlas. In: (France) Ards ed. *Histoire de l'Académie royale des sciences, avec les mémoires de mathématique et de physique*. Paris: Du Pont, 394-399

Desfontaines R. 1799. *Flora Atlantica, sive Historia Plantarum, quae in Atlante, Agro tunetano et algeriensi crescunt*: Panckouckes.

Desfontaines R. 1815. *Tableau de l'école de botanique du Muséum d'histoire naturelle*. Paris: J. A. Brosson.

Duchatre PES. 1847. *Revue botanique*. Paris: A. Franck.

Dumortier B-C. 1829. *Analyse des familles des plantes: avec l'indication des principaux genres qui s'y rattachent*. Tournay: J. Casterman, Ainé.

Endlicher S. 1847. *Generum plantarum supplementum quartum*. Vienna: Fr. Beck.

Espírito-Santo MDL, M., Costa, J.C., Capelo, J. 1995. Lonicero implexae-Querceto rotundifoliae sigmetum: uma nova série de vegetação do Divisório Português. . *XIV Jornadas de Fitosociologia*. Bilbao. 35.

Font Quer P. 1928. Iter Maroccanum 1927. Exsiccata schedula. *Natural Science Museum, Barcelona* **739**.

Franco J, González GL 1987. Notas referentes al género" Quercus". *Anales del Jardín Botânico De Madrid*: Real Jardín Botánico. 555-558.

Franco JA. 1971. *Nova Flora de Portugal (Continente e Açores) Lycopodiaceae-Umbelliferae*. Instituto Superior de Agronomia: Instituto Superior de Agronomia.

Franco JA 1990. Quercus L. In: S. C, al. e eds. *Flora Iberica, (Plantanaceae-Plumbaginaceae [Partim])*. Madrid: Real Jardín Botánico, CSIC, pp. 15-36.

Gay JE 1857. Notice sur une nouvelle espèce de chêne française sur les caractères qui la distinguent et sur la classification des chênes en général. In: J. BADD ed. *Annales des sciences naturelles. Botanique*. Paris: Libraire de Victor Masson, 223-246.

González-Albo J. 1936. *Nota sobre flora peninsular*: La Solana.

Govaerts R, Frodin DG. 1998. *World checklist and bibliography of Fagales*. Kew: Royal Botanic Gardens.

Grenier JCG, D.A. 1855. *Flore de France ou description des plantes qui croissent naturellement en France et en Corse*. Paris: J. B. Baillière.

Greuter W, Raus T. 1982. Med-checklist notulae, 5. *Willdenowia*: 33-46.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hickel R, Camus A. 1921. *Les Chénes d'Indo-chine*.

Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl A, Deng M, Denk T, Fitz-Gibbon S. 2020. Genomic landscape of the global oak phylogeny. *New Phytologist* **226**(4): 1198-1212.

Hohenacker M. 1838. Pflanzen der Provinz Talish. *Soc. Imp. Naturalists, Moskow, Russia*.

Hooker WJ. 1838. *Flora boreali-americana, or, the botany of the northern parts of British America*. London: H.G. Bohn.

Huang C, Zhang Y, Bruce B. 1999. Fagaceae. Flora of China. *CY Wu and PH Raven. Beijing: Science Press and St. Louis: Missouri Botanical Garden Press* **4**: 380-400.

Humboldt AB, A. . 1809. *Voyage de Humboldt et Bonpland. Plantes équinoxiales recueillies au Mexique.* Paris: F. Schoell.

Hy MlaF. 1895. Sur quelques chenes hybrides observés aux environs D'Angers. *Bulletin de la Société Botanique de France* **42**(6): 552-560.

Iamonico D, Peruzzi L. 2013. Lectotypification of Linnaean names in the genus Quercus (Fagaceae). *Taxon* **62**(5): 1041-1045.

Jaubert H-F. 1843. *Illustrationes plantarum orientalium auctoribus comite Jaubert et Eduardo Spach*: Roret.

Kasapligil B. 1981. Past and present oaks of Turkey. *Phytologia* **49**: 95-146.

Koch KHE. 1873. *Dendrologie: Die Cupuliferen, Coniferen und Monocotylen*. Erlangen: Enke.

Labillardière JJH. 1812. *Icones plantarum Syriae rariorum. Decas quinta et ultima*. Paris: Huzard.

Laguna M. 1883. *Flora Forestal Española*. Madrid: Imprenta del Colegio Nacional de Sordo-Mudos y de Ciegos.

Lamarck JB. 1785. *Encyclopédie méthodique. Botanique*. Paris: Panckoucke.

Lamarck JB, e Candolle AP 1805. Flore française, ou descriptions succinctes de toutes les plants qui croissent naturellement en France, disposées selon une nouvelle méthode d'analyse, et précédées par un exposé des principes élémentaires de la botanique. Troisième Édition. Tome second: Chez H. Agasse, Paris.

Lamarck JBPJLM. 1811. *Encyclopédie méthodique. Botanique. Supplement. Tome II.* Paris: Agasse.

Lange J. 1861. *Pugillus plantarum imprimís hispanicarum.* Kjóbenhavn: Typis Bianco Luno Bogtrykkeri.

Lapeyrouse P. 1813. *Histoire abrégée des plantes des Pyrénées*. Toulouse: De l'Imprimerie de Bellegarrigue.

Lieblein FK. 1784. *Flora fuldensis oder Verzeichniss der in dem Fürstenthume Fuld wildwachsenden Bäume*. Frankfurt: Sträucher und Pflanzen.

Liebmann FM. 1854. Mödet den 19de mai. *Oversigt over det kongelige danske videnskabernes selskabs forhandlinger og dets medlemmers arbeider* **5**: 159-191.

Linnaeus C. 1753. *Species Plantarum*. Stockholm: Impensis Laurentii Salvii.

Llamas F, Lence C, Acedo C. 2003. Una nueva nothoespecie de Quercus L. (Fagaceae) en el NO de España. *Lagascalia* **23**(1): 85-90.

Loidi J, Herrera M. 1990. The Quercus pubescens and Quercus faginea forests in the Basque Country (Spain): distribution and typology in relation to climatic factors. *Plant Ecology* **90**(1): 81-92.

Loudon JC. 1838. *Arboretum et fruticetum britannicum*. London: Longman, Orme, Brown, Green, and Longmans.

Loudon JC. 1843. *The gardener's magazine*.

Lowe JJ, Walker MJ. 1984. *Reconstructing Quaternary Environments*: London.

Lumaret R, Mir C, Michaud H, Raynal V. 2002. Phylogeographical variation of chloroplast DNA in holm oak (Quercus ilex L.). *Molecular Ecology* **11**(11): 2327-2336.

Maire R 1924. Études sur la végétation et la flore du Grand Atlas et du Moyen Atlas Marocains In: Maroc Sdsnd ed. *Mémoires de la Société des sciences naturelles du Maroc.* . Rabat: l'Institut Scientifique Chérifien, 1-220.

Maire R 1931. Contributions à l'étude de la flore de l'Afrique du Nord. In: d'Alger SFdS ed. *Bulletin de la Société d'histoire naturelle de l'Afrique du nord*. Argel: Minerva, 30-72.

Maire R 1933. Contributions à l'étude de la flore de l'Afrique du Nord. In: d'Alger SFdS ed. *Bulletin de la Société d'histoire naturelle de l'Afrique du nord*. Alger: Minerva.

Maire R. 1961. *Flore de l'Afrique du nord (Maroc, Algérie, Tunisie, Tripolitaine, Cyrénaique et Sahara)*: P. Lechevalier.

Maleev VP. 1935. A Review of Oak Trees in Caucasus through theirs Taxonomical and geographical relations and concerning to evolution of group Robur. *Bot. Zhur.* **20**(2): 156-172.

Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). *Molecular phylogenetics and evolution* **12**(3): 333-349.

Manos PS, Hipp AL. 2021. An updated infrageneric classification of the North American oaks (Quercus subgenus Quercus): Review of the contribution of phylogenomic data to biogeography and species diversity. *Forests* **12**(6): 786.

Marcet A. 1945. Plantas nuevas, raras o críticas del Montserrat. *Boletín de la Real Sociedad Española de Historia Natural* **43**: 31-39.

Martens M, Galeotti H. 1843. Enumeratio synoptica plantarum phanerogamicum ab Henrico Galeotii in regionibus mexicanis collectarum. *Bulletin de l´Academie Royale des Sciences et Belles-lettres de Bruxelles* **10**(1): 208–224.

Martrin-Donos MM, Bal-Lagrave T 1864. Observations sur quelques races ou variétés du Chêne-Vert (Quercus ilex L.), suivies de Luers Descriptions. In: France Sbd ed. *Bulletin de la Société Botanique de France*. Paris: La Société, 313.

Menitsky G. 1972. *Generis Quercus L. species asiae austro-occidentalis*.

Meyer CA. 1831. *Verzeichniss der pflanzen*. Kaiserlautern: Akademie der wissenschaften.

Michaux A. 1801. *Histoire des Chênes de l'Amérique, ou Descriptions et Figures de toutes les espèces et variétés de Chênes de l'Amérique Septentrionale*. Paris: l'imprimene de Crapelet.

Miller P. 1768. *The Gardeners Dictionary: Containing the Best and Newest Methods of Cultivating and Improving the Kitchen, Fruit, Flower Garden, and Nursery*. London: John and Francis Rivington.

Montserrat P. 1957. Algunos aspectos de la diferenciación sistemática de los Quercus ibéricos.

Muller CH. 1936. Studies in the oaks of the mountains of northeastern Mexico. *Journal of the Arnold arboretum* **17**(3): 160-179.

Née L. 1801. Descripciones de varias especies nuevas de encinos (Quercus de Linneo). *Annales de Ciencias Naturales* **3**: 260–276.

Newberry JS 1857. Report upon the Botany of the route. In: H. A ed. *Explorations for a Railroad Route, from the Sacramento Valley to the Columbia River. Beverley Tucker*. Washington: Beverly Tucker Printer, 20-102.

Nixon K, Muller C 1997. Quercus Sect. Quercus Linneus. In: Committee FoNAE ed. *Flora of North America North of Mexico*.

Nyman CF. 1881. *Conspectus florae europeae, seu enumeratio methodica plantarum phanerogamarum Europae indigenarum*. Örebro: Typis officinae Bohlinianae.

Olivier GA. 1807. *Voyage dans l'empire Othoman*. Paris: Henri Agasse.

Ørsted AS. 1866. *Bidrag til Egeslaegtens Systematik:(Hertill Tab. I-II Meddelt d. 2. Mars 1866)*.

Pau C. 1909. Carlos Pau, Plantae novae huescanae. *Repertorium novarum specierum regni vegetabilis* **7**(4-6): 83-86.

Penas A, Llamas F., Perez-Morales C, Acedo C. 1994. Aportaciones al conocimiento del género Quercus en la Cordillera Cantábrica. I. Tricomas foliares de las especies caducifolias. *Lagascalia* **17**(2): 311-324.

Pereira AJ, Francisco A, Porto M. 2016. Flora-On: Occurrence data of the vascular flora of mainland Portugal. *PhytoKeys*(69): 105.

Persoon CH. 1807. *Synopsis plantarum: seu enchiridium botanicum, complectens enumerationem systematicam specierum hucusque cognitarum*. Paris: C.F. Cramerum.

Petzold ECA, & Kirchner, G. . 1864. *Arboretum muscaviense*. Gotha: Bei W. Optez.

Pinto-Gomes C, Ladero M, Cano E, Meireles C, Aguiar C, Paiva-Ferreira R. 2010. The Teucrio salviastri-Quercetum rotundifoliae, a new forest association of holm-oak in the Center-North of Portugal. *Acta Botanica Gallica*(157): 25-36.

Poech J. 1842. *Enumeratio plantarum hucusque cognitarum insulae Cypri*. Vien: Caroli Ueberreuter.

Pomel AN. 1875. *Nouveaux matériaux pour la flore atlantique*. Paris: Savy.

Radic FJ. 1983. Hrastovi biokovskog područja. *Acta biocovica* **2**: 1-104.

Reichenbach HGL. 1832. *Flora Germanica excursoria ex affinitate regni vegetabilis naturali disposita, sive principia synopseos plantarum in Germania terrisque in Europa media adiacentibus sponte nascentium cultarumque frequentius*: Carolum Cnobloch.

Reynier A 1903. Espéce conventionelle "Quercus mixta". In: Rouy G ed. *Revue de botanique systématique et de géographie botanique*. Paris: E. Deyrolle, 204.

Rivas-Martínez S, Aguiar C, Aguilella A, Alonso R, Alvarez M, Amich F, Arnaiz C, Baccheta G, Barbero M, Barbour M. 2011. Map of series, geoseries and geopermaseries of vegetation in Spain [MEMORY OF MAP OF POTENTIAL VEGETATION OF SPAIN, 2011] PART II. *Itinera Geobotanica* **18**(II): 1-764.

Rivas-Martínez S, González-Días TE, González FF, Loidi JJ, Lousã MF, Merino ÁP. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica*(15): 433-922.

Rivas-Martínez S, Penas A, González TED, Cantó P, del Río S, Costa JC, Herrero L, Molero J 2017. Biogeographic Units of the Iberian Peninsula and Baelaric Islands to District Level. A Concise Synopsis. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 131-188.

Rivas-Martínez S, Rivas-Sáenz S, Penas A, Alcaraz F, Amigo J, Asensi A. 2011. World bioclimatic classification system. *Global Geobotany* **1**: 1–634.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rouy G, Foucaud J, Camus E. 1913. Flore de France ou description des plantes qui croissent spontanément en France, Corse et en Alsace-Lorraine. *Ann. Soc. nat. Charente-inférieure* **14**.

Saénz de Rivas C. 1967. Estudios sobre Quercus ilex L. y Quercus rotundifolia Lamk. . *Annales del Instituto Botanico de A.J. Cavanilles* **2**: 243-262.

Saénz de Rivas C 1969. Estudios biométrico-taxonómicos sobre Quercus faginea Lamk.In Sevilla Ud. *V Simposio de Flora Europaea*. Sevilla: Universidad de Sevilla. 335-350.

Saénz de Rivas C. 1975. Sobre Quercus pyrenaica Willd. (Fagaceae). *Annales del Instituto Botánico AJ Cavanilles* **32**(2): 779-792.

Saénz de Rivas C, Rivas-Martínez S. 1971. Híbridos meridionales ibéricos del Quercus faginea Lam. *Pharmacia Mediterránea* **7**: 489–501.

Salisbury RA. 1796. *Prodromus stirpium in horto ad Chapel Allerton vigentium*. London: Author Edition.

Sampaio G. 1909. Flora vascular de Odemira. *Boletim da Sociedade Broteriana* **24**: 7-132.

Sampaio G. 1910a. *Manual da Flora Portugueza*. Porto: Universidade do Porto.

Sampaio G. 1910b. Nota a propósito dos Quercus lusitanica Lamk., Q. humilis Lamk e Quercus faginea, Lamk. . *Annaes Scientificos da Academia Polytechnica do Porto* **5**(3): 161-165.

Sampaio G. 1947. *Flora de Portugal*. Porto: Imprensa Moderna.

Saporta MLMG 1893. Sur les rapports de l'ancienne flore avec celle de la région provençale actuelle. In: France Stbd ed. *Bulletin de la Société Botanique de France*. Paris: La Société, 202-207.

Sargent CS. 1896. *The silva of North America: a description of the trees which grow naturally in North America exclusive of Mexico*. Boston: Houghton, Mifflin and company.

Sargent CS. 1918. Notes on North American Trees. I. Quercus. *Botanical Gazette* **65**(5): 423-459.

Schlechtendal DFL. 1830. *Linnaea: Ein Journal für die Botanik in ihrem ganzen Umfange*. Berlin: Umfange. F. Dümmler.

Schneider K. 1904. *Handbuch der Laubholzkunde*. Jena: Gustav Fischer Vg.

Schneider K. 1906. *Illustriertes Handbuch der Laubholzkunde*. Jena: Gustav Fischer

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O. 1936a. Entwurf zu einem natürlichen System der Cupuliferen und der Gattung Quercus L. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*: 1-22.

Schwarz O. 1936b. Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* **8**: 65–100.

Schwarz O. 1937. Monographie der Eichen Europas und des Mittelmeergebietes. *Repertorium novarum speciarum regni vegetabilis* **1**: 1-200.

Schwarz O 1964. Quercus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, DA. W eds. *Flora Europaea*. Cambridge: Cambridge University Press, 61-64.

Sennen EG. 1932. Exsiccata «Plantes d'Espagne». Vingt-cinq ans de publication. *Bulletin de la Société Botanique de France* **79**(2): 227-230.

Serteser A, Kargıoğlu, M., Senkul, C., & Konuk, M. . 2009. An assessment on bioclimatic requirements of endemic Quercus aucheri Jaub. et Spach. communities spreading South-West Anatolia, Turkey. . *Asian Journal of Plant Sciences* **8**(1): 35-41.

Simonkai L. 1883. *Magyar növény lapok. Nyomatott K*. Budapest: Papp Miklósnál.

Skan SA. 1899. Cupuliferae: Quercineae. *Journal of the Linnean Society, Botany* **26**: 505–525.

Small JK. 1901. Shrubs and Trees of the Southern States-IV. *Bulletin of the Torrey Botanical Club* **28**(6): 356-361.

Spach É. 1842. *Histoire naturelle des végétaux: Phanérogames. Vol. 11. Librairie encyclopédique de Roret, Paris*. Paris.

Steudel EG. 1821. *Nomenclator botanicus enumerans ordine alphabetico nomina atque synonyma tum generica tum specifica et a Linnaeo et recentioribus de re botanica scriptoribus plantis phanerogamis imposita*. J.G. Cottae: J.G. Cottae.

Steven C 1857. Verzeichnis der auf der taurischen Halbinsel wildwachsenden Pflanzen. Buchdruckerei der Kaiserlichen Universität. In: prirody Mol ed. *Bulletin de la*

Société impériale des naturalistes de Moscou. Moscou: Société impériale des naturalistes de Moscou, 325-398.

Sweet R. 1830. *Hortus Britannicus: or, a Catalogue of Plants Cultivated in the Gardens of Great Britain.* London: Robert Sweet.

Taborda-de-Morais A. 1940. Novas Áreas da Fitogeografia Portuguesa. *Boletim da Sociedade Broteriana* **14**(2): 97-138.

Tenore M. 1813. Flora Napolitana (Prodromo), 1. *Stamperia Reale, Napoli*.

Tenore M. 1831. *Sylloge plantarum vascularium florae neapolitanae hucusque detectarum*.

Tenore M. 1836. *Flora Napolitana*. Napoli: Stampa Reale.

Thiers B 2022. Index Herbariorum: a global directory of public herbaria and associated staff. . New York Botanical Garden's Virtual Herbarium.

Thunberg C. 1784. Caroli a Linneì equitis Systema vegetabilium: secundum classes ordines genera species cum characteribus et differentiis.

Trelease W. 1917. Naming American hybrid oaks. *Proceedings of the American Philosophical Society* **56**(1): 44-52.

Trelease W. 1924. *The American oaks*. New York: Plant Monograph Reprints.

Turland N, Wiersema J, Barrie F, Greuter W, Hawksworth D, Herendeen P, Knapp S, Kusber W-H, Li D-Z, Marhold K. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vázquez, F.M. R, S., , Ruiz T. 2000. Hybridisation processes in Mediterranean oaks from South Spain. *International Oaks Journal* **12**: 108-117.

Vázquez FM. 1995. Híbridos de Quercus faginea subsp. broteroi (Coutinho) A.Camus en el suroeste de la Península Ibérica. *Annales del Jardín Botânico De Madrid* **53**(2): 247-251.

Vázquez FM, Coombes A. 2016. Aproximación al conocimiento del género Quercus L. Sect. Gallifera Spach (Fagaceae) en Extremadura (España). . *Folia Botánica Extremadurensis* **9**(1): 25-31.

Vazquez FM, Coombes A, Almeida R, Garcia-Alonso D, Marquez-Garcia F, Vila-Vicosa C. 2020. Lectotypification of names of Quercus spp.(Fagaceae) described by Lamarck from the Iberian Peninsula. *Phytotaxa* **455**(3): 205–213-205–213.

Vázquez FM, Coombes AJ. 2017. (2569) Proposal to conserve the name Quercus ilex (Fagaceae) with a conserved type. *Taxon* **66**(6): 1473-1475.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Vázquez FM, Ramos S, Doncel E, Coombes AJ, Rodríguez M. 2003. New oak hybrids from Spain. *International Oaks Journal* **14**: 49-60.

Vázquez FM, Ramos S, Garcia S. 2004. Diversity of Iberian oaks. *International Oaks Journal* **15**: 31-43.

Vázquez FM, Sanchez-Gullón E, Pinto-Gomes C., Pineda M., Alonso D., Márquez F., Barrena M., Blanco-Salas J., C. V-V. 2015. Three New Oak Hybrids from Southwest Iberia (Spain and Portugal). *International Oaks Journal* **26**: 43-56.

Vicioso C. 1942. Materiales para el estudio de la flora soriana. *Anales del Jardín Botânico De Madrid* **2**: 188-235.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C. 2012. *Os carvalhais marcescentes do Centro e Sul de Portugal. Estudo e Conservação.* MSc Dissertation, Évora Évora, Portugal.

Vila-Viçosa C, Arenas-Castro S, Marcos B, Honrado J, García C, Vázquez FM, Almeida R, Gonçalves J. 2020a. Combining Satellite Remote Sensing and Climate Data in Species Distribution Models to Improve the Conservation of Iberian White Oaks (Quercus L.). *ISPRS International Journal of Geo-Information* **9**(12): 735.

Vila-Viçosa C, Arraiano-Castilho R, Hipp A, Vázquez FM, Almeida R, García C, Beja-Pereira A, Azevedo H 2021. RAD-Seq unveils the phylogenetic backbone of the Iberian white oak (Quercus L. section Quercus) syngameon.In Pérez Badia RM, J.C. . *First Spanish Botanical Society Congress (SEBOT). Sociedad Española de Botanica*. Toledo. 175.

Vila-Viçosa C, Arsénio P 2021. Vegetação do Sudoeste Português. In: Capelo J, Aguiar C eds. *A vegetação de Portugal*. Lisbon: ENCM, 110-121.

Vila-Viçosa C, Fernandes TM, Moreira J, Junqueira J, Tinoco J, Frias I, Farinha-Marques P. 2022a. Developing the Oak Collection at the Jardim Botânico da Universidade do Porto (Portugal). *International Oaks* **33**: 159-172.

Vila-Viçosa C, Gonçalves J, Honrado J, Lomba Â, Almeida RS, Vázquez FM, Garcia C. 2020b. Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Scientific reports* **10**(1): 1-12.

Vila-Viçosa C, Mendes P, Meireles C, Pinto-Gomes C, Vázquez FM, Alves P, Almeida R, Capelo J 2017. Biogeographic analysis of Serrano-Monchiquense District and Southern Portugal. *European Meeting of Phytosociology Biogeography and Syntaxonomy of the Atlantic Regions*. Praia. Cabo Verde.

Vila-Viçosa C, Mendes P., del Río S, Meireles C., Quinto-Canas R, Arsénio P, Pinto-Gomes C. 2012. Temporihygrophilous Quercus broteroi forests in southern Portugal: analysis and conservation. *Plant Biosystems* **146**(1): 298-308.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vila-Viçosa C, Vázquez FM, Mendes P, Del Rio S, Musarella C, Cano-Ortiz A, Meireles C. 2015. Syntaxonomic update on the relict groves of Mirbeck's oak (Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* **149**(3): 512-526.

Vila-Viçosa C, Vieira C, Márquez F, Almeida R, Vázquez FM. 2022b. Notes on the original materials of the three western Mediterranean oaks (Quercus, Fagaceae) described by Desfontaines. *Mediterranean Botany* **43**: 1-11.

Villar E 1949. Les Quercus de la section galliferae de L'Afrique du Nord. *Mem. Soc. Hist. Nat: Afr. N.* Alger, 165-171.

Villar EH. 1935. Sur le nom de quelques Quercus et la systématique du faginea. *Cavanillesia* **7**: 57-70.

Villar EH 1938. Les Quercus de L`Herbier d´Alger. In: d'Alger SFdS ed. *Bulletin de la Société d'histoire naturelle de l'Afrique du nord*. Argel: Minerva, 432-478.

Villar EH 1943. Nouvelle note sur les Quercus de l'Afrique du Nord. In: Maroc SdSNd ed. *Bulletin de la Société des sciences naturelles du Maroc.* . Rabat: L'Institut Scientifique Chérifien, 2-3.

Villar EH. 1958. Estudios sobre los Quercus del Oeste mediterráneo. *Anales del Instituto Botanico de A.J. Cavanilles* **15**: 3-114.

Vinagre C, Pinto-Gomes, C., Vila-Viçosa, C., & Vázquez, F.M. . 2014. Anotaciones a la diversidad del género Quercus L.(Fagaceae) en la Estremadura Portuguesa. *Folia Botánica Extremadurensis* **8**: 4.

Webb P. 1838. *Iter Hispaniense.* Paris: Béthune and Plon.

Willdenow CL. 1796. *Berlinische Baumzucht oder Beschreibung der in den Gärten um Berlin im Freien ausdauernden Bäume und Sträucher für Gartenliebhaber und Freunde der Botanik*. Berlin: Nauck.

Willdenow CL. 1805. *Species plantarum exhibentes plantas rite cognitas ad genera relatas cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis naturalibus secundum systema sexuale digestas*. Berlin: Nauck.

Willdenow CL. 1809. *Enumeratio plantarum Horti Regii Berolinensis*. Berlin: Taberna libraria Scholae Realis.

Willkomm M, Lange J. 1861. *Prodromus florae Hispanicae. I.*: Stuttgart.

Zohary M. 1960. The maquis of Quercus calliprinos in Israel and Jordan. *Bulletin of the Research Council of Israel*(2): 51-72.

2.8. Supplementary information

Supplementary Information S1 – Taxonomic scheme (* cultivated):

Quercus Linnaeus (1753: 994)

I. *Quercus* subgen. *Cerris* Oersted (1866: 74)

i. Section *Cerris* Dumortier (1829: 15)

1. **Quercus acutissima* Carruthers (1862: 33)
2. **Quercus afares* Pomel (1875: 391)
3. **Quercus castaneifolia* C.A. Meyer (1831: 44)
4. **Quercus cerris* Linnaeus (1753: 997)
5. **Quercus ×crenata* Lamarck (1785: 724)
6. **Quercus ithaburensis* Decaisne (1835: 348)
7. **Quercus ×libanerris* Boom (1959: 157)
8. **Quercus macrolepis* Kotschy (1860: 16)
9. *Quercus suber* Linnaeus (1753: 995)
10. **Quercus variabilis* Blume (1851: 297)
11. **Quercus libani* G.Olivier (1801: 290)

ii. Section *Cyclobalanopsis* (Oerst.) Bentham & Hooker (1880: 408)

12. **Quercus glauca* Thunberg (1784: 858)
13. **Quercus lamellosa* Sm. (1814: 29)
14. **Quercus lineata* Blume (1826: 523)
15. **Quercus morii* Hayata (1911: 293)
16. **Quercus myrsinifolia* Blume (1851: 305)
17. **Quercus schottkyana* Rehder & E.H.Wilson (1916: 237) Sargent (1916)
18. **Quercus sessilifolia* Blume (1851: 305)
19. **Quercus stenophylloides* Hayata (1914: 21)

iii. Section *Ilex* Loudon (1838: 1899)

20. **Quercus floribunda* Lindl. ex A.Camus (1935: 131)
21. **Quercus franchetii* Skan (1899: 513)
22. **Quercus lanata* Sm. (1814: 29)
23. ** Quercus leucotrichophora* A.Camus (1935: 66)
24. **Quercus phillyreoides* A. Gray (1859: 406)

iii.i Subsection *Ilex* Oerst (1866: 69)

25. **Quercus ilex* Linnaeus (1753: 995)
26. *Quercus rotundifolia* Lam. (1785: 723)

iii.ii Subsection *Cocciferae* (Spach) Gürke (1897: 70)

27. **Quercus alnifolia* Poech (1842: 12)
28. **Quercus aucherii* Jaub. & Spach (1843: 113)
29. *Quercus airensis* Franco & Vasconcellos (1954: 119) prop. hybr.
30. **Quercus calliprinos* Webb (1838: 15)
31. *Quercus coccifera* L. (1753: 995)
32. *Quercus pseudococcifera* Desfontaines (1798: 349)
33. *Quercus pseudococcifera* subsp. *rivasmartinezii* (Capelo & J.C. Costa) Capelo & al. *comb. nov.*

II. Quercus subgen. *Quercus* Hicke l & Camus (1921: 379)

iv. Section Lobatae Loudon (1830: 385)

34. **Quercus alapensis* Bonplant (1809: 24) Humboldt & Bonplant (1809)
35. **Quercus ×benderi* Baenitz (1903: 85) Kneucker (1904)
36. **Quercus benthamii* A. De Candolle (1864: 29)
37. **Quercus brenesii* Trelease (1924: 186)
38. ** Quercus calophylla* Schltdl. & Cham. (1830:79)
39. **Quercus canbyi* Trel. (1924: 188)
40. **Quercus cupreata* Trel. (1936: 152)
41. **Quercus emoryi* Torr. (1848: 152)
42. **Quercus ×exacta* Trel. (1917: 49)
43. **Quercus frutex* Trelease (1924: 82)
44. **Quercus georgiana* M.A.Curtis (1849: 408)
45. **Quercus gravesii* Sudw. (1927: 86)
46. **Quercus humboldtii* Bonplant (1809: 155)
47. **Quercus imbricaria* Michaux (1801: 16)
48. **Quercus laurifolia* Michaux (1801: 17)
49. **Quercus laurina* Bonplant (1809: 32)
50. **Quercus ×leana* Nuttall (Michaux & Nuttall 1842: 13)
51. **Quercus mexicana* Bonplant (1809: 35)
52. **Quercus palustris* Münchhausen (1770: 253)
53. **Quercus phellos* Linnaeus (1753: 994)
54. **Quercus pinnativenulosa* C.H.Muller (1936: 171)
55. **Quercus ×rehderi* Trel. (1917: 51)
56. **Quercus ×richteri* Baenitz. (1903: 85) Kneucker (1904)
57. **Quercus ×robusta* C.H.Mull. (1934: 119)
58. **Quercus texana* Buck ley (1860: 444)

iv.i) Subsection *Agrifoliae* (Trel.) A. Camus (1952 : 46)

59. **Quercus agrifolia* Née (1801: 271)
60. **Quercus agrifolia* (Torr.) J.T.Howell var. *oxyadenia* (1931: 38)
61. **Quercus kelloggii* Newb. (1857: 89)
62. **Quercus wislizeni* A. DC. (1864: 67)

iv.ii) Subsection *Coccineae* (Trel.) A. Camus (1952 : 286)

63. **Quercus acerifolia* (E.J.Palmer) Stoynoff & Hess (1990: 268)
64. **Quercus buckleyi* Dorr & Nixon [1985: 225(-226)]
65. **Quercus coccinea* Münchhausen (1770: 254)
66. **Quercus ellipsoidalis* E.J.Hill (1899: 204)
67. **Quercus rubra* Linnaeus (1753: 996)
68. **Quercus shumardii* Buckley (1861: 444)
69. **Quercus velutina* Lamarck (1785: 721)

iv. iii) Subsection *Palustres* (Trel.) A. Camus (1952 : 360)

70. **Quercus palustris* Münch. (1770: 253)
71. **Quercus texana* Buckley (1860: 444)

iv. iv) Subsection *Phellos* (G. Don) A. Camus (1952 : 293)

72. **Quercus falcata* Michx. (1801: 28)
73. **Quercus georgiana* M.A.Curtis (1849: 408)
74. **Quercus hemisphaerica* Hort. ex Endl. (1848: 25)
75. **Quercus ilicifolia* Salisb. (1796: 392)
76. **Quercus imbricaria* Michx. (1801: 16)
77. **Quercus laevis* Walter (1788: 234)
78. **Quercus laurifolia* Michx. (1801: 17)
79. **Quercus ×ludoviciana* Sarg. (1913: 223)
80. **Quercus nigra ×georgiana*
81. **Quercus nigra* L. (1753: 995-996)
82. **Quercus phellos* L. (1753: 994)

v. Section Ponticae

83. **Quercus pontica* K.Koch (1849: 319)

vi. Section Protobalanus

84. **Quercus chrysolepis Liebm. (1854: 173)*
85. **Quercus tomentella Engelm. (1877: 393)*

vii. Section Quercus Nixon & Muller (1997); Denk et. al. (2017: 13)
(≡Section *Robur* Loudon (1838: 1731))

86. **Quercus arizonica* Sarg. (1895: 92)
87. **Quercus ×bebbiana* C.K.Schneid. (1904: 201)
88. **Quercus copeyensis* C.H. Muller (1942: 30)
89. **Quercus engelmannii* Greene (1889: 33)
90. **Quercus ×fernowii* Trel. (1917: 49)
91. **Quercus germana* Schlechtendal. & Chamisso (1830: 78) Schlechtendal (1830)

92. **Quercus* ×*haynaldiana* Simonk. (1883: 63)
93. **Quercus* ×*hillii* Trel. (1917: 49)
94. **Quercus insignis* M.Martens & Galeotti (1843: 219)
95. **Quercus invaginata* Trel. (1924: 138)
96. **Quercus* ×*jackiana* C.K.Schneid. (1904: 202)
97. **Quercus mongolica* Fisch. ex Turcz. (1838: 101)
98. **Quercus obtusata* Bonpl. (1809: 76)
99. **Quercus porphyrogenita* Trel. (1924: 51)
100. **Quercus rugosa* Née (1801: 275)
101. **Quercus* ×*saulii* C.K.Schneid. (1904: 203)
102. **Quercus serrata* Murray (1784: 858)
103. **Quercus stellata* × *Quercus muehlembergii*
104. **Quercus* ×*substellata Trel. (1924: 105)*
105. **Quercus turbinella* Greene (1889: 37)
106. **Quercus* ×*vilmoriniana* A.Camus (1935: 62)

vii.i) Subsection *Albae* (G. Don) A. Camus (1936 : 728)

107. **Quercus alba* L. (1753: 996)
108. **Quercus michauxii* Nuttall (1818: 215)

vii. ii) Subsection *Dumosae* (Trel.) A. Camus (1936 : 462)

109. **Quercus berberidifolia* Liebmann (1854: 172)
110. **Quercus douglasii* Hook. & Arn. (1840: 391)
111. **Quercus durata* Jeps. (1909: 356)
112. **Quercus* ×*eplingii* C.H.Mull. (1938: 585)
113. **Quercus gambelii* Nutt. (1847: 179)
114. **Quercus garryana* Douglas ex Hooker (1838: 159)
115. **Quercus garryana* (Engelm.) Jeps. *var. breweri* (1909: 354)
116. **Quercus lobata* Née (1801: 277)

vii. iii) Subsection *Macrantherae* (Stef.) Maleev (1935: 163)

117. *Quercus* ×*alentejana* C. Pinto-Gomes & F.M.Vázquez (Vázquez *et al.* 2015: 49)
118. *Quercus* ×*aruciencis* C. Vicioso (1950: 139)
119. **Quercus boissieri* Reuter (1853: 119)
120. *Quercus canariensis* Willd. (1809: 975)
121. **Quercus* ×*cerrioides* Willk. & Costa (1859: 123)
122. *Quercus* ×*diegoi* F.M. Vázquez, *et al.* (Vinagre *et al.* 2014: 95)
123. *Quercus faginea* Lam. (1785: 725)
124. **Quercus frainetto* Tenore (1813: 72 (lxxii))
125. *Quercus* ×*fontquerii* O.Schwarz (1936: 85)
126. *Quercus lusitanica* Lam. (1785: 719)
127. **Quercus macranthera* Fisch. & C.A.Mey. ex Hohen. (1838: 259)
128. **Quercus pubescens* Willd. (1796: 279)
129. *Quercus pyrenaica* Willd. (1805: 451)
130. *Quercus* ×*tlemcenensis* Trab. (Battandier & Trabut 1905: 308)
131. **Quercus virgiliana* (Ten.) Tenore (1838: 262)

132. **Quercus vulcanica* Boiss. ex Kotschy (1860: 18)

vii. iv) Subsection *Hartwissianae* (Maleev) Vila-Viçosa, Capelo, Alves, Almeida & F.M. Vázquez ***comb. & stat. nov.***

133. *Quercus estremadurensis* O. Schwarz (1935: 463)
134. **Quercus hartwissiana* Steven (1857: 387)
135. **Quercus huguetiana* (Franco & G.López) Rivas Mart. & Sáenz de Rivas (1991: 102)
136. *Quercus orocantabrica* Rivas-Martínez (2002: 706)
137. **Quercus petraea* (Matt.) Lieblein (1784: 403)
138. **Quercus robur* L. (1785: 725)
139. **Quercus robur* L. 'Fastigiata' Lamarck (1785: 725)
140. **Quercus robur* L. 'Alnarp'
141. **Quercus robur* L. 'Salicifolia' Hort. ex Loud. (1838)
142. **Quercus robur* subsp. *pedunculiflora* (K.Koch) Menitsky (1967: 129)

vii. vi) Subsection *Polymorphae*

143. **Quercus laceyi* Small (1901: 358)
144. **Quercus mohriana* Buckley ex Rydb. (1901: 219)
145. **Quercus polymorpha* Schltdl. & Cham. (1830: 78)
146. **Quercus pungens* Liebm. (1854: 171)
147. **Quercus vaseyana* Buckley (1883: 91)

vii. vii) Subsection *Prinoideae* (Trel.) A. Camus (1936 : 434)

148. **Quercus bicolor* Willd. (1801: 396)
149. **Quercus* ×*humidicola* E.J.Palmer (1937: 140)
150. **Quercus* ×*introgressa* P.M.Thomson (1977: 453)
151. **Quercus lyrata* Walter (1788: 235)
152. **Quercus macrocarpa* Michx. (1801: 2-3)
153. **Quercus* ×*megaleia* Laughlin (1962: 154)
154. **Quercus muehlenbergii* Engelm. (1877: 391)
155. **Quercus* ×*schuettei* Trel . (1917: 51)

v.vi) Subsection *Stellatae* (Trel.) A. Camus

156. **Quercus sinuata* Walter (1788: 235)
157. **Quercus sinuata* (Torr.) C.H.Muller var. *breviloba* (1944: 439)
158. **Quercus stellata* Wangenh. (1787: 78)

vii. section *Virentes* Loudon, (1838: 1918)

159. **Quercus oleoides* Schlechtendal. & Chamisso (1830: 79) Schlechtendal (1830)

160. **Quercus virginiana* Mill. (1768: 16)

IV. Interseccional Hybrids

161. *Quercus* ×*almeidae* Vila-Viçosa et. al. nothosp. nov.
162. *Quercus* ×*alvesii* Vila-Viçosa *et. al*. nothosp. nov.
163. *Quercus* ×*auzandri* Grenier & Godron (1855: 119)
164. *Quercus* ×*avellaniformis* Colmeiro & E. Boutelou (1854: 9)
165. *Quercus* ×*capeloana* Vila-Viçosa, Alves, Almeida & F.M. Vázquez nothosp. nov.
166. **Quercus* ×*caroppoi* Medagli, Turco, Albano & Accogli (2019:
167. *Quercus* ×*celtica* F.M. Vázquez *et al*. (2003: 52)
168. *Quercus* ×*coscojosuberiformis* Baonza (2007: 365)
169. *Quercus* ×*coutinhoi* Sampaio (1910a: 123)
170. **Quercus* ×*diosdadoi* F.M. Vázques, Coombes, Rodr.-Coombes, Ramos & Doncel (2003: 50)
171. *Quercus* ×*duriensis* Franco & Vasconcellos (1954: 33)
172. *Quercus* ×*eborense* Vila-Viçosa *et. al.* nothosp. nov
173. *Quercus* ×*gallaecica* F. Llamas *et al.* (2003: 87)
174. **Quercus* ×*kerneri* Simkovics (1883: 69)
175. *Quercus* ×*lousae* Vila-Viçosa *et al.* (2014: 145)
176. **Quercus* ×*morisii* Borzí (1881: 10)
177. *Quercus* ×*pacensis* F.M.Vázquez (1996: 249)
178. *Quercus* ×*prasina* Bosc ex Endlicher (Bosc 1807: 330)
179. *Quercus* ×*sampaioana* Vila-Viçosa *et al.* nothosp. nov.
180. *Quercus* ×*tavaresii* Samp. (1910a: 123)
181. *Quercus* ×*tentudaica* (F.M.Vázquez) F. M.Vázquez (Vázquez *et al.* 2015: 45)
182. **Quercus* ×*turneri* Willdenow (1809: 975)
183. *Quercus* ×*welwitschii* Samp. (1910a: 123)

Supplementary Information S2 – Digital Annex

See Digital Annex section at the end of the present thesis.

Chapter 3.

Notes on the original materials of the western Mediterranean oaks (*Quercus*, *Fagaceae*) described by Desfontaines

Carlos Vila-Viçosa[1,2,3,4*], Cristiana Vieira[1], Francisco Márquez[5], Rubim Almeida[1,2,3,4], Francisco María Vázquez[5] (2022) *Mediterranean Botany.* 43. 1-11.
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[1] MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto – Herbário PO, Universidade do Porto. Praça Gomes Teixeira, 4099-002, Porto, Portugal.
[2] CIBIO (Research Center in Biodiversity and Genetic Resources) - InBIO (Research Network in Biodiversity and Evolutionary Biology), University of Porto. Campus Agrário de Vairão; Rua Padre Armando Quintas; 4485-661 Vairão; Portugal.
[3] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal.
[4] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO. Campus de Vairão, 4485-661 Vairão, Portugal.
[5] HSS Herbarium. Dep. Forest Production and Biodiversity. CICYTEX. 06187. Guadajira, Badajoz, Spain

3.1. Abstract

We examined specimens from René Louiche Desfontaines, deposited in the “Herbier de la Flore Atlantique” (P-Desf) from MNHN-P and homologue specimens from P-Lam, LINN-HS, MPU, FI-Webb, and B-W, to assess three names of western Mediterranean oaks (Quercus L.) that are distributed across the Iberian Peninsula and North Africa. Specifically, we bring insights to the names *Quercus ballota*, *Q. pseudococcifera*, and *Q. pseudosuber*, after a thorough examination of the original specimens, combined with the analysis of the respective protologues. The results highlight the need for wider and detailed natural history and classic herbaria surveys to promote the discussion and better understanding of species delimitation and biogeographic awareness, especially in crucial groups, that are still involved in taxonomic and evolutionary discussion, as the trees that form the potential climacic forests of the Northern Hemisphere.

3.2. Introduction

The genus *Quercus* Linnaeus (1783: 994) is one of the most important groups of woody plants in the Northern Hemisphere, with around 435 species (Manos *et al.*, 1999; Carrero *et al.*, 2020). This genus taxonomy is target of substantial debate and is not yet consensual, mainly due to the intrinsic difficulty of defining species boundaries among groups of species, defined as a syngameon (Burger, 1975; Van Valen, 1976; Grant, 1981; Cannon & Petit, 2020; Carrero *et al.*, 2020; Hipp *et al.*, 2020). Consequently, there are diverse groups still under deep evolutionary and taxonomic study, especially around circummediterranean oaks in need of molecular scrutiny (Vila-Viçosa *et al.*, 2014; Hipp, 2015; Pham *et al.*, 2017; Vázquez *et al.*, 2018; Jiang *et al.*, 2019; Di Pietro *et al.*, 2020; Douaihy *et al.*, 2020; Vazquez *et al.*, 2020; Vila-Viçosa, 2021). This situation has been originated from the often-brief descriptions of many oak taxa and on the fact that some of their names have never been typified, hampering an established and commonly accepted nomenclature. In addition, original *Quercus* spp. specimens were not adequately studied, and a wealth of heterogeneous materials led to various assumptions, nomenclatural endorsements and hasty typifications by different authors. Consequently, this caused a profusion of names and synonyms, which remain an increasing problem in the accurate identification of well-delimited evolutionary entities, their accurate nomenclature and taxonomic rank. Downstream, this hampers biodiversity conservation, especially in the Mediterranean forests, woodlands and scrub Biome that is the richest

of extra-tropical areas, aggregating 20% of all planetary plant species (Cody, 1986; Regato, 2001; Mittermeier *et al.*, 2011; Bellard *et al.*, 2014).

Desfontaines (1791, 1799) described three oaks from North Africa, two belonging to the western Mediterranean clade of section Ilex (Denk *et al.*, 2017; Hipp *et al.*, 2020) - *Quercus ballota* Desfontaines (1791: 375), corresponding to the holm oaks group and *Quercus pseudococcifera* Desfontaines (1799: 349) corresponding to the kermes oaks group. The third oak, *Quercus pseudosuber* Desfontaines (1799: 348), is a member of the western Mediterranean gall oaks, that are placed in section Quercus (Denk *et al.*, 2017; Hipp *et al.*, 2020) in the traditionally circumscribed subsection *Galliferae* (Spach, 1842; Gürke, 1897; Tschan & Denk, 2012).

The Mediterranean arboreal kermes oaks are traditionally assigned to *Quercus calliprinos* Webb. (1838: 15), a tree originally described from northwest Africa (Tétouan, Morocco). The author (Webb, 1838) extended this original concept and species to the Middle East (Lebanon), in a comment to a plant, earlier named as *Q. pseudococcifera* Labillardière (1812: 9) (*non Q. pseudococcifera* Desfontaines 1799: 349). The western Mediterranean arboreal kermes oaks assigned to *Q. pseudococcifera* Desf. and *Quercus mesto* Boissier (1842: 579) (Vázquez et al., 2018) are extensively documented by Webb (1838), Boissier and Reuter (1842), Amo (1861), Martinoli (1953) and, more recently, by Capelo and Costa (2005). The latter authors proposed an endemic arboreal kermes oak (*Quercus rivasmartinezii* (Capelo & J.C. Costa) Capelo & J.C. Costa) from the Atlantic coast of Portugal. This taxon deserves further molecular in-depth studies once the highlighted characters related with leaf shape and cup scales are also observed and overlap most of the distribution of *Q. pseudococcifera* Desf. specimens across the western Mediterranean Basin.

The western Mediterranean holm-oaks traditionally includes two distinct taxa: the holm oak itself (*Quercus ilex* Linnaeus 1753: 995) and the round-leaf oak (*Quercus rotundifolia* Lamarck 1785: 723) (Rivas-Martínez & Saénz, 1991; Schwarz, 1993). Both taxa are discriminated by Saénz de Rivas (1967), Rivas-Martínez and Saénz (1991) and Franco (1990), followed by the molecular analysis of Lumaret et al. (2002) and respectively typified by Vázquez and Coombes (2017) and Vazquez *et al.* (2020). These species are taxonomically distinguishable by the wider lanceolate leaves of *Q. ilex* with a higher number of nerves (>(7)8) with a rectilinear midrib, in face of the smaller round-orbicular leaves with 5±7 secondary nerves and sinuous midrib, especially in the apex, of *Q. rotundifolia* (Rivas-Martínez & Saénz, 1991). Furthermore, *Q. ilex* is reported to have

tomentose leaves as a result of an indumentum formed with stellate trichomes with a higher number of rays (12±14) and larger in length (185±200 µm), in contrast to *Q. rotundifolia* with fewer (9±10) and smaller rays (135±150 µm) (Saénz de Rivas, 1967).

Traditional approaches and interpretations of the original protologue of *Quercus ballota* (Desfontaines, 1971), mentioning sweet edible acorns, led to the prompt synonymy to *Q. rotundifolia* (Sampaio, 1909; Sampaio, 1910; Taborda-de-Morais, 1940; Vasconcellos & Franco, 1954). Therefore, this taxon was included in Flora iberica (Franco, 1990) as *Quercus ilex* subsp. *ballota* (Desf.) Sampaio (1909: 102). Later, *Q. ballota* was lectotypified with materials preserved at MPU (MPU014008!) by Ferrer-Galego and Sáez (2019), although the author original materials deposited in Desfontaines personal herbarium (P-Desf), were disregarded by the latter authors.

The name of the approached gall oak (*Q. pseudosuber* Desf.) has been overlooked, once it was considered conspecific and a homonym of *Quercus pseudosuber* Santi (1795: 156). Both names have been traditionally incorporated as synonyms of *Quercus ×crenata* Lamarck (1785: 724), the broad-known hybrid between *Quercus cerris* Linnaeus (1753: 997) and *Quercus suber* Linnaeus 1753: 995) (Vázquez *et al.*, 2018).

Since consultations of authors' herbaria is a needed natural step, that is strongly recommended before further typifications, the main objective of this work was to revisit the previous typification of the three names (*Quercus ballota, Quercus pseudococcifera* and *Quercus pseudosuber*), complemented by the study of historical literature and the observation of the original materials, thus contributing to a better awareness of the western Mediterranean oaks' biogeography.

3.3. Materials and methods

The present study was directed to address previous typifications of the original plants collected in North Africa by Desfontaines and kept in his herbarium "Herbier de la Flore Atlantique" (P-Desf) at the Paris Muséum National d'Histoire Naturelle, and duplicated in P-Lam, the Smith Herbarium of Linnean Society (LINN-HS!), the herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B-W), at MPU! (Herbier de l'Université de Montpellier) and FI-Webb! (Webb herbarium from Herbarium Universitatis Florentinae).

Original Desfontaines materials were studied at the Paris Muséum National d'Histoire Naturelle herbarium: *Quercus* spp. specimens (P-Desf!: P00667223!; P00667224!; P00667227! and P00667225!), P-Lam (P00382520!), P! (P06861579!), together with Desfontaines (1791, 1799) original descriptions and protologues. This was done to assess their validity and role pertinence as type materials (Paris Herbarium Review – Digital Annex).

This task was complemented with further online analysis of (a) LINN-HS herbarium specimens (1478.5! and 1478.9!), collected and sent by Desfontaines to Linnaeus *filius*, alongside (b) B-W herbarium relevant specimens (B-W 17597!) and (c) specimens conserved in MPU collected, that were sent by Desfontaines (UM-MPU-MPU014006-9!).

Additionally, *Q. pseudosuber* Desf. was submitted to SEM analysis, to ascertain past inferences and typifications around this taxon. This was done *in loco,* following a SYNTHESIS grant (FR-TAF-280) and performed in the MNHN (Muséum national d'Histoire naturelle) Plateau Technique de Microscopie Electronique for SEM and BAOBAB facilities, UMS2700 2AD, for stereo-microscope imagery.

3.4. Results and discussion

Nomenclatural and taxonomic notes

Quercus ballota Desfontaines (1791: 375)
=*Quercus rotundifolia* Lamarck (1785: 723)

The specimen of *Q. ballota* Desf. deposited in the Smith Herbarium of the Linnaean Society of London (LINN-HS 1478.5!) collected by Desfontaines in 1786 (see LINN-HS 1478.5!; http://linnean-online.org/47990/) from the original and first location specified by Desfontaines (1791) as *locus classicus*: “Mount Atlas”, with his handwriting is identifiable as *Q. ilex* (Desfontaines 1791). Accordingly, the original materials examined in the Herbier de la Flore Atlantique (P-Desf: P00667223! http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667223); and P00667224! http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667224; see Figure 1), also correspond to *Q. ilex* and concur with the original collection site as written in several detailed manuscript notes by Desfontaines *in schedula* “(Alger, Maroc, Belide, Mascar,

Tlemsen)". Remarkably, we noticed that the specimen P00667224! (left exemplar) corresponds to the symmetrical image of the drawing presented by Desfontaines (1791) in his original protologue (see Figure 2), being the putative original plant used for such drawing. Additionally, the original description of *Q. ballota* (Desfontaines, 1971: 376-377) addresses two distinctive forms, referring *in schedula* "*J'en ai observé deux varietés bien saillantes, l'une à feulles orbiculaires, dont le diamètre n'etoit que de cinq à six lignes, celles de la seconde ètoient très-allongèes & terminées en pointe"*, referring clearly that the collected materials span the two addressed species inside the western Mediterranean holm oaks (Saénz de Rivas, 1967; Rivas-Martínez & Saénz, 1991), one with rounded and orbicular leaves with less than six secondary nerves, that corresponds to *Q. rotundifolia* and the second with large, acuminate and lanceolate leaves, that corresponds to *Q. ilex*. The specimens from Berlim (BW!) (Schwarz *in sched.*), together with P-Lam and LINN-HS were originated from P-Desf. and all correspond to the original protologue description (Desfontaines, 1799), besides the original diagnosis and image provided by Desfontaines (1791) (see Figure 2), where is common to count more than 8 secondary nerves in several acuminate leaves. Therefore, it is clear that these plants correspond to *Q. ilex*. However, the specimens from Montpellier herbarium (MPU014006!, MPU014007! and MPU014008!), referring to materials collected by Desfontaines in North Africa, were deposited only in 1791, and can be broadly assignable to the round-leaf oak (*Q. rotundifolia* Lam.), especially MPU014006! and MPU014007!. These MPU specimens are characterized by rounded leaves with entire to denticulate and spiny margins and less than 6-7 pairs of secondary nerves. However, the elected lectotype specimen from Ferrer-Galego and Sáez (2019) (MPU014008!) presents heterogeneous specimens, including leaves with 8 nerves, that could be broadly, but uncertainly, ascribed to *Q. rotundifolia*. The fact that Desfontaines collected heterogeneous materials, that might not correspond to the lectotype elected by Ferrer-Gallego & Sáez (2019) does not invalidate that there are more collected materials that are also original and were not mentioned in the previous lectotipification work. As Desfontaines (1791) proposed several places as *locus typicus* in *"Mount Atlas"* alongside "*Belide, Mascar & Tlemsen*", it enables multiple origins for the original materials, beyond the elected lectotype. Therefore, the original specimens collected by Desfontaines and kept at P-Desf (see Figure 1) are hereinafter discussed.



Figure 1 - Original materials of *Quercus ballota* Desf. studied *in-situ* at P-Desf. (a) P00667224! and b) P00667223!), corresponding to *Q. ilex* L.

We consider that the specimens originally collected by Desfontaines in 1786, unambiguously match the original description of the taxon and should have been selected from the author's personal herbarium (P-Desf) as the most appropriate types. However, the code (Turland *et al.*, 2018) prevents the superseding of the proposed MPU lectotype since the previous designation by Ferrer-Gallego and Sáez (l.c.) is not conflictual with the original protologue. Although, it is necessary to attain that the original gathered materials, collected in north Africa by Desfontaines, including the lectotype, are heterogeneous. Especially, the original materials at P-Desf (P00667224! and P00667223!) that presents leaves with up to 10 secondary nerves and notorious lauroid-lanceolate leaves (see Figure 3), are assignable to *Quercus ilex* L. This should address further questioning and scientific discussion around the holm oak nomenclature and biogeography in North Africa and western Mediterranean Basin. For this matter, we highlight a particular specimen (P00382520!) kept in Lamarck herbarium (P-Lam) (see Figure 4), that incorporates duplicate materials from P-Desf, including the three specimens distributed through P00667224! and P00667223!. The label from P00382520 mentions that all the three branches were offered by *"Monsieur Desfontaines"* and

includes the note "*appariement au meme arbre",* certifying that all specimens included in Desfontaines collection (P00667224! and P00667223!) belong to same tree (see Figure 4). This is also the case of the materials from B-W (B-W 17597!), that emulates the same segments of the branches retrieved from the three specimens kept at P00667224 and P00667223, as stated *in schedula* by Schwarz, confirming that they are the original plants associated to *Q. ballota* Desf.



Figure 2 - Original image used to illustrate *Q. ballota* Desf. (Desfontaines 1791). Symmetrical drawing of Figure 1 a) - P00667224! (left exemplar).



Figure 3 - a, Lectotype specimen of Quercus ballota Desfontaines (MPU014008!) with leaves presenting 8 pairs of secondary nerves; b, P-Desf specimen (P00667224!) with lauroid-lanceolate leaves presenting 10 pairs of secondary nerves; c, P-Desf specimen (P00667223!; left specimen) with lauroid-lanceolate leaves presenting 10 pairs of secondary nerves.



Figure 4 - Duplicated specimen from P-Desf (P00667224! and P00667223!), respectively deposited in P-Lam (P00382520!). Includes the statement that the three fragments belong to the same tree (Desfontaines pers. comm.).

The major output of this revision cohesively addresses that the name *Q. ballota* should be a synonym of *Q. ilex* rather than *Q. rotundifolia*, according to the original protologue, drawings, studied specimens and the abovementioned references and arguments. Herein, Desfontaines (1791), clearly described a different species without rounded and more tomentose leaves in opposition to the taxon previously described as "*chêne a feuilles rondes*", by Lamarck (1785). The own locations stated *in schedula "'en ai vu de valles forêts fur les montagnes de Belide, de Mascar, de Tlemsen…"* corresponds to the northern Algerian Atlas. In these locations, *Q. ilex* is a common tree, as known from herbaria review, namely the Holotype of *Quercus ilex* L. subvar. *oleoides* Trabut (MPU007892!; Figure 5), and fieldwork (Figure 6). This contradicts the major works of oak taxonomy and syntaxonomy of north Africa, that mostly recognises *Q. rotundifolia* as the dominant taxon in most forest associations (Barbero *et al.*, 1981; Benabid, 1982; Quézel *et al.*, 1987; Benabdellah *et al.*, 2010; Chkhichekh *et al.*, 2015; Taleb & Fennane, 2019).



Figure 5 - Holotype of *Quercus ilex* L. subvar. *oleoides* Trabut (Battandier, 1890: 824; MPU007892!) https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007892



Figure 6 - Specimens of *Quercus ilex* L. (PO-V 64578 and PO-V 64575) from Tlemcen (Algeria) at PO Herbarium collection. (Porto University, Natural History and Science Museum).

Yet, Meddour *et al.* (2017) addresses morphological uniqueness to the holm oak populations of Tlemcen, thus addressing the name *Q. ballota* to the local taxon. The local surrounding potential vegetation corresponds to marcescent forests of *Q. canariensis* Willd. (1809: 975) and *Q. faginea* Lam. (1785: 725) which distribution pattern supports an increase in higher mean rainfall, that is also related to favour *Q. ilex* ecologically. (Battandier, 1890; Saénz de Rivas, 1967; Alcaraz, 1989; Djellouli, 1992; Meddour *et al.*, 2017). Furthermore, these northern Algerian Atlas populations, that includes the limestone mountains (up to 1600 m), where Q. *ilex* var. *oleioides* (Battandier, 1890) is referenced, enhances its biogeographic and ecological vicariancy with the eastern Iberian and Italian known populations of *Q. ilex* (Saénz de Rivas, 1967; Quézel *et al.*, 1992; Biondi *et al.*, 2003). These are also known for entailing heavy morphological plasticity and corroborates the molecular results obtained by Lumaret *et al.* (2002). In spite that most of the original materials collected by Desfontaines, that are directly related to the original protologue, are assignable to *Q. ilex*, we preserved the traditional synonymy to *Q. rotundifolia*, once the only materials that were initially available online at the time of the lectotypification, were the ones from MPU that were allusive to *Q. rotundifolia*.

Quercus pseudococcifera Desfontaines (1799: 349)

This name was lectotypified by Vázquez *et al.* (2018), foreseeing the original materials from the Herbier de la Flore Atlantique (P00667225!; Figure 7; http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667225). Additional specimens were then studied, namely the ones preserved in Firenze (FI-011768!/ Webb-172233!), a LINN herbarium specimen (LINN-HS 1478.9!; http://linnean-online.org/47997/), sent to Linnaeus *Filius* by Desfontaines. and a Cosson herbarium specimen (P-Cosson P06861579!; http://coldb.mnhn.fr/catalognumber/mnhn/p/p06861579). This last specimen (P06861579!) is simultaneously the Lectotype (here designated) of *Quercus obtecta* Poiret (Vereecke, 2021). All these specimens were collected in populations distributed across the western Mediterranean basin (left of Tunisia).



Figure 7 - Lectotype of *Quercus pseudococcifera* Desf. (P00667225!). Designated by Vázquez *et. al.* (2018)

Quercus pseudococcifera lectotype corresponds to the broad descriptions of the arboreal Kermes oaks present in the western half of the Mediterranean basin (Desfontaines, 1799; Webb, 1838; Boissier & Reuter, 1842; Martinoli, 1953; Capelo & Costa, 2005). Regularly, the abovementioned lectotype presents sub-sessile, flat and oblong to elliptic-lanceolate or narrowly obovate leaves, sometimes with stellate trichomes near the midrib and proximate half of the leaf and petiole. Two key characters that distinguish this taxon from *Quercus coccifera* Linneaus (1753: 995) are (1) the presence of free large and flat scales on the cup (see Figure 8), that become retroflexed and acuminate or cuspidate in maturity, and (2) the acorn not exceeding the cup in more than 1/2 of the length of the cup (Capelo & Costa, 2005; Vázquez *et al.*, 2018).

Biogeographically this taxon is related to the Atlantic areas of the western Mediterranean Basin, normally located on the fringe of marcescent forests of *Quercus faginea* and *Q. canariensis*, included in the Iberian Peninsula and North Africa. Recently, Capelo and Costa (2005), described an independent species of kermes oak dedicated to Prof. Salvador Rivas-Martinez (1935-2020), in the already known populations of *Q. pseudococcifera* from Sintra and Arrábida (Portugal), with triangular-cuspidate and retroflexed cup-scales and natural arboreal development. This western Mediterranean distributed taxon has been related with the eastern arboreal kermes oak, which preserves similar characters (Vázquez *et al.*, 2018), linked with the eastern vicariant taxon that corresponds to the traditional concept of *Q. calliprinos* Webb (1838).



Figure 8 - Detail of cup scales in *Quercus pseudococcifera* Desf. (P-Desf: P00667225!).

Quercus pseudosuber Desfontaines (1799: 348)

=*Quercus faginea* Lamarck (1785: 725)

The name previously typified by Vázquez *et al.* (2018), overlooked the deposited specimens in P-Desf herbarium. Therefore, this taxon was assigned to the hybrid between *Quercus faginea* and *Q. suber* L. according to the original protologue that mentions a corky bark and following the proposal of Vicioso (1950). These trees (*Q. pseudosuber* Desf.) with lanceolate and serrate leaves, that can develop a corky bark, are common in the southern and western Iberian Peninsula and received several names by separate authors. For example, Webb (1838) relates it to *Q. hispanica*, while Vicioso (1950) brings the concept of *Q. lusitanica* subsp. *broteroi* var. *lanceolata* C. Vicioso (1950: 112), and in Vila-Viçosa *et al.* (2014) it was described as a new species (*Q. gaditana* F.M. Vázquez, C. Pinto-Gomes & C. Vila-Viçosa). However, this taxon is enclosed in the morphological plasticity of *Q. faginea*.

In the present study, the observation of the sheets preserved in P-Desf led to the conclusion that the lectotype of *Q. pseudosuber* corresponds to *Q. faginea*. (Figure 9; P-Desf P00667227! (left specimen); http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667227). This conclusion was achieved by following the recent study of the historical types of the Iberian oaks described by Lamarck (Vazquez *et al.*, 2020). This latter study helped to comprehend the extensive morphological plasticity and biogeographic outreach of *Q. faginea*, being conspecific of the P-Desf mentioned specimen (P00667227!). The name *Q. pseudosuber* has been traditionally synonymized with *Q. ×hispanica* Lam. and *Q. ×pseudosuber* Santi, both of which belong to subg. *Cerris* (Hipp *et al.*, 2020) and to the concept of *Q. ×crenata* L., as priority name (Cristofolini *et al.*, 2017).

The trichome analysis performed in this study (see Figure 10), confirms the presence of a single stellate indumentum with a high variation on the trichome ray length (100-230 µm). Thus we chose the left specimen (Figure 9 - P-Desf P00320363-798!; http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320363), while the right exemplar presents a double indumentum of the same type of stellate trichomes, plus the floccose-fasciculate, yellowish to orangish and fuzzy indumentum typical from *Q. canariensis*, especially on the midrib and secondary nerves. Thus, this exemplar was excluded, as it corresponds to a putative hybrid between *Q. faginea* and *Q. canariensis*.



Figure 9 - Lectotype of *Quercus pseudosuber* Desf. (P-Desf P00667227!; left specimen (790))

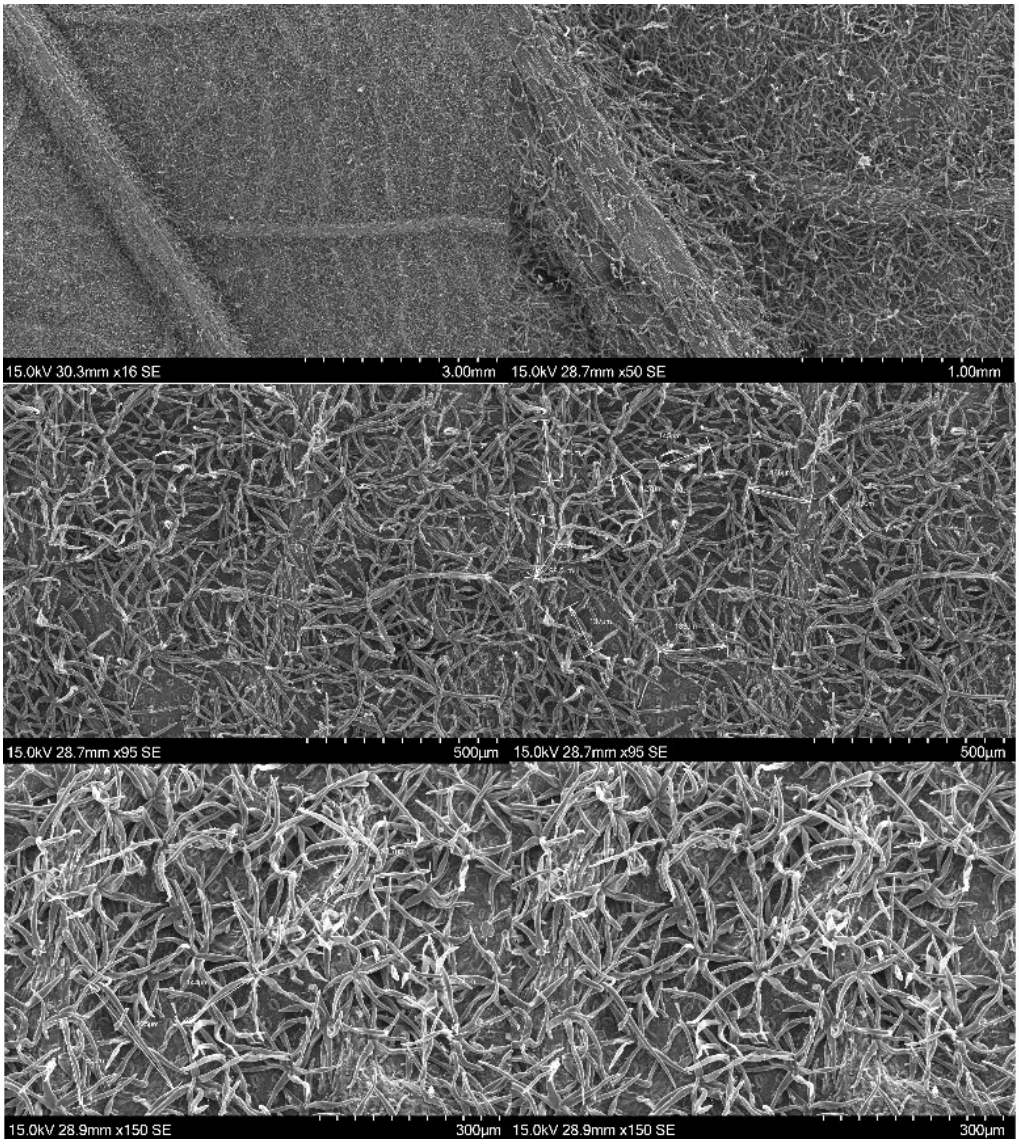


Figure 10 - SEM imagery of the abaxial leaf surface indumentum from *Q. pseudosuber* Desf. (P-Desf P00667227-790!; left specimen), revealing a single indumentum of stellate trichomes with large rays (100-230 µm).

3.5. Concluding remarks

This work reveals that the thorough review and examination of classic and personal herbaria is essential for accurate species delimitation, and nomenclatural endorsements, with special implications to the oak forest biogeography of the Mediterranean basin. This exercise is especially fundamental for continuing to explore the realms of evolution and plasticity of oaks, and can bring new biogeographic insights and updates, that are otherwise elusive, following prompt typifications and synonyms. This constructive exploration and incorporation of new insights are especially important in groups of species with blurred species boundaries still being established by modern phylogenetic

tools. Also, we recognize the importance of establishing and addressing the correct species names with a newly circumscribed biogeography, which influences the accurate conservation status of significant groups of oaks (ex: Sect. *Ilex* and *Quercus*). This is particularly fundamental for Mediterranean forests, which is a keystone biome that is severely threatened by Anthropocenic land use and climate change.

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3.6. References

Alcaraz C. 1989. Contribution à l'étude des groupements à Quercus ilex et Quercus faginea subsp. tlemcenensis, des monts de Tlemcen (Algérie). *Ecologia mediterranea* **15**(3): 15-32.

Amo M. 1861. *Memoria sobre la distribución geográfica de las familias de las plantas Crucíferas, Leguminosas, Rosáceas, Salsoláceas, Amentaceas, Coníferas y Gramíneas de la Peninsula Ibérica*. Madrid: Imprenta y librería de don Eusebio Aguado.

Barbero M, Quézel P, Rivas-Martínez S. 1981. Contribution à l'étude des groupements forestiers et préforestiers du Maroc. *Phytocoenologia*: 311-412.

Battandier JA. 1890. *Flore de l'Algérie: contenant la description de toutes les plantes signalées jusqu'a ce jour comme spontanées en Algérie et catalogue des plantes du Maroc*: Typographie Adolphe Jourdan.

Bellard C, Leclerc C, Leroy B, Bakkenes M, Veloz S, Thuiller W, Courchamp F. 2014. Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography* **23**(12): 1376-1386.

Benabdellah M-A, Amrani S-M, Elhaitoum A, Ollier S. 2010. Analyse phytoécologique des groupements à thuya (Tetraclinis articulata (Vahl) Masters) et à chêne vert (Quercus rotundifolia Lam.) dans les monts de Tlemcen (Algérie occidentale). *Ecologia mediterranea* **36**(2): 97-120.

Benabid A. 1982. Bref aperçu sur la zonation altitudinale de la végétation climacique du Maroc. *Ecologia mediterranea* **8**(1): 301-315.

Biondi E, Casavecchia S, Gigante D. 2003. Contribution to the syntaxonomic knowledge of the Quercus ilex L. woods of the Central European Mediterranean Basin. *Fitosociologia* **40**(1): 129-156.

Boissier E, Reuter GF. 1842. *Diagnoses plantarum novarum hispanicarum praesertim in Castella nova lectarum*: Typis Ferdinandi Ramboz.

Burger WC. 1975. The species concept in Quercus. *Taxon*: 45-50.

Cannon CH, Petit RJ. 2020. The oak syngameon: more than the sum of its parts. *New Phytologist* **226**(4): 978-983.

Capelo J, Costa JC. 2005. Quercus rivasmartinezii, uma espécie autónoma de carvalho, endémica de Portugal. *Silva Lusitana* **13**(2): 268-269.

Carrero C, Jerome D, Beckman E, Byrne A, Coombes A, Deng M, González-Rodríguez A, Hoang V, Khoo E, Nguyen N. 2020. The red list of oaks 2020. *The Morton Arboretum: Lisle, IL, USA*: 11-12.

Chkhichekh A, El Aboudi A, Aafi A, Wahid N, Benabid A. 2015. A contribution to the knowledge of the Moroccan forest ecosystems: association of Quercetum rotundifolio-suberis ass. nova in the Central Plateau of Morocco. *Plant Sociology* **52**(2): 57-68.

Cody ML. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions.

Cristofolini G, Managlia A, Crema S. 2017. Quercus crenata–the correct if long-forgotten name of the hybrid Quercus cerris× Quercus suber. *Israel Journal of Plant Sciences*: 1-7.

Denk T, Grimm GW, Manos PS, Deng M, Hipp AL. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Desfontaines R 1791. Observations sur le chêne Ballota ou à glands doux du Mont-Atlas. In: (France) Ards ed. *Histoire de l'Académie royale des sciences, avec les mémoires de mathématique et de physique*. Paris: Du Pont, 394-399

Desfontaines R. 1799. *Flora Atlantica, sive Historia Plantarum, quae in Atlante, Agro tunetano et algeriensi crescunt*: Panckouckes.

Di Pietro R, Conte AL, Di Marzio P, Gianguzzi L, Spampinato G, Caldarella O, Fortini P. 2020. A multivariate morphometric analysis of diagnostic traits in southern Italy and Sicily pubescent oaks. *Folia Geobotanica* **55**(3): 163-183.

Djellouli Y 1992. The Algerian Communities of Quercus Faginea Lamk. Distribution, Ecology and Phytosociology. Degradation and Preservation. a Case Study. *Responses of Forest Ecosystems to Environmental Changes*: Springer, 861-862.

Douaihy B, Saliba C, Stephan J, Simeone MC, Cardoni S, Farhat P, Bou Dagher Kharrat M. 2020. Tracking diversity and evolutionary pathways of Lebanese oak taxa through plastome analyses. *Botany Letters* **167**(3): 315-330.

Ferrer-Galego PP, Sáez L. 2019. Type designation of the oaks Quercus ballota and Q. rotundifolia (Fagaceae). *Nordic Journal of Botany* **37**(6).

Franco JA 1990. Quercus L. In: S. C, al. e eds. *Flora Iberica, (Plantanaceae-Plumbaginaceae [Partim])*. Madrid: Real Jardín Botánico, CSIC, pp. 15-36.

Grant V 1981. Plant speciation. *Plant Speciation*: Columbia university press.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hipp AL. 2015. Should hybridization make us skeptical of the oak phylogeny. *International Oak Journal* **26**: 9-18.

Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl AA, Deng M, Denk T, Fitz-Gibbon S. 2020. Genomic landscape of the global oak phylogeny. *New Phytologist* **226**(4): 1198-1212.

Jiang X-L, Hipp AL, Deng M, Su T, Zhou Z-K, Yan M-X. 2019. East Asian origins of European holly oaks (Quercus section Ilex Loudon) via the Tibet-Himalaya. *Journal of Biogeography* **46**(10): 2203-2214.

Labillardière JJH. 1812. *Icones plantarum Syriae rariorum. Decas quinta et ultima*. Paris: Huzard.

Lamarck JB. 1785. *Encyclopédie méthodique. Botanique*. Paris: Panckoucke.

Linnaeus C. 1753. *Species Plantarum*. Stockholm: Impensis Laurentii Salvii.

Lumaret R, Mir C, Michaud H, Raynal V. 2002. Phylogeographical variation of chloroplast DNA in holm oak (Quercus ilex L.). *Molecular Ecology* **11**(11): 2327-2336.

Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). *Molecular phylogenetics and evolution* **12**(3): 333-349.

Martinoli G. 1953. La Quercus coccifera L. var. imbricata DC. in Sardegna e suo significato fitogeografico. *Plant Biosystems* **60**(3): 518-564.

Meddour R, Meddour-Sahar O, Zeraia L, Mucina L. 2017. Syntaxonomic synopsis of the forest and tall scrub vegetation of Northern Algeria. *Lazaroa* **38**(2): 127-163.

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C 2011. Global biodiversity conservation: the critical role of hotspots. *Biodiversity hotspots*: Springer, 3-22.

Pham KK, Hipp AL, Manos PS, Cronn RC. 2017. A time and a place for everything: phylogenetic history and geography as joint predictors of oak plastome phylogeny. *Genome* **60**(9): 720-732.

Quézel P, Barbero M, Benabid A. 1987. Contribution à l'étude des groupements forestiers et pré-forestiers du Haut Atlas Oriental (Maroc). *Ecologia mediterranea* **13**(1): 107-117.

Quézel P, Barbero M, Benabid A, Rivas-Martínez S. 1992. Contribution a l'étude des groupements forestiers et pré-forestiers du Maroc oriental.

Regato P. 2001. The Mediterranean Forests, a New Conservation Strategy. *WWF-MedPO Ed, Rome*.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Saénz de Rivas C. 1967. Estudios sobre Quercus ilex L. y Quercus rotundifolia Lamk. . *Annales del Instituto Botanico de A.J. Cavanilles* **2**: 243-262.

Sampaio G. 1909. Flora vascular de Odemira. *Boletim da Sociedade Broteriana* **24**: 7-132.

Sampaio G. 1910. *Manual da Flora Portugueza*. Porto: Universidade do Porto.

Santi G. 1795. *Viaggio primo per la Toscana. Viaggio al Monte Amiata*. Pisa: Multigrafica.

Schwarz O 1993. Quercus L. In: al. TTe ed. *Flora Europaea*. Cambridge: Cambridge University Press., 72-76.

Spach É. 1842. *Histoire naturelle des végétaux: Phanérogames. Vol. 11. Librairie encyclopédique de Roret, Paris*. Paris.

Taborda-de-Morais A. 1940. Novas Áreas da Fitogeografia Portuguesa. *Boletim da Sociedade Broteriana* **14**(2): 97-138.

Taleb MS, Fennane M. 2019. *Vascular plant communities of Morocco*: Springer.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

Turland N, Wiersema J, Barrie F, Greuter W, Hawksworth D, Herendeen P, Knapp S, Kusber W-H, Li D-Z, Marhold K. 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017.

Van Valen L. 1976. Ecological species, multispecies, and oaks. *Taxon*: 233-239.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vazquez FM, Coombes A, Almeida R, Garcia-Alonso D, Marquez-Garcia F, Vila-Vicosa C. 2020. Lectotypification of names of Quercus spp.(Fagaceae) described by Lamarck from the Iberian Peninsula. *Phytotaxa* **455**(3): 205–213-205–213.

Vázquez FM, Coombes AJ. 2017. (2569) Proposal to conserve the name Quercus ilex (Fagaceae) with a conserved type. *Taxon* **66**(6): 1473-1475.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Vereecke P 2021. Quercus obtecta's hidden epithet uncovered. .In Blogs. IOS. *Patrick Vereecke's Blog*: International Oak Society.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C, Arraiano-Castilho, R., Hipp, A., Vázquez, F.M., Almeida, R., García, C., Beja-Pereira, A. & Azevedo, H. 2021. RAD-Seq unveils the phylogenetic backbone of the Iberian white oak (Quercus L. section Quercus) syngameon.In Pérez Badia RM, J.C. . *First Spanish Botanical Society Congress (SEBOT). Sociedad Española de Botanica*. Toledo. 175.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Webb P. 1838. *Iter Hispaniense.* Paris: Béthune and Plon.

Willdenow CL. 1809. *Enumeratio plantarum Horti Regii Berolinensis*. Berlin: Taberna libraria Scholae Realis.

SECTION B

Biogeography and Conservation of southern European white oaks

Chapter 4.

Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe

Carlos Vila-Viçosa [1,2,3,*], João Gonçalves[1,2], João Honrado[1,3], Ângela Lomba[1], Rubim S. Almeida[1,2,3], Francisco Maria Vázquez[4], Cristina García[1,5] (2020) *Scientific Reports* 10, 21598
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[1] CIBIO (Research Center in Biodiversity and Genetic Resources) - InBIO (Research Network in Biodiversity and Evolutionary Biology), University of Porto. Campus Agrário de Vairão; Rua Padre Armando Quintas; 4485-661 Vairão; Portugal
[2] MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto – Herbário PO, Universidade do Porto. Praça Gomes Teixeira, 4099-002, Porto, Portugal.
[3] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal.
[4] CICYTEX - Centro de Investigaciones Científicas y Tecnológicas de Extremadura; Agricultural Research Centre, Finca La Orden, Valdesequera; Ctra. A-V, Km372, 06187 Guadajira, Badajoz, España.
[5] Department of Evolution, Ecology and Behaviour, Institute of Integrative Biology (IIB), University of Liverpool, Bioscience Building, Liverpool, L69 7ZB, UK

4.1. Abstract

Marcescent forests are ecotones distributed across southern Europe that host increased levels of biodiversity, but their persistence is threatened by global change. Here we study the range dynamics of these forests in the Iberian Peninsula (IP) during the Late Quaternary, a period of profound climate and anthropic changes. We modeled and compared the distribution of eight oak taxa for the present and two paleoclimatic environments, the Last Glacial Maximum (LGM, ~ 21 ky) and the Mid-Holocene (MH, ~ 6 ky). Presence records were combined with bioclimatic and topographic data in an ensemble modelling framework to obtain spatial projections for present and past conditions across taxa. Substantial distribution shifts were projected between the three studied periods, that were explained by precipitation, winter cold and terrain ruggedness. Results were congruent with paleoclimatic records of the IP and showed that range shifts of these contact zones concurred with range dynamics of both Submediterranean and Temperate oaks. Notably, the distribution ranges of hybrid oaks and marcescent forests matched throughout the late Quaternary. This study contributes to unveil the complex Late-Quaternary biogeography of the ecotone belt occupied by marcescent forests and, more broadly, of Mediterranean oaks. Improved knowledge of species' responses to climate dynamics will allow us to anticipate and manage future range shifts driven by climate change.

4.2. Introduction

Ecotones are transitional areas between contrasting adjacent ecological systems integrating ecological features from neighbor regions (Hufkens *et al.*, 2009). They host complex and highly diverse communities that combine endemic species and those from adjacent neighboring zones that typically use these areas as refugia when environmental changes challenge their persistence across their native ranges (De Dios *et al.*, 2006). This combination of species makes ecotones hotspots of biodiversity and, therefore, they are of utmost importance if we are to preserve biodiversity in a changing world (Anderson & Stebbins Jr, 1954; Arnold, 1992; Risser, 1993). Although the distribution and extent of ecotones have changed widely over millennia in response to climate change (Weaver & Albertson, 1956), we still ignore whether and past climate changes have shaped the current distribution of species inhabiting ecotones.

Marcescent forests are ecotones located in the transition between temperate areas, with cold winters and mild rainy summers and Mediterranean ones, with dry and hot summers. They occur in the European Southern Peninsulas, through the Mediterranean Basin, including North Africa and Middle East regions (García-Mijangos *et al.*, 2015; Rivas-Martínez *et al.*, 2017). Marcescence, i.e., the absence of leaf fall abscission, is a life-history trait characteristic of tree species from ecotones between contrasted climatic zones, such as those across Temperate and Mediterranean Europe (Tschan & Denk, 2012; García-Mijangos *et al.*, 2015). Leaf retention was firstly interpreted as an adaptation to cold climates that would allow a direct uptake of soil minerals back to the tree (Otto & Nilsson, 1981). Further, marcescence proved to be adaptive in areas with summer drought and winter frosts by protecting leaf buds from desiccation and extreme cold (De Dios *et al.*, 2009). Despite the unclear adaptative value of marcescence, leaf retention is a trait highly responsive to environmental conditions that control distributional range fluctuations in response to climate changes (Greenwood, 2005).

Previous biogeographic studies in the Iberian Peninsula, a well-known hotspot of European and global biodiversity, confine the distribution of marcescent woodlands to the submediterranean bioclimatic belt, where these forests are fed by moderate summer precipitation, at least during one month of the dry season (De Dios *et al.*, 2006; De Dios *et al.*, 2009; García-Mijangos *et al.*, 2015). Such mild summers allow marcescent forests to host warm-temperate and even sub-tropical species (Svenning, 2003), acting as refugia for paleoclimatic relicts, including rare taxa that are otherwise common in the Atlantic islands (Rodrıguez-Sánchez & Arroyo, 2011). Model projections show that future climatic changes will likely hard-hit marcescent forests (De Dios *et al.*, 2009) and therefore, anticipating distributional range shifts of marcescent species in response to future climate changes is an urgent research goal. Tracking past range shifts can also improve our ability to forecast future changes. In this sense, the severe climatic conditions exhibited during cold periods in the late Pleistocene triggered massive migrations of the European flora towards the southern peninsulas, where they become confined. The Last Glacial Maximum (LGM, *ca.* 20 ky) was one of the most critical periods of the Quaternary for forest persistence because of their low temperatures and water availability (Lowe & Walker, 1984). Then, during the Bølling–Allerød period, the ice sheets retreated and the onset of the temperate and moister climate and mild winters triggered the expansion of Temperate and Mediterranean forest at the start of the late glacial (13 to 10 ky), interrupted during the Younger Dryas (12.9 to 11.7 ky). These forests recovered and achieved their maximum extent at the Early to Middle Holocene (*ca*. 6 ky) depending on the geographical location (Carrión *et al.*, 2010).

The magnitude of the distribution range shifts that marcescent forests have undergone in response to past climate changes is still poorly understood. We currently ignore the biogeographic trajectories that co-occurring oak species inhabiting this ecotone experienced in response to climate changes during the Late Quaternary. This is partly because most studies aimed to delineate past distributional ranges are based on fossil pollen records that provide a broad depiction of plant communities but fail to distinguish between deciduous oak species (Tzedakis, 1994; Muthreich *et al.*, 2020). Recent approaches based on species distribution modeling (SDM) can provide new insights to advance our understanding of the biogeographic past trajectories (Svenning *et al.*, 2011; Forester *et al.*, 2013; Maguire *et al.*, 2015) (https://www.nature.com/articles/s41598-020-78576-9 - ref-CR19). This is especially important to transiently co-occurring oak species at the boundary of two biogeographic regions in Southern Europe. This study aims to elucidate the late-Quaternary dynamics of the Temperate-Mediterranean transition in southern Europe by applying correlative SDMs to hindcast the past distribution of eighth oaks (seven marcescent and one deciduous) distributed across the Iberian Peninsula as model taxa. Specifically, we:

(i) Applied correlative species distribution models to identify the main climatic factors determining the current distribution ranges for each studied species;

(ii) Hindcasted projections of each species' past distribution and quantify distribution range shifts in response to climate changes;

(iii) Tracked the distribution shifts of oaks distributed across the submediterranean belt in the Iberian Peninsula based on the SDM's, and compare these shifts to those observed for temperate and mediterranean oak species; and

(iv) Compared current and past distributional ranges of parental species with the known occurrence of hybrids to infer ancient contact zones and the persistence or turn-over of hybrid-species.

We further discuss the implications of our results for preserving the biodiversity of marcescent forests that occupy the Temperate-Mediterranean transition in southern Europe in the face of projected climate change.

4.3. Material and Methods

4.3.1. Study area

The Iberian Peninsula, located in southwestern Europe and with a total area of 583,832 km^2 (Figure 1), holds a highly diverse geological history (Loidi, 2017) and a well-documented late Holocene climatic influence (Rodríguez-Sánchez *et al.*, 2010). The present climate ranges from dry Mediterranean in the Southeast to wet Temperate Atlantic in the North (Rivas-Martínez *et al.*, 2017). The former is considered to have a Submediterranean variant that represents 65.64% of its total area in the peninsula, where at least in one summer month, the average of rainfall in millimeters is 2.8 times lower than the average temperature. Under these conditions marcescent forests constitute the natural potential vegetation (De Dios *et al.*, 2009; García-Mijangos *et al.*, 2015; Rivas-Martínez *et al.*, 2017). Due to its high edaphoclimatic heterogeneity, the Iberian Peninsula is a major hotspot of European plant diversity, hosting 54% of all European species, with 22.7% percentage of endemicity, and a remarkable number of 21 endemic genera (Aedo *et al.*, 2017).

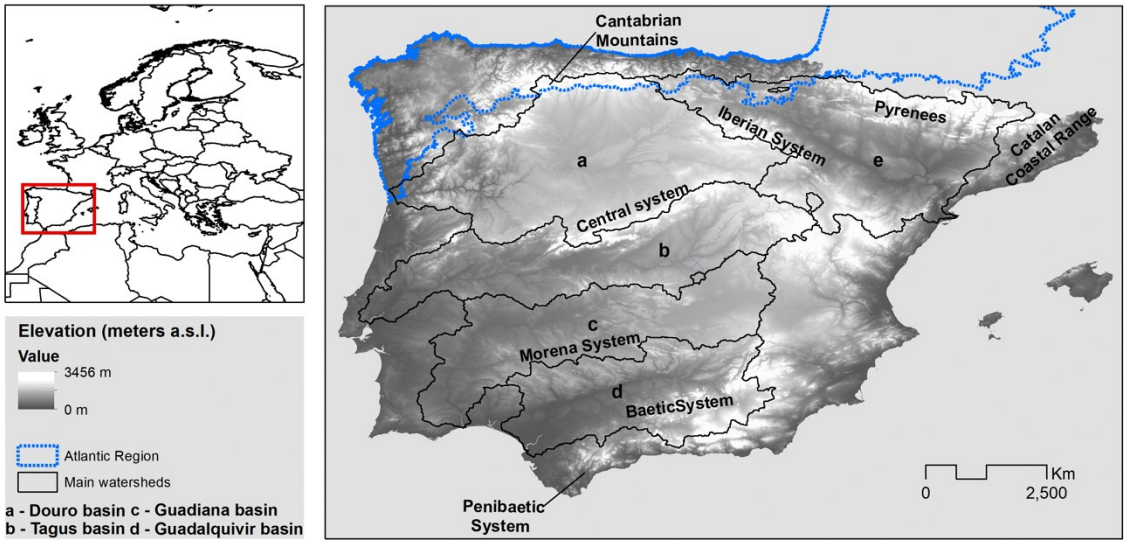


Figure 1 - Study area (Iberian Peninsula) European context (left), the boundary of the Atlantic region highlighted in blue (right) and major river basins and mountain systems.

4.3.2. Focal taxa and occurrence data

The European white oaks (Section *Quercus*) (Denk *et al.*, 2017) include a group traditionally segregated as a subsection (*Galliferae* (Spach) Guerke) (Gürke, 1897;

Tschan & Denk, 2012) that contains a group of oak species, considered strictly marcescent, with a broad (though disjoint) distribution across the Mediterranean Basin, from the Middle East to the Western Mediterranean region (Tschan & Denk, 2012). Five taxa belonging to this group (*Quercus broteroi, Q. canariensis, Q. faginea, Q. lusitanica*, including one hybrid *Q.* × *marianica*) plus two roburoid oaks (*Q. estremadurensis* and *Q. robur*) and the hybrid between them and the previous group (*Q.* × *coutinhoi*) were selected as focal taxa totalling eight taxa (Supplementary Note S1; Supplementary Figure S2).

Occurrence data was gathered through extensive fieldwork in Western Iberian Peninsula (since 2005), plus literature and herbaria review (Supplementary Table S1). Specimens were assigned to each taxa based on the authors' experience and supported in relevant literature (Vasconcellos & Franco, 1954; Rivas-Martínez & Saénz, 1991; Schwarz, 1993; Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018). To tackle taxonomic uncertainty, a thorough examination of more than 5000 vouchers of oak specimens was performed in 16 reference herbaria. This info was assessed and harmonized with other herbaria online collections and databases (Supplementary Information S1). Records for the target species (presence-only data) were aggregated to a 10 × 10 km grid (Supplementary Information S2 – Digital Annex).

4.3.3. Environmental variables (predictors)

Model development was based on regional/coarse-scale factors potentially influencing the target species distribution, related to bioclimatic and topographic descriptors of the niche environmental space.

For bioclimatic data we used the WorldClim v.1.4 dataset (URL: http://worldclim.org/version1), containing 19 bioclimatic indices, available between for the period 1960–1990 (Hijmans *et al.*, 2005). For obtaining model-based hindcasts, we used WorldClim's downscaled paleoclimate reconstructions for the Last Glacial Maximum (LGM; *ca.* 22 ky) and the Mid-Holocene (MH; *ca.* 6 ky). WorldClim infers the mean values of bioclimatic variables of the LGM based on three Global Circulation Models (GCMs) whereas it uses nine GCMs to estimate those values for current distributions. Therefore we opted for calculating the average of all available models as to reduce uncertainties linked to each specific GCM (Goberville *et al.*, 2015).

All bioclimatic data were later re-projected and re-sampled (average) to a common reference grid at 10 km spatial resolution (Datum WGS1984/UTM30N).

For portraying the 'static' influence of terrain morphology, wetness and its spatial heterogeneity on species distributions, we used the Topographic Ruggedness Index (TRI; as a proxy of slope and terrain complexity) and the Topographic Wetness Index (TWI; as a proxy of soil moisture and flow accumulation) both calculated from the SRTM (v.4) elevation data at 100 m of spatial resolution. For quantifying both variables, we aggregated/upscaled TRI and TWI values from their original resolution using the average (TRI_AVG) and the standard-deviation (TWI_STD).

We performed the pre-selection of bioclimatic variables based on preliminary models, using an exhaustive approach (similar to the one suggested by Cobos *et al.* (2019) which assessed all combinations of two variables for temperature and two variables for precipitation). This selection aimed to maximize per species model performance and parsimony (i.e. combinations with greater predictive performance where screened), balance variables linked to both temperature and precipitation, assess and prevent prediction issues related to non-analogous climatic conditions, and take advantage of previous knowledge regarding each species ecological requirements. Finally, six environmental variables were used for model fitting per species (Supplementary Table S2).

4.3.4. Modelling approach, model fitting and evaluation

Species Distribution Models (SDMs) were developed using the *biomod2* R package, which applies a multi-technique ensemble forecasting approach to analyze species-environment relations and to obtain spatiotemporal predictions (Thuiller *et al.*, 2009). Models were fitted using ten modelling techniques: GLM (Generalized Linear Models); GBM (Generalized Boosted Models); GAM (Generalized Additive Models); CTA (Classification Tree Analysis); ANN (Artificial Neural Networks); FDA (Flexible Discriminant Analysis); MARS (Multivariate Adaptive Regression Splines); RF (Random Forests); MAXENT.Phillips and MAXENT.Tsuruoka (Maximum Entropy Models) currently available in *biomod2*. Default parameters were used (with the exception of the smoothing degree term in GAM for Q*. canariensis*, which was set to k=2k=2 to avoid over-fitting issues (Guisan *et al.*, 2002). We only counted for presence data for focal species and therefore we obtained ten sets of randomly generated pseudo-absences

(PA), each one with ten times the number of presences to increment the representativeness of the environmental space of the study area (Barbet-Massin *et al.*, 2012). Since no previous information was assumed about species prevalence (pp), model weights were adjusted to p=0.5p=0.5 (*biomod2* default) thus giving similar weight to presences and pseudo-absences. We also verified that all species (either narrow or widespread ones) had sufficient presence records to train models following guidelines in previous research (Elith *et al.*, 2006; van Proosdij *et al.*, 2016). Holdout cross-validation was employed to evaluate the models, with 80% of the input records used for model fitting and 20% for model evaluation at each round. Twenty rounds were performed for model evaluation (plus one additional 'full calibration' round which uses all input records). For assessing model performance, the Area Under the Receiver-Operating Curve (AUC), the True-skill Statistic (TSS), and the Sensitivity and the Specificity values were calculated in *biomod2* (Thuiller et al., 2009).

Given that NT=2100NT=2100 models were fitted per species (with NT=Ntechniques×NPA_sets×Nevaluation_roundsNT=Ntechniques×NPA_sets×Nevaluation_rounds), the less performant models were filtered out before the final ensemble forecasting. Hence, we selected the top 21 models (the top 1% percentile) considering the AUC rank. Based on these top-performing models, an ensemble using the average was implemented, thus reducing inter-model uncertainty. To transform the predicted probabilities into binary predictions of suitable/unsuitable areas, we used a threshold minimizing the straight-line distance between the receiver operating curve and the upper-left corner of the unit square (Freeman & Moisen, 2008). To assess the importance of each variable in model fitting, we used *biomod2*'s internal method that calculates 1 – Pearson's correlation between reference predictions and predictions for a 'randomized' version of each variable. The highest the score the greater is the influence of a variable in model predictions. A value of zero assumes no influence of a given variable. Variable importance scores were averaged across the top-performing models.

4.3.5. Evaluating species range shift and overlap across time

After fitting the models and obtaining ensemble predictions for present conditions, we used the LGM or MH paleoclimate reconstructions of WorldClim (see above) to obtain model hindcasts for these periods. Niche conservatism (i.e., "*(…) retention of niche-related ecological traits over time.*" (Wiens *et al.*, 2010) was assumed which holds that models are reasonably transferable and thus allowing to obtain spatiotemporal

projections for past reference frames (see e.g. Wiens and Graham (2005); Wiens *et al.* (2010); Peterson (2011)). Then, we performed a spatial overlap between present and past projections to evaluate shifts in species distributions. This allowed us to identify stable areas (that remained suitable or unsuitable between time periods), gains (areas that gained environmental suitability between periods) and losses (areas that lost environmental suitability between periods). Afterwards, we spatially stacked all species distribution maps and obtained a binary matrix by extracting and transposing map values, later used to compute the Sorensen distance (Sd). Based on the Sd distance matrix, we then performed the hierarchical cluster analysis using the complete linkage method for each time step (Boccard *et al.*, 2011). This allowed to identify differences and similarities of distributions between species through time.

4.4. Results

4.4.1. Model performance and selection of environmental predictors

Selected models showed high performance scores for all species (Table 1), especially for *Quercus robur*, *Q. canariensis* and their hybrids. Model performance values (for details see Material and Methods section: *Modelling approach, model fitting and evaluation*) show that the lowest TSS values (True skill statistic bounded between [-1, 1], with values closer to one depicting better models) corresponded to *Q. faginea* (0.79) and *Q. broteroi* (0.77) up to *Q. robur* (0.98) which shows overall good to excellent model performance. The AUC (Area Under the Curve: [0, 1], values closer to one depict better models) were always above 0.96, also suggesting an excellent performance of the models. In addition, sensitivity and specificity scores (bounded between [0, 100]) were always above 85, confirming good and well-balanced performance of the models.

Table 1 - Evaluation scores per species for the ensemble of 21 top-models (TSS: True skill statistic; AUC: Area Under the Curve; Sensitivity also called true positive rate or recall; Specificity also defined as the true negative rate).

Species	TSS	AUC	Sensitivity	Specificity
Quercus robur	0.98	1.00	98.88	99.09
Quercus canariensis	0.94	0.99	100.00	94.01
Quercus × *coutinhoi*	0.93	0.99	97.67	95.53
Quercus × *marianica*	0.91	0.99	97.67	93.34
Quercus lusitanica	0.90	0.99	95.65	94.72
Quercus estremadurensis	0.88	0.98	95.52	92.66
Quercus faginea	0.79	0.97	85.71	92.87
Quercus broteroi	0.77	0.96	89.20	87.50

Bioclimatic predictors showed the highest importance scores when compared to topographic ones (Supplementary Figure S1). Exceptions were found for *Q. faginea* and *Q. canariensis*, for which the average topographic ruggedness index (TRI_AVG) was the most important variable. The contribution of variables related to the precipitation regime contributed the most to explain the present distribution of the focal species (Supplementary Figure S1), especially the precipitation of the warmest quarter (BIO_18), the annual precipitation (BIO_12), and precipitation seasonality (BIO_15). Winter cold temperatures also held substantial explanatory power, especially the Annual mean temperature (BIO_01), the Mean Temperature of Coldest Quarter (BIO_11), and Isothermality (BIO_03).

4.4.2. Changes in predicted distributions of marcescent oak species and their hybrids

When taking into account all taxa pat-present dynamics (Figure 4a), we observed an average loss of suitable areas from the LGM to the present of ca. 25%, offset by an overall gains of *ca*. 38% while about 37% of the range remained stable. From the MH to

the present, all selected oak species maintained 60% of their area, with ca. 16% of gains and ca. 23% of losses in terms of suitable area (Figures 2, 3 and 4).

Considering taxonomic groups, we observed that subsection *Galliferae* species expanded 43% of their overall area from LGM to MH, with losses of ca. 23% and 34% of their range remaining stable (Figures 2 and 4). Since the MH to the present, the range of these species remained stable for the most part (58%) (Figures 2, 3, 4 and 5). Regarding roburoid oaks, they showed limited latitudinal shifts, while the overall extension of their distribution area remained generally stable (Figures 3 and 4).

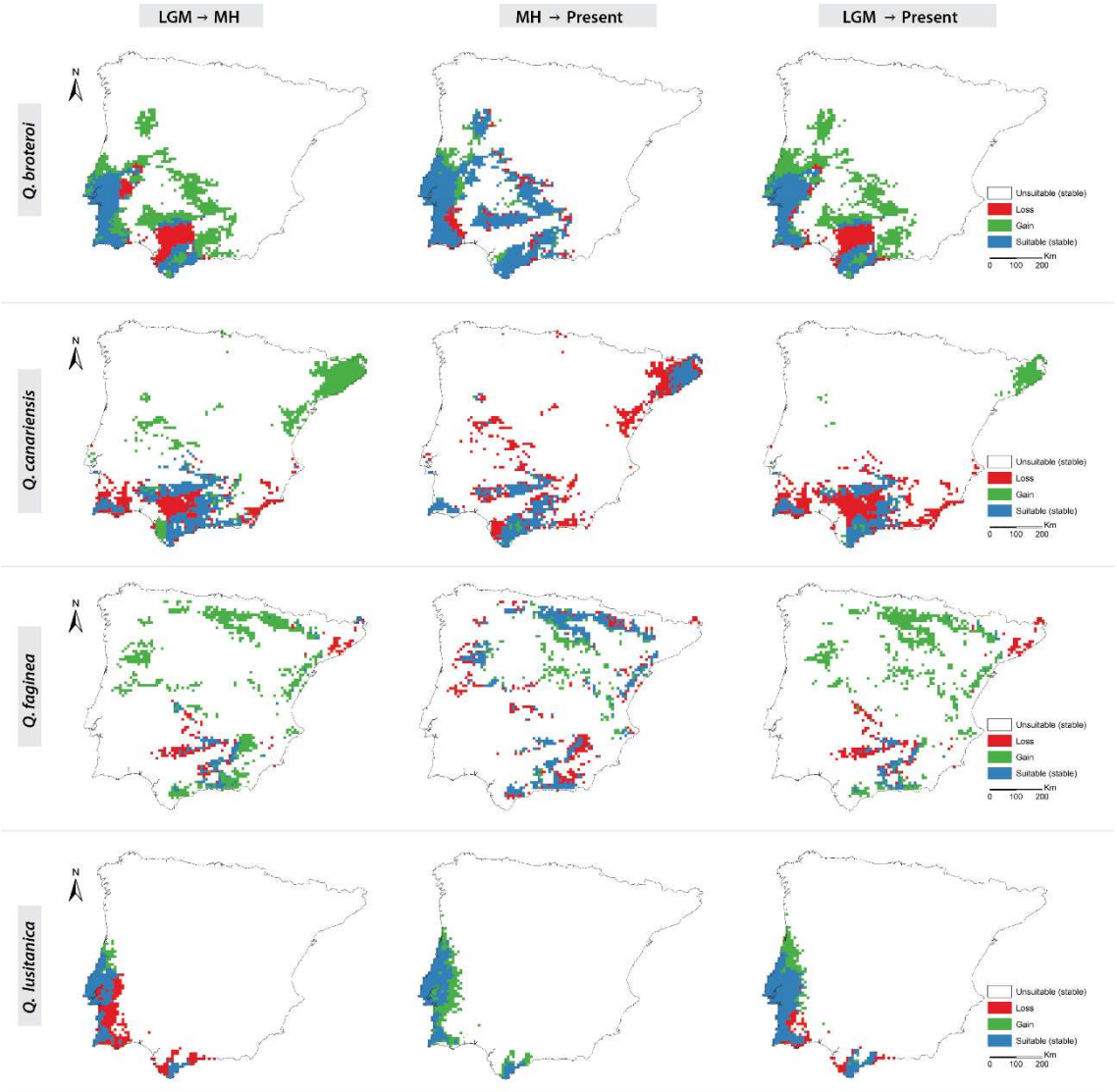


Figure 2 - Changes in predicted distributions (gained, lost, or stable) for *Galliferae* oak species for the studied periods. LGM-MH (left); MH-Present (center); LGM-Present (right). Maps were generated by JG and CVV in R v.4.0.3 (https://www.r-project.org) and assembled in ArcMap 10.5 (https://www.esri.com/en-us/arcgis).

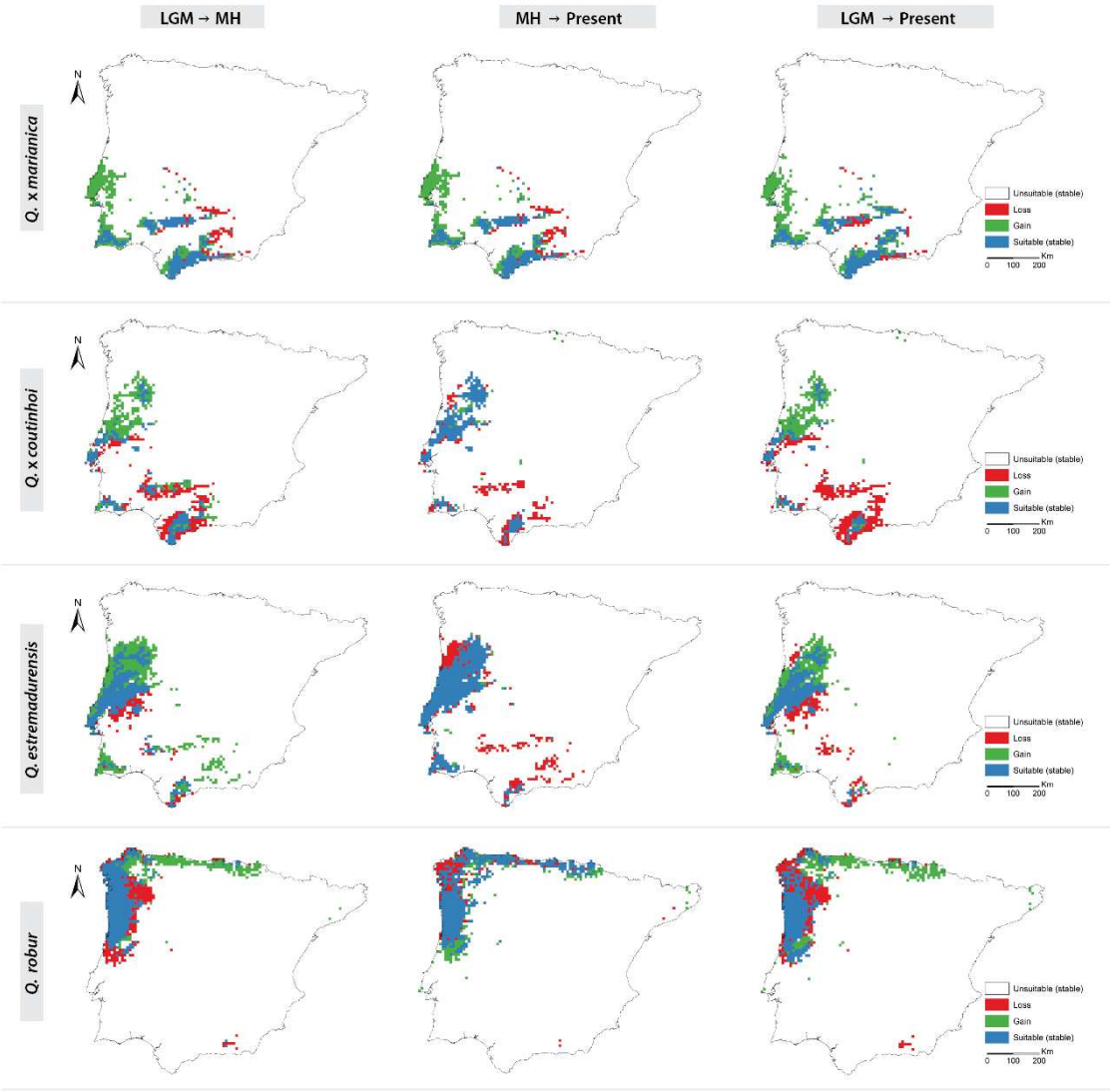


Figure 3 - Changes in the predicted distributions (gained, lost, or stable) of hybrids (*Q* × *marianica* and *Q.* × *coutinhoi*) *and* Roburoid oaks (*Q. estremadurensis* and *Q. robur*) for the studied periods. LGM-MH (left); MH-Present (center); LGM-Present (right). Maps were generated by JG and CVV in R v.4.0.3 (https://www.r-project.org) and assembled in ArcMap 10.5 (https://www.esri.com/en-us/arcgis).

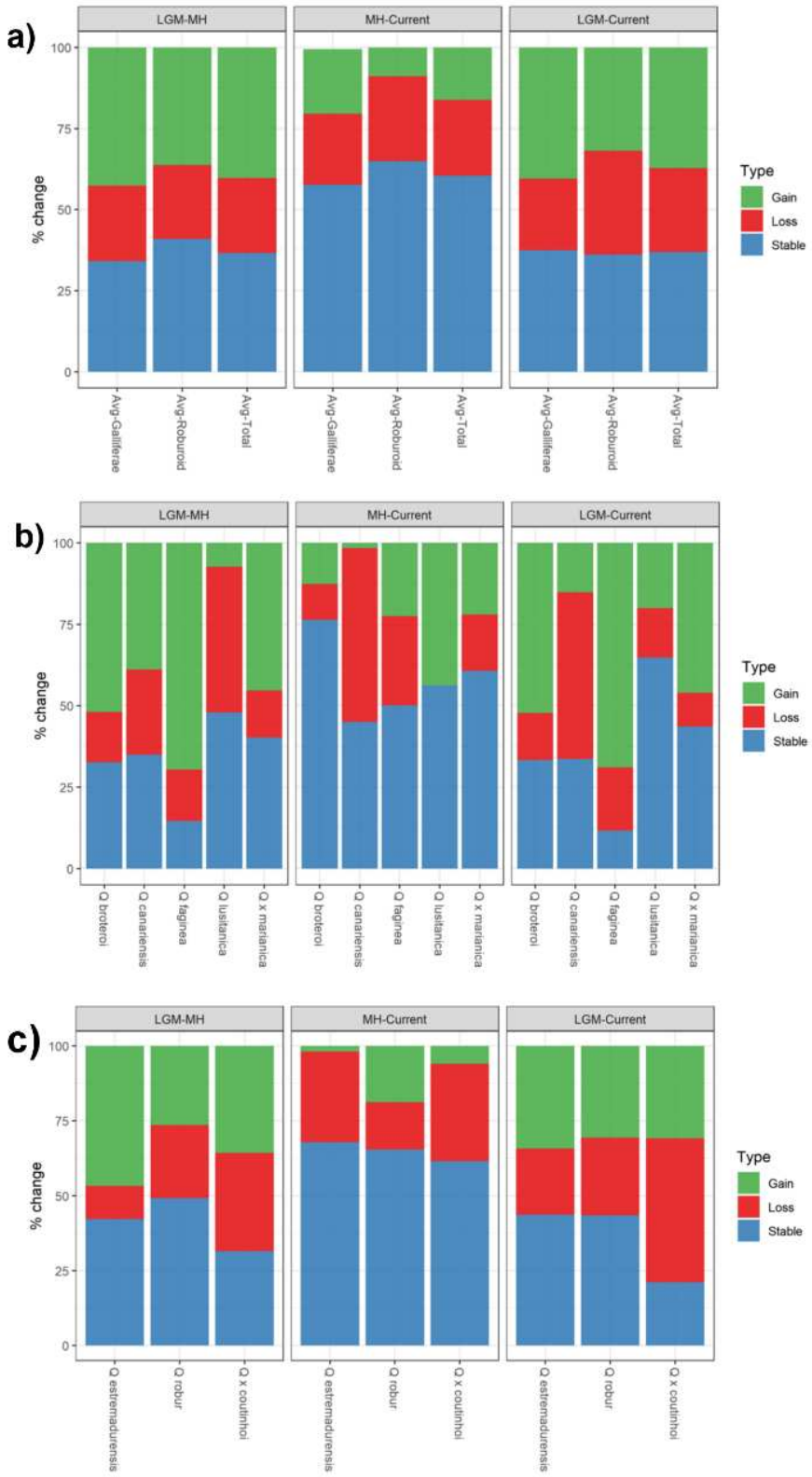


Figure 4 - Percentage of change (% change) of the predicted distributions (gained, lost, or stable) in the focal time frames. LGM-HM (left), MH-Present (center) and LGM-Present (right) (a) Broad taxonomic groups (*Galliferae*, Roburoid, and Total); (b) Individual species within the *Galliferae* group; (c) Individual species within the Roburoid group and the hybrid *Q.* × *coutinhoi*. Graphics were generated by JG and CVV in R v.4.0.3 (https://www.r-project.org).

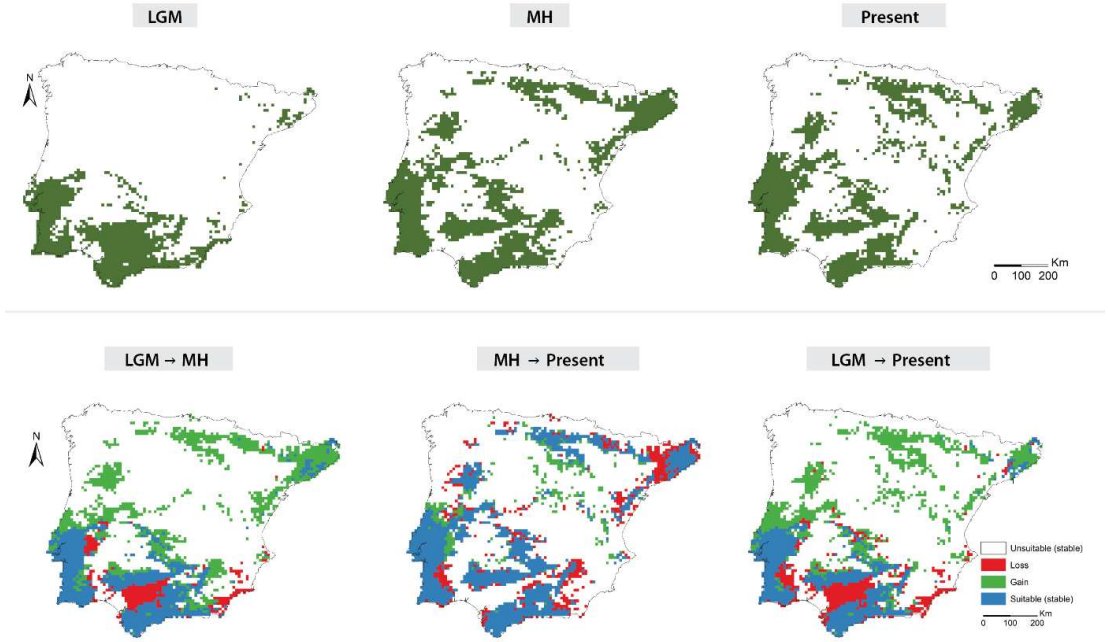


Figure 5 - Predicted distribution of the submediterranean belt in Iberian Peninsula, based in the distribution of the strictly marcescent oaks (*Q. broteroi, Q. canariensis, Q. faginea* and *Q. marianica*) (top row) and their distributional range changes across the three studied periods (bottom row). Maps were generated by JG and CVV in R v.4.0.3 (https://www.r-project.org) and assembled in ArcMap 10.5 (https://www.esri.com/en-us/arcgis).

Regarding individual species, *Quercus broteroi* had an expansion of 52% from LGM to the present, expanding from southern basins and mountains, towards the Central Iberian Peninsula and the Northern basins. This species showed the highest stability in its distribution range from MH to the present (76%) (Figures 2 and 4). In contrast, the distribution ranges of *Q. canariensis* contracted from LGM to the present (51%) with a fast-pace contraction from MH to present. Yet, this species experienced a notorious expansion of 39% towards the northeastern part of the Iberian Peninsula from LGM to MH (Figures 2 and 4). *Q. faginea* had the highest range expansion from LGM to MH (70%), mainly from Southern and Eastern Iberian Peninsula to the Northern Mountains, Central System and both Douro and Tagus basins, while 50% of the distribution area remained generally stable from MH to the present. The distribution range of *Q. lusitanica* contracted 45% from LGM to MH followed by an expansion of 44% from MH to present (Figures 2 and 4) when the species did not contract its distribution area. The distribution of *Q. estremadurensis* expanded (46%) from LGM to MH but ca. 40% of peripheral locations disappeared from MH to present. Finally, the distribution of *Q. robur* remained stable, particularly from the MH to the present (65%) (Figures 2 and 3).

As for hybrids, changes in the distribution range of *Q.* × *marianica* were very similar to those observed for the parental *Q. broteroi* (Figure 4). Changes in the distribution of *Q.* × *coutinhoi* resembled those observed for *Q. estremadurensis* expanding ca. 40% northwards and contracting ca. 30% in the southern areas (Figures 3 and 4).

Complementarily, the hierarchical clustering analysis, reflects the similarity of species projections in the three studied periods (Supplementary Figure S3).

4.4.3. Identification of contact zones

The contact zone between species of the two major groups (Roburoid oaks – Section *Quercus vs*. *Gall oaks* – Subsection *Galliferae*) was located across the Tagus basin in the LGM (with ca. 11% of overlap between distribution areas) and it expanded North in the MH, followed by a contraction of its area (ca. 20%) towards the present (Figures 3 and 5). The current distribution of *Q.* × *marianica* tracks the distribution of its parental species (*Q. canariensis* and *Q. broteroi*) that were predicted to co-exist during the LGM and MH periods mainly across southern and western areas (Figures 2 and 6).

The distribution areas of *Q. broteroi* and *Q. faginea* showed a residual overlap (3%) in the LGM located in southern Spanish mountains. This contact zone expanded in the MH to reach 12% from the expansion of *Q. faginea* towards North, which originated a second contact zone in the Douro basin (Figures 1 and 6). The distribution of the two roburoid oaks (*Q. robur* and *Q. estremadurensis*) also overlapped in the central and northern regions of Portugal. The area of this contact zone increased from 9 to 12% from LGM to the MH period and it remains generally stable since then (Figures 3 and 6).

4.5. Discussion

Our results reveal substantial distribution range shifts across Iberian Peninsula during the latest 20 ky for all studied species, suggesting a rather dynamic transition zone between two major biogeographic regions in Europe (Eurosiberian and Mediterranean). Overall, changes in precipitation and temperature during the late Quaternary were the main drivers of inferred distributional ranges. This also implies that future projected changes in precipitation regime and water balance will likely have strong effects on

species ranges, thus calling for improvements in regional and local scenarios based on global climate models.

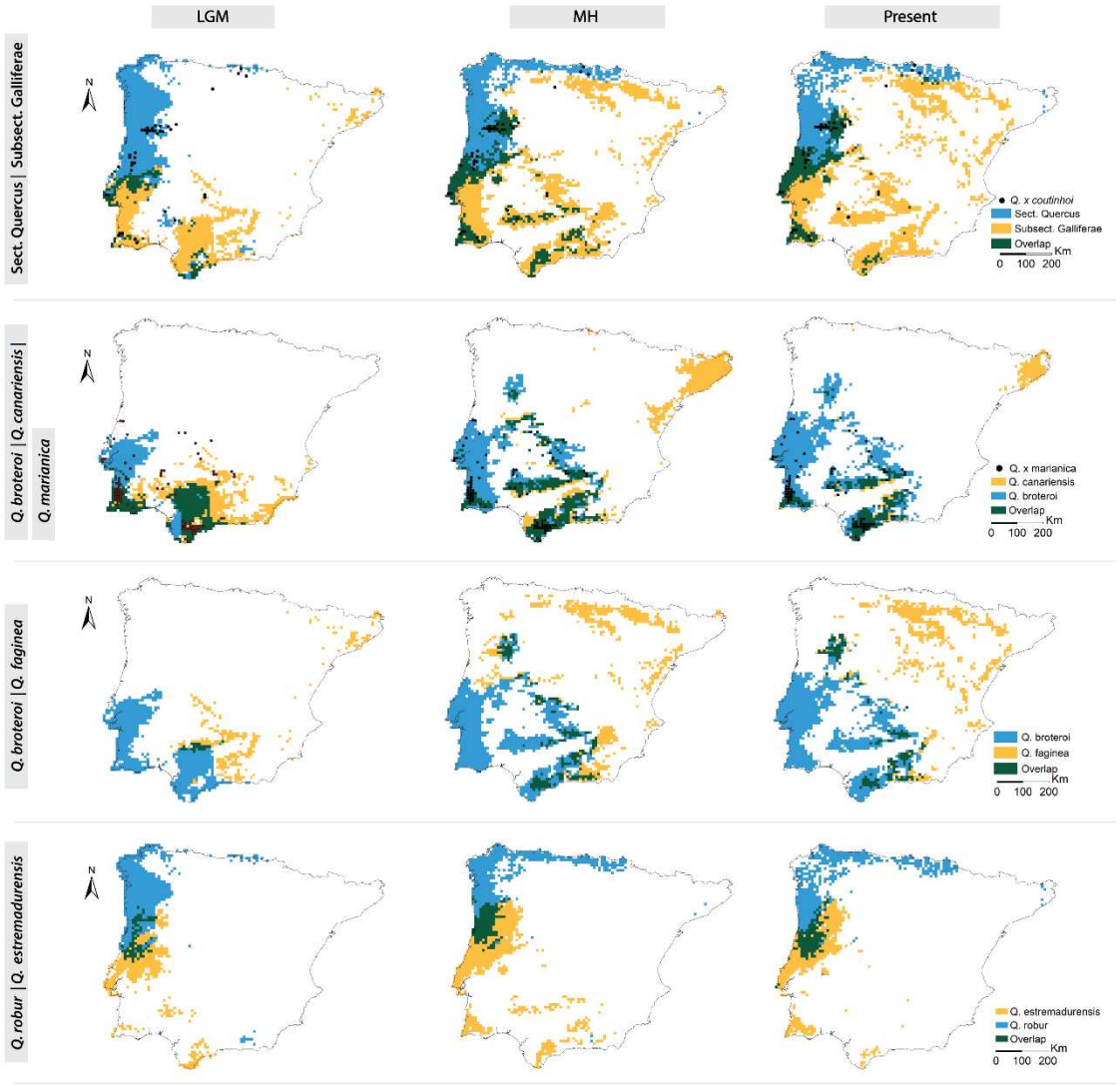


Figure 6 - Distribution of the contact zones (green) of main targeted taxa across time periods. LGM (left), MH (center), and the present (right), and current distribution of hybrids (*Q.* × *coutinhoi* and *Q.* × *marianica*). Sect. *Quercus* refers to the roburoid oaks (*Q. robur* and *Q. estremadurensis*) and Subsection *Galliferae* refers to the Gall oaks (*Q. broteroi* and *Q. faginea*) (Colours were chosen in way to enhance visual discrimination of different groups and their overlap). Maps were generated by JG and CVV in R v.4.0.3 (https://www.r-project.org) and assembled in ArcMap 10.5 (https://www.esri.com/en-us/arcgis).

We complemented previous projections on Iberian trees (Benito-Garzón *et al.*, 2007) and other studies that underline a broad association of marcescent forests with the submediterranean bioclimatic belt (De Dios *et al.*, 2006; De Dios *et al.*, 2009; García-Mijangos *et al.*, 2015). In fact, while the distribution range obtained for the deciduous *Quercus robur* closely tracked the Eurosiberian region, the distribution ranges

obtained for marcescent species (*Q. broteroi*, *Q. canariensis, Q. faginea* and *Q. marianica*) broadly corresponded to this submediterranean transition zone (Figure 5).

Our models also revealed that the distribution range of marcescent forests included the western coast of the Iberian Peninsula, an area with frequent advection fogs during summer that might compensate low annual precipitation values (De Dios *et al.*, 2009), thus favoring the expansion and establishment of marcescent forests. This overlooked source humidity has led previous biogeographic models to characterize *Q. broteroi* and *Q. canariensis* as thermophilic taxa inhabiting dry conditions (García-Mijangos *et al.*, 2015). On the contrary, they are maintained by frequent summer-fog regimes (Ward, 1952; Wheeler, 2001) that increase annual and summer precipitation and confer a submediterranean character to these areas. Also, this climatic and topographic heterogeneities favoured by small mountain ranges play a crucial role as identified across major refugia areas throughout the Mediterranean Basin (Médail & Diadema, 2009; Walas *et al.*, 2019).

The geographic patterns obtained for the different study periods are consistent with the known biogeography and dynamics of Iberian forests since the last glacial maximum (LGM) (Blanco-Castro *et al.*, 2005; Carrión *et al.*, 2010). Overall, climatic hardiness and increased annual precipitation in Southwest Iberian Peninsula during the LGM allowed the persistence of most marcescent oaks in the southern range limits of their present distribution. The distributional segregation between marcescent oaks and the deciduous *Q. robur* (Figures 2, 3 and Supplementary Figure S3) is evidenced by the range contraction of the latter between the LGM and MH, from the inland towards the Atlantic and Cantabrian coasts. This coastal expansion follows an increase in winter minimum temperatures, while the inland retreats are a response to increasing summer drought (i.e. more Mediterranean climate). Other roburoid oaks (*Q. estremadurensis* and *Q.* × *coutinhoi*) and *Q. lusitanica* follow the same general pattern.

The climatic amelioration during the MH explains most of the expansion of marcescent oaks towards Center and North Iberian Peninsula, followed by a slight contraction as the climate became drier towards the present. The present distribution of *Quercus faginea* approaches the roburoid taxa, unlike the remaining *Galliferae* oaks (Figures 2, 5 and Supplementary Figure S3). This is related with this species recent expansion through the Eurosiberian region, where it forms secondary forests in locally drier biotopes, in areas where the more favorable soils are occupied by deciduous primary forests of *Fagus sylvatica, Q. petraea* and *Q. pubescens* (Amigo *et al.*, 2017; Díaz-González & Penas, 2017). Terrain ruggedness followed by summer precipitation plays a

major role on *Q. faginea* and *Q. canariensis* distributions (Figure 2 and Supplementary Figure S1). Both are associated with increased summer precipitation, with the first expanding through interior mountainous areas, which is confirmed by the influence of precipitation and temperature seasonality, while *Q. canariensis* distribution is determined by a summer fog regime both in coastal and inland areas (Figure 2 and Supplementary Figure S1). The less fragmented distribution of *Q. canariensis* during the LGM, across southern Iberia, discloses an ancient contact between nowadays relict populations. This contact is supported by the current presence of vicariant assemblages of understory species, including relict taxa like *Frangula baetica, Cytisus baeticus, Davallia canariensis, Rhododendron ponticum* and *Myrica* spp. (Vila-Viçosa *et al.*, 2015).

Our results support ancient, but not current, sympatry between parental species during the LGM and MH at locations where their hybrids are currently present (Figure 6). The distribution of *Q.* × *marianica* tracks the distribution of *Q. canariensis* in the LGM but it progressively tracks the distribution range of its other parental species (*Q. broteroi*) during the MH and towards the present (Figure 6 and Supplementary Figure S3). This shows both adaptation towards drier conditions in face of *Q. canariensis* and expansion towards equilibrium considering the parental niches. Similarly, the spatial distribution of roburoid (*Q. estremadurensis* and *Q. robur*) and *Galliferae* parental species (*Q. broteroi* and *Q*. faginea) closely resembles the current distribution of the hybrid *Q.* × *coutinhoi* towards northern areas (Figures 3 and 6). Here, *Q. robur* may have shifted between submediterranean and temperate areas, benefitting from less severe summers and winters during the Holocene (Mauri *et al.*, 2015), which may explain the detected hybrid swarms during fieldwork in the Douro Basin and Central Portugal (Figure 1), in populations where roburoid oaks are absent.

The species-level segregation of *Q. broteroi* and *Q. faginea* is congruent with their exiguous overlap during the LGM, followed by the posterior expansion (MH) of *Q. faginea* to NW Iberia (Figures 2 and 6). The distribution of *Quercus lusitanica* is generally closer to roburoid oaks, especially in the LGM, but approaching other *Galliferae* species towards the present (Figure 5 and Supplementary Figure S3).

The projected distribution of *Q. estremadurensis* (Figure 3) is consistent with its thermophilic preferences and resembles the one obtained for *Q. canariensis* (Figure 2). This strengthens the hypothesis of *Q. estremadurensis* being a Tertiary relict oak that evolved under a subtropical paleo-environment (Vicioso, 1950; Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018). Herbaria review performed by the authors confirms the presence of this roburoid oak in northern Africa where it co-exists with other relicts such as *Q.*

canariensis and *Prunus lusitanica* (Paris Herbarium Review – Digital Annex). In contrast, the projected distribution of *Q. estremadurensis* is opposed to the well-established Eurosiberian distribution of *Q. robur* (Ülker et al., 2018). This projection dismisses any southern Iberian references of *Q. robur* enhancing the taxonomic dichotomy between these two roburoid oaks. Furthermore, the projected distribution of *Q. estremadurensis* in southwest Spain, emphasizes the role of Guadalquivir basin as a "dry" barrier for its expansion across southern Iberia (Figures 1, 3 and 6).

4.6. Conclusions

We provided insights into the late-Quaternary distribution range shifts of a set of oak species in response to past climate changes. By combining hindcast and current projections obtained from species distribution models, we provide novel insights to disentangle taxonomic uncertainties. The performance of the models and the major importance of climatic variables shows that these oaks are rather suitable model species to undergo paleo-environmental and biogeographic studies along transitional bioclimatic and biogeographic areas in southern Europe. Further, our methodology proved valid to infer the distributional range shifts of hybrid taxa that showed to be congruent with the biogeographic trajectories of their parental species. This is quite important in a group with low interspecific barriers to gene flow and, therefore, characterized by complex evolutionary and speciation patterns (Hipp, 2015; McVay *et al.*, 2017). Our work addresses a major gap in paleo-vegetation studies that typically rely on palinological data, which tend to fail in delimitating the distribution of tree species accurately, particularly in the case of deciduous oaks (Sect. *Quercus*) (Tzedakis, 1994; Muthreich *et al.*, 2020). Our study suggests that conservation efforts should target *Q. canariensis* and *Q. estremadurensis* because both taxa presently show a scattered (known and projected) distribution. In this regard, species distribution models prove useful to forecast the responses of these species to future climatic scenarios will contribute to prioritize conservation efforts.

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4.7. References

Aedo C, Buira A, Medina L, Fernández-Albert M 2017. The Iberian Vascular Flora: Richness, Endemicity and Distribution Patterns. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 101-130.

Amigo J, Rodríguez-Guitián MA, Honrado J, Alves P 2017. The lowlands and midlands of Northwestern Atlantic Iberia. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 191-250.

Anderson E, Stebbins Jr GL. 1954. Hybridization as an evolutionary stimulus. *Evolution*: 378-388.

Arnold ML. 1992. Natural hybridization as an evolutionary process. *Annual review of Ecology and Systematics*: 237-261.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**(2): 327-338.

Benito-Garzón M, Sánchez de Dios R, Sáinz Ollero H. 2007. Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography* **30**(1): 120-134.

Blanco-Castro E, Casado-Gonzáles M, Costa-Tenorio M, Escribano R, García-Antón M, Génova-Fuster M, Gómez-Mazaneque Á, Gómez-Mazaneque F, Moreno-Saiz JC, Juaristi CM, et al. 2005. *Los bosques ibéricos. Una interpretación geobotánica*. Barcelona: Editorial Planeta, Barcelona, Spain.

Boccard D, Gillet F, Legendre P. 2011. Numerical Ecology with R. Springer.

Carrión JS, Fernández S, González-Sampériz P, Gil-Romera G, Badal E, Carrión-Marco Y, López-Merino L, López-Sáez JA, Fierro E, Burjachs F. 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Review of Palaeobotany and Palynology* **162**(3): 458-475.

Castroviejo S, Aedo C, Medina L. 2006. Management of floristic information on the Internet: the Anthos solution. *Willdenowia* **36**(1): 127-137.

Cobos ME, Peterson AT, Osorio-Olvera L, Jiménez-García D. 2019. An exhaustive analysis of heuristic methods for variable selection in ecological niche modeling and species distribution modeling. *Ecological Informatics* **53**: 100983.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2006. Hybrid zones between two European oaks: a plant community approach. *Plant Ecology* **187**(1): 109-125.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology* **204**(2): 189-205.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Díaz-González TE, Penas Á 2017. The High Mountain Area of Northwestern Spain: The Cantabrian Range, the Galician-Leonese Mountains and the Bierzo Trench. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 251-321.

Elith J, Graham C, Anderson R, Dudık M, Ferrier S. 2006. Novel methods improve prediction of species' distribution models. *Ecography* **32**: 66-77.

Font X, Pérez-García N, Biurrun I, Fernández-González F, Lence C. 2012. The Iberian and Macaronesian Vegetation Information System (SIVIM, www. sivim. info), five years of online vegetation's data publishing. *Plant Sociology* **49**(2): 89-95.

Forester BR, DeChaine EG, Bunn AG. 2013. Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions* **19**(12): 1480-1495.

Franco JA 1990. Quercus L. In: S. C, al. e eds. *Flora Iberica, (Plantanaceae-Plumbaginaceae [Partim])*. Madrid: Real Jardín Botánico, CSIC, pp. 15-36.

Freeman EA, Moisen GG. 2008. A comparison of the performance of threshold criteria for binary classification in terms of predicted prevalence and kappa. *Ecological modelling* **217**(1-2): 48-58.

García-Mijangos I, Campos JA, Biurrun I, Herrera M, Loidi J 2015. Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: Box EO, Fujiwara K eds. *Warm-temperate deciduous forests around the Northern hemisphere*. London: Springer, 119-138.

Goberville E, Beaugrand G, Hautekèete NC, Piquot Y, Luczak C. 2015. Uncertainties in the projection of species distributions related to general circulation models. *Ecology and Evolution* **5**(5): 1100-1116.

Greenwood DR. 2005. Leaf form and the reconstruction of past climates. *New Phytologist* **166**(2): 355-357.

Guisan A, Edwards Jr TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological modelling* **157**(2-3): 89-100.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**(15): 1965-1978.

Hipp AL. 2015. Should hybridization make us skeptical of the oak phylogeny. *International Oak Journal* **26**: 9-18.

Holstein J. 2001. *GBIF: Global Biodiversity Information Facility*: University of Ulm.

Hufkens K, Scheunders P, Ceulemans R. 2009. Ecotones in vegetation ecology: methodologies and definitions revisited. *Ecological Research* **24**(5): 977-986.

Loidi J 2017. Introduction to the Iberian Peninsula, General Features: Geography, Geology, Name, Brief History, Land Use and Conservation. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 3-27.

Lowe JJ, Walker MJ. 1984. *Reconstructing Quaternary Environments*: London.

Maguire KC, Nieto-Lugilde D, Fitzpatrick MC, Williams JW, Blois JL. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. *Annual Review of Ecology, Evolution, and Systematics* **46**: 343-368.

Mauri A, Davis B, Collins P, Kaplan J. 2015. The climate of Europe during the Holocene: a gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science Reviews* **112**: 109-127.

McVay JD, Hipp AL, Manos PS. 2017. A genetic legacy of introgression confounds phylogeny and biogeography in oaks. *Proc. R. Soc. B* **284**(1854): 20170300.

Médail F, Diadema K. 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography* **36**(7): 1333-1345.

Muthreich F, Zimmermann B, Birks HJB, Vila-Viçosa CM, Seddon AW. 2020. Chemical variations in Quercus pollen as a tool for taxonomic identification: Implications for long-term ecological and biogeographical research. *Journal of Biogeography* **47**(6): 1298-1309.

Otto C, Nilsson LM. 1981. Why do beech and oak trees retain leaves until spring? *Oikos*: 387-390.

Pereira AJ, Francisco A, Porto M. 2016. Flora-On: Occurrence data of the vascular flora of mainland Portugal. *PhytoKeys*(69): 105.

Peterson AT. 2011. Ecological niche conservatism: A time-structured review of evidence. *Journal of Biogeography* **38**(5): 817-827.

Risser PG. 1993. Ecotones at local to regional scales from around the world. *Ecological Applications* **3**(3): 367-368.

Rivas-Martínez S, Penas A, del Río S, González T, Rivas-Sáenz S 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 29-80.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rodrıguez-Sánchez F, Arroyo J. 2011. Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past. *Climate change, ecology and systematics*: 280-303.

Rodríguez-Sánchez F, Hampe A, Jordano P, Arroyo J. 2010. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Review of Palaeobotany and Palynology* **162**(3): 507-521.

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O 1993. Quercus L. In: al. TTe ed. *Flora Europaea*. Cambridge: Cambridge University Press., 72-76.

Svenning J-C, Fløjgaard C, Marske KA, Nógues-Bravo D, Normand S. 2011. Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* **30**(21-22): 2930-2947.

Svenning JC. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology letters* **6**(7): 646-653.

Thuiller W, Lafourcade B, Engler R, Araújo MB. 2009. BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography* **32**(3): 369-373.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

Tzedakis P. 1994. Vegetation change through glacial—interglacial cycles: a long pollen sequence perspective. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **345**(1314): 403-432.

Ülker ED, Tavşanoğlu Ç, Perktaş U. 2018. Ecological niche modelling of pedunculate oak (Quercus robur) supports the 'expansion–contraction' model of Pleistocene biogeography. *Biological journal of the Linnean Society* **123**(2): 338-347.

van Proosdij AS, Sosef MS, Wieringa JJ, Raes N. 2016. Minimum required number of specimen records to develop accurate species distribution models. *Ecography* **39**(6): 542-552.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vila-Viçosa C, Vázquez FM, Mendes P, Del Rio S, Musarella C, Cano-Ortiz A, Meireles C. 2015. Syntaxonomic update on the relict groves of Mirbeck's oak (Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* **149**(3): 512-526.

Walas Ł, Sobierajska K, Ok T, Dönmez AA, Kanoğlu SS, Dagher-Kharrat MB, Douaihy B, Romo A, Stephan J, Jasińska AK. 2019. Past, present, and future geographic range of an oro-Mediterranean Tertiary relict: The juniperus drupacea case study. *Regional Environmental Change* **19**(5): 1507-1520.

Ward A. 1952. Fog at North Front, Gibraltar. *Meteorol. Mag* **81**: 272-279.

Weaver JE, Albertson FW. 1956. Grasslands of the great plains.

Wheeler D. 2001. Factors governing sunshine in south-west Iberia: A review of western Europe's sunniest region. *Weather* **56**(6): 189-197.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan Davies T, Grytnes JA, Harrison SP. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters* **13**(10): 1310-1324.

Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*: 519-539.

4.8. Supplementary Information

Supplementary Note S1

Focal taxa and occurrence data

- *Quercus broteroi* (Cout.) Rivas Mart. & C. Sáenz and *Q. faginea* Lam. were formerly considered subspecies (of *Q. faginea*) but are considered nowadays as independent taxa by the majority of Iberian botanists and experts of genus *Quercus* (Rivas-Martínez & Saénz, 1991; Vila-Viçosa *et al.*, 2014; García-Mijangos *et al.*, 2015), holding today a predominantly parapatric distribution. *Quercus broteroi* is indifferent for lithology and occupies areas with oceanic climate along the western coast , whereas *Q. faginea* is a strictly basophilous species, coping under sub-continental climates with cold winters (Franco, 1990).
- *Quercus canariensis* Willd. is a rare tree, disseminated in areas with moderate summer precipitation and/or fog condensation and mesic siliceous soils, being sympatric with *Q. broteroi* in its Southern distribution range (Vila-Viçosa *et al.*, 2015).
- To deal with taxonomic interactions and biogeographic patterns we considered the hybrids *Q.* × *marianica* C. Vicioso (*Q. canariensis* × *Q. broteroi*) to ascertain the past occurrence of *Q. canariensis* in these forests, or the breakthrough of this hybrid, departed from parental species.
- Additionally, we used the reference of *Q. estremadurensis* O. Schwarz (≡*Q. robur* subsp. *estremadurensis* (O.Schwarz) A. Camus), a relictual taxa occurring in transitional areas towards Mediterranean conditions in Southern Iberian Peninsula, presenting marcescent behavior and considered a Tertiary relictual taxon (Schwarz, 1935; Vicioso, 1950; Vila-Viçosa *et al.*, 2014).
- We add the Portuguese dwarf-oak (*Q. lusitanica* Lam.), as it shares synecological and biogeographical traits and belonging to the same infrageneric group of oaks (Subsect. *Gallifereae*) (Tschan & Denk, 2012).
- Finally, we also used broad references to *Q.* × *coutinhoi* Samp, which includes all taxonomic interactions between *Q. faginea* or *Q. broteroi* and roburoid oaks (*Q. robur* and *Q. estremadurensis*), which hybrid swarms are known from central
- and Northern Iberia.
- We add *Q. robur* to the analysis as parent species, in order to establish the comparison with a deciduous and temperate species, ecologically more demanding in terms of summer precipitation.

Supplementary Table S1

Supplementary Table S1– Focal species, their corresponding taxonomic filiation and number of available records at their native resolution (total records) and after aggregating into the 10x10 km resolution adopted for the modelling framework (standardized records).

Species	Section / Subsection	Total records	Standardized Records (10 x 10 km)
Q. broteroi	*Galliferae* (Spach) Guerke (Gürke, (1897: 68))	402	400
Q. canariensis	*Galliferae* (Spach) Guerke (Gürke, (1897: 68))	44	42
Q. ×coutinhoi	Interseccional hybrid (Sect. *Quercus* vs Subsection *Galliferae*)	43	41
Q. estremadurensis	Section *Quercus* (Denk et. al. (2017: 13)	67	67
Q. faginea	Galliferae (Spach) Guerke (Gürke, (1897: 68))	315	315
Q. lusitanica	Galliferae (Spach) Guerke (Gürke, (1897: 68))	140	140
Q. ×marianica	Galliferae (Spach) Guerke (Gürke, (1897: 68))	86	86
Q. robur	Section *Quercus* Denk et. al. (2017: 13)	2549	548
		Total: 3646	**Total 1639**

Supplementary Table S2

Supplementary Table S2 – Variables used in SDMs for each target species (BIO1 = Annual Mean Temperature; BIO3 = Isothermality; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO15 = Precipitation Seasonality; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter; TRI_AVG – Topographic Ruggedness Index average; TWI_STD – Topographic Wetness Index standard-deviation).

Species	Temperature related Bioclimatic variables					Precipitation related Bioclimatic variables				Topographic variables	
	BIO_01	BIO_03	BIO_06	BIO_07	BIO_11	BIO_12	BIO_15	BIO_18	BIO_19	TRI_AVG	TWI_STD
Q. broteroi	✓				✓	✓			✓	✓	✓
Q. canariensis	✓	✓				✓		✓		✓	✓
Q. coutinhoi	✓				✓	✓		✓		✓	✓
Q. estremadurensis	✓				✓	✓		✓		✓	✓
Q. faginea	✓			✓			✓	✓		✓	✓
Q. lusitanica		✓	✓			✓		✓		✓	✓
Q. marianica	✓				✓	✓		✓		✓	✓
Q. robur	✓		✓				✓	✓		✓	✓

Supplementary Information S1 - Herbaria list of studied physical and virtual collections (*Quercus* L) and consulted database

Studied herbaria collections (*Quercus* L.)

Herbarium Code	Institution	Location
AVE	Universidade de Aveiro	Portugal. Aveiro.
BCN	University of Barcelona	Spain. Catalonia. Barcelona
BRESA	Polytechnic Institute of Bragança - IPB	Portugal. Bragança.
COI	University of Coimbra	Portugal. Coimbra.
HSS	Research Centre of "La Orden-Valdesequera"	Spain. Extremadura. Mérida.
HVR	Universidade de Trás-os-Montes e Alto Douro	Portugal. Vila Real.
L	Naturalis	Netherlands. Leiden.

LISE		Portugal. Oeiras.
LISFA	Instituto Nacional de Investigação Agrária e Veterinária, I. P. (INIAV)	Portugal. Oeiras.
LISI	Instituto Superior de Agronomia	Portugal. Lisboa.
LISU	Museu Nacional de História Natural e da Ciência	Portugal. Lisboa.
MA	Real Jardín Botánico	Spain. Madrid.
P	Muséum National d'Histoire Naturelle	France. Paris.
PO	Museu de História Natural e da Ciência da Universidade do Porto	Portugal. Porto
SALA	Universidad de Salamanca	Spain. Salamanca.
SANT	Universidad de Santiago de Compostela	Spain. Galicia. Santiago de Compostela.
UEVH	Universidade de Évora	Portugal. Évora.

Online herbaria collections (*Quercus* L.)

Herbarium Code	Institution	Location
B	Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin	Germany. Berlin.
G	Conservatoire et Jardin botaniques de la Ville de Genève	Switzerland. Genève.
K	Royal Botanic Gardens	U.K. England. Kew.
MAIA	INIA (Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria)	Spain. Madrid.
MPU	Université de Montpellier	France. Montpellier.

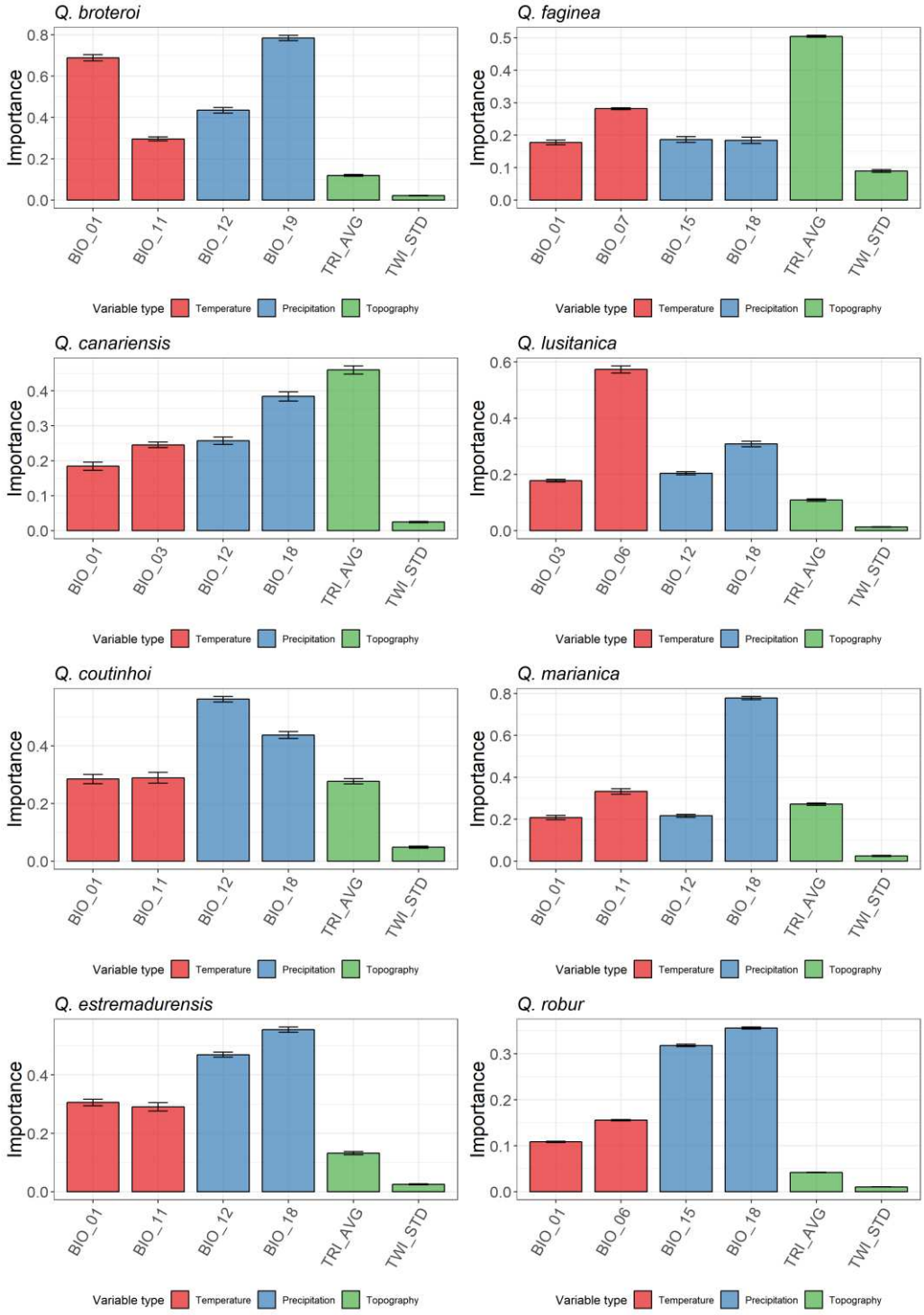
Online databases

Name	Site	Reference
ANTHOS: Spanish Plants Information System	http://www.anthos.es/	Castroviejo *et al.* (2006)
Flora-On: Flora de Portugal Interactiva	www.flora-on.pt	Pereira *et al.* (2016)
GBIF Global Biodiversity Information Facility	https://www.gbif.org/	Holstein (2001)
SIVIM: Iberian and Macaronesian Vegetation Information System	http://www.sivim.info/sivi/	Font *et al.* (2012)

Supplementary Information S2 – Digital Annex

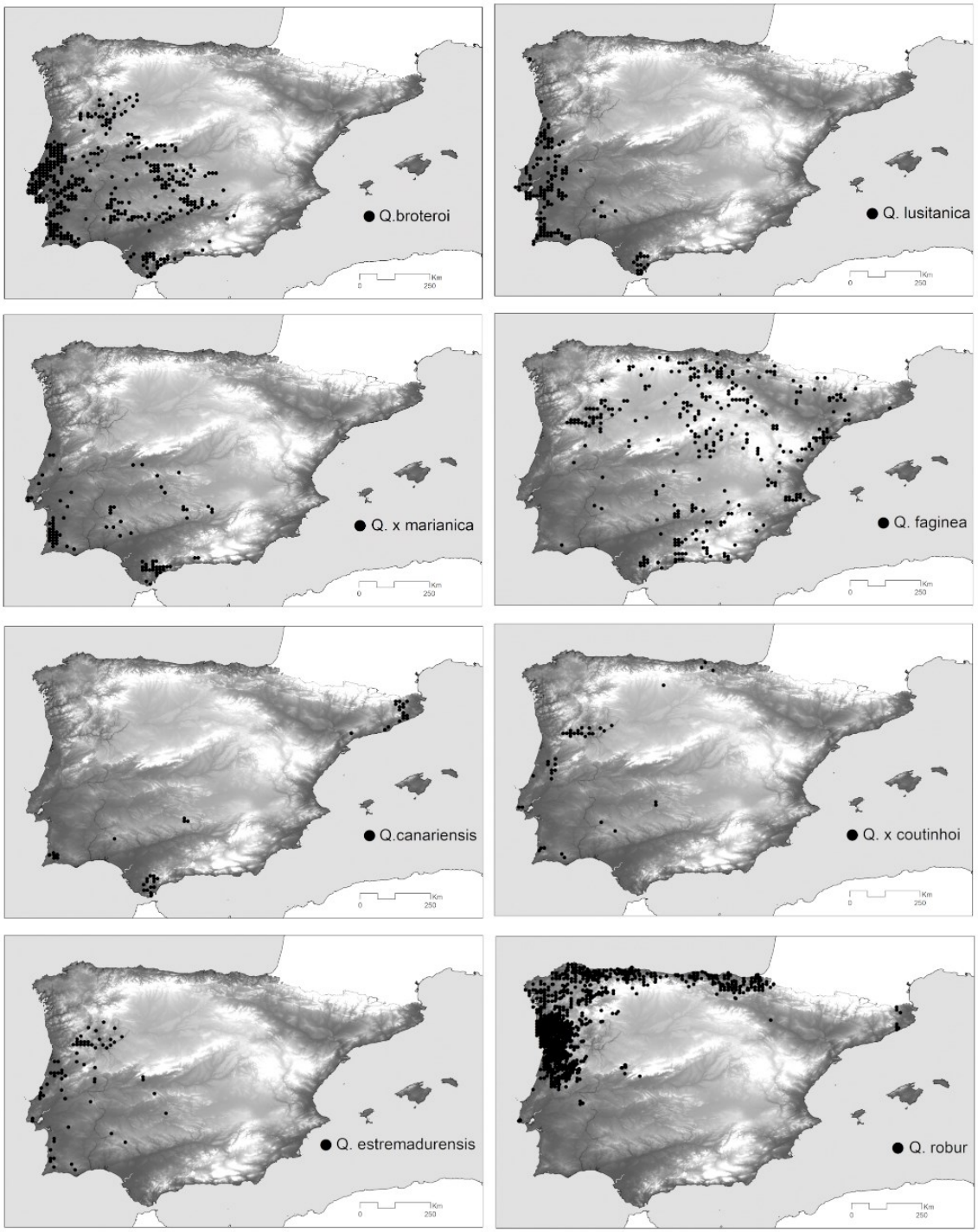
See Digital Annex section at the end of the present thesis.

Supplementary Figure S1



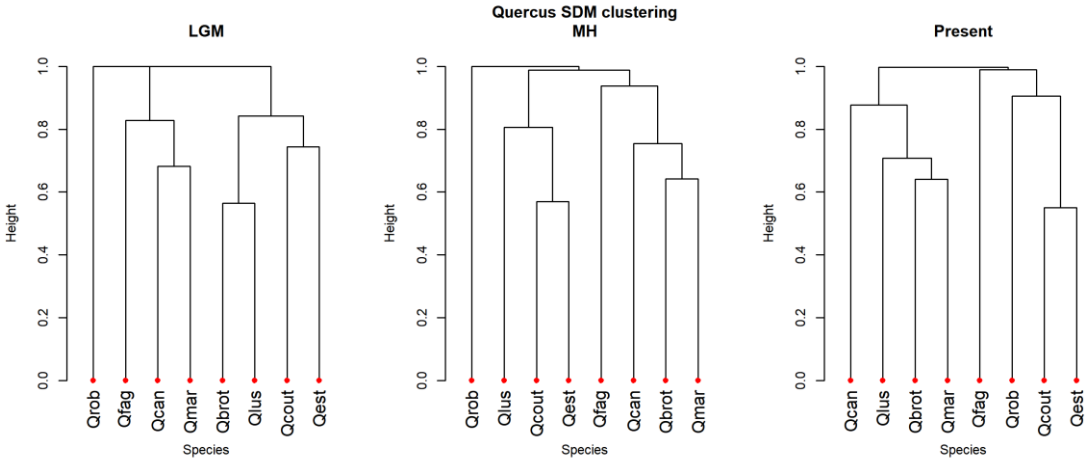
Supplementary Figure S1 – Variable importance scores, averaged across the top-performing models per species.

Supplementary Figure S2



Supplementary Figure S2 – Species records distribution.

Supplementary Figure S3



Supplementary Figure S3 – Hierarchical clustering analysis, with the similarity of species projections in the three studied periods.

Chapter 5.

Past projections of submediterranean oaks unveil future distribution range shifts of vulnerable taxa in the face of climate change

Carlos Vila-Viçosa[1,2,3,4*], Salvador Arenas-Castro[1,2,5], Antoine Guisan[6], Elif Deniz Ülker[7], Jean Stephan[8], Francisco M. Vázquez[9], João Honrado[1,2,3], Cristina García[1,2,10], Rubim Almeida[1,2,3,4], João Gonçalves[1,2,11]

Disclaimer: this chapter is an original contribution of this thesis in preparation for publication. Vila-Viçosa, C. led the work with contributions from all co-authors.

[1] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO. Campus de Vairão, 4485-661 Vairão, Portugal
[2] CIBIO (Research Center in Biodiversity and Genetic Resources) - InBIO (Research Network in Biodiversity and Evolutionary Biology), University of Porto. Campus Agrário de Vairão; Rua Padre Armando Quintas; 4485-661 Vairão; Portugal
[3] MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto – Herbário PO, Universidade do Porto. Praça Gomes Teixeira, 4099-002, Porto, Portugal.
[4] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal.
[5] Area of Ecology, Department of Botany, Ecology and Plant Physiology, University of Córdoba, Spain.
[6] Department of Ecology and Evolution, Faculty of Biology and Medicine, Université de Lausanne, UNIL Sorge Le Biophore CH – 1015, Lausanne, Switzerland.
[7] Functional Ecology Lab. Department of Biology (Ecology Section), Hacettepe University, Ankara, Turkey.
[8] Laboratory of Georesources, Geosciences and Environment, Faculty of Sciences 2, Lebanese University, Fanar, Lebanon.
[9] CICYTEX - Centro de Investigaciones Científicas y Tecnológicas de Extremadura; Agricultural Research Centre, Finca La Orden, Valdesequera; Ctra. A-V, Km372, 06187 Guadajira, Badajoz, España.
[10] Department of Biological Sciences. Bourne Building. Office 3-29B. Royal Holloway University of London (RHUL) Egham, Surrey, TW20 EX, UK.
[11] proMetheus—Research Unit in Materials, Energy and Environment for Sustainability, Instituto Politécnico de Viana do Castelo (IPVC), Avenida do Atlântico, No. 644, 4900-348 Viana do Castelo, Portugal.

5.1. Abstract

Mediterranean woodlands are amongst the most threatened forest ecosystems worldwide, predicted to be severely hit by extreme climatic events. Besides the typical evergreen oak species, the Mediterranean region hosts a group of narrowly distributed, marcescent oaks that evolved under Mediterranean-type climate regimes with higher annual precipitation and mild summers. In Europe, these oak species and their forests distinguish a continental-scale ecotone between the temperate deciduous forests of the Eurosiberian region and the typical evergreen woodlands and scrublands of the Mediterranean basin.

Current species distributions and biogeographic patterns are deeply related to recent past range shifts, especially since the Last Glacial Maximum (LGM). Analyzing past range dynamics may help us predict how responsive (and thus, how vulnerable) species are to climatic fluctuations and how they will respond in the face of future climate changes. Thus, we hypothesize that past abrupt climatic shifts, experienced in unfavourable periods, are more correlated with the expected future worsening scenarios. To validate this hypothesis, we use Species Distribution Models (SDMs) to explore the distribution dynamics of eight submediterranean oaks considering six past periods since the LGM (from 17.0 to 0.3 Kyr), current climate conditions, and future climatic scenarios for years 2070 and 2100. To calibrate niche models, we used a dataset of 12 450 occurrence records obtained from fieldwork, herbaria review and online resources, encompassing the distribution of the studied species across the Mediterranean basin. We used downscaled climate datasets from PaleoClim (past periods) and CHELSA (present conditions and future scenarios) to obtain the potential distribution of each species through an ensemble-modelling approach. The median latitude and longitude shifts, along with the relative loss and total change (combining gains and losses) of climatically suitable areas, were compared between past and future through linear regression.

Model performance was overall good to excellent. Our results show a positive correlation between past and future range shifts of marcescent oaks, which is generally higher for eastern Mediterranean species than western ones. Shifts in the distribution area attained higher correlation scores than geographical displacements. The amelioration periods (Bølling-Allerød (14.7-12.9 Kyr); early (11.7-8.326 Kyr) and mid-Holocene (8.326-4.2 Kyr)) generally recorded higher associations between past-future dynamics for the eastern Mediterranean taxa. We also found higher associations between past and future

range shifts for more “extreme” future scenarios, including SSP-370 and SSP-585 (CMIP-6). The pair-group of species that includes the eastern *Q. kotschyana* and *Q. vulcanica* and the western, narrowly distributed, *Q. canariensis* and *Q. lusitanica* are the ones who suffer higher range shifts and loss of suitable area and future-projected suitability into areas utterly outside their biogeographic outreach.

We demonstrate that studying past distribution range shifts of oak species helps to better predict future dynamics in the face of climate change and we support the main hypothesis, that past periods related with unfavourable conditions hold a higher predictive ability in relation to the studied future scenarios. We also shed light upon the role of climate change in determining the current biogeography of Mediterranean forests, especially those related to submediterranean areas. While this subset of oak species had wide-ranging distributions throughout optimal periods, future aridity conditions and extreme drought events will compromise their maintenance. Notably, inferring past distribution dynamics in response to climate change is an actionable framework to identify the most vulnerable tree species, regions where species may become extinct, and those where climatic suitability will be kept (refugia). We discuss the implications of our results for preserving submediterranean oaks in the face of severe climate change, thus contributing to the broader conservation efforts of Mediterranean forests.

5.2. Introduction

Climate change is a major threat to plant loss in the Mediterranean Basin, a well-known hotspot for plant diversity (Medail & Quezel, 1997; Myers *et al.*, 2000; Cramer *et al.*, 2018; Wang *et al.*, 2019). Accordingly, the Mediterranean forests, woodlands, and scrub Biome – which covers less than 0,5% of the Earth's surface – is the richest of the extra-tropical areas by aggregating almost 20% of the global plant diversity (Cody, 1986; Regato, 2001; Klausmeyer & Shaw, 2009; Mittermeier *et al.*, 2011; Bellard *et al.*, 2014; Cowling *et al.*, 2015; Safford & Vallejo, 2019). Additionally, the Mediterranean basin holds *ca*. 200 more tree species than Central Europe (Médail *et al.*, 2019). The forests distributed throughout this region are known for their multifunctionality and for providing essential ecosystem services (Van der Plas *et al.*, 2016). However, Mediterranean forests are predicted to be severely hit by climate change, with worst-case projections pointing it as the terrestrial biome that will experience the most significant proportional loss of biodiversity up to 2100 (Sala *et al.*, 2001; Ellison *et al.*, 2005; Klausmeyer & Shaw,

2009; Mori *et al.*, 2017; Aznar-Sánchez *et al.*, 2018; Cramer *et al.*, 2018; Acharya *et al.*, 2019; Allan *et al.*, 2021).

Oaks (*Quercus* L.) are one of the keystone groups of woody plants that feature most of the climax forest or scrub stages across contrasting geologic and bioclimatic conditions (Axelrod, 1983; Manos *et al.*, 1999; Nixon, 2006; Aldrich & Cavender-Bares, 2011; Vila-Viçosa *et al.*, 2020b). The primary source of environmental stress in the Mediterranean Basin is summer drought and the resulting lack of soil moisture in the growing season (Safford & Vallejo, 2019). These factors, coupled with the diminishing winter cold, establish the contrast and transition between the Mediterranean and Eurosiberian subregions (Rivas Martínez *et al.*, 2011). The distinct subset of oak species spans evergreen and deciduous or marcescent species that track the latter subregions' biogeography, broadly corresponding to the two main subgenus: *Cerris* and *Quercus* (Denk *et al.*, 2017). From the latter subgenus, all Palearctic species are known as the “white oaks” and are taxonomically ascribed to Section *Quercus* (Denk *et al.*, 2017). This Section covers mostly temperate distributed and deciduous oaks, from which the most emblematic European pair-species are *Q. robur* L. and *Q. petraea* (Matt.) Liebl. (Schwarz, 1936a; Manos *et al.*, 1999; Box & Fujiwara, 2016; Leroy *et al.*, 2020). However, in transitional areas towards Mediterranean climates, a subset of marcescent white oaks form a distinct forest ecotone between deciduous and evergreen oak forests. These are driven by moderate summer precipitation, predominant in Atlantic areas and shaping the potential forests of a submediterranean bioclimatic belt (Del Río & Penas, 2006; De Dios *et al.*, 2009; García-Mijangos *et al.*, 2015; Vila-Viçosa *et al.*, 2020b). Taxonomically, these oaks were traditionally ascribed to two subsections inside Section *Quercus* that broadly cover marcescent species: subsection *Galliferae* (Spach, 1842; Gürke, 1897; Tschan & Denk, 2012) and subsection *Dascia* (Schwarz, 1936a). This intricated taxonomic diversity of the Eurasian white oaks, which increases towards the southern European Peninsulas, North Africa, and the Near East, holds a corresponding growing ambiguity in species delimitation (Schwarz, 1935; Di Pietro *et al.*, 2021; Valencia-A.S., 2021). This ambiguity is naturally and intimately related to the paleobiogeography of the western Palearctic region (Manos & Stanford, 2001; Holm & Svenning, 2014).

This subset of oak species includes established, narrowly distributed and endangered species at global and local scales (Atalay & Efe, 2010; Ducousso, 2012; Arslan *et al.*, 2015; Vila-Viçosa *et al.*, 2015; Carrero *et al.*, 2020; Öney *et al.*, 2020; Vila-Viçosa *et al.*, 2020a), that are known to be susceptible to changes in precipitation seasonality and

water availability and therefore sensitive to projected drought scenarios (Salleo *et al.*, 2002; Blanco-Castro *et al.*, 2005; Fyllas & Troumbis, 2009; Kargıoğlu *et al.*, 2009; Karam *et al.*, 2011; Castagneri *et al.*, 2020; Vila-Viçosa *et al.*, 2020a; Vila-Viçosa *et al.*, 2020b; Allan *et al.*, 2021). Thus, this subset of oaks and the forests they form become a priority when overcoming plant loss in the Mediterranean Basin (Molina-Venegas *et al.*, 2020). Additionally, it is not only the species by themselves but all the submediterranean ecotone, provided by the maintenance of marcescent oak forests, that serve as reservoirs for warm-temperate and even some subtropical species (Svenning, 2003; Rodrıguez-Sánchez & Arroyo, 2011; Costa *et al.*, 2015; García-Mijangos *et al.*, 2015). This ecotone, distributed across the Mediterranean Basin, is biogeographically and phylogeographically related, establishing an amphimediterranean pattern between this basin's western and eastern sub-regions. Here, oaks' subset of species (Schwarz, 1935; Schwarz, 1936a) may be affected differently between both subregions, and it is yet to be solved how climate change will affect this subset of oaks species individually and as a group.

Henceforth, not only do recent environmental conditions reflect how past demographic processes of contraction and expansion shaped the current distribution of species, but also their history of persistence in climatically stable areas, as well as migration or dispersion from ancient refugia upon past abrupt climate change (Pearson, 1965; Svenning & Skov, 2007; Willner *et al.*, 2009; Stewart *et al.*, 2010; Hájek *et al.*, 2016). These complex dynamics make it necessary to understand the evolution of past geoclimates and how these affected all aspects of species distribution nowadays, including richness and diversity at the functional, phylogenetic and endemism levels. Considering these goals, species' model hindcasts, based on paleoclimatic reconstructions, emerge as a remarkable tool to identify the influence of past changes and how they shaped their current distribution and infer their responses to future scenarios (Fordham *et al.*, 2020). These hindcasts are especially important to improve our understanding of the drivers of species range shifts, especially throughout the Late Quaternary period (Araújo *et al.*, 2008; Pearman *et al.*, 2008; Wen & Ickert-Bond, 2009; Sandel *et al.*, 2011; Maiorano *et al.*, 2013; Robles *et al.*, 2013; Ordonez & Svenning, 2015; Saltré *et al.*, 2016; Vila-Viçosa *et al.*, 2020b). This period was the most critical for the persistence of forest ecosystems, essentially after dry and cold periods that were intercalated with climatic amelioration, such as in the Bølling-Allerød (14.7-12.9 Kyr) and the Early- to Mid-Holocene (11.7- 4.2 Kyr) periods (Lowe & Walker, 1984; Carrión *et al.*, 2010).

Relating past and future range shifts through geospatial analysis has become an essential mission of ecological and historical biology research, allowing us to assess the conservation and dynamics of species groups that are key for ecosystem functioning and biodiversity conservation. In particular, Species Distribution Models (SDMs) are one of the most widely used techniques to assess the impact of environmental change by researchers, practitioners and policymakers with a wide plethora of applications (Rodríguez-Sánchez *et al.*, 2010; Guisan *et al.*, 2017; Brunialti & Frati, 2021; Chakraborty *et al.*, 2021; Ferraz *et al.*, 2021; Blair *et al.*, 2022; Sanz-Arnal *et al.*, 2022). Recent approaches using SDMs provide new insights to advance our understanding of species' past and future trajectories and to test new hypotheses about range dynamics and demographic histories that can serve as a basis to mitigate further biodiversity losses driven by climate change (Wiens & Graham, 2005; Svenning *et al.*, 2011; Forester *et al.*, 2013; Fordham *et al.*, 2014; Maguire *et al.*, 2015; Fordham *et al.*, 2016; Saltré *et al.*, 2016). However, a comparative work that opposes past and future dynamics and how these relate to each other is still missing.

Climate change projections for the Mediterranean Basin indicate a decrease in precipitation and an increase in maximum summer temperatures (Cramer *et al.*, 2018; Allan *et al.*, 2021) that will hit the Mediterranean forests. Subsequently, these conditions will boost extreme drought scenarios, likely increasing these ecosystems' vulnerabilities (Margalef-Marrase *et al.*, 2020; Lloret *et al.*, 2022). However, the magnitude and how these extreme phenomena will affect this particular and biogeographically related subset of submediteranean oaks is still unknown.

This knowledge gap implies an uncertain future and a putative loss of a vital forest ecotone (Vila-Viçosa *et al.*, 2020b) as well as the plant diversity it holds inserted in a major phylogeographic hotspot (Quézel & Médail, 2003; Médail & Baumel, 2018; Médail *et al.*, 2019; Molina-Venegas *et al.*, 2020). Contributing to overcome this potential climatic threat and plant diversity loss, this study aims to infer if past distributional shifts of marcescent oaks, distributed across an East-to-West gradient in the Mediterranean Basin, can effectively inform about the vulnerability and susceptibility of species and their forests to future climate change. To address this, we employed SDMs to hindcast and forecast the distribution of eight marcescent oak species in the Mediterranean basin. Model hindcasts were used to explore each species' past range shifts across six periods since the LGM (from 17.0 to 0.3 Kyr): Heinrich Stadium, Bølling-Allerød, Younger Dryas, Early-Holocene, Middle-Holocene and Early-Holocene. We hypothesize that climatic shifts associated with past abrupt changes (e.g. extreme drought or cold) will hold a

higher predictive ability in relation to (expected) future periods of climatic worsening. Model forecasts (for two future periods, 2070 and 2100) were used to predict future distributional range shifts in response to Anthropocene climate change. Afterwards, we compared past and future range shifts between each species and group of species (i.e., those with western vs eastern distribution ranges) to assess correlations between distribution area losses or total change and global geographical range shifts (latitude and longitude) between past and future projections. By doing so, we intend to unveil which past period better predicts future species range shifts amongst all species and how west *versus* east Mediterranean oaks diverge in terms of their spatiotemporal dynamics. We further discuss the implications of our results for preserving submediterranean oaks in the face of severe climate change, thus contributing to the broader conservation efforts for the Mediterranean forests.

5.3. Materials and methods

5.3.1. Study area

The study area comprises a bounding box covering most of the Mediterranean Basin, with a total surface area of 8.107 million km^2. The Mediterranean Basin goes from Cabo Verde in the west, across the Iberian Peninsula, North Africa up to Jordan and Turkey in the east, crossing from Italy and France in the north to Tunisia, Algeria and Morocco in the south and through the Balkans, Greece, Turkey, and about 5.000 islands scattered around the Mediterranean Sea (See Figure 1). It is characterized by diverse geology and is dominated by the Mediterranean climate with hot, dry summers that contrast with cold and rainy winters (Barbéro *et al.*, 1998; Quézel *et al.*, 1999; Rivas-Martínez, S. *et al.*, 2017) and spans two major biogeographic subregions (Eurosiberian and Mediterranean) (Rivas-Martínez, Salvador *et al.*, 2017). We subdivided our bounding box into two sub-boxes, one for the western Mediterranean sub-Basin and the other for the eastern Mediterranean sub-Basin, with a buffer of 500 km of each species' distribution limits (Figure 1).

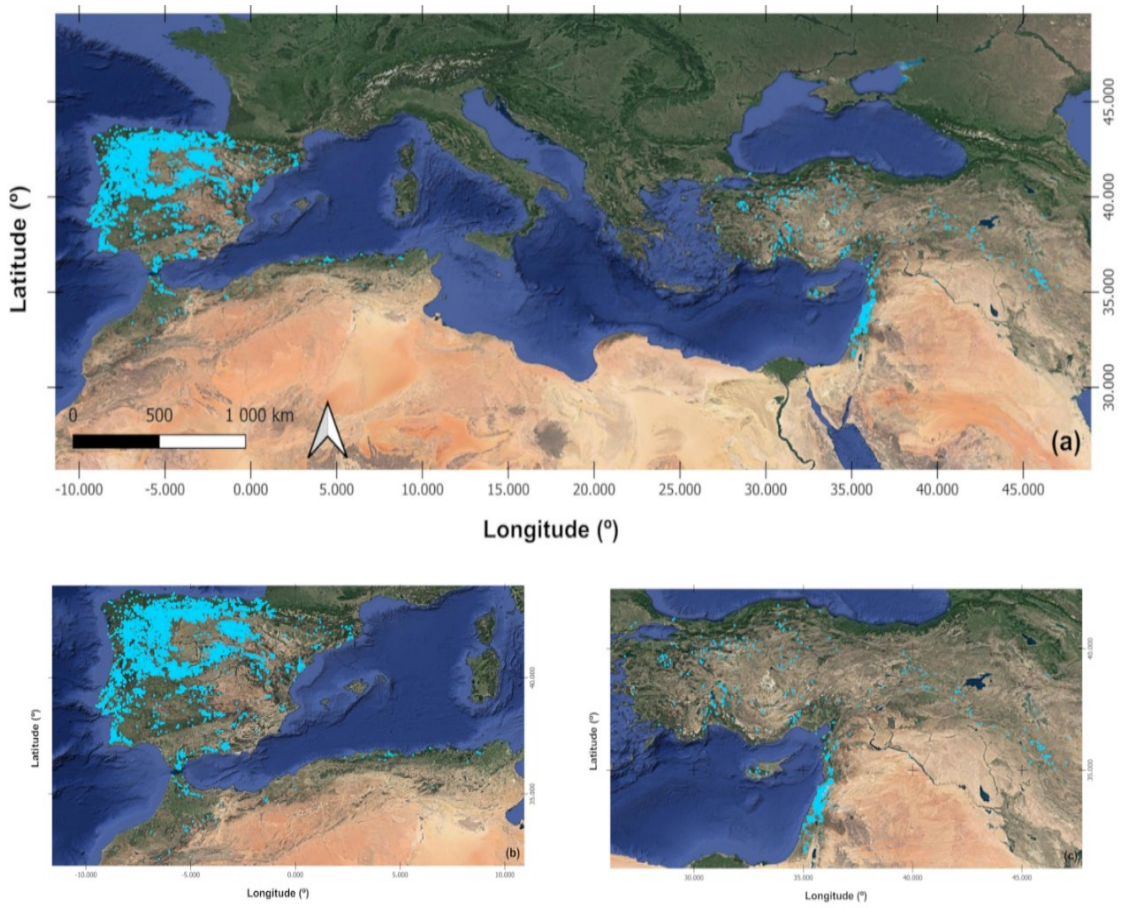


Figure 1 – Study area and selected bounding box with all oak species locations (upper row). Subsequent division into two sub-boxes featuring Western distributed oaks species (bottom row-left) and Eastern distributed oaks species (bottom row-right).

5.3.2. Focal species and occurrence data

The Circummediterranean white oaks include a sub-group of typically marcescent oaks, traditionally assigned to putative sections inside the former subgenus *Lepidobalanus* (Schwarz, 1935; Schwarz, 1936b; Schwarz, 1936a). This subgenus broadly covers the nowadays stablished Section *Quercus* (Denk *et al.*, 2017).

We chose a subset of eight marcescent oaks that are traditionally allocated in two infrasectional groups, including five common gall oaks (Subsection *Galliferae*) (Spach, 1842; Gürke, 1897; Tschan & Denk, 2012) and three species inside former Section *Dascia* (Schwarz, 1936a). These two subgroups entail *Quercus boissieri* Reut., *Q. canariensis* Willd., *Q. faginea* Lam., *Q. infectoria* G. Oliver and *Q. lusitanica* Lam. in the former first group and *Q. kotschyana* O. Schwarz, *Q. pyrenaica* Willd. and *Q. vulcanica* Boiss. & Heldr. ex Kotschy in the latter (Supplementary Data S1).

Occurrence data for the Iberian Peninsula was gathered through fieldwork (since 2005), combined with thorough literature and herbaria review, which served to tackle taxonomic uncertainty (Supplementary Data S1). The remaining area and targeted species were compiled from online collections (https://www.gbif.org/) and previous knowledge gathered by experts. Species records (presence-only data) were aggregated, cleaned and harmonized into a 10 km × 10 km grid (Supplementary Table S1 - Digital Annex and Supplementary Table S2).

5.3.3. Environmental variables (predictors)

Models were based on regional/coarse-scale bioclimatic factors potentially influencing the target species distribution and climatic niche. For model-based hindcasts, we used the 19 bioclimatic variables for six paleoclimate simulations hosted in the PaleoClim v.1.0 dataset (http://www.paleoclim.org/) (Supplementary Table S3) (Brown *et al.*, 2018). We chose the periods since the end of the Last Glacial Maximum once they reflect the most recent abrupt changes in climate from the Late Quaternary period. These covered the last 17-17.4 Ka, broadly since the Heinrich-Stadial (HS), and targeting all periods up to the present. These span both dry-cold periods, with heavier seasonality like the HS and the Younger-Dryas (YDS) at 12.9-11.7 Kyr (Ludwig *et al.*, 2018), but also those related to climatic amelioration like the Bølling-Allerød (BA) that covers the past 14.7-12.9 Kyr, and both Early and Mid-Holocene (EH and MH respectively that covers 11.7-8.326 Kyr and 8.326-4.2 Kyr respectively). Finally, we used the recent Late-Holocene (LH) that covers up to 300 years ago (4.2-0.3 Kyr).

For obtaining model-based forecasts, we used the CHELSA v.2.1 dataset (URL: https://chelsa-climate.org/downloads/), containing the same 19 bioclimatic indices available for the current calibration period 1981–2010 and two future periods (2070 and 2100). We derived future climate projections for this region based on averaged ensemble projections for five General Circulation Models (GCMs: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL) for the Coupled Model Intercomparison Project Phase 6 (CMIP-6), for three different Shared Socioeconomic Pathways scenarios (SSPs: 126, 370 and 585) and two future periods (2070 and 2100) (Karger et al., 2017). We selected these five GCMs because they showed good performance ('Satisfactory') for the European region based on the previous CMIP5 Project (McSweeney *et al.*, 2015). All bioclimatic data were later re-projected and re-sampled (average) to a common reference grid at 10×10 km spatial resolution (Datum

WGS1984/UTM30N). The bioclimatic variables were selected after collinearity exclusion through pairwise correlation analysis ($r < 0.7$). The variable selection process also accounted for a balance of temperature and precipitation-related variables. For the first set, we targeted the range variation of temperature (BIO2) and a measure of winter cold (BIO6), and for the second, a measure of summer and winter precipitation (BIO 18 and 19, respectively). These variables also allowed us to test the effect of precipitation variation and seasonality in hot and cold seasons, which are frequently relevant for this subset of white oaks.

5.3.4. Model calibration and evaluation

Species Distribution Models (SDMs) were developed in R statistical software (R 4.2.0) using the *biomod2* package (Thuiller *et al.*, 2009). This package implements a multi-model ensemble forecasting approach combining several statistical and machine-learning-based algorithms. Models were fitted using nine available modelling algorithms in biomod2: GLM (Generalized Linear Models); GBM (Generalized Boosted Models); GAM (Generalized Additive Models); CTA (Classification Tree Analysis); ANN (Artificial Neural Networks); FDA (Flexible Discriminant Analysis); MARS (Multivariate Adaptive Regression Splines); RF (Random Forests); MAXENT (Maximum Entropy Model).

Default model hyperparameters were employed for all modelling techniques, except for the smoothing degree term in GAM algorithm, which was set to $k = 4$, and the number of boosting trees in GBM (n.trees = 2000) to prevent over-fitting issues (Guisan *et al.*, 2002). Given that only presence data was available for the target species, we used ten sets of randomly generated pseudoabsences (PAs) in the model calibration. PAs were generated by assigning unoccupied grid cells with the following constraints: (1) generating the same number of PAs as of presences to avoid potential bias caused by different levels of prevalence in the presence/absence datasets (as recommended by (Manel *et al.*, 2001; Barbet-Massin *et al.*, 2012); and (2) defining a minimum distance between pseudoabsences, corresponding with the grain size (10 km), and without overlapping with presences (Wisz & Guisan, 2009), to avoid spatial autocorrelation and to cover the different ecological conditions in the study area. Since no previous information was assumed about species prevalence (p), model weights were adjusted to set $p=0.5$ (biomod2 default), thus giving similar weight to presences and the randomly generated pseudo-absences. Models were trained for current conditions, and projections for past and future were obtained by, respectively, replacing climate datasets with those

of PaleoClim and CHELSA v-2.1 future ensemble. To train and obtain model projections, we used the two separate bounding boxes defined by the subset of all occurrences for eastern or western species with a buffer of 500 kilometers surrounding each one. We used the threshold value maximizing the True Skill Statistic (TSS) to 'binarize' projections (i.e., dichotomous suitable/unsuitable habitat).

Holdout cross-validation was employed to evaluate the models, with 80% of the input records used for model fitting and 20% for model evaluation at each round. A total of 20 rounds were performed for model evaluation. For assessing model performance, the Area Under the Receiver-Operating Curve (AUC), TSS, and the Sensitivity and Specificity values were calculated (Thuiller *et al.*, 2009).

5.3.5. Comparisons between past, present and future range shifts

We spatially overlapped model projections to assess range shifts and calculated the percentage of area that remained stable (either climatically suitable or unsuitable), that lost climate suitability or otherwise gained it. The R package '*raster'* (Hijmans et al., 2005) was employed for overlap analyses and cross-tabulation. We used current conditions as the baseline for all pairwise comparisons against each projection horizon (past or future). As indices of past-to-present and present-to-future range shifts, we considered the % of total change (combining both distributional losses and gains, T_c, Eqn. 1), the % of loss (Eqn. 2) and shifts in the median centroid of each species distribution in latitude and longitude. A many-to-many matrix was assembled by combining all possible past and future comparisons for each species, thus allowing for more exhaustive statistical screening and analysis. Data joins (by species) were performed in R using packages '*dplyr'* and '*tidyr'* (Wickham *et al.*, 2022; Wickham & Girlich, 2022).

		Past or future model projections	
Current projection (baseline)		**Unsuitable**	**Suitable**
	Unsuitable	Stable unsuitable (S_u)	Gain (G)
	Suitable	Loss (L)	Stable suitable (S_s)

$$\%Tc = \left(\frac{L+G}{S+G+L}\right) \times 100, \text{ with } S = S_u + S_s \text{ (Eqn.1)}$$

$$\%L = \left(\frac{L}{S+G+L}\right) \times 100 \text{ (Eqn. 2)}$$

$p_i = (\varphi_i, \lambda_i)$, with i={1,…,n}, equal to the longitude (φ) and latitude (λ) of all suitable locations (n, as pixels)

$c(\varphi, \lambda) = (median(\{\varphi_i\}), median(\{\lambda_i\}))$, with as the median centroid (c) of each species distribution. The percent relative shift in longitude and latitude are given for past and future range shifts as:

$$\%c(\varphi, \lambda) = \left(\frac{c(\varphi, \lambda)_{past} - c(\varphi, \lambda)_{cur}}{c(\varphi, \lambda)_{cur}}\right) \times 100$$

(Eqn. 3)

$$\%c(\varphi, \lambda) = \left(\frac{c(\varphi, \lambda)_{fut} - c(\varphi, \lambda)_{cur}}{c(\varphi, \lambda)_{cur}}\right) \times 100$$

(Eqn. 4)

Linear regression was performed to compare past and future range shifts across species and periods. The coefficient of determination (R^2) was used to measure the magnitude of past vs future range dynamics association or correlation. Panel regression plots allowed us to explore differences in the association between past and future shifts for (i) species groups (eastern vs western), (ii) past periods, i.e., by fixing one specific past period against all future horizons (composed of year and SSP), and (iii) the reverse, i.e., fixing one future horizon against all past periods. The first set of plots allows exploring which species group tends to have a higher association concerning past vs future trajectories, while the second assesses which past periods may hold greater predictive value to investigate future shifts. Finally, the third explores which future scenarios may become more likely considering past dynamics. These analyses employed R package *ggplot2* (Wickham *et al.*, 2016).

5.4. Results

5.4.1. Models performance

Overall, model performance results showed high True Skill Statistic scores (TSS; bounded between "-1, 1") (Supplementary Table S4), especially for the narrow-distributed oaks species, such as *Q. kotschyana* (1.00) and *Q. lusitanica* (0.96), followed by *Q. vulcanica* (0.91) and *Q. canariensis* (0.90). In contrast, the lowest scores were obtained by *Q. infectoria* (0.84) and *Q. faginea* (0.82), which still evidence very good-to-excellent performances. Also, the lowest value for the Area Under the Curve (AUC: "0, 1") was 0.97 for two species, with values above 0.99 for the remaining taxa, supporting outstanding performances. As for sensitivity and specificity scores "0, 100", these were consistently above 86, evidencing a well-balanced performance of the models.

5.4.2. Variables contribution

The overall contribution of precipitation predictors surpassed that of temperature variables for most of the analysed species (Figure 2). Exceptions occurred for *Q. pyrenaica* and *Q. vulcanica,* where the mean diurnal temperature range (BIO02, which measures the mean of the month difference between the maximum and minimum temperatures) overcomes the predictive importance of winter and summer precipitation. Winter precipitation (BIO19) was crucial for most oaks, except for *Q. vulcanica*, where summer rain is the most important variable (BIO18). A quick overview of all graphics (Figure 2) evidenced notable relationships of bioclimatic vicariance between some eastern and western Mediterranean taxa. This effect is especially notorious for *Q. boissieri* and *Q. canariensis* and, in some part, for *Q. vulcanica* and *Q. pyrenaica*, where the variables' contributions have an equivalent weight.

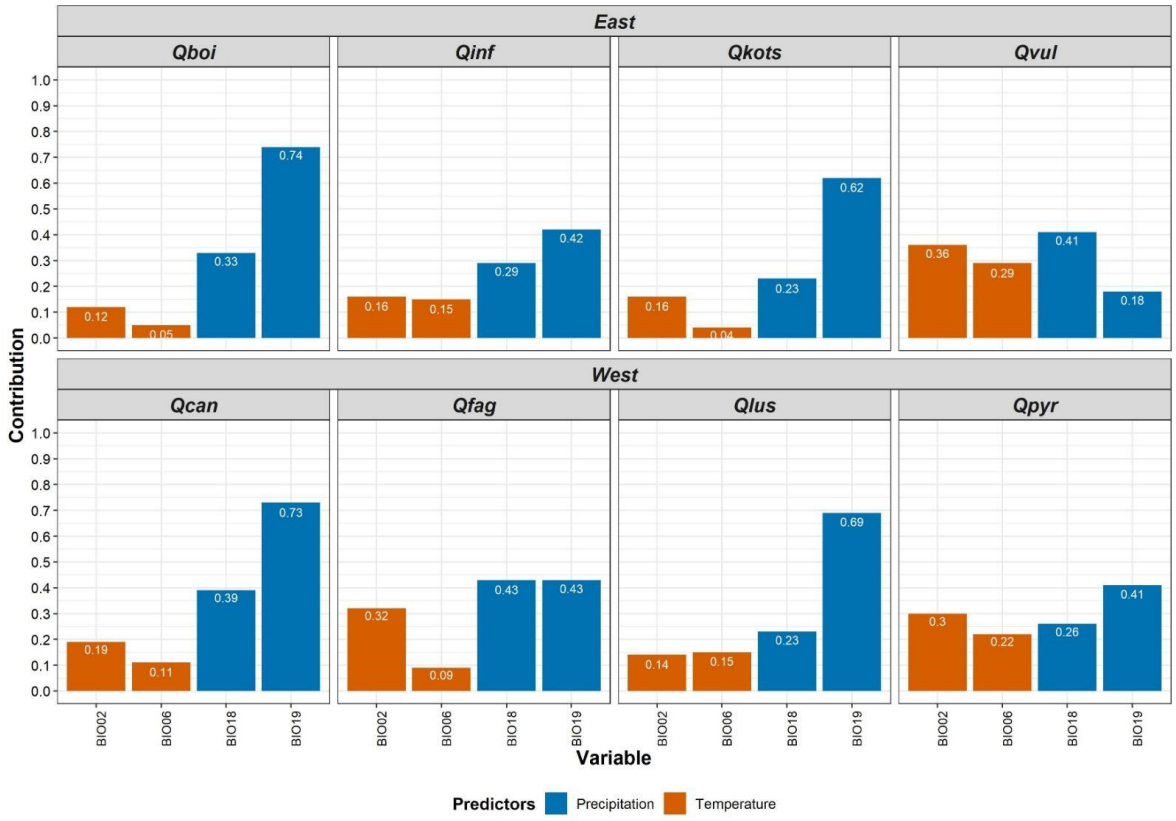


Figure 2 - Average variable importance per species and region (East vs West).

5.4.3. Past distribution range shifts

Geographic range shifts

Results on geographic range shifts evidenced that most past latitude alterations were southern-driven in most periods for all species. However, exceptions were found for *Q. pyrenaica* with northern-driven shifts, especially since the YDS, *Q. boissieri* since the EH and for *Q. vulcanica* in the LH, which also experienced residual northern-driven shifts (Supplementary Figure S1a; Supplementary Maps 1, 7 and 8 - Digital Annex).

As for the longitude, changes for past periods compared to the current distribution, results showed a constant eastern shift for *Q. canariensis* across all periods, with *Q. faginea* showing eastern migrations since the YDS, followed by *Q. lusitanica* that only contracts towards the seashore during the Late-Holocene. *Q. pyrenaica* only migrated east since the Middle Holocene, showing a considerable contraction to the seashore in the YDS (Supplementary Figure S1b; Supplementary Maps 2, 3, 6 and 7 – Digital Annex).

Past area range shifts (total area and losses)

When considering past total change (gains and losses), species distribution dynamics showed that the broadly distributed *Q. faginea* and *Q. pyrenaica* evidence more considerable changes in suitable area until the EH, only surpassed by *Q. infectoria* in the YDS and across the Holocene periods. For the most recent periods (MH and LH), our results evidenced that *Q. canariensis* is the taxon with the most significant changes, alongside *Q. infectoria* and *Q. vulcanica*. Overall, the narrowly distributed species *Q. lusitanica* and *Q. kotschyana* showed lesser total area changes (gains and losses) (Figure 3; Supplementary Maps 2-5, 7 and 8 – Digital Annex).

When analysing past distribution losses, our results evidence that *Q. infectoria* was the taxon with the most significant decrease of suitable area in almost all periods, except for the Late-Holocene, where *Q. canariensis* appears again as the oak species with the most recent and major area loss. On the other hand, minor changes were again observed for narrowly distributed *taxa* such as *Q. kotschyana*, *Q. vulcanica* and *Q. lusitanica* (Supplementary Figure S2; Supplementary Maps 2, 4-6, 8 – Digital Annex).

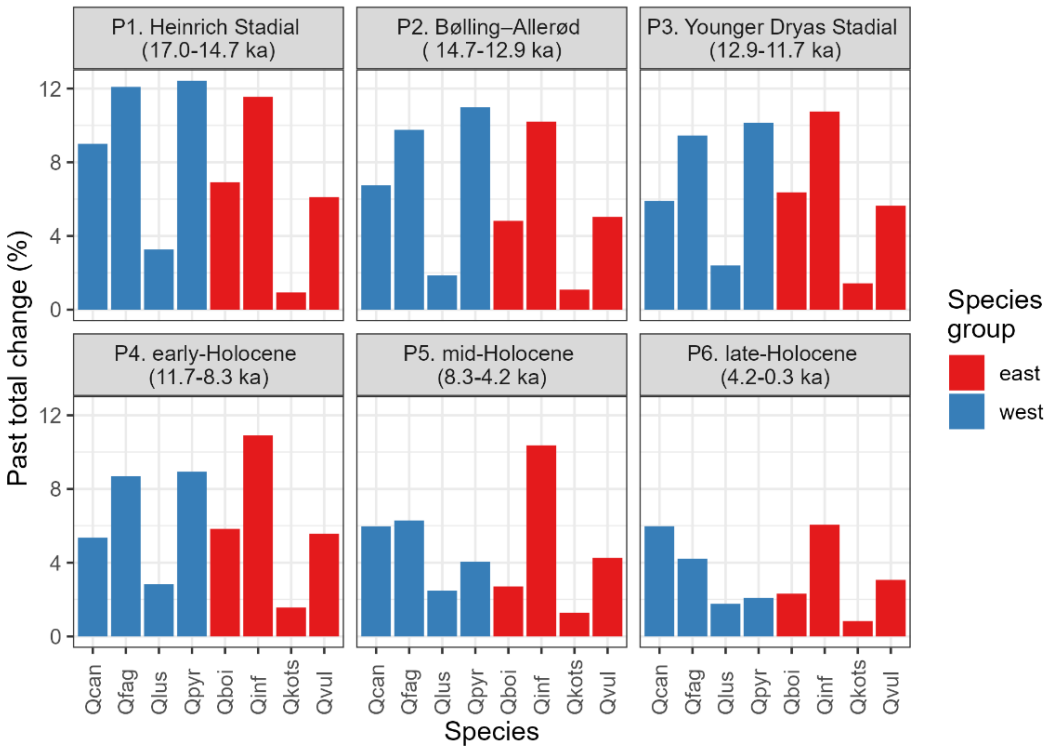


Figure 3 - Past total change (%) by species and period.

5.4.4. Future distribution range shifts

Geographic range shifts

Results for future latitude changes highlight that most circummediterranean oaks' climatic suitability will suffer northern-driven range shifts, except the eastern *Q. boissieri* and *Q. kotschyana*, which show evident southern driven range shifts in the worst scenarios (i.e., SSP-585) (Supplementary Maps 9 and 13 – Digital Annex). This projection horizon also evidences major latitudinal shifts for the western Mediterranean oaks, especially for the year 2100 (Figure 4a; Supplementary Maps 10, 11, 14 and 15 – Digital Annex). Regarding future longitude shifts, our results evidence eastern shifts in almost all scenarios, growing towards the more pessimistic SSPs, with the western Mediterranean species evidencing more remarkable changes, especially *Q. faginea*, *Q. pyrenaica* and in 2100 also *Q. canariensis* (Figure 4b; Supplementary Maps 10, 11 and 15 – Digital Annex).

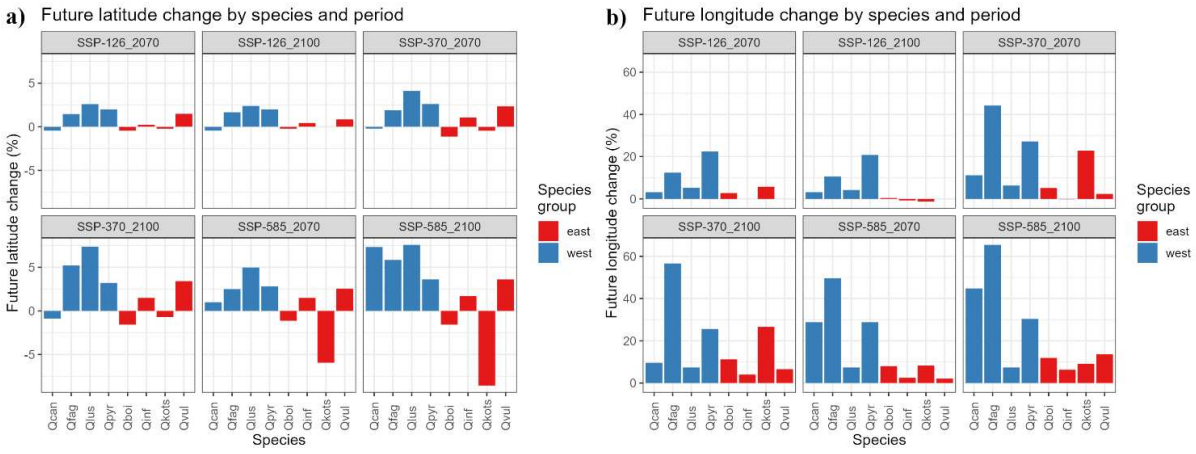


Figure 4 - a) Future latitude change by species and period; b) Future longitude change by species and period.

Total area range shifts (and losses)

Total area change (i.e., considering both gains and losses of suitable area) for 2070 and 2100 and the three SSP scenarios (totalling six future projection horizons) highlight *Q. faginea* as the taxon that will suffer more extensive range shifts, followed by *Q. pyrenaica* for the SSP-126 in both future horizons. *Q. infectoria* then surpasses the latter oak species in the remaining projection horizons. *Q. canariensis* and *Q. vulcanica* evidence significant range shifts in total area, especially for the SSP-375 and SSP-585 in 2100 (Figure 5; Supplementary Maps 10-12, 16 – Digital Annex).

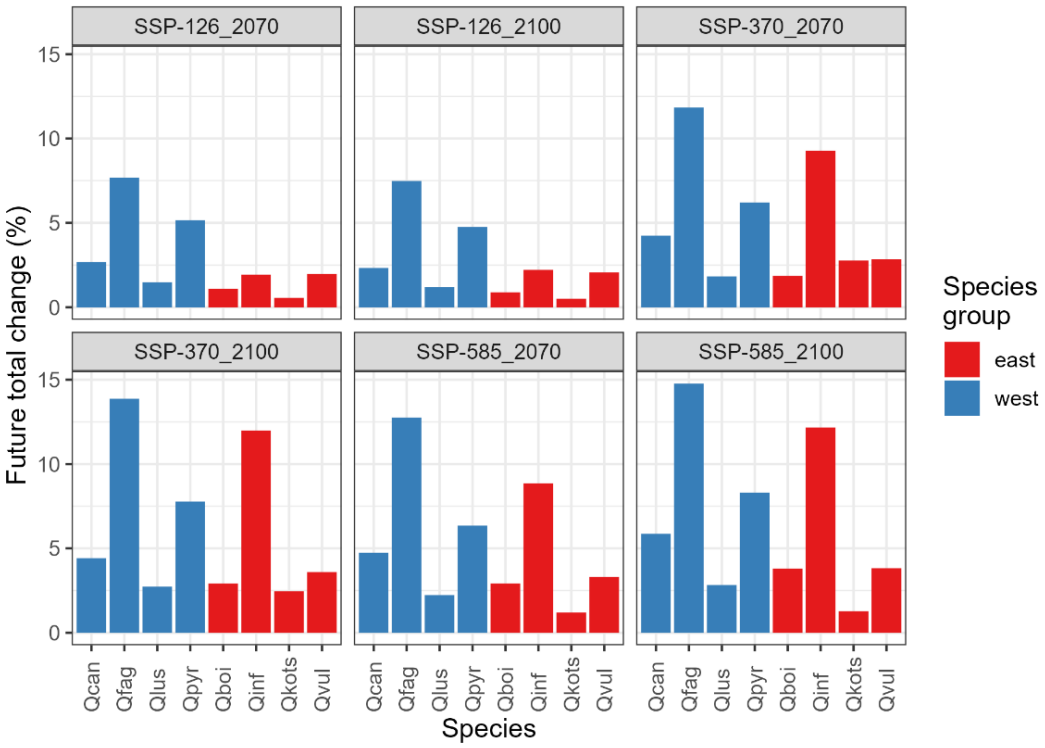


Figure 5 - Future total change (%) by species and period (2070-2100).

As for total future loss, *Q. faginea* remains the species experiencing a more considerable area decrease for the six past projection horizons, followed by the broadly distributed *Q. pyrenaica* in the SSP-126 for 2070 and 2100. *Q. infectoria* is the second species to suffer more extensive contractions in the remaining four projection horizons, followed by *Q. canariensis* and *Q. vulcanica* (Supplementary Figure S3; Supplementary Maps 10-12, 16 – Digital Annex).

5.4.5. Future scenarios for vulnerable taxa

Model projections for the worst future scenarios (SSP-585), specifically considering the four narrowly distributed taxa (*Q. canariensis, Q. lusitanica, Q. kotschyana* and *Q. vulcanica*), confirm the previous future range dynamics with significant losses in terms of suitable area and vast range shifts for the considered vulnerable species (Figures 6 and 7).

Eastern Mediterranean sensitive taxa

The narrowly distributed *Q. vulcanica* presents a global contraction pattern in 2070 towards the mountainous areas of its distribution range. The easternmost subpopulation

(Osmaniye, Turkey) will face significant losses in suitable area, while the other subpopulations persist stably at higher altitudes (Figure 6). Besides, the species displays an expansion around its northernmost populations (Küre and Ilgaz Mountains, Turkey), reflecting that this region will climatically contain suitable areas for the species' persistence. The 2100 projections evidence substantial losses of climatically suitable area in most subpopulations, where notably the southeastern ones will suffer significant range contractions, besides the total loss of climatic suitability to the type and emblematic location for the species (Kara Dağ, Karaman, Turkey). The mountain areas of the westernmost distribution of the species, including the best-preserved subpopulations, will be critical for preserving climatic suitability, especially around Isparta and Ankara (Turkey). As for the Lebanese narrow endemic *Q. kotschyana*, its constrained distribution in Mount Lebanon to a restricted altitudinal range (1600-2000m) makes it a highly vulnerable oak, considering the impacts of future climate change scenarios. The projected scenarios for 2070 and 2100 (SSP 585) do not exhibit any gain in terms of suitable areas for the potential range shift of this species while projecting significant losses towards the end of the century. These losses will confine it to a narrower range, restricted to the western slopes of Mount Lebanon, or a shift towards higher altitudes (>2000 m.a.s.l.).

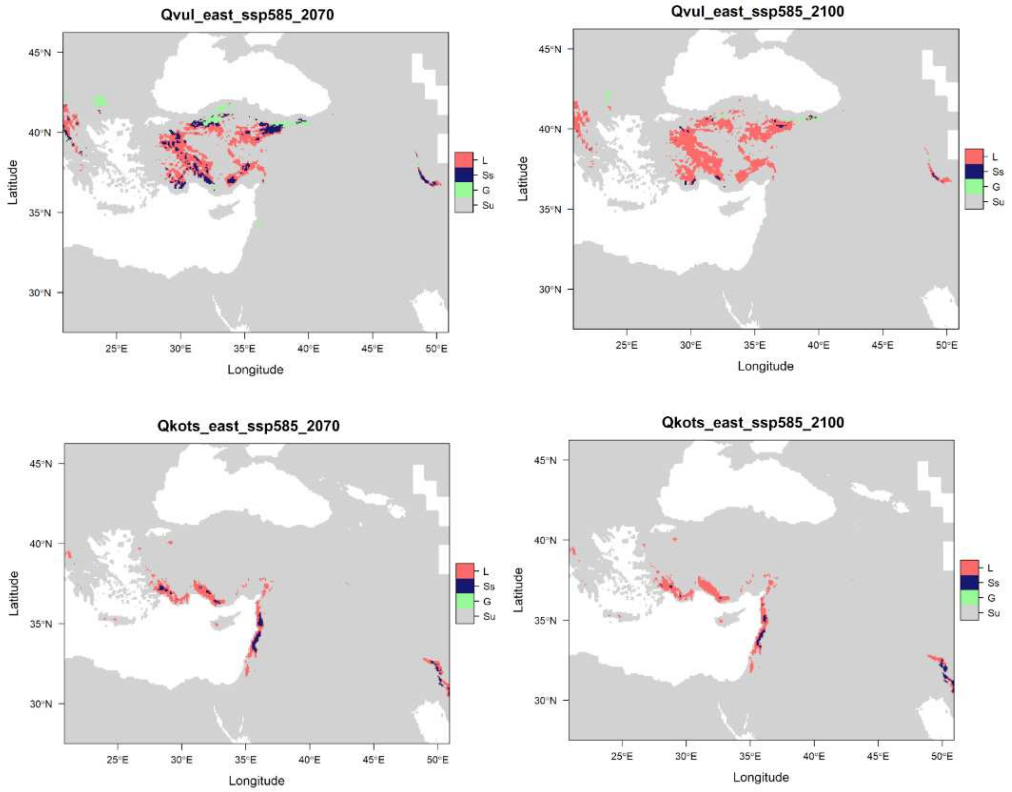


Figure 6 – *Q. kotschyana* and *Q. vulcanica* future range shifts (SSP585) for 2070 (left maps) and 2100 (right maps). L-Loss; Ss-Stable suitable; G-Gain; Su-Stable unsuitable.

Western Mediterranean sensitive taxa

The Western narrowly distributed *Q. canariensis* presents a contraction of its climatically suitable area, with the remaining populations of southwest Portugal (Monchique), Spain (Aracena and Algeciras), the Moroccan Rif and Middle Atlas, plus the Algerian Atlas, up to Tunisia potentially accountable for preserving the species towards 2070. In contrast, the Catalonian subpopulation appears as the one that may suffer more considerable contractions in this period (Figure 7). Towards 2100, model results show that this oak may suffer relevant contractions with the putative total loss of climatic suitability for the Catalonian subpopulation and a significant contraction of the remaining ones, mainly the Portuguese and northern African. Notably, results for this species evidence an upward shift of climatic suitability towards the northern Iberian Peninsula, from where the species is not native. As for the narrowly distributed *Q. lusitanica*, we observe a contraction from inland subpopulations, with the maintenance of the littoral ones and putative loss of climatic suitability of the subpopulation of Aracena Mountains already in 2070. At the end of the century, the SSP-585 scenario worsens the situation of the southern distributed subpopulations, maintaining climatic suitability only in the mountain areas of southern Portugal (Monchique), Spain (Algeciras) and North Morocco. In contrast, the centre-western, northern Portugal and the Galician subpopulation may be preserved and become the best suitable areas for this species (Figure 7).

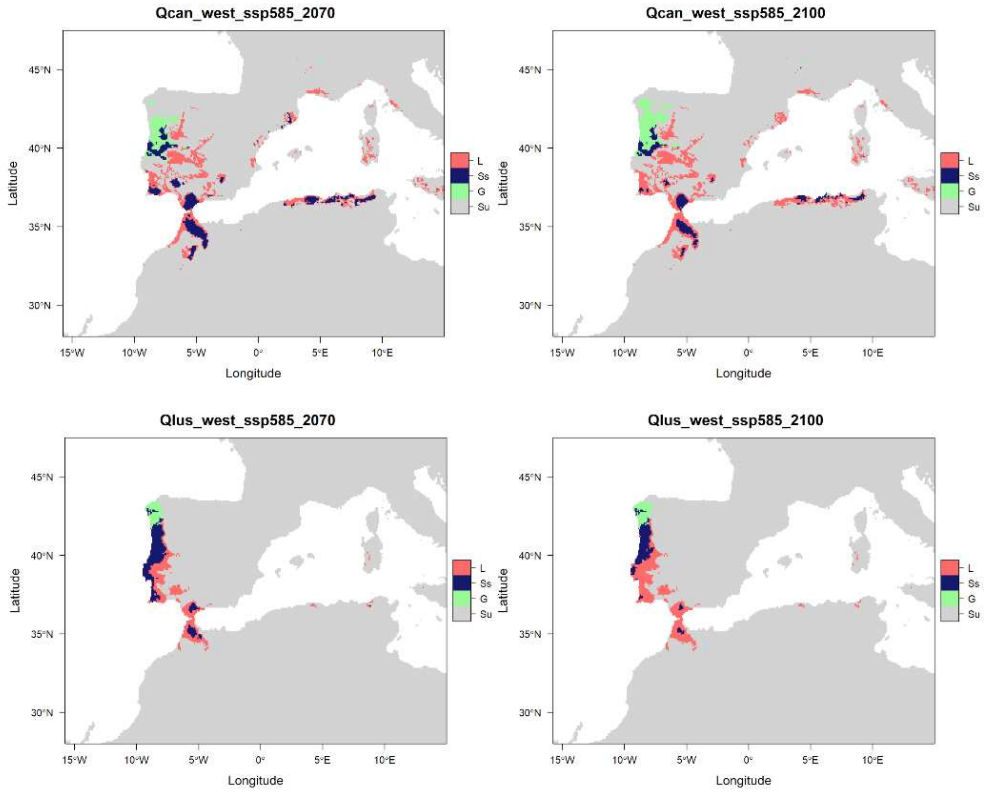


Figure 7 – *Quercus lusitanica* and *Q. canariensis* future range shifts (SSP585) for 2070 (left maps) and 2100 (right maps). L-Loss; Ss-Stable suitable; G-Gain; Su-Stable unsuitable.

5.4.6. Associations between past and future range shifts

Associations between past and future geographic shifts

Associations between past and future latitude shifts for all species (Supplementary Figure S4a) and between species groups (Supplementary Figure S4b) are mostly neglectable. A single positive correlation in latitude change was obtained for the eastern Mediterranean group of species, from which the most recent change (LH) presents a positive capability of predicting future range shifts (Supplementary Figure S5a). Lower correlation and inconsistencies in trend signals were found for the remaining periods. Eastern species mainly showed a higher correlation in past vs future latitude shifts compared to western ones. When comparing future scenarios vs all past periods (Supplementary Figure S5b), higher R^2 values were found for eastern species and SSP-370 (R^2=0.12) and especially for western species for the 2100/SSP-570 projection horizon (R^2=0.38).

Similarly, the correlation between past and future longitude shifts for all species (Supplementary Figure S6a) and between species groups (Supplementary Figure S6b) is mostly neglectable. Some positive correlations with consistent trends between eastern and western oak species were found (Supplementary Figure S7a) for the MH (8.3-4.2 ka; R^2: 0.14 – 0.16) and LH (4.2-0.3 ka; R^2: 0.22 – 0.27) periods. As for comparisons with specific future scenarios (Supplementary Figure S7a,b), we found lower correlations and inconsistent trends between species groups. Generally, past vs future trajectories' associations decreased from the SSP-126 to the SSP-570 climate scenarios.

Associations between past and future range shifts for total area change and loss

When analysing temporal trends in species' suitable area (Figure 8), the association between increases and decreases and climatic amelioration and aggravation periods was notable, with exception for *Q. canariensis,* which showed a continuous decline from the HS to the LH. All species experienced an increase of suitable area towards the Bølling–Allerød (BA), followed by a considerable decrease across the YDS to the Early-Holocene. This situation is then inverted towards the Middle Holocene. It tends to attenuate in the LH (Late-Holocene), except for growth in suitable areas for this period experienced by the eastern distributed oaks like *Q. vulcanica, Q. kotschaya*, *Q. infectoria*, and *Q. lusitanica* in the western Iberian Peninsula. The future trends exhibit smaller losses in suitable area for *Q. boissieri*, *Q. infectoria*, *Q. canariensis* and *Q. lusitanica*, with the most evident decreases in total suitable area being experienced by *Q. vulcanica, Q. pyrenaica* and *Q. faginea* (Figure 8).

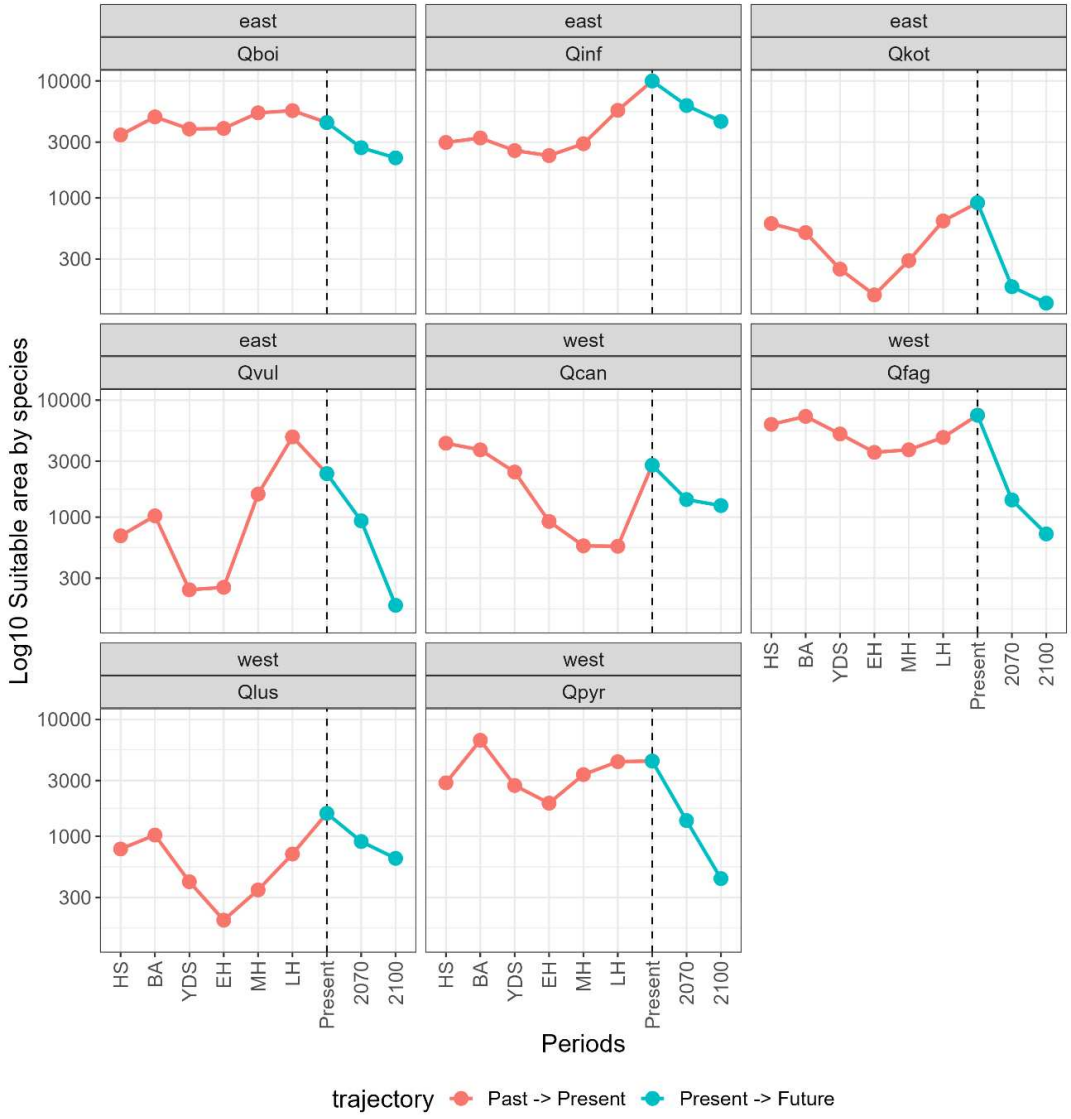


Figure 8 – Temporal changes in suitable area (Log10 transformed) across all periods (HS – Heinrich Stadium; BA - Bølling–Allerød; YDS – Younger Dryas; EH – Early-Holocene; MH – Medium-Holocene; LH – Late-Holocene; Present; SSP-585 2070 and SSP-585 2100).

Overall results show that the magnitude of correlations between past and future range shifts is much higher for areal-related indices (either for total change, combining both gains and loss in distributions, or losses) than latitude/longitude displacements. We also found that the total change in species distributions between past and future ranges is positively correlated, not only for all species across all period combinations (Supplementary Figure S8; R^2=0.35, p<0.001), but more evident when separating by species groups and especially for the eastern oaks (eastern, R^2=0.41, p<0.001 vs western, R^2=0.27, p<0.001; Figure 9).

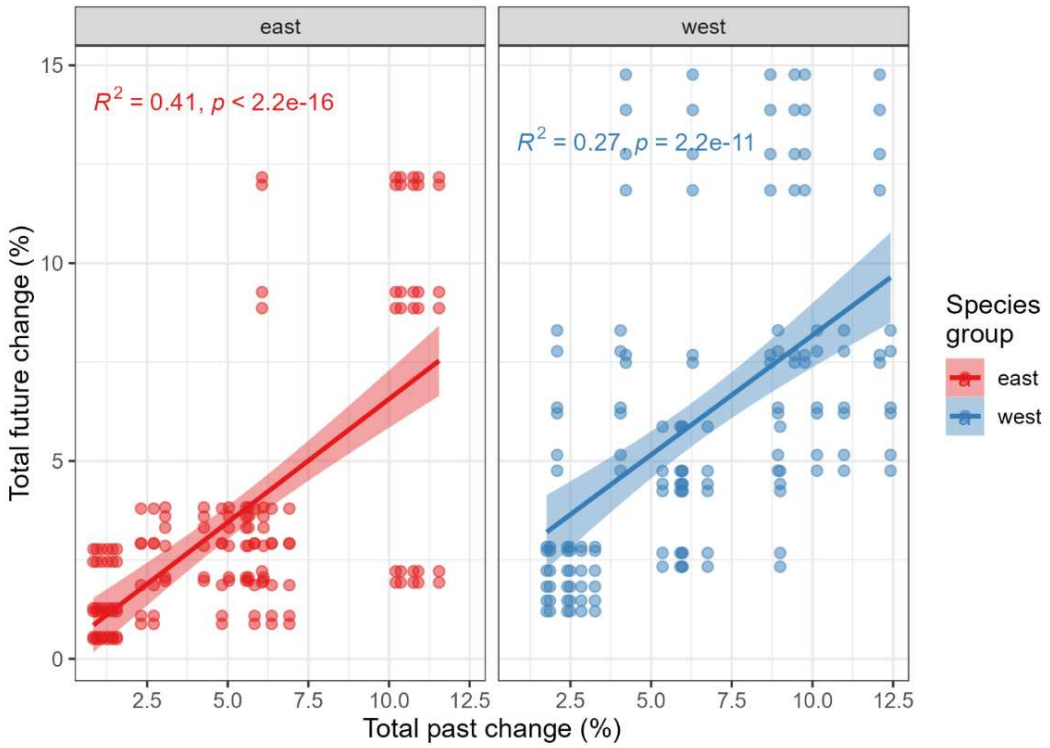


Figure 9 - Past vs. future total change (%) by species group (East vs West).

The analysis of each past period's total range shifts compared with all future horizons (Figure 10a) evidenced higher positive correlations for western Mediterranean species, except for the BA and the recent Holocene periods (MH and LH). Hence, past range shifts of eastern Mediterranean oaks are more positively correlated to future projections over the last six millennia. Conversely, future range shifts of eastern Mediterranean oaks are more positively correlated to changes suffered in past periods than western ones (Figure 10b). In particular, the eastern species group tends to have higher correlations to past periods in the most extreme climate change scenarios (SSP-370, R^2: 0.60 – 0.70 and especially SSP-585, R^2: 0.79 – 0.80). Conversely, western species have considerably less variability across projected horizons (R^2: 0.31 – 0.37).

Results for the % loss between past and future periods/scenarios revealed remarkably similar results to total area change with positive associations for all species and period combinations (Supplementary Figure S9a). Similarly, the eastern oak species group also showed higher R^2 values (0.36 vs 0.22) than western Mediterranean oaks (Supplementary Figure S9b). When considering the correlation between past and future losses for each past period (Supplementary Figure S10a), results evidenced higher

correlations for the BA, EH and MH periods for eastern species (R^2: 0.48 – 0.49) and, somewhat similarly, the BA, YDS and EH periods for western species (R^2: 0.49 – 0.64).

As for the total loss percentage for the future horizons, we found no substantial change in correlation across scenarios for the western species group (R^2: 0.26 – 0.27), while for the eastern one a strong correlation was found towards the more "extreme" SSP-585 scenario (R^2=0.76; Supplementary Figure S10b).

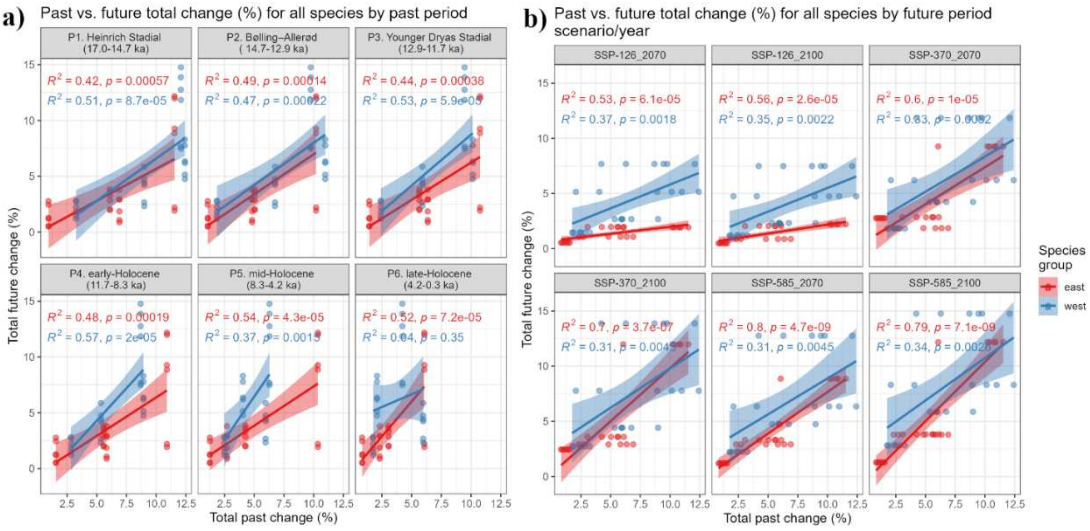


Figure 10 - a) Past vs. future total change (%) for all species by past period; b) - Past vs. future total change (%) for all species by future period scenario/year.

5.5. Discussion

5.5.1. Past and future range shifts

Our results evidence significant correlations between past and future range shifts across the Mediterranean basin for the selected oak species since the Last Glacial Maximum (ca. 20 Kyr). These results also suggest analogous dynamics between western- and eastern-distributed oaks that are phylogenetically and morphologically related (Hipp *et al.*, 2020; Vila-Viçosa *et al.*, 2021). Overall, precipitation variables related to rain availability and seasonality significantly shaped past and future range shifts, followed by the mean diurnal temperature ranges, specifically for *Q. vulcanica* and *Q. pyrenaica*. This output highlights the relevance of future projected changes in precipitation regimes and how these will affect this subset of oaks, calling for conservation measures directed to these species at the local level.

We observed an evident correlation between past and future model projections (See Figures 9 and 10). Similarly, future trends, which reflect a global decrease in rainfall, especially for the worst-case scenarios (SSP585), present higher correlations with past changes (Figure 10b). These correlations are higher in the worsening periods (Bølling-Allerød and Early-Holocene), which supports the hypothesis that past periods with abrupt climate changes and worsening conditions are more correlated and informative regarding (expected) future climatic scenarios.

By incorporating eastern distributed oaks, which are phylogenetically related with the western Mediterranean taxa, we complement previous works on Mediterranean marcescent forests (García-Mijangos *et al.*, 2015; Vila-Viçosa *et al.*, 2020b), while enhancing the knowledge and revamping the remarkable biogeographical vicariance among their species (Humphries *et al.*, 2017). This outcome is observable when considering similarities in the importance of model predictors and the obtained climatic envelopes between *Q. boissieri* and *Q. canariensis* or *Q. vulcanica* and *Q. pyrenaica* (see Figure 2). Notably, the ecological models contribute to validate the subsectional units inside the European white oaks (Denk *et al.*, 2017). Therefore, these oaks, which are morphologically related, enclose two traditionally circumscribed taxonomic groups established by Schwarz (1936a) (*Dascia* vs *Galliferae*) (See Supplementary Data S1). It is also notable that the projections obtained for the eastern oaks inside former Section *Dascia* (*Q. kotschyana* and *Q. vulcanica*) show a remarkable overlap of their individual projected distributions (Supplementary Maps 5, 8, 13 and 16 – Digital Annex). This evidence leverages future analysis about phylogenetic reconstruction among this species. Such analysis should focus putative ancestral or time sequencing relationships among taxa and lineages and how vicariance events affected speciation or the retention of ancestral morphological characteristics between them. This analysis can further be applied between eastern and western subgroups of species and within them, unravelling the biogeographic factors beneath this phenomenon.

Past range shifts highlight southern migrations for most species, except for the cold-tolerant *Q. pyrenaica* in the Younger Dryas and *Q. vulcanica* in the 'recent' Late-Holocene (Supplementary Figure S1; Supplementary Maps 7.4 and 8.4 – Digital Annex) (Kargıoğlu *et al.*, 2009; Vilches *et al.*, 2016). On the other hand, the longitude migration shows a constant migration of *Q. canariensis* towards the east, putatively after a major contraction following the Last Glacial Maximum period and the climatic amelioration of the Bølling-Allerød (Carrión *et al.*, 2010), while most species found climatic suitability towards western longitudes. As for total area change, the past dynamics evidence that

present-day broadly distributed species suffered higher range fluctuations when compared to the narrow-distributed ones (Figure 3; Supplementary Maps 1-8 – Digital Annex). In particular, the paleoclimatic relict *Q. canariensis* shows the highest and most recent fluctuation due to the loss of suitable climatic conditions (Figure 3; Supplementary Map 2 – Digital Annex) entailing a decrease in precipitation seasonality and higher annual rainfall, provided by its predominantly coastal distribution (Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2020b). This loss of climatic suitability is reinforced when we analyse the total loss for *Q. canariensis* especially in the Late-Holocene (Supplementary Figure S2; Supplementary Map 2.1 – Digital Annex).

Future range shifts projected for circummediterranean white oaks evidence significant changes in suitable area, mostly towards northern latitudes, sometimes to areas widely distant from these species' current distributions (Figures 4, 5, 8; Supplementary Figure S3; Supplementary Maps 9-16 – Digital Annex). The widespread *Q. faginea* shows the most extensive changes when considering future climatic scenarios, followed by *Q. pyrenaica* and *Q. infectoria* (Figures 5 and 8; Supplementary Figure S3; Supplementary Maps 11, 12, 15 – Digital Annex). These results highlight that the more ecologically plastic species will potentially suffer greater changes, and suggests that the submediterranean ecotone, dominated by marcescent oaks, may shrink its area. Probably this shrinkage will be followed by suitability lost to dry-adapted Mediterranean and evergreen oaks (Vila-Viçosa *et al.*, 2019; Vila-Viçosa *et al.*, 2020b), despite the evidenced northern migration in terms of climatic suitability. This may lead to a substitution of deciduous oaks in the southern distribution limits of the temperate forests belt by these marcescent oaks (Figures 4 and 5; Supplementary Figure S3; Supplementary Maps 9-16 – Digital Annex).

Past temporal trends in suitable area evidence expected critical scenarios with successive losses for all species from the Bølling-Allerød towards the Early-Holocene. These dynamics vary among species with broader distributions (*e.g., Q. faginea* or *Q. pyrenaica*) when facing narrow-distributed oaks (*Q. kotschyana, Q. canariensis* or *Q. vulcanica*), despite similar observed trends (See Figure 8). For instance, *Q. faginea* and *Q. pyrenaica* evidence more considerable losses in terms of future suitable area, which is translated effectively in the disappearance from areas that correspond to their actual presence (Figure 1; Supplementary Maps 3 and 7 – Digital Annex). At the same time, the attenuated losses presented by *Q. canariensis*, *Q. infectoria* and *Q. boissieri* are related to the significant latitudinal gains in terms projected area for these species. This

fact compensates for the heavy losses presented by the same oaks (Figure 8; Supplementary Maps 9, 10 and 12 – Digital Annex).

5.5.2. Future conservation of sensitive taxa

Sensitive taxa, selected by their narrow distribution or vulnerability, highlight the extreme need to act and monitor their populations, especially considering the 'worst' climatic scenarios (SSP 585). For both elected subregions, sensitive oaks present a constant pattern of higher altitude refugia or northern-driven displacement mainly due to the maintenance of available precipitation. This effect is particularly important for the eastern-distributed *Q. kotschyana* and *Q. vulcanica*, which exhibit significant losses towards the end of the century (See Figures 4, 5, 6, and 8; Supplementary Figure S3). The contraction of *Q. kotschyana* towards higher altitudes of Mount Lebanon may be unbalanced by the inhospitality of depleted soils, decrease of minimal temperatures, and increase in frost-wind damage, which enhances it as a high-priority species for conservation efforts. Likewise, *Q. vulcanica* exhibits a similar pattern with the potential loss of its southeastern subpopulations and maintenance of the northern ones, with a displacement of climatic suitability to the mountain areas of Trabzon (Figures 4, 5, 6 and 8; Supplementary Figure S3). In the western Mediterranean region, the geographically circumscribed *Q. canariensis* appears as the most vulnerable species since the worst-case scenarios for future climatic indicate considerable shrinking of the southwest Iberian and Northern African populations, primarily due to the decrease in annual precipitation. They include the tentative disappearance of the Catalonian subpopulation by 2100 (Figures 4, 5, 7 and 8; Supplementary Figure S3). Also, *Q. lusitanica* contraction patterns highlight a northern-driven migration of its climatic envelope, with the southwestern populations becoming restricted to the higher altitudes of Monchique and Algeciras, followed by a northern-driven shift towards the Northwestern Iberian Peninsula, where winter cold will be absent, and enough amount of annual rainfall will permit its survival. At the same time, all inland populations will lose climatic suitability, including Aracena, São Mamede and most of the Cenozoic Tagus-Sado Basin (Figures 4, 5, 7 and 8; Supplementary Figure S3).

5.5.3. East vs West Mediterranean dynamics

While the association between past and future latitude/longitude shifts are mostly neglectable (Supplementary Figures S4-7), the magnitude of correlations between past and future range shifts is higher (both for total area change and losses). This effect is directly observable for all species and periods, especially for the eastern Mediterranean Oak species (Figures 8 and 10; Supplementary Figures S8 and S9; Supplementary Maps 1-16 – Digital Annex). These results evidence that the eastern subset of oaks that suffered major changes in the past are susceptible to the most significant future changes, especially across the Holocene (EH to MH and LH). This period between the Early and Middle Holocene is known for a growing decrease in white oak forests, up to 60-80% in the Middle East (Dormoy *et al.*, 2009), which confirms these total changes (Figure 10a) and especially the losses in climatically suitable area (Supplementary Figure S10a). Likewise, future range shifts of eastern Mediterranean oaks are also more positively correlated with total changes and losses suffered in past periods, and this is particularly relevant for the losses in the worst-case scenarios (SSP 370 and 585) (See Figures 10b and Supplementary Figure S10b). These results become quite interesting since future scenarios seem to emulate the same magnitude of range shifts and losses in climatic suitability that this subgroup of oaks (Eastern Mediterranean) experienced from the Middle Holocene towards the present, highlighting the predictive capability of the models. Conversely, western-distributed species presented higher correlations in the Heinrich Stadial and the Younguer Dryas (Figure 10a), corroborating the largest bloom of temperate forests in the Near East in the Bølling-Allerød period (Dormoy *et al.*, 2009). This is supported by the higher correlation in distribution losses in the BA observed for the Western Mediterranean species (Supplementary Figure S10a).

Globally, the east and western Mediterranean oaks' expansions and contractions support the paleoenvironmental reconstructions brought by palynological data. On the one hand, the Early to Mid-Holocene, in the western Mediterranean basin, showed an increase in summer rainfall and, at the same time, cooler summers (Dormoy *et al.*, 2009; Baldini *et al.*, 2019), which favored the Iberian white oaks expansion and maintenance in the edge of their distributions (Vila-Viçosa *et al.*, 2020b). On the other hand, the near east witnessed a contemporary decrease in summer precipitation, with a dry interval at 6.5 Kyr observed in Turkey (Roberts *et al.*, 2001). This effect evidences a decreasing humidity gradient, especially in summer precipitation, from West to Eastern Mediterranean areas, as suggested by Dormoy *et al.* (2009). This effect is reflected in the higher correlation values in past (MH to EH) to future trajectories, for the eastern

Mediterranean oaks. Consequently, this explains the higher predictive power of the past range-shifts towards the future scenarios presented by these species, and vice-versa, whereas future range shifts are also more positively correlated with changes suffered in the past (Figure 10).

5.5.4. Vicariance Biogeography

The models' performance (Supplementary Table S4), denote a high species filiation to well defined bioclimatic and biogeographic gradients, while climatic overlap of *Q. boissieri* and *Q. canariensis* (Figure 2) suggests vicariance between both subregions. This bioclimatic pattern corresponds to the well-known East-West Mediterranean (or amphi-Mediterranean) biogeographic outline, by which lineages show current distributions at both extremes of the longitudinal axis of the Mediterranean basin, and a gap of occurrences in between (Willkomm, 1896; Lumaret & Lobo, 1996; Nieto-Feliner, 2014). The origin of the pattern has been hypothesised as result of fragmentation of Tertiary circum-mediterranean Laurel Forest biome and related thermophilic-mesophytic communities (Kalkman, 1966; Mai, 1989; Thompson, 2020). Climatic deterioration, with increasingly cooler and drier conditions since late Pliocene and during the Quaternary glaciations, would have led to species extirpation and biotic replacement affecting most precedent mesic and warmth-loving communities, while a few relict lineages managed to remain in western and eastern glacial refugia that harboured suitable environmental conditions (Mai, 1989; Denk *et al.*, 2001; Denk *et al.*, 2019). Consequently, the pattern can be found in some broadleaf evergreen woody elements with sister lineages occurring at the extremes of the Mediterranean basin, sometimes with Macaronesian outposts. Typical examples are the sister species *Prunus lusitanica* and *P. laurocerasus* (Bortiri et al., 2002; Calleja et al., 2009), the group of hollies that includes *Ilex aquifolium, I. perado* and *I. colchicum* (Manen *et al.*, 2010; Yao *et al.*, 2021), the western and eastern subspecies of *Rhodondendrum ponticum* (Ferrer-Gallego & Laguna, 2018), or the phylogeographic disjunction within *Buxus sempervirens* (Rossello *et al.*, 2007). The pattern is also found in perennial herbs as *Erophaca* (Casimiro-Soriguer *et al.*, 2010) or the basal most clade of the speciose genus *Campanula* s.l, with a western lineage including the SW Iberian-NW African *C. primulifolia-C. alata* group and the Macaronesian genus *Musschia*, and an eastern lineage including *C. lactiflora*, *C. peregrina* and *C. axilaris* from the Near East, Balkan and Black sea areas (Mansion *et al.*, 2012). Most of these taxa appear in relatively warm mesophytic habitats with deciduous and lauroid elements, and it is remarkable how their distribution pattern broadly overlaps with the

areas with highest habitat suitability inferred for *Q. canariensis* and *Q. boissieri*. It emphasises the role as glacial refugia and the relict character of these oak forests, as well as its connection to plant communities with Tertiary and sub-tropical elements, otherwise common in Atlantic areas with mild climates (Svenning, 2003; Rodríguez-Sánchez & Arroyo, 2011; Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2020b). Nevertheless, other historical processes have been invoked to explain the East-West Mediterranean pattern, particularly when it applies to taxa with arid environmental envelopes. In these cases, current disjunct ranges in western Mediterranean areas probably arose after dispersal from Asian deserts during cold and dry Pleistocene periods, as it was suggested for both plant and animal taxa (Sanmartín, 2003; Kadereit & Yaprak, 2008). More work is needed to unravel the different underlying processes of the complex biogeography of the Mediterranean. Meanwhile the vicariant bioclimatic envelopes of *Q. canariensis* and *Q. boissieri* recovered by our analyses (Figure 2), and the projected overlap of the individual modelling *Q. kotschyana* and *Q. vulcanica* in the Near East, which are also projected in the native area of *Q. frainetto* (Supplementary Maps 5, 8, 13 and 16 – Digital Annex), suggest niche conservatism of relict environmental conditions. Thus, this offers additional hypothesizing and scientific questioning to support to late Neogene climatic deterioration and subsequent distribution disruption as explanatory suggestion for the East-West biogeographic pattern.

5.5.5. Future conservation perspectives

Our projected past and future climatic refugia highlight the biogeographic areas that will likely provide climatic stability and persistence for the studied species and their forests. These refugia include new areas with climatic suitability for vulnerable taxa that were otherwise inhospitable by an adverse regional climate. The maintenance of these areas, which include past and future climatic refugia, are fundamental for conservation networks, climate change management and decision planning (Fordham *et al.*, 2016), and of vital importance for conserving biodiversity in the long run (Keppel & Wardell-Johnson, 2012; Davis *et al.*, 2013). The protection of these essential relicts and biogeographic transitional forests (Vila-Viçosa *et al.*, 2020b) is of paramount importance, since they are enclosed in a major phylogeographic hotspot with high diversity levels (Médail & Baumel, 2018). These diversity levels includes not only their own endemic lineages but, at the same time, all the genetic diversity from its adjacent areas, thus

serving as refugia in the face of anthropogenic climatic transition (De Dios *et al.*, 2006; Barrett & Schluter, 2008; Keppel *et al.*, 2012; Carnaval *et al.*, 2014; Yannic *et al.*, 2014).

Our work also outlines that biological data quality is crucial for developing modelling frameworks that feed conservation planning and decision-making. Future improvements should include unrepresented taxa that received dubious and still have unsolved nomenclatural and taxonomic delimitation (See Supplementary Data S1) (Vila-Viçosa *et al.*, 2022). Here, the role of fieldwork, botanical expeditions and the deep study of biological collections kept in Natural History Museums and Herbaria are fundamental to tackle the societal challenges of the 'biodiversity crisis' (Nogués-Bravo *et al.*, 2018). The minutiae associated with accurate biological records are crucial to provide accurate spatial and temporal projections that can better depict the ecological drivers shaping biogeographic and evolutionary responses to past climate changes. In turn, as Fordham *et. al.* (2017) suggested, this will help to predict how species respond to future climatic modifications. This is especially relevant for the most significant and contrasting periods of the recent deglaciation event of the Late Quaternary, in the face of the limited use of the more common static and narrow environments of the Last Glacial Maximum (ca. 21 Ka) and Middle Holocene (8.326-4.2 Kyr) (Walas *et al.*, 2019; Dagtekin *et al.*, 2020; Salvà-Catarineu *et al.*, 2021). This is also especially important once we can analyze a higher and more continuous number of intervals/periods (Fordham *et al.*, 2017), which better depict distinct scenarios related with climatic amelioration or worsening, bringing more accuracy to evaluate past-to-future trajectories.

5.6. Conclusions

The use of retrospective information from hindcasted SDMs helped to improve projections about how climatic shifts will hard-hit vulnerable oaks across the Mediterranean Basin towards the end of the 21st century. Although using SDMs to develop strategies that may inform policies aiming to reduce biodiversity loss is not novel, the idea of looking into past processes to predict how they can predict future responses to climate change remains underdeveloped. Here, we fulfilled this gap in which evidence of past range shifts might be used to gain deeper insights into the likely effects of future shifts in climate on eight circummediterranean white oaks, and consequently foresee the preservation of their forests. The model's performance and the importance of climatic variables, mostly related to precipitation availability and seasonality, enables oaks to

become model species to undergo paleobiogeographic assessments, with further insights into their demographic and evolutionary history, especially in transitional areas that cross two major biogeographic subregions across southern Europe, North Africa and the Near East.

In what concerns the four narrowly distributed taxa, model projections for the worst future scenarios (*Q. canariensis, Q. lusitanica, Q. kotschyana* and *Q. vulcanica*) evidenced significant losses in suitable area and vast range shifts, especially towards higher latitiudes and coastal areas. These results highlights these species as priority conservation targets, namely *Q. kotschyana, Q. vulcanica* and *Q. canariensis*. Thus, their conservation status at the IUCN level should be revisited (Carrero *et al.*, 2020). Not only do they already present narrowly distributed and reduced populations, but simultaneously evidence disproportionate range shifts, namely to areas where the species do not exist and cannot reach naturally by themselves, demanding human and conservation planning efforts.

We advocate that this approach, relating past range shifts with future scenarios, should be broadly implemented to better inform policies that will help overcome the human-driven loss of plant diversity, resulting in effective conservation strategies for conservation of the Mediterranean Biome.

5.7. References

Acharya RP, Maraseni T, Cockfield G. 2019. Global trend of forest ecosystem services valuation–An analysis of publications. *Ecosystem Services* **39**: 100979.

Aldrich PR, Cavender-Bares J 2011. Quercus. *Wild crop relatives: Genomic and breeding resources*: Springer, 89-129.

Allan RP, Hawkins E, Bellouin N, Collins B. 2021. IPCC, 2021: Summary for Policymakers.

Araújo MB, Nogués-Bravo D, Diniz-Filho JAF, Haywood AM, Valdes PJ, Rahbek C. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography* **31**(1): 8-15.

Arslan M, Karataş R, Güner ŞT, Özkan K, Toprak O, Müdürlüğü EAE. 2015. Threat categories and endemism status of plants in the distibution areas of pulley oak in the Lakes District. *BioDiCon (Biological Diversity and Conservation)* **8**(1): 7-15.

Atalay I, Efe R. 2010. Structural and distributional evaluation of forest ecosystems in Turkey. *Journal of Environmental Biology* **31**(1): 61.

Avcı M. 1996. Endemik bir meşe türü, kasnak meşesi (Quercus vulcanica (Boiss. Heldr. ex) Kotschy)'nin Türkiye'deki yeni bir yayılış alanı. *Türk Coğrafya Dergisi*(31): 283-289.

Avishai M. 1967. *Taxonomic-Geographic Studies in the Middle East Oaks.* Master, The Hebrew University of Jerusalem Jerusalem.

Axelrod DI. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden*: 629-657.

Aydınözü D. 2004. Kasnak meşesi (quercus vulcanica (boiss. and heldr. ex) kotschy)'nin Türkiye'deki ikinci yeni bir yayılış alanı.

Aznar-Sánchez JA, Belmonte-Ureña LJ, López-Serrano MJ, Velasco-Muñoz JF. 2018. Forest ecosystem services: An analysis of worldwide research. *Forests* **9**(8): 453.

Babali B, Hasnaoui A, Medjati N, Bouazza M. 2013. Note on the vegetation of the mounts of tlemcen (Western Algeria): Floristic and phytoecological aspects. *Open Journal of Ecology* **3**(05): 370.

Baldini LM, Baldini JU, McDermott F, Arias P, Cueto M, Fairchild IJ, Hoffmann DL, Mattey DP, Müller W, Nita DC. 2019. North Iberian temperature and rainfall seasonality over the Younger Dryas and Holocene. *Quaternary Science Reviews* **226**: 105998.

Barbéro M, Loisel R, Quézel P, Richardson DM, Romane F. 1998. Pines of the Mediterranean basin. *Ecology and biogeography of Pinus*: 153-170.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**(2): 327-338.

Barrett RD, Schluter D. 2008. Adaptation from standing genetic variation. *Trends in ecology & evolution* **23**(1): 38-44.

Battandier JA, Trabut LC. 1905. *Flore analytique et synoptique de l'Algérie et de la Tunisie.* . Argel: Vve Giralt, Imprimeur-Éditeur.

Bellard C, Leclerc C, Leroy B, Bakkenes M, Veloz S, Thuiller W, Courchamp F. 2014. Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography* **23**(12): 1376-1386.

Blair ME, Le MD, Xu M. 2022. Species distribution modeling to inform transboundary species conservation and management under climate change: promise and pitfalls. *Frontiers of Biogeography* **14**(1): 1-11.

Blanco-Castro E, Casado-Gonzáles M, Costa-Tenorio M, Escribano R, García-Antón M, Génova-Fuster M, Gómez-Mazaneque Á, Gómez-Mazaneque F, Moreno-Saiz JC, Juaristi CM, et al. 2005. *Los bosques ibéricos. Una interpretación geobotánica*. Barcelona: Editorial Planeta, Barcelona, Spain.

Boissier E. 1853. *Diagnoses plantarum orientalium novarum.... Ser. 1: Vol. secundum: Fasc. No. 12*: Wolfrath.

Bortiri E, Oh SH, Gao FY, Potter D. 2002. The phylogenetic utility of nucleotide sequences of sorbitol 6-phosphate dehydrogenase in Prunus (Rosaceae). *American Journal of Botany* **89**(10): 1697-1708.

Box EO, Fujiwara K. 2016. *Warm-temperate deciduous forests around the Northern Hemisphere*: Springer.

Brown JL, Hill DJ, Dolan AM, Carnaval AC, Haywood AM. 2018. PaleoClim, high spatial resolution paleoclimate surfaces for global land areas. *Scientific data* **5**(1).

Brunialti G, Frati L. 2021. Modeling of Species Distribution and Biodiversity in Forests. *Forests* **12**(3): 319.

Calleja JA, Benito Garzón M, Sáinz Ollero H. 2009. A Quaternary perspective on the conservation prospects of the Tertiary relict tree Prunus lusitanica L. *Journal of Biogeography* **36**(3): 487-498.

Capelo JH, Costa JC, Lousã MF, Mesquita S. 2002. A aliança Quercion fruticosae Rothmaler 1954 em. Rivas-Martínez, Lousã, T.E. Díaz, Fernández-González & J.C. Costa 1990. *Quercetea* **3**: 99-110.

Carapeto A, Francisco A, Pereira P, Porto M 2020. Lista vermelha da flora vascular de Portugal Continental: Sociedade Portuguesa de Botânica, Associação Portuguesa de Ciência da ….

Carnaval AC, Waltari E, Rodrigues MT, Rosauer D, Vanderwal J, Damasceno R, Prates I, Strangas M, Spanos Z, Rivera D, et al. 2014. Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal Society B: Biological Sciences* **281**(1792): 20141461.

Carrero C, Jerome D, Beckman E, Byrne A, Coombes A, Deng M, González-Rodríguez A, Hoang V, Khoo E, Nguyen N. 2020. The red list of oaks 2020. *The Morton Arboretum: Lisle, IL, USA*: 11-12.

Carrión JS, Fernández S, González-Sampériz P, Gil-Romera G, Badal E, Carrión-Marco Y, López-Merino L, López-Sáez JA, Fierro E, Burjachs F. 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Review of Palaeobotany and Palynology* **162**(3): 458-475.

Casimiro-Soriguer R, Talavera M, Balao F, Terrab A, Herrera J, Talavera S. 2010. Phylogeny and genetic structure of Erophaca (Leguminosae), a East–West Mediterranean disjunct genus from the Tertiary. *Molecular phylogenetics and evolution* **56**(1): 441-450.

Castagneri D, Carrer M, Regev L, Boaretto E. 2020. Precipitation variability differently affects radial growth, xylem traits and ring porosity of three Mediterranean oak species at xeric and mesic sites. *Science of The Total Environment* **699**: 134285.

Chakraborty D, Móricz N, Rasztovits E, Dobor L, Schueler S. 2021. Provisioning forest and conservation science with high-resolution maps of potential distribution of major European tree species under climate change. *Annals of Forest Science* **78**(2).

Cody ML 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. In: Soule ME ed. *Conservation biology : the science of scarcity and diversity*. Sunderland, Mass. (USA): Sinauer Associates.

Costa JC, Monteiro-Henriques T, Bingre P, Espírito-Santo D 2015. Warm-temperate forests of central Portugal: a mosaic of syntaxa. *Warm-temperate deciduous forests around the Northern hemisphere*: Springer, 97-117.

Coutinho AXP. 1888. Os Quercus de Portugal. *Boletim da Sociedade Broteriana* **6**: 47-116.

Cowling RM, Potts AJ, Bradshaw PL, Colville J, Arianoutsou M, Ferrier S, Forest F, Fyllas NM, Hopper SD, Ojeda F. 2015. Variation in plant diversity in mediterranean-climate ecosystems: The role of climatic and topographical stability. *Journal of Biogeography* **42**(3): 552-564.

Cramer W, Guiot J, Fader M, Garrabou J, Gattuso J-P, Iglesias A, Lange MA, Lionello P, Llasat MC, Paz S, et al. 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change* **8**(11): 972-980.

Dagtekin D, Şahan EA, Denk T, Köse N, Dalfes HN. 2020. Past, present and future distributions of Oriental beech (Fagus orientalis) under climate change projections. *PloS one* **15**(11): e0242280.

Davis J, Pavlova A, Thompson R, Sunnucks P. 2013. Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Global Change Biology* **19**(7): 1970-1984.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2006. Hybrid zones between two European oaks: a plant community approach. *Plant Ecology* **187**(1): 109-125.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology* **204**(2): 189-205.

Del Río S, Penas Á. 2006. Potential distribution of semi-deciduous forests in Castile and Leon (Spain) in relation to climatic variations. *Plant Ecology* **185**(2): 269-282.

Denk T, Frotzler N, Davitashvili N. 2001. Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). *Biological journal of the Linnean Society* **72**(2): 287-332.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Denk T, Güner HT, Bouchal JM. 2019. Early Miocene climate and biomes of Turkey: Evidence from leaf fossils, dispersed pollen, and petrified wood. *Palaeogeography, Palaeoclimatology, Palaeoecology* **530**: 236-248.

Di Pietro R, Conte AL, Di Marzio P, Fortini P, Farris E, Gianguzzi L, Müller M, Rosati L, Spampinato G, Gailing O. 2021. Does the genetic diversity among pubescent white oaks in southern Italy, Sicily and Sardinia islands support the current taxonomic classification? *European Journal of Forest Research* **140**(2): 355-371.

Dormoy I, Peyron O, Combourieu Nebout N, Goring S, Kotthoff U, Magny M, Pross J. 2009. Terrestrial climate variability and seasonality changes in the Mediterranean region between 15 000 and 4000 years BP deduced from marine pollen records. *Climate of the Past* **5**(4): 615-632.

Douaihy B, Saliba C, Stephan J, Simeone MC, Cardoni S, Farhat P, Bou Dagher Kharrat M. 2020. Tracking diversity and evolutionary pathways of Lebanese oak taxa through plastome analyses. *Botany Letters* **167**(3): 315-330.

Ducousso A. 2012. Endangered Oak Resources in Europe and Around the Mediterranean Basin: Marginal Populations and Minor Species. *International Oaks* **24**: 108-115.

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**(9): 479-486.

Ferraz KMPMdB, Morato RG, Bovo AAA, da Costa COR, Ribeiro YGG, de Paula RC, Desbiez ALJ, Angelieri CSC, Traylor-Holzer K. 2021. Bridging the gap between researchers, conservation planners, and decision makers to improve species conservation decision-making. *Conservation Science and Practice* **3**(2): e330.

Ferrer-Gallego PP, Laguna E. 2018. (2663) Proposal to conserve the name Rhododendron ponticum (Ericaceae) with a conserved type. *Taxon* **67**(6): 1226-1227.

Fordham DA, Akçakaya HR, Alroy J, Saltré F, Wigley TM, Brook BW. 2016. Predicting and mitigating future biodiversity loss using long-term ecological proxies. *Nature Climate Change* **6**(10): 909-916.

Fordham DA, Brook BW, Moritz C, Nogués-Bravo D. 2014. Better forecasts of range dynamics using genetic data. *Trends in ecology & evolution* **29**(8): 436-443.

Fordham DA, Jackson ST, Brown SC, Huntley B, Brook BW, Dahl-Jensen D, Gilbert MTP, Otto-Bliesner BL, Svensson A, Theodoridis S. 2020. Using paleo-archives to safeguard biodiversity under climate change. *Science* **369**(6507): eabc5654.

Fordham DA, Saltré F, Haythorne S, Wigley TML, Otto-Bliesner BL, Chan KC, Brook BW. 2017. PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. *Ecography* **40**(11): 1348-1358.

Forester BR, DeChaine EG, Bunn AG. 2013. Integrating ensemble species distribution modelling and statistical phylogeography to inform projections of climate change impacts on species distributions. *Diversity and Distributions* **19**(12): 1480-1495.

Fyllas NM, Troumbis AY. 2009. Simulating vegetation shifts in north-eastern Mediterranean mountain forests under climatic change scenarios. *Global Ecology and Biogeography* **18**(1): 64-77.

García-Mijangos I, Campos JA, Biurrun I, Herrera M, Loidi J 2015. Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: Box EO, Fujiwara K eds. *Warm-temperate deciduous forests around the Northern hemisphere*. London: Springer, 119-138.

Ghazal A. 2008. Landscape ecological, phytosociological and geobotanical study of eumediterranean in west of Syria.

Guisan A, Edwards Jr TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological modelling* **157**(2-3): 89-100.

Guisan A, Thuiller W, Zimmermann NE. 2017. *Habitat suitability and distribution models: with applications in R*: Cambridge University Press.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hájek M, Dudová L, Hájková P, Roleček J, Moutelíková J, Jamrichová E, Horsák M. 2016. Contrasting Holocene environmental histories may explain patterns of species richness and rarity in a Central European landscape. *Quaternary Science Reviews* **133**: 48-61.

Hedge I, Yaltırık F. 1982. Quercus L. *Flora of Turkey and the East Aegean Islands* **7**: 659-683.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**(15): 1965-1978.

Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl A, Deng M, Denk T, Fitz-Gibbon S. 2020. Genomic landscape of the global oak phylogeny. *New Phytologist* **226**(4): 1198-1212.

Holm SR, Svenning J-C. 2014. 180,000 years of climate change in Europe: avifaunal responses and vegetation implications. *PloS one* **9**(4): e94021.

Humphries CJ, Escudero M, Martín-Bravo S 2017. Vicariance biogeography. In: Roitberg B ed. *Reference Module in Life Sciences*. Cambridge, UK: Elsevier, 1-13.

Jablonski E. 2016. Karl Georg Theodor Kotschy and the Kotschy Oak.

Kadereit G, Yaprak AE 2008. " Microcnemum coralloides"(Chenopodiaceae-Salicornioideae): an example of intraspecific East-West disjunctions in the Mediterranean region. *Anales del Jardín Botânico De Madrid*: Real Jardín Botánico. 415-426.

Kalkman C. 1966. The Old World species of Prunus subg. Laurocerasus including those formerly referred to Pygeum. *Blumea: Biodiversity, Evolution and Biogeography of Plants* **13**(1): 1-115.

Karam F, Doulis A, Ozturk M, Dogan Y, Sakcali S. 2011. Eco - physiological behaviour of two woody oak species to combat desertification in the east Mediterranean-a case study from Lebanon. *Procedia - Social and Behavioral Sciences* **19**: 787-796.

Kargıoğlu M, Şenkul Ç, Serteser A, Konuk M. 2009. Bioclimatic requirements of Quercus vulcanica Boiss et Heldr. ex Kotschy an endemic species in Turkey. *Polish Journal of Ecology* **57**(1): 197-200.

Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* **21**(4): 393-404.

Keppel G, Wardell-Johnson GW. 2012. Refugia: keys to climate change management. *Global Change Biology* **18**(8): 2389-2391.

Ketenoglu O, Tug G, Bingol U, Geven F, Kurt L, Guney K. 2010. Synopsis of syntaxonomy of Turkish forests. *Journal of Environmental Biology* **31**(1): 71.

Klausmeyer KR, Shaw MR. 2009. Climate change, habitat loss, protected areas and the climate adaptation potential of species in Mediterranean ecosystems worldwide. *PloS one* **4**(7): e6392.

Kotschy T. 1862. *Die Eichen Europa's und des Orient's*. Wien und Olmütz: E. Hölzel.

Lamarck JB. 1785. *Encyclopédie méthodique. Botanique*. Paris: Panckoucke.

Leroy T, Louvet JM, Lalanne C, Le Provost G, Labadie K, Aury JM, Delzon S, Plomion C, Kremer A. 2020. Adaptive introgression as a driver of local adaptation to climate in European white oaks. *New Phytologist* **226**(4): 1171-1182.

Lloret F, Jaime L, Margalef-Marrase J, Pérez-Navarro M, Batllori E. 2022. Short-term forest resilience after drought-induced die-off in Southwestern European forests. *Science of The Total Environment* **806**: 150940.

Lowe JJ, Walker MJ. 1984. *Reconstructing Quaternary Environments*: London.

Ludwig P, Shao Y, Kehl M, Weniger G-C. 2018. The Last Glacial Maximum and Heinrich event I on the Iberian Peninsula: A regional climate modelling study for understanding human settlement patterns. *Global and Planetary Change* **170**: 34-47.

Lumaret J-P, Lobo JM. 1996. Geographic distribution of endemic dung beetles (Coleoptera, Scarabaeoidea) in the Western Palaearctic region. *Biodiversity Letters*: 192-199.

Maguire KC, Nieto-Lugilde D, Fitzpatrick MC, Williams JW, Blois JL. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. *Annual Review of Ecology, Evolution, and Systematics* **46**: 343-368.

Mai DH 1989. Development and regional differentiation of the European vegetation during the Tertiary. *Woody plants—evolution and distribution since the Tertiary*: Springer, 79-91.

Maiorano L, Cheddadi R, Zimmermann N, Pellissier L, Petitpierre B, Pottier J, Laborde H, Hurdu B, Pearman P, Psomas A. 2013. Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. *Global Ecology and Biogeography* **22**(3): 302-317.

Manel S, Williams HC, Ormerod SJ. 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**(5): 921-931.

Manen J-F, Barriera G, Loizeau P-A, Naciri Y. 2010. The history of extant Ilex species (Aquifoliaceae): evidence of hybridization within a Miocene radiation. *Molecular phylogenetics and evolution* **57**(3): 961-977.

Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). *Molecular phylogenetics and evolution* **12**(3): 333-349.

Manos PS, Stanford AM. 2001. The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. *International Journal of Plant Sciences* **162**(S6): S77-S93.

Mansion G, Parolly G, Crowl AA, Mavrodiev E, Cellinese N, Oganesian M, Fraunhofer K, Kamari G, Phitos D, Haberle R. 2012. How to handle speciose clades? Mass taxon-sampling as a strategy towards illuminating the natural history of Campanula (Campanuloideae). *PloS one* **7**(11): e50076.

Margalef-Marrase J, Pérez-Navarro MÁ, Lloret F. 2020. Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species. *Global Change Biology* **26**(5): 3134-3146.

McSweeney C, Jones R, Lee RW, Rowell D. 2015. Selecting CMIP5 GCMs for downscaling over multiple regions. *Climate dynamics* **44**(11): 3237-3260.

Médail F, Baumel A. 2018. Using phylogeography to define conservation priorities: The case of narrow endemic plants in the Mediterranean Basin hotspot. *Biological Conservation* **224**: 258-266.

Médail F, Monnet A-C, Pavon D, Nikolic T, Dimopoulos P, Bacchetta G, Arroyo J, Barina Z, Albassatneh MC, Domina G. 2019. What is a tree in the Mediterranean Basin hotspot? A critical analysis. *Forest Ecosystems* **6**(1): 1-19.

Medail F, Quezel P. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden*: 112-127.

Meddour R, Meddour-Sahar O, Zeraia L, Mucina L. 2017. Syntaxonomic synopsis of the forest and tall scrub vegetation of Northern Algeria. *Lazaroa* **38**(2): 127-163.

Meikle RD. 1985. *Flora of Cyprus 2*. London: Royal Botanic Gardens, Kew.

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C 2011. Global biodiversity conservation: the critical role of hotspots. *Biodiversity hotspots*: Springer, 3-22.

Molina-Venegas R, Ramos-Gutiérrez I, Moreno-Saiz JC. 2020. Phylogenetic Patterns of Extinction Risk in the Endemic Flora of a Mediterranean Hotspot as a Guiding Tool for Preemptive Conservation Actions. *Frontiers in Ecology and Evolution* **8**: 571587.

Mori AS, Lertzman KP, Gustafsson L. 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology* **54**(1): 12-27.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**(6772): 853-858.

Nieto-Feliner G 2014. Patterns and processes in plant phylogeography in the Mediterranean Basin: a review. Perspect Pl Ecol Evol Syst 16: 265–278.

Nixon KC 2006. Global and neotropical distribution and diversity of oak (genus Quercus) and oak forests. *Ecology and Conservation of Neotropical Montane Oak Forests*: Springer, 3-13.

Nogués-Bravo D, Rodríguez-Sánchez F, Orsini L, de Boer E, Jansson R, Morlon H, Fordham DA, Jackson ST. 2018. Cracking the code of biodiversity responses to past climate change. *Trends in ecology & evolution* **33**(10): 765-776.

Olivier GA. 1807. *Voyage dans l'empire Othoman*. Paris: Henri Agasse.

Öney SB, Nihal Ö, Gugger PF, Özkan K. 2020. Endemik kasnak meşesinin (Quercus vulcanica [Boiss. et Heldr. ex] Kotschy) yeni bir yayılış alanı. *Turkish Journal of Forestry* **21**(1): 6-14.

Ordonez A, Svenning J-C. 2015. Geographic patterns in functional diversity deficits are linked to glacial-interglacial climate stability and accessibility. *Global Ecology and Biogeography* **24**(7): 826-837.

Pearman PB, Randin CF, Broennimann O, Vittoz P, Knaap WO, Engler R, Lay GL, Zimmermann NE, Guisan A. 2008. Prediction of plant species distributions across six millennia. *Ecology letters* **11**(4): 357-369.

Pearson R. 1965. Problems of post-Glacial refugia. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **161**(984): 324-330.

Quézel P, Médail F. 2003. *Ecologie et biogéographie des forêts du bassin méditerranéen*: Elsevier Paris.

Quézel P, Médail F, Loisel R, Barbero M. 1999. Biodiversity and conservation of forest species in the Mediterranean basin. *UNASYLVA-FAO*-: 21-28.

Regato P. 2001. The Mediterranean Forests, a New Conservation Strategy. *WWF-MedPO Ed, Rome*.

Rivas-Martínez S, González-Días TE, González FF, Loidi JJ, Lousã MF, Merino ÁP. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica*(15): 433-922.

Rivas-Martínez S, Penas A, del Río S, González T, Rivas-Sáenz S 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 29-80.

Rivas-Martínez S, Penas A, González TED, Cantó P, del Río S, Costa JC, Herrero L, Molero J 2017. Biogeographic Units of the Iberian Peninsula and Baelaric Islands to District Level. A Concise Synopsis. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 131-188.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rivas Martínez S, Rivas Sáenz S, Penas Á, del Río S 2011. Biogeographic map of Europe. Second concise advance. *1st International Symposium of the FIP - Global Strategy for plant conservation*. Valencia: Società Italiana Scienza della Vegetazione.

Roberts N, Reed J, Leng M, Kuzucuoğlu C, Fontugne M, Bertaux J, Woldring H, Bottema S, Black S, Hunt E. 2001. The tempo of Holocene climatic change in the eastern Mediterranean region: new high-resolution crater-lake sediment data from central Turkey. *The Holocene* **11**(6): 721-736.

Robles S, Barrón E, Cebolla C. 2013. Estudio paleobotánico preliminar del afloramiento plioceno de Camp dels Ninots (Caldes de Malavella, Girona, España). Macroflora del sector de Can Argilera. *Soc. Esp. Hist. Nat. Sec. Geol* **17**: 75-89.

Rodrıguez-Sánchez F, Arroyo J. 2011. Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past. *Climate change, ecology and systematics*: 280-303.

Rodríguez-Sánchez F, Arroyo J. 2011. Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past. *Climate change, ecology and systematics*: 280-303.

Rodríguez-Sánchez F, Hampe A, Jordano P, Arroyo J. 2010. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Review of Palaeobotany and Palynology* **162**(3): 507-521.

Rossello JA, Lazaro A, Cosín R, Molins A. 2007. A phylogeographic split in Buxus balearica (Buxaceae) as evidenced by nuclear ribosomal markers: when ITS paralogues are welcome. *Journal of Molecular Evolution* **64**(2): 143-157.

Safford HD, Vallejo VR 2019. Ecosystem management and ecological restoration in the Anthropocene: integrating global change, soils, and disturbance in boreal and Mediterranean forests. *Developments in Soil Science*: Elsevier, 259-308.

Sala OE, Chapin FS, Huber-Sannwald E 2001. Potential biodiversity change: global patterns and biome comparisons. *Global Biodiversity in a Changing Environment*: Springer, 351-367.

Salleo S, Pitt F, Nardini A, Hamzé M, Jomaa I. 2002. Differential drought resistance of two Mediterranean oaks growing in the Bekaa Valley (Lebanon). *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology* **136**(1): 91-99.

Saltré F, Rodríguez-Rey M, Brook BW, Johnson CN, Turney CS, Alroy J, Cooper A, Beeton N, Bird MI, Fordham DA. 2016. Climate change not to blame for late Quaternary megafauna extinctions in Australia. *Nature communications* **7**(1): 1-7.

Salvà-Catarineu M, Romo A, Mazur M, Zielińska M, Minissale P, Dönmez AA, Boratyńska K, Boratyński A. 2021. Past, present, and future geographic range of the relict Mediterranean and Macaronesian Juniperus phoenicea complex. *Ecology and Evolution* **11**(10): 5075-5095.

Sampaio G. 1910. Nota a propósito dos Quercus lusitanica Lamk., Q. humilis Lamk e Quercus faginea, Lamk. . *Annaes Scientificos da Academia Polytechnica do Porto* **5**(3): 161-165.

Sandel B, Arge L, Dalsgaard B, Davies R, Gaston K, Sutherland W, Svenning J-C. 2011. The influence of Late Quaternary climate-change velocity on species endemism. *Science* **334**(6056): 660-664.

Sanmartín I. 2003. Dispersal vs. vicariance in the Mediterranean: historical biogeography of the Palearctic Pachydeminae (Coleoptera, Scarabaeoidea). *Journal of Biogeography* **30**(12): 1883-1897.

Sanz-Arnal M, Benítez-Benítez C, Miguez M, Jiménez-Mejías P, Martín-Bravo S. 2022. Are Cenozoic relict species also climatic relicts? Insights from the macroecological evolution of the giant sedges of Carex sect. Rhynchocystis (Cyperaceae). *American Journal of Botany* **109**(1): 115-129.

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O. 1936a. Entwurf zu einem natürlichen System der Cupuliferen und der Gattung Quercus L. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*: 1-22.

Schwarz O. 1936b. Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* **8**: 65–100.

Spach É. 1842. *Histoire naturelle des végétaux: Phanérogames. Vol. 11. Librairie encyclopédique de Roret, Paris*. Paris.

Stephan J. 2018. Quercus kotschyana. The IUCN Red List of Threatened Species 2018:.

Stephan J, Chayban L, Vessella F. 2016. Abiotic factors affecting the distribution of oaks in Lebanon. *Turkish Journal of Botany* **40**(6): 595-609.

Stephan J, Teeny P. 2017. Revealing the taxonomy of an endemic oak of Lebanon. *Pl Sociol* **54**(Suppl. 1): 97-100.

Stephan JM, Teeny PW, Vessella F, Schirone B. 2018. Oak morphological traits: between taxa and environmental variability. *Flora* **243**: 32-44.

Stewart JR, Lister AM, Barnes I, Dalén L. 2010. Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B: Biological Sciences* **277**(1682): 661-671.

Svenning J-C, Fløjgaard C, Marske KA, Nógues-Bravo D, Normand S. 2011. Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* **30**(21-22): 2930-2947.

Svenning JC. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology letters* **6**(7): 646-653.

Svenning JC, Skov F. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography* **16**(2): 234-245.

Taleb MS, Fennane M. 2019. *Vascular plant communities of Morocco*: Springer.

Thiers B 2022. Index Herbariorum: a global directory of public herbaria and associated staff. . New York Botanical Garden's Virtual Herbarium.

Thompson JD. 2020. *Plant evolution in the Mediterranean: insights for conservation*: Oxford University Press, USA.

Thuiller W, Lafourcade B, Engler R, Araújo MB. 2009. BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography* **32**(3): 369-373.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

Ugurlu E, Senol SG. 2005. Quercus-dominated vegetation units in the Aegean region of Turkey. *Botanika Chronika* **18**(1): 283-291.

Valencia-A.S. 2021. Species delimitation in the genus Quercus (Fagaceae). *Botanical Sciences* **99**: 1-12.

Van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L. 2016. Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature communications* **7**(1): 1-11.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vazquez FM, Coombes A, Almeida R, Garcia-Alonso D, Marquez-Garcia F, Vila-Vicosa C. 2020. Lectotypification of names of Quercus spp.(Fagaceae) described by Lamarck from the Iberian Peninsula. *Phytotaxa* **455**(3): 205-213.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C. 2012. *Os carvalhais marcescentes do Centro e Sul de Portugal. Estudo e Conservação.* MSc Dissertation, Évora Évora, Portugal.

Vila-Viçosa C, Arenas-Castro S, Marcos B, Honrado J, García C, Vázquez FM, Almeida R, Gonçalves J. 2020a. Combining Satellite Remote Sensing and Climate Data in Species Distribution Models to Improve the Conservation of Iberian White Oaks (Quercus L.). *ISPRS International Journal of Geo-Information* **9**(12): 735.

Vila-Viçosa C, Arraiano-Castilho R, Hipp A, Vázquez FM, Almeida R, García C, Beja-Pereira A, Azevedo H 2021. RAD-Seq unveils the phylogenetic backbone of the Iberian white oak (Quercus L. section Quercus) syngameon.In Pérez Badia RM, J.C. . *First Spanish Botanical Society Congress (SEBOT). Sociedad Española de Botanica*. Toledo. 175.

Vila-Viçosa C, Gonçalves J, Honrado J, Lomba Â, Almeida RS, Vázquez FM, Garcia C. 2020b. Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Scientific reports* **10**(1): 1-12.

Vila-Viçosa C, Marcos B, Garcia C, Gonçalves J 2019. Biogeography from space—A new tool to disentangle Iberian Forests Ecology and Distribution. *Proceedings of the SIBECOL. 1st Meeting of the Iberian Ecological Society & XIV AEET Meeting, Barcelona, Spain*. 4-17.

Vila-Viçosa C, Mendes P., del Río S, Meireles C., Quinto-Canas R, Arsénio P, Pinto-Gomes C. 2012. Temporihygrophilous Quercus broteroi forests in southern Portugal: analysis and conservation. *Plant Biosystems* **146**(1): 298-308.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vila-Viçosa C, Vázquez FM, Mendes P, Del Rio S, Musarella C, Cano-Ortiz A, Meireles C. 2015. Syntaxonomic update on the relict groves of Mirbeck's oak (Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* **149**(3): 512-526.

Vila-Viçosa C, Vieira C, Márquez F, Almeida R, Vázquez FM. 2022. Notes on the original materials of the three western Mediterranean oaks (Quercus, Fagaceae) described by Desfontaines. *Mediterranean Botany* **43**: 1-11.

Vilches B, Sánchez-Mata D, Gavilán RG 2016. Marcescent Quercus pyrenaica Forest on the Iberian Peninsula. *Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales*: Springer, 257-283.

Villar EH. 1958. Estudios sobre los Quercus del Oeste mediterráneo. *Anales del Instituto Botanico de A.J. Cavanilles* **15**: 3-114.

Walas Ł, Sobierajska K, Ok T, Dönmez AA, Kanoğlu SS, Dagher-Kharrat MB, Douaihy B, Romo A, Stephan J, Jasińska AK. 2019. Past, present, and future geographic range of an oro-Mediterranean Tertiary relict: The juniperus drupacea case study. *Regional Environmental Change* **19**(5): 1507-1520.

Wang C-J, Zhang Z-X, Wan J-Z. 2019. Vulnerability of global forest ecoregions to future climate change. *Global Ecology and Conservation* **20**: e00760.

Webb P. 1838. *Iter Hispaniense.* Paris: Béthune and Plon.

Wen J, Ickert-Bond SM. 2009. Evolution of the Madrean-Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. *Journal of Systematics and Evolution* **47**(5): 331-348.

Wickham H, Chang W, Wickham MH. 2016. Package 'ggplot2'. *Create elegant data visualisations using the grammar of graphics. Version* **2**(1): 1-189.

Wickham H, Francois R, Henry L 2022. Müller K. dplyr: A grammar of data manipulation. R package version 0.4. 3. R Found Stat Comput, Vienna. 2015.

Wickham H, Girlich M. 2022. tidyr: Tidy Messy Data. *CRAN. URL: https://cran. r-project. org/package= tidyr [accessed 2022-06-15]*.

Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*: 519-539.

Willdenow CL. 1805. *Species plantarum exhibentes plantas rite cognitas ad genera relatas cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis naturalibus secundum systema sexuale digestas*. Berlin: Nauck.

Willdenow CL. 1809. *Enumeratio plantarum Horti Regii Berolinensis*. Berlin: Taberna libraria Scholae Realis.

Willkomm M. 1896. *Grundzüge der Pflanzenverbreitung auf der iberischen Halbinsel*: W. Engelmann.

Willner W, Di Pietro R, Bergmeier E. 2009. Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography* **32**(6): 1011-1018.

Wisz MS, Guisan A. 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC ecology* **9**(1): 1-13.

Yaltırık F. 1984. *Türkiye'nin Meşeleri Teşhis Kılavuzu*. İstanbul.

Yannic G, Pellissier L, Ortego J, Lecomte N, Couturier S, Cuyler C, Dussault C, Hundertmark KJ, Irvine RJ, Jenkins DA, et al. 2014. Genetic diversity in caribou linked to past and future climate change. *Nature Climate Change* **4**(2): 132-137.

Yao X, Song Y, Yang JB, Tan YH, Corlett RT. 2021. Phylogeny and biogeography of the hollies (Ilex L., Aquifoliaceae). *Journal of Systematics and Evolution* **59**(1): 73-82.

Yücedağ C, Müller M, Gailing O. 2021. Morphological and genetic variation in natural populations of Quercus vulcanica and Q. frainetto. *Plant systematics and evolution* **307**(1): 1-15.

5.8. Supplementary Information

Supplementary Data S1 - Focal taxa and occurrence data

The present study benefited from previous taxonomic research, exclusively directed to the study of the type materials of most of the circummediterranean oaks, deposited at the Paris Muséum National d' Histoire Naturelle. This revealed to be crucial for the presented nomenclatural and taxonomic endorsements and was done through a SYNTHESIS Grant (FR-TAF-280). This analysis was further complemented with the available online collections of the Smith Herbarium of Linnean Society (LINN-HS!), the herbarium of the Botanic Garden and Botanical Museum of Berlin-Dahlem (B-W!), the Herbier de l'Université de Montpellier (MPU), the Webb Herbarium from Herbarium Universitatis Florentinae (FI-Webb), the Herbarium from the Conservatoire et Jardin botaniques de la Ville de Genève (G), the Herbarium from Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (MAIA), the Herbarium from the Swedish Museum of Natural History (S) and the Herbarium from the Royal Botanic Gardens (K). Furthermore, we revised the Iberian oak collections of more fourteen Herbaria, spanning ten Portuguese (AVE, BRESA, COI, HVR, LISE, LISFA, LISI, LISU, PO and UEVH); three Spanish (BCN; HSS and MA) and one from the Netherlands (L) (Thiers, 2022).

We sustain the focal taxa, based in the original proposals of Lamarck (1785), Willdenow (1805); Olivier (1807); Willdenow (1809), Boissier (1853), Kotschy (1862) and Schwarz (1935), from which taxonomic circumscription and nomenclatural endorsements were revisited by Avishai (1967), Stephan and Teeny (2017), Öney *et al.* (2020) and Yücedağ *et al.* (2021) for the near eastern oaks, while for the Iberian Peninsula and north Africa, other authors like Vasconcellos and Franco (1954), and more recently Vázquez *et al.* (2018) and Vazquez *et al.* (2020), as follows:

Section *Quercus* Denk *et al.* (2017)

Subsection *Galliferae* (Spach) Gürke (1897)

***Quercus canariensis* Willd.** (1809: 975)

The Algerian oak is a relictual tree, with five small subpopulations in the Iberian Peninsula (Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2020a; Vila-Viçosa *et al.*, 2020b). In Europe it occurs above siliceous bedrock, always in mesophytic conditions, in spite of being largely distributed above limestones in Africa. It has an higher demand on annual and summer precipitations, when compared with the remaining western *Galliferae* species (Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2020a; Vila-Viçosa *et al.*, 2020b). It is Critically Endangered in Portugal (Carapeto *et al.*, 2020) and has a Data Deficient status according to Carrero *et al.* (2020). Its conservation status is ambiguous since it is known to form hybrid swarms with other sympatric oaks like *Quercus faginea* Lam. (*Q.* ×*tlemcenensis* Trab.) and *Q. pubescens* Willd. (*Q.* ×*cerrioides* Willk. & Costa) (Battandier & Trabut, 1905; Vicioso, 1950; Vázquez *et al.*, 2018), which hampers taxonomic identification and the proper georeferentiation of pure stands dominated by this species.

Quercus faginea Lam. (1785: 725)

The Portuguese oak congregated two widely known subspecies, that were traditionally considered two independent taxa: 1 – *Q. broteroi* and 2 – *Q. faginea* respectively (Rivas-Martínez & Saénz, 1991; Rivas-Martínez *et al.*, 2002; Vila-Viçosa, 2012; Vila-Viçosa *et al.*, 2014; Vazquez *et al.*, 2020). However, the study of the type material of *Q. faginea* carried by Vazquez *et al.* (2020) at the Lamarck herbarium (P-Lam), concluded that the name formerly assigned to the Western and Southern Iberian species as *Q. broteroi* corresponds, in fact, to the own original concept of *Q. faginea* described by Lamarck (1785). This outcome is in accordance with the nomenclatural endorsements given by Schwarz (1936a) and Vasconcellos and Franco (1954), while later the correct taxonomic and geographic circumscription of the Portuguese Oak is well-stablished by Villar (1958). This taxon is distributed across the submediterranean and Atlantic areas of the Iberian Peninsula and North Africa (Morocco, Algeria and Tunisia), preferably in base-rich soils, being common in limestone areas. It is the white oak that better stands lower annual precipitations, in stations that are often fed by an increase in summer rainfall (Blanco-Castro *et al.*, 2005; Vila-Viçosa *et al.*, 2012; Babali *et al.*, 2013; Vila-Viçosa *et al.*, 2014; Meddour *et al.*, 2017; Taleb & Fennane, 2019; Vila-Viçosa *et al.*, 2020a).

Quercus lusitanica Lam. (1785: 719)

The Lusitanian dwarf-oak is a geoxylic shrub, that is exclusive of siliceous bedrock and occurs in the extreme western areas of the Iberian Peninsula, with a sub-population in Morocco. It has a sharp Atlantic distribution, being sensitive to winter cold (Capelo *et al.*, 2002; Vila-Viçosa *et al.*, 2020b). It has a past nomenclatural entanglement with *Q. faginea*, since traditional works often mixed up both names and address the name *Q. lusitanica* to the Portuguese oak (*Q. faginea*) (Webb, 1838; Coutinho, 1888; Vicioso, 1950). The correct nomenclatural endorsement for this shrub was correctly solved and addressed by Sampaio (1910).

Quercus boissieri Reut. (1853: 119)

The Boissier Oak grows preferably in deep and base-rich soils that are often poor in humus and may vary from sandstones to loam-rich soils. However, it is also compatible with dry and skeletical soils, in places with higher annual rainfall (Ugurlu & Senol, 2005; Ghazal, 2008; Ketenoglu *et al.*, 2010). The name *Q. boissieri* has been traditionally synonymized to the subspecies of *Q. infectoria* (*Q. infectoria* subsp. *veneris* (A.Kern.) Meikle) by several authors and following the priority name proposed by Meikle (1985). None withstanding, when comparing the type material of *Q. boissieri* available in Geneve Herbarium (G00150110!) to the original plants used for the description of *Q. infectoria* G. Olivier, properly studied in Paris (P00753892!), it became notorious that they should be treated as taxonomically distinct, agreeing with both proposals of Avishai (1967) and Schwarz (1936a). The presence of totally glabrous leaves and hybrids with *Q. cerris* among the type materials of *Q. infectoria* (P00753892!), are opposed to the lanceolate to oblong leaf blade, with serrate to crenate margin, and the common presence of a flake indumentum observed in the nerves of *Q. boissieri* specimens. This last character gives a bluish tonality to the abaxial leaf blade of the latter species, and the sum of these characters appear as major reliable source to segregate both *taxa*. Simultaneously, this character, led to the proposition of the Series *Orientales* by Schwarz (1936a), where the author congregates *Q. boissieri* and *Q. canariensis* as related species. Avishai (1967), also segregates *Q. boissieri* by its distribution, mostly through southern and some central parts of Anatolia, Cyprus, Syria, Lebanon, Caucasus and reaching Zagros Mountains in Iran, as farther eastern distribution, normallly in scrub and anthropogenic changed landscapes, up to 1850 m.a.s.l. (Hedge & Yaltırık, 1982). It forms mostly pure stands, or sometimes mixes with other oak species (*Q. brantii, Q. cerris, Q. calliprinos, Q. ithaburensis, Q. libani, Q. pubescens*), with direct implication to several suggested hybrids with other oaks (Stephan *et al.*, 2018; Douaihy *et al.*, 2020). It occupies both

Mediterranean and Irano-Turanian regions, and this is reflected in the plasticity of its leaf traits, when changing from mesic to xeric and continental conditions (Stephan *et al.*, 2018).

Quercus infectoria G.Olivier (1801: 14-15)

Q. infectoria is mainly distributed across north and western Anatolia, from the Aegean to the Black Sea, from which revised materials in Paris Herbarium helped to solve this biogeographic dichotomy against *Q. boisseri* (Paris Herbarium Review – Digital Annex). It can be generally recognized by its shorter petioles, broadly obovate leaves, and prominently crenate or serrate margins, with mostly glabrous leaves, when in contrast to *Q. boisseri*. It occurs often intermixed with *Q. cerris* and *Q. pubescens* stands and sometimes *Pinus brutia* mixed stands, or in pseudo-maquis (*Paliurus sp*., *Arbutus sp*.) up to 850 m, preferably in humus-poor, loamy and base-rich soils (Avishai, 1967). As it is a Euro-Siberian and temperate element, it mainly distributes across the Euxine and sub-Euxine sectors, being tolerant to winter cold.

Subsection *Dascia* (Kotschy) Schwarz (1936a)

Quercus kotschyana O.Schwarz (1935: 466)

The Kotschy Oak have traditionally suffered of a long history of taxonomic and nomenclatural misinterpretations, being often ascribed to a taxon resultant from putative introgression with *Q. pubescens,* or *Q. cerris,* and even to a petraeoid oak related to the concepts of *Q. subalpina* O. Schwarz and *Quercus cedrorum* Kotschy (Jablonski, 2016; Stephan & Teeny, 2017; Douaihy *et al.*, 2020). Douaihy et al. (2020) conducted a preliminary molecular survey of this species and suggested that together with *Q. vulcanica* Boiss. ex Kotschy, and possibly *Q. macranthera* subsp. *syspirensis* (K.Koch) Menitsky it might represent a member of an ancient stock of closely related, disjoint oaks from section *Quercus*. This entanglement comes from a plethora of multiple interpretation of the morphological plasticity of its leaf blade, expressed by the type population in Bscharri (Lebanon) (Paris Herbarium Review – Digital Annex). This plasticity encompasses the leaf that ranges from a pinnatifid to pinnatilobate margin, with a tomentose leaf blade (Stephan *et al.*, 2018). This species has been correctly recovered and solved by Stephan and Teeny (2017) as an Endangered oak that occurs in fragmented eight sub-populations in Lebanon. The distribution is characterized by isolated trees among *Cedrus libani* mountain forests mixed with other species such as

Quercus petreae subsp. pinnatiloba (Q. cedrorum), Acer hyrcanum tauricolum, Abies cilicica and *Juniperus spp.* (Stephan, 2018). The species thrives mainly in cool mesic conditions, and accommodates with different soil conditions but is restricted between 1600 and 2000 m.a.s.l (Stephan *et al.*, 2016).

***Quercus pyrenaica* Willd.** (1805: 451)

The Pyrenean oak has a wide distribution, mostly through the submediterranean and temperate belts of the western Mediterranean basin, with important relictual subpopulations in mountain areas of the Mediterranean half of the Iberian Peninsula and North Africa, reaching up to France. It's a totally edaphic-indifferent species, being more common above siliceous bedrock, and supporting slight summer drought, especially when in comparison to *Q. robur* L (Blanco-Castro *et al.*, 2005; Vilches *et al.*, 2016).

Quercus vulcanica Boiss. & Heldr. ex Kotschy (1859: 18)

The Kasnak oak is an endemic tree that was originally described from central Anatolia (Karadağ Mountain), which is an extinct volcano located between Konya and Karaman (Hedge & Yaltırık, 1982). Its main distribution range is across the western Central Anatolia to the upper Mediterranean Turkey region (known as Turkish Lakes), in a Natural Conservation area for the species. Some few isolated populations have also been recorded towards the east in Kayseri (Ahır and Gediz Mountains), Hatay (Amanos and Murat Mountains), Ankara (Sarıçalı Mountain) and towards the north in the Western Black Sea Region of Turkey (Yaltırık, 1984; Avcı, 1996; Aydınözü, 2004; Öney *et al.*, 2020). It prefers mesophytic conditions, ocurring on limestone bedrock, basalt rocks, volcanic rocks, and ophiolite, normally as pure stands or intermixed with *Pinus* spp.*, Cedrus libani, Acer hyrcanum,* and other oaks (*Q. infectoria, Q. pubescens, Q. cerris, Q. petraea, Q. robur, Q. trojana*) from 1100-2000 m (Kargıoğlu *et al.*, 2009; Öney *et al.*, 2020). Kasnak oak differs from *Q.petraea subsp. pinnatiloba* (K.Koch) Menitsky by having flat cup scales, and leaves with truncated lobes and intercalary veins, and from *Q. frainetto* Ten. by having longer petioles and the leaves evenly distributed across the shoots (Hedge & Yaltırık, 1982).

Supplementary Table S1 – Digital Annex

See Digital Annex section at the end of the present thesis.

Supplementary Table S2

Supplementary Table S2 – Species record numbers.

Sub-Region	Species	Number of records
Western Mediterranean	*Q. pyrenaica*	8689
Western Mediterranean	*Q. faginea*	1321
Western Mediterranean	*Q. lusitanica*	613
Western Mediterranean	*Q. canariensis*	165
Eastern Mediterranean	*Q. boissieri*	1470
Eastern Mediterranean	*Q. vulcanica*	154
Eastern Mediterranean	*Q. infectoria*	118
Eastern Mediterranean	*Q. kotschyana*	15

Supplementary Table S3

Supplementary Table S3 - Models' summary for past, current and future projections.

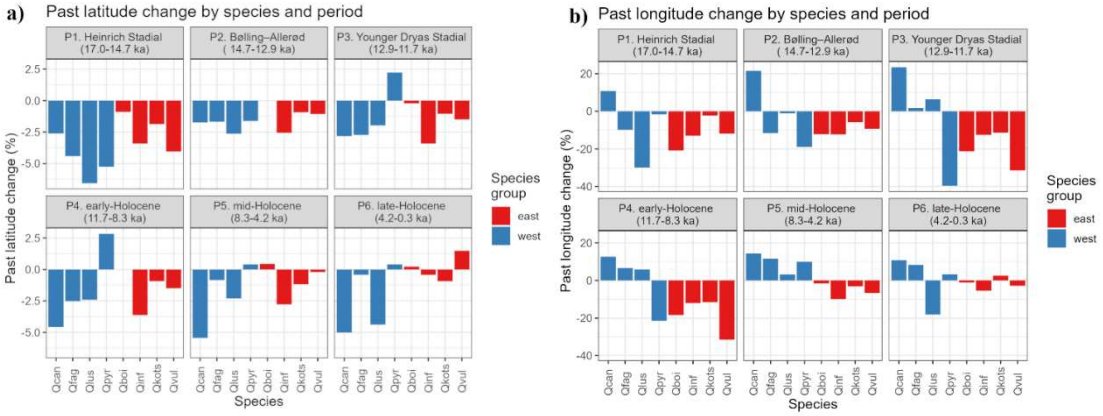
Projections	Model	Code	Time period
Past	Heinrich Stadial 1	HS	17.0-14.7 Kyr
	Bølling-Allerød	BA	14.7-12.9 Kyr
	Younger Dryas Stadial	YDS	12.9-11.7 Kyr
	Early-Holocene	EH	11.7-8.3 Kyr
	Mid-Holocene	MH	8.3-4.2 Kyr
	Late-Holocene	LH	4.2-0.3 Kyr
Current	Average model of 5 GCMs	Current	1981-2010
Future	Average model of 5 GCMs × 3 SSP (126, 370, 585)	sspXX_2070	2070
		sspXX_2100	2100

Supplementary Table S4

Supplementary Table S4 - Evaluation scores per species for the ensemble of best models (TSS: True skill statistic; AUC: Area Under the Curve; Sensitivity also called true positive rate or recall; Specificity also defined as the true negative rate)

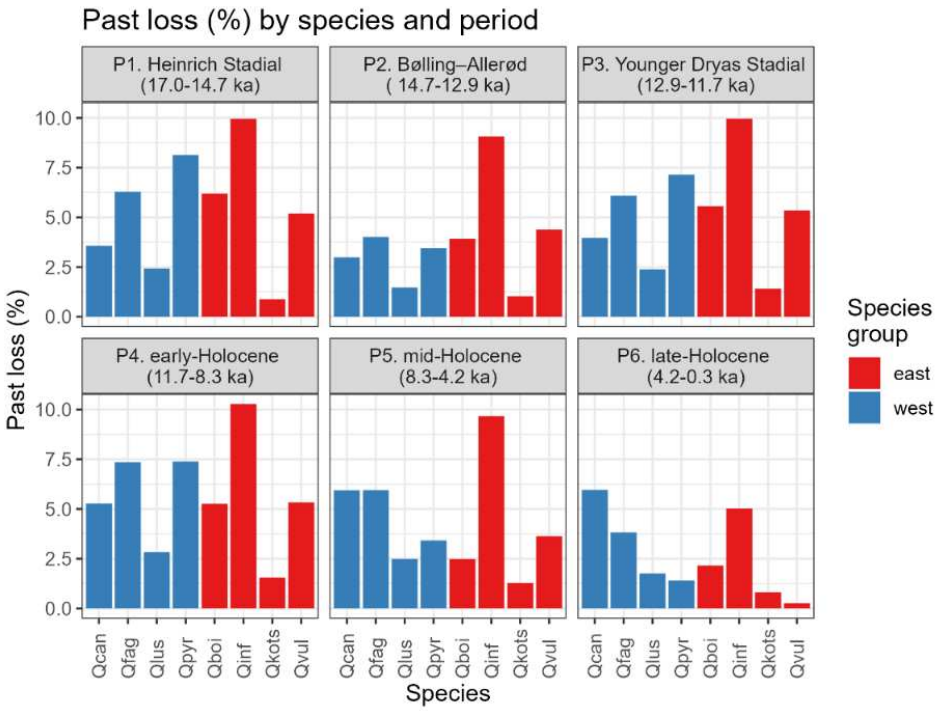
Region	Species	TSS	AUC	Sensitivity	Specificity
Eastern Mediterranean	*Quercus kotschyana*	1,00	1,00	100,00	100,00
Western Mediterranean	*Quercus lusitanica*	0,96	1,00	100,00	96,42
Eastern Mediterranean	*Quercus vulcanica*	0,91	0,99	97,67	93,29
Western Mediterranean	*Quercus canariensis*	0,90	0,99	96,43	93,52
Western Mediterranean	*Quercus pyrenaica*	0,90	0,99	96,65	92,79
Eastern Mediterranean	*Quercus boissieri*	0,88	0,99	97,02	90,48
Eastern Mediterranean	*Quercus infectoria*	0,84	0,97	97,39	86,16
Western Mediterranean	*Quercus faginea*	0,82	0,97	93,32	88,90

Supplementary Figure S1



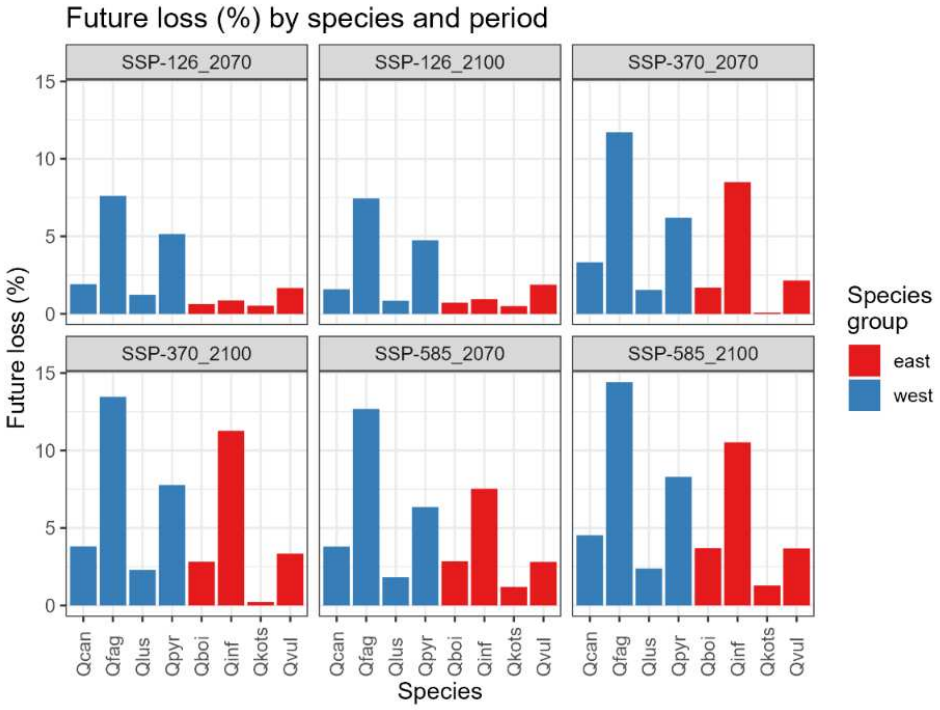
Supplementary Figure S1 - Past latitude (a) and longitude (b) changes by species and period. Positive increases in latitude represent northern-driven shifts, while for longitude, these are eastern-driven shifts.

Supplementary Figure S2



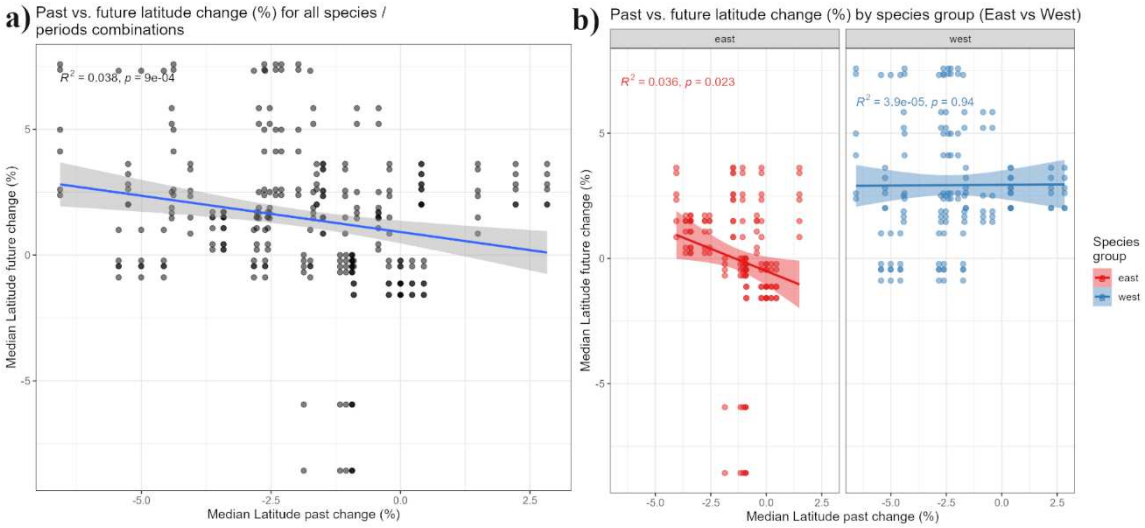
Supplementary Figure S2 - Past loss (%) by species and period.

Supplementary Figure S3



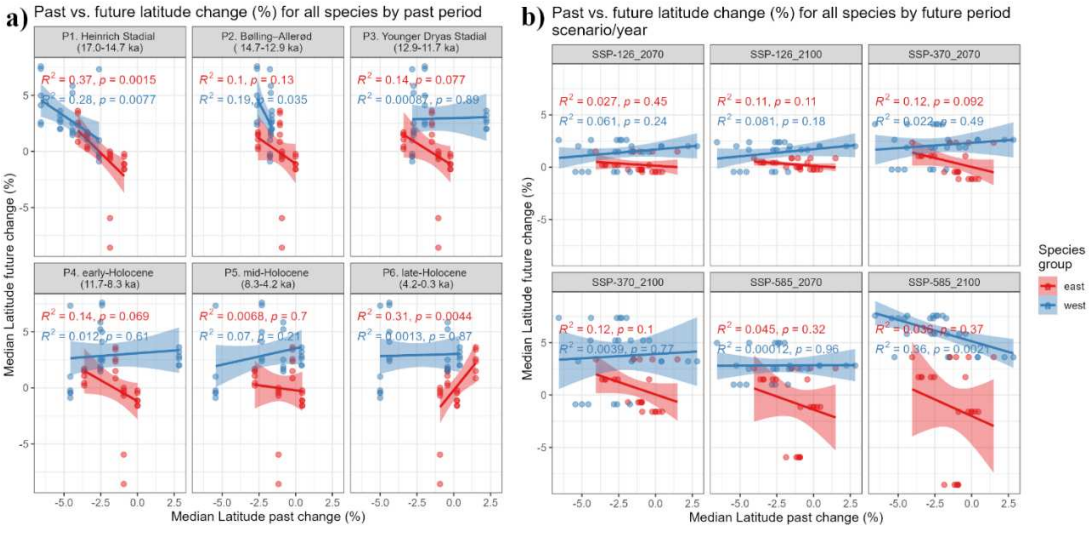
Supplementary Figure S3 - Future loss (%) by species and period.

Supplementary Figure S4



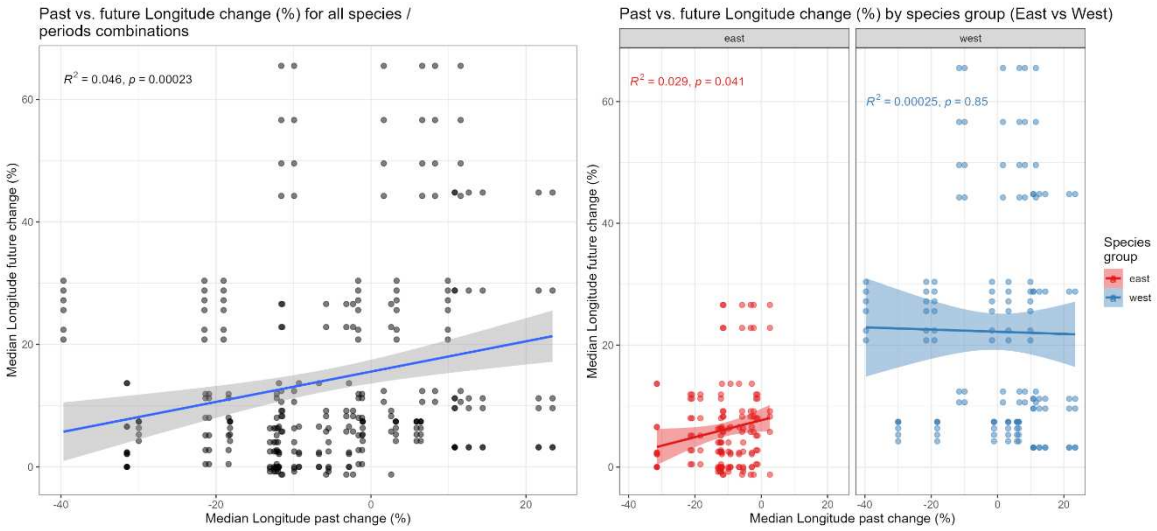
Supplementary Figure S4 - a) Past vs. future latitude change (%) for all species / periods combinations; b) Past vs. future latitude change (%) by species group (East vs West).

Supplementary Figure S5



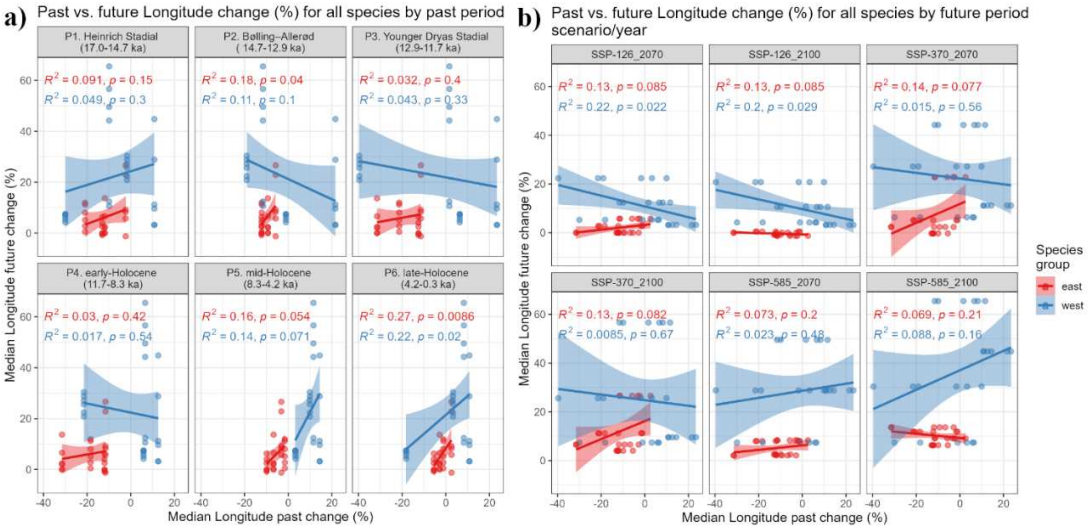
Supplementary Figure S5 - a) Past vs. future latitude change (%) for all species by past period; b) Past vs. future latitude change (%) for all species by future period scenario/year.

Supplementary Figure S6



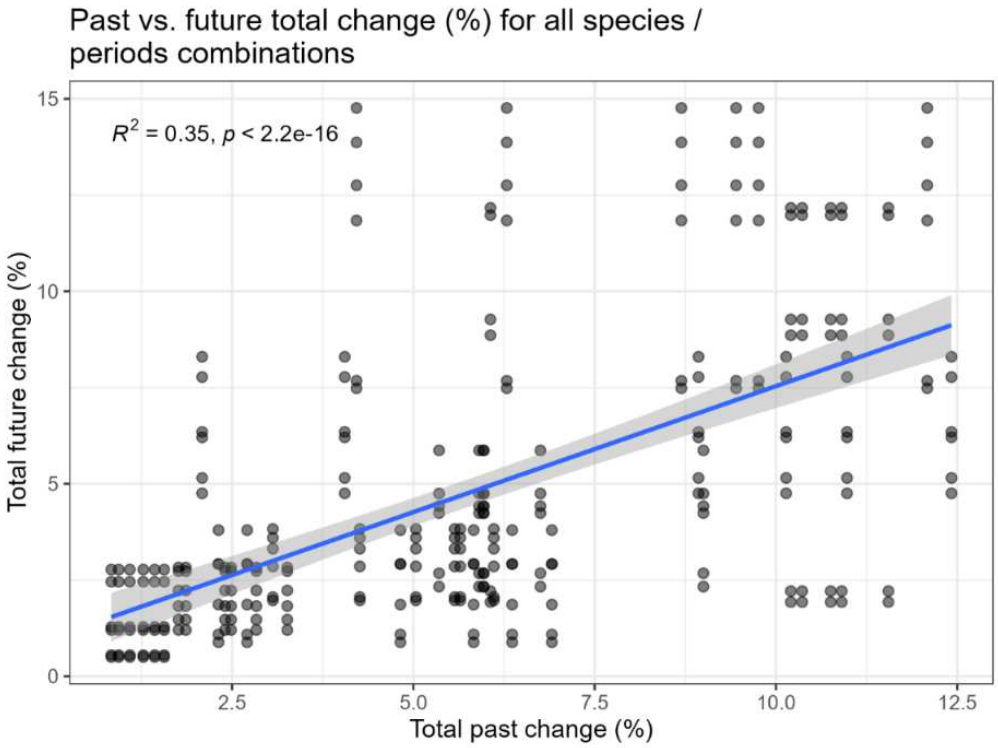
Supplementary Figure S6 - a) Past vs. future longitude change (%) for all species/periods combinations; b) Past vs. future longitude change (%) by species group (east vs west).

Supplementary Figure S7



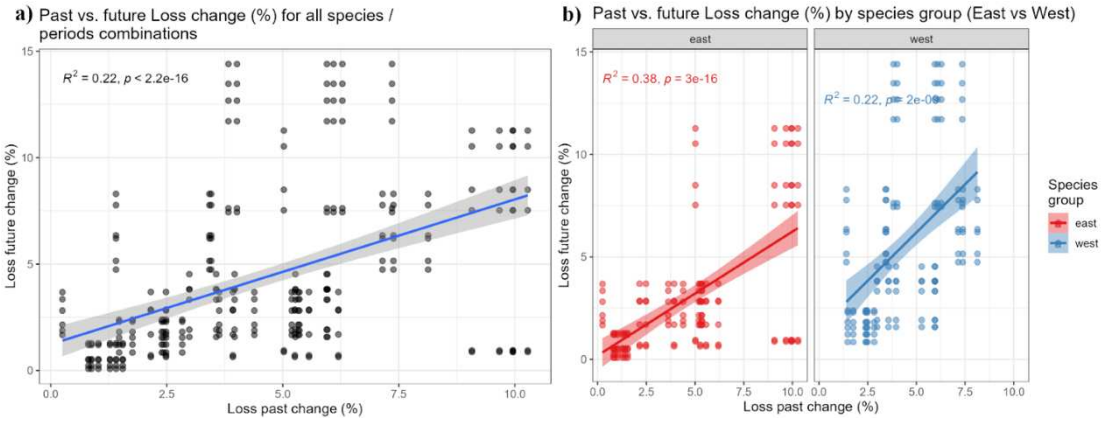
Supplementary Figure S7 - a) Past vs. future Longitude change (%) for all species by past period; b) Past vs. future Longitude change (%) for all species by future period scenario/year.

Supplementary Figure S8



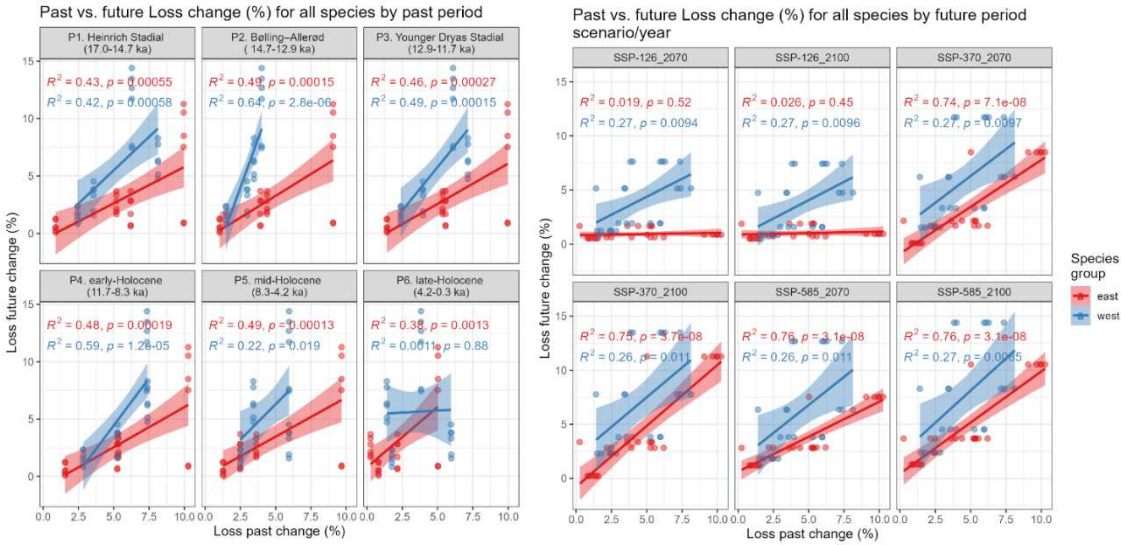
Supplementary Figure S8 - Past vs. future total change (%) for all species and period combinations.

Supplementary Figure S9



Supplementary Figure S9 – a) Past vs. future Loss change (%) for all species/periods combinations; b) Past vs. future Loss change (%) by species group (East vs West).

Supplementary Figure S10



Supplementary Figure S10 - a) Past vs. future Loss change (%) for all species by past period; b) Past vs. future Loss change (%) for all species by future period scenario/year.

Supplementary Maps – Digital Annex

See Digital Annex section at the end of the present thesis.

Chapter 6.

Combining Satellite Remote Sensing and Climate Data in Species Distribution Models to Improve the Conservation of Iberian White Oaks (*Quercus* L.)

Carlos Vila-Viçosa[1,2,3*], Salvador Arenas-Castro[1,4,5] Bruno Marcos[1,3], João Honrado[1,3], Cristina García[1,6], Francisco M. Vázquez[7], Rubim Almeida[1,2,3], João Gonçalves[1] (2020)
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Disclaimer: This chapter is an original contribution of this thesis, published in *ISPRS International Journal of Geo-Information* under the same title. Vila-Viçosa, C. led the work with contributions from all co-authors.

[1] CIBIO (Research Center in Biodiversity and Genetic Resources) - InBIO (Research Network in Biodiversity and Evolutionary Biology), University of Porto. Campus Agrário de Vairão; Rua Padre Armando Quintas; 4485-661 Vairão; Portugal
[2] MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto – Herbário PO, Universidade do Porto. Praça Gomes Teixeira, 4099-002, Porto, Portugal.
[3] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal.
[4] Instituto Politécnico de Viana do Castelo, Escola Superior de Tecnologia e Gestão, 4900-347 Viana do Castelo, Portugal
[5] CICGE—Centro de Investigação em Ciências Geo-Espaciais, Faculdade de Ciências, Universidade do Porto, Observatório Astronómico “Prof. Manuel de Barros”, Alameda do Monte da Virgem, 4430-146 Vila Nova de Gaia, Portugal
[6] Department of Evolution, Ecology and Behaviour, Institute of Integrative Biology (IIB), University of Liverpool, Bioscience Building, Liverpool L69 7ZB, UK
[7] CICYTEX—Centro de Investigaciones Científicas y Tecnológicas de Extremadura, Agricultural Research Centre, Finca La Orden, Valdesequera, Ctra. A-V, Km372, 06187 Guadajira, Badajoz, Spain

6.1. Abstract

The Iberian Peninsula hosts a high diversity of oak species, being a hot-spot for the conservation of European White Oaks (*Quercus*) due to their environmental heterogeneity and its critical role as a phylogeographic refugium. Identifying and ranking the drivers that shape the distribution of White Oaks in Iberia requires that environmental variables operating at distinct scales are considered. These include climate, but also ecosystem functioning attributes (EFAs) related to energy–matter exchanges that characterize land cover types under various environmental settings, at finer scales. Here, we used satellite-based EFAs and climate variables in species distribution models (SDMs) to assess how variables related to ecosystem functioning improve our understanding of current distributions and the identification of suitable areas for White Oak species in Iberia. We developed consensus ensemble SDMs targeting a set of thirteen oaks, including both narrow endemic and widespread taxa. Models combining EFAs and climate variables obtained a higher performance and predictive ability (true-skill statistic (TSS): 0.88, sensitivity: 99.6, specificity: 96.3), in comparison to the climate-only models (TSS: 0.86, sens.: 96.1, spec.: 90.3) and EFA-only models (TSS: 0.73, sens.: 91.2, spec.: 82.1). Overall, narrow endemic species obtained higher predictive performance using combined models (TSS: 0.96, sens.: 99.6, spec.: 96.3) in comparison to widespread oaks (TSS: 0.80, sens.: 92.6, spec.: 87.7). The Iberian White Oaks show a high dependence on precipitation and the inter-quartile range of Normalized Difference Water Index (NDWI) (i.e., seasonal water availability) which appears to be the most important EFA variable. Spatial projections of climate–EFA combined models contribute to identify the major diversity hotspots for White Oaks in Iberia, holding higher values of cumulative habitat suitability and species richness. We discuss the implications of these findings for guiding the long-term conservation of Iberian White Oaks and provide spatially explicit geospatial information about each oak species (or set of species) relevant for developing biogeographic conservation frameworks.

6.2. Introduction

The genus *Quercus* L. is one of the most abundant and economically important group of woody plants in the Northern Hemisphere (Manos *et al.*, 1999), and oak forests are the keystone species in many Mediterranean and Temperate forests and woodlands, providing fundamental regulation, provision, support and cultural ecosystem services for people and nature (Neophytou *et al.*, 2010; Cramer *et al.*, 2018; Sabatini *et al.*, 2018;

Anderegg *et al.*, 2020; Balzan *et al.*, 2020). The Iberian Peninsula (IP) harbours half of the European diversity of oak species, when excluding intraspecific variation (Coutinho, 1888; Schwarz, 1964; Franco, 1990; Rivas-Martínez & Saénz, 1991). The IP is a major glacial refugia (Olalde *et al.*, 2002) and a major hotspot for the White Oaks group (*Sect. Quercus*) (Denk *et al.*, 2017) partly due to its paleoclimatic history and the presence of two major biogeographic regions (Eurosiberian and Mediterranean). The ecotone between these two biogeographic regions is widely occupied by marcescent forests dominated by White Oaks either deciduous or marcescent spanning across the sub-Mediterranean belt (Del Río & Penas, 2006; De Dios *et al.*, 2009; Rivas-Martínez *et al.*, 2017; Vila-Viçosa *et al.*, 2020). Climate change seriously threatens these transition zones, as summer periods become increasingly arid and warm in the coming decades (Pachauri *et al.*, 2014; Balzan *et al.*, 2020). Additionally, land use/cover changes, forest management practices that favour fast growing tree species (e.g., *Eucalyptus* spp.), and invasive species along with wildfires and other disturbances (García-Valdés *et al.*, 2015; Senf & Seidl, 2020) also pose serious threats to these already marginal and fragile ecosystems in the IP.

Traditionally, seven White Oak species are considered to be native to the IP, when excluding infraspecific variation (Franco, 1990). However, the known low interspecific barriers to gene flow give this genus a complex evolutionary and speciation pattern, which includes the formation of new species as a result of hybridization (i.e., nothotaxa) (Hipp, 2015; McVay *et al.*, 2017). Previous studies refer to cryptic taxa that are notable in the IP (Schwarz, 1935; Vicioso, 1950; Vasconcellos & Franco, 1954; Montserrat, 1957; Rivas-Martínez & Saénz, 1991), including narrow distributed and endemic (NDE) species or relict taxa (Schwarz, 1936; Rivas-Martínez *et al.*, 2002; Vila-Viçosa *et al.*, 2014). This confers to the Iberian White Oak forests with high phylogeographic value in addition to the value for human well-being and especially relevance for mitigating climate-driven risks (Sabatini *et al.*, 2018; Anderegg *et al.*, 2020).

Given their eco-evolutionary importance, White Oak species and related ecosystems require suitable geospatial analysis tools to assess their conservation status and demographic trends (Rodríguez-Sánchez *et al.*, 2010). In this regard, species distribution models (hereafter SDMs, i.e., habitat suitability models or ecological niche models) are among the most widely used tools to assess the impact of global change on biodiversity, and to inform policy makers (Guisan *et al.*, 2013). In a nutshell, SDMs allow to understand species–environment relations by modelling between the occurrence or abundance of species and environmental predictors (e.g., temperature, rainfall, soil type,

vegetation cover) that determine it. This is done through empirical/correlative and mainly static approaches, based on statistical or machine learning algorithms which use as input species field observations, and/or museum-type records. The obtained species–environment responses are thought to best reflect the realized ecological niche of the study species (Guisan *et al.*, 2017). Trained models are used to obtain spatiotemporal projections of species distributions based on current, past or future conditions to gain insights on the environmental drivers that shape the potential (or actual) occurrence of study species at multiple spatial scales.

Complementarily to innovative SDM approaches, recent advances in satellite remote sensing (SRS), with the ever increasing availability of data with enhanced spatial and spectral features, allow us to continuously depict Earth system dynamics in its multiple facets relevant for species and biodiversity monitoring (Luque *et al.*, 2018). These are capable of capturing the intra-annual dynamics of ecosystem functioning such as the average annual conditions, intra-annual seasonal variation, phenology or extreme values for several relevant dimensions. In particular, satellite-based ecosystem functioning attributes (EFAs) (Alcaraz *et al.*, 2006; Alcaraz-Segura *et al.*, 2009) defined as spatiotemporal integrative descriptors of ecosystem functioning and dynamics computed from time series of satellite products (e.g., spectral indices for vegetation or water) are providing new opportunities to push the boundaries of SDMs. EFAs inform on several relevant features of ecosystem functioning such as primary productivity, evapotranspiration, land surface temperature, and albedo, thereby encompassing several dimensions including carbon gains, water and energy balance (Alcaraz-Segura *et al.*, 2017; Arenas-Castro *et al.*, 2018; Arenas-Castro *et al.*, 2019). EFAs are considered essential biodiversity variables (EBVs) describing the 'Ecosystem Function' class (Pereira *et al.*, 2013). Therefore, the EFA framework provides key variables to model the ecosystem processes that maintain suitable environmental and habitat conditions for keystone species (Gonçalves *et al.*, 2016; Regos *et al.*, 2020). This will allow us to anticipate species' range shifts under global change (Rodríguez-Sánchez *et al.*, 2010). Overall, EFAs offer an alternative and cost-effective approach to improve predictions on the distribution of species and support biodiversity monitoring once these are capable of capturing the intra-annual dynamics of ecosystem functioning.

Although the use of SDMs has played a major role in oak forest conservation (Hernández-Lambraño *et al.*, 2019; Sun *et al.*, 2020), they have been mainly applied to iconic oak species, like cork oak (*Q. suber* L.) (Vessella *et al.*, 2017; Matías *et al.*, 2019), or to broadly distributed species (e.g., *Q. robur*) or species groups (Noce *et al.*, 2017;

Ülker *et al.*, 2018), sometimes at smaller and regional scales (Duque-Lazo *et al.*, 2018; López-Tirado & Hidalgo, 2018). We lack to date studies encompassing narrow distributed and endemic (NDE) relict species, especially in a phylogeographic hotspot such as the IP. This knowledge gap mainly derives from issues related to the taxonomic uncertainty and delimitation of species, which in turn hampers data quality and quantity. These data are typically based on inflated nomenclatural inaccuracy and outdated, due to misleading identification that results from ancient herbaria reviews. Still, it is the biggest bulk of information available in worldwide databases (e.g., https://www.gbif.org/), but its limitations hinder the process of accurately predicting species distributions across geographic space, hampering conservation efforts (Ahrends *et al.*, 2011; Ely *et al.*, 2017; Coleman & Radulovici, 2020). Furthermore, previous modelling techniques mostly rely on climatic envelopes that perform better at broad global scales, and they tend to overlook ecosystem functioning features at a fine spatial scale. To overcome this situation, SRS-based ecosystem functioning attributes integrate the effects of vegetation structure, edaphic conditions, and climate at the fine local/meso scale. This makes these variables suitable to improve predictions regarding species optimal environmental conditions, to forecast the effects of environmental change, to monitor biodiversity hotspots, or to model habitat quality from local/regional to global scales (Gonçalves *et al.*, 2016; Arenas-Castro *et al.*, 2018; Regos *et al.*, 2020).

This study aimed to assess whether the combination of EFA and climate variables improves the performance of SDMs using seven narrow distributed or endemic Iberian White Oaks: *Quercus canariensis, Q. ×cerrioides, Q. estremadurensis, Q. lusitanica, Q. marianica, Q. orocantabrica* and *Q. subpyrenaica* along with six widespread species *Q. broteroi*, *Q. faginea, Q. pyrenaica, Q. petraea, Q. pubescens* and *Q. robur*. For this aim, we developed a set of combined models (integrating EFA and climate variables) and partial models (either EFA or climate variables). We compared their performance through several metrics and identified the most suitable areas to preserve threatened species. With this goal in mind, we specifically:

(i) Compared the performance of SRS-EFAs as predictors in SDMs, separately and combined with climate data, to determine the current potential distribution of the thirteen target species;

(ii) Identified the most suitable potential areas for the conservation of vulnerable NDE oak species by comparing the spatial projections of habitat suitability derived from SDMs based on different sets of predictors;

(iii) Depict the fittest biogeographic areas for oak conservation based on a species-richness map obtained through stacking individual SDM's.

6.3. Materials and Methods

6.3.1. Study Area

The Iberian Peninsula (IP) is located in southwestern Europe (bounded by longitudes -9.55° W to 3.35° E and latitudes 35.87° N to 43.80° N) and has a total area of 583 832 km^2 (Figure 1). The region holds a highly diverse geological history (Loidi, 2017) and a climate that ranges from a dry Mediterranean in the southeast to a wet Temperate Atlantic in the north (Rivas-Martínez *et al.*, 2017). As result of its biogeographic idiosyncrasies and diverse edaphoclimatic conditions, the IP is a major hotspot of European plant diversity, hosting 54% of all European species (22.7% of endemicity), including 21 genera (Aedo *et al.*, 2017) and 13 recognized phylogeographic refugia (Médail & Baumel, 2018).

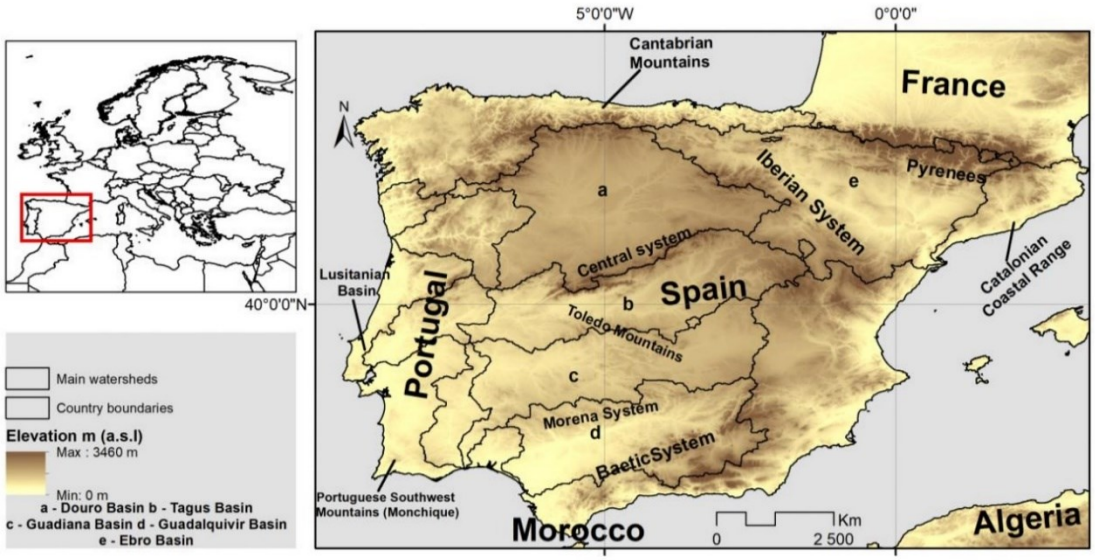


Figure 1 - Study area - Iberian Peninsula - with major river basins and mountain chains where most phylogeographic refugia are located.

6.3.2 Occurrence Data and Focal Taxa

Oak species geographic information was obtained through extensive fieldwork in western IP (since 2005), classic literature and herbaria review. To tackle taxonomic geographic uncertainty, we gathered the information through the thorough examination of 17 reference herbaria, in more

than 6000 vouchers. This info was scrutinized and homogenized with online collections and digital databases (Supplementary Information S1). Geographical records for the target *taxa* were subsumed and aggregated to a 1 x 1 km grid (Datum WGS1984/UTM30N), using both accurately georeferenced points and UTM grid centroids (Supplementary Information S2). We used ESRI ArcGIS 10.3 for spatial data processing and R version 3.3.1 (R Core Team, 2019) for data management and analysis.

We selected a set of thirteen Iberian White Oaks (Sect. *Quercus*) (Denk *et al.*, 2017), which included six roburoid taxa (former Sect. Robur Endlicher (1847) and seven Gall Oaks (subsection *Galliferae* Gurke) (Gürke, 1897; Villar, 1958; Tschan & Denk, 2012). This taxonomic set comprises traditional and updated taxonomic approaches, including infraspecific variation and the existence of stabilized nothotaxa (Supplementary Information S3).

6.3.3. Predictor Variables

Satellite-Based Ecosystem Functioning Attributes (EFAs)

Satellite remote sensing data from the Moderate Resolution Imaging Spectrometer (MODIS) on-board the Terra satellite platform were used to extract EFA variables. The MOD09A1 product, delivering global surface reflectance imagery with 8 days of temporal resolution, 500 m of spatial resolution and with an archive spanning from the year 2000 to the present day, was employed to calculate two spectral indices: (i) the enhanced vegetation index (EVI) (Huete *et al.*, 2002) as a proxy of vegetation greenness, biomass and leaf area index — with values ranging from −1 to 1, with healthy vegetation generally holding values between 0.20 and 0.80; and (ii) the Normalized Difference Water Index (NDWI) (Gao, 1996) as a proxy for the amount of vegetation and soil water contentv— with values varying between −1 and +1, with higher values corresponding to high vegetation/soil water content.

To describe the intra-annual properties of each spectral index and aiming to obtain EFAs linked to carbon and water cycles (Alcaraz-Segura *et al.*, 2017; Arenas-Castro *et al.*, 2018; Arenas-Castro *et al.*, 2019), we calculated the median (as a descriptor of central tendency and quantity), the inter-quartile range (IQR; as a measure of intra-annual seasonal variation or seasonality) and the sine and cosine transformations of the day of maximum annual value, respectively, related to spring and winter peaks (DMaxSpring or DMaxWinter as a descriptor of phenology). These statistical measures were calculated for each complete year. To capture the multi-year normal conditions of each EFA variable, thus reducing the effect of stochastic annual climatic fluctuations, we computed

the overall median. Calculations were performed in Google's Earth Engine (GEE) cloud-based platform (Gorelick *et al.*, 2017). All 8-day image composites available in the GEE archive spanning from 2001 to 2019 (i.e., all complete years) were used, totalling 873 available images/dates (Supplementary Information S4 – Digital Annex). Data were exported from GEE at 1 km of final spatial resolution, totalling eight variables: median, IQR, sine and cosine transformations, and DMax for both EVI and NDWI.

Climatic Data

Bioclimatic variables (derived from monthly temperature and rainfall data to generate more ecologically meaningful variables) were used to portray the temperature and precipitation regimes of the study area. These climatic data were obtained for historical conditions (1970–2000) from the WorldClim dataset version-2.1 (released in January 2020; https://www.worldclim.org/data/worldclim21.html) at a spatial resolution of 30 arc-sec (~1 km). Based on a preliminary assessment (supported by the correlation and variable importance assessment from preliminary models (Vila-Viçosa, Carlos *et al.*, 2019; Vila-Viçosa, C. *et al.*, 2019), three temperature-related and two precipitation variables were used, namely: BIO01—Annual Mean Temperature, BIO03—Isothermality, BIO06—Minimum Temperature of Coldest Month, BIO12—Annual Precipitation and, BIO18—Precipitation of Warmest Quarter.

6.3.4. Model Development, Evaluation and Multi-Algorithm Ensembling

Species distribution models (SDMs) were developed in *R* statistical software (Team R, 2019) using the biomod2 package (Araújo & New, 2007; Thuiller *et al.*, 2009). This package implements a multi-model ensemble forecasting approach which combines several existing statistical and machine-learning-based algorithms thus enabling to assess and prevent a range of methodological uncertainties in each individual modelling algorithm, as well as the examination of species–environment relationships. Models were fitted using nine modelling techniques: generalized linear model (GLM); generalized boosted model (GBMs); generalized additive model (GAM); classification tree analysis (CTA); artificial neural networks (ANN); flexible discriminant analysis (FDA); multivariate adaptive regression splines (MARS); random forests (RF); and MAXENT.Phillips2 (Maximum Entropy Model), currently available in biomod2. Given the subpar performance of the surface range envelop method (also called BIOCLIM; see e.g., Elith *et al.* (2006)) and the similarity of MAXENT.Phillips (also a maximum entropy-

based model available in the biomod2 package) these two algorithms were not considered. Default parameters were employed (with the exception of the smoothing degree term in GAM which was set to k = 4 to prevent over-fitting issues (Guisan *et al.*, 2002) and the number of boosting trees in GBM, n.trees = 2000). Previously to modelling, all candidate variables were inspected for multicollinearity issues using Spearman's non-parametric pair-wise correlation. By setting a threshold of $|\rho| < 0.8$, we retained a total of ten variables (out of 13) including: all bioclimatic variables (BIO 01, 03, 06, 12 and 18) and EVI annual median, EVI IQR, EVI DMax-Spring, NDWI median and NDWI IQR. Given that only presence data were available for the selected species, we established a total of five sets of randomly generated pseudo-absences, each set with ten times the number of presence records allowing to diversify environmental conditions in the data used for model training. Since no previous information was available about the species prevalence (p) nor a robust way to accurately estimate it and after checking the comparative results by Barbet-Massin *et al.* (2012), model weights were adjusted to set $p = 0.5$ (biomod2 default) thus giving a similar weight to presences and generated pseudo-absences (Barbet-Massin *et al.*, 2012). A spatial thinning procedure implemented in the *spThin* R package (Aiello-Lammens *et al.*, 2014) was applied prior to modelling which imposes a minimum spatial separation between input records (through subsampling) with a distance equal to 3 km, thus decreasing autocorrelation and sampling bias effects.

Holdout cross-validation was employed to evaluate the models, with 80% of the input records used for model fitting (train data set) and 20% for model evaluation at each round (test data set). A total of ten rounds were performed for the model evaluation. For assessing the model performance, the area under the receiver-operating curve (ROC), the true-skill statistic (TSS), Cohen's Kappa (KAPPA) and the sensitivity and the specificity values were calculated (Thuiller *et al.*, 2009). Given that 450 models were generated per species, the less performant models were filtered out before the final ensemble forecasting. Hence, we selected the top 10% percentile best models for the six best performing techniques, considering the TSS rank (n = 30). Based on these top performing models, an ensemble using the average was implemented, thus reducing inter-model uncertainty. To 'binarize' projections (to dichotomous suitable/unsuitable habitat) the threshold value maximizing the TSS statistic was used. A linear mixed-effects model was devised through the R package lme4 (Bates *et al.*, 2014) to check if there was an effect of the set of predictive variables (either the combined set including the climate and EFA variables, climate-only or EFA-only; i.e., fixed factor) on the predictive performance scores (i.e., response variable) while controlling for the species

and evaluation metric (i.e., random factors). An ANOVA analysis was then performed to assess if the effect of the set of predictive variables was statistically significant. Finally, given the different number of variables between models setups (partial vs. combined), we also calculated the Akaike information criterion (with finite sample size correction; AICc) for GLM's allowing to rank models (Burnham & Anderson, 2004; Burnham *et al.*, 2011) while accounting for a different number of variables in each set (i.e., partial climate or satellite EFA's models vs. combined ones).

6.4. Results and Discussion

6.4.1 Model Performance and Added Value of EFAs as Predictors

Overall, the models combining EFAs and climate variables obtained a higher performance and predictive ability (average values for TSS: 0.88, ROC: 0.98, KAPPA: 0.72, sensitivity: 99.6, specificity: 96.3), in comparison to climate-only models (TSS: 0.86, ROC: 0.97, KAPPA: 0.68, sensitivity: 96.1, specificity: 90.3) and EFA-only models (TSS: 0.73, ROC: 0.93, KAPPA: 0.54, sensitivity: 91.2, specificity: 82.1). In addition, narrow endemic species obtained higher predictive performances using combined models (average TSS: 0.96, ROC: 0.99, KAPPA: 0.80, sensitivity: 99.6, specificity: 96.3) in comparison to the widespread oaks (TSS: 0.80, ROC: 0.96, KAPPA: 0.66, sensitivity: 92.6, specificity: 87.7). These results show that the modelling performance for the different sets of variables and taxonomic groups increase in performance when combining Climate and EFA variables for all metrics but especially for Kappa and TSS, whereas ROC is less sensitive to improvements, followed by climate-only and a consistent lower performance for the EFA-only set (Figure 2). This is particularly true for the NDE species-group, with the slightest differences between climate and EFA and climate-only in TSS and ROC for the remaining White Oaks. When comparing performance metrics, it is also important to consider their scale of variation; while Cohen's Kappa and TSS vary between −1 and 1 (with better models nearing one), ROC varies between 0 and 1 (also with better models nearing one) and hence the later lower ability to discriminate across good performing models holding a lower variance and saturating at the upper-end part of the spectrum. The increase in the performance by the combined set of climate and EFA is also reflected in terms of sensitivity (true positive rate), but especially in terms of specificity (true negative rate) (Figure 3). As before, these gains are reflected especially in the NDE group, and particularly for species such as Q.

×cerrioides, *Q. canariensis*, *Q. orocantabrica* and *Q. estremadurensis* (Table 1 and Supplementary Figure S1).

Results from the post hoc ANOVA test based on linear mixed-effects modelling (with a species and evaluation metric as random factors) showed a significant effect of the set of predictive variables on performance scores ($p < 0.001$). Estimated coefficients show that (despite variability) the "climate-only" and the "EFA-only" sets both have on average less performant models in relation to the combined climate–EFA set, since both coefficients are negative and, respectively, equal to: −0.018 ± 0.015 and −0.124 ± 0.014 (estimate ± std. error). These estimates also show that performance gains are higher in relation to the "EFA-only" set but less in relation to the "climate-only" (see Supplementary Information S5 for more details). The AICc-based model ranking (which measures model fitting performance while accounting for the number of variables in the models; Supplementary Table S1) also showed that for nine (out of thirteen) species, including *Q. broteroi*, *Q. canariensis*, *Q. ×cerrioides, Q. lusitanica, Q. marianica, Q. orocantabrica, Q. pubescens, Q. pyrenaica* and *Q. subpyrenaica*, better model performances are attained for the climate–EFA combined models. For *Q. faginea*, *Q. petraea* and *Q. robur* the EFA-only models obtained better performances according to the AICc-based ranking, while for *Q. estremadurensis* the climate-only model was the best one. This evidences that the higher number of variables in combined models (i.e., higher complexity) does not affect the overall ranking.

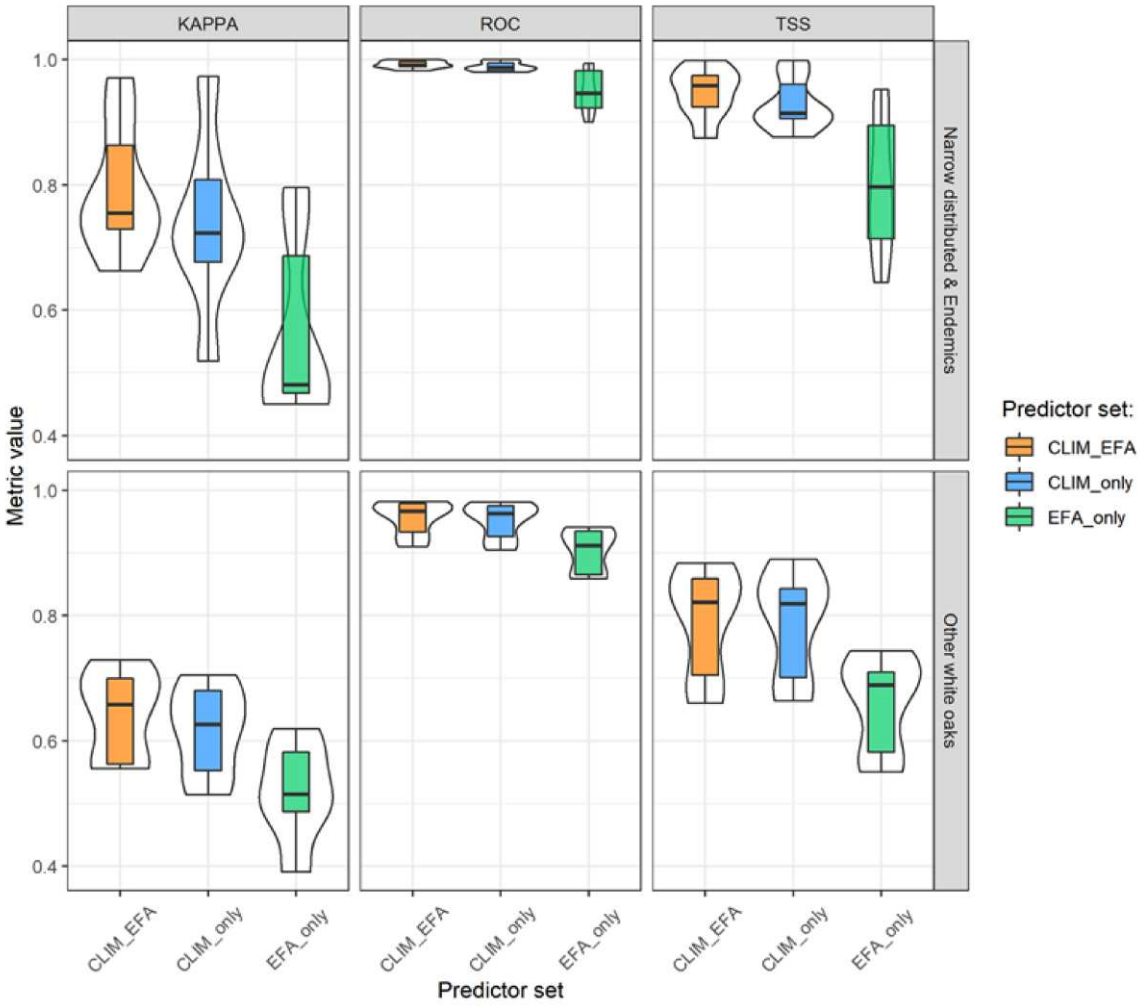


Figure 2 - Combined boxplot/violin plot of model performance values for the species group. (KAPPA—Cohen Kappa, ROC—area under the receiver operating curve, and TSS—true skill statistic) for each set of predictor variables: "CLIM_EFA" (climate and ecosystem functioning attributes (EFAs) combined), "CLIM_only" (climate variables only) and "EFA_only" (satellite EFA variables only). Boxes display (from bottom to top) the 25%, 50% (median) and 75% quartiles of the distribution. Whiskers present the minimum and maximum values.

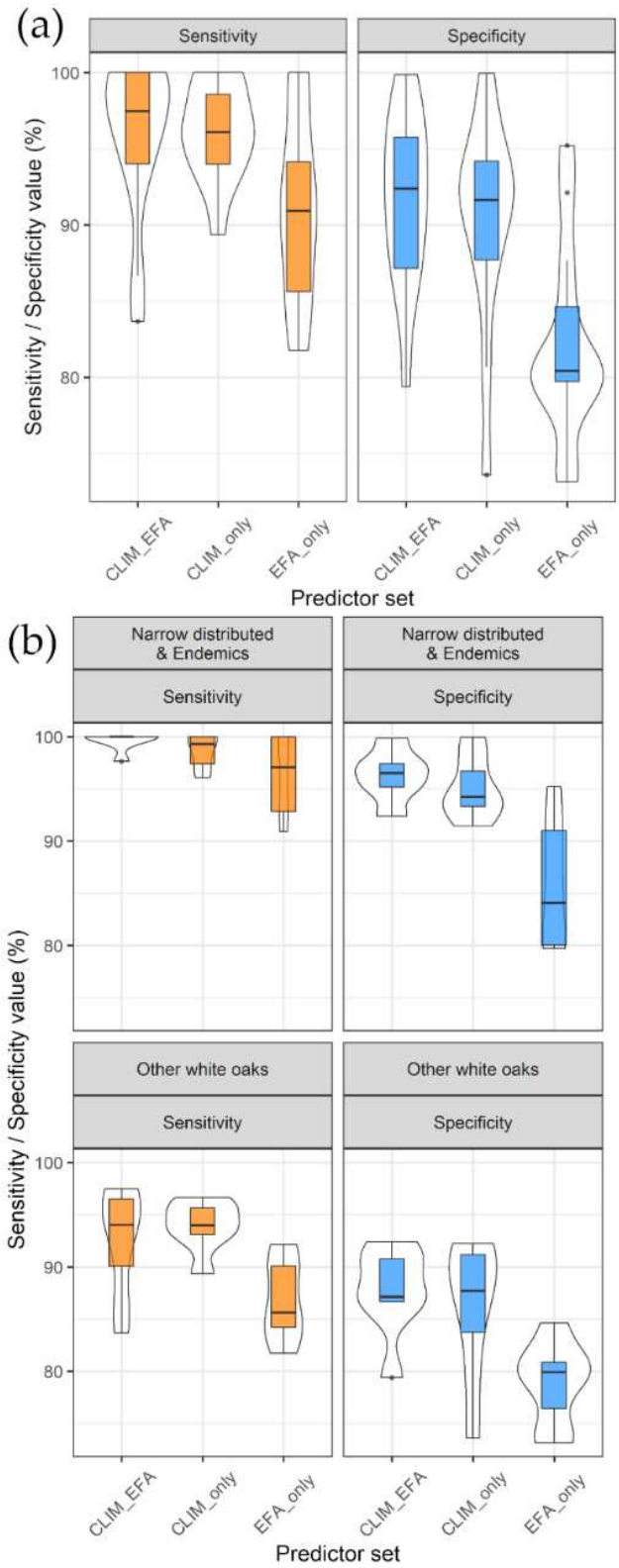


Figure 3 - (a) Combined boxplot/violin plot with the comparison of sensitivity (or true positive rate) and specificity (or true negative rate) for all species between groups of variables. Boxes display (from bottom to top) the 25%, 50% (median) and 75% quartiles of the distribution: (b) the comparison of specificity values between different groups of species. Whiskers present the minimum and maximum values without outliers (shown as points). Sets of predictive variables (x axis) are: “CLIM_EFA” (climate and EFA combined), “CLIM_only” (climate variables only) and “EFA_only” (satellite EFA variables only).

Table 1 - Evaluation scores per studied species for the ensemble of 30 top-models combining both climate and satellite-based EFA variables (TSS: true skill statistic; ROC: area under the receiver operating curve; KAPPA: Cohen's Kappa; sensitivity (also called true positive rate or recall); specificity (also defined as the true negative rate)). The number of species records presented are computed after removing duplicates and applying the spatial thinning algorithm for imposing a minimum separation distance of 3 km between points (*spThin*). * narrow distributed; ** endemic.

Species Names	TSS	ROC	KAPPA	Sensitivity	Specificity	Number of Species Records
Quercus ×cerrioides **	1.00	1.00	0.97	100.0	99.9	18
Quercus canariensis *	0.98	1.00	0.78	100.0	97.5	96
Quercus orocantabrica **	0.97	1.00	0.89	100.0	97.2	33
Quercus estremadurensis *	0.96	0.99	0.66	100.0	95.8	46
Quercus lusitanica *	0.93	0.99	0.72	97.6	95.0	212
Quercus marianica **	0.92	0.99	0.75	100.0	92.4	70
Quercus pubescens	0.88	0.98	0.73	97.5	90.9	473
Quercus subpyrenaica **	0.88	0.98	0.76	96.8	90.6	375
Quercus broteroi	0.86	0.98	0.70	93.5	92.4	306
Quercus robur	0.83	0.97	0.64	96.2	86.8	901
Quercus petraea	0.81	0.97	0.68	94.0	87.1	753
Quercus faginea	0.71	0.93	0.56	83.7	86.6	301
Quercus pyrenaica	0.66	0.91	0.56	86.7	79.4	3282

The consistent better performance of combined climate and EFA models, despite the relatively small increment for some species (Figures 2 and 3; Supplementary Figure S1), suggests that these two types of variables, when combined, improve the predictive models. Results improved especially for NDE species which have narrower biogeographic ranges and ecological niche breadths. In contrast, models based solely on EFA variables show the lowest performances, even when compared with climate-only models. This may be explained by the coarse scale of the models developed (i.e., with low spatial resolution and a large areal extent) for which regional variations of climate patterns hold substantial more predictive power than finer/local ecosystem functioning patterns depicted by satellite EFA variables. This may be due to the particularly high

affinity of most White Oak species to climate gradients, which constrain or control several important physiological aspects of these species' environmental tolerances at a regional scale (Veloz *et al.*, 2012). The scale of the influence of variables capturing primary to secondary (or regional to local) patterns structuring species habitat given each one's spatial autocorrelation patterns, has been previously identified for SDMs (Vicente *et al.*, 2014). This may also mean that when used at a narrower extent and higher spatial resolution (i.e., finer scale), EFA variables may prove more relevant by their ability to describe small scale variation, heterogeneity and environmental gradients in species habitat patterns, and thus present distinct predictive abilities given species attributes and modelling scale (Arenas-Castro *et al.*, 2018).

At a regional/coarser scale, EFAs are mainly driven by climate patterns while in contrast these are more linked to land-cover and land-use patterns at a finer/local scale and thus capturing human influence on ecosystems (Alcaraz-Segura *et al.*, 2017; Arenas-Castro *et al.*, 2018; Arenas-Castro *et al.*, 2019). As such, EFAs offer an integrative, quicker and more up-to-date view of ecosystem responses to environmental factors and changes, in comparison to attributes of structure (e.g., patch size, fragmentation) or composition (e.g., percent cover of certain habitats) (Alcaraz-Segura *et al.*, 2017; Arenas-Castro *et al.*, 2018; Civantos *et al.*, 2018; Arenas-Castro *et al.*, 2019) and thus linking species responses to pressures on ecosystem functioning and its state (Alcaraz-Segura *et al.*, 2017). This holds advantages for implementing species-monitoring programs (Cabello *et al.*, 2012; Honrado *et al.*, 2016; Regos *et al.*, 2020) and at the same time, satellite-based EFAs also have the virtue of inserting more 'realism' into the spatial predictions of models. For example, implementing EFA variables in models may aid by removing unsuitable areas occupied by artificial or shrubby vegetation (both with a lower mean and seasonal variation in annual EVI or productivity) that may appear as suitable in climate-only models (which solely portray the potential distribution) while in combined models they likely do not. By including integrative, finer-scale attributes of ecosystem functioning linked to each species habitat and suitable environmental conditions, models may better approximate the realized distribution of species which may present several advantages for conservation, management and restoration efforts. Nonetheless, it is important not to blur the distinction between modelling a species distribution or its environmental suitability from actually detecting it through satellite imagery using spectral signatures or indices (Bradley *et al.*, 2012).

A frequent limitation linked to SDMs is that species occurrences (one of SDM's key inputs) are usually available at coarse resolutions (McPherson *et al.*, 2006) while their

conservation and management are often required at a much finer spatial resolution (Nagendra *et al.*, 2013; Fernandes *et al.*, 2014). Moreover, many predictive variables are also not measurable or available at the required spatiotemporal resolution and consequently, surrogates and interpolated data (e.g., from weather stations) have to be used instead (Pearson & Dawson, 2003; Lassueur *et al.*, 2006). Structural predictors from thematic maps (e.g., land-cover) also bear limitations by often not representing key landscape features nor the ecosystem processes relevant for characterizing a certain species status and change. Moreover, both occurrence data and predictive variables can have inappropriate or distinct spatial, thematic and/or temporal resolutions which impacts model quality and performance (Pôças *et al.*, 2014).

6.4.2 Combined Models for Individual Species

Overall, combined models (i.e., with both satellite-based EFA and climate variables) showed higher performance scores for all NDE taxa than other White Oaks (TSS > 0.88; Figure 2), especially for *Quercus* ×*cerrioides*, *Q. canariensis*, *Q. orocantabrica*, and *Q. estremadurensis* (Table 1). The lowest TSS values corresponded to *Q. faginea* and *Q. pyrenaica* (0.71 and 0.66, respectively). ROC values were always above 0.9, suggesting an overall excellent performance of the NDE models. Cohen's Kappa values (typically more sensitive to true negative rates) varied between 0.56 and 0.97, also showing a strong performance of combined (climate and EFA) models with variations across species. In addition, sensitivity and specificity scores were always above 80% (with a slight exception for the widespread *Q. pyrenaica*), confirming the good and well-balanced performance of the models (Table 1; Supplementary Table S2 – Digital Annex).

Generally, we observe a bigger relevance of precipitation-related variables and a fluctuation of the importance of a second group of predictors, either related with temperature, or with EFA variables. When considering all species, climatic variables are generally the most important ones, especially the precipitation of the warmest quarter (BIO18), followed by annual precipitation (BIO12), annual mean temperature (BIO01) and winter cold (BIO06) (Figure 4 and Supplementary Figure S2). The same pattern is noticeable for the widely distributed White Oaks, but temperature-related variables (BIO01 and BIO06) become the second and third most important variables for the NDE group, followed by BIO12, with NDWI_MED, occupying the fifth position for these group of species (Supplementary Figure S2).

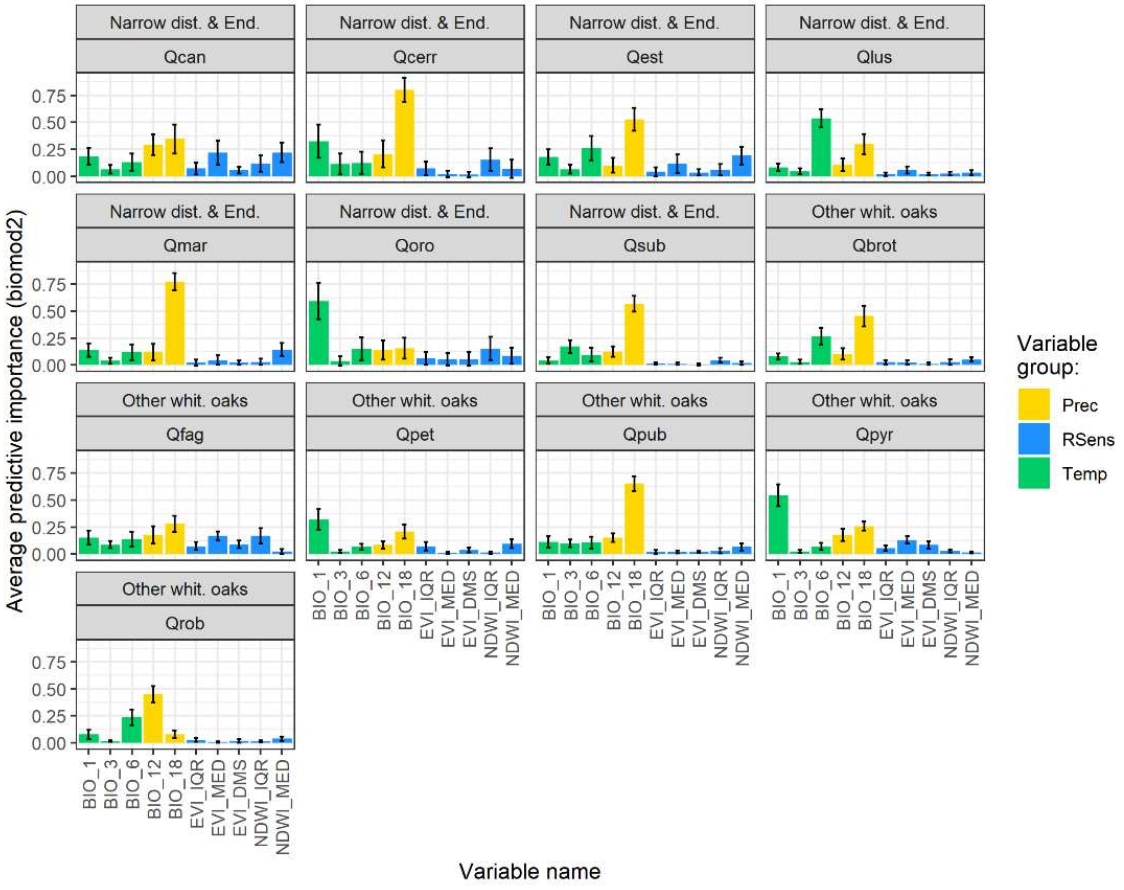


Figure 4 - Variable importance (average ± standard deviation across all models) for each oak species considering the two groups of predictors, climatic (precipitation and temperature) and satellite-based EFAs. BIO_1—annual mean temperature; BIO_4—temperature seasonality; BIO_6—min temperature of coldest month; BIO_12—annual precipitation; BIO_18—precipitation of warmest quarter; EVI_IQR—seasonality (EVI intra-annual variation); EVI_MED—productivity (EVI median); EVI_DMS—phenology (EVI day of maximum—spring). Precipitation-related variables ("Prec", shown in yellow), temperature ("Temp" in green) and remotely-sensed EFA's ("RSens", in blue).

When taking into account individual species (Figure 4), summer precipitation (BIO18) is predominantly the most important variable for most of the Iberian White Oaks, only superseded by winter cold (BIO6) for *Q. lusitanica*, annual mean temperature (BIO01) for *Q. orocantabrica*, *Q. petraea* and *Q. pyrenaica*, and annual precipitation (BIO12) for Q. robur. EFA-related variables occupy the third and fourth positions for several NDE oaks, like *Q. canariensis*, *Q. ×cerrioides*, *Q. marianica, Q. estremadurensis* and *Q. orocantabrica*, especially EVI_MED and NDWI_MED. *Q. faginea* seems to be the species with the most balanced equilibrium between variables (Figure 4).

Regarding EFAs, its contribution was found to be more important as predictors in models of NDE species than other White Oak species as before, regarding model performances. More specifically, the inter-quartile range of the NDWI (a descriptor of seasonality in water balance/content) was the most relevant variable across all of the studied species,

followed by the median of NDWI and EVI (descriptors of water balance/content and primary productivity, respectively) (Figure 4).

These results reflect the high dependence of precipitation for these group of oaks, especially in the dry season (BIO18) for most of the Gall Oaks, or those geographically distributed throughout the sub-Mediterranean and southern areas of the IP. The winter cold (BIO06) importance explains the distribution of *Q. lusitanica* in the Atlantic shore of the IP, showing this species' intolerance for winter cold, while the annual precipitation (BIO12) marks the distribution of *Q. robur* as it cannot withstand low precipitation levels and summer drought. The third and fourth position occupied by EFA predictors for some NDE species, represent the importance of the vegetation state/quality, for the maintenance of some of these oaks, especially for the relicts *Q. canariensis* and *Q. estremadurensis* and the endemics *Q. ×cerrioides* and *Q. marianica*. These taxa are dependent on shady and moist environments, normally in deep canyons of Atlantic areas. Herein, EVI-related EFA's were found suitable to depict primary production and water availability patterns of these areas with higher levels of humidity linked to the maintenance of these species (Ward, 1952; Wheeler, 2001; Vila-Viçosa *et al.*, 2015; Soriano & Costa, 2017).

The visual inspection of suitability maps for the seven NDE taxa shows the best areas for the preservation and recovery of the selected species. Here, we can compare the combined model (with satellite EFA and climate variables), with the spatial overlap of partial models (RS and climate) (Figure 5 and Figure 6). Overall, the contribution of EFA predictors brings higher accuracy for the spatial delimitation of these species' recovery areas, by reflecting the vegetation state through primary productivity and moisture conditions (better captured by NDWI-related EFA variables), and by adding it to the climatic suitability for each species.

When analysing the narrowly distributed oaks (Figure 5), *Q. canariensis* evidences suitable environmental conditions in its "typical" locations, from the Iberian southwest (Monchique and Algeciras) and Catalonian sub-populations, with the maintenance of residual areas in Morena System and suitable areas and Littoral shore of Centre Portugal (around Lisbon) (Figure 1). A similar pattern is followed by *Q. estremadurensis*, with a wider suitable area, through central Portugal up to Montes de Toledo (Spain) and an incursion in the Portuguese Douro thermophilic areas. *Q. lusitanica* preserves most of its known distribution (Franco, 1990; Schwarz, 1993), with the overlap of partial models being considerably smaller than the combined models (Figure 5).

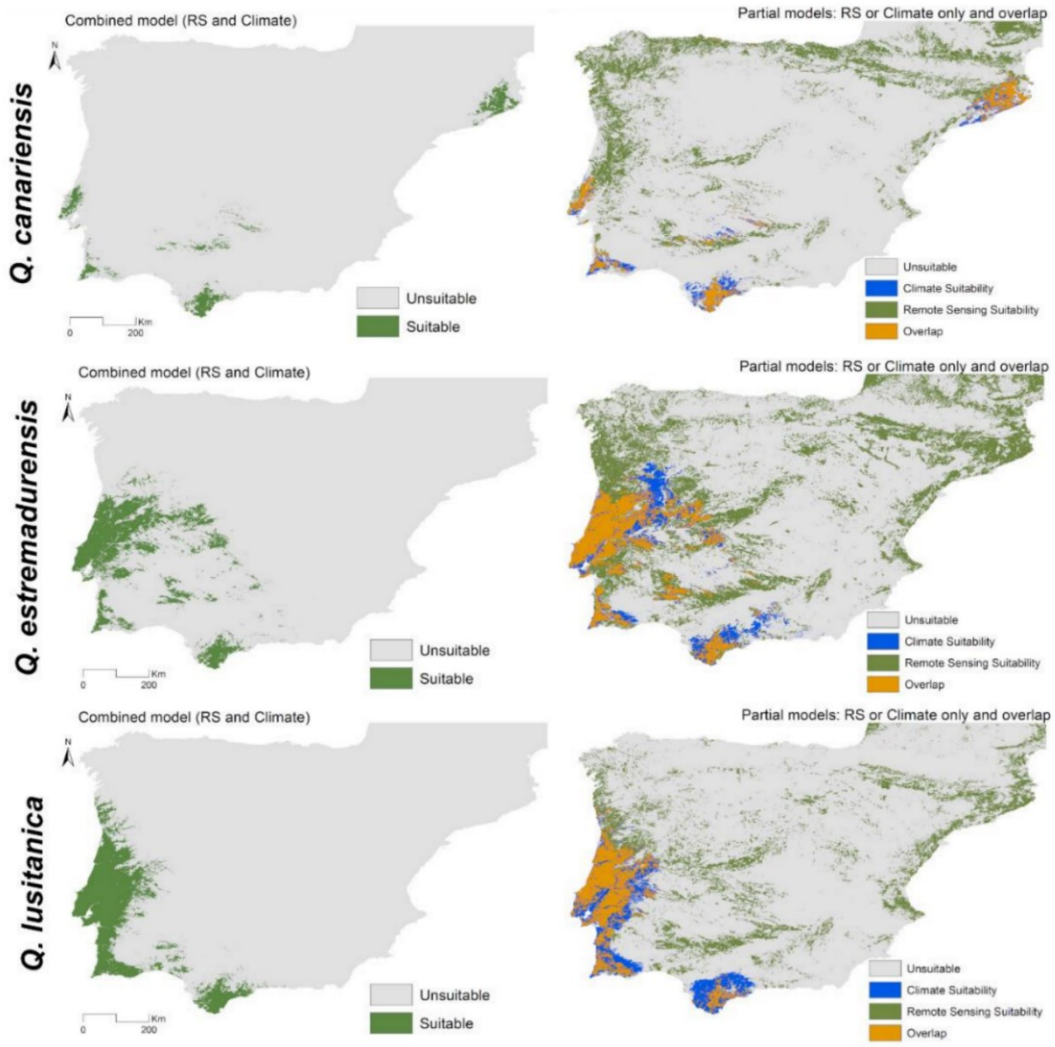


Figure 5 - Combined models (remote sensing EFA-–and climate) (left) and partial models (remote sensing EFA in green or climate in blue and their spatial overlap in orange) (right). Narrow distributed White Oaks (*Q. canariensis*, *Q. estremadurensis* and *Q. lusitanica*).

When looking at endemic oaks (Figure 6), *Q. marianica* shows a larger suitable area with a higher ecological plasticity in comparison to its parental species *Q. canariensis*, extending throughout Morena mountain chain and the western Portuguese coast. By tracking the remaining parental species (*Q. broteroi*) it enhances the role of hybridization by adapting to new ecological conditions as a strategy for survival in growing drier habitat types and conditions, where at least one of the parentals lost fitness (*Q. canariensis*) (Anderson, 1948; Anderson & Stebbins, 1954). *Q. orocantabrica* shows a wider area out of its currently known range, across the Cantabrian mountains and three disjoint subpopulations in Rioja, Cuenca and the Central system (Figure 1), with the EFA predictors contributing to diagnose orophile conditions in the suitable environmental space. These novel spatial inferences may in turn help managers and stakeholders to

devise much-needed restauration, recovery or re-introduction efforts (Gauquelin *et al.*, 2018; Cruz-Alonso *et al.*, 2019; Löf *et al.*, 2019; Safford & Vallejo, 2019). Likewise *Q. marianica*, the nothotaxa *Q. subpyrenaica*, show a wider and more continuous distribution in comparison to the parental *Q. pubescens* (Supplementary Figure S4), however, in reverse, a more reticulated distribution in the overlap of the partial models. This shows a higher ecological plasticity by matching the other parental species (*Q. faginea*) and tracking the sub-Mediterranean belt of northeast IP, while *Q. pubescens* presents a more continuous temperate distribution in the partial models and a reticulated distribution in the combined ones, being a more restrict taxon in terms of distribution. The endemic nothotaxa *Q. ×cerrioides* has a reduced suitable area in the littoral Catalonian mountains, as it results from contact with the residual *Q. canariensis* forests.

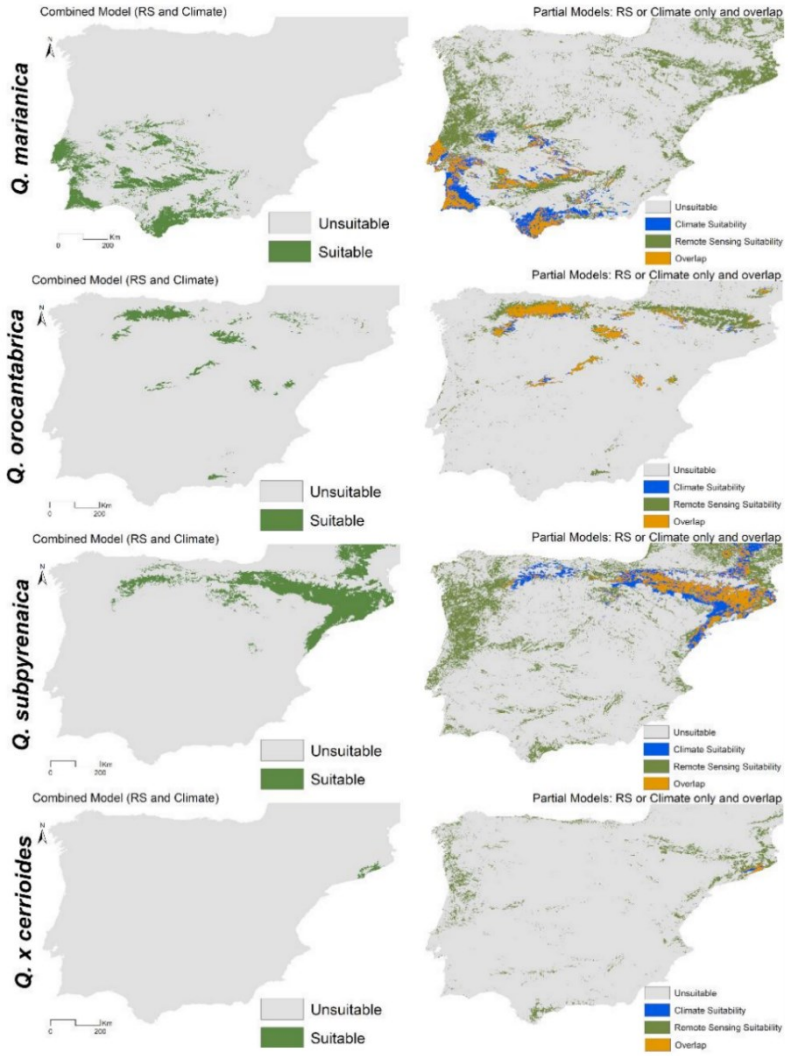


Figure 6 - Combined models (remote sensing (RS) EFA and climate) (left) and partial models (remote sensing EFA in green or climate in blue and their spatial overlap in orange) (right). Narrow endemic oaks (*Q. marianica, Q. orocantabrica, Q. subpyrenaica, Q. ×cerrioides*).

The remaining Iberian White Oaks, with wider distributions, frequently present smaller overlap areas between partial models than the combined ones, highlighting more detailed areas where to recover this species group when taking into account the EFA predictors (Supplementary Figures S3 and S4). The *Quercus broteroi* combined model shows a continuous area in western Iberia and throughout the Morena System and Montes de Toledo, with the overlap of partial models evidencing the best areas for this species recovery. By opposite, *Q. faginea* combined models show a wider area in the Douro Basin and throughout the Cantabrian mountains, Iberian and Betic Systems, and eastern IP, while the overlap shows a more conservative area for its recovery (Figure 1). Likewise, *Q. pyrenaica* presents a similar pattern, while including the central system and northwest Iberian Mountain areas, with disjoint relict subpopulations in southern Iberia. *Q. petraea* and *Q. robur* present complementary projected areas that reflect their ecological requirements, both with a larger overlap between combined models and the overlap of partial models. *Q. pubescens* shows similar patterns of the nothotaxa *Q. subpyrenaica*, with the first having a temperate distribution while the second enters into sub-Mediterranean areas (Himrane *et al.*, 2004; De Dios *et al.*, 2009). Both species evidence notorious differences between the combined models when in comparison to the overlap of the partial ones, with larger areas in the first ones.

6.4.3 Spatial Projections and Patterns of Species Richness

Model projections for all Iberian White Oak species (Figure 7) reveal areas with cumulative suitability up to seven oak taxa, highlighting the Iberian southwest mountains, the Lusitanian Basin, Montes de Toledo and to sub-littoral Catalonian mountains (Figure 1) as highly relevant. These areas can be considered the largest hotspots and the most important “lost” areas for the Iberian White Oaks conservation, being suitable for the highest diversity of oak taxa. Oaks in general show strong niche conservatism (Veloz *et al.*, 2012), particularly the Subgenus *Quercus* (Denk et al., 2017), that comprises temperate lineages of oaks (Wu & Al-Shehbaz, 1999), which were heavily constrained in the IP by its biogeography, prevailing only in areas with similar climates. This way water availability and the Atlantic influence plays a major role, especially when in a seasonal climate like the Mediterranean one (Rivas-Martínez *et al.*, 2017). Thus, our study provides a lacking approach to assess these woody temperate plants species richness which can provide useful data for promoting their persistence (Xu *et al.*, 2019), while unveiling the importance of multiple drivers of ecosystem functioning and their

interaction with the climate in a biogeographic transitional area between Temperate and Mediterranean Europe.

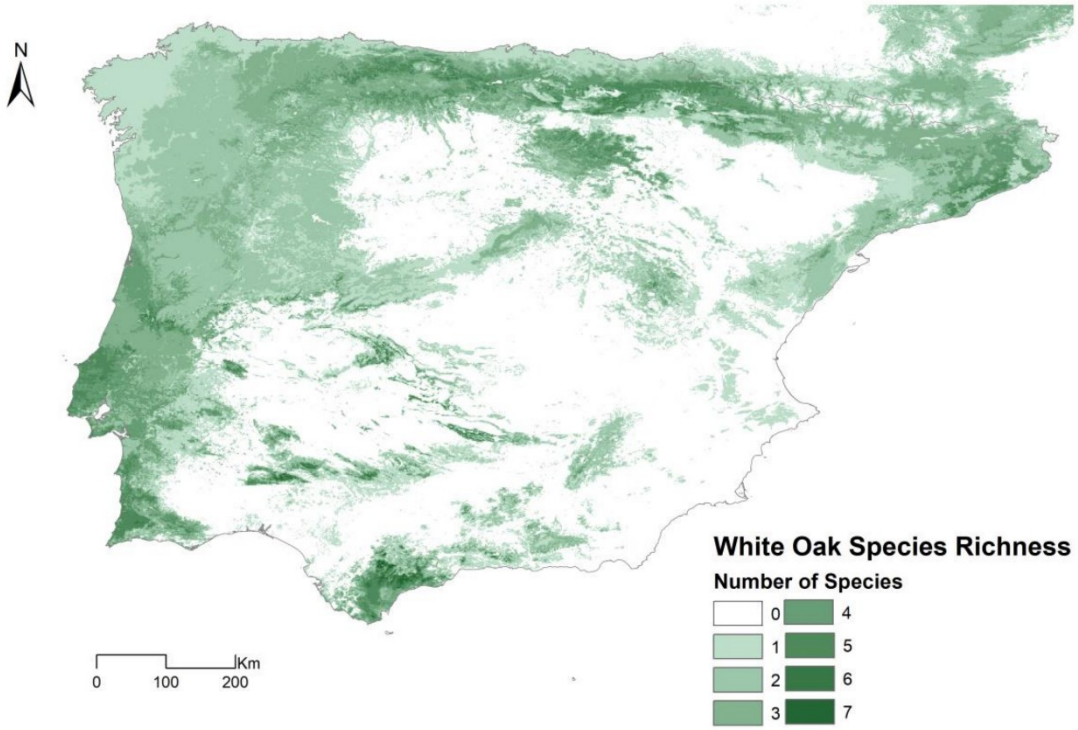


Figure 7 - Spatial patterns of predicted species richness for the Iberian White Oaks.

Such results allow to better understand the co-distribution and the spatial patterns of potential species richness of these taxa and therefore to know and prioritize areas with higher biogeographic conservation value. The central and western IP show the best areas for the Gall Oaks, where *Q. canariensis*, *Q. broteroi*, *Q. lusitanica* and *Q. marianica* have suitable environmental conditions to co-occur, together with *Q. estremadurensis*, which is a relict species, and also the presence of the widespread *Q. pyrenaica*, that in these thermophilic areas is also rare but potentially distributed. This area is only matched by the littoral Catalonian range, where *Q. canariensis* co-occurs with the roburoid *Q. pubescens, Q. petraea* and *Q. robur*, with an intricated legacy of introgression (Schwarz, 1936). This pattern is also present in the pre-Pyrenees area, where *Q. subpyrenaica* marks the transition from the submediterraenan to the temperate belt alongside the contact of *Q. pubescens* and *Q. faginea*. The northern and western mountain ranges, including the Iberian, Cantabrian and Gallaecian Systems are also quite important for the preservation of the European southernmost suitable areas for *Q. robur*, *Q. petraea* and the endemic *Q. orocantabrica*. Moreover, this area has a major relevance for the evolutionary history of these group of oaks in terms of the European

forests (Olalde *et al.*, 2002) and their inherent relevance for forest conservation when confronted with projected climatic shifts.

6.5. Conclusions

We highlighted the importance of incorporating satellite-derived ecosystem functioning attributes for mapping the potential distribution and habitat suitability of oak species, especially to those with a narrow distribution and relict-like character (NDE), in a biodiversity hotspot such as the Iberian Peninsula. Our results show that EFAs are able to improve predictions of the distribution of both narrow- and wide-ranged oak species at the regional scale and confirm its robustness as predictors of habitat features that complement the climate influence by describing relevant complementary dimensions of the carbon cycle and water balance at the ecosystem level. Thus, satellite-based predictors such as EFAs can nowadays be computed from imagery available at high frequencies and several spatial resolutions, which allow to match the scale of the relevant processes in each study, and to anticipate species' responses to different disturbances. By doing this, our combined modelling framework illustrates the great potential of EFAs to contribute for monitoring and conservation through the essential biodiversity variables framework (EBV class 'ecosystem function').

By incorporating and combining these variables with climatic data, our work addresses the best areas for the conservation of each taxa, for which vegetation state and ecosystem functioning attributes are generally overseen in climate-only studies. The good performance of the models helped to predict the best areas for the preservation of the studied species, while variable importance measures aided to explain the main factors behind species' distributions in the geographic space. Therefore, this work also serves as base for forecasting the impact of climate change in the Iberian oak forests, in the face of future scenarios. Furthermore, our methodology proved to be suitable to be applied to analogous situations and throughout the Mediterranean Basin and targeting oak forests worldwide. This is of paramount importance in a group characterized by a complex and reticulate evolutionary history. Globally, our results show that species distribution models are a suitable tool to accurately predict oak species distribution which holds great potential to accurately depict the 'best' areas for the conservation of the studied taxa. Our study highlights the Iberian Southwest, the Lusitanian Basin and the Catalonian littoral mountains, as the most important biogeographic areas, with greater

overall habitat suitability for a larger number of species, functioning as hotspots and relict-like areas for the broad-scale conservation of the Iberian white Oaks.

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6.6. References

Aedo C, Buira A, Medina L, Fernández-Albert M 2017. The Iberian Vascular Flora: Richness, Endemicity and Distribution Patterns. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 101-130.

Ahrends A, Rahbek C, Bulling MT, Burgess ND, Platts PJ, Lovett JC, Kindemba VW, Owen N, Sallu AN, Marshall AR. 2011. Conservation and the botanist effect. *Biological Conservation* **144**(1): 131-140.

Aiello-Lammens M, Boria R, Radosavljevic A, Vilela B, Anderson R, Bjornson R, Weston S. 2014. spThin: Functions for spatial thinning of species occurrence records for use in ecological models. *R package version 0.1. 0*.

Alcaraz-Segura D, Cabello J, Paruelo JM, Delibes M. 2009. Use of descriptors of ecosystem functioning for monitoring a national park network: a remote sensing approach. *Environmental Management* **43**(1): 38-48.

Alcaraz-Segura D, Lomba A, Sousa-Silva R, Nieto-Lugilde D, Alves P, Georges D, Vicente JR, Honrado JP. 2017. Potential of satellite-derived ecosystem functional attributes to anticipate species range shifts. *International journal of applied earth observation and geoinformation* **57**: 86-92.

Alcaraz D, Paruelo J, Cabello J. 2006. Identification of current ecosystem functional types in the Iberian Peninsula. *Global Ecology and Biogeography* **15**(2): 200-212.

Anderegg WR, Trugman AT, Badgley G, Anderson CM, Bartuska A, Ciais P, Cullenward D, Field CB, Freeman J, Goetz SJ. 2020. Climate-driven risks to the climate mitigation potential of forests. *Science* **368**(6497): eaaz7005.

Anderson E. 1948. Hybridization of the habitat. *Evolution*: 1-9.

Anderson E, Stebbins GL. 1954. Hybridization as an evolutionary stimulus. *Evolution*: 378-388.

Araújo MB, New M. 2007. Ensemble forecasting of species distributions. *Trends in ecology & evolution* **22**(1): 42-47.

Arenas-Castro S, Gonçalves J, Alves P, Alcaraz-Segura D, Honrado JP. 2018. Assessing the multi-scale predictive ability of ecosystem functional attributes for species distribution modelling. *PloS one* **13**(6): e0199292.

Arenas-Castro S, Regos A, Gonçalves JF, Alcaraz-Segura D, Honrado J. 2019. Remotely sensed variables of ecosystem functioning support robust predictions of abundance patterns for rare species. *Remote Sensing* **11**(18): 2086.

Balzan MV, Hassoun AER, Aroua N, Baldy V, Dagher MB, Branquinho C, Dutay J-C, El Bour M, Médail F, Mojtahid M. 2020. *Ecosystems*. Marseille: Plan Bleu.

Barbet-Massin M, Jiguet F, Albert C, Thuiller W 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3: 327–338.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* **3**(2): 327-338.

Bates D, Mächler M, Bolker B, Walker S. 2014. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.

Blanco-Castro E, Casado-Gonzáles M, Costa-Tenorio M, Escribano R, García-Antón M, Génova-Fuster M, Gómez-Mazaneque Á, Gómez-Mazaneque F, Moreno-Saiz JC, Juaristi CM, et al. 2005. *Los bosques ibéricos. Una interpretación geobotánica*. Barcelona: Editorial Planeta, Barcelona, Spain.

Bradley BA, Olsson AD, Wang O, Dickson BG, Pelech L, Sesnie SE, Zachmann LJ. 2012. Species detection vs. habitat suitability: are we biasing habitat suitability models with remotely sensed data? *Ecological modelling* **244**: 57-64.

Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological methods & research* **33**(2): 261-304.

Burnham KP, Anderson DR, Huyvaert KP. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral ecology and sociobiology* **65**(1): 23-35.

Cabello J, Fernández N, Alcaraz-Segura D, Oyonarte C, Pineiro G, Altesor A, Delibes M, Paruelo JM. 2012. The ecosystem functioning dimension in conservation: insights from remote sensing. *Biodiversity and Conservation* **21**(13): 3287-3305.

Castroviejo S, Aedo C, Medina L. 2006. Management of floristic information on the Internet: the Anthos solution. *Willdenowia* **36**(1): 127-137.

Civantos E, Monteiro AT, Gonçalves J, Marcos B, Alves P, Honrado JP. 2018. Patterns of landscape seasonality influence passerine diversity: Implications for conservation management under global change. *Ecological Complexity* **36**: 117-125.

Coleman CO, Radulovici AE. 2020. Challenges for the future of taxonomy: talents, databases and knowledge growth. *Megataxa* **1**(1): 28–34-28–34.

Coutinho AXP. 1888. Os Quercus de Portugal. *Boletim da Sociedade Broteriana* **6**: 47-116.

Cramer W, Guiot J, Fader M, Garrabou J, Gattuso J-P, Iglesias A, Lange MA, Lionello P, Llasat MC, Paz S, et al. 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change* **8**(11): 972-980.

Cruz-Alonso V, Ruiz-Benito P, Villar-Salvador P, Rey-Benayas JM. 2019. Long-term recovery of multifunctionality in Mediterranean forests depends on restoration strategy and forest type. *Journal of Applied Ecology* **56**(3): 745-757.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology* **204**(2): 189-205.

Del Río S, Penas Á. 2006. Potential distribution of semi-deciduous forests in Castile and Leon (Spain) in relation to climatic variations. *Plant Ecology* **185**(2): 269-282.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Díaz-González TE, Penas Á 2017. The High Mountain Area of Northwestern Spain: The Cantabrian Range, the Galician-Leonese Mountains and the Bierzo Trench. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 251-321.

Duque-Lazo J, Navarro-Cerrillo R, Ruíz-Gómez F. 2018. Assessment of the future stability of cork oak (Quercus suber L.) afforestation under climate change scenarios in Southwest Spain. *Forest ecology and management* **409**: 444-456.

Elith J, Graham C, Anderson R, Dudık M, Ferrier S. 2006. Novel methods improve prediction of species' distribution models. *Ecography* **32**: 66-77.

Ely CV, de Loreto Bordignon SA, Trevisan R, Boldrini II. 2017. Implications of poor taxonomy in conservation. *Journal for Nature Conservation* **36**: 10-13.

Endlicher S. 1847. *Generum plantarum supplementum quartum*. Vienna: Fr. Beck.

Fernandes RF, Vicente JR, Georges D, Alves P, Thuiller W, Honrado JP. 2014. A novel downscaling approach to predict plant invasions and improve local conservation actions. *Biological invasions* **16**(12): 2577-2590.

Font X, Pérez-García N, Biurrun I, Fernández-González F, Lence C. 2012. The Iberian and Macaronesian Vegetation Information System (SIVIM, www. sivim. info), five years of online vegetation's data publishing. *Plant Sociology* **49**(2): 89-95.

Franco JA 1990. Quercus L. In: S. C, al. e eds. *Flora Iberica, (Plantanaceae-Plumbaginaceae [Partim])*. Madrid: Real Jardín Botánico, CSIC, pp. 15-36.

Gao B-C. 1996. NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote sensing of environment* **58**(3): 257-266.

García-Valdés R, Svenning JC, Zavala MA, Purves DW, Araújo MB. 2015. Evaluating the combined effects of climate and land-use change on tree species distributions. *Journal of Applied Ecology* **52**(4): 902-912.

Gauquelin T, Michon G, Joffre R, Duponnois R, Génin D, Fady B, Dagher-Kharrat MB, Derridj A, Slimani S, Badri W. 2018. Mediterranean forests, land use and climate change: a social-ecological perspective. *Regional Environmental Change* **18**(3): 623-636.

Gonçalves J, Alves P, Pôças I, Marcos B, Sousa-Silva R, Lomba Â, Honrado JP. 2016. Exploring the spatiotemporal dynamics of habitat suitability to improve conservation management of a vulnerable plant species. *Biodiversity and Conservation* **25**(14): 2867-2888.

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote sensing of environment* **202**: 18-27.

Guisan A, Edwards Jr TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological modelling* **157**(2-3): 89-100.

Guisan A, Thuiller W, Zimmermann NE. 2017. *Habitat suitability and distribution models: with applications in R*: Cambridge University Press.

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AI, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C. 2013. Predicting species distributions for conservation decisions. *Ecology letters* **16**(12): 1424-1435.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hernández-Lambraño RE, de la Cruz DR, Sánchez-Agudo JÁ. 2019. Spatial oak decline models to inform conservation planning in the Central-Western Iberian Peninsula. *Forest ecology and management* **441**: 115-126.

Himrane H, Camarero JJ, Gil-Pelegrín E. 2004. Morphological and ecophysiological variation of the hybrid oak Quercus subpyrenaica (Q. faginea× Q. pubescens). *Trees* **18**(5): 566-575.

Hipp AL. 2015. Should hybridization make us skeptical of the oak phylogeny. *International Oak Journal* **26**: 9-18.

Holstein J. 2001. *GBIF: Global Biodiversity Information Facility*: University of Ulm.

Honrado JP, Pereira HM, Guisan A. 2016. Fostering integration between biodiversity monitoring and modelling. *Journal of Applied Ecology* **53**(5): 1299-1304.

Huete A, Didan K, Miura T, Rodriguez EP, Gao X, Ferreira LG. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote sensing of environment* **83**(1-2): 195-213.

Lassueur T, Joost S, Randin CF. 2006. Very high resolution digital elevation models: Do they improve models of plant species distribution? *Ecological modelling* **198**(1-2): 139-153.

Löf M, Castro J, Engman M, Leverkus AB, Madsen P, Reque JA, Villalobos A, Gardiner ES. 2019. Tamm Review: Direct seeding to restore oak (Quercus spp.) forests and woodlands. *Forest ecology and management* **448**: 474-489.

Loidi J 2017. Introduction to the Iberian Peninsula, General Features: Geography, Geology, Name, Brief History, Land Use and Conservation. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 3-27.

Loidi J, Herrera M. 1990. The Quercus pubescens and Quercus faginea forests in the Basque Country (Spain): distribution and typology in relation to climatic factors. *Plant Ecology* **90**(1): 81-92.

López-Tirado J, Hidalgo PJ. 2018. Predicting suitability of forest dynamics to future climatic conditions: the likely dominance of Holm oak [Quercus ilex subsp. ballota (Desf.) Samp.] and Aleppo pine (Pinus halepensis Mill.). *Annals of Forest Science* **75**(1): 1-11.

Luque S, Pettorelli N, Vihervaara P, Wegmann M. 2018. Improving biodiversity monitoring using satellite remote sensing to provide solutions towards the 2020 conservation targets. *Methods in Ecology and Evolution* **9**(8): 1784-1786.

Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). *Molecular phylogenetics and evolution* **12**(3): 333-349.

Matías L, Abdelaziz M, Godoy O, Gómez-Aparicio L. 2019. Disentangling the climatic and biotic factors driving changes in the dynamics of Quercus suber populations across the species 'latitudinal range. *Diversity and Distributions* **25**(4): 524-535.

McPherson JM, Jetz W, Rogers DJ. 2006. Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions—possibilities and limitations. *Ecological modelling* **192**(3-4): 499-522.

McVay JD, Hipp AL, Manos PS. 2017. A genetic legacy of introgression confounds phylogeny and biogeography in oaks. *Proc. R. Soc. B* **284**(1854): 20170300.

Médail F, Baumel A. 2018. Using phylogeography to define conservation priorities: The case of narrow endemic plants in the Mediterranean Basin hotspot. *Biological Conservation* **224**: 258-266.

Montserrat P. 1957. Algunos aspectos de la diferenciación sistemática de los Quercus ibéricos.

Nagendra H, Lucas R, Honrado JP, Jongman RH, Tarantino C, Adamo M, Mairota P. 2013. Remote sensing for conservation monitoring: Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecological Indicators* **33**: 45-59.

Neophytou C, Aravanopoulos FA, Fink S, Dounavi A. 2010. Detecting interspecific and geographic differentiation patterns in two interfertile oak species (Quercus petraea (Matt.) Liebl. and Q. robur L.) using small sets of microsatellite markers. *Forest ecology and management* **259**(10): 2026-2035.

Noce S, Collalti A, Santini M. 2017. Likelihood of changes in forest species suitability, distribution, and diversity under future climate: The case of Southern Europe. *Ecology and Evolution* **7**(22): 9358-9375.

Olalde M, Herrán A, Espinel S, Goicoechea PG. 2002. White oaks phylogeography in the Iberian Peninsula. *Forest ecology and management* **156**(1-3): 89-102.

Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, Church JA, Clarke L, Dahe Q, Dasgupta P. 2014. *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*: IPCC.

Pasta S, de Rigo D, Caudullo G 2016. Quercus pubescens in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G,

Houston Durrant T, Mauri A eds. *European atlas of forest tree species*. Luxembourg: Publications Office of the European Union, 156-157.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**(5): 361-371.

Pereira AJ, Francisco A, Porto M. 2016. Flora-On: Occurrence data of the vascular flora of mainland Portugal. *PhytoKeys*(69): 105.

Pereira HM, Ferrier S, Walters M, Geller GN, Jongman R, Scholes RJ, Bruford MW, Brummitt N, Butchart S, Cardoso A. 2013. Essential biodiversity variables. *Science* **339**(6117): 277-278.

Pôças I, Gonçalves J, Marcos B, Alonso J, Castro P, Honrado JP. 2014. Evaluating the fitness for use of spatial data sets to promote quality in ecological assessment and monitoring. *International Journal of Geographical Information Science* **28**(11): 2356-2371.

Regos A, Gómez-Rodríguez P, Arenas-Castro S, Tapia L, Vidal M, Domínguez J. 2020. Model-assisted bird monitoring based on remotely sensed ecosystem functioning and atlas data. *Remote Sensing* **12**(16): 2549.

Rivas-Martínez S, Aguiar C, Aguilella A, Alonso R, Alvarez M, Amich F, Arnaiz C, Baccheta G, Barbero M, Barbour M. 2011. Map of series, geoseries and geopermaseries of vegetation in Spain [MEMORY OF MAP OF POTENTIAL VEGETATION OF SPAIN, 2011] PART II. *Itinera Geobotanica* **18**(II): 1-764.

Rivas-Martínez S, González-Días TE, González FF, Loidi JJ, Lousã MF, Merino ÁP. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica*(15): 433-922.

Rivas-Martínez S, Penas A, del Río S, González T, Rivas-Sáenz S 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 29-80.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rodríguez-Sánchez F, Hampe A, Jordano P, Arroyo J. 2010. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Review of Palaeobotany and Palynology* **162**(3): 507-521.

Sabatini FM, Burrascano S, Keeton WS, Levers C, Lindner M, Pötzschner F, Verkerk PJ, Bauhus J, Buchwald E, Chaskovsky O. 2018. Where are Europe's last primary forests? *Diversity and Distributions* **24**(10): 1426-1439.

Safford HD, Vallejo VR 2019. Ecosystem management and ecological restoration in the Anthropocene: integrating global change, soils, and disturbance in boreal and Mediterranean forests. *Developments in Soil Science*: Elsevier, 259-308.

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O. 1936. Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* **8**: 65–100.

Schwarz O. 1937. Monographie der Eichen Europas und des Mittelmeergebietes. *Repertorium novarum speciarum regni vegetabilis* **1**: 1-200.

Schwarz O 1964. Quercus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, DA. W eds. *Flora Europaea*. Cambridge: Cambridge University Press, 61-64.

Schwarz O 1993. Quercus L. In: al. TTe ed. *Flora Europaea*. Cambridge: Cambridge University Press., 72-76.

Senf C, Seidl R. 2020. Mapping the coupled human and natural disturbance regimes of Europe's forests. *bioRxiv*.

Soriano P, Costa M 2017. The coastal Levantine area. *The vegetation of the Iberian Peninsula*: Springer, 589-625.

Sun S, Zhang Y, Huang D, Wang H, Cao Q, Fan P, Yang N, Zheng P, Wang R. 2020. The effect of climate change on the richness distribution pattern of oaks (Quercus L.) in China. *Science of The Total Environment* **744**: 140786.

Taleb MS, Fennane M. 2019. *Vascular plant communities of Morocco*: Springer.

Team R C 2019. R Version 3.5.3: A language and environment for statistical computing.In Computing: RFfS. Vienna, Austria. https://www.R-project.org.

Thuiller W, Lafourcade B, Engler R, Araújo MB. 2009. BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography* **32**(3): 369-373.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

Ülker ED, Tavşanoğlu Ç, Perktaş U. 2018. Ecological niche modelling of pedunculate oak (Quercus robur) supports the 'expansion–contraction' model of Pleistocene biogeography. *Biological journal of the Linnean Society* **123**(2): 338-347.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Veloz SD, Williams JW, Blois JL, He F, Otto-Bliesner B, Liu Z. 2012. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology* **18**(5): 1698-1713.

Vessella F, López-Tirado J, Simeone MC, Schirone B, Hidalgo PJ. 2017. A tree species range in the face of climate change: cork oak as a study case for the Mediterranean biome. *European Journal of Forest Research* **136**(3): 555-569.

Vicente JR, Gonçalves J, Honrado JP, Randin CF, Pottier J, Broennimann O, Lomba A, Guisan A. 2014. A framework for assessing the scale of influence of environmental factors on ecological patterns. *Ecological Complexity* **20**: 151-156.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C, Gonçalves J, Honrado J, Lomba Â, Almeida RS, Vázquez FM, Garcia C. 2020. Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Scientific reports* **10**(1): 1-12.

Vila-Viçosa C, Gonçalves J, Honrado J, Silva R, Vazquez F, Stephan J, García C. 2019. Past, Present, and Future of Marcescent Mediterranean Forests. *Biodiversity Information Science and Standards* **3**.

Vila-Viçosa C, Marcos B, Garcia C, Gonçalves J 2019. Biogeography from space—A new tool to disentangle Iberian Forests Ecology and Distribution. *Proceedings of the SIBECOL. 1st Meeting of the Iberian Ecological Society & XIV AEET Meeting, Barcelona, Spain*. 4-17.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vila-Viçosa C, Vázquez FM, Mendes P, Del Rio S, Musarella C, Cano-Ortiz A, Meireles C. 2015. Syntaxonomic update on the relict groves of Mirbeck's oak (Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* **149**(3): 512-526.

Villar EH. 1935. Sur le nom de quelques Quercus et la systématique du faginea. *Cavanillesia* **7**: 57-70.

Villar EH. 1958. Estudios sobre los Quercus del Oeste mediterráneo. *Anales del Instituto Botanico de A.J. Cavanilles* **15**: 3-114.

Ward A. 1952. Fog at North Front, Gibraltar. *Meteorol. Mag* **81**: 272-279.

Wheeler D. 2001. Factors governing sunshine in south-west Iberia: A review of western Europe's sunniest region. *Weather* **56**(6): 189-197.

Wu Z-y, Al-Shehbaz IA. 1999. *Flora of China. 4. Cycadaceae through Fagaceae [Hauptbd.]*: Science Press.

Xu X, Dimitrov D, Shrestha N, Rahbek C, Wang Z. 2019. A consistent species richness–climate relationship for oaks across the Northern Hemisphere. *Global Ecology and Biogeography* **28**(8): 1051-1066.

6.7. Supplementary Information

Supplementary Information S1 - Herbaria list of studied physical and virtual collections (*Quercus* L) and consulted databases.

Studied herbaria collections (*Quercus* L.)

Herbarium Code	Institution	Location
AVE	Universidade de Aveiro	Portugal. Aveiro.
BCN	University of Barcelona	Spain. Catalonia. Barcelona
BRESA	Polytechnic Institute of Bragança - IPB	Portugal. Bragança.
COI	University of Coimbra	Portugal. Coimbra.
HSS	Research Centre of "La Orden-Valdesequera"	Spain. Extremadura. Mérida.
HVR	Universidade de Trás-os-Montes e Alto Douro	Portugal. Vila Real.
L	Naturalis	Netherlands. Leiden.
LISE	Instituto Nacional de Investigação Agrária e Veterinária, I. P. (INIAV)	Portugal. Oeiras.
LISFA	Instituto Nacional de Investigação Agrária e Veterinária, I. P. (INIAV)	Portugal. Oeiras.
LISI	Instituto Superior de Agronomia	Portugal. Lisboa.
LISU	Museu Nacional de História Natural e da Ciência	Portugal. Lisboa.
MA	Real Jardín Botánico	Spain. Madrid.
PO	Museu de História Natural e da Ciência da Universidade do Porto	Portugal. Porto
SALA	Universidad de Salamanca	Spain. Salamanca.
SANT	Universidad de Santiago de Compostela	Spain. Galicia. Santiago de Compostela.
UEVH	Universidade de Évora	Portugal. Évora.

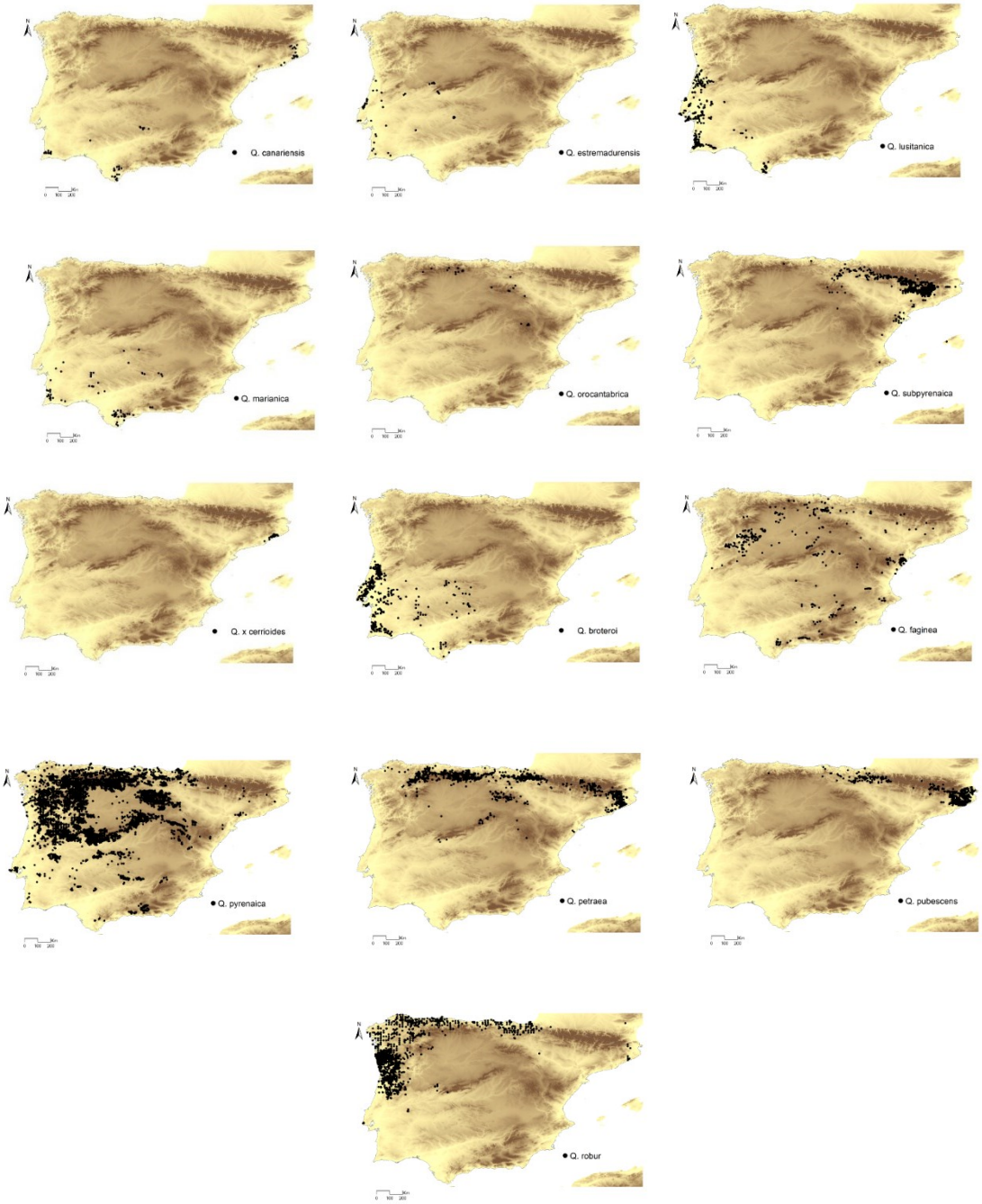
Online collections

Herbarium Code	Institution	Location
B	Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin	Germany. Berlin.
G	Conservatoire et Jardin botaniques de la Ville de Genève	Switzerland. Genève.
K	Royal Botanic Gardens	U.K. England. Kew.
MAIA	INIA (Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria)	Spain. Madrid.
P	Muséum National d'Histoire Naturelle	France. Paris.
MPU	Université de Montpellier	France. Montpellier.

Online databases

Name	Site	Reference
ANTHOS: Spanish Plants Information System	http://www.anthos.es/	Castroviejo *et al.* (2006)
Flora-On: Flora de Portugal Interactiva	www.flora-on.pt	Pereira *et al.* (2016)
GBIF Global Biodiversity Information Facility	https://www.gbif.org/	Holstein (2001)
SIVIM: Iberian and Macaronesian Vegetation Information System	http://www.sivim.info/sivi/	Font *et al.* (2012)

Supplementary Information S2 – Species records



Supplementary Information S3 - Focal taxa information.

Roburoid Oaks (Section *Robur* Endlicher) (Endlicher, 1847)

Quercus robur L. is a Eurosiberian widespread oak not standing summer drought (Ülker *et al.*, 2018) and distributed across the Atlantic belt of IP. We opted to refer to the broad concept of *Q. robur* in spite of the majority of the taxonomic reference, herbaria review and fieldwork refers to *Q. robur* subsp. *broteroana* O. Schwarz (Schwarz, 1937). *Quercus estremadurensis* O. Schwarz (=*Q. robur* subsp. *estremadurensis* (O.Schwarz) A. Camus) is considered to be a relictual taxa, distributed through the western IP in transitional areas towards thermophilic Mediterranean and Submediterranean conditions (Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018). It can also be found in Morocco (North Africa), which presence was confirmed by herbaria review. *Quercus orocantabrica* Rivas Mart. & al. is an endemic oak from the northern range of the Cantabrian mountains (Rivas-Martínez *et al.*, 2002; Rivas-Martínez *et al.*, 2011; Díaz-González & Penas, 2017) with disjoint populations in la Rioja and Cuenca. *Quercus petraea* (Matt.) Liebl. distributes throughout northern and continental areas of the IP. The biogeographic overlap of characters between broad *Q. petraea* and the subspecies *Q. petraea* subsp. *huguetiana* Franco & G.López (Franco, 1990), observed throughout its entire distribution range, and in accordance with the scattered distribution of *Q. petraea* stated in SIVIM database (Font *et al.*, 2012), led us to assume this subspecies to be the widespread taxon in IP, as putative tertiary relictual taxa (Schwarz, 1936; Vicioso, 1950). *Quercus pyrenaica* Willd. is a common taxon throughout the IP, tolerating summer drought, being distributed in almost all mountain areas of IP, in places with higher annual precipitation and important relictual subpopulations in the Mediterranean half of the IP and North Africa (Blanco-Castro *et al.*, 2005). *Quercus pubescens* Willd. is the oak species with wider distribution worldwide. It is related with thermophilic areas in basophile soils, that encompasses the Northeast IP, normally in temperate areas, but also in the submediterrenan belt (Pasta *et al.*, 2016) , where it contacts with *Q. faginea* Lam., resulting in hybrid masses of *Q. subpyrenaica* Villar (Villar, 1935).

Gall Oaks (Subsection *Galliferae* Gurke) (Gürke, 1897; Villar, 1958; Tschan & Denk, 2012)

Quercus broteroi (Cout.) Rivas Mart. & C. Sáenz and Q. faginea Lam. are predominantly parapatric and independent taxa (Rivas-Martínez & Saénz, 1991). The first has a predominant western distribution in areas with oceanic climate, in deep valleys protected from winter cold, while Q. faginea endures winter cold and continental climates. *Quercus*

canariensis Willd. is a critically endangered tree, with five subpopulations in IP. Normally, this species occurs in places with higher annual and summer horizontal precipitation in mesophytic conditions. Its sympatric distribution along *Q. broteroi* led to the formation of hybrid masses dominated by the nothotaxa *Quercus* ×*marianica* C. Vicioso (Vila-Viçosa *et al.*, 2014; Vila-Viçosa *et al.*, 2015) which is also included in this study as an endemic oak. The formation of nothotaxa with roburoid Oaks was also considered, so *Q. subpyrenaica* (Villar, 1935; Himrane *et al.*, 2004) was also included in the study. This taxon is the stabilized hybrid between *Q. pubescens* and *Q. faginea* and its forests are mostly found in the Spanish Pre-Pyrenees, mainly in the central and western area, reaching the Douro River basin (Loidi & Herrera, 1990). The outreach of *Q. subpyrenaica* to the Littoral Catalonian mountains (Fig. 1), is addressed to be related in the formation of the narrow endemic nothotaxa *Q.* ×*cerrioides* Willk. & Costa, referring to the introgression with *Q. canariensis*. The study of type material and fieldwork done in the type location for both taxa (*Q. subpyrenaica* and *Q.* ×*cerrioides*) was carefully performed to attain an accurate geographical segregation of both. Finally, we add the Portuguese dwarf-oak (*Q. lusitanica* Lam.), as a narrow-distributed species, living in the westernmost areas of IP, not tolerating winter cold and with a subpopulation in Morocco (North Africa) (Taleb & Fennane, 2019).

Supplementary Information S4 – Digital Annex

See Digital Annex section at the end of the present thesis.

Supplementary Information S5 - Linear Mixed Model Effects and post-hoc ANOVA results

Definitions

mod0: "null-model "with intercept-only effect

mod1: model including a single fixed-effect term related to the set of predictive variables used in SDM's

Response variable is named "TestEvalValue" i.e., the performance score for either TSS, ROC or KAPPA

Fixed effect: "set" i.e. the name of the set of predictive variables, either: combined climate and EFA ("CLIM_EFA"), climate-only ("CLIM_only") or EFA-only ("EFA_only")

Random factors are: "Species" (species name: 13 in total) and "EvalMetrics" (the evaluation score type: 3 in total, TSS, ROC and KAPPA)

Model results

Model formulae used in R lmer function:

mod0: TestEvalValue ~ 1 + (1 | Species) + (1 | EvalMetrics)

mod1: TestEvalValue ~ set + (1 | Species) + (1 | EvalMetrics)

Table 1 - Scaled residuals

Minimum	1st Quartile (25%)	Median (50%)	3rd Quartile (75%)	Maximum
-2.436	-0.477	0.018	0.681	2.488

Figure 1 - Histogram of residuals

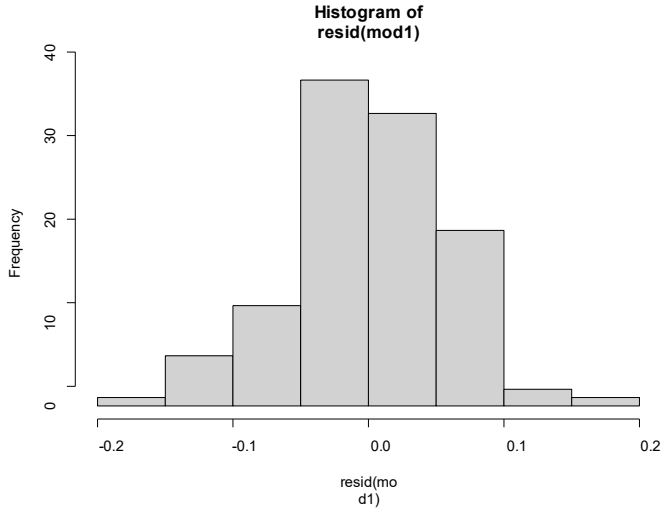


Table 2 – Random effects estimates

Groups	Name	Variance	Std.Dev.
Species	(Intercept)	0.005	0.074
EvalMetrics	(Intercept)	0.024	0.155
Residual		0.004	0.062

Number of observations: 117, groups: Species, 13; EvalMetrics, 3

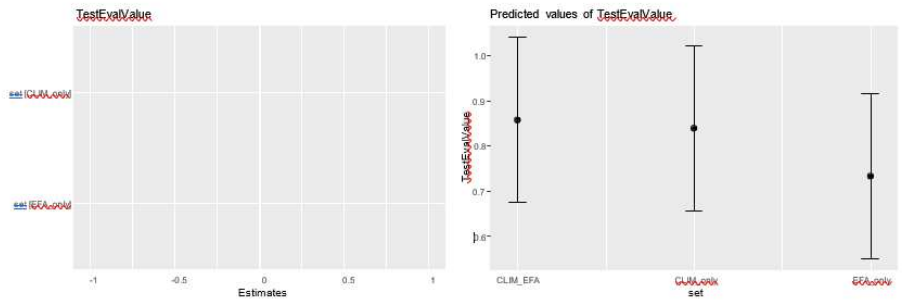
Results show overall greater variation in performance scores across evaluation metrics than across species.

Table 3 – Fixed effects estimates

Model term	Estimate	Std. Error	t-value
(Intercept)	0.858	0.093	9.274
set [CLIM_only]	-0.018	0.015	-1.298
set [EFA_only]	-0.124	0.014	-8.715

Figure 2 – Linear mixed model results

(a) (b)



Diagnostic: negative model coefficients (Table 3 and Fig. 2 – a) show that (despite uncertainty in coefficient estimates) the set[CLIM_only] and set[EFA_only] both have on average less performant models in relation to the combined set[CLIM_EFA]. That effect is more noticeable for the EFA_only set (Fig. 2 – b).

ANOVA results:

```
mod0 <- lmer(TestEvalValue ~ 1 + (1|Species) + (1|EvalMetrics), data =
perfEvalAll) mod1 <- lmer(TestEvalValue ~ set + (1|Species) +
(1|EvalMetrics), data = perfEvalAll) anova(mod0, mod1)
```

Table 4 – ANOVA post-hoc test results

Model	Number of parameters	AIC	BIC	Log likelihood	Deviance	Chi-square test value	Degrees of freedom	Pr(>Chisq)
mod0	4	-198.1	-187.14	103.09	-206.19			
mod1	6	-258.8	-242.24	135.41	-270.81	64.62	2	**p=9.269 x 10^{-15} (***)**

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Diagnostic: the model including the "set" term (mod1) is significant at p<<0.001

Data used for analysis (Supplementary information S5)

Supplementary Table S1

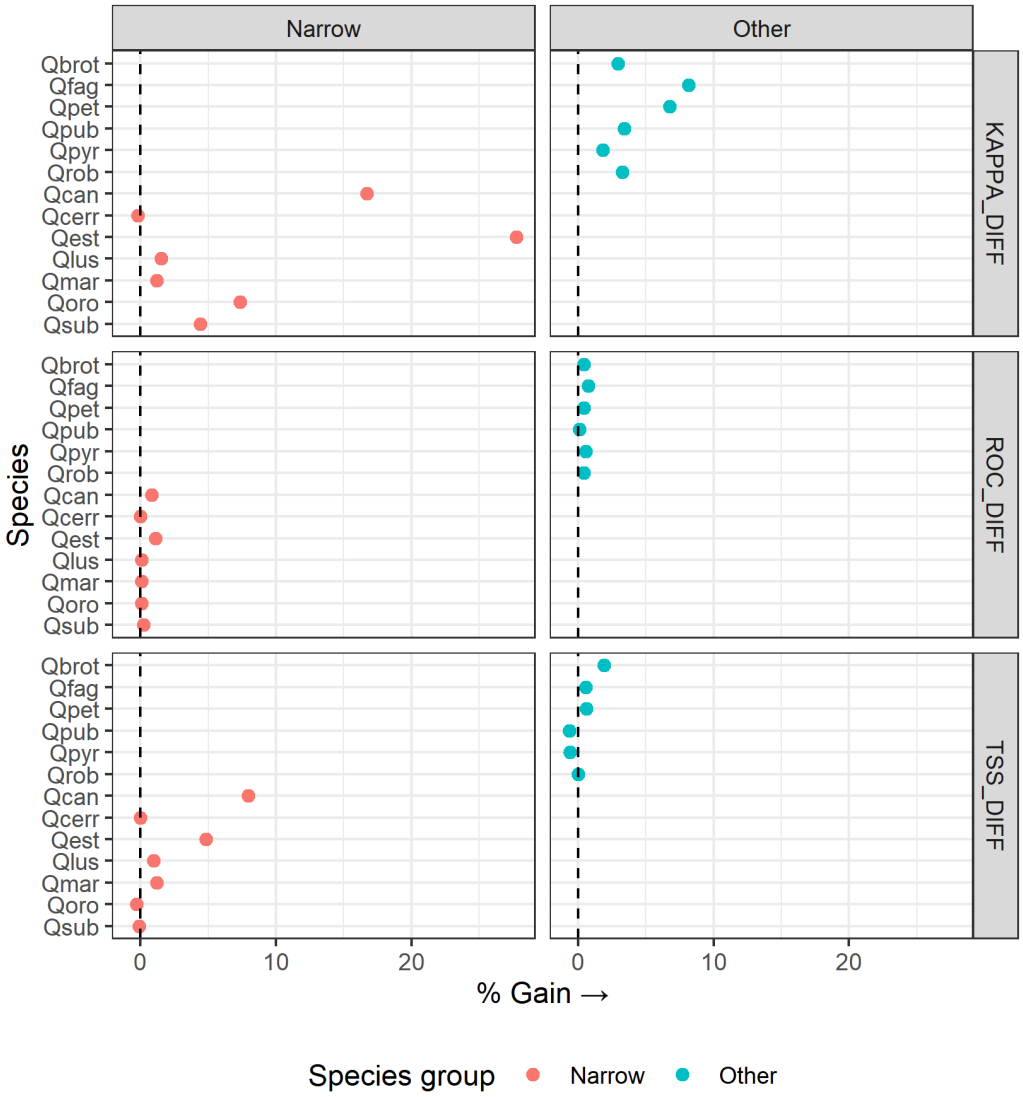
Supplementary Table S1 - GLM AICc-based model ranking. Models signaled with an asterisk (*) in bold are the best models for each species (i.e., lowest values) according to different sets of variables: CLIM – models only with climatic variables, EFA – only satellite-based Ecosystem Functioning Attributes (EFA), and CLIM_EFA – combined models using both climate and EFA variables. * Narrow distributed; ** Endemic

Species name	Group of predictor variables	AICc value
Quercus broteroi	**CLIM_EFA (*)**	**797.57**
	CLIM	883.66
	EFA	1049.73
*Quercus canariensis**	**CLIM_EFA (*)**	**214.43**
	EFA	356.75
	CLIM	431.02
*Quercus ×cerrioides***	**CLIM_EFA (*)**	**8.13**
	CLIM	10.19
	EFA	97.58
*Quercus estremadurensis**	**CLIM (*)**	**190.11**
	CLIM_EFA	193.88
	EFA	284.12
Quercus faginea	**EFA (*)**	**1263.09**
	CLIM_EFA	1674.71
	CLIM	1674.71
*Quercus lusitanica**	**CLIM_EFA (*)**	**440.53**
	CLIM	554.18
	EFA	714.17
*Quercus marianica***	**CLIM_EFA (*)**	**186.03**
	CLIM	276.67
	EFA	327.38
*Quercus orocantabrica***	**CLIM_EFA (*)**	**20.96**
	CLIM	73.11
	EFA	84.93
Quercus petraea	**EFA (*)**	**1153.95**
	CLIM_EFA	1041.36
	CLIM	1811.36
Quercus pubescens	**CLIM_EFA (*)**	**1041.36**
	CLIM	1173.35
	EFA	1185.59
Quercus pyrenaica	**CLIM_EFA (*)**	**5119.22**
	CLIM	5510.87
	EFA	7145.01
Quercus robur	**EFA (*)**	**1448.22**
	CLIM_EFA	1642.69
	CLIM	1715.53
*Quercus ×subpyrenaica***	**CLIM_EFA (*)**	**915.54**
	CLIM	1002.90
	EFA	1332.10

Supplementary Table S2 – Digital Annex

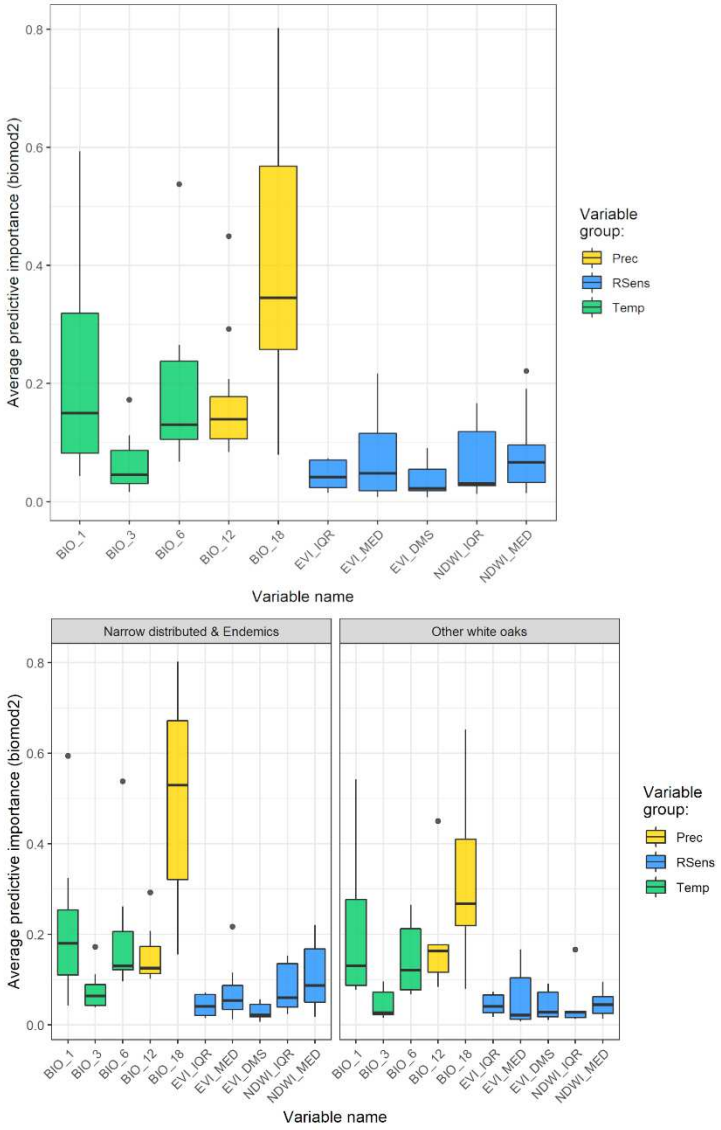
See Digital Annex section at the end of the present thesis.

Supplementary Figure S1



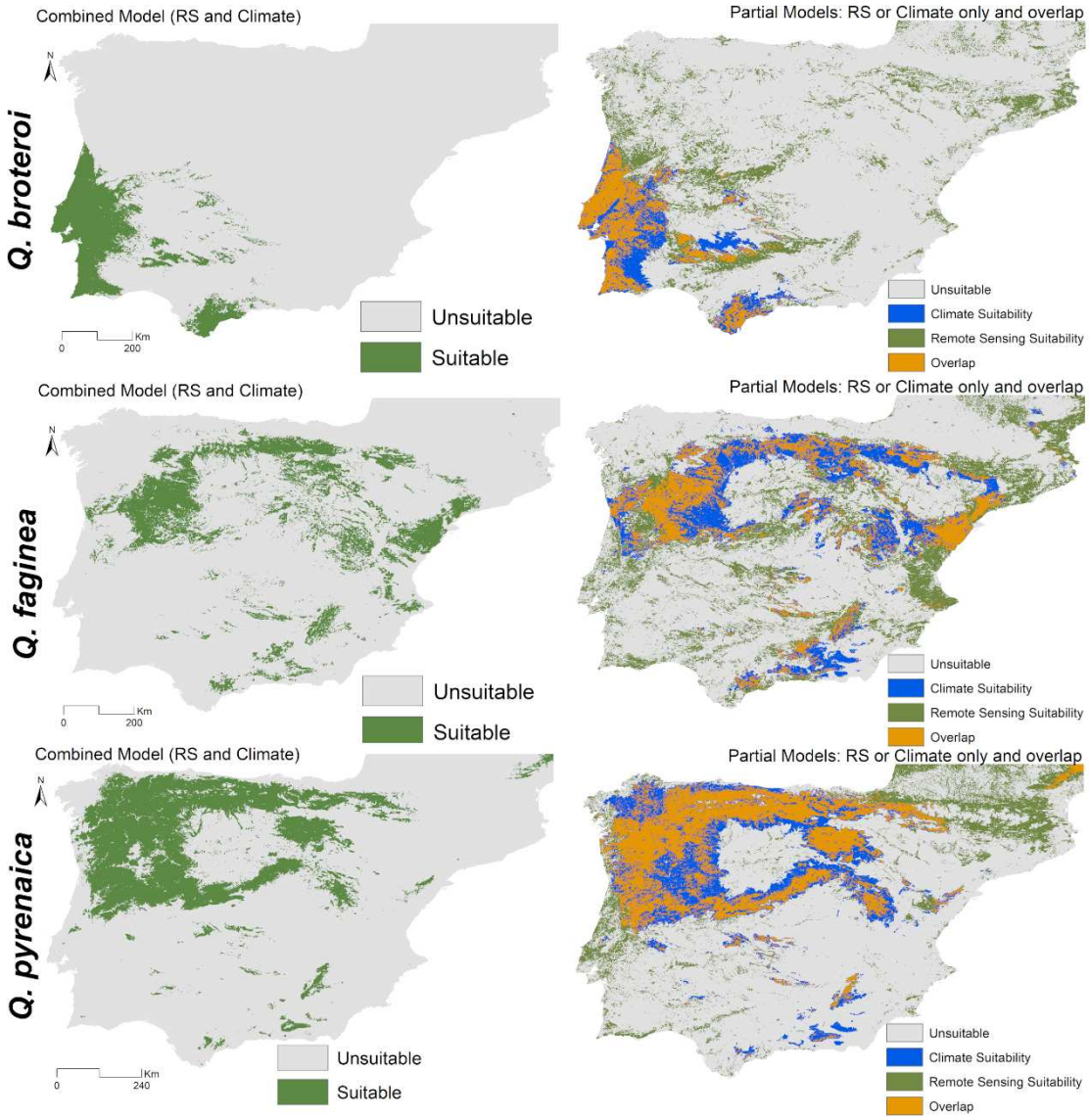
Supplementary Figure S1 - Increased performance of the models (Gains) in NDE (left) and other oaks (right).

Supplementary Figure S2



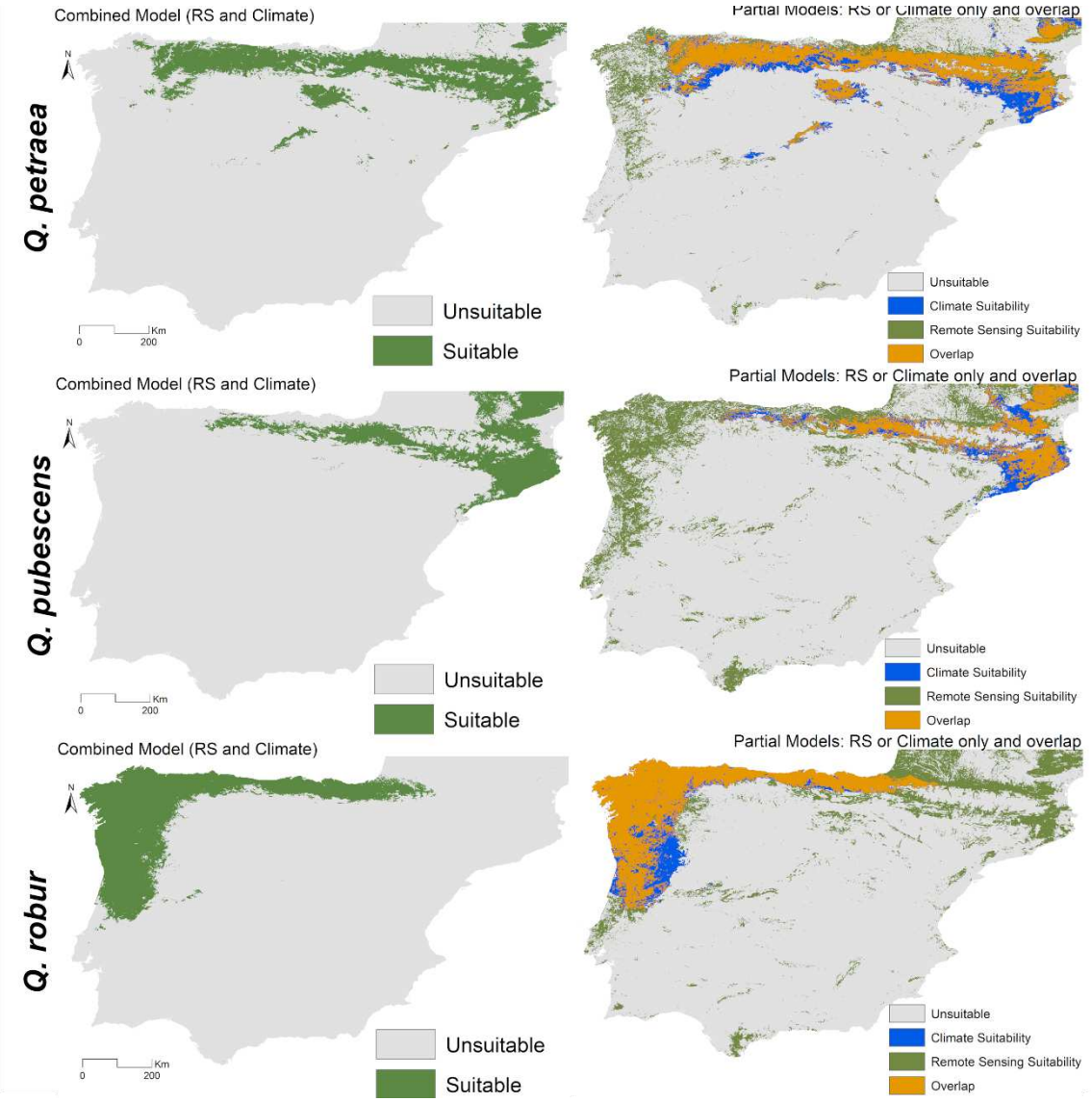
Supplementary Figure S2 - Variables contributions; all species (above); NDE and other oaks (bellow).

Supplementary Figure S3



Supplementary Figure S3 - Combined models (remote sensing—RS and climate) (Left) and partial models (RS or climate and overlap) (Right) for *Q. broteroi, Q. faginea* and *Q. pyrenaica.*

Supplementary Figure S4



Supplementary Figure S4 - Combined models (remote sensing—RS and climate) (Left) and partial models (RS or climate and overlap) (Right) for *Q.petraea*, *Q. pubescens* and *Q. robur*.

SECTION C

Molecular phylogeny and Evolution of Iberian white-oaks

Chapter 7.

The Iberian White-Oaks' Syngameon, a legacy of introgression in southern Europe

Carlos Vila-Viçosa [1,2,3,4*]Ricardo Castilho[5], Andrew Hipp[6], Francisco M. Vázquez[7], Rubim Almeida[1,2,3,4], Cristina García[1,2,8], Albano Beja-Pereira[1,2,9], Herlander Azevedo[1,2,4]

*Equally contributing authors.

Disclaimer: this chapter is an original contribution of this thesis in preparation for publication. Carlos Vila-Viçosa and Ricardo Castilho led the experimental work with contributions from all co-authors; Carlos Vila-Viçosa was involved in taxonomic filtering, sample collection, generation of molecular data, analysis of molecular data and integration of results.

[1] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO. Campus de Vairão, 4485-661 Vairão, Portugal
[2] CIBIO (Research Center in Biodiversity and Genetic Resources) - InBIO (Research Network in Biodiversity and Evolutionary Biology), University of Porto. Campus Agrário de Vairão; Rua Padre Armando Quintas; 4485-661 Vairão; Portugal
[3] MHNC-UP - Museu de História Natural e da Ciência da Universidade do Porto – Herbário PO, Universidade do Porto. Praça Gomes Teixeira, 4099-002, Porto, Portugal.
[4] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal.
[5] Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland
[6] The Morton Arboretum, Lisle IL 60532-1293, USA
[7] Department of Forest Production and Vegetal Biodiversity, Institute of Agricultural Research "Finca La Orden Valdesequera" (CICYTEX), A5 km 372, 06187 Guadajira, Spain
[8] Department of Biological Science. Centre for Evolution, Ecology and Behaviour. Bourne Building, Office 3-29B. Royal Holloway University of London, Egham, Surrey, TW20 EX, United Kingdom
[9] DGAOT, Faculdade de Ciências, Universidade do Porto, Rua Campo Alegre 687, 4169-007 Porto, Portugal

7.1. Abstract

Oaks are among the most important tree genera around the world. Their intricate history is reflected on a reticulated phylogeny, deeply influenced by introgression and diversification among contrasting biogeographic regions, followed by ecological divergence within regions. In this study we investigated the particular contribution of the Iberian white oaks to the evolutionary history of the Eurasian Roburoid clade, and we scrutinized the prevalence and biogeographic meaning of hybrids and hybrid swarms among their populations. Towards this end we implemented the RADSeq characterization of 38 putative taxa and nothotaxa. Results show a strong infrasectional differentiation among the Eurasian white oaks, separating typical temperate and Atlantic distribution species from their submediterranean marcescent counterparts. The latter are rich in hybrid swarms, confirming extensive gene flow despite the maintenance of parentals as strong species and integrative interbreeding evolutionary units. Results also amplify the significance of biogeographical vicariance among east and western Mediterranean oaks, and the importance of transitional ecotones in driving species differentiation at both macro and microevolutionary scales, despite the confounding effect provided by the convergence and plasticity of morphological characters. Work significantly contributed to the resolution of important pending taxonomic questions, and helped re-position the Iberian oak species inside the world phylogenetic tree. Ultimately, the Iberian Peninsula emerges as a major hotspot for oak conservation, placed between two major subregions (Eurosiberian and Mediterranean).

7.2. Introduction

Oaks (*Quercus* L.) are one of the most speciose tree taxa in the Northern Hemisphere, where they are keystone elements spanning various types of forest typologies and multiple edaphic and climatic niches (Axelrod, 1983; Manos *et al.*, 1999; Hipp *et al.*, 2020). There are ca. 435 species known to date, distributed across the world and displaying a notoriously complex morphological diversity. This originates from a geographic and ecological diversification of over 56 million years of evolution of wide-range lineages (Denk, T. *et al.*, 2017; Carrero *et al.*, 2020; Hipp *et al.*, 2020). Inside the Eurasian continental area, the Iberian Peninsula (IP) displays a unique biogeographic positioning within Europe and the Mediterranean Basin. Its contrasting bioclimatic gradients (Loidi, 2017) and the presence of a single major biogeographic border to

Europe (Pyrenees), turns it into a powerful model for the characterization of refugia and speciation events, associated with past bioclimatic abrupt changes (Williams *et al.*, 2011; Veloz *et al.*, 2012; Birks & Tinner, 2016). We hypothesize that the biodiversity of the IP's white oaks has been consistently undervalued, and that the generation of novel insights that adequately link biogeography distribution of these species with speciation and hybridization will be much improved by an in-depth molecular re-visiting of Iberian white oak populations.

Section *Quercus*, commonly referred to as the white oaks (Denk, T. *et al.*, 2017), contain the Eurasian Roburoid clade which shows particularly outstanding levels of diversification rate throughout the Late Miocene (Hipp *et al.*, 2020). They present several subclades that incorporate both temperate and submediterranean distributed taxa, the latter being adapted to the drier Mediterranean climate without clear phylogenetic differentiation (Hipp *et al.*, 2020). Some of these submediterranean and dry adapted species have been traditionally assigned to the *Galliferae* subsection or section, depending on the authors (Spach, 1842; Gürke, 1897; Schwarz, 1936a; Schwarz, 1936c). It has been suggested that dry adapted taxa share a convergent adaptation that emulates an ecological alliance, rather than geographic or phylogenetic congruent groups (Hipp *et al.*, 2020). Together with former Section *Dascia* (Schwarz, 1936a), they form a notable biogeographic and morphological correspondence within all circummediterranean white oaks, namely in areas where annual and summer precipitations played a major role on the maintenance of submediterranean oaks . However, their relationship with the temperate-dominant species and northern-distributed taxa (*Q. robur* and *Q. petraea*) is yet unclear. Remarkably, the IP harbours almost half of the European oak species and is a well-documented refugia for these species (Schwarz, 1964; Franco, 1990; Rivas-Martínez & Saénz, 1991; Olalde *et al.*, 2002; Vila-Viçosa *et al.*, 2020a). The IP's specific biogeographic positioning reinforce its status as an extraordinary model for evolutionary studies.

Sympatric oaks are not reproductively isolated, and their significance as a species syngameon has been recently reaffirmed (Cannon & Petit, 2020). The *species syngameon* concept differs from the *species complex* concept. The latter corresponds to species that are both taxonomically difficult to distinguish and display blurred molecular species boundaries. Conversely, the species that compose a syngameon are quite distinguishable, particularly at the molecular level, despite common gene flow and pervasive introgression between sympatric species (Cannon & Petit, 2020). This extant taxonomic complexity is reflected at the genome level, with various and unique species-

level phylogenetic histories, as a result either of introgression or lineage sorting (Eaton *et al.*, 2015; McVay *et al.*, 2017). In this sense, hybridization complicates the reconstruction of the oak syngameon, especially when using traditional organellar DNA markers (e.g. chloroplast or mitochondrial DNA markers) or a combination of a few nuclear genes. Broadly, their lack of resolution strongly hinders the capacity to unveil the history of speciation in the reticulated mosaic that is characteristic of oak genomes (Pham *et al.*, 2017; Hipp *et al.*, 2020). Thus, there is a need to accurately identify the phylogenetic backbone of Section *Quercus,* as a basis for the interpretation of its diversification in space and time.

Considering their biogeographical complexity, Iberian white oaks have attracted many taxonomic investigations. Inside broad taxonomic groups, Quercus species are often difficult to distinguish due the profusion of convergent characters and the presence of introgression among sympatric species (Schwarz, 1936c). In that regard, studies often lack accurate identification and well-circumscribed bona fide species to be used as references. Natural history artifacts hamper downstream works, from ecological modelling to phylogeny, up to forest conservation, urging the need for state-of-the-art molecular characterization of oak biodiversity (Vila-Viçosa *et al.*, 2022). Next generation sequencing (NGS) technologies and new computational techniques have inaugurated the genomics era, producing unprecedented knowledge on the evolutionary history of living organisms (Crowl *et al.*, 2020; Leroy *et al.*, 2020; Plomion & Martin, 2020; Backs & Ashley, 2021; Gugger *et al.*, 2021). including *Fagaceae* (Petit et al., 2013). Amongst NGS-associated technologies, Restriction-site Associated DNA sequencing (RADSeq) has been amply used in ecological, evolutionary and conservation genomics studies. It enables discovery of thousands of polymorphic genetic markers across the genome, offering robust sampling by targeting a subset of the genome with major depth of coverage per locus (Andrews *et al.*, 2016). In particular, RADSeq has impacted significantly on our present knowledge of the oak genomic landscape, through multiple studies that addressed phylogeny, population genomics, adaptation and introgression events (Hipp *et al.*, 2014; Cavender-Bares *et al.*, 2015; Eaton *et al.*, 2017; Fitz-Gibbon *et al.*, 2017; Deng *et al.*, 2018; Hipp *et al.*, 2020; Lazic *et al.*, 2021; Tóth *et al.*, 2021; Ulaszewski *et al.*, 2021).

The biogeographic significance of the IP in the evolution of the Eurasian white oaks is yet to be fully understood. The profusion of names and unclear taxonomic assumptions make their phylogenetic resolution urgent. It is also critical to assess the role of the IP as a diversity hot spot within the context of the macro and microevolutionary processes that

shaped the evolutionary history of Eurasian white oaks. In the present study, we tackled the IP's white oaks, their species and nomenclature uncertainties, by filtering target-taxa, through extensive literature and field work survey. We subsequently used RADSeq to carry out a phylogenomic analysis of the Iberian bulk of species, including hybrids, to address species delimitation and phylogenetic relationships amongst individuals. We analysed 263 individuals from our sampling set, and added 60 individuals from previously published RADSeq data, in a total of 38 putative taxa and nothotaxa (i.e. hybrids) of Iberian and non-Iberian origins. A combination of phylogenetic and complexity reduction methods was used to resolve the backbone of the western Mediterranean white oaks within the Eurasian clade of *Roburoid* oaks (*sensu* Hipp *et al.* (2020)), developing and extending the role of hybrids in the Iberian syngameon.

7.3. Material and methods

7.3.1. Focal species/groups and study area

To interrogate the phylogeny of Iberian White Oaks, we collected 263 samples (Figure 1) using the IP as study area (Figure 1; Supplementary Methods S1). This included 5-10 plants for each subpopulation, representing 8 species across a west-to-east gradient, which initially targeted *Galliferae* oaks (Gürke, 1897; Schwarz, 1936a; Tschan & Denk, 2012) and their known putative hybrids and related parents inside Section *Quercus*. We favoured collections in the historical type locations, so we also added particular populations assigned to taxonomic and own nomenclatural endorsements that are considered narrow endemics (ex: *Q. alpestris*, *Q. orocantabrica* and *Q. pauciradiata*), in order to unveil their phylogenetic backbone. Our sampling was mostly distributed across the submediterranean belt of the IP, with incursions in Eurosiberian and strictly Mediterranean areas (Vila-Viçosa *et al* 2020b) (Figure 1). The Iberian White oaks sampling distribution map was spatialized in ESRI ArcGIS v10.3 and overlapped with the Iberian life zones (Temperate, Transitional Temperate-Submediterranean, Submediterranean, strictly Mediterranean), based on the SDM's of the deciduous and brevi-deciduous (marcescent) species, which were retrieved by Vila-Viçosa and co-workers (2019; 2020a). A descriptive overview of each taxon and nothotaxon is summarized in Supplementary Notes S1.

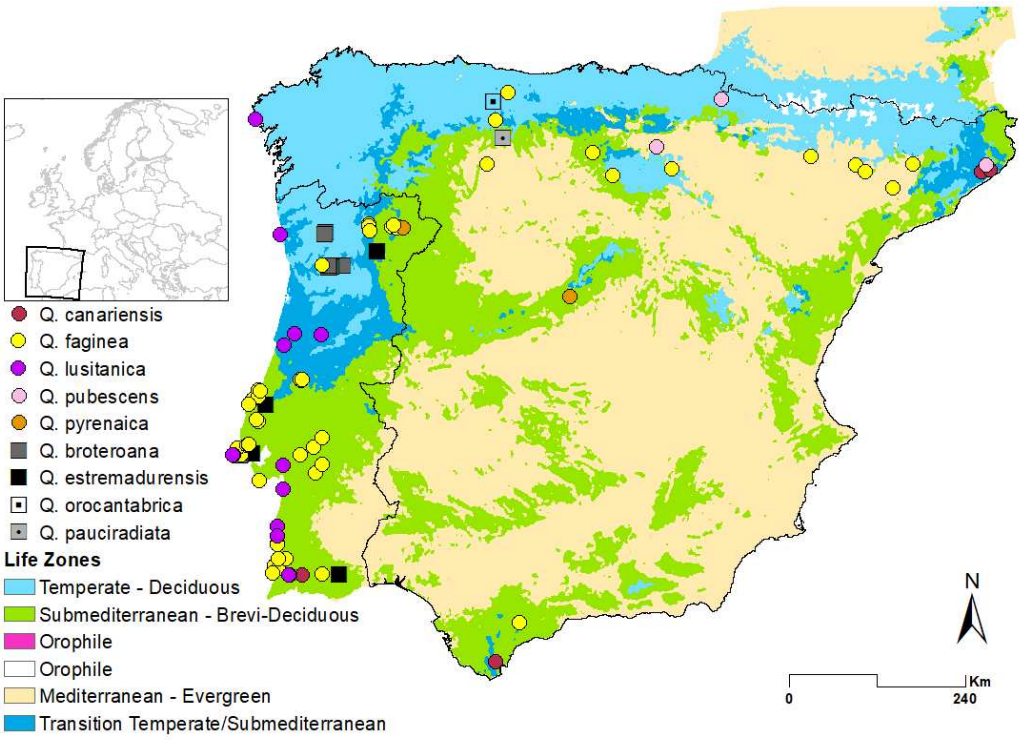


Figure 1 - Iberian White oaks sampling distribution. Sampling locations are placed above the main biogeographic lifezones obtained by the modelling of deciduous (Temperate-Eurosiberian) and brevi-deciduous/marcescent (Submediterranean) oaks, with the overlap of both lifezones considered to be transitional (Eurosiberian-Submediterranean). Squares represent true roburoid oaks and circles represent former Sect. *Dascia* and Sect. *Galliferae* species. Adapted from Vila-Viçosa *et al.* (2019).

7.3.2. Genomic DNA extraction and sequencing

Genomic DNA (gDNA) was extracted from *ca*. 70 mg of dry or frozen (-80ºC) leaf material, using the CTAB-based variation of the NucleoSpin Plant II kit (Macherey-Nagel), according to the manufacturer's instructions except for an increased (1 h) buffer incubation period. DNA purity, concentration and integrity were inferred from spectrophotometry (Nanodrop 2000, ThermoFisher Scientific), Qubit dsDNA HS Assay Kit, Picogreen Quant-iT dsDNA Assay kit (Invitrogen, ThermoFisher Scientific) and agarose gel electrophoresis. DNA was normalized to 20 ng/µl in a 50 µl volume for each sample. RADSeq libraries were prepared using the restriction enzyme *Pst I*, barcoded by individual, and sequenced in 100 bp single-end reactions on an Illumina Hiseq 4000 at the University of Oregon Genomics and Cell Characterization Core Facility (Eugene, OR, USA) following the RAD protocol of Baird *et al.* (2008).

7.3.3 RAD loci call and matrix assembly

Raw sequencing reads were processed using *ipyrad* v0.9.31 (Eaton & Overcast, 2020). FASTQ files were demultiplexed and filtered to remove sequences with >5 bases of quality score <20. High quality reads were clustered at an 85% similarity threshold, with a maximum depth within clusters of 10,000 reads, and mapped back to the latest version of the *Q. robur* haploid genome (HAPLOME 2.3; https://urgi.versailles.inra.fr/Data/Genome/Genome-data-access; Plomion *et al.* (2016). All the remaining parameters were set to default, except for the minimum number of samples with data at a given locus, which was set differently for each individual analysis (see below).

7.3.4. Phylogenetic analysis and species tree inference

To investigate the position of the Iberian clade within the Eurasian white-oaks (Sect. *Quercus*) context, we used a total of 69 samples, including 17 from our field sampling effort and previously published samples representing 38 Eurasian samples and 14 American white oaks (Hipp *et al.*, 2020). The RAD loci data matrix was generated using the *ipyrad* assembly previously described and filtered to accommodate only loci that were present in a minimum of 52 individuals (*i.e*., 75% of the total number of individuals). The concatenated sequence matrix was assembled based on 28,473 filtered RAD loci with a total size of 5,298,608 base pairs (29.33% of missing sites). The maximum likelihood phylogenetic analysis was conducted locally in *RAxML* v.8.2.9 (Stamatakis, 2014) using the GTRCAT implementation of the general time reversible model of nucleotide evolution, with branch support assessed using the RELL bootstrapping method (Minh *et al.*, 2013).

To assess the phylogenetic relationships among the Iberian white oaks, we collected 28 representative samples of the currently recognized Iberian clades, which were complemented with previously published data from 22 Eurasian and 3 American white oaks (Hipp *et al.*, 2020). The RAD loci data matrix was generated using the *ipyrad* assembly feature described earlier and filtered to accommodate only loci that were present in a minimum of 40 individuals (*i.e.*, 75% of the total number of individuals). The concatenated sequence matrix was assembled based on 30,951 filtered RAD loci with a total size of 5,702,695 base pairs (29.09% of missing sites). The maximum likelihood phylogenetic analysis was conducted locally in *RAxML* v.8.2.9 as previously described. Species tree inference was based on the SVDQuartets algorithm (Chifman & Kubatko,

2014) using the coalescent-based method tetrad as implemented in *ipyrad*. Briefly, it uses phylogenetic invariants to resolve quartet trees from SNPs for all sets of quartets in a larger tree, and then joins the quartets together into a supertree using quartets MaxCut algorithm (Snir & Rao, 2012). Here, we subsampled a single SNP from every locus separately for every quartet set in the analysis and repeated this independently over 100 bootstrap replicates. Using this approach, we maximised the amount of unlinked SNP information used in every quartet inference. The average number of unlinked SNPs used to infer each quartet was 27,287 ± 132.

7.3.5. Genetic diversity assessment using PCA and Neighbor-net analysis

Principal component analysis (PCA) was used to evaluate the genetic diversity among the morphologically similar species and their relatives within the Iberian clade. We aligned all samples from each putative subsections inside sect. *Quercus* (Group A and Group B) to the *Q. robur* reference genome (see above). The dataset of the Clade Group A was composed of eight taxa (*Q. broteroana, Q. dalechampii, Q. estremadurensis, Q. hartwissiana, Q. orocantabrica, Q. pauciradiata, Q. petraea* and *Q. robur*) while the dataset of the Clade Group B was composed of ten taxa (*Q. boissieri, Q. canariensis, Q. faginea, Q. frainetto, Q. lusitanica, Q. macranthera, Q. kotschyana, Q. pubescens, Q. pyrenaica* and *Q. vulcanica*). These datasets incorporated both high-confidence Iberian species and their putative hybrids (*Q. ×cerrioides*, *Q. faginea* × *Q. pyrenaica*, *Q. ×marianica* and *Q. ×subpyrenaica*) (Supplementary Notes S1). RAD loci were called individually in each analysis. Only loci observed in at least 75% of the individuals in each of the two datasets were selected. In addition, SNPs present in less than 50% of all the samples in each dataset were discarded and, to reduce the effect of linkage in PCA results, only one SNP was randomly selected per each RAD locus. The SNP subsampling was replicated 25 times to include a different random set of unlinked SNPs, with the total number of selected SNPs per dataset being the following: all species (10,801), Group A (25,021), Group B with hybrids (12,947), Group B without the hybrids (13,535) and all species with hybrids (9,598). To reduce the effects of missing data in all datasets, we tested the imputation methods *sample* and *k-means* as implemented in *ipyrad*. Both yielded similar results and for that reason only the *sample* imputation method results were presented.

Additionally, we inferred three phylogenetic networks based on the maximum-likelihood (GTR+γ) pairwise distance matrix estimated in RAxML. The networks were visualized

using the neighbor-net algorithm (Bryant & Moulton, 2004) in *SplitsTree* v4.16.1 (Huson & Bryant, 2006). The first Neighbor-Net features the Asian taxa (*Q. aliena, Q. dentata, Q. yunannensis, Q. griffithii, Q. fabrii and Q. mongolica*) as outgroup, and the bonafide identified species (*Q. robur, Q. broteroana, Q. estremadurensis, Q. petraea, Q. pauciradiata, Q. pubescens, Q. macranthera, Q. vulcanica, Q. kotschyana, Q. boissieri, Q. faginea, Q. canariensis, Q. faginea, Q. lusitanica,* and *Q. pyrenaica*), while the second includes the studied hybrids (Q. ×*cerrioides, Q.* ×*coutinhoi, Q.* ×*duriensis, Q.* ×*fontquerii, Q.* ×*marianica, Q.* ×*subpyrenaica* and *Q. faginea* × *Q. pyrenaica*), among the putative parent species. Here, we excluded an outgroup to provide bigger resolution to the syngameon.

7.4. Results

7.4.1. Phylogenetic analysis of European and Iberian white oaks

The phylogeny of European and circummediterranean white oaks offers a series of challenges. Here, we used RADSeq data to generate a new species phylogeny targeting these taxa (Figure 2). Sampling incorporated wild populations based on type-locations for multiple taxon and nothotaxon (Supplementary Note S1). The white oak species sampled resolved into American, Asian, and European clades, as shown previously (Hipp *et al.*, 2020). A key finding of our phylogeny was the segregation, within the European white oaks, of two distinct groups, addressing the circumscription of two subsections inside Section *Quercus,* hereafter designated as Group A and Group B (Figure 2). Group A includes the so called “true” roburoid oaks, encompassing former Sections *Roburoides* and *Robur* (Schwarz, 1936c; Schwarz, 1936a). Here, all taxa were ascribed to two subgroups, tentatively designated as “broad robur” (*Q. robur* L.; *Q. broteroana* (=*Quercus robur* subsp. *broteroana* O.Schwarz); *Q. orocantabrica* Rivas Mart., Penas, T.E.Díaz & Llamas; *Q. estremadurensis* O. Schwarz*; Q. hartwissiana* Steven*; Quercus robur* subsp. *imeretina* (Steven ex Woronow) Menitsky (=*Quercus imeretina* Steven ex Woronow); *Quercus robur* subsp. *pedunculiflora* (K.Koch) Menitsky (=*Q. pedunculiflora* K.Koch) and *Q. robur* L.)*,* and “broad petraea” (*Q. dalechampii* Ten. *Q. pauciradiata* Penas, Llamas, Pérez Morales & Acedo; *Q. petraea* (Matt.) Liebl and *Quercus petraea* subsp. *iberica* (Steven ex M.Bieb.) Krassiln (=*Quercus iberica* M.Bieb). Group B comprised all taxa from former sections *Dascia* (*Q. frainetto* Ten.*, Q. kotschyana* O.Schwarz*, Q. pubescens* Willd.; *Q. pyrenaica* Willd. and *Q. vulcanica* Boiss. ex Kotschy) and *Galliferae* (*Q. boissieri* Reut. *Q. canariensis* Willd.*, Q. faginea* Lam. and

Q. lusitanica Lam.) (Schwarz, 1936a). Group B displayed two large clades. The first clade contains an Iberian set of species, also distributed across the Western Mediterranean Basin, including North Africa. The second clade could be further divided into three subclades, comprising: 1) broadly distributed *Q. pubescens*; 2) species from Caucasus and Anatolia; 3) species from the Near East.

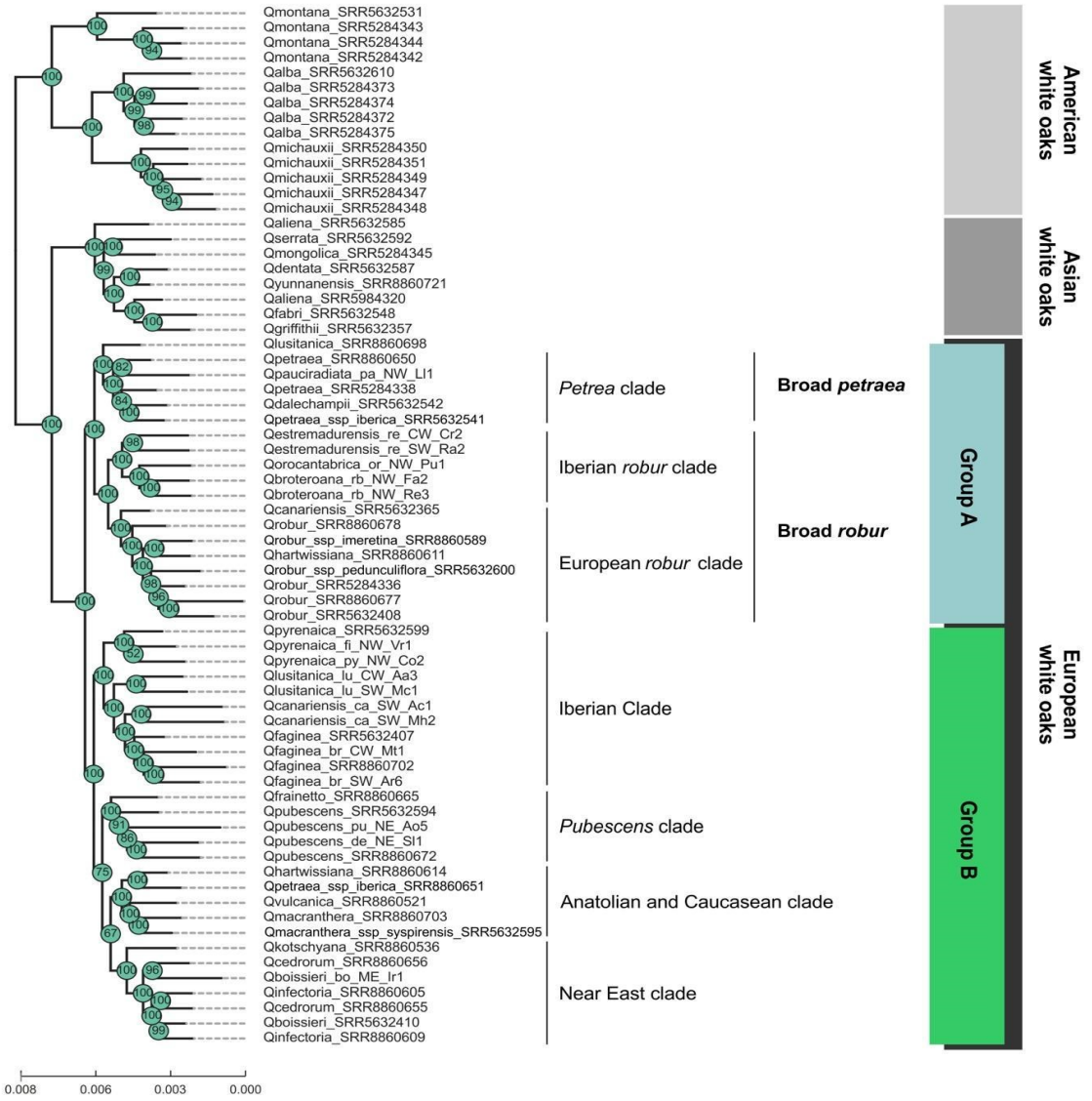


Figure 2 - Phylogeny of the Eurasian white-oaks (*Sect. Quercus*), including subsets of American and Asian species used as outgroups.

We focused further on Iberian white Oaks in a second phylogenetic analysis. It was complemented by the species tree inference obtained via tetrad testing, which is based on the SVDQuartets algorithm of Chifman and Kubatko (2014) (TETRAD test) and accommodates for the presence of incomplete lineage sorting (Figure 3). By using three

American oaks (*Q. alba, Q. michauxii, Q. montana*) and two Asian oaks (*Q. fabri* and *Q. yunnanensis*) as outgroups, we observed a segregation of three species: the two existing Anatolian and Caucasian clade members (*Q. macranthera* and *Q. vulcanica*), plus *Q. frainetto*, previously positioned in the *pubescens* clade member (though it presents weaker support in the tetrad tree in Figure 3B). Positionally, samples were then resolved into the previously reported Groups A and B. In the latter, results replicated the differentiation of the *Iberian clade* versus remaining clades observed in Figure 2. They cohesively aggregated Series *Dascia* and *Galliferae* species but failed to present sub-structuring of *Dascia* versus *Galliferae* (Figure 3). The *Iberian clade* incorporated most Iberian oaks (*Q. canariensis, Q. faginea*, *Q. lusitanica* and *Q. pyrenaica*). Unlike in Figure 2, *Q. canariensis* genotypes were ascribed to two separate clades (Figure 3). Samples from Iberian SW [Monchique (Portugal) and Algeciras (Spain)] remained in the *Iberian clade*, while samples from NE Spain (Catalunya) clustered within the *pubescens clade*, which contains all *Q. pubescens* sample with other Southern European origins.

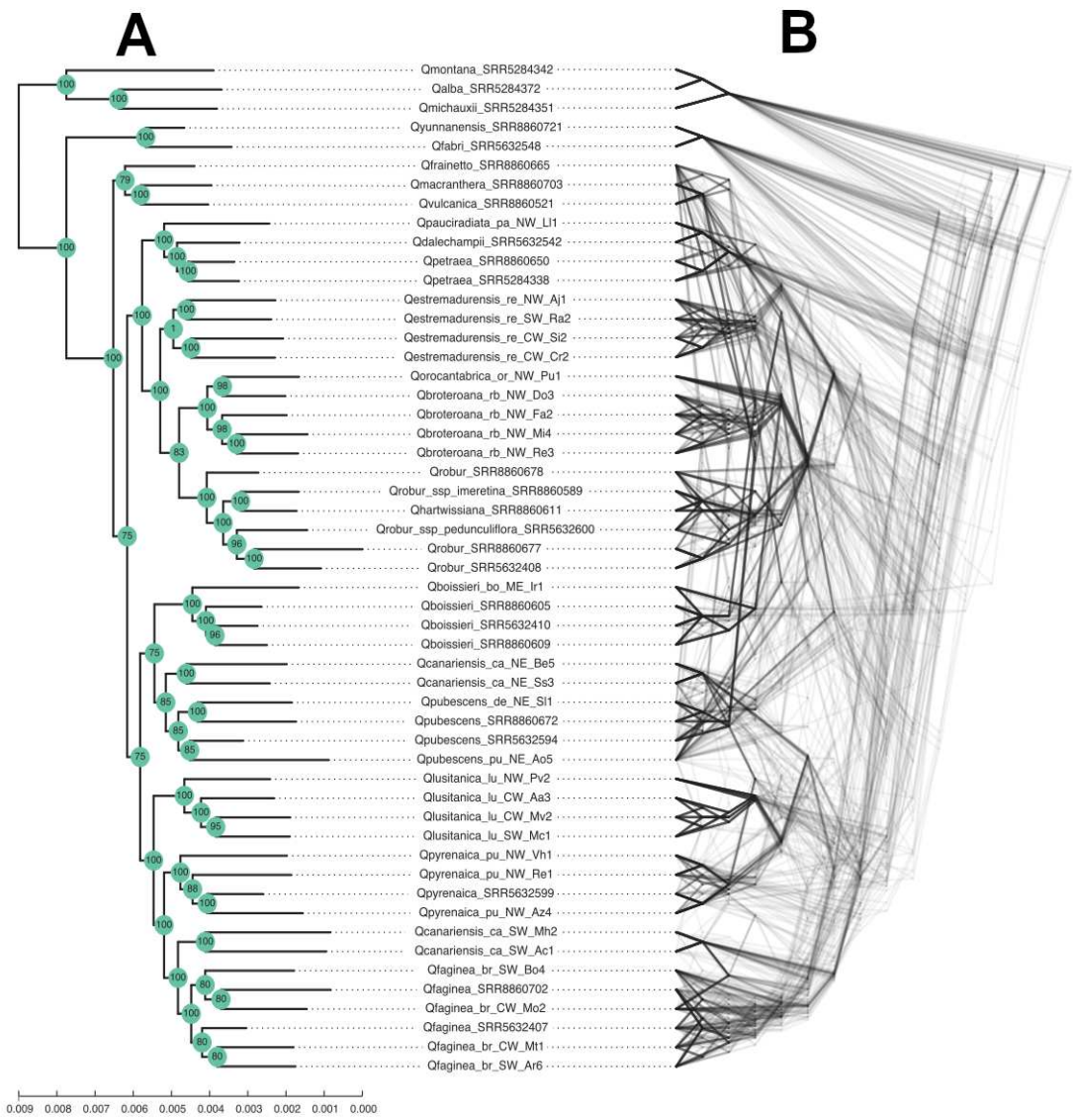


Figure 3 - Phylogeny of Iberian white oaks. Phylogenomic analysis (A), and species tree inference based on the SVDQuartets algorithm (TETRAD test) (B).

7.4.2. Complementary analysis of species-level phylogenies

Additionally, we carried out principal component analysis (PCA) of previous samples (Figures 1 and 2) complemented with added population samples. Results separated samples into Groups A and B (PC1; 7.4% of variance) (Figure 4A), in line with previous phylogenetic insights. A second component (PC2; 2.9% of variance) was driven by *Q. lusitanica*, which appears as a clear outlier species. Then, PC2 resolved geographically distinctive Eastern-distributed species (Near East, Caucasus and Anatolia), clustering Iberian taxa (Figure 4A). Focusing specifically on Group A species (Figure 4B), we observed a main component (PC1; 9% of variance) delimiting European *Q. robur* and

"broad petraea" species against the *taxa* related with the *Iberian robur* group *Q. broteroana, Q. orocantabrica* and *Q. estremadurensis*. This last one notably occupied an intermediate position with "broad petraea". Analysis of Group B species (Figure 4C) evidenced once again the clear segregation of *Q. lusitanica*, strongly influencing PC1 (4.3% of variance). PC2 (2.7% of variance) reflected biogeography, gradually resolving Near East *Q. boissieri, Q. kotschyana,* the Anatolian and Caucasian *Q. vulcanica* and *Q. macranthera,* followed by *Q. pubescens*, and finally all Iberian Group B species.

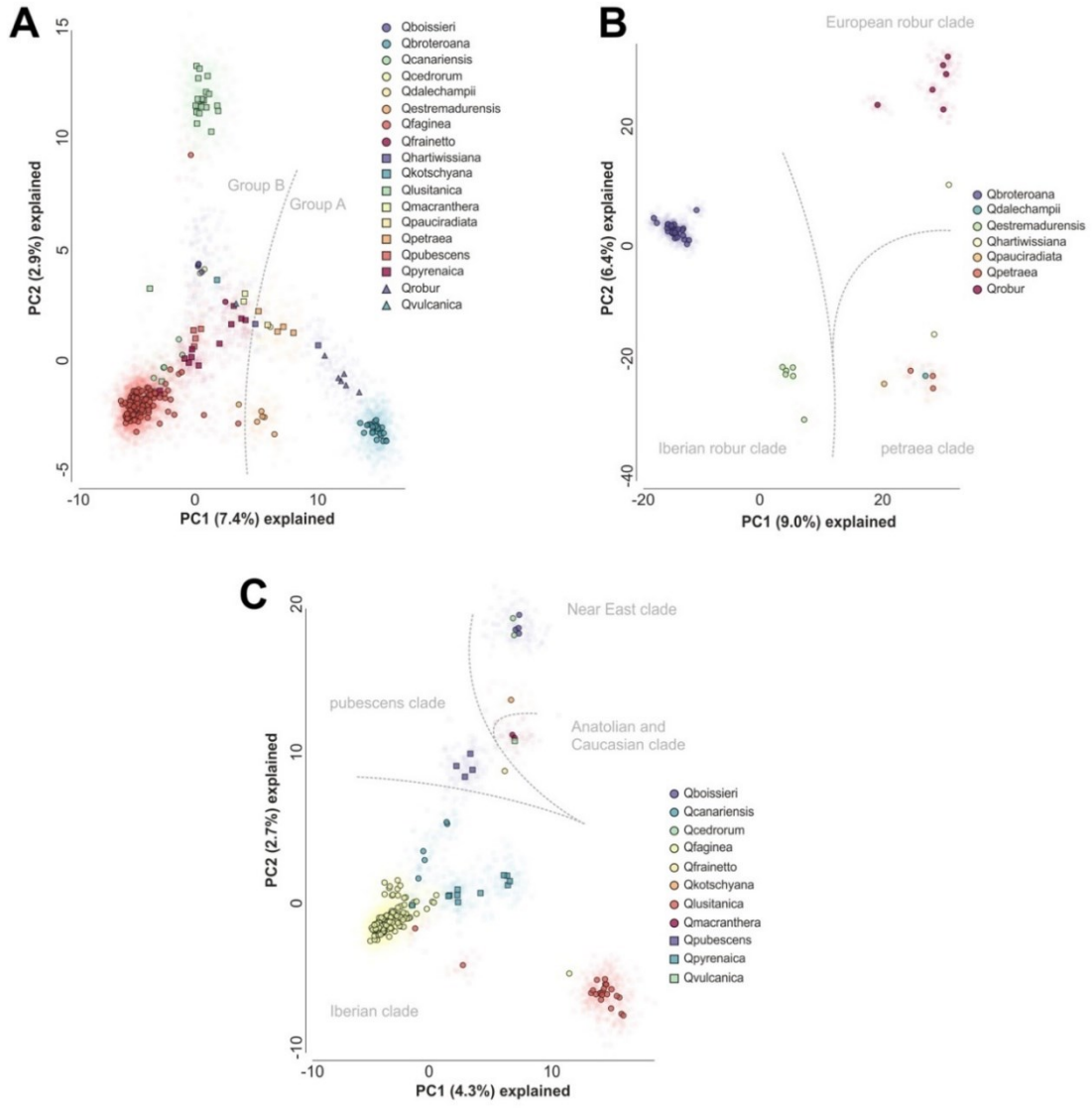


Figure 4 - Principal component analysis of Eurasian white oaks. (A) Global overview with all species; dashed grey line delimits Groups A and B. (B) Group A species; dashed grey line delimits the presently established Group A clades (see Figure 1); (C) Group B species; dashed grey line delimits the presently established Group B clades (see Figure 1).

The same sampling spectrum was then used to generate a neighbor-net (Figure 5). Despite some degree of reticulation at the bases of the clades, it evidenced proper clustering of within-species replicate samples, translating into well-established species-groups. The net was polarized by outgroup Asian species (to the right), which clustered closer to Group A species. Notably, in the latter, *Q. robur* and its former subspecies *Q. broteroana,* which includes *Q. orocantabrica*, simultaneously differentiated against the remaining species and between themselves. The neighbor-net suitably resolved groups A and B, with the exception of *Q. estremadurensis*, which reflects on the observed low split length. Group B species incorporated a subset of European and Euroasiatic species, where one sample of *Q. pubescens* grouped with *Q. frainetto*, followed by Caucasian (Q. *macranthera*) and Anatolian (Q. *vulcanica*) samples. Curiously, the near East *Q. kotschyana* shares some splitting, between *Q. vulcanica* and *Q. boissieri*, complementing the Near East clade. The Iberian set of Group B samples resolved the main species (*Q. faginea*, *Q. canariensis*, *Q. lusitanica* and *Q. pyrenaica*), while reflecting the transitional gradient of Catalonian *Q. canariensis* samples towards *Q. pubescens*. Notably, species were broadly resolved between Iberian and non-Iberian provenances, regardless of their Group A or B attribution (Figure 4). For instance, inside the “broad petraea” group, a major splitting was observed in the Iberian *Q. pauciradiata* with regards to remaining European *Q. petraea*.

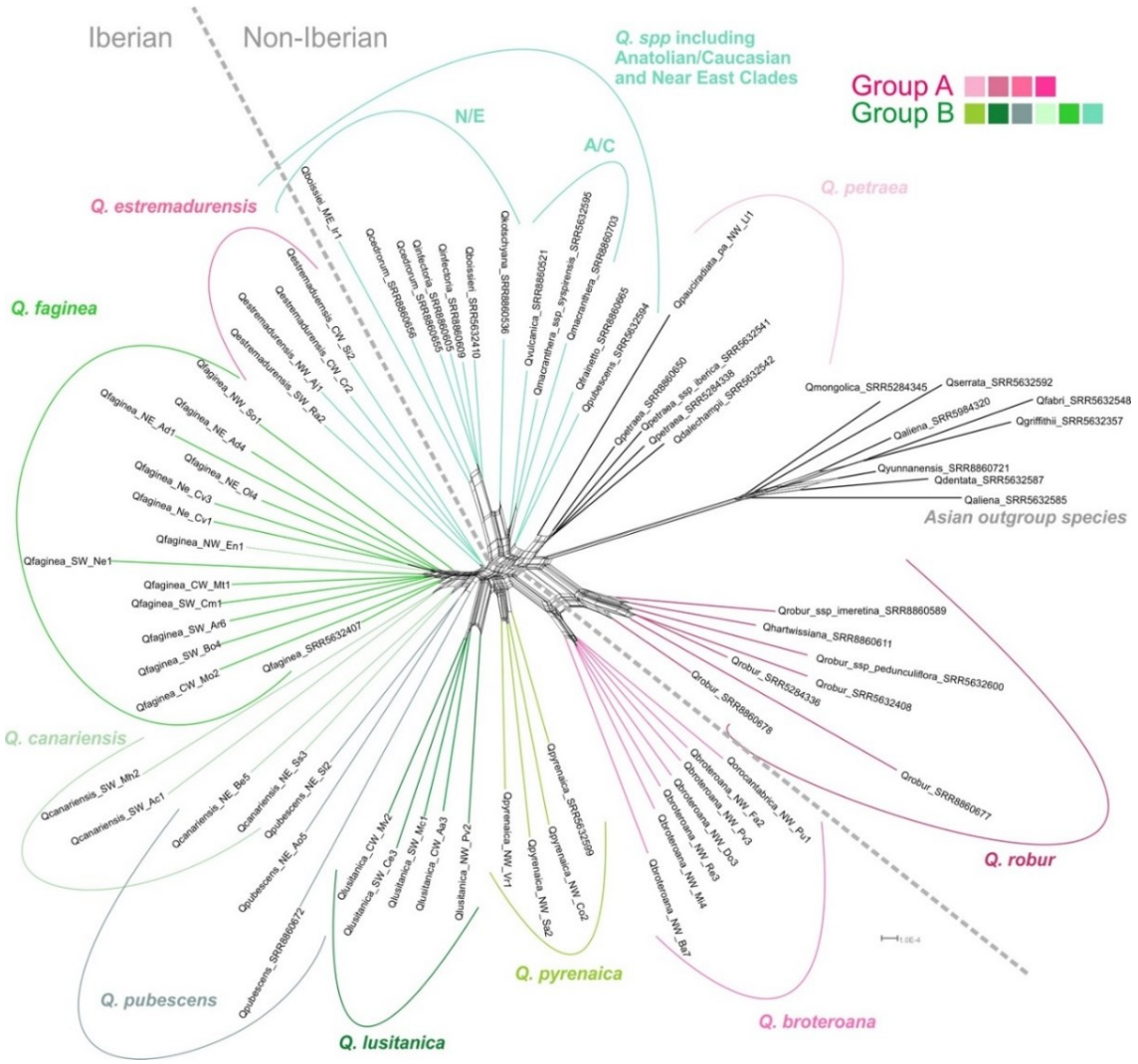


Figure 5 - Phylogenetic network computed using the neighbor-net method based on pairwise maximum likelihood distances and focusing on a species-level analysis of Iberian white oaks and related taxa. Coloured lines group phylogenetically cohesive species samples from Group A (purples), Group B (greens) and outgroup Asian species (light grey). Dashed grey lines represent a large biogeographic split delimiting Iberian from non-Iberian samples.

7.4.3. Characterization of white oak taxa and nothotaxa relationships

Subsequently, we addressed taxa and nothotaxa relationships by extending our analysis to additional populations of hybrids (known nothotaxa). Considering that PCA enables exploratory analysis without the constraints that hybrids would impose on phylogeny, the first analysis consisted of a birds-eye view of all sampled populations following incorporation of hybrids (Figure 6A). Here, we also observed the segregation between Groups A and B reflected onto PC1 (6.1% of variance). PC2 (2.4% of variance) translated a Mediterranean East-to-West gradient. Our dataset did not incorporate any tentative hybrids within Group A species. Intergroup A/B hybrids represent a special

case. A combination of literature and biogeographic evidence have led to the grouping, under the name *Q.* ×*coutinhoi*, of two sets of hybrids. They share the same Group B parent species (i.e. *Q. faginea*), but differ in the Group A parent species (the Iberian *robur* clade members *Q. estremadurensis* and *Q. broteroana*). For PCA analysis, our sampling incorporated two tentative *Q.* ×*coutinhoi*. One, sympatric with *Q. estremadurensis*, was visible halfway between *Q. estremadurensis* and *Q. faginea* (Figure 6A, Supplementary Figure S1A). A second, sympatric with *Q. broteroana*, was visible halfway between *Q. broteroana and Q. faginea*, albeit superimposing with *Q. estremadurensis* (Figure 6A, Supplementary Figure S1B). A new PCA that removed the confounding effect of remaining Group B members was subsequently able to separate the latter *Q.* ×*coutinhoi* from *Q. estremadurensis* (Supplementary Figure S1C). By resolving both *Q.* ×*coutinhoi* samples at the population level, we were able to observe a tentative origin from two separate provenances (*Q. broteroana* × *Q. faginea* and *Q. estremadurensis* × *Q. faginea*). This supports the previous nomenclatural attribution and taxonomic rearrangement providaded by Vasconcellos and Franco (1954) of Q. ×*duriensis* which we adopted henceforth regarding the hybrid between *Q. broteroana* and *Q. faginea* (Figure 6C; Supplementary Notes S1).

Group B displayed several tentative intra-group hybrids, and was subjected to a group-specific PCA (Figure 6B). Results consistently evidenced the studied nothotaxa in intermediate positions between putative parents. The first segregation level (PC1; 3.4% of variance) of *Q. lusitanica* was followed by the eastern distributed species (*Q. boisseri, Q. frainetto, Q. kotshyana, Q. macranthera* and *Q. vulcanica*) and *Q. pyrenaica*. PC2 (2.7% of variance) reflected multiple hybrids and parent species. Top-to-bottom, segregation evidences a gradient between *Q. pubescens,* followed by *Q.* ×*cerrioides* and the Catalonian samples of *Q. canariensis*. This hybrid swarm was followed by *Q.* ×*subpyrenaica* intermediate with *Q. faginea*. Finally, samples of *Q.* ×*marianica* were also positioned between *Q. canariensis* and *Q. faginea*. A summary of hinted parent/hybrid lineages is depicted in Figure 6C.

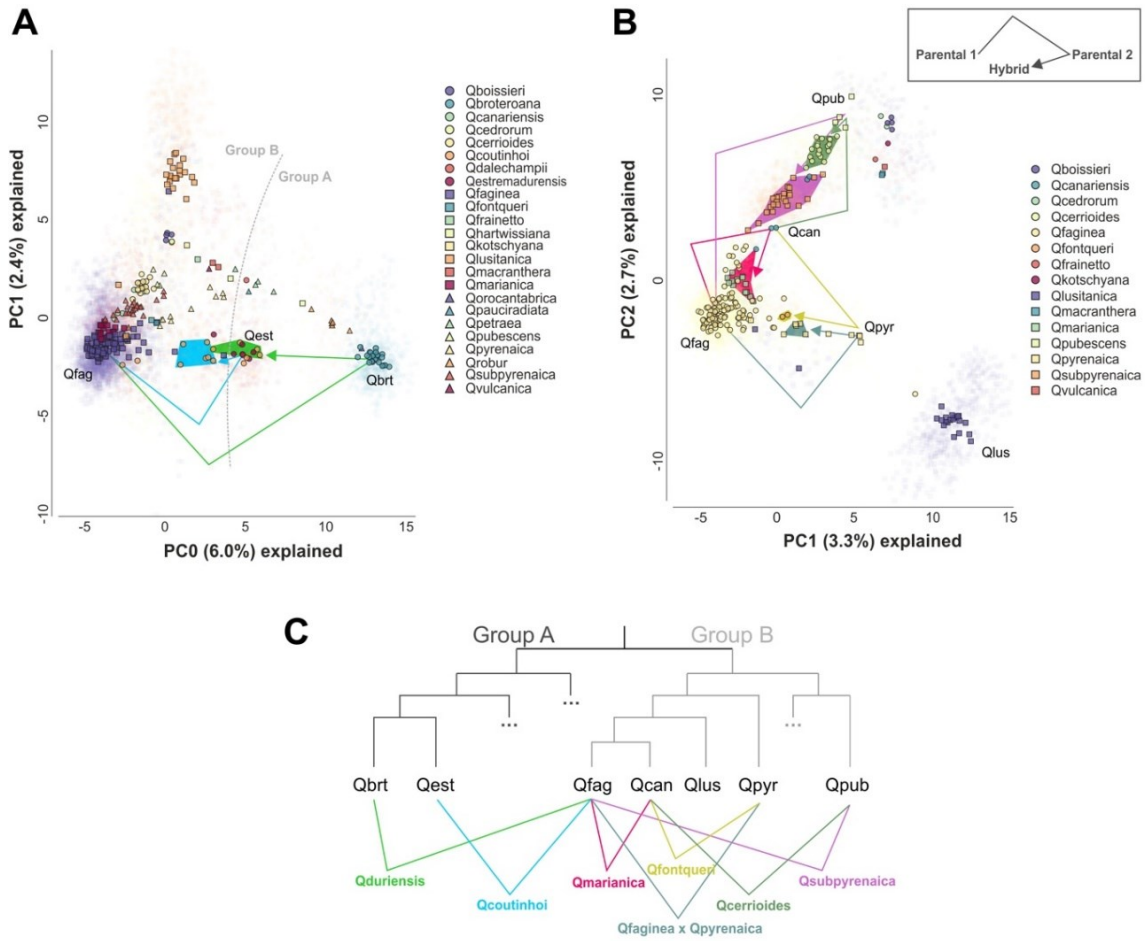


Figure 6 - Principal component analysis addressing hybridization in Iberian white oaks. (A,B) PCA featuring all taxa and hybrids (A), and all group B species and their hybrids (B). Arrows depict both parents pointing towards the hybrid; hybrids are singled out by coloured fields. (C) Schematic representation of the relations between hybrids and parent species. Qbrt – *Q. broteroana*; Qcan - *Q. canariensis*; Qest – *Q. estremadurensis*; Qfag - *Q. faginea*; Qlus - *Q. lusitanica*; Qpub – *Q. pubescens*; Qpyr - *Q. pyrenaica*.

Neighbor-net analysis of the complete hybrid dataset (Figure 7) mirrored previous results (Figure 5), by portraying relationships between the main species and putative parents. There was an expected confounding effect by the incorporation of hybrids, as shown by the relative splitting among parents. The four hybrids formed with *Q. faginea* displayed either intermediate positioning among parents (*Q.* ×*marianica* and *Q.* ×*subpyrenaica*) or positioning close to one parent (*Q. faginea* × *Q. pyrenaica* and Q. ×*coutinhoi*). We observed a Northeastern Iberia hybrid swarm, which incorporates the adequately positioned *Q.* ×*subpyrenaica*, and Catalonian *Q.* ×*cerrioides* samples, the latter being equally distributed among the parents *Q. canariensis* and *Q. pubescens*. Meanwhile, *Q.* ×*fontquerii* (*Q. canariensis* × *Q. pyrenaica*), correctly adopted an intermediate position

between parents. Collectively, results revealed important new insights on the intrinsic nature of the Iberian syngameon.

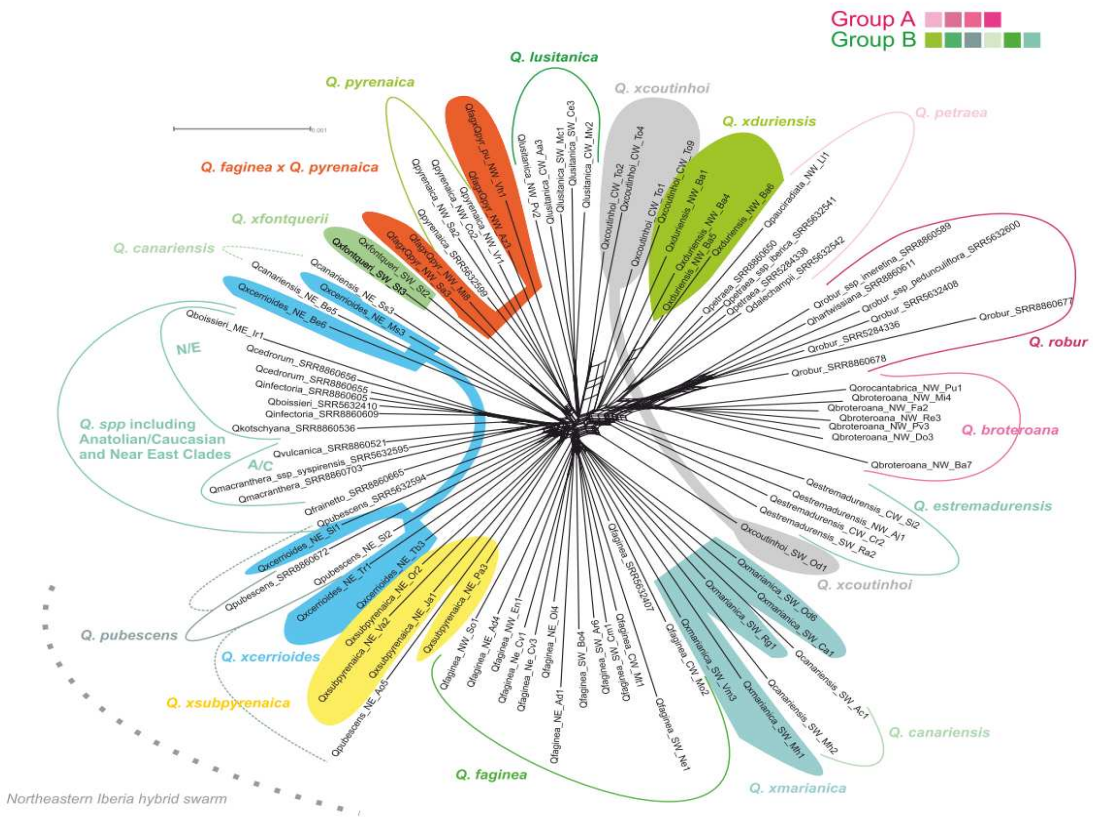


Figure 7 - Phylogenetic network computed using the neighbor-net method based on pairwise maximum likelihood distances, focusing on Iberian white oaks including their hybrids. Coloured lines group phylogenetically cohesive species samples from Group A (purples), and Group B (greens). Coloured fill areas group cohesive hybrid samples.

7.5. Discussion

7.5.1. The European white oaks reflect two major groups

Previous phylogenetic works have endorsed monophyly followed by radiation (increasing of diversification) of Eurasian *Roburoid* (Sect. *Quercus*) oaks, and consequently suggested the convergence of the submediterranean and dry-adapted species that were traditionally ascribed to subsections *Galliferae* and *Dascia*, inside four assigned subclades (Schwarz, 1936a; Hipp *et al.*, 2020; Vila-Viçosa *et al.*, 2020c). The present work's input of a larger set of Iberian samples suggests a reassessment of these assumptions, highlighted by one key finding: we consistently observed two well defined

clades (Groups A and B), which should underpin two new subsections inside Section *Quercus*. This hypothesis contradicts the previous assignment of four subclades, all of which carried dry-adapted (*Galliferae*) species and were suggestive of convergent evolution towards adaptation (Hipp *et al.*, 2020). This misassignment possibly originated in the imperfect identification of the *Galliferae* representative (*Q. canariensis*) (Hipp *et al.*, 2020). In the present report, the phylogenetic analysis of the Iberian white oaks revealed deep intraspecific interconnection and solid geographic structuring in samples from both groups (A and B), which were ascribed to former taxonomic groups (sections), but with different and newly solved circumscriptions. We unveiled a clade (Group A) that incorporates the temperate true roburoid species ("broad robur" and "broad petraea"). Group B species include mostly circummediterranean marcescent oaks, which occur predominantly in the transitional areas towards the Mediterranean climate (De Dios *et al.*, 2009; Mauri *et al.*, 2016; Vilches *et al.*, 2016; Dorado-Liñán *et al.*, 2017; Gil-Pelegrín *et al.*, 2017; Kavgacı *et al.*, 2021).Their distribution is related with an increase of annual and summer precipitation, which confers a submediterranean character to those forest ecotones between fully deciduous and evergreen sclerophyll species (García-Mijangos *et al.*, 2015; Hipp *et al.*, 2020; Vila-Viçosa *et al.*, 2020c).

7.5.2. Group A members highlight the uniqueness of Iberian oak diversity

Three aspects highlight the richness of Iberian white oaks within Group A members. First, the Iberian *Quercus pauciradiata* presents noticeable divergence from its European "broad petraea" counterparts, as suggested by branch distance (Figures 2 and 3) and PCA analysis (Figure 4B). This result is supported by *Q. pauciradiata*'s described morphological variation, with an exclusive and different type of fasciculate indumentum (Penas *et al.*, 1997) when compared to remaining "broad petraea". This case resembles the example of another Southern European "broad petraea" oak, the Italian *Q. dalechampii,* which also shares taxonomic ambiguity due to morphological plasticity (Di Pietro *et al.*, 2020; Proietti *et al.*, 2021). Second, results suggest the existence of two Iberian "broad robur" species (*Q. estremadurensis* and *Q. broteroana*), which are consistently differentiated from remaining European "broad robur" (Figures 2, 3 and 5). Relationships between Iberian and European "broad robur" may be legacies of past populational expansion and contraction events, which left a mark on these sister species. We also highlight the observation that *Q. orocantabrica* is nested within *Q. broteroana*. *Q. orocantabrica* was previously proposed as a new species by having a larger petiole (Rivas-Martínez *et al.*, 2002) and other sets of intermediate characters shared with *Q.*

petraea (Supplementary Notes S1). However, our phylogenetic and PCA analysis (Figures 2, 3, 4 and 5) suggest that the morphological variation ascribed to *Q. orocantabrica* is morphological variation within the westernmost *Q. broteroana* populations. Likewise, the analysis of both TETRAD analysis (Figure 3) and PCA positioning (Figure 4B) corroborates an interesting pattern around *Q. estremadurensis*, where the number of topologies linking either with “broad petraea” or ”broad robur” may suggest a shared ancestry between both and broader groups of taxa inside Group A. Morphologically, this is reflected in *Q. estremadurensis*’ features such as a larger petiole and rhomboidal leaf shaping (Schwarz, 1935; Schwarz, 1936a; Vicioso, 1950; Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018). It remains to be established whether this reproduces a past hybridization event between lineages, or the presence of ancestor footprint in *Q. estremadurensis* populations, in which case the Western IP may have acted as a putative center of origin for the temperate oaks (Group A). Notwithstanding, our results enhance the IP’s positioning as a biogeographic hotspot for white oaks.

7.5.3. Group B species reflect an East-to-West geographic gradient

Group B segregate between the *Iberian* and *pubescens* clades, the former encompassing Iberian samples but reflecting a broader geographical distribution of species across the Western Mediterranean. The latter clustered with Anatolian, Caucasean and Near East species (Figures 2 and 4C). This broadly reflects an East-to-West biogeographical structuring across the Mediterranean basin. *Quercus canariensis* is an interesting case of this biogeographic continuum. Our analysis revealed that a subset of Catalonian samples was geographically related to *Q. pubescens* and *Q. ×cerrioides,* (perceived as the hybrid swarm of *Q. canariensis* x *Q. pubescens*) (Figures 3, 6B and 7). Results therefore indicate that Catalonian populations of *Q. canariensis* display high levels of admixture with southern France and Italian *Q. pubescens*. Most importantly, the molecular evidence for this East-to-West continuum seems to contradict previous assignment of Western Mediterranean *Q. faginea, Q. canariensis*, *Q. lusitanica* and the Near Eastern *Q. boissieri*, into a single Section *Galliferae* (Boissier, 1853; Gürke, 1897; Tschan & Denk, 2012). Such evidence may reflect either: 1) convergent evolution between species occupying the same ecological niche but occupying extremes in the Mediterranean distribution range, with phenotypic plasticity of *Q. pubescens* (the link species) towards temperate climates. or 2) biogeographic vicariance between *Q. canariensis* and *Q. boissieri*. Similarly, four species with morphological similarities (the

Iberian *Q. pyrenaica,* the Italo-Hungarian *Q. frainetto*, the Anatolian *Q. vulcanica* and the Lebanese *Q. kotschyana*), all traditionally assigned to former Series *Confertae* (Section *Dascia*) (Schwarz, 1936a), appear in our data as phylogenetically segregated. This indicates an additional putative case of either convergent evolution, phenotypic plasticity, or common ancestry with posterior gene flow with local species, deserving deeper population genetics and phylogenetic surveys to infer on past demographic history across southern Europe.

Another interesting finding relates to *Q. lusitanica*, a species consistently assigned to Group B (Figures 2 and 3). In PCAs, *Q. lusitanica* was responsible for much of the observed variance, whether analysis referred to Group B species (Figure 4C, PC1) or the global oak analysis (Figure 4A, PC2; Figure 6). Unlike remaining European white oaks, *Q. lusitanica* is a shrub. It has been morphologically and historically associated with *Q. faginea*, resulting in ancient nomenclatural entanglement with this species (Coutinho, 1888; Sampaio, 1910; Vicioso, 1950; Vázquez *et al.*, 2018). This shrub alternates between marcescent and evergreen leaf behaviour. Ecologically, it is limited to siliceous bedrocks, requires moderate-to-high annual precipitation, and is highly susceptible to winter cold, making its distribution restricted to the Atlantic front of the IP and North Africa (Capelo *et al.*, 2002; Vila-Viçosa *et al.*, 2020a; Vila-Viçosa *et al.*, 2020c). This ecological specificity, coupled with being a geoxylic shrub, may have led to extensive genetic differentiation via adaptation. Genetic differentiation may have also resulted from genetic bottlenecks, associated with severe dry and cold periods or adaptation to cycles of recurrent fires, in stages of degradation of the Mediterranean forest into shrubland and grassland mosaics, observed in the western Iberian Peninsula in the past, especially in hot periods (Daniau *et al.*, 2007; Connor *et al.*, 2012; Camuera *et al.*, 2019; Genet *et al.*, 2021).

7.5.4. The Iberian white oaks reflect a legacy of pervasive hybridization

Our analysis was strongly sustained by the intermediate positioning of tentative hybrids between their putative parents, validating and redesigning classic taxonomic inferences (Schwarz, 1936a; Vicioso, 1950; Villar, 1958; Schwarz, 1964; Rivas-Martínez & Saénz, 1991; Vila-Viçosa *et al.*, 2014). More specifically, using a combination of morphological identification, literature review (Supplementary Notes S1) and molecular inference, we were able to assign a large set of Group B intra-hybrids, and two (albeit complex) Group A-B inter-hybrids. The latter show a gradient with putative hybrids positioned

intermediately among parents, going as far as to suggest cases of backcrosses (Figure 6, Figure 7, Supplementary Figure S1). Results respectively associate *Q.* ×*duriensis* and *Q.* ×*coutinhoi* with known individualized hybrid swarms that occur either in the Northern Douro Basin (for the contact between *Q. faginea* and *Q. broteroana*), or the Center and Southwest Portugal (for the contact between *Q. faginea* and *Q. estremadurensis*) (Vila-Viçosa *et al.*, 2020c). The most notorious case that celebrates the syngameon comes from Group B nothotaxa, where we observed a nexus of four species and multiple intermediate nothotaxa, that occur as hybrid-swarms with geographic outreach, like *Q.* ×*cerrioides, Q.* ×*subpyrenaica*, *Q.* ×*marianica* and *Q. faginea* × *Q. pyrenaica* (Figure 6B). The relatedness between *Q. pubescens*, *Q. boissieri* and *Q. canariensis* is corroborated by both PCA and the phylogenetic analysis, and seems to reflect an East-to-West gradient. Figures 6 and 7 also highlight the Northeastern Iberia hybrid swarm composed of *Q. canariensis*, *Q. pubescens* and their hybrid *Q.* ×*cerrioides*. Figure 7 highlights hybrid swarms well fitted amongst parent samples. Here, we highlight *Q. faginea* as one of the species most prone to hybridize with multiple Iberian oaks. This can be explained by the higher ecological plasticity of *Q. faginea,* as the most dry-adapted species of all Iberian white oaks, spanning across typical Mediterranean areas but also capable of contacting with temperate and continental areas (Kouba *et al.*, 2011; Vila-Viçosa *et al.*, 2012; Amigo *et al.*, 2017; Vila-Viçosa *et al.*, 2020c). Collectively, our data showcases the intricate network of pervasive hybridization currently underpinning the Iberian white oaks syngameon.

7.5.5. Macro and micro evolutionary processes as simultaneous drivers for both Groups

The Iberian syngameon brings to the fore the notable relations of the submediterranean ecotone as a major driver for understanding the evolutionary history of the clade represented by the Group B Mediterranean oaks (Vila-Viçosa *et al.*, 2020c). This transitional ecotone may have played a major evolutionary role by linking thermophilic conditions to a lower precipitation seasonality, emulating the subtropical conditions that were observed in the late Miocene. Such conditions are commonly associated with the geographical areas where relictual lauroid and broad-leafed flora is still present (Suc, 1984; Rodríguez-Sánchez *et al.*, 2010; Rodríguez-Sánchez & Arroyo, 2011; Vila-Viçosa *et al.*, 2020c). Also, for Group A species, we should highlight the microevolutionary singularity of *Q. estremadurensis* inside “broad robur”. *Q. estremadurensis* is distributed

peripherally throughout the submediterranean fringe (Figure 1), and is a species in need of further evolution-based studies towards a better phylogeographical resolution. Since this species is phylogenetically related with remaining temperate-distributed Group A species, we advocate the need for future in-depth molecular characterization of other Group A species distributed across all of Southern Europe. Many of these taxa share intermediate features between *Q. robur* and *Q. petraea* (Supplementary Notes S2). Thorough sampling of *bona fide* taxonomic representatives of "broad robur" and "broad petraea" should help us scrutinize the role of southern European Peninsulas as Miocene refugia (Vargas *et al.*, 2018). Ultimately, it will lead to a better understanding of the significance and evolutionary meaning of Southern European Peninsulas, either as sources or sinks of the diversity or origin of temperate distributed oaks, by possibly containing relict genotypes or even ancient taxa that matter to solve and filter the microevolutionary processes of the European white oaks.

7.5.6. The Iberian Peninsula syngameon is a major hotspot for oak conservation

Present results enhance the significance of the Iberian Peninsula syngameon as a major hotspot for oak conservation. A major output of the present work is the resolution of the phylogenetic backbone and species validation for forest dominant trees, in an important area (the IP) placed between two major biogeographic subregions (Eurosiberian and Mediterranean). First, by refining the taxonomy inside the "broad robur" group, we showcase *Q. estremadurensis* and *Q. broteroana* as taxa that should be considered as species due to the considerable phylogenetic divergence with European pedunculate oaks (*Q. robur* L. *senso strictu).* Earlier, we also highlighted a potential Iberian origin for Group A oaks, based on molecular and morphological data coming from *Q. estremadurensis*. *Q. estremadurensis* is distributed across Western IP in very small patches of scattered individuals among *Q. faginea* forests, where frequently the presence of *Q.* ×*coutinhoi* is dominant over *Q. estremadurensis* (Vila-Viçosa *et. al.* 2020b). Thus, this species is deserving of major conservation efforts and inclusion in the *Species of Concern and genetic research focus* list (Backs & Ashley, 2021). Second, while the Iberian sister species of *Q. robur* L., *Q. broteroana*, appears to be a valid species, *Q. orocantabrica* requires further population genetic studies to understand its substructure inside *Q. broteroana*. Similarly, *Q. pauciradiata*, which belongs to the "broad petraea" in our analysis, also deserves further studies alongside *Q. huguetiana,* an Iberian petraeoid oak appearing as a sister species to *Q. petraea* (Papini *et al.,* 2011). Finally, the validation of several nothotaxa and amplification of the Iberian syngameon

profile urges novel conservation efforts, due to the possible ongoing hybridization in known hotspots, like Catalonian sub littoral mountains (*Q.* ×*cerrioides*), the Pre-Pyrenean (*Q.* ×*subpyrenaica*), and the ongoing extensive introgression of both *Q. broteroana* and *Q. estremadurensis* with *Q. faginea* related with *Q.* ×*duriensis* and *Q.* ×*coutinhoi*. This peripheral natural hybrid zones emerge as notable case-studies to address adaptation and adaptive introgression of genomic variation (Suarez-Gonzalez *et al.*, 2016; Holliday *et al.*, 2017). Our conservation concerns are even more pressing in face of the fast pace of climate change, where bioclimatic and ecological adaptation will certainly play a major role in species migration, survival rates and isolation, thus shaping sympatry patterns and exposure to introgression with other oaks.

7.6. Concluding remarks

The present analysis contributed to the resolution of several pending taxonomic questions, by assessing the Western European white oaks' evolutionary history, which is well-known for its rapid diversification. In parallel, we helped re-position the Iberian oak species inside the world phylogenetic tree and enlarged the current understanding of the phylogeography of the Eurasian white oaks. In this sense the Iberian white oaks evidence the celebration of the syngameon concept (Grant, 1981; Cronk & Suarez-Gonzalez, 2018; Cannon & Petit, 2020), improved after a robust genomic analysis. This syngameon is substantiated by a deep biogeographical imprint that is notorious across the circummediterranean oaks from Group B, and especially across the IP. Here, hybrid swarms confirm the extensive gene exchange among taxa, despite the maintenance of parents as strong species and integrative interbreeding evolutionary units (Suarez-Gonzalez *et al.*, 2018). Also, the analysis of Group A ("broad robur" and "broad petraea") solidifies the Iberian Peninsula as a major hotspot for white oak diversity with putative relict genotypes. Our findings also amplify the significance of biogeographical vicariance and transitional climate ecotone in driving species differentiation despite the confounding effect of character morphology convergence. Our dichotomic monophyly of two segregated Groups (A and B) enhances the notable inferences made by Otto Schwarz (1935; 1936c; 1936a), which are one of the major references for the European white oak's taxonomy. Traditional arguments suggested the presence of cohesive groups inside *Section Quercus* that were ultimately reflected in our molecular data (see Supplementary Notes S3 for details). Ultimately, our approach improves on the knowledge obtained at the micro and macroevolutionary levels in the European white

oaks, after the development of oak genomics (Plomion *et al.*, 2016; Sork *et al.*, 2016; Ramos *et al.*, 2018). It fosters novel conservation strategies, especially regarding the paleo-biogeographic history of European white oaks and the role of Southern European Peninsulas as reservoirs and refugia for cryptic biological diversity, with major insights to the evolutionary history of the key species that rule forests in the Northern Hemisphere.

7.7. References

Aedo C, Buira A, Medina L, Fernández-Albert M 2017. The Iberian Vascular Flora: Richness, Endemicity and Distribution Patterns. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 101-130.

Amigo J, Rodríguez-Guitián MA, Honrado J, Alves P 2017. The lowlands and midlands of Northwestern Atlantic Iberia. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 191-250.

Andrews KR, Good JM, Miller MR, Luikart G, Hohenlohe PA. 2016. Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics* **17**(2): 81-92.

Axelrod DI. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden*: 629-657.

Backs JR, Ashley MV. 2021. Quercus conservation genetics and genomics: past, present, and future. *Forests* **12**(7): 882.

Baird NA, Etter PD, Atwood TS, Currey MC, Shiver AL, Lewis ZA, Selker EU, Cresko WA, Johnson EA. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PloS one* **3**(10): e3376.

Battandier JA, Trabut LC. 1905. *Flore analytique et synoptique de l'Algérie et de la Tunisie.* . Argel: Vve Giralt, Imprimeur-Éditeur.

Birks HJB, Tinner W. 2016. Past forests of Europe.

Boissier E. 1838. Elenchus plantarum novarum minusque cognitarum in Hispania australi collectarum. *Typographia Nador et Ramboz, Geneve*.

Boissier E. 1853. *Diagnoses plantarum orientalium novarum.... Ser. 1: Vol. secundum: Fasc. No. 12*: Wolfrath.

Bryant D, Moulton V. 2004. Neighbor-net: an agglomerative method for the construction of phylogenetic networks. *Molecular biology and evolution* **21**(2): 255-265.

Camuera J, Jiménez-Moreno G, Ramos-Román MJ, García-Alix A, Toney JL, Anderson RS, Jiménez-Espejo F, Bright J, Webster C, Yanes Y. 2019. Vegetation and climate changes during the last two glacial-interglacial cycles in the western Mediterranean: A new long pollen record from Padul (southern Iberian Peninsula). *Quaternary Science Reviews* **205**: 86-105.

Cannon CH, Petit RJ. 2020. The oak syngameon: more than the sum of its parts. *New Phytologist* **226**(4): 978-983.

Capelo JH, Costa JC, Lousã MF, Mesquita S. 2002. A aliança Quercion fruticosae Rothmaler 1954 em. Rivas-Martínez, Lousã, T.E. Díaz, Fernández-González & J.C. Costa 1990. *Quercetea* **3**: 99-110.

Carapeto A, Francisco A, Pereira P, Porto M 2020. Lista vermelha da flora vascular de Portugal Continental: Sociedade Portuguesa de Botânica, Associação Portuguesa de Ciência da ….

Carrero C, Jerome D, Beckman E, Byrne A, Coombes A, Deng M, González-Rodríguez A, Hoang V, Khoo E, Nguyen N. 2020. The red list of oaks 2020. *The Morton Arboretum: Lisle, IL, USA*: 11-12.

Cavender-Bares J, González-Rodríguez A, Eaton DA, Hipp AA, Beulke A, Manos PS. 2015. Phylogeny and biogeography of the American live oaks (Quercus subsection Virentes): a genomic and population genetics approach. *Molecular Ecology* **24**(14): 3668-3687.

Chifman J, Kubatko L. 2014. Quartet inference from SNP data under the coalescent model. *Bioinformatics* **30**(23): 3317-3324.

Connor SE, Araújo J, van der Knaap WO, van Leeuwen JF. 2012. A long-term perspective on biomass burning in the Serra da Estrela, Portugal. *Quaternary Science Reviews* **55**: 114-124.

Coutinho AXP. 1888. Os Quercus de Portugal. *Boletim da Sociedade Broteriana* **6**: 47-116.

Cronk QC, Suarez-Gonzalez A 2018. The role of interspecific hybridization in adaptive potential at range margins: Wiley Online Library.

Crowl AA, Manos PS, McVay JD, Lemmon AR, Lemmon EM, Hipp AL. 2020. Uncovering the genomic signature of ancient introgression between white oak lineages (Quercus). *New Phytologist* **226**(4): 1158-1170.

Daniau A-L, Sánchez-Goñi M, Beaufort L, Laggoun-Défarge F, Loutre M-F, Duprat J. 2007. Dansgaard–Oeschger climatic variability revealed by fire emissions in southwestern Iberia. *Quaternary Science Reviews* **26**(9-10): 1369-1383.

De Dios RS, Benito-Garzón M, Sainz-Ollero H. 2009. Present and future extension of the Iberian submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology* **204**(2): 189-205.

Deng M, Jiang X-L, Hipp AL, Manos PS, Hahn M. 2018. Phylogeny and biogeography of East Asian evergreen oaks (Quercus section Cyclobalanopsis; Fagaceae): insights into the Cenozoic history of evergreen broad-leaved forests in subtropical Asia. *Molecular phylogenetics and evolution* **119**: 170-181.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Denk T, Grimm GW, Manos PS, Deng M, Hipp AL. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *bioRxiv*.

Di Pietro R, Conte AL, Di Marzio P, Gianguzzi L, Spampinato G, Caldarella O, Fortini P. 2020. A multivariate morphometric analysis of diagnostic traits in southern Italy and Sicily pubescent oaks. *Folia Geobotanica* **55**(3): 163-183.

Dorado-Liñán I, Zorita E, Martínez-Sancho E, Gea-Izquierdo G, Di Filippo A, Gutiérrez E, Levanic T, Piovesan G, Vacchiano G, Zang C. 2017. Large-scale atmospheric circulation enhances the Mediterranean East-West tree growth contrast at rear-edge deciduous forests. *Agricultural and Forest Meteorology* **239**: 86-95.

Douaihy B, Saliba C, Stephan J, Simeone MC, Cardoni S, Farhat P, Bou Dagher Kharrat M. 2020. Tracking diversity and evolutionary pathways of Lebanese oak taxa through plastome analyses. *Botany Letters* **167**(3): 315-330.

Eaton DA, Hipp AL, González-Rodríguez A, Cavender-Bares J. 2015. Historical introgression among the American live oaks and the comparative nature of tests for introgression. *Evolution* **69**(10): 2587-2601.

Eaton DA, Overcast I. 2020. ipyrad: Interactive assembly and analysis of RADseq datasets. *Bioinformatics* **36**(8): 2592-2594.

Eaton DA, Spriggs EL, Park B, Donoghue MJ. 2017. Misconceptions on missing data in RAD-seq phylogenetics with a deep-scale example from flowering plants. *Systematic biology* **66**(3): 399-412.

Fitz-Gibbon S, Hipp AL, Pham KK, Manos PS, Sork VL. 2017. Phylogenomic inferences from reference-mapped and de novo assembled short-read sequence data using RADseq sequencing of California white oaks (Quercus section Quercus). *Genome* **60**(9): 743-755.

Franco JA 1990. Quercus L. In: S. C, al. e eds. *Flora Iberica, (Plantanaceae-Plumbaginaceae [Partim])*. Madrid: Real Jardín Botánico, CSIC, pp. 15-36.

García-Mijangos I, Campos JA, Biurrun I, Herrera M, Loidi J 2015. Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: Box EO, Fujiwara K eds. *Warm-temperate deciduous forests around the Northern hemisphere*. London: Springer, 119-138.

Genet M, Daniau A-L, Mouillot F, Hanquiez V, Schmidt S, David V, Georget M, Abrantes F, Anschutz P, Bassinot F. 2021. Modern relationships between microscopic charcoal in marine sediments and fire regimes on adjacent landmasses to refine the interpretation of marine paleofire records: An Iberian case study. *Quaternary Science Reviews* **270**: 107148.

Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D. 2017. Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.

Grant V 1981. Plant speciation. *Plant Speciation*: Columbia university press.

Gugger PF, Fitz-Gibbon ST, Albarrán-Lara A, Wright JW, Sork VL. 2021. Landscape genomics of Quercus lobata reveals genes involved in local climate adaptation at multiple spatial scales. *Molecular Ecology* **30**(2): 406-423.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Himrane H, Camarero JJ, Gil-Pelegrín E. 2004. Morphological and ecophysiological variation of the hybrid oak Quercus subpyrenaica (Q. faginea× Q. pubescens). *Trees* **18**(5): 566-575.

Hipp AL, Eaton DA, Cavender-Bares J, Fitzek E, Nipper R, Manos PS. 2014. A framework phylogeny of the American oak clade based on sequenced RAD data. *PloS one* **9**(4): e93975.

Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl A, Deng M, Denk T, Fitz-Gibbon S. 2020. Genomic landscape of the global oak phylogeny. *New Phytologist* **226**(4): 1198-1212.

Holliday JA, Aitken SN, Cooke JE, Fady B, González-Martínez SC, Heuertz M, Jaramillo-Correa JP, Lexer C, Staton M, Whetten RW 2017. Advances in ecological genomics in forest trees and applications to genetic resources conservation and breeding: Wiley Online Library.

Huson DH, Bryant D. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular biology and evolution* **23**(2): 254-267.

Kavgacı A, Balpınar N, Öner HH, Arslan M, Bonari G, Chytrý M, Čarni A. 2021. Classification of forest and shrubland vegetation in Mediterranean Turkey. *Applied Vegetation Science* **24**(2): e12589.

Kotschy T. 1862. *Die Eichen Europa‘s und des Orient‘s*. Wien und Olmütz: E. Hölzel.

Kouba Y, Alados CL, Bueno CG. 2011. Effects of abiotic and anthropogenic factors on the spatial distribution of Quercus faginea in the Spanish Central Pyrenees. *Plant Ecology* **212**(6): 999-1007.

Lamarck JB. 1785. *Encyclopédie méthodique. Botanique*. Paris: Panckoucke.

Lazic D, Hipp AL, Carlson JE, Gailing O. 2021. Use of genomic resources to assess adaptive divergence and introgression in oaks. *Forests* **12**(6): 690.

Leroy T, Plomion C, Kremer A. 2020. Oak symbolism in the light of genomics. *New Phytologist* **226**(4): 1012-1017.

Loidi J 2017. Introduction to the Iberian Peninsula, General Features: Geography, Geology, Name, Brief History, Land Use and Conservation. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*: Springer, 3-27.

Manos PS, Doyle JJ, Nixon KC. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). *Molecular phylogenetics and evolution* **12**(3): 333-349.

Mauri A, Enescu C, Houston Durrant T, De Rigo D, Caudullo G. 2016. Quercus frainetto in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg*: 1-4.

McVay JD, Hipp AL, Manos PS. 2017. A genetic legacy of introgression confounds phylogeny and biogeography in oaks. *Proc. R. Soc. B* **284**(1854): 20170300.

Médail F, Baumel A. 2018. Using phylogeography to define conservation priorities: The case of narrow endemic plants in the Mediterranean Basin hotspot. *Biological Conservation* **224**: 258-266.

Minh BQ, Nguyen MAT, von Haeseler A. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular biology and evolution* **30**(5): 1188-1195.

Olalde M, Herrán A, Espinel S, Goicoechea PG. 2002. White oaks phylogeography in the Iberian Peninsula. *Forest ecology and management* **156**(1-3): 89-102.

Papini A, Simeone M, Bellarosa R, Spada F, Schirone B. 2011. Quercus macranthera Fisch. & Mey. ex Hohen. and Quercus iberica M. Bieb.: Taxonomic definition and systematic relationships with European oaks inferred from nuclear internal transcribed spacer (ITS) data. *Plant Biosystems* **145**(1): 37-49.

Pasta S, de Rigo D, Caudullo G 2016. Quercus pubescens in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A eds. *European atlas of forest tree species*. Luxembourg: Publications Office of the European Union, 156-157.

Penas A, Llamas F, Perez-Morales C, Acedo C. 1997. A new species of Quercus L. (Fagaceae) from NW Spain. *Botanica Helvetica* **107**: 75-82.

Petit RJ, Brewer S, Bordács S, Burg K, Cheddadi R, Coart E, Cottrell J, Csaikl UM, van Dam B, Deans JD. 2002. Identification of refugia and post-glacial colonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *Forest ecology and management* **156**(1): 49-74.

Petit RJ, Carlson J, Curtu AL, Loustau M-L, Plomion C, González-Rodríguez A, Sork V, Ducousso A. 2013. Fagaceae trees as models to integrate ecology, evolution and genomics. *New Phytologist* **197**(2): 369-371.

Pham KK, Hipp AL, Manos PS, Cronn RC. 2017. A time and a place for everything: phylogenetic history and geography as joint predictors of oak plastome phylogeny. *Genome* **60**(9): 720-732.

Plomion C, Aury JM, Amselem J, Alaeitabar T, Barbe V, Belser C, Bergès H, Bodénès C, Boudet N, Boury C. 2016. Decoding the oak genome: public release of sequence data, assembly, annotation and publication strategies. *Molecular ecology resources* **16**(1): 254-265.

Plomion C, Martin F. 2020. Oak genomics is proving its worth. *New Phytologist* **226**(4): 943-946.

Proietti E, Filesi L, Di Marzio P, Di Pietro R, Masin R, Conte AL, Fortini P. 2021. Morphology, geometric morphometrics, and taxonomy in relict deciduous oaks woods in northern Italy. *Rendiconti Lincei. Scienze Fisiche e Naturali* **32**(3): 549-564.

Ramos AM, Usié A, Barbosa P, Barros PM, Capote T, Chaves I, Simões F, Abreu I, Carrasquinho I, Faro C. 2018. The draft genome sequence of cork oak. *Scientific data* **5**(1): 1-12.

Rivas-Martínez S, Báscones J.E., Díaz T., F. F-G, J. L. 1991. Vegetación del Pirineo occidental y Navarra. *Itinera Geobotanica* **5**: 530.

Rivas-Martínez S, González-Días TE, González FF, Loidi JJ, Lousã MF, Merino ÁP. 2002. Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica*(15): 433-922.

Rivas-Martínez S, Penas A, del Río S, González T, Rivas-Sáenz S 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi J ed. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 29-80.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rodríguez-Sánchez F, Arroyo J. 2011. Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past. *Climate change, ecology and systematics*: 280-303.

Rodríguez-Sánchez F, Hampe A, Jordano P, Arroyo J. 2010. Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Review of Palaeobotany and Palynology* **162**(3): 507-521.

Sampaio G. 1910. Nota a propósito dos Quercus lusitanica Lamk., Q. humilis Lamk e Quercus faginea, Lamk. . *Annaes Scientificos da Academia Polytechnica do Porto* **5**(3): 161-165.

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O. 1936a. Entwurf zu einem natürlichen System der Cupuliferen und der Gattung Quercus L. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*: 1-22.

Schwarz O. 1936b. *Monographie der Eichen Europas und des Mittelmeergebietes*: Selbstverlag.

Schwarz O. 1936c. Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* **8**: 65–100.

Schwarz O. 1937. Monographie der Eichen Europas und des Mittelmeergebietes. *Repertorium novarum speciarum regni vegetabilis* **1**: 1-200.

Schwarz O 1964. Quercus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, DA. W eds. *Flora Europaea*. Cambridge: Cambridge University Press, 61-64.

Snir S, Rao S. 2012. Quartet MaxCut: a fast algorithm for amalgamating quartet trees. *Molecular phylogenetics and evolution* **62**(1): 1-8.

Sork VL, Fitz-Gibbon ST, Puiu D, Crepeau M, Gugger PF, Sherman R, Stevens K, Langley CH, Pellegrini M, Salzberg SL. 2016. First draft assembly and annotation of the genome of a California endemic oak Quercus lobata Née (Fagaceae). *G3: Genes, Genomes, Genetics* **6**(11): 3485-3495.

Spach É. 1842. *Histoire naturelle des végétaux: Phanérogames. Vol. 11. Librairie encyclopédique de Roret, Paris*. Paris.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**(9): 1312-1313.

Suarez-Gonzalez A, Lexer C, Cronk QC. 2018. Adaptive introgression: a plant perspective. *Biology letters* **14**(3): 20170688.

Suarez-Gonzalez A, Hefer CA, Christe C, Corea O, Lexer C, Cronk QC, Douglas CJ. 2016. Genomic and functional approaches reveal a case of adaptive introgression from Populus balsamifera (balsam poplar) in P. átrichocarpa (black cottonwood). *Molecular Ecology* **25**(11): 2427-2442.

Suc J-P. 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* **307**(5950): 429-432.

Tarkhnishvili D, Gavashelishvili A, Mumladze L. 2012. Palaeoclimatic models help to understand current distribution of Caucasian forest species. *Biological journal of the Linnean Society* **105**(1): 231-248.

Tóth EG, Köbölkuti ZA, Cseke K, Kámpel JD, Takács R, Tomov VT, Ábrán P, Stojnic S, Vastag E, Mataruga M. 2021. A genomic dataset of single-nucleotide polymorphisms generated by ddRAD tag sequencing in Q. petraea (Matt.) Liebl. populations from Central-Eastern Europe and Balkan Peninsula. *Annals of Forest Science* **78**(2): 1-13.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

Ulaszewski B, Meger J, Burczyk J. 2021. Comparative analysis of SNP discovery and genotyping in Fagus sylvatica L. and Quercus robur L. using RADseq, GBS, and ddRAD methods. *Forests* **12**(2): 222.

Vargas P, Fernández-Mazuecos M, Heleno R. 2018. Phylogenetic evidence for a Miocene origin of Mediterranean lineages: species diversity, reproductive traits and geographical isolation. *Plant Biology* **20**: 157-165.

Vasconcellos JC, Franco JA. 1954. Os Carvalhos de Portugal. *Anais do Instituto Superior de Agronomia* **21**: 1–135.

Vazquez FM, Coombes A, Almeida R, Garcia-Alonso D, Marquez-Garcia F, Vila-Vicosa C. 2020. Lectotypification of names of Quercus spp.(Fagaceae) described by Lamarck from the Iberian Peninsula. *Phytotaxa* **455**(3): 205-213.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Veloz SD, Williams JW, Blois JL, He F, Otto-Bliesner B, Liu Z. 2012. No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology* **18**(5): 1698-1713.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C, Arenas-Castro S, Marcos B, Honrado J, García C, Vázquez FM, Almeida R, Gonçalves J. 2020a. Combining Satellite Remote Sensing and Climate Data in Species Distribution Models to Improve the Conservation of Iberian White Oaks (Quercus L.). *ISPRS International Journal of Geo-Information* **9**(12): 735.

Vila-Viçosa C, Gonçalves J, Honrado J, Lomba Â, Almeida RS, Vázquez FM, Garcia C. 2020b. Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Scientific reports* **10**(1): 21598.

Vila-Viçosa C, Gonçalves J, Honrado J, Lomba Â, Almeida RS, Vázquez FM, Garcia C. 2020c. Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Scientific reports* **10**(1): 1-12.

Vila-Viçosa C, Marcos B, Garcia C, Gonçalves J 2019. Biogeography from space—A new tool to disentangle Iberian Forests Ecology and Distribution. *Proceedings of the SIBECOL. 1st Meeting of the Iberian Ecological Society & XIV AEET Meeting, Barcelona, Spain*. 4-17.

Vila-Viçosa C, Mendes P., del Río S, Meireles C., Quinto-Canas R, Arsénio P, Pinto-Gomes C. 2012. Temporihygrophilous Quercus broteroi forests in southern Portugal: analysis and conservation. *Plant Biosystems* **146**(1): 298-308.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vila-Viçosa C, Vázquez FM, Mendes P, Del Rio S, Musarella C, Cano-Ortiz A, Meireles C. 2015. Syntaxonomic update on the relict groves of Mirbeck's oak

(Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* **149**(3): 512-526.

Vila-Viçosa C, Vieira C, Márquez F, Almeida R, Vázquez FM. 2022. Notes on the original materials of the three western Mediterranean oaks (Quercus, Fagaceae) described by Desfontaines. *Mediterranean Botany* **43**: 1-11.

Vilches B, Sánchez-Mata D, Gavilán RG 2016. Marcescent Quercus pyrenaica Forest on the Iberian Peninsula. *Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales*: Springer, 257-283.

Villar EH. 1935. Sur le nom de quelques Quercus et la systématique du faginea. *Cavanillesia* **7**: 57-70.

Villar EH. 1958. Estudios sobre los Quercus del Oeste mediterráneo. *Anales del Instituto Botanico de A.J. Cavanilles* **15**: 3-114.

Willdenow CL. 1796. *Berlinische Baumzucht oder Beschreibung der in den Gärten um Berlin im Freien ausdauernden Bäume und Sträucher für Gartenliebhaber und Freunde der Botanik*. Berlin: Nauck.

Willdenow CL. 1805. *Species plantarum exhibentes plantas rite cognitas ad genera relatas cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis naturalibus secundum systema sexuale digestas*. Berlin: Nauck.

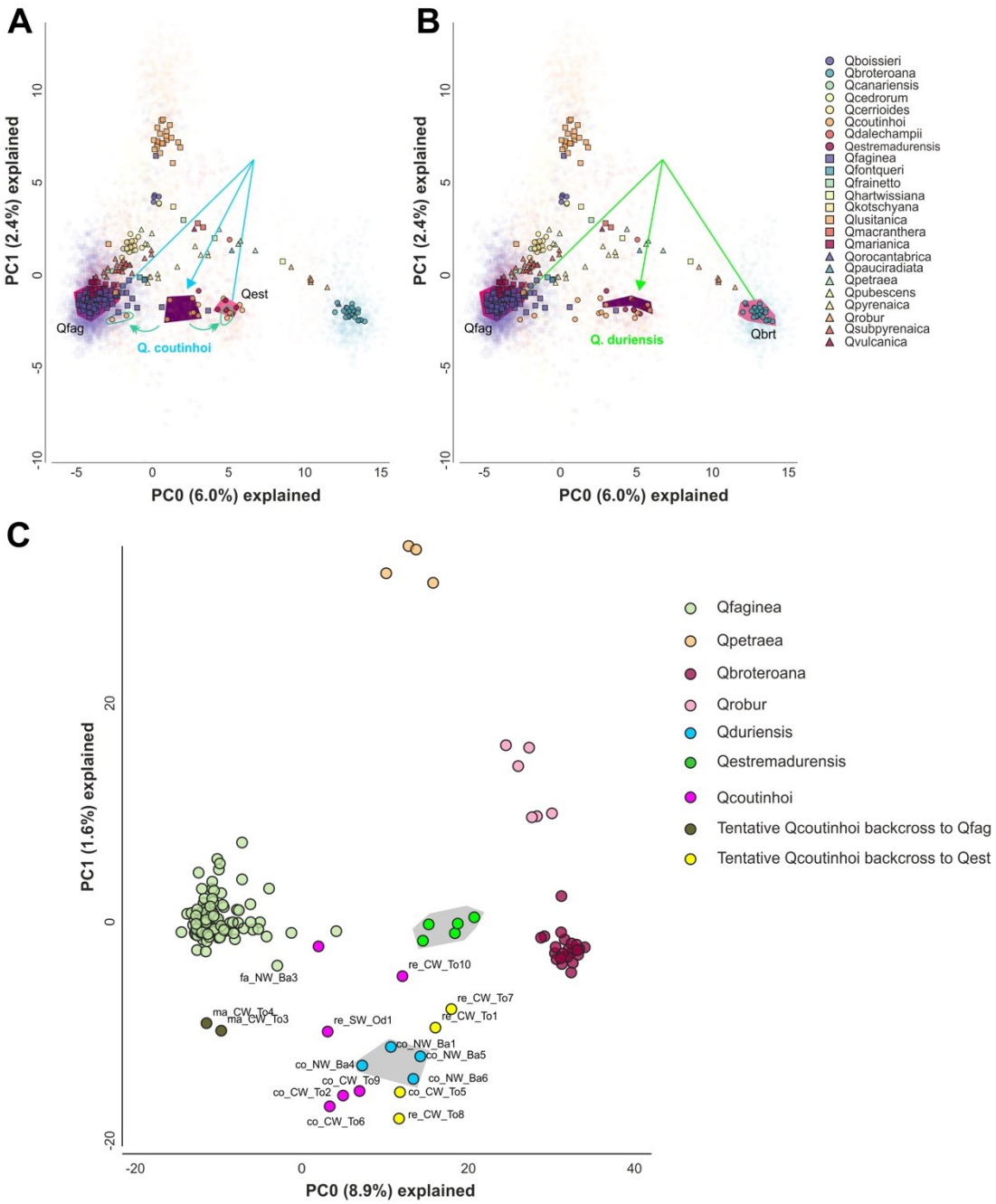
Williams JW, Blois JL, Shuman BN. 2011. Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *Journal of Ecology* **99**(3): 664-677.

Willkomm HM. 1859. *Pugillus plantarum novarum peninsulae pyrenaicae*: Journal für die Botanik.

Willkomm M, Lange J. 1861. *Prodromus florae Hispanicae. I.*: Stuttgart.

7.8. Supplementary information

Supplementary Figure S1



Supplementary Figure S1 - Principal component analysis addressing hybridization in Iberian white oaks. (A) PCA featuring all taxa and hybrids, highlighting samples that reflect the hybrid *Q.* ×*coutinhoi* and tentative backcrosses (green arrows). (B) PCA featuring all taxa and hybrids, highlighting samples that reflect the hybrid *Q.* ×*duriensis*. (C) PCA that removed the confounding effect of Group B members in order to resolve *Q.* ×*duriensis* from *Q. estremadurensis* in the bi-dimensional space (highlighted grey areas).

Supplementary Methods S1. Characterization of the study area.

The Iberian Peninsula is located in the southwest of the European continent and the extreme west of the Mediterranean Basin (between latitudes -9.55º W to 3.35º E and latitudes 35.87º N to 43.80º N). The IP holds a highly diverse geological history, with a geographic location that places it under the influence of two strong climatic determinants: a wet Temperate Atlantic climate in the Northwest, and a dry Mediterranean climate in the Southeast (Loidi, 2017; Rivas-Martínez *et al.*, 2017). Its biogeographic positioning and orographic characteristics turn it into a hotspot for European phytocoenotic diversity. The Iberian total flora displays almost 30% of endemicity rate (including 21 genera and 13 phylogeographic refugia) (Aedo *et al.*, 2017; Médail & Baumel, 2018), and it specifically hosts circa half of the European oak species (Schwarz, 1964).

Supplementary Notes S1. Focal taxa information.

Section *Quercus* Denk, Thomas *et al.* (2017)

Subsection *Robur* Schwarz (1936a)

Quercus estremadurensis O. Schwarz *(=Q. robur* subsp. *estremadurensis* (O.Schwarz) A. Camus)

General information: Taxon earlier described by Schwarz (1935) as an independent species of *Q. robur* L.. Together with *Quercus hartwissiana* Steven, both species present common characteristics that led the author to create a Series “Primitivae”, inside Section *Robur* with characters related with cup scales and leaf development, morphology and venation (Schwarz, 1936b). Together with *Q. hartwissiana*, it develops large petioles, and petraeoid leaves. In the original protologue, the author already refers problems of introgression with sympatric *Quercus robur*, assuming that all the plants that he studied were already severely hybridized with the “European” *Quercus robur*. This taxon is considered to be relictual and distributes across the western Iberian Peninsula, especially in thermophilic areas and river basins. Related specimens from Northern Africa (Paris Herbarium – Digital Annex) can also be addressed to this taxon (Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018).

Differential morphological traits: Regular and rhomboidal leaf structure, relative higher number of acute and equal lobes and often absence of sinual nerves, the higher

number of scales, which are large at the base of the cup and becoming smaller towards the apex. It tends to develop large petioles (up to 1 cm) and large peduncles (>10 cm) (Schwarz, 1935; Vila-Viçosa *et al.*, 2014; Vázquez *et al.*, 2018).

Quercus broteroana (=*Q. robur* subsp. *broteroana* O.Schwarz; =*Q. orocantabrica* Rivas Mart., Penas, T.E.Díaz & Llamas)

General information: Taxon immediately described after the publication of *Q. estremadurensis,* where the author defines this new Iberian subspecies as the putative introgressive gradient of *Q. estremadurensis* and the European *Q. robur* L. The author refers leaf, cup-scales and peduncle sizes, as differential for this taxon, with an exclusive Northwestern Iberian distribution and a new biogeographic frontier facing European *Q. robur* in North Leon (Spain) (Schwarz, 1937). In the later European Flora, Schwarz (1964) gives up both *Q. estremadurensis* and *Q. broteroana* after observing convergent characters alongside several European specimens of broad *Q. robur*. Regardless, the insights given about Iberian pedunculate oaks, whereas he finds a higher relative frequency of distinguished morphological characters, are quite pertinent as shown in this work. Advanced nomenclatural treatments should envisage the adoption of *Q. orocantabrica* as valid name for this oak, since it was already validly published as species (Rivas-Martínez *et al.*, 2002) and revealed to be conspecific of *Q. broteroana. Q. orocantabrica* was described as a relict endemic roburoid oak, distributed in high elevation areas from the Cantabrian Mountains, by having a disjunct distribution from *Q. robur* (Rivas-Martínez *et al.*, 2002; Vila-Viçosa *et al.*, 2020a). Regarding differential morphological traits, possesses a larger petiole and larger cups (as in *Q. broteroana*) and has distinguished cup scales (pubescent and reddish).

Differential morphological traits: In comparison to *Q. robur* L., *Q. broteroana* tends to have a thicker and coriaceous blade, with oblong to oblong-transovate shape. Normally the leaves are wider and glossy, with unequal lobes and more then 6(8) secondary nerves, which are often sinual. It has big cups 18-25 mm, with brownish scales, larger and free in the base becoming smaller and merged in the apex cups. It tends to have a bigger petiole and peduncle when in comparison with *Q. robur* (Schwarz, 1937; Rivas-Martínez & Saénz, 1991).

Subsection *Roburoides* (Schwarz, 1936a)

Quercus pauciradiata Penas, Llamas, Pérez Morales & Acedo

General information: Taxon described as another narrow endemic species for León Province. The original description segregates it from the surrounding roburoid oaks, namely *Q. petraea* and *Q. pyrenaica*, by having exclusive fasciculate trichomes that are absent in the former, and distinguishable leaf phenology and morphology from the latter (Penas *et al.*, 1997).

Differential morphological traits: Lobate to pinnatifid leaves, presenting a different foliation period among sympatric oaks (*Q. petraea* and *Q. pyrenaica*), with shorter fasciculate trichomes possessing only 2-4 rays in a “cross-like” shape pattern (Penas *et al.*, 1997).

Subsection *Galliferae* Spach (1842); Gürke (1897)

***Quercus canariensis* Willd.**

General information: is a relictual tree, with five subpopulations in the Iberian Peninsula. In spite of being largely distributed above limestones in North Africa, in the Iberian Peninsula it is related with silicious bedrock, in places with mesophytic conditions. It has a higher demand on annual and summer precipitations in comparison with all *Galliferae* species (Vila-Viçosa *et al.*, 2015; Vila-Viçosa *et al.*, 2020b). It is known to form hybrid swarms with other sympatric oaks like *Quercus faginea* Lam. (*Q. ×marianica* C. Vicioso and *Q. ×tlemcenensis* Trab.) and *Q. pubescens* Willd. (*Q. ×cerrioides* Willk. & Costa) (Battandier & Trabut, 1905; Vicioso, 1950; Vazquez *et al.*, 2020).

Differential morphological traits: Glabrescent leaves obovate or progressively obovate towards the apex, crenate to serrate, sometimes with sinuate-lobulated margin; with short obtuse lobes, acute in young leaves, having a single indumentum of fasciculate-trichomes (sometimes reddish in dryer stations) that can detach, forming a cotton like fuzzy indumentum, mainly in the midrib and secondary veins, which are rectilinear (almost parallel and in higher number (>11)). Absence of stellate trichomes (present in the remaining *Galliferae* species *Quercus faginea* and *Q. lusitanica*) (Willdenow, 1805; Rivas-Martínez & Saénz, 1991). *Q. canariensis* has been a hallmark for conservation in the Iberian Peninsula, being Critically Endangered in Portugal

(Carapeto *et al.*, 2020), and encompassing peculiar Miocene forests with special conservation interest (Ojeda et al., 2000), where we retrieved samples from the three main populations (Monchique, Algeciras and Catalonia).

Quercus faginea Lam.

General information: congregates the concepts of *Q. broteroi* and *Q. faginea*, usually considered as two independent taxa (Franco, 1990; Rivas-Martínez & Saénz, 1991). Following recent reviews of the type material for this taxon, the conclusion that the name formerly ascribed to the Western and Southern Iberian oak as *Q. broteroi* is in fact the original concept of *Q. faginea* (Vazquez *et al.*, 2020). The taxon with North and Northeast distribution that could be considered as different species should be addressed to the concept of *Q. muricata* Palau, as suggested by Villar (1958). This taxon has a broad distribution in submediterranean and Atlantic areas of the Iberian Peninsula and through North Africa up to Algeria, with a preference for base-rich soils, being common in limestone areas with an increased annual or summer precipitation (Vila-Viçosa *et al.*, 2014; Vila-Viçosa *et al.*, 2020a). Anther subspecies addressed to the concept of *Q. alpestris* Boiss (Boissier, 1838) was collected in its typical loci (Serra das Neves) in Southern Spain, to infer about its segregation as a different species of *Q. faginea*.

Differential morphological traits: Oblong to obovate and ovate leaves, with crenate to serrate margin, sometimes denticulate and mucronated; tomentose to pubescent bellow, with stellate and multiradiate trichomes (Lamarck, 1785; Schwarz, 1964).

Quercus lusitanica Lam.

General information: is a dwarf (shrub) oak that occurs in the extreme western areas of Iberian Peninsula with a mostly Atlantic distribution, not tolerating winter cold and with a sub-population in Northern Africa (Morocco).

Differential morphological traits: Shrubs with oblong to obovate and ovate leaves (occasionally lobulated), with flat and almost sessile cuneate leaves with partial entire margin in the proximal third (Lamarck, 1785; Sampaio, 1910; Rivas-Martínez & Saénz, 1991).

Subsection *Dascia* (Kotschy) Schwarz (1936a)

***Quercus pyrenaica* Willd.**

General information: has a wide distribution through the submediterranean and temperate belts of the Iberian Peninsula. Being an edaphic indifferent, it is more common above siliceous bedrock, supporting summer drought in comparison to *Q. broteroana* (Vila-Viçosa et al., 2020a).

Differential morphological traits: Crenate to pinnatifid heavily tomentose leaves, with fasciculate trichomes with >0.5 mm rays.

***Quercus pubescens* Willd.**

General information: has its far west European limit in northeast Iberian Peninsula, in spite of being the most widely distributed oak in Europe. It is a typical temperate species that can occur in submediterranean areas (Vila-Viçosa *et al.*, 2020a), with preference for base-rich soils, and a complex history of infraspecific taxonomic inflation in Southern Europe (Kotschy, 1862; Schwarz, 1964; Pasta *et al.*, 2016). This taxon forms known hybrid swarms either with *Q. faginea* (*Q.* ×*subpyrenaica* Villar), or *Q. canariensis* (*Q.* ×*cerrioides* Willk. & Costa).

Differential morphological traits: Crenate to pinnatilobate leaves, with tomentose nerves and with fasciculate trichomes (<0.3 mm) (Willdenow, 1796; Schwarz, 1936c; Schwarz, 1964).

Hybrids

***Quercus* ×*coutinhoi* Samp.**

General information: was described as a hybrid between *Q. faginea* and *Q. robur*. This was based on several heterogeneous materials retained at the LISU herbarium relating plants earlier described by Coutinho (1888). Most were collected in the Sintra, Caldas da Rainha and Coimbra regions. This hybrid raises concerns on the putative parent species, with both *Q. broteroana* and *Q. estremadurensis* as putative parents. Thus, we used this name for the contact of *Q. faginea* and the subpopulations of *Q. estremadurensis*.

Differential morphological traits: Highly polymorphic taxon, sharing characters of both *Galliferae* and *Robur* Sections (Schwarz, 1936a). Tendentially, the leaves have acute lobes and are glabrescent, with scattered stellate trichomes in the abaxial leaf surface. Short petioles and larger peduncles in face of *Q. faginea* tends to indicate the participation of a broad *Q. robur* oak in the admixture.

***Quercus ×cerrioides* Willk. & Costa**

General information: Taxon originally described for the littoral Catalonian mountains and ascribed to the variation of *Q. pubescens*, adding a leaf shape closer to broad *Q. cerris* Lam. (Willkomm, 1859). For this particular reason, this plant has been traditionally assigned to the putative hybrid between *Q. canariensis* and *Q. ×subpyrenaica*. This is due to the dentate-to-serrate leaf shape, which should include a *Galliferae* species as putative parent, besides the obvious participation of *Q. canariensis* (Rivas-Martínez et al., 1991; Vázquez et al., 2018). However, our study confirms the most probable hypothesis, which is that *Q. pubescens* is the second parent species that participates in the establishment of this nothotaxon. Schwarz (1936c) and Willkomm and Lange (1861) traditionally addresses the name *Q. ×cerrioides* Willk. & Costa to hybrids between *Q. pubescens* and *Q. faginea* (*Q. ×subpyrenaica* Villar), and this still brings nomenclatural confusion and incorrect taxonomic assignment to both taxa in Catalonia and Pre-Pyrenean regions.

Differential morphological traits: Crenate to serrate and lobulated margins, sharing the redish fuzzy indument of *Q. canariensis* (Willkomm, 1859; Schwarz, 1936c) and simultaneously.

Quercus ×duriensis Franco & Vasconcellos (≡*Quercus ×coutinhoi* f. *duriensis* Franco & Vasc.)

General information: This hybrid was originally described by Vasconcellos and Franco (1954) taking in to account the participation of broad *Q. robur* and a recognized variety of *Q. faginea* (*Quercus lusitanica* f. *salicifolia* Cout.) that includes some *Q. faginea* subpopulations from the Douro river basin (Portugal). The type-locations from where this hybrid was originally described concurs with the distribution of *Q. broteroana*. Samples of hybrids with *Q. faginea* were collected in one of these locations, where *Q. broteroana* was also sampled and confirmed through our molecular analysis.

Differential morphological traits: Highly polymorphic (as *Q.* ×*coutinhoi*), has smaller leaves with crenate to lobated margins, showing uneven rounded lobes with glabrescent cuneate leaves, sparse stellate trichomes and short peduncles.

***Quercus* ×*marianica* C.Vicioso** (=*Q.* ×*tlemcenensis* Trab.)

General information: Is mostly distributed in southwest Iberian Peninsula, in areas of mixed stands where *Q. canariensis* lives in sympatry with *Q. faginea*, normally in siliceous bedrock (Vicioso, 1950; Vila-Viçosa *et al.*, 2015).

Differential morphological traits: Lanceolate leaves, either glabrescent with scarce stellate trichomes (*Quercus* ×*marianica* C.Vicioso), or tomentose with both stellate and fuzzy fuzzy-like indumentum of fasciculate trichomes (*Q.* ×*tlemcenensis* Trab.), normally with rectilinear nerves (Battandier & Trabut, 1905; Vicioso, 1950).

***Quercus* ×*subpyrenaica* Villar**

General information: This taxon forms a continuous hybrid swarm in Pre-Pyrenees mountains with *Q. pubescens* and *Q. faginea* as parent species (Villar, 1935; Villar, 1958) and has a typical transitional submediterranean distribution (Himrane *et al.*, 2004; Vila-Viçosa *et al.*, 2020a).

Differential morphological traits: Lobate to dentate and serrate margins, with both stellate and fasciculate trichomes, the former notoriously in the midrib (Villar, 1935; Villar, 1958; Rivas-Martínez & Saénz, 1991).

Supplementary Notes S2. Note on Group A species.

We advocate the need for future in-depth molecular characterization of Group A species distributed across the biogeographical range of Southern Europe. Frequently, these taxa share common characteristics, evidencing intermediate features between *Q. robur* and *Q. petraea.* It is common to assign to *broad robur* oaks the presence of larger and usually pubescent petioles and wider and thicker leaves, typically with a higher number of even lobes (*Q. broteroana, Q. brutia, Q. estremadurensis*, *Q. haas*, *Q. hartwsissiana, Q. imeritina* and *Q. pedunculiflora*). Conversely, *broad petraea* oaks are associated with developed peduncles (*Q. abietum, Q. cedrorum, Q. mannifera*). Sampling of these species should consist of *bona fide* taxonomic representatives collected in type-

populations. Ensuing molecular characterization should help address important aspects on the evolutionary significance of Southern European Peninsulas.

Supplementary Notes S3. Note on natural history insights to oak evolution.

We observe consistencies between the dichotomic monophyly of two segregated Groups (A and B) highlighted in our molecular data analysis, and the important inferences made by Otto Schwarz in his works (Schwarz, 1935; Schwarz, 1936c; Schwarz, 1936a), traditionally considered the major references for the European white oak's taxonomy. Foremost, our obtained phylogeny binds, within Group A, the former Section *Robur* and part of Section *Roburoides* (Series *Sessiliflorae*). It also reflects a close biogeographic segregation of the main Southern European refugia, which includes former Sections *Galliferae* and *Dascia* (Schwarz, 1936a). Species from former Section *Dascia* that were expected to be phylogenetically related, in fact now group within their biogeographically nearest taxa, namely Iberian (*Q. pyrenaica*), Near Eastearn (*Q. kotschyana*) and Anatolian and Caucasian (*Q. vulcanica*) ones. Near Eastern, Anatolian and Caucasian species derive from a well-known hotspot for oak radiation and diversity (Petit *et al.*, 2002; Tarkhnishvili *et al.*, 2012), and were also grouped by Camus (1935) in a common subsection *(Macrantherae*), relating *Q. macranthera* with *Q. frainetto* and *Q. pyrenaica*. Our results reinforce the cohesiveness of this group of species, by highlighting the proximity of *Q. vulcanica* and *Q. macranthera*, with *Q. kotschyana* and *Q. pyrenaica* being similarly resolved by component 1 of the PCA (Figure 5C). Furthermore, Figures 2, 3 and 4 evidenced how *Q. vulcanica* and *Q. kotschyana*, which are morphologically related species (Schwarz, 1936a), fell into cohesive subgroups reflecting their biogeography (*Q. vulcanica* and *Q. boissieri* in the Near East; *Q. kotschyana* and *Q. macranthera* in Anatolia/Caucasus). This suggests either convergent evolution, or a common origin followed by isolation and posterior gene flow with sympatric species. Here, we also highlight the Series *Esculiformes* (Sect. Dascia) described by Schwarz (1936a), and specifically *Q. macranthera*, as a taxon that congregates intermediate morphological characters with all Group B species, suggestive of the Caucasian area as a putative hotspot or centre of origin for the Group B species (Douaihy *et al.*, 2020).

In addition, the biogeographic relationship of the taxa traditionally ascribed to the Section *Galliferae* is addressed in our study. All analyses reflect the proximity among Series *Orientales* (*Q. canariensis and Q. boissieri*) (Schwarz, 1936a), by sharing the same fuzzy indumentum of fasciculate trichomes and leaf morphological resemblances, as a

notorious case of biogeographic vicariance between east and west Mediterranean areas (Humphries *et al.*, 2017). Also, Series *Lanuginosae* (*Q. pubescens*) was accurately circumscribed and included in the Section *Dascia* by Schwarz (1936c), relating *Q. pubescens* as a putatively older taxa formed by an ancient hybrid swarm, since it aggregates characters of several species it contacted with (e.g. *Q. faginea, Q. canariensis, Q. boissieri* and *Q. petraea*), and with whom it shares biogeographic affinities and sympatry across submediterranean areas of Southern Europe (Pasta *et al.*, 2016). This relationship is also reenforced by the Northeastern Iberia *Q. ×cerroides* hybrid swarm, relating extensive introgression among *Q. pubescens* and *Q. canariensis*. This is a novel output from our study, since *Q. ×cerroides* was traditionally ascribed to the cross between *Q. ×subpyrenaica* and *Q. canariensis* (which inappropriately attributed the participation of *Q. faginea* in the admixture) (Rivas-Martínez & Saénz, 1991; Rivas-Martínez *et al.*, 2002).

All these arguments (natural history and molecular data) favor the circumscription of two subsections inside *Section Quercus*. One aggregates all temperate roburoid oaks, which include former Sections *Robur* and *Roburoids*, the other aggregates former Sections *Galliferae* and *Dascia* (Schwarz, 1936a). This analysis urges deeper intraspecific studies in order to infer on its evolutionary and phylogeographic history and putative introgression legacy, based on a wide geographic coverage, plus sample collection in type populations, neighbor areas, and known hybrid swarms retrieved from grey historical literature. Looking back, Schwarz's natural history contributions were of outstanding value, to infer and serve as a basis for the Eurasian White-Oaks evolutionary history and were done by solely studying herbaria vouchers. This enhances the necessity to keep on studying natural history and classic collections, as a way to provide new clues on oak biogeography and evolutionary history, properly complemented by novel genome-level molecular studies.

Chapter 8.

General discussion, concluding remarks and future perspectives

8.1. General discussion

The scientific advances and knowledge update incorporated into the present thesis comprise a set of six studies that aimed to advance our fundamental and applied knowledge about the genus *Quercus* in the Mediterranean Basin, its species assessment, patterns, and evolutionary trends. These studies were complementary, and all fed a final model that was established by three transversal areas of this challenging plant genus (Figure 1). Although each section represents specific areas of knowledge in the Biological and Ecological Sciences, the original research plan addressed distinct cross-level interconnections, enabling a holistic approach to address pressing taxonomic-specific knowledge gaps from Ecosystems to Genes.

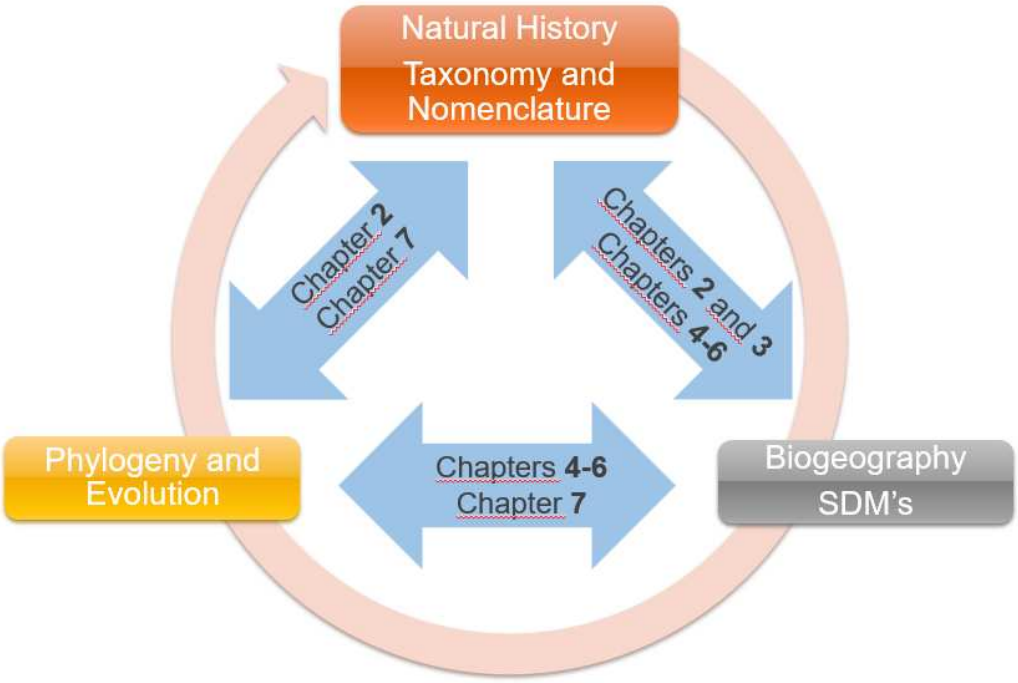


Figure 1 – Schematic representation summarizing thesis chapters interdependence with three key topics.

This research aimed to integrate the information retrieved from Natural History data sources to inform species distribution models that predicted past and future changes in oak distribution patterns and to test evolutionary hypothesis on the drivers and patterns that underlie speciation patterns of complex genus. By doing so, this sutdy improves the current knowledge on the Iberian oaks' taxonomy and the ecological drivers that shape

their actual and future distributions. In this context, our ultimate goal was to provide guidance to practitioners committed to conservation of highly threatened Mediterranean forests, supported by the integration of taxonomic, biogeographic and evolutionary tools. This section presents a summary of research contributions from Chapters 2 to 7, followed by a broader synthesis of the holistic contributions of this thesis under the three vectors of Natural History and Taxonomy, Biogeography and Ecological Modelling, and Phylogenomics and Evolution.

8.1.1. Species delimitation and nomenclatural update of Mediterranean Oaks

Species are the fundamental units for the study and conservation of biodiversity and historical biogeography on Earth (Mayr, 1982; De Queiroz, 2005; Hohenegger, 2014). In oaks, establishing species limits has been an historically challenging task for botanists (Burger, 1975; Van Valen, 1976). Final proposals for the most coherently possible species' limit are a major task for conservationists and taxonomists to tackle, as well as to understand the underneath evolutionary processes that led to a species or population to occur in a given area. Species delimitation is particularly important when in the presence of a biodiversity hot spot like the Mediterranean Basin. Thus, the present work shed light on the controversial species limits among the Iberian white oaks brought up by multiple authors (Axelrod, 1983; Medail & Quezel, 1997; Olalde *et al.*, 2002; Valladares *et al.*, 2014; Dernegi, 2017; Médail & Baumel, 2018; Médail *et al.*, 2019; Buira *et al.*, 2021). Also, this work highlighted the role of the Iberian Peninsula as a biogeographic landmark and phylogeographic hot spot across the Western Palearctic region, especially on the circummediterranean context.

We dedicated two works of nomenclatural and taxonomic revision and update (**Section A** with **Chapters 2** and **3**), where the first simultaneously nourished and was fed by the molecular analysis, regarding the white oaks subset of species (**Chapter 7**). Hence, a necessary overview and full nomenclatural update of the Portuguese oaks was provided (**Chapter 2**), with insights to a considerable part of the Western Mediterranean oak forests. This was performed after thorough herbaria and literature review and complemented with extensive fieldwork across the Iberian Peninsula for almost a decade. This work upgraded the number of species and nothotaxa in the country and updated their synonym lists with regards to 11 oaks and 23 hybrids. Five of these hybrids became new or renamed to science. We highlighted and commented on relevant type specimens that simultaneously reduced the existing nomenclatural inflation and

inaccurate naming-attribution to disaccording taxa. These were previously ascribed as different species or hybrids, immersing most taxonomic designations in a thread of speculative assignments at both the specific and infraspecific ranks, which were here consistently resolved. The paradigmatic example comes from the kermes oaks (*Q. coccifera* s.l.), which were decomposed in each vicariant taxon across the East-to-West gradient in the Mediterranean Basin, relating *Q. calliprinos* with *Q. pseudococcifera* and *Q. airensis* with *Q. aucherii,* and solving the nomenclatural conundrum among taxa (see **Section A, Chapter 2**). Essentially, **Section A** brought important insights to future scientific questioning trough phylo or population genomics, not only for the circummediterranean white oaks but also about Section *Ilex* across the Mediterranean Basin. In this sense, **Chapter 3** brought species-specific novelties and also synonym update, especially to the Northern African oaks, reinstating *Q. ilex* L. to the Algerian Atlas, unknown to the African continent until now, and addressing the correct name for the western Mediterranean arboreal kermes oak (*Q. pseudococcifera*), firstly described by Desfontaines (1799). Also, the name *Q. pseudosuber* that was erroneously enrolled in the concept of *Q.* ×*crenata* L. and *Q.* ×*hispanica* Lam. was synonymized to *Q. faginea*, since it brought past confusion around the putative hybridization of *Q. faginea* and *Q. suber* (Linnaeus, 1753; Colmeiro & Boutelou, 1854; Vicioso, 1950; Cristofolini *et al.*, 2017; Vázquez *et al.*, 2018). This chapter (**Chapter 3**) brought important insights to species delimitation that will contribute for oak forests conservation.

8.1.2. Biogeography and conservation of Mediterranean white oaks

Forest ecosystems are crucial ecosystems that are currently targeted in United Nations' Decade on Ecosystems Restoration for restauration (Cruz-Alonso *et al.*, 2019; Mansuy *et al.*, 2022; United Nations & FAO, 2022). Specifically, the biome that includes all Mediterranean forests is considered the second most important reservoir of plant diversity in the extra-tropical realm (Cody, 1986; Medail & Quezel, 1997; Mittermeier *et al.*, 2011; Valladares *et al.*, 2014). Its forest species, namely trees, hold a high value in terms of conservation, especially for providing crucial ecosystems services and importance for humanity (Quézel, 1976; 1985; Quézel *et al.*, 1999; Marañón *et al.*, 2012; Mori *et al.*, 2017; Médail *et al.*, 2019). These forests are predicted to be severely knocked by climate change, emerging as the terrestrial biome with heavier projected proportional biodiversity loss until 2100 (Sala *et al.*, 2001; Ellison *et al.*, 2005; Klausmeyer & Shaw, 2009; Acharya *et al.*, 2019). These changes are mainly related to increased maximum summer temperatures and decreased precipitation associated with extreme events that

will increase Mediterranean forests susceptibility (Cramer *et al.*, 2018; Margalef-Marrase *et al.*, 2020; Allan *et al.*, 2021; Lloret *et al.*, 2022). The way how vulnerable tree species will respond to these changes is an unsolved question. This effort demands the usage of SDMs (among other modelling tools) to define species niches and how it varies across the geographical space, hypothesizing about species' past and future range dynamics allowing to anticipate future biodiversity losses driven by climate change (Wiens & Graham, 2005; Svenning *et al.*, 2011; Fordham *et al.*, 2016).

Section B linked biogeographical analysis with conservation. In **Chapter 4** we developed a framework that intended to depict how the ecotone projected by marcescent forests, which borders the major European regions (Eurosiberian and Mediterranean), has changed across the late quaternary period. For that, we combined presence records of eight marcescent oaks (including two hybrids) with bioclimatic and topographic predictors and obtained spatial projections for current and past conditions for all taxa. We observed that precipitation, winter cold and ruggedness were the most important variables to explain the substantial changes and refugia for most of the studied white oaks. The analysis of both submediterranean and temperate oaks and their hybrids across the two subsections obtained in this thesis (**Chapters 1 and 7**) matched important past contact between parents and nowadays existence of hybrid swarms. For example, results obtained for the hybrid swarms between *Q. faginea* and broad *robur* oaks matched ancient contact of nowadays known populations of *Q.* ×*coutinhoi* and *Q.* ×*duriensis*. On the other hand, model projections for *Q. orocantabrica* (=*Q. broteroana*) and *Q. estremadurensis* highlighted disjunct distributions in the past and helped to postulate species delimitation hypotheses, further scrutinized in **Chapter 7**. Also, the LGM projections of nowadays segregated populations of *Q. canariensis* that share similar floristic casts were highlighted in this work in areas that kept higher summer rainfall in Atlantic areas, that served as important refugia (Vila-Viçosa *et al.*, 2015). These results emphasize *Q. canariensis* and *Q. estremadurensis* as target species to be considered in future conservation efforts of Iberian Oaks. Globally this chapter improved our knowledge about species' responses to climatic dynamics, which allows us to anticipate potential range shifts due to climatic worsening projections.

Consequently, **Section B**'s **Chapter 5** aimed to construct the next logical step and consider the future dynamics of marcescent oaks using a dominant conservationist perspective, which was done in view of their past range shifts. Here, the questioning on how correlated the past projections with future scenarios could be, established by a "back-to-the-future" framework, finally extended to the entire Mediterranean basin. For

that purpose, we also applied SDMs to eight marcescent oaks (four western Mediterranean distributed species and four eastern Mediterranean distributed ones), considering six past periods from 17.0 to 0.3 ka, current climate conditions, and future climatic scenarios (2070 and 2100). We then compared past and future range shifts through linear regression to latitude and longitude shifts, relative area loss and total change (accounting for gains and losses) of climatically suitable areas. In this study, we also hypothesized that worst past periods, related to extreme cold or drought and the abrupt climatic shifts that these species endured then, could be more correlated with the expected future worsening scenarios, also related to dryer periods.

Results show that precipitation predictors had overall higher contributions for all species, with a clear positive correlation between past and future range dynamics. This correlation is predominantly higher for the eastern subset of species that present a higher correlation in the amelioration periods (BA and Holocene) with future trends than western distributed oaks. Also, eastern oaks tend to have higher correlations to past periods in the most extreme climate change scenarios (SSP 370 and 585) and higher loss percentages between past and future periods/scenarios. This study highlights the relevance of changes in precipitation regimes (past and future) and how these will affect this particular group of oaks, demanding conservation measures directed to particular species, such as *Q. canariensis, Q. kotschyana, Q. lusitanica* and *Q. vulcanica*. Moreover, the study revamped the remarkable biogeographic vicariance observed between species and groups of species (Humphries *et al.*, 2017), namely *Q. boissieri* and *Q. canariensis* in the former subsection *Galliferae* and *Q. vulcanica* with *Q. kotschyana* in former Section *Dascia*. This output was observable when comparing the climatic variables contributions of the first group (*Q. boissieri* vs. *Q. canariensis*) and the overlap of their individual projected distributions in the obtained maps (**Chapter 5** - Supplementary Information SM – Digital Annex). This pattern that relates to a notorious “amphi-Mediterranean” biogeographic outline, where several lineages are distributed at both extremes of the longitudinal axis of the Mediterranean basin, with well-known gap-occurrences in between (Willkomm, 1896; Lumaret & Lobo, 1996; Nieto-Feliner, 2014). Meanwhile, our obtained projections suggest niche conservatism of environmental conditions, offering further scientific questioning or complementing phylogenomic hypotheses about subsection *Macrantherae* (**Chapters 2 and 7**).

Finally, **Chapter 5**’s projected future scenarios that evidence significant losses in suitable area and vast range shifts for vulnerable oaks, highlights these species as priority

conservation targets, with imperative conservation status review at the IUCN level (Carrero *et al.*, 2020). Since they broadly present already narrowly distributed and reduced populations, or concurrently evidence projected range shifts to areas far departed from their native range, these cannot reach them naturally, thus demanding human and conservation planning efforts. Overall, **Chapter 5** binds together all the sections outlined in this thesis by accurately congregating and resuming information from natural history and biogeography, which allows further evolutionary questioning around the circummediterranean white oaks, with significant insights for future forest conservation.

In **Section B**'s **Chapter 6**, we addressed another conservation framework by exploring the combination of climatic variables with satellite-based EFAs in SDMs, to assess how ecosystem functioning predictors may improve the knowledge of oaks potential distribution and ecological requirements to unveil the best suitable areas to preserve the Iberian white oaks. As a complement to classic SDMs approaches that consider common environmental predictors like temperature, rainfall, soil type or vegetation cover, other relevant features of ecosystems functioning like primary productivity, evapotranspiration, land surface temperature or albedo also encompass several dimensions that include carbon gains or water and energy balance (Alcaraz-Segura *et al.*, 2017; Arenas-Castro *et al.*, 2018; Arenas-Castro *et al.*, 2019). We targeted 13 oaks (including hybrids) distributed across two subsets of narrow endemics and broad distributed taxa. The results and discussion revealed that models combining EFAs and climate variables had higher predictive performance than EFAs or climate alone, whereas narrow endemic oaks obtained higher predictive performance in combined models than widespread oaks. Precipitation and seasonal water availability (NDWI) appear as the best predictors in each climate or EFAs, highlighting the water-dependence of the Iberian white oaks, especially in the dry season, when intermixed in altered landscape mosaics. Herein the related EFAs were found suitable to depict areas with higher humidity levels, linked with higher primary production and seasonal water availability. This result revealed to be particularly important for the two narrow endemics *Q. canariensis* and *Q. estremadurensis*, preserved in relictual Atlantic areas, or areas with available summer rainfall (Ward, 1952; Wheeler, 2001; Vila-Viçosa *et al.*, 2015; Soriano & Costa, 2017) (See **Chapter 4**).

Additionally, the combined climate-EFA models allowed us to identify the hotspots with higher white oak diversity by holding higher cumulative habitat suitability and species richness, fostering smart geographic planning for conservation measures. These areas

encompass the Iberian Southwest mountains, the Lusitanian Basin, Montes de Toledo, the Penibaetic System and the sub-littoral Catalonian mountains. Results highlight highlight the importance of these highly relevant biogeographic areas as a home for several known hybrid swarms like *Q.* ×*cerrioides, Q.* ×*coutinhoi*. *Q.* ×*subpyrenaica, Q.* ×*tlemcenensis (*=*Q.* ×*marianica*) (See **Chapter 7**), retrieved by SDMs and enhancing the bio and phylogeographic questioning carried out in this thesis.

8.1.3. Molecular phylogeny and evolution of Iberian white-oaks

After both natural history and biogeographical approaches, the yet-to-solve species delimitation of the Iberian white oaks demanded an urgent molecular essay that could provide new insights at the macro and microevolutionary scales. As mentioned, the implemented conundrum around species name and taxonomic ranking emerges as a natural history artifact (See **Chapters 2 and 3**). In order to address species nomenclatural validity and scrutinize the role of introgression on traditionally assigned hybrid swarms, **Chapter7** was directed towards the implementation of a RADSeq characterization of 38 taxa that included most of the circummediterranean white oaks, albeit with a preferable sampling of Iberian taxa and nothotaxa. This study enabled a desired infrasectional resolution among the western Paleartic white oaks (Denk *et al.*, 2017). Results resolved two major groups. One group (Group B) contains the main subset of species that were initially the focus of this work, related with the submediterranean marcescent oaks (Subsection *Macrantherae*) that were included in Section *Dascia* and *Galliferae* by traditional authors (Gürke, 1897; Schwarz, 1936a; Tschan & Denk, 2012). The second group (Group A) contains the typical temperate and Atlantic distributed oaks. Results evidenced new relationships inside the subsection (*Hartwissianae*) that grouped broad *Q. robur* and broad *Q. petraea* oaks. Both these groups (A and B) resulted in newly circumscribed subsections that were respectively formalized in **Chapter 2** whilst taking into consideration the existence of previous proposals (Maleev, 1935).

Chapter 7 provided additional important insights. Group A (subsection *Hartwissianae*) revealed high differentiation from the European pedunculate and sessile oaks (broad *robur* and broad *petraea*), with the emergence of both *Q. orocantabrica* (=*Q. broteroana*) and *Q. estremadurensis* as noteworthy taxa inside the evolutionary timeline of broad *Q. robur*. These two taxa previously segregated by Schwarz (1935; 1937) may consist of past populational expansion and contraction events, which left a mark on these sister

species at the end of the Tertiary and during the Quaternary periods (Schwarz, 1935; Vicioso, 1950; Montserrat, 1957; Olalde *et al.*, 2002). Results also suggest a relation between *Q. estremadurensis* and *Q. petraea* that is accompanied by shared morphological features, which may unveil putative ancestry inside this temperate oaks' lineage. Also *Q. pauciradiata* evidenced noticeable divergence inside the broad *Q. petraea* clade, showing again a notorious divergence between Iberian oaks inside Subsection *Hartwissianae* and the remaining European oaks from the same group. This includes all the deciduous to brevi-deciduous trees, with subsessile to long petiolate leaves and lobate to lobulate margins. Normally, leaves have vestigial intercalary nerves, seldom with tertiary ones that are subparallel to each other and coarsely and regularly reticulate. A major character is that they often possess glabrous to glabrescent or pubescent leaves and twigs (**Chapter 2**). Beside the most common *Q. robur* and *Q. petraea*, this subsection includes the southern distributed oaks related with them like *Q. brutia, Q. dalechampii*, *Q. haas*, *Q. huguetiana*, *Q. iberica*, *Q. imeretina*, *Q. pedunculiflora*, *Q. petraea* and *Q. pinnatiloba*.

As for the oak trees from Group B (subsection *Macrantherae*), they possess brevi-deciduous or marcescent leaves, with crenate or ± deeply lobed to pinnatifid margins, that can become toothed or crenate. Often, they possess divaricate and irregular secondary nerves, with pubescent to tomentose abaxial leaf surfaces composed of a tomentum with simple, stellate, multistellate or fasciculate trichomes. An important character to segregate them from oaks belonging to Section *Cerris* (ex: *Q. cerris* L.) is that their cups have small and normally fat or gibbose scales (sometimes flat), always appressed and never free or loosely imbricated and long. These oaks are commonly distributed across the borders between Temperate and Mediterranean biomes, i.e. the transition between Euro-Siberian and the Mediterranean or Irano-Turanian Regions, namely across southern Europe, North Africa, and Near East, and reaching the Transcaucasus and Iran (Zagros) (Rivas Martínez *et al.*, 2011; Rivas-Martínez *et al.*, 2017). Conversely, subsection *Hartwissianae* comprises oaks that need an increased annual and especially summer rainfall, and are dominantly distributed across the Temperate bioclimatic belt, albeit preserved in Atlantic or Tertiary paleoclimatic refugia inside the submediterranean ecotone across southern European Peninsulas (Svenning, 2003; Rodrıguez-Sánchez & Arroyo, 2011; Costa *et al.*, 2015; García-Mijangos *et al.*, 2015).

Our analysis suggests solutions for doubtful past relationships between both groups/subsections, and generically speaking between southern-distributed oak

populations against northern-driven temperate ones. For example, it positioned *Q. pubescens* in Subsection *Macrantherae*, solving its questionable phylogenetic relation with broad *Q. petraea*, which was an ancient interrogation associated with the Palearctic white oaks, due to *Q. pubescens*' morphological resemblance to the broad sessile oaks (See **Chapter 7**) (Fortini *et al.*, 2015; Pasta *et al.*, 2016; Martínez & Llamas, 2022).

The pervasive hybridization, especially among Group B oaks (subsection *Macrantherae*) was sustained by the transitional positioning of hybrids between their putative parents, validating and redesigning classic taxonomic inferences (Schwarz, 1936a; Vicioso, 1950; Villar, 1958; Schwarz, 1964; Rivas-Martínez & Saénz, 1991; Vila-Viçosa *et al.*, 2014). These included *Q.* ×*cerrioides, Q.* ×*coutinhoi*. *Q.* ×*subpyrenaica, Q.* ×*tlemcenensis (=Q.* ×*marianica*) and the hybrid between *Q. faginea* and *Q. pyrenaica* (*Q.* ×*alentejana,* See **Chapter 2**). Also, the hybrid swarms between *Q. faginea* and the roburoid *Q. orcantabrica* (=*Q. broteroana*) and *Q. estremadurensis* were highlighted in the analysis as the only relating hybridization among both subsections (*Hartwissianae* and *Macrantherae*).

At the end, the positioning of the circummediterranean white oaks also complemented the analysis from **Chapter 5**, where the vicariance relations between *Q. boissieri* and *Q. canariensis* and the subset of species of former Section *Dascia* (*Q. frainetto, Q. kotschyana, Q. vulcanica*) emerge as intriguing in **Chapter 7**'s phylogenetic trees, PCA and NeighborNet, often suggesting these species as being close to the tentatively older *Q. pubescens* (Schwarz, 1936b). Finally, this final study enhanced the importance of the Iberian white oak syngameon as a major hotspot for oak conservation. We greatly advanced the knowledge about species delimitation trough phylogenomic backbone resolution, by assessing the Western European white oaks' evolutionary history. Furthermore, we fostered innovative conservation approaches, when looking at the paleo-biogeographic history of European white oaks and particularly the role of Southern European Peninsulas as reservoirs for elusive oak diversity, with major insights into the evolutionary history of the vital trees that rule the circummediterranean forests.

8.2. Concluding remarks

Based on a holistic framework that include different areas of biological sciences, this thesis aimed to improve the knowledge about one of the most paradigmatic genera of woody plants worldwide. From the methodological viewpoint, three complementary

areas of knowledge were used to access the genus *Quercus* in the western Mediterranean subregion: Natural History, Biogeography and Evolution.

Section A reinstated the value of preserving scientific collections and the in-situ study of type specimens, complemented by historical and literature review to improve the awareness about discernible morphological plasticity and its geographical and ecological variation. Hence, distinctive characters that are commonly ascribed to a given taxon can posthumously change its established status once they are detected across the geographic space. That is to say, one can use a name and address it to a given taxon, but the type-specimen proves it to be wrongly assigned. These errors can be perpetuated for decades and hamper all downstream works related with phylogenetic backbone resolution, along with further conservation efforts that might be dedicated to oak forest conservation. Thus, natural history and extensive herbaria reviewing become mandatory steps for any kind of evolutionary study, particularly when they entail difficult groups of plants and species syngameons.

A more consistent and accurate species identification and delimitation framework also became crucial for exercising species distribution models (**Section B**), which allowed the capturing of the realized niche of each oak taxa. This provided more accurate and conservative hindcasts, with insights to recent demographic range-shifts of given species, and forecasts that foresee the conservation of vulnerable oaks when facing climate change. Our niche-modelling approaches demonstrated the suitability of oaks as model species to undergo paleobiogeographic assessments, with insights into their demographic and evolutionary history.

The decision-making at the species-level solely based on traditional morphological or genetic data alone is potentially problematic. None the less, our taxonomic and biogeographic awareness developed upon the Iberian white oaks (**Sections A and B**), strongly favoured the ensuing molecular analysis presented in the current work (**Sections C**). Here, we acknowledge the need for reduced-representation and/or full genome-level molecular analysis of oak diversity. In this context, RADSeq strategies have been amply used by the Quercus community to resolve the phylogenetic backbone of worldwide oak species. As such, this was the molecular strategy we resorted to. Our results strengthened the phylogenetic backbone resolution of the Iberian white oaks, by adding a considerable set of samples to previous RADSeq efforts. We were able to unveil a much needed infrasectional resolution that highlighted two subsections inside section *Quercus*. These results provided insights to both macro and microevolutionary processes in the circummediterranean white oaks, and their reciprocal contributions for

shaping the evolutionary history and success of the Roburoid oaks across the Temperate Northern Hemisphere. This effort was achieved by scrutinizing a fundamental piece of the puzzle provided by circummediterranean white oaks, especially by focusing on this southern European Peninsula, whose biogeographic positioning discloses an outstanding diversity among the western Palearctic white oaks.

We suggest that similar bioclimatic envelopes and thresholds (i.e. niche conservatism), may have played a major role in preserving species and clades, and even species inside clades, at the evolutionary scale. This is noteworthy for the relationships presented inside subsection *Macrantherae* between former *Galliferae* oaks like *Q. boissieri* and *Q. canariensis*, which present an amphi-mediterranean vicariance among their forests (see **Chapter 5**). Also of note worth are the morphological, climatic, and molecular resemblances presented by former *Dascia'* oaks, like the ones that *Q. pubescens* has with *Q. vulcanica, Q. kotschyana* and *Q. pyrenaica*, with the latter growing predominantly in acidic bedrock, contrarily to the previous ones that thrive in base-rich soils. This last group of oaks presents a disjoint positioning in the phylogenetic trees, grouping among its biogeographic related species, which may evidence past splits followed by gene-flow with close sympatric oaks belonging to the same subsection (*Macrantherae*) (See **Chapters 5** and **7**).

We advocate that the biogeographic processes *per se* are potentially the major drivers of speciation, and it is by understanding the underlying vicariance among edaphoclimatic envelopes and how they vary across time and space that we may infer about the persistence of (older) genotypes, which dispersed across past climatically homogenous conditions. Such conditions were likely posthumously disrupted by abrupt climate change, while the representatives inside the same lineage got retained within edaphoclimatic islands that preserved similar conditions to the preterit geographically continuous ecological ones. These abrupt climate changes were most likely driven by alterations in precipitation cycles (annual rainfall and seasonality), with additional topographic mediated compensations in water availability. Winter cold may have played, to a lesser extent, an important role for submediterranean oaks, which preserved marcescent behaviour in transitional areas towards the mediterranean climate. The relatively modern submediterranean ecotone, which mimics a subtropical environment with an ample amount of warmth and lower seasonality in precipitation during the grow season, may have promoted the prevalence of Subsection *Macrantherae* species across southern Europe, North Africa, and the Near East. We hypothesize the survival of ancestral phenotypes and older or less-evolved genotypes (ex: *Q. boissieri* and *Q.*

canariensis), while the remnant oaks adapted to growing totally Mediterranean climates or radiated into fully temperate regions (underwent niching). We envisage that the present work's historical biogeography of the circummediterranean white oaks is determined by chronological sequences of taxa (evolutionary snapshots), inside the same lineage or clade, that got retained in vicariant edaphoclimatic envelopes, from which past contact was disrupted by abrupt climate change.

Broadly, we advanced the current knowledge concerning western Mediterranean oak species and oak forest biogeography, focusing on the Iberian phylogeographic hotspot. These advances and methodological approaches can serve as models to be replicated across all circummediterranean forests. They may focus on several other hotspots (Anatolia, Balkans, Caucasus, Mediterranean Islands, Near East, North African Atlas), in order to better serve species delimitation, applied to conservation efforts and decision making in such an important Biome: the Mediterranean forests, woodlands and scrub.

8.3. Future perspectives

8.3.1. Integrating remotely-sensed Earth Observations in Taxonomy and Phylogenomics

Recent developments in Earth Observation technologies, particularly imaging spectroscopy, allow depicting plant functional traits and diversity at unprecedented spatial scales. Binding information about leaf structure and chemistry and how it fits evolutionary models can be applied to unveil fundamental links between leaf spectra and the Tree of Life in oaks. In this sense, hyperspectral data from field spectroradiometers can be used for accurate taxonomic classification and species-specific detection. Here, leaf-level spectral data can be coupled with phylogenomic data to differentiate among species or inside oak populations. Such a task could also be approached by hyperspectral satellite missions such as PRISMA or EnMAP or even by using the fine spatial resolution of multispectral missions such as Sentinel-2. Such data would allow the detection of rare and narrow endemic oaks with benefits for characterizing population-level attributes and targeting their conservation. At the Iberian level, *Q. canariensis* and *Q. estremadurensis* could be depicted in broader biogeographic areas, isolated populations, or even isolated trees among *Q. faginea* forests.

Also, new Light detection and ranging (LiDAR) missions (such as GEDI), terrestrial laser scanning (TLS) and radar satellites (such as Sentinel-1) have been increasingly used to assess forest structure and quantify forest biomass due to their ability to provide high-

resolution, three-dimensional (3D) information about the forest canopy. The 3D point clouds obtained from LiDAR can be used to extract various measures of forest structure, including tree height, crown diameter, and canopy cover. LiDAR also offers an alternative, remote sensing-based approach for measuring forest structure and biomass, which can be faster, more cost-effective, and more accurate than field-based methods. New missions launched until the end of the decade, and new sensors will provide accessible and more affordable data.

Plant health can be affected by various factors, including droughts, pests, diseases, and nutrient deficiencies, among other environmental stressors. Traditional methods for assessing plant health, such as field-based observations and laboratory analyses, are often time-consuming, labour-intensive, and have limited spatial coverage. As such, satellite remotely-sensed Earth observations offer an alternative approach to assess plant health, which can be more efficient, cost-effective, and spatially extensive. Time series of satellite images are also employed for assessing forest stability, disturbance, and overall status, which can provide valuable information for managing vulnerable oak species and their habitats. Among other aspects, satellite remote sensing time series can also capture several features of ecosystem functioning across multiple spatial and temporal scales. These aspects are linked with primary productivity, evapotranspiration, land surface temperature or albedo, and relate to several ecosystemic dimensions like carbon gains, water content and energy balance. Data on surface phenology extracted from satellites can also provide a deeper understanding of the dynamics and timing of ecosystems and gather insights into the impacts of climate change. In addition, multiband thermal imagers and new imagers that measure chlorophyll fluorescence provide unprecedented information about plant and ecosystem functioning, composition and species response to stress.

All these tools can support evolutionary exploration and test the influence of biogeographic legacies on ecosystems by assessing the level of spectral variation at several scales, from individual plants to ecosystems. These examples demonstrate the potential of remote sensing for ecological applications as well as for assessing genetic and phylogenetic diversity.

8.3.2. Further biogeographic and phylogenomic targeting on Mediterranean Oaks

This work shed light onto critical biogeographic areas for taxonomic, phylogenomic and population genetics questioning around the evolutionary history of Mediterranean Oaks.

In this sense, we have chosen a group of taxonomic groups and biogeographic areas that may become the subject of choice for future studies, particularly with regards to in-depth molecular characterization of population genomics and phylogenetic backbones. Future work on circummediterranean oaks phylogeny should target both taxonomic-specific and biogeographic approaches. The taxonomic-directed approach should address the white oaks at the subsection level, where phylogenomics could solve the macro-evolutionary processes inside both subsections, then population genomics should solve species syngameons and introgression issues between the former resolved species. Examples are the southern European oaks belonging to subsection *Hartwissianae,* especially the potential ancestor relationships from Iberian species among European *Q. robur* (*Q. estremadurensis* and *Q. orocantabrica*) and *Q. petraea* (*Q. pauciradiata* and *Q. huguetiana*). All the circummediterranean subsection *Macrantherae* should be targeted to unveil species-relationships, namely around *Q. pubescens* and the vicariants *Q. frainetto, Q. pyrenaica, Q. kotschyana* and *Q. vulcanica* or *Q. boissieri*, with the Iberian *Q. canariensis, Q. faginea* and *Q. lusitanica* (**Chapters 2** and **7**). Analysis should also address Subgenus *Cerris,* with a wide range review of both Sections *Cerris* and *Ilex.* The biogeographic-directed approach should target the know Mediterranean hotspots (Médail & Baumel, 2018). First, the spotted areas unveiled in this thesis like the Littoral Catalonian Mountains, the Iberian Southwest and the Lusitanian Basin, together with the Pyrenees mountains should be scrutinized, to unveil species syngameons and introgression among different oak species. The North African Atlas would allow to complete all analysis around *Q. canariensis* and *Q. faginea*. They could extend to the Near East and depict relations with *Q. boissieri* and all Section *Ilex.* The remaining southern European Peninsulas are also fundamental for solving Section *Cerris* and both Subsections *Macrantherae* and *Hartwissianae* (**Chapters 2** and **7**).

8.3.3. Future genomic approaches to Mediterranean Oaks

The previous section (8.3.2.) highlights several res earch questions that require the incorporation of genomics data for further resolution, either as a stand-alone approach or in combination with biogeographic analysis. Here, we provide a broad overview on how oak biology might be shaped by the fast-paced developments in plant genomics.

As stated previously, many recent molecular studies have been carried out using reduced representation strategies, and particularly RADSeq, to tackle issues related with population, landscape genomics or global phylogenies, amongst others. Interestingly,

RADSeq studies (including the present effort) have been established with mostly the same technical platform (FLORAGENEX) and the same *Pst* I restriction enzyme digestion. This may enable, in the future, the meta re-use of RADSeq data to address further issues. Briefly, we suggest two interesting paths. The first pertains to a reassessment of the global oak phylogeny, as carried out previously (Hipp *et al.*, 2020), this time complemented with the additional sampling provided by our dataset. This should help further resolve section Quercus. Second, we see the potential for cross-comparison of biogeographic-common assemblages, namely the ecologically Mediterranean oaks of the Mediterranean basin versus the Californian oaks, considering the existence of fairly overlapping datasets of the former (present study) and the latter (Kim *et al.*, 2018). Such a study would be particularly timely given the known susceptibility of the Mediterranean areas to climate change (Cramer *et al.*, 2018; Allan *et al.*, 2021).

We envisage that the field of oak genomics should move beyond reduced representation strategies towards the use of full genomic sequence information. There are already several quality *De novo* genomes within *Quercus* and advances in long-read sequencing technologies, spearheaded by PacBio Hi-FI technology, along with advances in algorithms for sequence assembly, should rapidly increase the number of *De novo* genomes associated with Oaks. Currently they include taxa such as *Q. lobata, Q. mongolica, Q. robur, Q. rotundifolia, Q. suber*, *Q. acutissima* (Sork *et al.*, 2016; Plomion *et al.*, 2018; Ramos *et al.*, 2018; Ai *et al.*, 2022; Fu *et al.*, 2022; Rey *et al.*, 2022). The near saturation of representative genomes across the *Quercus* genus should be sought, as it would minimize the bias associated with the lack of proximal reference genomes in population and adaptation level studies. It would also be interesting to tackle comparative genomics within the genus, namely by checking whether expansion or contraction of genes families may correlate with adaptative or ecological characteristics of certain oaks. Immediately, we envisage the need for representative species from sections *Virentes*, *Protobalanus* and *Ponticae*, and advocate the need for thorough infrasectional sampling, including species with narrow distributions or related to peculiar climatic envelopes inside each clade. For example, our infrasectional resolution highlights the need to develop a quality *De novo* genome inside subsection *Macrantherae* directed to target species like the potential carrier of ancient genomic stock *Q. macranthera*, or narrowly distributed and endangered species like *Q. canariensis, Q. lusitanica, Q. kotschyana* or *Q. vulcanica.*

De novo genome availability should impact massively on whole genome resequencing (WGS) approaches, in which shotgun short-read sequencing data is mapped onto these reference genomes. As stated, the vast taxonomic coverage of complete genomes will improve the quality of the WGS strategies and diminish associated bias. Already we witness the increasing availability of high-profile genomic studies that make use of WGS approaches (Gailing et al., 2021; Gugger et al., 2021; Zhou et al., 2021; Fu et al., 2022; Liang et al., 2022), which sum up to hundreds of resequenced genomes that can be applied to address multiple aspects of oak biology, ecology, evolution and adaptation. WGS approaches can be used to cover population-level interrogations, benefiting from the increased economic accessibility of short-read sequencing data (e.g. Illumina platform). On this matter there are several interesting topics that derive from recent works, including the present thesis. At the phylogenomic backbone resolution, we envisage the need to continuously increase the number of species represented by WGS efforts, expanding the efforts already initiated for 50+ *Quercus* species within the Fagaceae context (Zhou *et al.*, 2022). On a more specific note, we suggest the resequencing effort dedicated to the Subgenus *Cerris* in the Western Paleartic Region. As a follow-up to the work developed in the present thesis, a much-needed time calibration could simultaneously solve all inter-specific and sequential relationships among all species inside the Groups/subsections (and in between them) that we have obtained for the circummediterranean white oaks. This work would then nurture phylogeographic inferences upon trajectory routes of their linages. A broader approach including American (ex: subsection *Albae*) and Asian white oaks (ex: *Q. dentata, Q. fabri, Q. mongolica, Q. serrata,* among others) could serve to test interesting hypotheses related with the origin of subsections *Hartwissiana* and *Macrantherae*. This approach should be merged with information from geotectonical and palaeoclimatic history. It would help to unveil if prototypical roburoid oaks may have reached Western Europe through Greenland and Iceland and started to develop marcescence from when reaching inland continental areas of the Paratethys and Taurus mountains, then reflooding Western areas when the Mediterranean dried up, across south Europe and North Africa.

Also, the known pervasive introgression of oaks should envisage the quantification of introgression extent, and the mapping of chromosome regions where introgression may preferably occur. WGS should provide added resolution by enabling the deployment of statistics such as D- and Fd-statistics that enable the quantification of introgression and identification of introgression blocks within the genome. Uncovering the genetic basis of adaptation is another critical aspect that is improved upon use of WGS approaches. The most enticing aspect of this added resolution is the prospect of identifying the genes

underlying important traits, whether morphological or adaptive. For instance, it will be interesting to quantify the existence (or not) of convergent adaptive evolution between oaks from vicariant areas, that share similar morphological traits, like the aforementioned comparison between Californian and Mediterranean white oaks, or at a smaller scale, between both extremes of the Mediterranean Basin. It will also be critical to assess the impact of introgression, and the importance and types of selection that have operated in shaping genetic variation, particularly with regards to studying the cost or adaptive value of hybrids and syngameons.

Another interesting aspect deriving from ample genomics data across the genome, pertains to the merging of adaptive genetic variation data and biogeography. Thus, an analysis directed considering the role of multiple environmental gradients across the Iberian landscape could enable us to find evidence of local adaptation by combining population genomics and spatial ecological modelling across the distribution range of a given species (for example *Q. faginea*). This would enable a guided decision making for conservational reforestation, genetically well-informed through explicit predictive spatial models, to facilitate adaptation to future climate changes and prioritize conservation areas (e.g. the establishment of certified seed zones).

At the speciation and nomenclatural assignment levels, the usage of aDNA is of particular interest within the context of museomics, to resolve taxonomic doubts with types when revisiting original Herbarium collections. The extraction of aDNA in order to establish molecular phylogenies in a weighted comparison between all ancient nomenclatural type-specimens and a saturated array of modern DNA samples based on high coverage genome resequencing, will allow us to produce a robust species assignment and develop a final and accurate checklist of western Palearctic (or worldwide) oaks. This will assure each phylogenetic name positioning and unveil potential hybridization signalling of each oak name, that can be nowadays misassigned. Museomics can also be used to document genetic erosion in endangered oaks, or to establish molecular population genomics analysis, documenting population genetic diversity and targeting a comparative analysis between past (prior to the current climate crisis) and current conditions.

We foresee additional challenges and prospects that relate to advancements in the capacity to generate *De novo* genomes. First, we are increasingly accomplishing the capacity to generate diploid phased genomes, which encase the full genetic variability within the sequenced individual, rather than depending on a haploid reference sequence. We expect this field to develop strongly, with the parallel development of tools that are

able to manage and mine this type of data, particularly with regards to large structural variation across the genome. Second, development of multiple genomes within a species will lead to a pangenomics age, in which the core and unique genomes of Quercus are dissected. Lastly, in forthcoming years as a combination of *De novo* genome availability and increased economic feasibility of long-read technology and computational power, we foresee an era where population-level studies may be conducted with *De novo* reference genomes rather than WGS approaches, unlocking the impact of large structural variation on oak performance. This may be associated with population-level studies, the uncovering of the genetic basis of adaptation, and estimates on the impact of hybridization.

It is important to reinstate once more that all future genomic approaches will benefit from accurate taxonomic identification, and geobotanical insights from which the phylogenetic backbone is totally dependent. Thus, a sampling approach that privileges the type-location of each putative oak species or name, followed by the total coverage of the morphological and infraspecific variation spanned across all biogeographic gradients of a given species' distribution, is a key task when developing molecular studies target phylogenies, introgression relationships and species syngameons. This can be then complemented with ecological niche modelling to infer the spatial variation of the genetic data, by testing the role of niche divergence in driving morphological evolution or lineage divergence, and infer on how spatial genetic heterogeneity can shape the ability of trees to respond to quick shifts in climate (Martins *et al.*, 2018; Du *et al.*, 2020). Ultimately, it would be strategic to confront the phylogenetic data retrieved from modern fieldwork with a phylogeny based on the analysis of ancient DNA from herbaria type specimens, covering all names given to oak taxa and nothotaxa. There is also a high potential in the analysis of extant genetic diversity within the species using multiple *De novo* genomes, to tackle the increasingly important aspect of the pangenome. Globally, genomics strategies will be crucial to reveal the evolutionary success history of oaks and help predict how these vital group of trees will cope with climate change. This will allow the development of strategic frameworks to equip decision-makers, giving them tools to prevent species extinction and ensure the maintenance of the extant diversity that spans from genomes to forests and habitats.

8.4. References

Acharya RP, Maraseni T, Cockfield G. 2019. Global trend of forest ecosystem services valuation–An analysis of publications. *Ecosystem Services* **39**: 100979.

Ai W, Liu Y, Mei M, Zhang X, Tan E, Liu H, Han X, Zhan H, Lu X. 2022. A chromosome-scale genome assembly of the Mongolian oak (Quercus mongolica). *Molecular ecology resources* **22**(6): 2396-2410.

Alcaraz-Segura D, Lomba A, Sousa-Silva R, Nieto-Lugilde D, Alves P, Georges D, Vicente JR, Honrado JP. 2017. Potential of satellite-derived ecosystem functional attributes to anticipate species range shifts. *International journal of applied earth observation and geoinformation* **57**: 86-92.

Allan RP, Hawkins E, Bellouin N, Collins B. 2021. IPCC, 2021: Summary for Policymakers.

Arenas-Castro S, Gonçalves J, Alves P, Alcaraz-Segura D, Honrado JP. 2018. Assessing the multi-scale predictive ability of ecosystem functional attributes for species distribution modelling. *PloS one* **13**(6): e0199292.

Arenas-Castro S, Regos A, Gonçalves JF, Alcaraz-Segura D, Honrado J. 2019. Remotely sensed variables of ecosystem functioning support robust predictions of abundance patterns for rare species. *Remote Sensing* **11**(18): 2086.

Axelrod DI. 1983. Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Garden*: 629-657.

Buira A, Fernández-Mazuecos M, Aedo C, Molina-Venegas R. 2021. The contribution of the edaphic factor as a driver of recent plant diversification in a Mediterranean biodiversity hotspot. *Journal of Ecology* **109**(2): 987-999.

Burger WC. 1975. The species concept in Quercus. *Taxon*: 45-50.

Carrero C, Jerome D, Beckman E, Byrne A, Coombes A, Deng M, González-Rodríguez A, Hoang V, Khoo E, Nguyen N. 2020. The red list of oaks 2020. *The Morton Arboretum: Lisle, IL, USA*: 11-12.

Cody ML 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. In: Soule ME ed. *Conservation biology : the science of scarcity and diversity*. Sunderland, Mass. (USA): Sinauer Associates.

Colmeiro M, Boutelou E. 1854. Examen de las Encinas y demás arboles de la Peninsula Iberica que producen bellotas, con la designación de los que se llaman mestos. *Imprenta de D. Jose M, Geofrin*.

Costa JC, Monteiro-Henriques T, Bingre P, Espírito-Santo D 2015. Warm-temperate forests of central Portugal: a mosaic of syntaxa. *Warm-temperate deciduous forests around the Northern hemisphere*: Springer, 97-117.

Cramer W, Guiot J, Fader M, Garrabou J, Gattuso J-P, Iglesias A, Lange MA, Lionello P, Llasat MC, Paz S, et al. 2018. Climate change and interconnected risks to sustainable development in the Mediterranean. *Nature Climate Change* **8**(11): 972-980.

Cristofolini G, Managlia A, Crema S. 2017. Quercus crenata–the correct if long-forgotten name of the hybrid Quercus cerris× Quercus suber. *Israel Journal of Plant Sciences*: 1-7.

Cruz-Alonso V, Ruiz-Benito P, Villar-Salvador P, Rey-Benayas JM. 2019. Long-term recovery of multifunctionality in Mediterranean forests depends on restoration strategy and forest type. *Journal of Applied Ecology* **56**(3): 745-757.

De Queiroz K. 2005. Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences* **102**(suppl_1): 6600-6607.

Denk T, Grimm GW, Manos PS, Deng M, Hipp A. 2017. An updated infrageneric classification of the oaks: review of previous taxonomic schemes and synthesis of evolutionary patterns. *Oaks physiological ecology. Exploring the functional diversity of genus Quercus L.*: 13-38.

Dernegi D. 2017. Ecosystem profile: Mediterranean basin biodiversity hotspot. Critical Ecosystem Partnership Fund: CEPF - Critical Ecosystem Partnership Fund.

Desfontaines R. 1799. *Flora Atlantica, sive Historia Plantarum, quae in Atlante, Agro tunetano et algeriensi crescunt*: Panckouckes.

Du Z-Y, Harris A, Xiang Q-YJ. 2020. Phylogenomics, co-evolution of ecological niche and morphology, and historical biogeography of buckeyes, horsechestnuts, and their relatives (Hippocastaneae, Sapindaceae) and the value of RAD-Seq for deep evolutionary inferences back to the Late Cretaceous. *Molecular phylogenetics and evolution* **145**: 106726.

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**(9): 479-486.

Fordham DA, Akçakaya HR, Alroy J, Saltré F, Wigley TM, Brook BW. 2016. Predicting and mitigating future biodiversity loss using long-term ecological proxies. *Nature Climate Change* **6**(10): 909-916.

Fortini P, Di Marzio P, Di Pietro R. 2015. Differentiation and hybridization of Quercus frainetto, Q. petraea, and Q. pubescens (Fagaceae): insights from macro-morphological leaf traits and molecular data. *Plant systematics and evolution* **301**(1): 375-385.

Fu R, Zhu Y, Liu Y, Feng Y, Lu R-S, Li Y, Li P, Kremer A, Lascoux M, Chen J. 2022. Genome-wide analyses of introgression between two sympatric Asian oak species. *Nature Ecology & Evolution*: 1-12.

Gailing O, Hipp AL, Plomion C, Carlson JE 2021. Oak population genomics. Springer.

García-Mijangos I, Campos JA, Biurrun I, Herrera M, Loidi J 2015. Marcescent forests of the Iberian Peninsula: floristic and climatic characterization. In: Box EO, Fujiwara K eds. *Warm-temperate deciduous forests around the Northern hemisphere*. London: Springer, 119-138.

Gugger PF, Fitz-Gibbon ST, Albarrán-Lara A, Wright JW, Sork VL. 2021. Landscape genomics of Quercus lobata reveals genes involved in local climate adaptation at multiple spatial scales. *Molecular Ecology* **30**(2): 406-423.

Gürke M 1897. Quercus. In: Richter K ed. *Plantae Europaeae [Enumeratio systematica et synonymica plantarum phanerogamicarum in Europa sponte crescentium vel mere inquilinarum]*. Leipzig: Engelmann, 54–72.

Hipp AL, Manos PS, Hahn M, Avishai M, Bodénès C, Cavender-Bares J, Crowl A, Deng M, Denk T, Fitz-Gibbon S. 2020. Genomic landscape of the global oak phylogeny. *New Phytologist* **226**(4): 1198-1212.

Hohenegger J. 2014. Species as the basic units in evolution and biodiversity: Recognition of species in the Recent and geological past as exemplified by larger foraminifera. *Gondwana Research* **25**(2): 707-728.

Humphries CJ, Escudero M, Martín-Bravo S 2017. Vicariance biogeography. In: Roitberg B ed. *Reference Module in Life Sciences*. Cambridge, UK: Elsevier, 1-13.

Kim BY, Wei X, Fitz-Gibbon S, Lohmueller KE, Ortego J, Gugger PF, Sork VL. 2018. RADseq data reveal ancient, but not pervasive, introgression between Californian tree and scrub oak species (Quercus sect. Quercus: Fagaceae). *Molecular Ecology* **27**(22): 4556-4571.

Klausmeyer KR, Shaw MR. 2009. Climate change, habitat loss, protected areas and the climate adaptation potential of species in Mediterranean ecosystems worldwide. *PloS one* **4**(7): e6392.

Liang YY, Shi Y, Yuan S, Zhou BF, Chen XY, An QQ, Ingvarsson PK, Plomion C, Wang B. 2022. Linked selection shapes the landscape of genomic variation in three oak species. *New Phytologist* **233**(1): 555-568.

Linnaeus C. 1753. *Species Plantarum*. Stockholm: Impensis Laurentii Salvii.

Lloret F, Jaime L, Margalef-Marrase J, Pérez-Navarro M, Batllori E. 2022. Short-term forest resilience after drought-induced die-off in Southwestern European forests. *Science of The Total Environment* **806**: 150940.

Lumaret J-P, Lobo JM. 1996. Geographic distribution of endemic dung beetles (Coleoptera, Scarabaeoidea) in the Western Palaearctic region. *Biodiversity Letters*: 192-199.

Maleev VP. 1935. A Review of Oak Trees in Caucasus through theirs Taxonomical and geographical relations and concerning to evolution of group Robur. *Bot. Zhur.* **20**(2): 156-172.

Mansuy N, Hwang H, Gupta R, Mooney C, Kishchuk B, Higgs E. 2022. Forest Landscape Restoration Legislation and Policy: A Canadian Perspective. . *Land* **11**(10): 1747.

Marañón T, Ibáñez B, Anaya-Romero M, Muñoz-Rojas M, Pérez-Ramos I. 2012. Oak trees and woodlands providing ecosystem services in Southern Spain. *Trees beyond the wood: An exploration of concepts of woods, forests and trees. Wildtrack Publishing, Sheffield*: 291-299.

Margalef-Marrase J, Pérez-Navarro MÁ, Lloret F. 2020. Relationship between heatwave-induced forest die-off and climatic suitability in multiple tree species. *Global Change Biology* **26**(5): 3134-3146.

Martínez AC, Llamas F. 2022. Quercus petraea (Matt.) Liebl. y otros robles del Sistema Ibérico septentrional. *Flora Montiberica* **84**: 15-17.

Martins K, Gugger PF, Llanderal-Mendoza J, González-Rodríguez A, Fitz-Gibbon ST, Zhao JL, Rodríguez-Correa H, Oyama K, Sork VL. 2018. Landscape genomics provides evidence of climate-associated genetic variation in Mexican populations of Quercus rugosa. *Evolutionary Applications* **11**(10): 1842-1858.

Mayr E. 1982. *The growth of biological thought: Diversity, evolution, and inheritance*: Harvard University Press.

Médail F, Baumel A. 2018. Using phylogeography to define conservation priorities: The case of narrow endemic plants in the Mediterranean Basin hotspot. *Biological Conservation* **224**: 258-266.

Médail F, Monnet A-C, Pavon D, Nikolic T, Dimopoulos P, Bacchetta G, Arroyo J, Barina Z, Albassatneh MC, Domina G. 2019. What is a tree in the Mediterranean Basin hotspot? A critical analysis. *Forest Ecosystems* **6**(1): 1-19.

Medail F, Quezel P. 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden*: 112-127.

Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C 2011. Global biodiversity conservation: the critical role of hotspots. *Biodiversity hotspots*: Springer, 3-22.

Montserrat P. 1957. Algunos aspectos de la diferenciación sistemática de los Quercus ibéricos.

Mori AS, Lertzman KP, Gustafsson L. 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology* **54**(1): 12-27.

Nieto-Feliner G 2014. Patterns and processes in plant phylogeography in the Mediterranean Basin: a review. Perspect Pl Ecol Evol Syst 16: 265–278.

Olalde M, Herrán A, Espinel S, Goicoechea PG. 2002. White oaks phylogeography in the Iberian Peninsula. *Forest ecology and management* **156**(1-3): 89-102.

Pasta S, de Rigo D, Caudullo G 2016. Quercus pubescens in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A eds. *European atlas of forest tree species*. Luxembourg: Publications Office of the European Union, 156-157.

Plomion C, Aury J-M, Amselem J, Leroy T, Murat F, Duplessis S, Faye S, Francillonne N, Labadie K, Le Provost G, et al. 2018. Oak genome reveals facets of long lifespan. *Nature Plants* **4**(7): 440-452.

Quézel P. 1976. Les forêts du pourtour méditerranéen. *Forêts et maquis méditerranéens: écologie, conservation et aménagement*: 9-33.

Quézel P. 1985. Definition of the Mediterranean region and the origin of its flora. *Geobotany*.

Quézel P, Médail F, Loisel R, Barbero M. 1999. Biodiversity and conservation of forest species in the Mediterranean basin. *UNASYLVA-FAO-*: 21-28.

Ramos AM, Usié A, Barbosa P, Barros PM, Capote T, Chaves I, Simões F, Abreu I, Carrasquinho I, Faro C. 2018. The draft genome sequence of cork oak. *Scientific data* **5**(1): 1-12.

Rey M-D, Labella-Ortega M, Guerrero-Sanchez VM, Carleial R, Castillejo M-A, Rodriguez-Franco A, Buggs R, Ruggieri V, Jorrin-Novo JV. 2022. A first draft genome of Holm oak (Quercus ilex L.), the most representative species of the Mediterranean forest and the Spanish agrosilvopastoral ecosystem dehesa. *bioRxiv*.

Rivas-Martínez S, Penas A, González TED, Cantó P, del Río S, Costa JC, Herrero L, Molero J 2017. Biogeographic Units of the Iberian Peninsula and Baelaric Islands to District Level. A Concise Synopsis. *The Vegetation of the Iberian Peninsula*. Utrecht: Springer, 131-188.

Rivas-Martínez S, Saénz C. 1991. Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* **6**: 101-110.

Rivas Martínez S, Rivas Sáenz S, Penas Á, del Río S 2011. Biogeographic map of Europe. Second concise advance. *1st International Symposium of the FIP - Global Strategy for plant conservation*. Valencia: Società Italiana Scienza della Vegetazione.

Rodrıguez-Sánchez F, Arroyo J. 2011. Cenozoic climate changes and the demise of Tethyan laurel forests: lessons for the future from an integrative reconstruction of the past. *Climate change, ecology and systematics*: 280-303.

Sala OE, Chapin FS, Huber-Sannwald E 2001. Potential biodiversity change: global patterns and biome comparisons. *Global Biodiversity in a Changing Environment*: Springer, 351-367.

Schwarz O. 1935. Einige neue Eichen des Mediterrangebiets und Vorderasiens. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* **114**: 461-469.

Schwarz O. 1936a. Entwurf zu einem natürlichen System der Cupuliferen und der Gattung Quercus L. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem*: 1-22.

Schwarz O. 1936b. Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* **8**: 65–100.

Schwarz O. 1937. Monographie der Eichen Europas und des Mittelmeergebietes. *Repertorium novarum speciarum regni vegetabilis* **1**: 1-200.

Schwarz O 1964. Quercus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, DA. W eds. *Flora Europaea*. Cambridge: Cambridge University Press, 61-64.

Soriano P, Costa M 2017. The coastal Levantine area. *The vegetation of the Iberian Peninsula*: Springer, 589-625.

Sork VL, Fitz-Gibbon ST, Puiu D, Crepeau M, Gugger PF, Sherman R, Stevens K, Langley CH, Pellegrini M, Salzberg SL. 2016. First draft assembly and annotation of the genome of a California endemic oak Quercus lobata Née (Fagaceae). *G3: Genes, Genomes, Genetics* **6**(11): 3485-3495.

Svenning J-C, Fløjgaard C, Marske KA, Nógues-Bravo D, Normand S. 2011. Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* **30**(21-22): 2930-2947.

Svenning JC. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology letters* **6**(7): 646-653.

Tschan GF, Denk T. 2012. Trichome types, foliar indumentum and epicuticular wax in the Mediterranean gall oaks, Quercus subsection Galliferae (Fagaceae): implications for taxonomy, ecology and evolution. *Botanical Journal of the Linnean Society* **169**(4): 611-644.

United Nations, FAO 2022. UN Decade on Ecosystem Restoration. https://www.decadeonrestoration.org/

Valladares F, Benavides R, Rabasa S, Díaz M, Pausas J, Paula S, Simonson W 2014. Global change and Mediterranean forests: Current impacts and potential responses. In: Coomes D, Burslem D, D. S eds. *Forests and global change*. Cambridge: Cambridge University Press, 47-75.

Van Valen L. 1976. Ecological species, multispecies, and oaks. *Taxon*: 233-239.

Vázquez FM, Coombes AJ, García D, Márquez F, Meireles C, Barrena MJ, Vila-Viçosa C. 2018. Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. . *Folia Botánica Extremadurensis* **12**: 5-79.

Vicioso C. 1950. *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa C, Vázquez F.M., Meireles C, Pinto-Gomes C. 2014. Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* **35**: 139–153.

Vila-Viçosa C, Vázquez FM, Mendes P, Del Rio S, Musarella C, Cano-Ortiz A, Meireles C. 2015. Syntaxonomic update on the relict groves of Mirbeck's oak (Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* **149**(3): 512-526.

Villar EH. 1958. Estudios sobre los Quercus del Oeste mediterráneo. *Anales del Instituto Botanico de A.J. Cavanilles* **15**: 3-114.

Ward A. 1952. Fog at North Front, Gibraltar. *Meteorol. Mag* **81**: 272-279.

Wheeler D. 2001. Factors governing sunshine in south-west Iberia: A review of western Europe's sunniest region. *Weather* **56**(6): 189-197.

Wiens JJ, Graham CH. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*: 519-539.

Willkomm M. 1896. *Grundzüge der Pflanzenverbreitung auf der iberischen Halbinsel*: W. Engelmann.

Zhou BF, Shi Y, Chen XY, Yuan S, Liang YY, Wang B. 2021. Linked selection, ancient polymorphism, and ecological adaptation shape the genomic landscape of divergence in Quercus dentata. *Journal of Systematics and Evolution* **60**(6): 1344–1357.

Zhou BF, Yuan S, Crowl AA, Liang Y-Y, Shi Y, Chen X-Y, An Q-Q, Kang M, Manos PS, Wang B. 2022. Phylogenomic analyses highlight innovation and introgression in the continental radiations of Fagaceae across the Northern Hemisphere. *Nature communications* **13**(1).

Annex: List of additional publications

Muthreich, F., Zimmermann, B., Birks, H. J. B., **Vila-Viçosa, C. M.**, & Seddon, A. W. (2020). Chemical variations in *Quercus* pollen as a tool for taxonomic identification: Implications for long-term ecological and biogeographical research. *Journal of Biogeography*, *47*(6), 1298-1309. https://doi.org/10.1111/jbi.13817

Author contributions: FM, AWRS, BZ and HJBB conceived the idea. FM and CMVV conducted the fieldwork and collected the data. FM, BZ and AWRS analysed the data. FM and AWRS led the writing with assistance from BZ, HJBB and CMVV.

Vázquez, F.M., Coombes, A., Almeida, R., Garcia-Alonso, D., Marquez-Garcia, F., & **Vila-Viçosa, C.** (2020). Lectotypification of names of *Quercus* spp. (Fagaceae) described by Lamarck from the Iberian Peninsula. *Phytotaxa*, 455(3), 205-213. https://doi.org/10.11646/phytotaxa.455.3.3

Co-authoring contributions: The candidate led the taxonomic research at the Herbarium of the Paris Muséum National d'Histoire Naturelle (P) together with the first author, unveiling and providing insights to the studied type materials.

Digital Annex

The Digital Annex can be found at the link:

https://zenodo.org/record/7520511#.Y72ElXbP25c

The Digital Annex comprises the following information:

Chapter 2

Supplementary Information S2 – Digital Annex

Chapter 4

Supplementary Information S2 – Digital Annex

Chapter 5

Supplementary Table S1 – Digital Annex

Supplementary Maps – Digital Annex

Chapter 6

Supplementary Information S4 – Digital Annex

Supplementary Table S2 – Digital Annex

Chapters 2-5

Paris Herbarium Review P Full - List of the 792 circummediterranean oaks specimens studied at Paris Herbarium (P), of which 672 were subjected to new nomenclatural or taxonomic determinations, while 120 were unveiled as nomenclatural types that were elusive in the general collection.