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Assessing interactive effects of climate and land use changes on Mediterranean farmland bird species

João Faria

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João Pedro Leite Faria
Doctoral Programme in Biodiversity, Genetics and Evolution
Faculty of Sciences of the University of Porto and Faculty of Sciences of the University of Lisbon

2024

Assessing interactive effects of climate and land use changes on Mediterranean farmland bird species

João Pedro Leite Faria

Thesis carried out as part of the Doctoral Programme in Biodiversity, Genetics and Evolution
Department of Biology
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Em memória da minha Mãe
(1958-2008)

In memory of my Mother
(1958-2008)

Nota prévia

Na elaboração desta dissertação, e ao abrigo do n.º 2 do Artigo 4º do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31º do DL n.º 74/2006, de 24 de março, com a nova redação introduzida pelo DL n.º 65/2018, de 16 de agosto, foi efetuado o aproveitamento total de um conjunto coerente de trabalhos de investigação objecto de publicação em revistas internacionais indexadas e com arbitragem científica, os quais integram alguns dos capítulos da presente tese. Tendo em conta que os referidos trabalhos foram realizados com a colaboração de outros autores, o candidato esclarece que, em todos eles, participou ativamente na sua conceção, na obtenção, análise e discussão de resultados, bem como na elaboração da sua forma publicada. Adicionalmente, o candidato foi coautor em um artigo publicado em revista internacional não diretamente relacionado com o tema da tese. Esse artigo publicado em coautoria, não incluído como capítulo da tese, está detalhado no *Appendix A*.

Este trabalho foi apoiado pela Fundação para a Ciência e Tecnologia (FCT) através da atribuição de Bolsas de Investigação para alunos de doutoramento SFRH/BD/131809/2017 e COVID/BD/151946/2022. Foi também financiado pela atribuição de uma bolsa pela Associação BIOPOLIS (BIOPOLIS 2022-46), no âmbito do projeto BIOPOLIS – Enhancing the transference of scientific and technological knowledge through a new Centre of excellence in Environmental Biology, Ecosystems and AgroBiodiversity (NORTE-01-0246-FEDER-000063), financiado pelo Programa Operacional Regional do Norte (NORTE2020), sob o acordo de parceria do PORTUGAL 2020, do Fundo Europeu de Desenvolvimento Regional (FEDER). Finalmente, contou com o apoio do projeto financiado pela FCT: EDGES (PTDC/BIA-BIC/2203/2012).

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Lista de capítulos publicados / Published chapters (*Appendix B*):

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Acknowledgements

In February of 2017, while working on a small research project after completing my MSc degree and still very unsure of what to do next, earlier than anticipated calls for the major national program of PhD fellowships were announced. As I was currently working on another project and this came sooner than expected, I hadn't given serious consideration to this idea. After some talks with my soon to be supervisors, we decided to give it try, putting together a project with great effort… but little time. Suffice it to say, we weren't terribly hopeful. Alas, it paid off! And nearly 7 years after being more than a little abstract concept in my mind, here it is in all its glory.

I would like to say these were 7 wonderful years, but that would simply be untruthful. While I was aware of the high rates of stress, anxiety, and burnout of PhD fellows, I was still not prepared to face what lay before me. These were without a doubt the most challenging and difficult years of my life. After battling with constant feelings of anxiety, depression, chronic back pain and impostor syndrome, the isolation brought about by the pandemic crisis was just an additional nail in the coffin. It strikes me as ironic how an event that was experienced by all of us could still be so isolating. However, much like every PhD journey, it is still a highly individualized experience for every person undertaking it. While these words may not feel particularly appropriate in this section, I think that they serve precisely to highlight the importance of every single person acknowledged here, as they are the most fundamental reason for why I was able to arrive at this point. If I learned one thing, is the value of a strong community, researchers and otherwise, surrounding you through this journey. Or as they say: "*It takes a village"*.

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Abstract

Afforestation initiatives are expanding globally, aiming to mitigate climate change through carbon emissions' reduction and sequestration, soil quality improvement and habitat restoration. However, their implementation often falls short regarding both carbon goals and effects on biodiversity. Despite potential benefits to overall biodiversity, afforestation can negatively impact species associated with unique habitats such as open grasslands, through direct habitat loss and fragmentation, with edge effects deteriorating habitat quality of resulting smaller grassland patches. Open-grassland specialist birds are particularly affected, with species richness and abundance declining near plantation edges. This may result from several factors, from the selective habitat requirements to the increased predator abundance and consequent nest-predation risk. Plantation type and grassland matrix structure also influence afforestation responses, by modulating edge effects, and providing different nest concealment capabilities and resource availability. Furthermore, increasingly pervasive climatic conditions interact with land uses to affect present and future farmland bird species' distribution.

This thesis aims to address these issues by focusing on three main objectives in a Mediterranean farmland context of relevance for the conservation of emblematic open grassland specialists. Namely, i) evaluating the contrasting effects of different plantation types used in afforestation on the nest-predation risk of grassland birds; ii) examining how climate-mediated changes to the local grassland structure modulate the response of different groups to afforestation; and iii) assessing the combined effects and relative importance of land use and climate on farmland bird ecological niches and distributions.

Higher predation rates were expectedly observed near plantation edges, however, these effects varied with the adjacent plantation type, reflecting the importance of plantation edge structure (i.e., understorey vegetation, tree density and height). Grasslands associated with eucalyptus plantations had larger predator abundance, mostly corvids, but predation risk was lower near edges, increasing into the grassland matrix to levels that surpassed oak and pine plantation edges, highlighting the increased risk for open habitat specialist birds. Changes to grassland vegetation height in two periods of contrasting climatic conditions revealed mixed effects on afforestation responses, which appeared to vary according to habitat preferences. Taller vegetation usually observed during a period of milder climatic conditions resulted in increased abundance of avian species associated with cereal fields and most ground-nesting birds. Furthermore, the benefits of taller vegetation appeared to be more pronounced in grasslands adjacent to eucalyptus plantations. Conversely, open habitat specialist birds associated with ploughed fields were more abundant in association with shorter

vegetation, during the drier period, but also when adjacent to oak and pine plantations. Finally, land use, particularly planted forests and non-intensive farmland, emerged as determining factors in farmland species' distributions at a regional scale. These factors often outweighed the importance of climatic predictors, particularly for open habitat specialists. Nonetheless, a combination of land-use and climatic factors was essential in accurately predicting individual farmland birds' distributions at a finer scale.

Overall, this thesis sheds light on the impacts of afforestation as a major driver of land-use change within the Mediterranean farmland context, along agricultural intensification and land abandonment, revealing key factors that influence farmland bird diversity and distribution within these ecosystems. Moreover, these results underscore the need for nuanced conservation strategies to address these impacts, highlighting the complexities and possible pathways that need to be considered to adequately implement measures able to benefit a group of farmland species with varying habitat requirements.

Keywords: Mediterranean farmland conservation, habitat fragmentation, plantation edges, nest-predation risk, farmland birds, steppe specialists, vegetation height, land-use effects, climatic conditions, species distribution models, ecological niches.

Resumo

As iniciativas de reflorestação estão a expandir-se globalmente, com o objetivo de mitigar as alterações climáticas através da redução das emissões de carbono e do seu sequestro, da melhoria da qualidade do solo e da restauração do habitat. No entanto, a sua implementação muitas vezes fica aquém dos objetivos relativos ao carbono e nos efeitos na biodiversidade. Apesar dos potenciais benefícios para a biodiversidade global, a reflorestação pode impactar negativamente espécies associadas a habitats únicos, como as pastagens abertas, através da perda direta de habitat e a sua fragmentação, com efeitos de orla que deterioram a qualidade do habitat das pequenas manchas de pastagens resultantes. As aves especialistas de pastagem aberta são particularmente afetadas, com a diminuição da riqueza e abundância de espécies perto da orla das plantações. Isto pode derivar de vários fatores, desde os requisitos seletivos do habitat até ao aumento da abundância de predadores e ao consequente risco de predação dos ninhos. O tipo de plantação e a estrutura da matriz das pastagens também influenciam as respostas à reflorestação, ao modular os efeitos de orla e ao fornecer diferentes capacidades de ocultação de ninhos e disponibilidade de recursos. Além disso, as condições climáticas cada vez mais pervasivas interagem com os usos do solo para afetar a distribuição presente e futura das espécies de aves de áreas agrícolas.

Esta tese pretende abordar estas questões, focando-se em três objetivos principais num contexto agrícola mediterrânico, relevante para a conservação de especialistas de pastagens abertas emblemáticos. Nomeadamente, i) avaliar os efeitos contrastantes de diferentes tipos de plantação, utilizados na reflorestação, no risco de predação de ninhos de aves de pastagem; ii) examinar como as mudanças na estrutura da pastagem local, mediadas pelo clima, modulam a resposta de diferentes grupos à reflorestação; e iii) avaliar os efeitos combinados e a importância relativa do uso do solo e do clima nos nichos ecológicos e distribuição de aves de áreas agrícolas.

Tal como esperado, perto das orlas das plantações foram observadas taxas de predação mais elevadas. No entanto, estes efeitos variaram com o tipo de plantação adjacente, refletindo a importância da estrutura da orla da plantação (ou seja, vegetação do sub-bosque, densidade e altura das árvores). As pastagens associadas a plantações de eucaliptos apresentaram uma maior abundância de predadores, principalmente corvídeos, mas o risco de predação foi menor perto das orlas, aumentando para a matriz de pastagem para níveis que ultrapassaram os das orlas de plantações de carvalhos e pinheiros, evidenciando o aumento do risco para as aves especialistas em habitats

abertos. As mudanças na altura da vegetação da pastagem em dois períodos de condições climáticas contrastantes revelaram efeitos mistos nas respostas à reflorestação, que pareceram variar de acordo com as preferências de habitat. Vegetação mais alta, observada normalmente durante um período de condições climáticas mais suaves, resultou num aumento da abundância de espécies de aves associadas a campos de cereais e da maioria das aves nidificantes no solo. Além disso, os benefícios da vegetação mais alta pareceram ser mais pronunciados em pastagens adjacentes a plantações de eucaliptos. Pelo contrário, as aves especialistas em habitats abertos associados a campos lavrados foram mais abundantes em associação com vegetação mais baixa, durante o período mais seco, mas também quando adjacentes a plantações de carvalhos e pinheiros. Finalmente, o uso do solo, em particular as florestas plantadas e as áreas agrícolas não intensivas, emergiram como fatores determinantes na distribuição das espécies de áreas agrícolas a nível regional. Estes fatores muitas vezes superaram a importância dos preditores climáticos, especialmente para especialistas em habitats abertos. No entanto, uma combinação de fatores de uso do solo e climáticos foi essencial para prever com precisão a distribuição individual das aves agrícolas a uma escala mais fina.

No geral, esta tese esclarece sobre os impactos da reflorestação, como um dos principais impulsionadores da mudança, no uso do solo no contexto agrícola mediterrânico, juntamente com a intensificação agrícola e o abandono de terras, revelando fatores-chave que influenciam a diversidade e distribuição de aves de áreas agrícolas nestes ecossistemas. Além disso, estes resultados destacam a necessidade de estratégias de conservação bem ponderadas, versáteis, para abordar estes impactos, sublinhando as complexidades e possíveis caminhos que precisam ser considerados para implementar medidas capazes de beneficiar um grupo de espécies de áreas agrícolas com requisitos variados de habitat.

Palavras-chave: Conservação de áreas agrícolas mediterrânicas, fragmentação de habitat, orlas de plantação, risco de predação de ninhos, aves de áreas agrícolas, especialistas de estepe, altura de vegetação, efeitos de uso do solo, condições climáticas, modelos de distribuição de espécies, nichos ecológicos.

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List of abbreviations

AIC	Akaike Information Criteria
AICc	Akaike Information Criteria corrected for small samples
ASL	Above Sea Level
AUC	Area Under the Curve
AWMSI	Area Weighted Mean Shape Index
BRT	Boosted Regression Trees
CAP	Common Agricultural Policy
CLIM	Climatic
COR	Correlation
DF	Degrees of Freedom
DOI	Digital Object Identifier
ED	Edge Density
EEC	European Economic Council
ELSA	Entropy-based Local Spatial Association
EN	Ensemble Model
EVI	Enhanced Vegetation Index
EU	European Union
GDP	Gross Domestic Product
GLM	Generalized Linear Model
GLMM	Generalized Linear Mixed Model
GPS	Global Positioning System
HNVF	High Nature Value Farmland
HRI	Highest Relative Importance
ICNF	Nature and Forests Conservation Institute
IR	Infra-Red
IUCN	International Union of Conservation of Nature
LC	Least Concern
LED	Light-Emitting Diode
LRT	Likelihood Ratio Test
LU	Land Use
MARS	Multivariate Adaptive Regression Splines
MPS	Mean Patch Size
NT	Near Threatened
P	Statistical significance value
P-A	Presence- Absence
REDD+	Reducing Emissions from Deforestation and Forest Degradation
RF	Random Forests
ROC	Receiver Operating Characteristic
Rpart	Recursive Partitioning
SAF	Agroforestry Systems
SD	Standard Deviation

SDM	Species Distribution Model
SE	Standard Error
SPA	Special Protection Area, Directive 2009/147/EC
TSS	True Skill Statistic
VU	Vulnerable
Z	Standard score
β	model coefficient estimates
Δabund	Difference in abundance between periods
X^2	Chi-squared test statistic

Chapter 1

General Introduction

1.1. Global overview of Afforestation

Large-scale afforestation can be classified as an establishment of forest plantations on farmland, grassland and other previously unforested land (Brockerhoff *et al*., 2008; Jacoboski *et al*., 2019). Globally, it is an increasingly common land-use change (Hansen *et al*., 2013; Arakwiye *et al*., 2017; Brazeiro *et al*., 2018; Jacoboski and Hartz, 2020). From a 35-year satellite analysis of global land-use dynamics (1982-2016), Song *et al*. (2018) concluded that contrary to the prevailing view of a declining forest area, tree cover increased by 2.24 million km^2, representing a 7.1% increase over this period. During the latter half of that period (2001-15), global afforestation represented nearly the same level of land-cover changes as deforestation (26 and 27%, respectively), being much more predominant than the latter in Europe (Curtis *et al*., 2018).

For a long time, afforestation measures were mainly explored in northern hemisphere countries with low forest cover and higher GDPs (Ewers, 2006), as these usually rely less on environmental capital such as forest resources, contrasting with developing nations which often rely on forests (and deforesting) for their economic development (Ewers, 2006). In Europe, there are several large-scale schemes and policies directing funds for the conservation, restoration and development of forest plantations. For instance, the Common Agricultural Policy (CAP), implemented under the European Council regulation EEC 2080/92 (Burrascano *et al*., 2016) has historically encouraged forest expansion and protection of existing forests through direct payments to farmers. However, according to recent assessments, only ca. 5% of these funds were applied for sustainable forest management (Varela *et al*., 2020). In more recent times, we have seen an expansion of afforestation initiatives worldwide, including low-income areas (Newbold *et al*., 2017; Arakwiye *et al*., 2017). This expansion mostly occurs on the tropics (Ribas *et al*., 2016; Curtis *et al*., 2018; Song *et al*., 2018) and the southern hemisphere (Fernandes *et al*., 2016; Arakwiye *et al*., 2017; Bond *et al*., 2019), and has seen large initiatives, often under the guidance of climatic change mitigation (García *et al*., 2020), aiming to plant or reforest large areas to help reduce carbon emissions, deforestation and forest degradation, and increase carbon sequestration, soil quality and habitat restoration capabilities (Loyn *et al*., 2007; Curtis *et al*., 2018; Bond *et al*., 2019; Holl *et al*., 2020). For instance, in Africa, *ca.* 1 million km^2 of mostly grassy biomes have been targeted for habitat restoration and carbon sequestration through large-scale plantations (Bond *et al*., 2019). However, some of these initiatives are often too general in their aims and targets chosen for application. For instance, these “deforested” or “degraded” areas, can often be ancient savanna landscapes of highly important national parks, which were classified as such due to tree cover being reduced by elephants,

antelopes, and the long-term effects of grass-fuelled fires (Bond *et al*., 2019). These grassy biomes are intrinsically integrated into a community of forest-averse species that will be greatly impacted by a careless implementation of afforestation measures. Indeed, since the 2000s, when afforestation measures have started to be encouraged in these areas, nearly 90% of afforested and reforested areas are patchy monocultures of eucalyptus and alnus species, with some direct and immediate economic value (Bradshaw *et al*., 2013; Lin *et al*., 2013), but relatively low potential to provide equivalent ecosystem services to those likely being compromised (Arakwiye *et al*., 2017).

In southern America, afforestation and reforestation initiatives are often implemented with large-scale pine and eucalyptus monocultures (Fernandes *et al*., 2016; Ribas *et al*., 2016). Brazil has seen a recent increase of 18.3% in area planted with pines and eucalyptus from 2005 to 2012, often coinciding with areas covered by *Cerrado* (savannah) vegetation (Ribas *et al*., 2016). While, at a local scale, they may appear economically appealing, these plantations often replace areas of *Cerrado*, ultimately leading to a loss of native vegetation and hindering local biodiversity as well as habitat connectivity which at a large scale can result in environmental losses and economic unsustainability (Hoffmann and Franco, 2003; Ribas *et al*., 2016). In addition to a lesser capacity for water absorption and retention, these monocultures also exhaust superficial water at a higher rate (Wang *et al*., 2017). The effects of eucalyptus plantations in the native grasslands of Brazil, Uruguay and Argentina also reflected in a decline in species richness and a change in community structure (Phifer *et al*., 2017), including a decrease in taxonomic and functional bird diversity (Jacobobski and Hartz, 2020) and avian species richness and abundance (Martínez-Lanfranco, 2017; Brazeiro *et al*., 2018; Pretelli *et al*., 2018).

It is expected that these initiatives continue to expand, with several initiatives such as: Reducing Emissions from Deforestation and Forest Degradation (REDD+; Corbera and Schroeder, 2011), the Trillion Trees campaign (Brancalion and Holl, 2020), the Bonn Challenge (Laestadius *et al*., 2015; Bond *et al*., 2019; García *et al*., 2020), the European Green Deal (European Commission, 2019) and the United Nations' Decade on Ecosystem Restoration (2021–2030) (Brancalion and Holl, 2020), all contributing to unprecedented political and socio-economic support for afforestation policies (Brancalion and Holl, 2020). Thus, it is imperative to understand and weigh the potential environmental and biodiversity benefits and consequences and develop methods and alternatives to improve their implementation to maximize carbon sequestration while minimizing harm to or even benefitting overall biodiversity (see example: **Figure 1.1**).

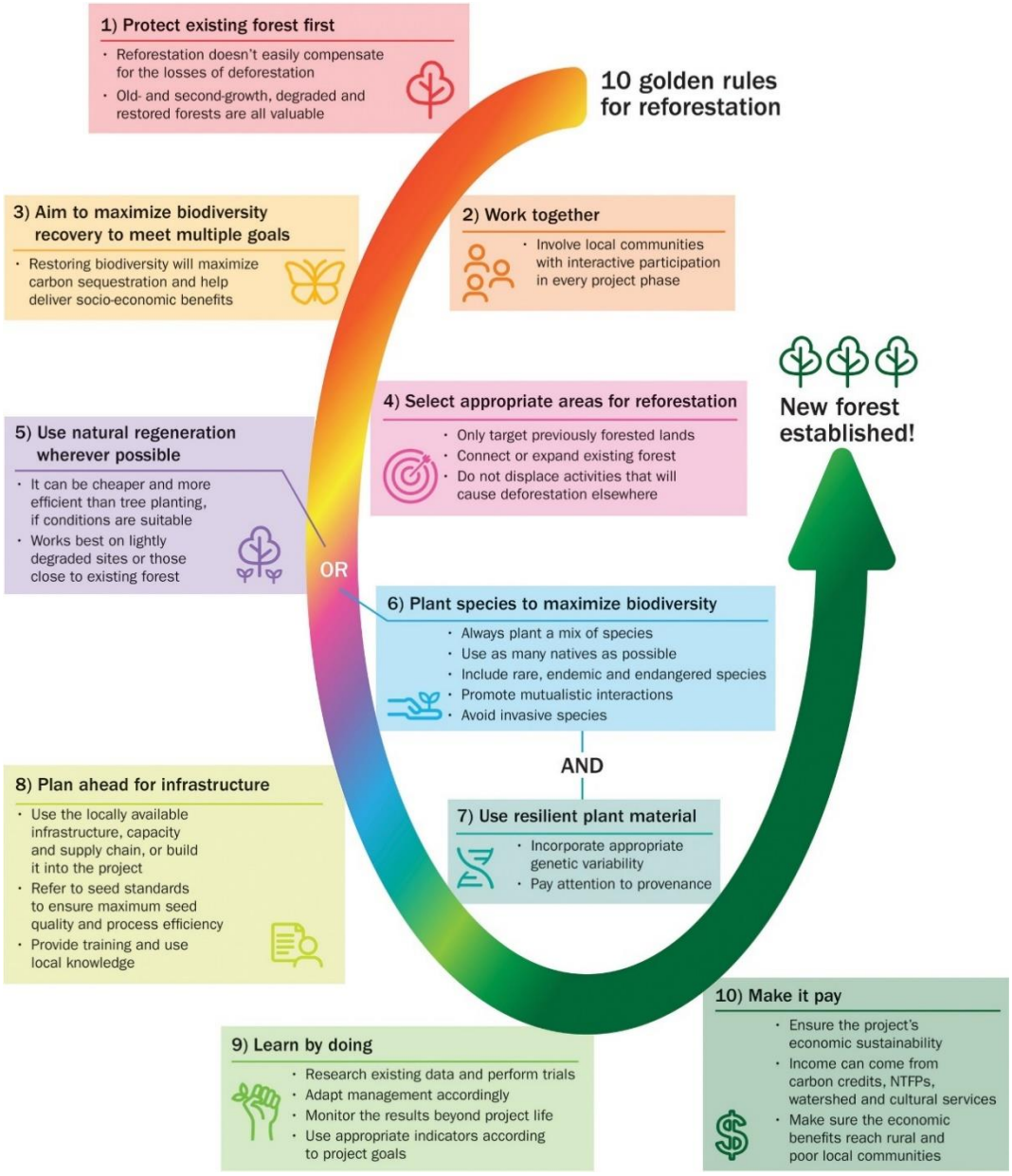

Figure 1.1 - Diagram depicting the Ten golden rules for successfully implementing forest ecosystem restoration projects that maximize rates of both carbon sequestration and biodiversity recovery while improving livelihoods. *Source:* Di Sacco *et al.,* 2021.

1.2. Conservation concerns may outweigh afforestation benefits

The major focus of discussion regarding afforestation is usually its potential for carbon sequestration and reduction (Potter *et al*., 2007; Lin *et al*., 2013; García *et al*., 2020), or to serve as carbon offset for projects with large carbon production rates (Van Kooten *et al*., 2004; Polonsky *et al*., 2010). However, an increasingly growing body of research is revealing several issues that may occur because of large-scale afforestation projects

(Gries *et al*., 2012; Van Kooten and Johnston, 2016; Pretelli *et al*., 2018; Jacoboski *et al*., 2019). The effects of afforestation can be widely diverse, depending on the affected fauna and flora, associated habitats and ecosystem services impacted, as well as the implementation methods (e.g., diversity of species used and the scale of individual plantations) (Brancalion and Holl, 2020; Holl *et al*., 2020). Afforestation can lead to neutral or even beneficial effects to species richness and diversity (Loyn *et al*., 2007; Reino *et al*., 2009; Pita *et al*., 2009; Graham *et al*., 2017; Jacoboski and Hartz, 2020).

However, these changes often involve generalist or widespread species with high potential of adaptability, thus requiring less focus regarding their conservation. Negatively affected are species generally requiring more unique or diverse habitats to thrive. For instance, flora and fauna associated with early-successional habitats or vast open grassland areas, have been shown to be negatively impacted by afforestation (Reino *et al*., 2009; Bremer and Farley, 2010; Felton *et al*., 2010; Morgado *et al*., 2010; Gries *et al*., 2012; Bunce *et al*., 2014; Burrascano *et al*., 2016; Pretelli *et al*., 2018; Jacoboski *et al*., 2019; Vasconcelos *et al*., 2019). These areas are transformed from natural or semi-natural ecosystems, such as extensive pastures or meadows covered by herbaceous vegetation with unique communities (Burrascano *et al*., 2016; Squires *et al*., 2018), into smaller and more fragmented habitats (Liu *et al*., 2019). This loss and fragmentation of habitats can be particularly taxing for grassland bird species (Shochat *et al*., 2001; Brotons *et al*., 2005; Reino *et al*., 2009; Morgado *et al*., 2010; Pretelli *et al*., 2018; Jacoboski *et al*., 2019).

1.3. How afforestation can affect grassland species

The effects that afforestation may have on grassland biodiversity can be influenced by several factors. From increased fragmentation and increased plantation edges, to increases in predation pressures, all varying according to the types of plantation and plantation edges, as well as the structure and heterogeneity of the remaining grassland.

1.3.1. Habitat loss, fragmentation and edge effects

From the previous examples, the loss of open habitat is the most direct consequence of afforestation. The invading trees can lead to a decrease in species richness, besides altering plant and animal communities (Lautenbach *et al*., 2017). As a result, species associated with grassland and shrubland areas are often absent or scarce near planted areas (Fletcher Jr., 2005), giving way to those associated with forest or woody vegetation covered habitats, which are commonly generalist or widespread species (Shochat *et al*.,

2001; Reino *et al*., 2009). The impacts of habitat loss extend beyond the afforested areas, likely reducing the quality of the remaining open habitat fragments due to the proliferation of newly formed edges, which have highly profound effects on animal population dynamics (Ries *et al*., 2004; Ewers and Didham, 2007; Fletcher Jr. *et al*., 2018). Large-scale fragmentation can inclusively affect species distribution, at least at a regional scale (Reino *et al*., 2013; Liu *et al*., 2019). This does not always lead to a negative outcome. Indeed, several species prefer more fragmented landscapes (Coppedge *et al*., 2004; Reino *et al*., 2009). Thus, edges may sometimes constitute a richer and more diverse habitat than either of the adjacent areas, though this is highly conditioned by assemblage composition, as edge responses are often guild or species-specific, depending on habitat preferences and species traits (Balestrieri *et al*, 2015). For instance, early successional forest species of conservation concern can benefit from newly planted areas (Sanderson *et al*., 2006). In addition, if there is careful implementation of the afforestation process, with small-scale variation in habitat heterogeneity, bird and insect diversity can increase (van Halder *et al*., 2011, Terraube *et al*., 2016; Graham *et al*., 2017). Edge distance is also an important factor, as species responses can usually vary in different ways from the plantation edge (Reino *et al*., 2009; Terraube *et al*., 2016). Moreover, the magnitude of edge effects may increase with the contrast between plantation edge and the adjacent open habitat, as well as the degree of landscape fragmentation, though this is not always the case (Fletcher Jr., 2005; Reino *et al*., 2009; Andrieu *et al*., 2018).

Birds have been shown to constitute good models for the effects of landscape matrices on biodiversity in fragmented habitats (Prevedello and Vieira, 2010; Pretelli *et al*., 2018). Open-grassland specialist birds constitute one of the groups most negatively impacted by afforestation (Brotons *et al*., 2005; Morgado *et al*., 2010; Lautenbach *et al*., 2017; Pretelli *et al*., 2018; Jacoboski *et al*., 2019). They usually show lower abundance and overall species richness (Reino *et al*., 2009; Terraube *et al*., 2016; Brazeiro *et al*., 2018) near wooded edges, with their numbers steadily increasing with larger grassland patches and away from forest plantations (Reino *et al*., 2009; Pretelli *et al*., 2018). This may occur due to several factors. For instance, edge avoidance behaviour may result from highly sensitive habitat requirements (Morgado *et al*., 2010; Zurita and Bellocq, 2012; Pretelli *et al*., 2018), reduced habitat quality and lack of resources (Lautenbach *et al*., 2017). It may also result from a strong aversion forming due to an unfamiliarity with wooded structures, given the evolution of grassland species in expansive prairies and steppes (Bota *et al*., 2005; Renfrew *et al*., 2005). Perhaps more importantly is the risk of

increased nest predation, which is often one of the most likely reasons explaining edge avoidance (Vickery *et al*., 1992; Santos *et al*, 2006; Reino *et al*., 2010a).

1.3.2. Nest predation

Afforestation is often associated with an increase in predator abundance in the open grassland areas surrounding these forest plantations, driven by higher resource and refuge availability for avian and mammalian predators (Evans, 2004; Santos *et al*., 2006; Pita *et al*., 2009; Reino *et al*., 2010b; Hansen *et al*., 2019). Predators may also benefit from the proliferation of fragmented landscapes (Andrén, 1992; Chalfoun *et al*., 2002), potentially due to higher abundances of prey populations, which commonly thrive in plantation-grassland edge areas, and the increased cover provided by planted trees (Reino *et al*., 2010b; Batáry *et al*., 2014; Terraube *et al*., 2016; Fahrig *et al*., 2019). Several species in grasslands adjacent to plantations are ground-nesting species, which are one of bird groups in larger decline across Europe, a decline which correlates with an increase in abundance of generalist predators (McMahon *et al*., 2020). Indeed, nest predation is one of the main causes of nest mortality and it is known to affect reproductive strategies of birds (Yanes and Suárez, 1997). Avian predators hunting by sight may use the trees on plantation edges as elevated perches to increase prey detection rate on adjacent grasslands (Andersson *et al*., 2009). A key avian predator group, corvids are often associated with nest predation near wooded areas (Andrén, 1992; Söderström *et al*., 1998; Aebischer *et al*., 2016; Madden *et al*., 2015; Bravo *et al*., 2020; McMahon *et al*., 2020). Some of these species are generalist predators known to benefit from the availability of forest patches interspersed with agricultural land, as they can find reliable food sources around farms and other human settlements in addition to plantations (Andrén, 1992). Crows are significantly more likely to have a negative impact on prey species productivity than other corvids (Madden *et al*., 2015).

All these factors may lead to increasing nest predation pressures in grasslands adjacent to forest plantations, whether through incidental or targeted predation (Vickery *et al*., 1992; Yanes and Suárez, 1996), particularly near edges where predator activity is concentrated (Santos *et al*., 2006; Morris and Gilroy, 2008; Šálek *et al*., 2010; Cox *et al*., 2012; Sánchez-Oliver *et al*., 2014a; Hansen *et al*., 2019). It can also lead to a decline in ground-nesting species abundance near wooded edges, as these tend to select nesting habitats to reduce nest predation (Bellamy *et al*., 2018). As such, grassland structure and vegetation cover are crucial in mitigating the effects of increased nest-predation rates through afforestation.

1.3.3. Grassland and climatic conditions

The structure of the landscape matrix surrounding forest fragments can markedly influence plantation edge effects (Terraube *et al*., 2016). Indeed, in the adjacent semi-natural grassland or farmland patches, vegetation density and cover are of great importance (Moreira, 1999; Laidlaw *et al*., 2020) as they may provide protection, food, and nesting resources for numerous species (Batáry *et al*., 2007; Erdös *et al*., 2009). Although predation rates are not always related to the degree of nest concealment (Howlett and Stutchbury, 1996; Evans, 2004), an increase in vegetation cover and heterogeneity often leads to a decrease in nest predation rates, as nest crypsis is improved (Willson *et al*., 2001; Evans *et al*., 2004). Furthermore, different grassland types (e.g., cereal, fallow, or pastures) and structures (e.g., vegetation height, litter depth and shrub cover) can be favoured by different grassland bird species (Jacobs *et al*., 2012; Santana *et al*., 2014; 2017a). Vegetation height likely becomes increasingly important near plantation edges, since these present avian predators with taller perching sites, which increase prey detection rates (Andersson *et al*., 2009). As such, taller vegetation swards should play a crucial role in mitigating predator searches and improving nest survival rates in open-grassland habitats. However, changes to farming systems, often in the context of agricultural policy reforms, such as the CAP introduced in Europe in 2003, can directly reflect changes in grassland vegetation structure, for instance by shifting from arable farmland to intensively grazed and permanent crop systems, resulting in grassland heterogeneity declines (Ribeiro *et al*., 2014). Additionally, through habitat modifications usually associated with the simplification of habitat structures through anthropogenic land management, nests become less inconspicuous and are likely to be more prone to predation (Evans, 2004; Bellamy *et al*., 2018). The consequent reduction in grassland vegetation heterogeneity may lead to a decline in breeding success (Erdös *et al*., 2009), although some grassland specialist species tend to favour homogeneous landscapes (Morris and Gilroy, 2008). Changes in climatic conditions can also influence grassland structure and suitability (Conrey *et al*., 2016; Zuckerberg *et al*., 2018), ultimately affecting the magnitude of plantation edge effects, which also likely influences the different impacts observed in tropical and temperate regions (Vetter *et al*., 2013; Terraube *et al*., 2016; Fletcher Jr. *et al*., 2018). Increasingly frequent droughts and heat waves can lead to changes in soil properties and less overall biomass production (Wu *et al*., 2022), which can decrease vegetation cover (Conrey *et al*., 2016). In combination with increasing intensive grazing patterns (Reino *et al*., 2010b; Ribeiro *et al*., 2014; Li *et al*., 2018), vulnerability to nest-predators is likely to increase, particularly near plantation edges (Beja *et al*., 2014). For instance, Bellamy *et al* (2018)

showed how some ground-nesting species prefer to place their nests on steeper slopes and areas with taller canopies. In areas with greater cover of medium to high vegetation, the correlation between nest-predation rate and vegetation structure was relatively low, although predation rates were generally lower. Contrastingly, in areas of very low vegetation cover (due to grazing pressure), predation pressures increase greatly, which is likely to result in an increased importance of nest cover when conditions become more extreme. As such, an increasing need arises for clarifying the role of different types of plantation edge habitats in a Mediterranean farmland context, and their influence on the distribution and diversity of bird species in adjacent grassland areas (Lindenmayer *et al*., 2015; Terraube *et al*., 2016).

1.3.4. A note on different plantation types

Afforestation introduces changes to the landscape composition and configuration, which can be linked to increased generalist predator abundances at a wider scale (Reino *et al*., 2010a). However, effects on predation rates and predator activity often depend on the type of plantation and overall area covered (Reino *et al*., 2010a; Sliwinski and Koper, 2012). Based on tree composition and the intensity of plantation, among other potential factors, plantations have varying degrees of understory vegetation, canopy structure and tree height and density (Reino *et al*., 2010a; Calviño-Cancela *et al*., 2012). These factors can result in a higher contrast between the plantation and adjacent grassland areas (Ries *et al*., 2004), which can influence the suitability for certain species while also increasing predation pressures (Santos *et al*., 2006; Reino *et al*., 2010a). As an example, eucalyptus plantations are often composed of tall trees, densely populated, which provides more contrast with the adjacent area (**Figure 1.2** – left side), as well as suitable perching sites for roosting and search-hunting (Rice, 1983; Santos *et al*., 2006; Andersson *et al*., 2009). Conversely, plantation oak stands are often composed by slower growing trees with shorter and sparser canopies (Vasconcelos *et al*., 2019), which contrast less with the adjacent area (**Figure 1.2.** – right side). It would therefore be interesting to understand how afforestation with different plantation types interacts with adjacent grassland features (e.g., vegetation cover), and the resulting effects on grassland bird species abundance and diversity across the grassland area.

Figure 1.2 - Contrast of plantation grassland edge of eucalyptus (left side) and oak (right side) plantations (Photos by: Juan Sánchez-Oliver and Luís Reino).

1.4. Mediterranean farmland – A unique setting

The Mediterranean basin is considered a global biodiversity hotspot of important conservation priority (Myers *et al*., 2000; **Figure 1.3**). An afforestation program by the EU (the CAP) has, since 1993, resulted in the afforestation of millions of ha of Mediterranean farmland to date (Sánchez-Oliver *et al*., 2014b). However, most EU funds related to afforestation programmes are mostly targeting conservation or restoration of low-priority areas, with few financial incentives for sustainable forest management and maintenance of multifunctional agro-silvo-pastoral mosaics (Varela *et al*., 2020).

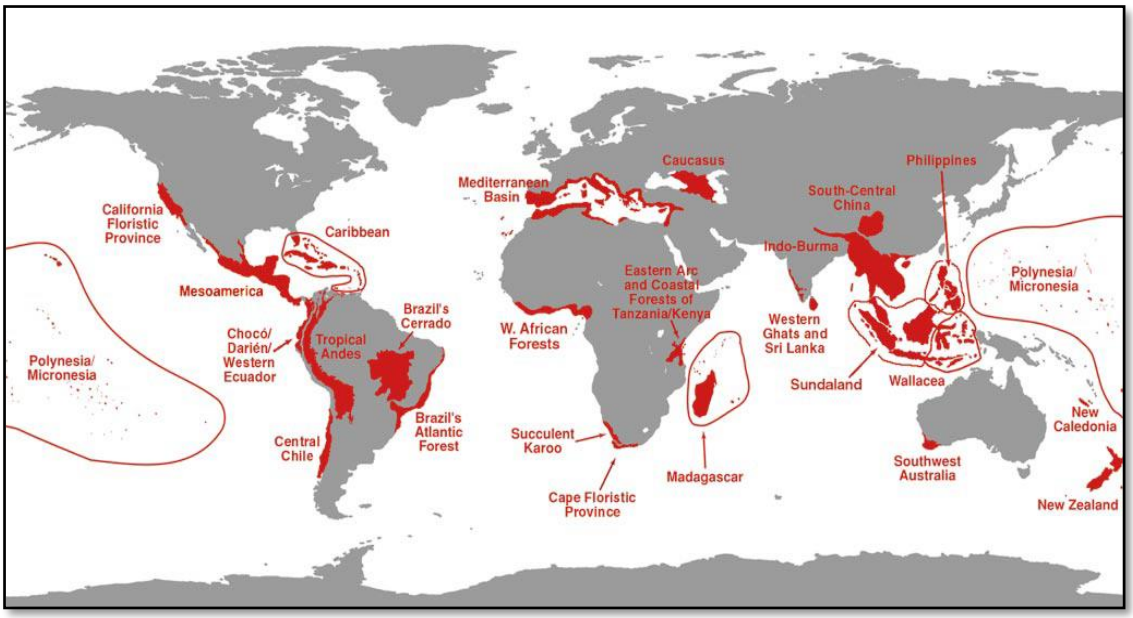

Figure 1.3 - Mediterranean Basin as one of the 25 Global biodiversity hotspots comprising nearly 35% of all species in four vertebrate groups. *Source: Myers et al., 2000.*

The Mediterranean farmland region of southern Portugal contains the Special Protection Area (SPA) of Castro Verde, an area designated to safeguard steppe birds under the European Union Birds Directive 2009/147/EC, and used to be mostly representative of the characteristic Mediterranean landscapes, with a mostly flat or gently undulating landscape composed by a mosaic of different cereal and fallow crops and semi-natural or natural grassland patches interspersed with woody vegetation and sparsely populated trees (Ribeiro *et al*., 2014; Morgado *et al*., 2020). It also possesses a Mediterranean climate, characterised by hot and dry summers and mild winters, with >75% of annual rainfall concentrated in October-March (Moreira *et al*., 2005; Morgado *et al*., 2020). However, the last decades have shown shifts in land uses as well as climatic conditions (Ribeiro *et al*., 2016; Santana *et al*., 2017a; FFMS, 2022). Indeed, an area that was traditionally dominated by mosaics of shrubland interspersed with old fallow fields or agricultural fields cultivated with dry cereal crops in long rotations with fallows grazed at low densities (Delgado and Moreira, 2000; Moreira *et al*., 2007), as recently seen a decline in cereal and fallow land replaced by permanent pastures and increasingly intensive crops (e.g., highly intensive olive orchards), accompanied by an increase in specialised livestock systems (Ribeiro *et al*., 2014; Ren *et al*., 2018; Morgado *et al*., 2020; 2022). Additionally, whereby tree cover was mostly composed of open oak plantations with a few areas of eucalyptus stands, the CAP implementation saw a great increase in afforestation with umbrella pines and a few oak plantations in the periphery of the SPA (Institute for Forestry Development, 2001; Reino *et al*., 2010b).

Open-grassland communities are often one of the most specialized in terms of habitat (Devictor *et al*., 2010; Terraube *et al*., 2016). Because of this, grassland associated species can be negatively impacted by large-scale afforestation, especially when exotic tree species are used (Vasconcelos *et al*., 2019). This can be particularly concerning when afforestation occurs in open habitats of conservation significance (Reino *et al*., 2009; Bond *et al*., 2019; Jacoboski *et al*., 2019).

In the cereal steppes of the SPA of Castro Verde, we find many bird species of high conservation value which can be significantly impacted by afforestation practices (Delgado and Moreira, 2000; Reino *et al*., 2009; Santana *et al*., 2017b). Among cereal fields, fallow land, stubbles, and ploughed land, one can find populations of emblematic species (Silva *et al*., 2024), such as the little and great bustard (*Tetrax tetrax* and *Otis tarda*, respectively), as well as tawny pipits (*Anthus campestris*), stonechats (*Saxicola rubicola*), short-toed larks (*Calandrella brachydactyla*), Galerida larks (*Galerida* spp.), corn bunting (*Emberiza calandra*), among others. Most of these species are highly sensitive to the type of grassland and vegetation structure they inhabit. Hence, changes

through afforestation as well as grazing regimes and agricultural intensification could lead to very distinct outcomes for different species (Moreira, 1999; Delgado and Moreira, 2000; Santana *et al*., 2017b), and a highly specific analysis is needed to understand how these changes affect the distributions of different groups.

1.5. General aims and objectives

This thesis is broadly focused on the impacts of human-led afforestation and its interaction with land-use changes and climatic conditions, on the avian community of Euro-Mediterranean open farmlands, an important biodiversity and conservation hotspot. Using several Mediterranean farmland bird species of southern Portugal as model organisms, the general aim is to understand how, at different scales, species and different functional groups respond to land-use changes and the local and landscape-scale factors influencing these responses. Within this context, three specific objectives were defined:

1- Evaluate how contrasting plantation types used in afforestation may affect nest predation risk on grassland bird species (**Chapter 2**).
2- Determine if temporal variation in local grassland structure, potentially driven by changes in climatic conditions, may affect bird responses to afforestation, and how different grassland preferences may shape this response (**Chapter 3**).
3- Explore the principal land-uses affecting farmland species distribution, and how these interact with climatic factors to influence a range of distributions, from farmland generalists to open habitat specialists (**Chapter 4**).

1.6. Chapters' overview

This thesis is divided into five chapters. **Chapter 1** provides a general introduction and overview of the historical and current understanding of afforestation around the globe, followed by conservation concerns that have been raised regarding potential impacts on grassland species, which are then contextualized in a Mediterranean farmland setting to be approached in the following chapters. **Chapter 2** (Faria *et al*., 2022) presents the first study, in which afforestation effects of pine, oak and eucalyptus trees on nest predation risk of grassland birds were evaluated. This was achieved using artificial nests baited with quail eggs in a camera trapping setup in a farmland bird protected area (SPA of Castro Verde). Identification of nest predators in grasslands adjacent to different plantation types, the probability of depredated nests and the local grassland conditions were used to examine how different plantations influence predator's

abundance, whether grassland cover could positively affect predation risk and how these factors interacted together. The obtained results were used to discuss the distinct impacts of afforestation with different tree species on nest-predation risk in the Mediterranean farmlands and conservation strategies to mitigate negative effects on species of conservation concern. In **Chapter 3** (Faria *et al*., 2024), the effects of grassland vegetation height on Mediterranean farmland bird responses to plantation edges were examined. Using bird counts performed over 38 grassland parcels on two different occasions which differed significantly in climatic conditions, the effects of changes in grassland sward height on bird responses to afforestation were examined. The combined effects of vegetation height, plantation type and distance to plantation edges on bird assemblages was then analysed for each guild and a group of key species, to infer and discuss about the importance of field and landscape-level management focused on the preservation of grassland heterogeneity in Mediterranean farmland landscapes. **Chapter 4** (Faria *et al*., *in prep.*), aims to evaluate the main land-use effects on farmland bird species distribution and their interactions with climatic conditions at a regional level. To achieve this, bird counts were performed across 148 sampled sites in southern Portugal and nine of the most widespread and ecologically relevant species were selected. After categorizing the region in eight broadly significant land-uses, five climatic predictors, a productivity and a heterogeneity index, species distribution models were constructed to identify the probability of occurrence of these species over a larger area and the relative importance of land-use and climatic variables at this scale. Results were used to discuss how ongoing and future land-use changes (whether human-mediated or through increasingly extreme climatic conditions), could impact the distribution of key open grassland specialist birds. Finally, **Chapter 5** is composed of a general discussion which serves to highlight the overall findings and main conclusions of this thesis and to propose potential conservation actions and future research possibilities in Mediterranean farmland areas.

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Chapter 2

Contrasting effects of eucalyptus, pine and oak plantations on nest predation risk in Mediterranean grasslands

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2.1. Abstract

Large scale afforestation (i.e., establishment of forests on farmland, grassland and other land not previously forested) is increasingly regarded as a cost-effective option to mitigate climate change by promoting carbon sequestration. However, this strategy can have negative biodiversity impacts, potentially causing the loss and fragmentation of open habitats of conservation value, as well as edge effects that can extend well beyond forest boundaries. Mitigating impacts of afforestation programs thus requires a detailed understanding of the mechanisms whereby they affect biodiversity, particularly where new plantations are established close to areas important for open habitat species. Here, we examined how afforestation with oak, pine or eucalyptus trees, commonly planted in Mediterranean Europe, may have distinct effects on nest predation risk of grassland birds in southern Portugal. We used artificial nests with quail eggs and camera traps to: (i) identify nest predators and estimate predation risk of ground-nesting birds in grasslands adjacent to oak, pine and eucalyptus plantations across a distance gradient (0 m to 300 m) from the plantation edge; and (ii) examine how predation risk was influenced by avian predator abundance, sward height and vegetation clearing for photo-monitoring (nest-site manipulation), and their interactions with plantation type. Carrion crow was by far the main egg predator identified, followed by Montagu's harrier, raven and magpie. Overall, nest predation risk and predator abundance were higher around eucalyptus plantations, compared to either pine or oak plantations. Predation decreased with increasing sward height, but this effect was less noticeable when vegetation around nests was cleared. In pine and oak plantations, predation risk was slightly higher close to edges, and decreased with distance from the edge. Conversely, in eucalyptus plantations predation was lower close to edges, and increased with distance to edges. Distance effects around eucalyptus plantation were, however, absent in manipulated nests. Overall, results show that afforestation with different tree species has distinct impacts on predation risk of artificial nests in Mediterranean farmland. This is probably a consequence of an increasing structural complexity of the plantations, from oak to eucalyptus, driven by differences in tree growth rates and undergrowth cover. These findings suggest that farmland afforestation should favour agro-forest plantations with slow growing species (oak and pine) to mitigate negative effects on breeding grassland birds in adjacent open habitats.

2.2. Introduction

Large-scale afforestation (i.e., establishment of forest on farmland, grassland and other land not previously forested) is an increasingly common land-use change worldwide (Hansen *et al*., 2013; Arakwiye *et al*., 2017; Brazeiro *et al*., 2018; Jacoboski and Hartz, 2020). Initially, afforestation occurred mainly in northern hemisphere countries with high income and low forest cover (Ewers, 2006), where it was promoted by schemes such as the Common Agricultural Policy (CAP) under the European Council regulation EEC 2080/92 (Burrascano *et al*., 2016). Recently, however, afforestation is becoming more widespread, also affecting low-income countries, mainly in the tropics (Ribas *et al*., 2016; Curtis *et al*., 2018; Song *et al*., 2018) and southern hemisphere (Fernandes *et al*., 2016; Arakwiye *et al*., 2017; Bond *et al*., 2019). This is likely to expand even more in the near future, as a result of current and planned initiatives such as Reducing Emissions from Deforestation and Forest Degradation (REDD+; Corbera and Schroeder, 2011), the Trillion Trees campaign (Brancalion and Holl, 2020), the Bonn Challenge (Laestadius *et al*., 2015; Bond *et al*., 2019; García *et al*., 2020), the European Green Deal (European Commission, 2019) and the United Nations' Decade on Ecosystem Restoration (2021–2030) (Brancalion and Holl, 2020). These initiatives aim to mitigate the impacts of climate change (García *et al*., 2020) by increasing carbon sequestration, while also improving soil quality, reducing deforestation, forest degradation and promoting habitat restoration (Loyn *et al*., 2007; Curtis *et al*., 2018; Holl *et al*., 2020). Afforestation policies will thus receive unprecedented financial, political and societal support in the next decade (Brancalion and Holl, 2020).

Despite their potential environmental benefits, the biodiversity consequences of afforestation schemes are often ignored or presumed to be positive with limited supporting evidence (Barcena *et al*., 2014; Burrascano *et al*., 2016; Pretelli *et al*., 2018; Liu *et al*., 2019; Varela *et al*., 2020). While afforestation can be neutral or beneficial to certain widespread species (Loyn *et al*., 2007; Reino *et al*., 2009; Pita *et al*., 2009; Phifer *et al*., 2017; Jacoboski and Hartz, 2020), it often leads to declines in different fauna and flora species associated with early-successional or otherwise open habitat types (Bremer and Farley, 2010; Felton *et al*., 2010; Morgado *et al*., 2010; Gries *et al*., 2012; Bunce *et al*., 2014; Vasconcelos *et al*., 2019). This is a case in point where afforestation involves semi-natural grasslands, i.e., extensive pastures or meadows, mainly covered by spontaneous herbaceous vegetation, which often have diverse and unique plant and animal communities (Burrascano *et al*., 2016; Squires *et al*., 2018). While afforestation can increase the overall biodiversity of these systems, concerns have been raised about

its negative impacts on grassland biodiversity (Reino *et al*., 2009; Burrascano *et al*., 2016; Pretelli *et al*., 2018; Jacoboski *et al*., 2019). Moreover, there is still limited information on how to reduce impacts of forests that have been planted in the past, and how to plan and mitigate impacts of new plantations (Brancalion and Holl, 2020; García *et al*., 2020; Varela *et al*., 2020).

Afforestation can have particularly serious impacts on grassland birds, mainly through habitats loss and fragmentation (Shochat *et al*., 2001; Reino *et al*., 2009; Morgado *et al*., 2010; Pretelli *et al*., 2018; Jacoboski *et al*., 2019; Jacoboski and Hartz, 2020), but also by increasing nest predation in surrounding open areas (Santos *et al*., 2006; Sánchez-Oliver *et al*., 2014). In fact, forest plantations can provide refuges for avian predators such as corvids and generalist mammalian predators (Santos *et al*., 2006; Pita *et al*., 2009; Reino *et al*., 2010b), which can also benefit from the proliferation of highly fragmented landscapes (Chalfoun *et al*., 2002). Corvids, in particular, are frequently identified as major predators in grasslands associated with forest plantations (Andrén, 1992; Söderström *et al*., 1998; Draycott *et al*., 2008; Aebischer *et al*., 2015; Madden *et al*., 2015). These predators may also be favoured by increases in the populations of key prey, which often thrive in more fragmented landscapes (Reino *et al*., 2010a; 2010b; Batáry *et al*., 2014; Terraube *et al*., 2016; Fahrig *et al*., 2019). This is expected to increase nest predation risk in grassland habitats surrounding planted forests, particularly at habitat edges where predator activity is often concentrated (Morris and Gilroy, 2008; Šálek *et al*., 2010, Cox *et al*., 2012).

It is likely, however, that predator impacts are not uniform across plantation types, as predator abundance and activity may differ between forests with different tree composition and development (Reino *et al*., 2010a). For example, previous studies found that farmland afforestation with eucalyptus may favour particularly strong increases in predator abundances, probably because it results in tall and dense plantations that likely provide avian predators with suitable nesting sites, as well as perches for roosting and hunting (Santos *et al*., 2006, Reino *et al*., 2009, 2010a). In contrast, plantations with slower growing species such as oak or pine may take more time to develop conditions for generalist predators, with shorter trees also likely to provide less favourable lookouts for avian predators. Additionally, afforestation effects on nest predation risk may be conditional on the characteristics of the adjacent swards. For instance, while taller swards of vegetation may decrease nest detectability and negatively impact nest predation risk (Beja *et al*., 2014; Bellamy *et al*., 2018), high perching sites may provide vantage points for avian predators (Rice, 1983), which could lessen the nest cover provided by taller vegetation. While one or a subset of these factors have been previously

addressed, their combined effects have not been investigated (Reino *et al*., 2009; 2010a; Burrascano *et al*., 2016), thus making it difficult to have a full understanding of the mechanisms driving changes in grassland bird communities, which is crucial to minimise biodiversity impacts of afforestation schemes.

Here, we provide a case study focusing on the most common planted trees in Mediterranean Europe (oak, pine and eucalyptus), to analyse the effects of afforestation on nest predation risk in semi-natural grasslands of southern Portugal. The study area is representative of the Iberian cereal steppes, which are among the European farmland landscapes with highest conservation relevance to grassland birds (EEA, 2004; Bota *et al*., 2005). Nest predation risk was evaluated using a camera trap set up for predator identification, with artificial nests baited with quail (*Coturnix spp.*) eggs (quails are commonly found in the region) and placed at different distances (0-300 m) from the edge of each plantation type (oak, pine and eucalyptus) into the surround grassland matrix. We then analysed how nest predation rates varies with distance to plantations, and with the abundance of local predators and sward height. As camera traps can cause inaccuracies or potential bias in the outcomes of the experiment (Meek *et al*., 2016), we also considered the effects of placing a camera-trap near the nest, because this involved the removal of vegetation to clear the line of sight between the nest and cameras, and might thus affect nest detectability. Specifically, we tested the following hypotheses: (i) corvids are the main nest predators; (ii) main avian predator abundance is higher in grasslands surrounding eucalyptus plantations; (iii) predation risk is higher in grassland: (iii.a) adjacent to eucalyptus plantations compared to oak and pine plantations; (iii.b) with lower sward height due to increased nest detectability; (iii.c) and closer to plantation edges due to increased predator presence and nest detectability. Results from this study have implications for the design of policies aiming to support conservation management of current and future forest plantations on Mediterranean grasslands.

2.3. Methods

2.3.1 Study area

The study was conducted in southern Portugal, mostly within the Special Protection Area (SPA) of Castro Verde (**Figure 2.1**) designated to protect steppe birds under the European Union Birds Directive 79/409/EEC. The climate is Mediterranean, with mild winters (averaging 9°C [5-14°C] in January) and hot summers (24 °C [16-32°C] in July) and >75% of annual rainfall (500-600 mm) concentrated in October through March. The landscape is either flat or gently undulating (100-300 m a.s.l) and was traditionally dominated by either mosaics of shrubland interspersed with old fallow fields (up to 10

years) or agricultural fields cultivated with dry cereal crops in long rotations with fallows (2 to 5 years), mostly grazed by sheep at low densities (Delgado and Moreira, 2000; Moreira *et al*., 2007). In recent years the traditional system has shifted to a specialized production of either cattle or sheep (Ribeiro *et al*., 2016), with declines in cereal and fallow land, and increases in forage crops and permanent pastures (Ribeiro *et al*. 2014; 2016; Santana *et al*., 2017). Until the early 1990s, tree cover was largely restricted to some exotic eucalypt (*Eucalyptus* sp.) plantations and a few native open holm and cork oak (*Quercus rotundifolia* and *Q. suber*, respectively) woodlands grazed by livestock, mainly cattle and sheep, but also horses and pigs (Delgado and Moreira, 2000; Moreira *et al*., 2005; Reino *et al*., 2009). From 1994 to 1999, following the implementation of EEC regulation 2080/92 (Institute for Forestry Development, 2001), there was an increase in afforestation with native umbrella pines (*Pinus pinea*) and holm and cork oaks in the periphery of the SPA (Reino *et al*., 2010b). Oak plantations in the study area (**Figure 2.1**) contain sparsely spaced trees, with understories of pastures and fallow lands with a diverse coverage of grass and forb species, broadly similar to the grassland matrix (Vasconcelos *et al*., 2019). Pine plantations have more closely spaced trees, while still maintaining a mix of grasses and forbs with patches of bare rocky ground (Vasconcelos *et al*., 2019). Contrastingly, eucalypt plantations are usually older (50 to 70 years old), although several of these are regularly cut for wood due to their faster growth rate, thus resulting in overall taller trees and closed canopies, with very sparse herbaceous vegetation and, occasionally, dense patches of shrubs in the understory (Vasconcelos *et al*., 2019).

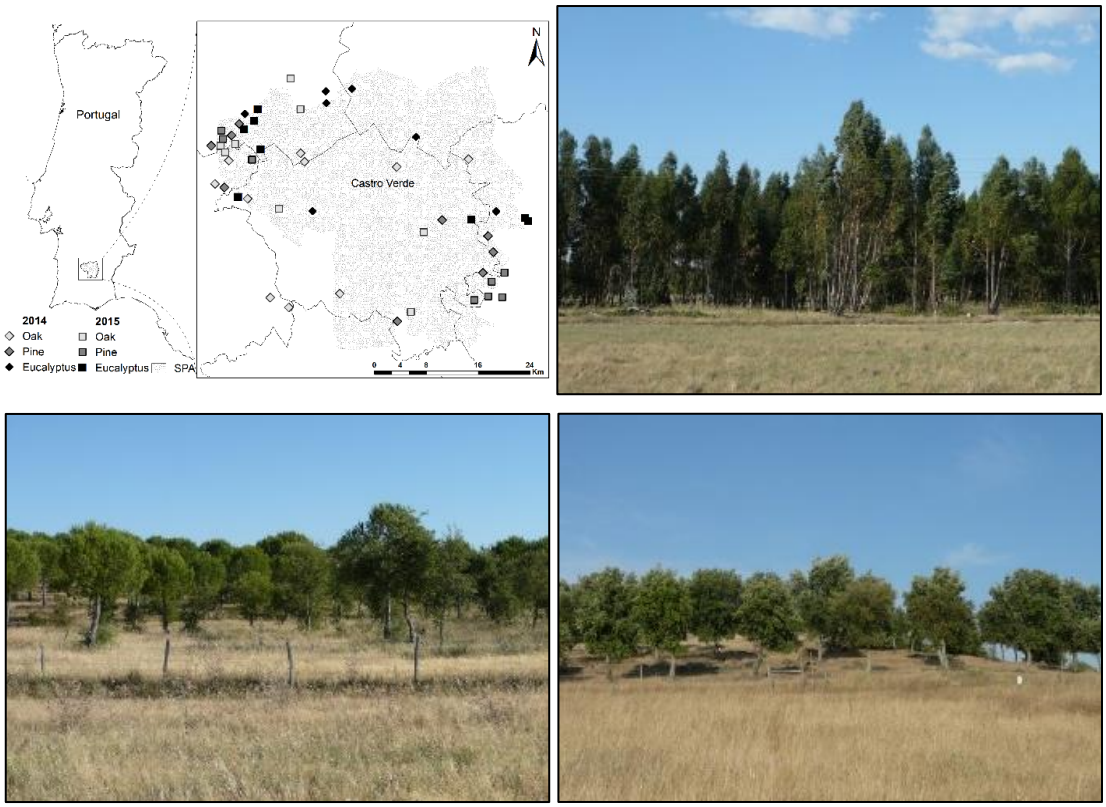

Figure 2.1 - a) Location of the study area in Southern Portugal, showing the Special Protection Area (SPA) of Castro Verde, and the distribution of the 51 sites sampled in 2014 (n= 26, in grey) and 2015 (n= 25, in black) across eucalyptus (n = 15), pine (n = 18) and oak (n = 18) plantations. Below, we provide examples of the **b)** Eucalyptus, **c)** Pine and **d)** Oak plantations and adjacent grassland (photo credits: J.S. Sánchez-Oliver).

2.3.2 Sampling design

Sampling was carried out at 51 sites (26 in 2014 and 25 in 2015; **Figure 2.1**). Site selection was based on sampling sites originally established in 2005 to study the effects of forest plantations on farmland birds (Reino *et al*., 2009). Briefly, plantations of the most common tree species were selected if the adjacent grassland parcel was at least 600 m long and wide, to allow sampling at distances up to 300 m from the nearest plantation edge. Selection was based on 1:25,000 land cover maps from 1990, updated through systematic field checking of new forest stands planted up to the beginning of 2005 (Reino *et al*., 2009). Of those, only sites that did not undergo considerable land use changes in 2014–2015, including, for instance, ploughing or cereal cultivation in grassland and tree harvesting in plantations, were retained. Additional sites were selected using satellite images from 2014 (GoogleEarth®), refined with field checking in 2014–2015 (Vasconcelos *et al*., 2019). The resulting sites consisted of a grassland parcel of fallow or pastureland, adjacent to a forest plantation stand (18 oak, 18 pine and 15 eucalyptus; **Figure 2.1**). Only one grassland parcel per plantation was established to avoid pseudo-replication and spatial autocorrelation (Fortin and Dale, 2009; Vasconcelos *et al*., 2019).

At each site, we established four 50-m radius sampling circles placed at 100-m intervals along a transect within the grassland parcel, perpendicular to the plantation-grassland edge (**Figure 2.2**). To adequately cover grassland and edge habitats, the 50-m circles were located as follows: (i) one circle centered on the plantation-grassland edge, and (ii) three circles in grassland centered at 100, 200, and 300 m from the plantation-grassland edge (**Figure 2.2**), as these distances appear to adequately encompass farmland bird responses to plantation edges (Reino *et al*., 2009; 2010a). In each site, and for each distance point, we identified the nest predators and estimated nest predation rate, sward structure and the abundance of avian predators.

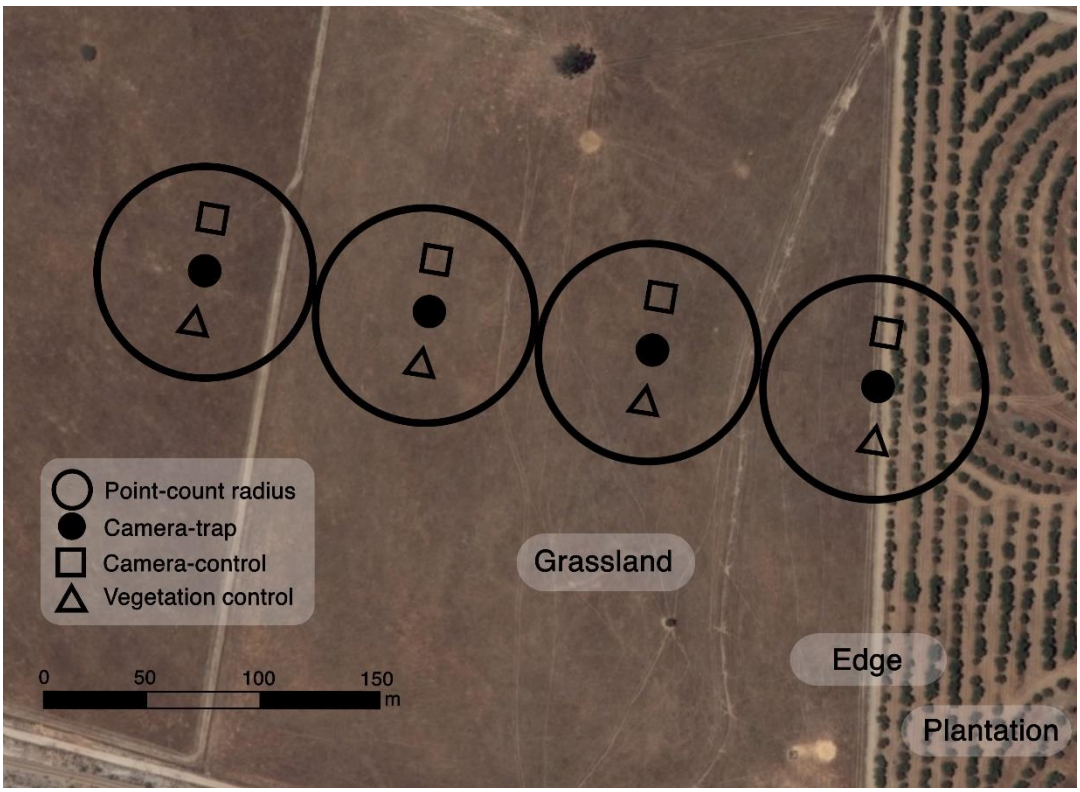

Figure 2.2 - Example of the spatial distribution of sampling sites in grasslands (fallow or pastureland) adjacent to forest plantations (oak, pine or eucalyptus; oak plantation in the photo), and schematic representation of the location of nests (camera-trap, camera-control and vegetation-control nests) and avian predator point-counts (50 m radius) along the 300 m long transects distributed at 100 m intervals (Image source: IFAP/ICNF, 2018).

2.3.3 Nest predators and nest predation risk

We identified nest predators and estimated nest predation risk at each site between April 17th and June 4th in 2014 and between April 7th and June 5th in 2015, with different plantations randomly selected to avoid temporal effect of breeding season. This study was based on an artificial nest experiment, commonly used due to cost-effectiveness and flexibility of experimental design (Batáry and Báldi, 2004; Sánchez-Oliver *et al*.,

2014; Huhta *et al*., 2015). Although the use of artificial nests has been criticised because they do not necessarily reflect predation rates on natural nests (e.g., Thompson and Burhans, 2004; Burke *et al*., 2004; but see Hoset and Husby, 2019), the method remains widely used to assess variation in predation risk in relation to habitats and predator communities (Batáry and Báldi, 2004; Huhta *et al*., 2015; Krüger *et al*., 2018; Bravo *et al*., 2020). The set-up consisted of three artificial nests placed 25-m apart, parallel to the plantation edge, in each 50-m circle (**Figure 2.2**). The nest at the centre of the circle (hereafter camera-monitored nest) was made with herbaceous vegetation collected near the nesting area and baited with two fresh quail eggs (*Coturnix* sp.), and then monitored using an automatic camera (Scoutguard SG570-6M; http://www.trail-camera.co.uk/scoutguard20SG570_6M.html) to identify predators and estimate predation risk. These are automatic cameras equipped with infra-red (IR) sensors and built-in IR LEDs functioning as a flash during the night, set to automatically take three sequential photos (trigger speed: 1.2 seconds) upon movement detection, with a 15 second delay between the following triggers. Cameras (n = 29) were placed in a metal bracket nailed to the ground (in grassland) or attached to trees (in plantation edges) and were supplied with 6V lead acid batteries. The camera and battery set-up were stored in a camouflaged box (Herranz *et al*., 2002; **Figure S2.1a**), to minimise their potential effects on the behaviour of nest predators (Meek *et al*., 2014; 2016). Herbaceous vegetation between the camera and the nest-site was manually trimmed or removed as needed to ensure an adequate field of view during shooting of photographs, and to avoid continuous camera-shooting due to the movement of herbs. All photographs were manually processed by a researcher (JF).

Since site manipulation can increase nest detectability (Suvorov *et al*., 2012), two types of artificial nests were used as controls to evaluate the effect of the camera (hereafter camera-control nest) and vegetation removal (hereafter vegetation-control nest) on nest predation risk (**Figure S2.1b-c**). The camera-control nest was similar to the camera-monitored nest but without camera (**Figure S2.1b**), while in the vegetation-control nest, the eggs were placed in a small depression in the soil and surrounding vegetation was not removed (**Figure S2.1c**). In total, 532 artificial nests were placed and verified after seven days, 204 of which were camera-monitored, and 164 nests for each control situation (camera- and vegetation-control nests), as we were unable to place controls for the first 10 sites where nests were deployed in 2014.

Vegetation-control nests represent non-manipulated nest-sites (manipulation = 0). Since nest-predation risk between camera-monitored and camera-control nests did not significantly differ (Fisher's exact test, F= 0.79; P = 0.295), we pooled their data in a

single variable describing nest-site manipulation (manipulation = 1). This variable aims to control for the effects of both camera presence and vegetation removal on nest predation risk potentially due to any increased nest detectability by avian predators.

Nests were set by two researchers (JSSO and JF), who avoided trampling the vegetation around the nests and wore rubber gloves and rubber boots to minimize potential human scent influence (Duncan *et al*., 2002), and to avoid potential biases due to variation in nest placement criteria. Nests position was recorded with a GPS tracker during placement and checked only once at the time of equipment removal to reduce potential observer effects and preserve nest concealment (Reino *et al*., 2010a; Ekanayake *et al*., 2015). We considered a predation event either the clear displacement or complete removal of an egg, along with beak, bite or claw marks visible on the eggshell (Reino *et al*., 2010a; Sánchez-Oliver *et al*., 2014). Images obtained by camera traps for each parcel were thoroughly verified to corroborate each predation event and identify nest predators at the species level. Multiple visits by the same species to a nest were only counted once and visits to the nest-site subsequent to the predation event were disregarded. Nest predation risk was characterized as a binary variable of the different outcomes: 0 if not depredated and 1 if at least one egg was depredated (**Table 2.1**).

2.3.4 Sward height

Sward height was characterized as the mean height of the herbaceous vegetation, which was estimated from four measurements evenly spaced in a ca. 50-cm radius around each nest, just outside the manipulated area (**Table 2.1**); measurements were taken during nest placement (**Figure S2.1**). This variable is uncorrelated with nest-site manipulation (Pearson's correlation coefficient = - 0.042; P = 0.331, **Table S2.1**), and conceptually different: sward height aims to measure the increase in nest safety from predators due to increased cover surrounding the nests, while nest-site manipulation intends to account for the impacts of manipulation on the protection normally offered by sward cover.

2.3.5 Avian predator abundance

Avian predators were surveyed at each site between April 1st and June 5th in 2014, and between April 11th and June 5th, 2015. Point-count surveys at each camera-monitored nest-site were performed to record all birds seen or heard during 10 minutes on nearly windless and rainless days (Bibby *et al*., 2000; Reino *et al*., 2009). To maximize detection probability, every point-count station was surveyed either at dawn or dusk. At each point, individual birds and flocks were identified and recorded on maps if they were <50 m from

the observer (**Figure 2.2**). Double counting of individuals between survey points was minimized because birds flying over without landing were not counted and when birds were suddenly flushed, extra care was taken to check if they landed in a potential survey point further ahead (Reino *et al*., 2009).

Predator abundance was defined as a discrete quantitative variable corresponding to the total number of individuals of each of the main avian predator species observed at each site, obtained by adding the counts of all four distance points together (**Table 2.1**). We grouped the four point counts because it was difficult to associate each bird with a single distance point given the short distances between consecutive points. Avian predators considered included the corvids carrion crow (*Corvus corone*), common raven (*Corvus corax*), and common magpie (*Pica pica*), and Montagu's harrier (*Circus pygargus*) (Arroyo, 1997; Terraube *et al*., 2010). The corvids Azure-winged magpie (*Cyanopica cooki*) and Eurasian Jay (*Garrulus glandarius*) were not considered as predators because there is, to our knowledge, no documented evidence of their nest-predation in grassland areas, likely due to their strong preference for woodland areas (Badge, 2020).

Table 2.1 - Variables considered in analyses, with respective description and prediction according to relevant references.

Variable	Type	Description	Prediction
Parcel	Random - Categorical	The sampling site associated with each grassland parcel and adjacent plantation stand	Used to account for lack of independence among sites at different distances within each parcel (Reino *et al*., 2009)
Plantation type	Fixed - Categorical	The type of plantation adjacent to where nests were placed (Eucalyptus, Pine and Oak)	Steeper decreases in risk associated with Eucalyptus than Pine or Oak (Reino *et al*., 2009; 2010a)
Distance	Fixed - Continuous	Distance starting from the edge of the plantation and extending into the adjacent grassland (0, 100, 200 and 300 meters)	Linear decrease of predation risk with increasing Distance (Reino *et al*., 2010a)
Predator abundance	Fixed - Discrete quantitative	Total number of individuals of the main avian predator species detected per site	Linear increase associated with higher predator abundance (Beja *et al*., 2014; Bravo *et al*., 2020)
Sward height	Fixed - Continuous	The mean height of 4 evenly spaced measures of the herbaceous vegetation surrounding the nest	Linear decrease associated with higher sward height (Bellamy *et al*., 2018)
Manipulation	Fixed - Binary (0/1)	The effects of camera presence and consequent removal of herbaceous vegetation to clear the camera field of view	Higher predation risk associated with Manipulated nests (Meek *et al*., 2014; 2016)

2.3.6 Statistical analysis

To begin, we investigated if there were noticeable differences in the total abundance of the main avian predators found across plantations. For this, we tested the relationship

between predator abundance and plantation type (oak, pine and eucalyptus), using a generalized linear model (GLM) with Poisson errors and a log link function after testing for overdispersion (dispersion parameter = 1.16; *P* = 0.057; Kleiber and Zeileis, 2008). Pair-wise Chi-squared tests were also performed to estimate the differences in predator abundance between each plantations type.

Then, we investigated how nest predation risk varied with distance from edges (0 m,100 m, 200 m, 300 m), forest plantation type (oak, pine and eucalyptus), predator abundance, sward height, and nest-site manipulation, using generalized linear mixed models (GLMM; Bates *et al*., 2015) with binomial errors and a logit link function. Interaction terms were added to test how distance effects varied with plantation type and predator abundance, and how sward height effects varied with nest site manipulation. Distance was specified as a continuous variable despite responses being estimated only at 100-m intervals, because categorisation would reduce the power of analysis by increasing the degrees of freedom (i.e., one versus three, for each term including distance), and because this specification allowed for detecting monotonic increases (or decreases) of the response variables even if only approximately linear. Detecting more complex non-linear responses (e.g. unimodal), would require a denser sampling of distances and larger sample sizes. GLMM was used to account for lack of independence among sites at different distances within each parcel, treating parcels as random effect (Zuur *et al*., 2009), resulting in the following candidate full model:

$$Predation \sim distance + plantation + pred.abundance + sward\ height + manipulation + distance{:}\,plantation + plantation{:}\,pred.abundance + sward\ height{:}\,manipulation + (1|parcel).$$

Lastly, we modelled predation risk separately for nests placed close to oak, pine and eucalyptus plantations, to examine how nest manipulation effects interacted with distance from the edge and sward height simultaneously, in different plantation types. This modelling strategy was used instead of incorporating plantation type and the interaction terms in the global model described above, due to lack of convergence. We used GLMM with binomial errors and logit link function with the same fixed and random effects described above, except plantation type, resulting in the following candidate model for each type of plantation:

$$Predation_{plantation} \sim distance + pred.abundance + sward\ height + manipulation + distance{:}\ sward\ height + distance{:}\ manipulation + sward\ height{:}\ manipulation + distance{:}\ sward\ height{:}\ manipulation + (1|parcel).$$

Model selection was performed by starting from a candidate full model and sequentially dropping the least significant variables and testing the effects of removing them in the model deviance with a chi-square test. We kept only variables whose removal caused significant decreases in model deviance ($P < 0.10$). If multiple variables simultaneously did not meet these criteria, we prioritized dropping the most complex interaction first.

Overdispersion tests were performed using "dispersiontest" function from the AER package (Kleiber and Zeileis, 2008). GLMM models were developed using "glmer" function, from the lme4 package (Bates *et al*., 2015), and model selection was performed using "drop1" function from the stats package (R Core Team 2020). All analyses were performed using R 3.6.4 software (R Core Team 2020).

2.4. Results

2.4.1 Overall patterns

Overall, the mean proportion of nests depredated was higher at the plantation edge (mean ± SE = 0.50 ± 0.04) than at any other distance point in the grassland matrix (mean ± SE = 0.43 ± 0.02; **Figure 2.3a**, **Table 2.2**). This overall pattern was found for pine and oak plantations, but not for the eucalyptus plantations, which had lower mean predation rates at edges than farther away (**Figure 2.3a, Table 2.2**).

Overall, mean sward height was higher in grassland than at plantation edges (**Figure 2.3b, Table 2.2**). For different plantation types (**Figure S2.2**), mean sward height was highest around eucalyptus but lowest at its edges. Sward in the grassland matrix near oak plantations was comparatively shorter but with similar mean sward height at the edges. Mean sward height was lowest in the grassland matrix associated with pine plantations, being particularly low at the plantation edge.

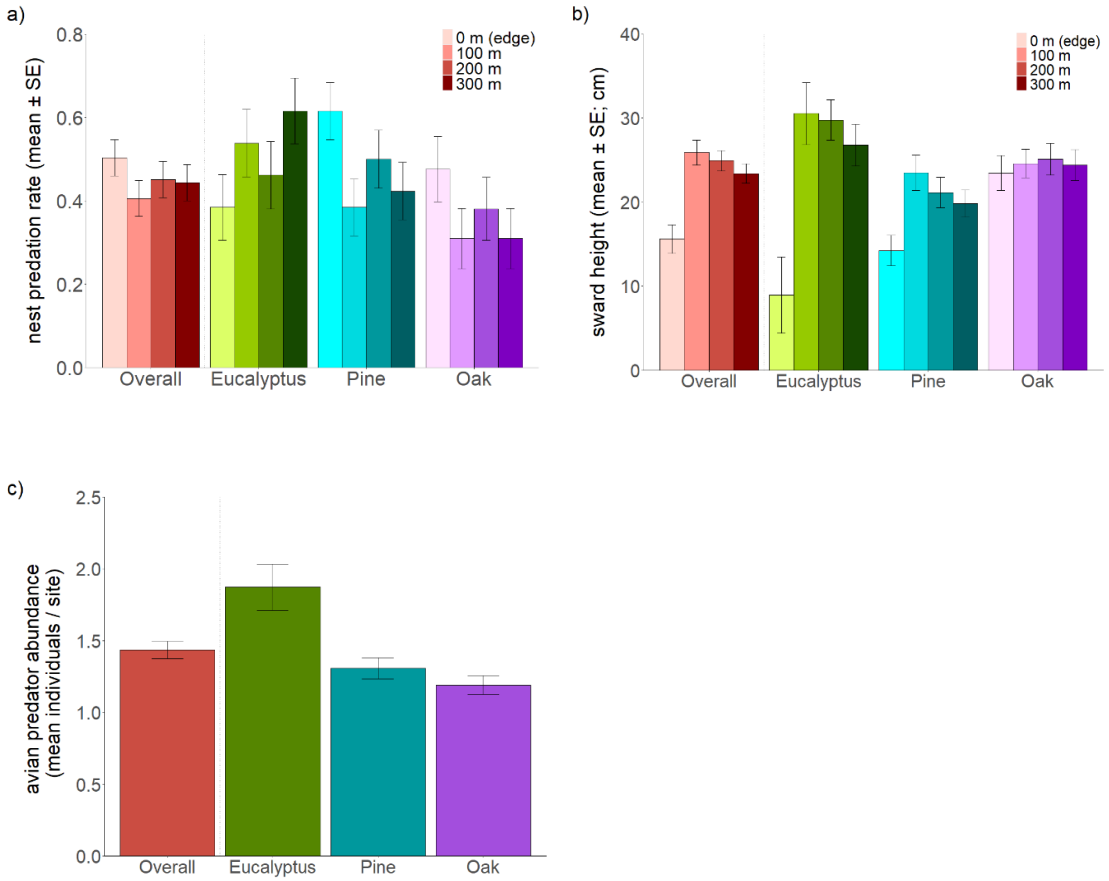

Figure 2.3 - Mean ± SE (before model tests) for: a) nest predation rate in relation to distance points; b) sward height (cm) surrounding the nest in relation to distance points; and c) avian predator abundance per site in relation to plantation types. Transparency scale in legend applies for each plantation colour.

2.4.2 Avian predator abundance

The most abundant (mean count per site ± standard error) avian predators recorded were the carrion crow (0.63 ± 0.12) and the Montagu's harrier (0.43 ± 0.10), followed by the common raven (0.20 ± 0.08) and common magpie (0.18 ± 0.08) (**Figure 2.4; Table S2.2**). The abundance of avian predators varied significantly across plantation types (X^2 = 28.77; P < 0.001), being higher near eucalyptus plantations (1.87 ± 0.16), compared to pine (1.31 ± 0.07, *Z* = -2.35; *P* = 0.019) and oak plantations (1.19 ± 0.07, *Z* = -2.82; *P* = 0.005; **Figure 2.3c; Table 2.2**).

Table 2.2 - Description and summary statistics [mean ± SE (min-max)] describing variation between habitat type (grassland and edge) and plantation type (edge + grassland: eucalyptus, oak and pine) in predation rate, sward height and predator abundance. Predator abundance was surveyed at each sampling site without distinction between grassland and edge due to the difficulty in associating each counted bird with the correct habitat type given the short distances between survey points and bird movements between each point count.

Variable	Description	Total	Habitat type		Plantation type (Edge + Grassland)		
			Grassland	Edge	Eucalyptus	Oak	Pine
Predation rate	Presence (1) / absence (0) of nest predation per transect.	0.45 ± 0.02 (0-1)	0.43 ± 0.02 (0-1)	0.50 ± 0.04 (0-1)	0.50 ± 0.04 (0-1)	0.37 ± 0.04 (0-1)	0.48 ± 0.03 (0-1)
Sward height	Mean height of herbaceous vegetation in cm, estimated from 4 measurements taken around each nest.	22.38 ± 0.72 (0-175)	24.64 ± 0.74 (2.5-98.5)	15.60 ± 1.70 (0-175)	23.99 ± 1.82 (0-175)	24.38 ± 0.93 (0-64)	19.56 ± 0.94 (0-65)
Predator abundance	Total number of individuals of the main avian predator species in the sampling site.	2.53 ± 0.13 (0-17)	-	-	4.23 ± 0.75 (0-17)	1.33 ± 0.15 (0-3)	2.23 ± 0.22 (0-6)

Figure 2.4 - Camera trap photos of the main nest-predators. In order of abundance, the carrion crow (top-left), the common raven (top-right), the common magpie (bottom-left) and the Montagu's harrier (bottom-right).

2.4.3 Nest predator identification

We obtained more than 770,000 photos for the 204 camera-trapped nests (up to 4000 photos/nest). Predators appeared in ca 0.35% of the photos (2153 photos, an average of 42.2 predator photos/parcel). After excluding nests trampled by cattle (18 out of 532 nests, 3.4%), nearly half (46.1%) of the camera-monitored nests were depredated (94 out of 204) by at least 13 different species, which were successfully identified in 72% of the predation events (**Figure S2.4; Table S2.3**).

Carrion crow was the main nest predator (**Table S2.3**), accounting for 40.4% of depredated nests (n = 38), followed by Montagu's harrier (n = 8; 8.5%), common raven (*Corvus corax*, n = 4; 4.3%) and common magpie (n = 2; 2.1%). Mammals represented only 11.7% of total depredated nests, involving mainly cattle (*Bos taurus*, n = 4; 4.3%, excluding trampling), garden dormouse (*Eliomys quercinus*) (n = 2; 2.1%) and red fox (*Vulpes vulpes*) (n = 2; 2.1%).

2.4.4 Factors affecting overall nest predation rate

Nest predation rate was significantly related to all predictors, except predator abundance, including the main effects of sward height and nest-site manipulation, and the interactions between distance * plantation type and sward height * nest-site manipulation (**Table 2.3**). Nest predation increased with distance from eucalyptus plantations, but no significant distance effects were found for oak and pine plantations (**Figure 2.5; Table 2.5 and 2.6**). Overall predation rate was lower in grasslands adjacent to oak (mean ± SE = 0.37 ± 0.04) and pine plantations (mean ± SE = 0.48 ± 0.03), than eucalyptus plantations (mean ± SE = 0.50 ± 0.04; **Figure 2.5, Table 2.2**).

Table 2.3 - Goodness of fit tests of the predation risk for the overall generalized linear mixed model (GLMM) obtained after variable selection. For each model term we provide degrees of freedom (Df), Akaike Information Criteria (AIC) scores, Likelihood Ratio Test (LRT) outputs and significance level (*P*). **Bold** denotes $P < 0.10$.

	Df	**AIC**	***LRT***	***P***
NULL	NA	639.17	NA	NA
distance	0	639.17	0.00	0.999
plantation type	2	637.31	2.14	0.541
sward height	1	656.07	18.90	**<0.001**
manipulation	1	647.16	10.00	**0.002**
distance : plantation type	2	648.75	13.58	**0.001**
sward height : manipulation	1	644.05	6.89	**0.009**

Manipulation significantly affected overall nest predation rate (**Table 2.3**). Nest predation rate was consistently ca. 20% lower in non-manipulated nests irrespective of plantation type, and it decreased with increasing sward height, particularly in non-manipulated nests (**Figure 2.5; Table 2.4**). In manipulated nests around eucalyptus plantations there were no significant effects of distance and sward height (**Figure 2.5a-b**).

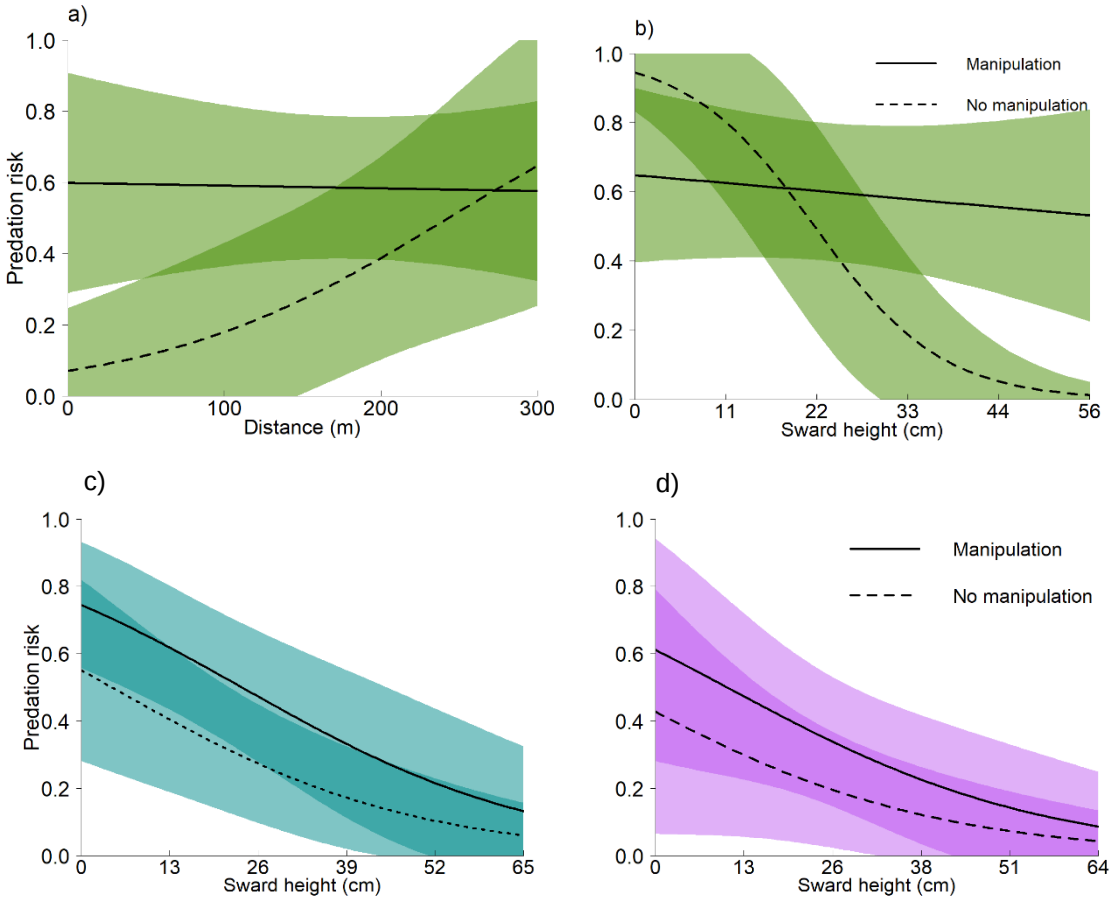

Figure 2.5 - Predicted nest predation risk in grassland adjacent to (a-b) eucalyptus, (c) pine, and (d) oak plantation forests, in relation to distance to grassland-plantation edge (a) and sward height (b-d). Predicted values (black line) and 95% confidence intervals (shaded area), for manipulated (filled line) and non-manipulated (dashed line) nests are represented. See also **Tables 2.5 and 2.6.**

Table 2.4 - GLMM of overall predation risk with selected parameters. For each parameter we provide the coefficient estimate (β), its standard error (SE), *z*-value and significance level (*P*). **Bold** denotes $P < 0.05$.

	β	**SE**	**Z-value**	***P***
(Intercept)	-1.34	0.51	-2.59	0.010
distance	**0.56**	**0.19**	**3.02**	**0.003**
pine	0.90	0.63	1.46	0.150
oak	0.41	0.65	0.62	0.530
sward height	**-1.08**	**0.27**	**-3.99**	**<0.001**
manipulation	**0.74**	**0.24**	**3.13**	**0.002**
distance : pine	**-0.76**	**0.24**	**-3.23**	**0.001**
distance : oak	**-0.80**	**0.25**	**-3.21**	**0.001**
sward height : manipulation	**0.71**	**0.28**	**2.55**	**0.011**

2.4.5 Effects of plantation type on predation rate

There was a significant effect of distance to eucalyptus edge, which negatively interacted with manipulation ($\beta_{euc.} = -1.15$; $P_{euc.} = 0.028$). Additionally, there was a positive interaction between sward height and nest-site manipulation ($\beta_{euc.} = 2.67$; $P_{euc.} = 0.0024$; **Table 2.5** and **2.6**), with predation rate of non-manipulated nests increasing with distance from the plantation edge and decreasing with sward height (**Figure 2.5a-b**).

Predation rate was significantly affected by sward height and nest-site manipulation around pine ($X^2_{pine} = 11.38$; $P < 0.001$) and oak ($X^2_{oak} = 4.21$; $P = 0.041$) plantations (**Table 2.5b-c** and **2.6b-c**), with stronger effects for sward height (LRT = 3.75, $P = 0.053$) than for manipulation (LRT = 2.92, $P = 0.087$) around oak plantations (**Table 2.5c**). Predation risk significantly decreased with sward height around pine ($\beta_{pine} = -0.61$; $P_{pine} = 0.007$), but less so around oak plantations ($\beta_{oak} = -0.53$; $P_{oak} = 0.063$).

Manipulation affected predation rate in eucalyptus plantations by reducing the effects of the other predictors, with nest-predation rates becoming largely similar irrespective of distance to edge and sward height (**Figure 2.5a-b**). Predation rate increased with nest-site manipulation in pine plantations ($\beta_{pine} = 0.86$; $P_{pine} = 0.02$) and weakly so in oak plantations ($\beta_{oak} = 0.74$; $P_{oak} = 0.09$) (**Figure 2.5c-d**, **Table 2.5** and **2.6**).

Table 2.5 - Goodness of fit tests of the predation risk GLMM for each plantation type model obtained after variable selection. For each model term we provide degrees of freedom (Df), Akaike Information Criteria (AIC) scores, Likelihood Ratio Test (LRT) outputs and significance level (*P*). **Bold** denotes $P < 0.10$.

	Df	AIC	*LRT*	*P*
Eucalyptus				
NULL	NA	193.79	NA	NA
distance	1	203.29	11.50	**<0.001**
sward height	1	209.92	18.12	**<0.001**
manipulation	1	198.97	7.18	**0.007**
distance : manipulation	1	197.43	5.63	**0.018**
sward height : manipulation	1	205.69	13.89	**<0.001**
Pine				
NULL	NA	246.18	NA	NA
sward height	1	251.83	7.65	**0.006**
manipulation	1	249.94	5.76	**0.016**
Oak				
NULL	NA	202.72	NA	NA
sward height	1	204.47	3.75	**0.053**
manipulation	1	203.65	2.92	**0.087**

Table 2.6 - GLMM of predation risk for each plantation type with selected parameters. For each parameter we provide the coefficient estimate (β), its standard error (SE), *z*-value and significance level (*P*). **Bold** denotes $P < 0.05$ and **grey** denotes $P < 0.10$.

	β	SE	Z-value	*P*
Eucalyptus				
(Intercept)	-2.69	0.98	-2.76	**0.006**
distance	1.42	0.48	2.93	**0.003**
sward height	-2.73	0.84	-3.23	**0.001**
manipulation	2.45	1.01	2.43	**0.015**
distance : manipulation	-1.15	0.52	-2.19	**0.028**
sward height : manipulation	2.67	0.88	3.04	**0.002**
Pine				
(Intercept)	-0.68	0.44	-1.55	0.120
manipulation	0.86	0.36	2.38	**0.017**
sward height	-0.61	0.23	-2.71	**0.007**
Oak				
(Intercept)	-1.36	0.55	-2.11	**0.014**
manipulation	0.74	0.44	1.69	**0.090**
sward height	-0.53	0.29	-1.86	**0.063**

2.5. Discussion

This study showed that corvids, and particularly the carrion crow, were the most important nest predators in our Mediterranean grasslands surrounding forest plantations. Specifically, we found that predator abundance was generally higher in grassland areas adjacent to eucalyptus plantations. Our study also showed that nest predation risk around eucalyptus plantations was lower near edges and increased into the grassland, contrasting with oak and pine plantations where predation risk was similar across all distances from edge, although highest at the edges. Furthermore, this study supported the idea that nest predation risk increases with decreasing sward height, likely because nests are less concealed in shorter vegetation and consequently more detectable by predators (Lyons *et al*., 2015; Bellamy *et al*., 2018). Our results provide insight for ongoing and future afforestation schemes, highlighting potentially different impacts on grassland birds depending on the type of adjacent plantation.

2.5.1 Predators identity and abundance

Our study supported the idea that corvids are important nest predators in Mediterranean farmland (Rodewald *et al*., 2011; Beja *et al*., 2014; Sánchez-Oliver *et al*., 2014). Carrion crows depredated almost half of the nests monitored with camera-traps, while ravens and common magpies were only responsible for a few nest losses. Of these corvid species, the carrion crow is considered the most important predator near edges of forest plantations, leading to increased predation rates (Andrén, 1992). This is corroborated by a recent camera-trap study where corvids were also the main predators, and carrion crows accounted for more than half of predation events (Bravo *et al*., 2020). Although less important, Montagu's harrier was also responsible for the loss of several nests, confirming the opportunistic foraging strategy of this raptor (Terraube and Arroyo, 2011). The abundance of avian predators was significantly higher around eucalyptus plantations than around pine or oak plantations, probably reflecting differences in the structure of forest plantations. Eucalyptus plantations are composed of faster growing trees with taller and denser canopies (Reino *et al*., 2009; Vasconcelos *et al*., 2019), which provide more suitable habitat for generalist predators such as corvids (Chalfoun *et al*., 2002; Pita *et al*., 2009) than pine and oak plantations. In contrast, oak and pine plantations were composed of shorter trees because of their slower growth, which are sparsely spaced with pasture understories broadly similar to the grassland matrix (Vasconcelos *et al*. 2019, **Figure 2.1**), thus offering less breeding and foraging habitat for avian predators than eucalyptus plantations (Reino *et al*., 2009).

All the species identified as important nest predators were also the most abundant predators detected in the study area, suggesting that a higher availability of predators may lead to increased nest predation risk. However, predator abundance was not selected as a significant predictor of predation risk, nor was it significantly related to predation events (result not presented). This may be because our surveys did not differentiate between breeding pairs and floaters, as only the former was found to relate significantly to risk of predation by corvids (Erikstad *et al*., 1982; Bravo *et al*., 2020). As such, if we detected mostly floaters, it is likely that our predictor of predator abundance poorly correlates with predation risk (Bravo *et al*., 2020). Additionally, the most common predator, carrion crow, tended to occur very frequently near eucalyptus patches, due to their need of forest cover for breeding. But most contacts with this species during counts were mainly vocal, as the birds were persistently vocalizing through their common contact calls. This should help alleviate any potential bias that could occur due to lower detection probability around the taller and denser eucalyptus forest edges.

Our results are in line with other studies conducted in Mediterranean farmland areas that also observed a significant majority of avian predators (Reino *et al*., 2010a; Krüger *et al*., 2018; Ponce *et al*., 2018). However, mammal and reptile predators such as foxes, domestic dog, rats, hedgehogs or snakes may also play a role in shaping nest predation (Batáry and Báldi, 2004; Reino *et al*., 2010a; Beja *et al*., 2014; Arbeiter and Franke, 2018). Although mammals represented a small part of the total predation events detected in camera-traps in our study (ca. <11%), we do not know the real dimension of their impacts on predation as we were unable to identify predators in ~30% of the depredated nests. Despite this, in the unlikely chance that all unknown events were from mammals, corvids would still dominate nest-predation events. Livestock grazing may also contribute to reduce nest survival rates (Beja *et al*., 2014) through nest destruction caused by livestock trampling or nest predation. In our study, trampling by cattle represented 3.4% of total nests destroyed, while 4.3% of all depredated nests were depredated by cattle. Despite their impact being low when compared to overall corvid predation (55.3%), it still represents a higher impact than several individual species. However, this is unlikely to change the main conclusions of this study, as we were primarily interested in the effects of afforestation on nest predation risk. While livestock may significantly reduce nest survival, their occurrence and abundance in grassland stands is driven by human decisions for grazing purposes independent of adjacent plantation stand composition.

2.5.2 Contrasting edge effects by plantation type on nest predation risk

Contrary to expectations, overall nest predation risk remained unchanged with distance to plantation edge, though there was a significant positive effect for the main distance predictor in the general model. The lack of an overall distance effect likely results from the contrasting effects of this variable for different plantation types, and should be carefully interpreted without such context, following the principle of marginality (Nelder, 1977). Indeed, we found that nest predation risk increased significantly with distance from the edge in eucalyptus plantations, but remained stable and overall lower in the grasslands adjacent to oak and pine plantations.

The increase in nest predation risk farther into the grassland around eucalyptus plantations likely occurs because these have generally taller trees that can provide a better vantage point near the plantations' edges, thus increasing nest detectability into the adjacent grassland (Rice, 1983; Eggers *et al*., 2008). This can also increase the likelihood of the spill-over of carrion crow (Reino *et al*., 2009; 2010a), as they often nest in tall trees (Santos *et al*., 2006) and feed in adjacent open farmland (McCollin, 1998) by adapting to their prey's habitat preferences in order to opportunistically consume them (Anderson and Burgin, 2008).

In the case of oak and pine plantations, the lack of differences in predation risk across distances may reflect the similarity between the plantation understory and the adjacent grassland, with very similar sward heights and sparse and shorter trees, especially in the case of oak plantations (Vasconcelos *et al*. 2019). Contrary to eucalyptus plantations, these trees would also provide less advantage in detecting prey at increasing distances into the grassland (Rice, 1983), resulting in similar predation efforts between edge and the adjacent grassland matrix.

While reduced predation risk near the plantation edge may appear to be a potential benefit of eucalyptus plantations, careful analysis actually suggests otherwise. In this study, the use of artificial nests allowed us to place them evenly along a gradient in distance from plantation edges. However, grassland birds, particularly grassland specialists such as the calandra lark (*Melanocorypha calandra*) and short-toed lark (*Calandrella brachydactyla)*, are more likely to nest farther into the grassland, as several of these species are known to be edge avoiders, placing their nests far from plantation edges (Reino *et al*., 2009; 2010a; Morgado *et al*., 2010; Pretelli *et al*., 2018), where plantation risk was found to be higher.

2.5.3 Camera trapping effects on nest predation

The effects of nest-site manipulation, consisting of camera placement and vegetation removal in front of the camera-trap to reduce the number of photos from vegetation in

movement due to the wind, led to consistently higher levels of nest predation. This likely reflects the potential of cameras to sometimes attract animals (Meek *et al*., 2016), thus increasing nest detection and inherent predation risk. Moreover, vegetation removal may have increased the detectability of nests by reducing the camouflage effects normally provided by the higher sward height. In our study, interaction effects between nest-site manipulation, distance to edge, and sward height were found in eucalyptus plantations. Predation risk in grasslands surrounding these plantations became unchanged by sward height and distance when nests were manipulated. In the case of pine and oak plantations, manipulation increased the overall predation risk across the entire sward height gradient. This difference could be explained by the higher number of corvids in eucalyptus plantations compared to other areas, which can lead to changes in predation rates in the adjacent area (Andrén, 1992; Lyons *et al*., 2015; Bellamy *et al*., 2018). For instance, corvids may take advantage of the higher perches of eucalyptus trees (Santos *et al*., 2006) to optimize their foraging abilities, extending their ability to detect nests farther into the taller swards of grassland (Rice, 1983; Eggers *et al*., 2008; Bellamy *et al*. 2018). This detection is enhanced by increased visibility due to vegetation removal in nest sites, even with higher sward height surrounding it. Overall, despite generally increasing predation risk associated with distance and sward height effects in eucalyptus plantations, nest-site manipulation did not significantly affect predator identity or nest predation risk by plantation type.

2.5.4 Management Implications

Our results highlight a major concern in the conservation of several key species associated with Mediterranean farmland, such as calandra larks, little and great bustards (*Tetrax tetrax*), Montagu's harrier or greater short-toed larks. These species, normally associated with open habitats, are directly affected through habitat loss due to former and current plantation practices (Bremer and Farley, 2010; Morgado *et al*., 2010; Jacoboski and Hartz, 2020). We fear this effect may be further exacerbated by loss of habitat quality due to increased nest predation, as these open farmland species normally opt to breed at safer distances further from plantations (Fletcher Jr., 2005; Reino *et al*., 2009; Morgado *et al*., 2010). This may lead to an asymmetrical impact by eucalyptus plantations compared to oak or pine stands, due to the observed increase in nest predation risk away from edges.

Several studies have suggested that afforestation practices worldwide should avoid areas preferred by open-habitat species of conservation concern to avoid exacerbating potentially negative consequences on them (see also: Graham *et al*., 2017;

Brazeiro *et al*., 2018; Gómez-Catasús *et al*., 2018; Cravino and Brazeiro, 2021). Although we did not aim to assess the impacts of afforestation by plantation forests on nest predation risk, we should note that a previous study conducted in a relatively close area but without nearby plantations observed noticeably lower predation rates (0.18 ± 0.23 SD, Beja *et al*., 2014), compared to our observed overall predation risk (ca. 0.45). Regarding plantation type, afforestation practices that focus on eucalyptus or other fast-growing tree species could represent an increased risk for grassland bird specialists (Reino *et al*., 2009; 2010a; Saccol *et al*., 2017; Jacoboski and Hartz, 2020). In situations where these are of particular concern, afforestation policies could instead prioritise plantations with lesser impact on local biodiversity such as oak, pine, or other slower growing native species (Sánchez-Oliver *et al*., 2014; Bellamy *et al*., 2018; Magnano *et al*., 2019; Vasconcelos *et al*., 2019). These species also seem to provide an additional advantage in one of the main targets of current and future afforestation policies: greater carbon accumulation and sequestration (He *et al*., 2018; García *et al*., 2020; Xiong *et al*., 2020).

Moreover, efforts should be made to preserve the quality of areas of grassland habitat when these harbour grassland specialists. This could be achieved by removing small tree rows whenever possible, and the use of selective patch-burn grazing, focusing on maintaining taller swards of vegetation to provide refuge for ground-nesters and decrease predation risk (Klug *et al*., 2010; Ellison *et al*., 2013; Arbeiter and Franke, 2018; Skagen *et al*., 2018).

A more controversial management option (Beja *et al*., 2009; Treves *et al*., 2016; 2019) would be the culling of key predators such as the carrion crow, which seems to have a disproportionately higher predation impact compared to other predators in our and other Mediterranean grasslands (Smith *et al*., 2010; Phifer *et al*., 2017; Bond *et al*., 2019). However, this approach is costly, time-consuming and sometimes ineffective (Bolton *et al*., 2007; Madden *et al*., 2015), with a high likelihood of increasing dispersal and replacement rates (Marzluff and Heinrich, 1991; Bodey *et al*., 2009). As such, a better approach could be to understand in detail the feeding behaviour of corvids, by comparing nest predation between areas rich and poor in alternative corvid food (i.e., insects and worms) and testing the provision of alternative food sources in areas where nests may be at a higher risk (Bravo *et al*., 2020). We believe that careful consideration and selective implementation of these measures can economically and environmentally benefit the outcome of these afforestation schemes.

2.6. Conclusions

The carrion crow was the principal nest predator in our Mediterranean grassland area. Different plantation types can have different impacts on predation risk in the surrounding grasslands by providing potentially distinct advantages for predators targeting grassland bird species. Among oak, pine and eucalyptus, the latter was associated with significantly more predator presence than other plantation types. Furthermore, while its impact on predation risk was lower near edges, it seemed to extend farther into the grassland area, potentially exacerbating its negative effects on certain species. Considering these results, we advise that afforestation practices should carefully consider between the use of eucalyptus or other fast-growth species, and slower growing species such as oak and pine, particularly when targeting grassland patches with high conservation value. Finally, we suggest potential alternatives to reduce predation risk, from the less favourable culling of the main corvid predators, to focusing instead on alternative resource availability and habitat improvement, which may tie into the suggested afforestation measures. The successful consideration of these measures in ongoing and future large-scale afforestation schemes may not only reduce their impacts, but also help achieve carbon sequestration goals while keeping sustainable grassland biodiversity levels.

2.7. Credit authorship contribution statement

João Faria: Data curation, Formal analysis, Investigation, Writing - original draft, Writing – review & editing**. Juan S. Sánchez-Oliver:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing**. Pedro Beja:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing**. Francisco Moreira:** Investigation; Writing – review & editing**. Inês Catry:** Investigation; Writing – review & editing**. Sasha Vasconcelos** Investigation; Writing – review & editing**. Sílvia Pina:** Investigation; Writing – review & editing**. John T. Rotenberry:** Investigation; Writing – review & editing**. Luís Reino:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing**. Joana Santana:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – review & editing**.**

2.8. Declaration of conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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2.11. Supplementary material

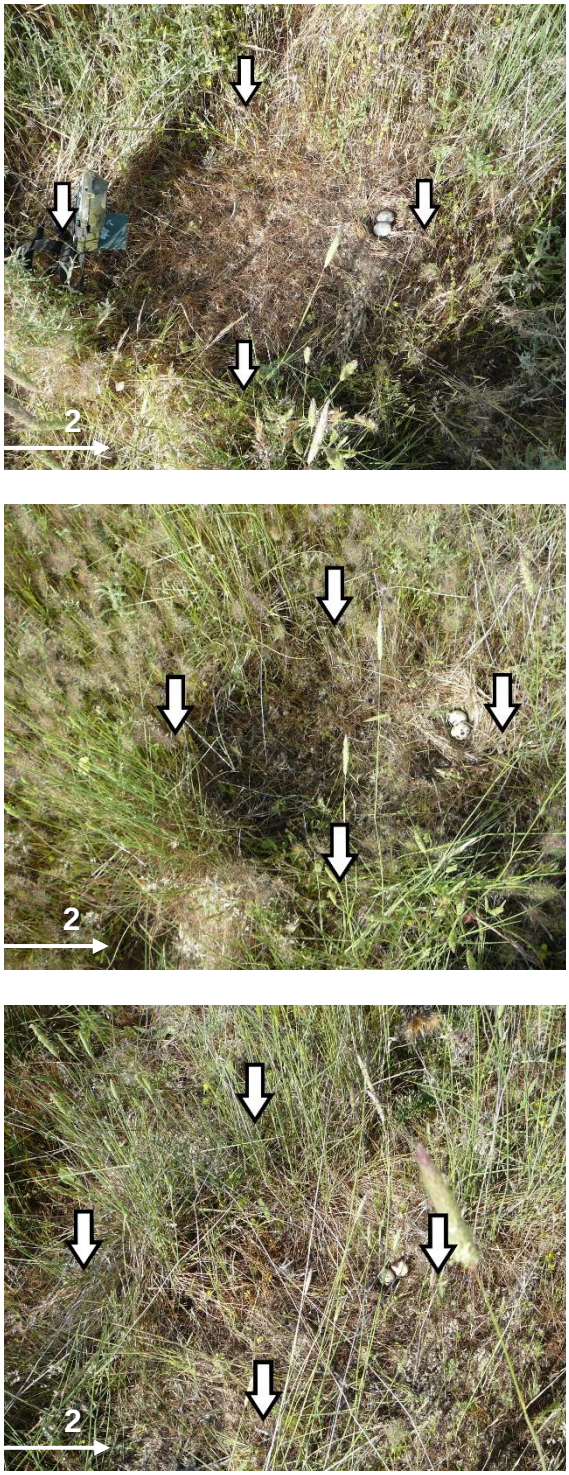

Figure S2.1 - Images from the three types of experimental nests in grassland. (A) camera-monitored nest (with camouflaged camera); (B) camera control nest (with no camera); (C) vegetation control nest (with no camera and no vegetation clearing). The white arrows (ca. 50 cm apart) indicate the four points where we measured vegetation height.

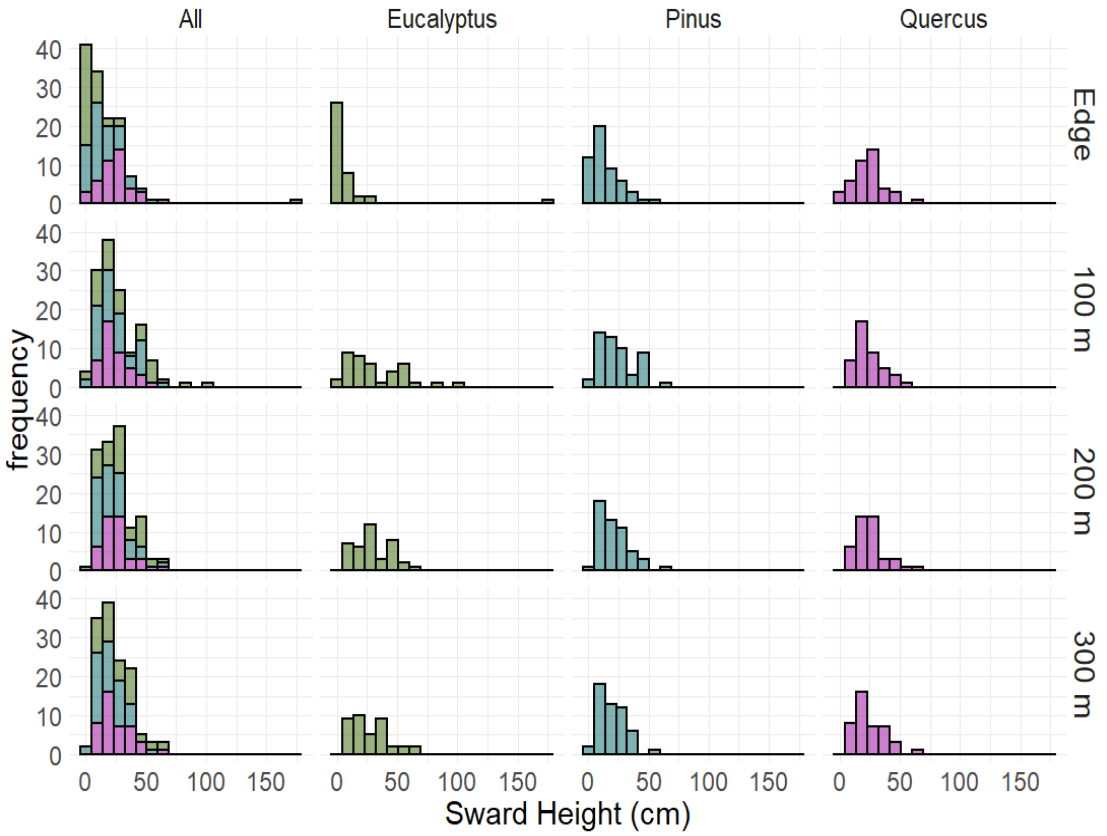

Figure S2.2 - Histogram of mean sward height values around the nests by distance (Edge; 100; 200; 300) and plantation type (Eucalyptus – Green; Pinus – Orange; Oak – Blue).

Figure S2.3 - Camera trap photo examples of other nest-predators, as presented in **Table S2.2**. From left to right and top to bottom: common buzzard, great bustard, cow, garden dormouse, red fox, mouse, sheep and wild boar.

Table S2.1 - Correlation tests between the fixed factors sward height and nest-site manipulation. Test statistic and correlation value obtained from Pearson's product moment correlation coefficient. P-values presented.

Data	cor	df	t statistic	p-value
Overall	-0.042	530	-0.973	0.331
Overall (edge only)	-0.109	131	-1.258	0.211
Eucalyptus	-0.104	154	-1.293	0.198
Eucalyptus (edge only)	-0.243	37	-1.524	0.136
Pine	-0.034	206	-0.486	0.627
Pine (edge only)	-0.042	50	-0.300	0.766
Oak	0.020	166	0.252	0.802
Oak (edge only)	-0.018	40	-0.114	0.910

Table S2.2 - List of main predators recorded between April-June 2014 and 2015 in open semi-natural grassland adjacent to eucalyptus, oak and pine plantations. For each species we provide the abundance (**Abund**) expressed as the mean count per site ± standard error (minimal - maximum) and the percentage of sites where the species was recorded (**% occur**) for overall, eucalyptus, oak and pine plantations. Species are ordered by overall % occurrence inside their respective families.

Species	Common name	Overall (n=51)		Eucalyptus (n=15)		Oak (n=18)		Pine (n=18)	
		Abund	% occur	Abund	% occur	Abund	% occur	Abund	% occur
Accipitriformes									
Accipitridae									
Circus pygargus	Montagu's harrier	0.43 ± 0.1 (0-4)	33.3	0.53 ± 0.27 (0-4)	33.3	0.61 ± 0.16 (0-2)	50.0	0.17 ± 0.09 (0-1)	16.7
Passeriformes									
Corvidae									
Corvus corone	Carrion crow	0.63 ± 0.12 (0-4)	43.1	1.07 ± 0.28 (0-4)	66.7	0.33 ± 0.14 (0-2)	27.8	0.56 ± 0.18 (0-2)	38.9
Corvus corax	Common raven	0.2 ± 0.08 (0-3)	13.7	0.33 ± 0.23 (0-3)	13.3	0 ± 0 (0-0)	0.0	0.28 ± 0.11 (0-1)	27.8
Pica pica	Common magpie	0.18 ± 0.08 (0-3)	9.8	0 ± 0 (0-0)	0.0	0.17 ± 0.17 (0-3)	5.6	0.33 ± 0.16 (0-2)	22.2

Table S2.3 - List of the avian and mammal nest predator species identified by camera traps placed from April-June 2014 and 2015 in open semi-natural grassland adjacent to eucalyptus, oak and pine plantations. For each species the number of nests depredated per habitat and plantation type are provided. * Nest depredated by both carrion crow and Montagu´s harrier.

Species	Common name	Habitat type (% Depredated nests)		Plantation type (% Depredated nests)						Total Nests
		Grassland	Edge	Eucalyptus		Oak		Pine		
				edge	grassland	edge	grassland	edge	grassland	
Avian										
Corvus corone	**Carrion crow**	**29 (30.9)**	**9 (9.6)**	**3 (3.2)**	**14 (14.9)**	**4 (4.3)**	**9 (9.6)**	**2 (2.1)**	**6 (6.4)**	**38 (40.4)**
Circus pygargus	**Montagu's harrier**	**8 (8.5)**	**0 (0)**	**0 (0)**	**2 (2.1)**	**0 (0)**	**3 (3.2)**	**0 (0)**	**3 (3.2)**	**8 (8.5)**
Corvus corax	**Common raven**	**3 (3.2)**	**1 (1.1)**	**0 (0)**	**0 (0)**	**0 (0)**	**0 (0)**	**1 (1.1)**	**3 (3.2)**	**4 (4.3)**
Pica pica	**Magpie**	**0 (0)**	**2 (2.1)**	**0 (0)**	**0 (0)**	**1 (1.1)**	**0 (0)**	**1 (1.1)**	**0 (0)**	**2 (2.1)**
Buteo buteo	Common buzzard	0 (0)	1 (1.1)	0 (0)	0 (0)	1 (1.1)	0 (0)	0 (0)	0 (0)	1 (1.1)
Otis tarda	Great bustard	1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.1)	0 (0)	0 (0)	1 (1.1)
C. corone & C. pygargus	Carrion crow & Montagu's harrier*	1 (1.1)	0 (0)	0 (0)	1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.1)
Mammal										
Bos taurus	Cow	3 (3.2)	1 (1.1)	0 (0)	1 (1.1)	0 (0)	0 (0)	1 (1.1)	2 (2.1)	4 (4.3)
Eliomys quercinus	Garden dormouse	0 (0)	2 (2.1)	0 (0)	0 (0)	1 (1.1)	0 (0)	1 (1.1)	0 (0)	2 (2.1)
Vulpes vulpes	Red fox	1 (1.1)	1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.1)	1 (1.1)	2 (2.1)
Murid sp.	Mouse	1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.1)	1 (1.1)
Ovis aries	Sheep	0 (0)	1 (1.1)	0 (0)	0 (0)	1 (1.1)	0 (0)	0 (0)	0 (0)	1 (1.1)
Sus scrofa	Wild boar	1 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1.1)	1 (1.1)
Unknown events		22 (23.4)	6 (6.4)	2 (2.1)	7 (7.4)	1 (1.1)	5 (5.3)	3 (3.2)	10 (10.6)	28 (29.8)
Total events		70 (74.5)	24 (25.5)	5 (5.3)	25 (26.6)	9 (9.6)	18 (19.1)	10 (10.6)	27 (28.7)	94 (100)

Table S2.4 - Variable selection for candidate full overall model, using drop1 function. For each model term we provide degrees of freedom (Df), Akaike Information Criteria (AIC) scores, Likelihood Ratio Test (LRT) outputs and significance level (P). **Bold** denotes P < 0.10).

	Df	**AIC**	***LRT***	***P***
NULL	NA	644.66	NA	NA
distance	0	644.66	-1.77E-09	0.999
plantation type	2	641.89	1.23E+00	0.541
predator abundance	0	644.66	-3.25E-09	0.999
sward height	1	661.64	1.90E+01	**<0.001**
manipulation	1	652.75	1.01E+01	**0.001**
distance : plantation type	2	654.27	1.36E+01	**0.001**
plantation type : predator abundance	2	640.98	3.15E-01	0.854
sward height : manipulation	1	649.66	7.00E+00	**0.008**

Table S2.5 - Variable selection for candidate models for each plantation type, using drop 1 function. For each model term we provide degrees of freedom (Df), Akaike Information Criteria (AIC) scores, Likelihood Ratio Test (LRT) outputs and significance level (P). **Bold** denotes P < 0.10.

	Df	**AIC**	***LRT***	***P***
Eucalyptus				
NULL	NA	193.07	NA	NA
distance	1	197.96	6.89	**0.009**
sward height	1	194.16	3.09	**0.079**
manipulation	1	195.68	4.61	**0.032**
distance : sward height	1	192.09	1.01	0.314
distance : manipulation	1	195.24	4.17	**0.041**
sward height : manipulation	1	196.17	5.10	**0.024**
distance : sward height : manipulation	1	191.08	0.01	0.916
Pine				
NULL	NA	247.81	NA	NA
distance	1	251.24	5.43	**0.020**
sward height	1	245.92	0.11	0.745
manipulation	1	245.83	0.02	0.896
distance : sward height	1	249.78	3.96	**0.047**
distance : manipulation	1	249.26	3.45	**0.063**
sward height : manipulation	1	247.89	2.08	0.149
distance : sward height : manipulation	1	249.99	4.18	**0.040**
Oak				
NULL	NA	208.32	NA	NA
distance	1	206.72	0.40	0.529
sward height	1	210.51	4.20	**0.041**
manipulation	1	207.49	1.17	0.279
distance : sward height	1	207.41	1.10	0.295
distance : manipulation	1	206.32	0.01	0.943
sward height : manipulation	1	207.44	1.12	0.289
distance : sward height : manipulation	1	206.71	0.39	0.534

Chapter 3

Grassland vegetation height affects bird responses to forest edges in Mediterranean open farmland

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3.1. Abstract

Afforestation affects Mediterranean farmland biodiversity due to loss and fragmentation of grassland habitats. While the influence of landscape context and plantation edges on farmland bird responses to afforestation is well-documented, less is known about the influence of grassland vegetation height and how it interacts with afforestation to influence bird communities. Here, we examined how changes in grassland vegetation height affect bird responses to afforestation in a farmland region in southern Portugal, and how these are affected by plantation type and edge. This region has experienced afforestation with eucalyptus, pine and oak stands, agricultural intensification, and frequent dry periods. To capture local and landscape-level changes, we collected data in two periods (2005 and 2014-15). Grassland vegetation height varied between sampling periods, emerging as a key factor affecting changes observed. Ground-nesting and cereal-associated species increased in abundance with taller vegetation in 2014-15, while in 2005, with drier weather and shorter vegetation, the species associated with ploughed fields were more abundant. Vegetation height effects on bird assemblages depended on plantation type and distance to plantation edges. Farmland bird abundance, including ground-nesting and cereal crops-associated species, increased with taller vegetation, particularly near oak and pine plantations. Conversely, species associated with ploughed fields declined with taller vegetation, especially near eucalyptus plantations. Results highlight complex interactions between vegetation height, plantation type, and edge proximity shaping avian assemblages. This study supports the importance of field and landscape-level management with special focus on grassland vegetation height and landscape heterogeneity for preserving open-farmland birds in fast-changing Mediterranean farmland landscapes.

Keywords: Mediterranean farmland conservation; open farmland birds; vegetation height; plantation edges; steppe specialists.

3.2. Introduction

Afforestation, prominently discussed for its potential in carbon reduction and sequestration (Potter *et al*., 2007; Lin *et al*., 2013), poses conservation concerns due to its transformation of natural and semi-natural ecosystems into smaller fragmented habitats (Liu *et al*., 2019). This is particularly concerning when open habitats of conservation significance are replaced (Reino *et al*., 2009; Bond *et al*., 2019; Jacoboski *et al*., 2019; Faria *et al*., 2022), as newly formed plantation edges reinforce fragmentation effects, potentially reducing the quality of the remaining open-habitat fragments (Ries *et al*., 2004; Ewers and Didham, 2007). Open farmland bird species are particularly affected by this (Brotons *et al*., 2005; Reino *et al*., 2009; Morgado *et al*., 2010; Pretelli *et al*., 2018; Jacoboski *et al*, 2019; Jacoboski and Hartz, 2020), experiencing increased nest predation in grasslands adjacent to these plantations (Santos *et al*., 2006; Sánchez-Oliver *et al*., 2014a; Faria *et al*. 2022). Afforestation effects on farmland biodiversity are influenced by various factors. Different plantations provide varying understorey vegetation and tree species composition, which influences avian community composition adjacent to open habitats, including potential predators and competitors (Reino *et al*., 2010a; Calviño-Cancela *et al*., 2012, Faria *et al*., 2022). Additionally, taller tree growth and higher density may amplify edge effects, modifying suitability for certain species and increasing predation pressure in the adjacent grasslands (Santos *et al*., 2006; Reino *et al*., 2010a; Faria *et al*., 2022).

Grassland vegetation height is thus of particular importance in the resulting grassland fragments (Moreira, 1999), as in addition to protection from nest predation (Faria *et al*., 2022), taller vegetation can provide adequate cover, food and nesting resources to numerous open farmland species (Batáry *et al*., 2007; Erdös *et al*., 2009). Vegetation height may be directly affected by changes to farming systems, e.g., in the context of agricultural policy reforms, such as the Common Agricultural Policy (CAP) introduced by the EU in 2003 (Ribeiro *et al*., 2014). The Mediterranean farmlands of southern Portugal are part of the cereal-steppes of the Iberian Peninsula, representing a High Nature Value Farmland (HNVF) system critical for the conservation of a range of open farmland birds (Suárez *et al*., 1997; Bota *et al*., 2005, Reino *et al*., 2009). It was mostly composed of extensively farmed traditionally mixed-rotational systems of dry cereal, fodder crops and fallow land and pastures grazed by sheep (Ribeiro *et al*., 2014). However, this is currently changing with the increased cultivation of intensive woody crops and the establishment of specialised livestock systems, associated with an increased cover by permanent improved pastures (Ribeiro *et al*., 2014; Ren *et al*., 2018; Morgado *et al*., 2020).

Concerns regarding the impact of extreme climatic conditions (i.e., droughts and heat waves) on grasslands have also been raised (Conrey *et al*., 2016; Zuckerberg *et al*., 2018). These result in less biomass production and changes to soil properties (Wu *et al*., 2022) decreasing vegetation cover (Conrey *et al*., 2016), and shifting grazing patterns (Li *et al*., 2018). Lower vegetation height, driven by droughts (Conrey *et al*., 2016), intensive grazing (Reino *et al*., 2010b; Ribeiro *et al*., 2014), or a combination of both, likely raises nest-detectability (Bellamy *et al*., 2018) and vulnerability to predators near plantation edges (Beja *et al*., 2014; Faria *et al*., 2022). Thus, farmland birds inhabiting these habitats are expected to be particularly susceptible to changes in grassland vegetation height. However, while both the effects of afforestation and (to a lesser extent) vegetation heights on bird communities have been studied, little is known about the interaction of these two factors, i.e., how variations in vegetation height may affect farmland bird responses to afforestation differentially depending on plantation type.

In this study we aimed to analyse afforestation's impact on Mediterranean open farmland bird communities in two periods (2005, 2014-15) with contrasting vegetation heights in grasslands adjacent to different plantation types. We focused on a representative area of Iberian cereal steppes that has experienced recent afforestation (Reino *et al*., 2010a) and has been facing increasing drought severity (García-Ruiz *et al*., 2011; FFMS, 2022). This area is also among the European farmland landscapes with the highest conservation relevance to farmland birds (Bota *et al*., 2005; EEA, 2006). Specifically, we examined: 1) variations in bird composition and local and landscape characteristics, and 2) the influence of those characteristics that changed significantly between periods on avian assemblages' responses to plantation edges and types. We hypothesise that (i) grassland vegetation is shorter in the drier period (Conrey *et al*., 2016); (ii) ground-nesting species, especially those associated with cereal fields, increase in abundance with taller vegetation due to the role played by vegetation cover in nest survival (Delgado and Moreira, 2000), while those specifically associated with ploughed fields decrease; and (iii) steppe birds benefit from increased vegetation height in grasslands adjacent to the softer edges of oak plantations and higher distances to the plantation edge (Reino *et al*., 2009; Sliwinsky and Koper, 2012; Besnard *et al*., 2016).

3.3. Methods

3.3.1 Study area

The study was conducted in southern Portugal, mostly within the Special Protection Area (SPA) of Castro Verde. Since 1995, this area has benefitted from an agri-environment scheme targeting the conservation of steppe birds under the European Union Birds Directive 2009/147/EC, through the maintenance of traditional farming systems (Ribeiro *et al*., 2014) (**Fig. 3.1**). The region has a Mediterranean climate, characterised by mild winters (averaging 9 ºC [5–14 ºC] in January) and hot summers (24 ºC [16–32 ºC] in July), with >75% of annual rainfall (500–600 mm) concentrated between October and March (Moreira *et al*., 2005; Morgado *et al*., 2020). Over the past 30 years, there has been a decrease in annual rainfall (from 584 to 547 mm) and an increased number of days without rain (from 150 to 155) (FFMS, 2022).

The landscape is predominantly flat or gently undulating (100–300 m a.s.l) (Moreira *et al*., 2005) and consists mostly of open farmland, traditionally composed of old fallow fields (lasting up to 10 years) or agricultural fields cultivated with dry cereal crops in rotations with fallows (2 to 5 years). Historically, these farmlands were grazed by sheep at low densities (Delgado and Moreira, 2000; Santana *et al*., 2017). Following the implementation of the European Economic Community regulation 2080/92 in the mid to late 1990s (Institute for Forestry Development, 2001), there was an increase in afforestation with umbrella pines (*Pinus pinea*) and holm and cork oaks (*Quercus rotundifolia* and *Q. suber*, respectively) in the periphery of the SPA (Reino *et al*., 2010). Until then, tree cover largely consisted of eucalyptus plantations (*Eucalyptus* sp.) and a few open-oak woodlands, grazed by livestock (Delgado and Moreira, 2000; Moreira *et al*., 2005; Reino *et al*., 2009). More recently, the traditional mixed system has shifted towards specialised production of cattle or sheep (Ribeiro *et al*., 2016), with declines in cereal and fallow land, and increases in forage crops and permanent pastures (Ribeiro *et al*. 2014; 2016; Santana *et al*., 2017).

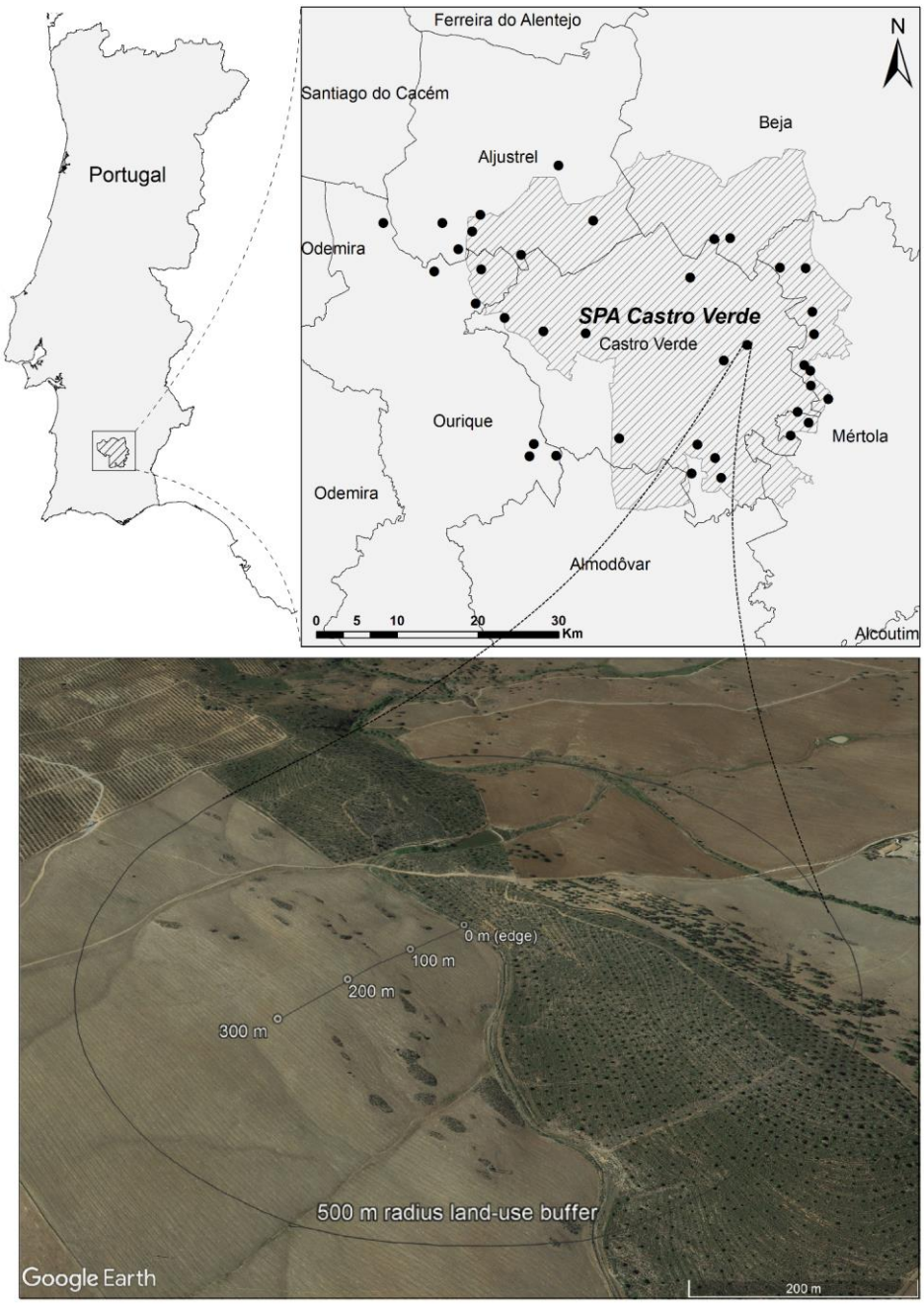

Figure 3.1 - Study area located in Southern Portugal, showing the Special Protection Area (SPA) of Castro Verde (Alentejo region), and the distribution of the 38 sampled sites. Below is highlighted an example of the spatial distribution of the survey points used in the grasslands (fallow or pastureland) adjacent to each forest plantations (oak, pine or eucalyptus; oak plantation in the photo). See methods section for further details. Image source Google Earth Pro (ver. 7.3.4.857).

3.3.2 Sampling design

We sampled 38 grassland parcels twice in each sampling period (2005, 2014-15), each time along 300-m transects perpendicular to the edge of one of three types of forest plantations commonly found in the region, including younger pine, and oak stands (mean age = 15.4 ± 4.9 years and 12.9 ± 5.9 years, respectively) and older eucalyptus stands

(mean age = 41.8 ± 18.1 years). Grassland parcels consisted of fallow fields and pastures (i.e. rainfed cereal fields were excluded) to reduce variation unrelated to the variables tested, and due to their particular importance for steppe bird species (Delgado and Moreira, 2000; Reino *et al*., 2009).

Site selection was carried out prior to the 2005 sampling period, based on 1:25,000 land cover maps from 1990, updated through systematic field checking of new forest stands planted up to early 2005 (Reino *et al*., 2009). Each site included a grassland parcel plus an adjacent plantation, selected only if the grassland parcel was at least 600 m long and wide, to allow sampling up to 300 m from the nearest plantation edge. Additionally, only one grassland parcel per plantation was considered to avoid pseudo-replication and spatial autocorrelation (Fortin and Dale, 2009; Vasconcelos *et al*., 2019). For the 2014-15 sampling period, we were able to resample several of the original sites, retaining 38 sites that did not undergo major land-use changes, such as ploughing or cereal cultivation in the grassland parcel, and tree harvest or thinning in the adjacent plantations (Vasconcelos *et al*., 2019, Faria *et al*. 2022). These included grassland parcels adjacent to 8 eucalyptus, 13 pine and 17 oak plantation stands.

3.3.3 Bird Data

Bird surveys were conducted during the breeding season in 2005 (from April 1st to May 31st), and again in either 2014 or 2015 (from April 1st to June 5th, 2014, and April 11th to June 5th, 2015). Surveys were conducted twice per sampling period. They consisted of four sequential point-counts performed at 0, 100, 200, and 300 m perpendicularly from the plantation edge, where for 10 minutes, each bird seen or heard within 50 m from the observer was recorded. Sampling was conducted preferably at dawn, or at either dawn or dusk in the two sampling occasions for each period, as Mediterranean farmland birds have similar peaks of activity during these periods (Caro *et al*., 2015). To help reduce detectability problems, surveys were only conducted on nearly windless and rainless days on mostly flat grassland parcels (Bibby *et al*., 2000; Reino *et al*., 2009) by two experienced observers (LR and RM). At each point, individual birds and flocks were identified and mapped (**Fig. 3.1**). To minimise double counting of individuals, birds in flight were not recorded, except in the case of song flights (e.g., calandra lark). Additionally, extra care was taken to not count any birds flushed between counts that landed at a subsequent survey point, which was always within sight (Reino *et al*., 2009). To address identification challenges in the field, crested and Thekla larks (*Galerida cristata* and *G. theklae*, respectively) and common and Spanish sparrows (*Passer domesticus* and *P. hispaniolensis*, respectively) were categorised at the genus level.

For each sampling period, we estimated bird abundance (i.e., the highest number of birds counted between the two surveys per distance point per site) for the overall assemblage and at a species level. To evaluate differences in responses in the bird community according to their habitat affinities, we categorised species into guilds: woodland and farmland (more general groups); ground-nesting; open-farmland (steppe) specialists (contained within farmland; Reino *et al*., 2009); cereal, fallow or ploughed fields (different classification of farmland species, according to species traits; Delgado and Moreira, 2000; Santana *et al*. 2014); and threatened species (all within farmland group), including near threatened, vulnerable or endangered on the IUCN European red list of birds (Birdlife International, 2022; **Table S3.1**). Species-specific analyses were carried out for the 13 most widespread bird species in either period (higher than 25% occurrence, **Table S3.2**): tawny pipit (*Anthus campestris*), red-legged partridge (*Alectoris rufa*), greater short-toed lark (*Calandrella brachydactyla*), European goldfinch (*Carduelis carduelis*), zitting cisticola (*Cisticola juncidis*), carrion crow (*Corvus corone*), corn bunting (*Emberiza calandra*), Galerida larks (*Galerida* spp.), common linnet (*Linaria cannabina*), calandra lark (*Melanocorypha calandra*), European stonechat (*Saxicola rubicola*), little bustard (*Tetrax tetrax*) and Eurasian hoopoe (*Upupa epops*).

3.3.4 Variable selection

Plantation structure was characterised by tree height and edge density, estimated using ground-level photographs taken at 70-100m perpendicular to the plantation edge. A field scale was employed at the edge to determine pixel size, which was then used to calculate average tree height. Tree density was derived from the total number of trees per metre of edge captured in the photographs. Additionally, plantation type was included to account for other potential effects of different plantation characteristics, such as plantation age, vegetation structure and composition, and avian predator abundance.

For vegetation height, grassland vegetation height was estimated from the average of four measurements evenly spaced in a ca. 50-cm radius centred at each sampling point, using a 50-cm ruler. This process was repeated in both periods (**Table S3.3**). The potential influence of livestock grazing on vegetation height was also considered by recording the occurrence (presence/absence) of livestock (sheep and cattle) at each grassland parcel during counts.

Furthermore, we also considered weather conditions in the study area for both periods. Data from the nearest weather station (Beja weather station) (https:www.pordata.pt; FFMS, 2022), was used to extract three precipitation indicators: annual precipitation (annual rainfall), maximum monthly precipitation (max. precipitation)

and total number rainless days. To accommodate the potential influence of the preceding year's precipitation on grassland conditions (Zuckerberg *et al*., 2018), annual data from 2004 and 2005 were used for the first sampling period (2005), and data from 2013 to 2015 were used for the second (2014-2015).

For landscape context, land cover maps for both periods were created within 500-m radius buffers centred on the plantation-grassland edge (**Fig. 3.1**). Images from Google Earth Pro (ver. 7.3.4.857) from 2005-2007 and 2015-2016 were used. Land-use categories were obtained from a governmental database (DGT, 2007; 2015), and included agricultural area; eucalyptus, pine, and oak plantations; shrubland; wood-pastures; water bodies; urban areas; and olive groves. These were selected to broadly reflect all land-use types within the area, with greater detail provided for plantation cover (**Table S3.3**). Landscape heterogeneity metrics (Elkie *et al*., 1999), including area-weighted mean shape index (AWMSI), mean patch size (MPS), and edge density (ED) were computed using the Patch Analyst plugin in ArcGIS (ver. 10.2.2; ESRI Inc., 2014).

3.3.5 Statistical analysis

Variation in the abundance of avian assemblages at each site (i.e., relative abundance per site, including all distance points) and local and landscape variables between periods was evaluated through individual paired t-tests or Wilcoxon rank-sum test with continuity correction, preceded by Shapiro-Wilk tests for sample normality (Hollander *et al*., 2013).

Then, we modelled how changes in guilds and species abundance between 2005 and 2014-2015 were associated with variables that differed significantly between these periods (i.e., vegetation height; see **Table S3.3**), across distances from different plantation edge types. Bird abundance differences were measured by subtracting bird counts at each distance in 2005 from those in 2014–2015 (i.e., dif. abundance = bird abund [2014–2015] – bird abund [2005]). Changes in vegetation height were estimated likewise, after being standardised (dif. height = veg height [2014–2015] – veg height [2005]). Generalised Linear Mixed Models (GLMMs) were used with a Gaussian distribution and identity link function (Bolker, 2015). To address the lack of independence among samples, transect (representing the site) was used as a random factor (Zuur *et al*., 2009; Santana *et al*., 2014).

Model selection was performed using a Multi-model Inference approach (Burnham and Anderson, 2002), generating a table of subset model combinations using standardised coefficients and ranking them based on weights derived from Akaike Information Criteria corrected for small samples (AICc). Model averaging was then conducted for models with delta AICc < 2, using partial standardized regression

coefficients to estimate the relative importance of each coefficient on the final models (Cade, 2015).

All analyses were performed using R (ver. 4.2.0; R Core Team 2022). GLMM models were developed using “glmer” function, from the lme4 package (Bates *et al*., 2015), and model selection and averaging were performed using “dredge” and “model.avg” functions from MuMIn package (Bartoń, 2023).

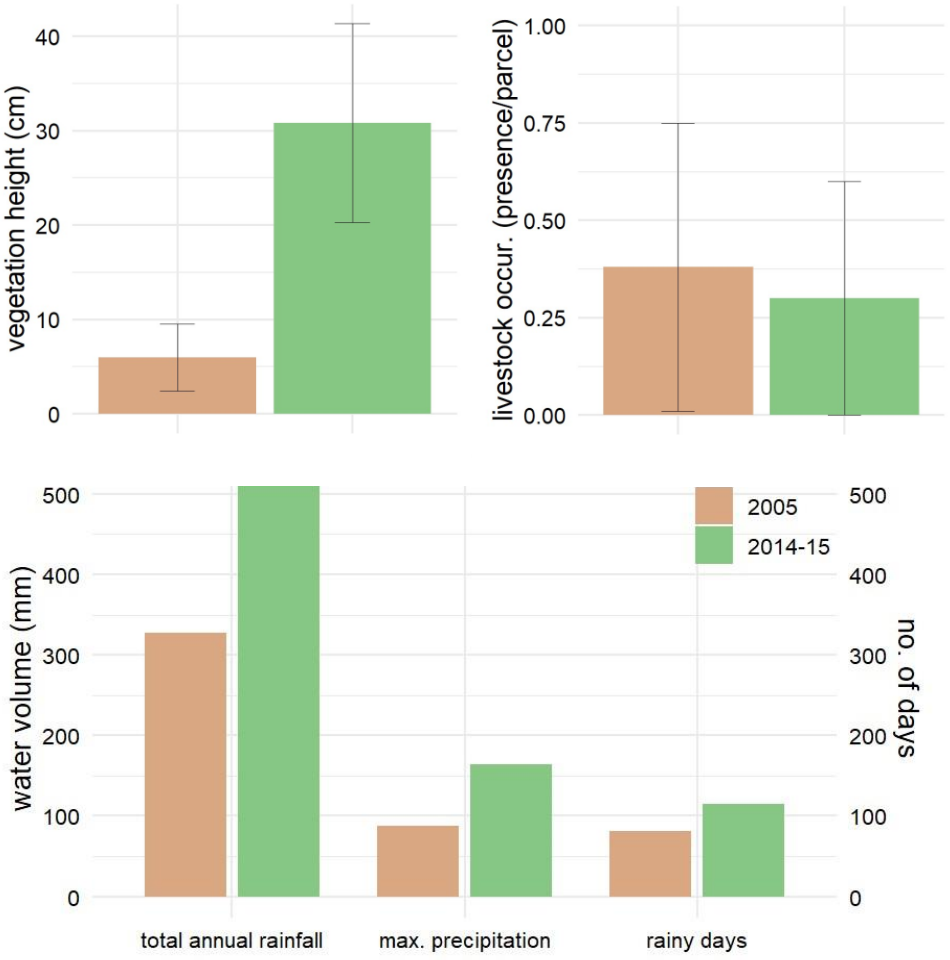

Figure 3.2 - Temporal changes in vegetation height, livestock occurrence and precipitation variables between periods. Error bar represents 95% C.I. Full details and tests on landscape context and plantation attribute variables provided in **Table S3.3.**

3.4. Results

3.4.1 Overall patterns

Overall bird abundance was significantly higher in the second period (Δ_{abund}, **Table 3.1**), primarily driven by an increase in farmland birds. Contrastingly, woodland birds decreased during this time (**Table 3.1**). Among farmland species, there were significant increases in ground-nesting birds (Δ_{abund} = 3.79, p <0.001) and those associated with cereal fields (3.63; p < 0.001), while species associated with ploughed fields decreased. Abundance of steppe specialists, birds associated with fallow fields and threatened species remained relatively stable (**Table 3.1**).

The corn bunting, Eurasian hoopoe, Galerida larks and zitting cisticola were significantly more abundant in 2014-15, while the red-legged partridge and the tawny pipit were more abundant in 2005. Short-toed lark abundance decreased slightly, whereas other species remained relatively constant (**Table 3.1**).

Vegetation height was significantly higher in the second period (**Fig 3.2**). This period (2014-15) was characterised by heightened annual rainfall, maximum precipitation, and number of rainy days. Livestock occurrence and all other variables regarding plantation attributes and landscape context remained stable between periods and were thus not included in further analyses (**Fig 3.2**; **Table S3.3**).

3.4.2 Effects of vegetation height and distance from different plantation edges

As initially expected, vegetation height significantly influenced various guilds and species abundance (**Table 3.1**; **Table S3.4**). Increased vegetation height was positively related to woodland birds' abundance regardless of plantation type (β_{heig} = 0.55). However, the impact of grassland vegetation height on farmland bird abundance varied based on adjacent plantation types. Vegetation height negatively influenced farmland bird abundance near eucalyptus plantations but was associated with their abundance near oak and pine plantations ($\beta_{oak:heig}$ = 0.45; $\beta_{pine:heig}$ = 0.11). Ground-nesting birds slightly decreased with increasing vegetation height (β_{heig} = -0.11). Steppe birds' abundance showed a positive association with higher vegetation height near plantation edges, with this effect diminishing at greater distances ($\beta_{D:heig}$ = -0.43).

Table 3.1 – Average number of birds detected per site per period (site abund 05, site abund 15) and respective differences in relative bird abundance (guilds and species) (Δabund) between periods (2005 and 2014-15) and *p*-value of the t-test; **bold** signs denote $P < 0.05$. For each guild and species, we provide model averaging (GLMM) coefficient estimates (β) for effects of vegetation height (veg. height), distance, plantation type (young oak; young pine; old eucalyptus - default level) and two-level interactions.

	site abund 05	site abund 15	Δabund	*P*-value	veg. height	distance	young oak	young pine	distance: veg. height	oak:veg. height	pine:veg. height
Bird guilds											
All species	**15.92**	**20.34**	**4.42**	**<0.001**		1.48	2.17	2.29			
Woodland	**6.03**	**5.58**	**-0.45**	**0.017**	0.55	1.98	2.16	2.36			
Farmland	**9.84**	**14.76**	**4.92**	**<0.001**	-0.55		0.58	0.53		0.45	0.11
Ground-nesting	**8.34**	**12.13**	**3.79**	**<0.001**	-0.11		0.55	0.18			
Steppe	4.63	4.45	-0.18	0.301	0.15	0.24	0.16	0.08	-0.43		
Cereal related	**1.82**	**5.45**	**3.63**	**<0.001**	0.35	0.06			0.17		
Fallow related	2.63	2.95	0.32	0.859	-0.04	0.25	0.20	-0.06	-0.29		
Ploughed related	**1.68**	**0.82**	**-0.87**	**0.002**	-0.10	-0.13	0.04	0.10	-0.08		
Threatened species	1.13	1.74	0.61	0.114		-0.13	-0.03	0.12			
Species											
Calandra lark	**2.16**	**2.29**	0.13	0.874	-0.09	0.20	0.15	-0.07	-0.23		
Carrion crow	**0.21**	**0.53**	0.32	0.433			-0.11	-0.11			
Common linnet	**0.37**	**0.37**	0	1		0.06					
Corn bunting	**1.53**	**3.68**	**2.16**	**<0.001**	0.02	-0.07			0.19		
Eurasian hoopoe	0.08	0.29	0.21	**0.050**	-0.07	-0.05			0.06		
European goldfinch	**0.53**	**0.53**	0	0.899	0.05						
European stonechat	0.47	0.50	0.03	0.828	-0.07	-0.06			0.07		
Galerida larks (spp.)	1.32	1.95	0.63	**0.039**	-0.16		0.11	0.04			
Little bustard	0.47	0.66	0.18	0.660	0.03						
Red-legged partridge	**0.37**	**0.05**	**-0.32**	**0.012**	-0.02	0.01					
Short-toed lark	1.11	0.63	-0.47	0.053	-0.09	-0.16	0.07	0.10	-0.04		
Tawny pipit	**0.42**	**0.11**	**-0.32**	**0.005**	-0.04	-0.01	0.05	0.06	-0.04	-0.02	0.01
Zitting cisticola	**0.05**	**1.45**	**1.39**	**<0.001**	0.23	-0.02			-0.06		

Distance to the plantation edge played an important role in the overall assemblage's abundance, as well as that of woodland birds, depending on the adjacent plantation type (i.e., increased distances only had a positive effect in eucalyptus plantations) (**Table 3.1**; **Table S3.4**). It also interacted with vegetation height in several cases. For instance, species linked to fallow and ploughed fields not only decreased slightly with taller vegetation, but also exhibited a more pronounced decrease as distance to the plantation edge increased (respectively, $\beta_{D:heig}$ = -0.29; $\beta_{D:heig}$ = -0.08). Contrastingly, cereal crops-associated species marginally increased in abundance with greater distance to the plantation edge (β_{D} = 0.06), with larger increases where vegetation was significantly taller ($\beta_{D:heig}$ = 0.17).

The abundance of farmland, ground-nesting and fallow-related species increased in certain plantation types regardless of distance, generally favouring oak plantations (respectively, β_{oak} = 0.58; β_{oak} = 0.55; and β_{oak} = 0.20). Indeed, farmland bird abundance increased with taller vegetation, primarily in grasslands adjacent to oak plantations ($\beta_{oak:heig}$ = 0.45).

At the species level, vegetation height influenced the abundance of all but two (woodland) species (**Table 3.1**). Vegetation height was negatively related to red-legged partridge (β_{heig} = -0.02) and Galerida larks abundances (β_{heig} = -0.16), and positively so to goldfinch (β_{heig} = 0.05) and little bustard (β_{heig} = 0.03). For other species, the vegetation height effect was contingent on the distance to the plantation edge. The positive association of vegetation height with corn bunting abundance (β_{heig} = 0.02) increased with distance from the forest edge ($\beta_{D:heig}$ = 0.19), while species like the calandra lark, experienced a negative relationship (β_{heig} = - 0.09) exacerbated by distance ($\beta_{D:heig}$ = - 0.23). Vegetation height had an overall positive relationship with zitting cisticola (βheig = 0.23), though that decreased with distance to the plantation edge ($\beta_{D:heig}$ = - 0.06). Contrastingly, the abundance of stonechat and hoopoe was negatively associated with increased vegetation height (β_{heig} = - 0.07 in both cases), especially near wooded edges ($\beta_{D:heig}$ = 0.07; 0.06) (**Table 3.1**). Linnet abundance increased solely with distance from the edge (β_{D} = 0.06). Regarding plantation type, oak plantations had a positive association with Galerida, calandra and short-toed larks, while eucalyptus plantations positively associated with carrion crow (β_{oak} and β_{pine} = - 0,11).

3.5. Discussion

Our results demonstrate that forest edges may impact avian communities differently, depending on locally varying factors such as grassland vegetation height and its interactions with different adjacent plantations and proximity to edge in open-farmland Mediterranean landscapes. Specifically, farmland bird abundance was higher in the wet period (2014-15) and thrived with taller vegetation near oak and pine plantations. Cereal-field associated species benefitted from taller vegetation cover regardless of adjacent plantation type, but preferred greater distances from the forest edge. Conversely, ploughed-field associated species declined, negatively impacted by taller vegetation in 2014-15, particularly close to plantation edges. Thus, results suggest that local field management, such as a more sustainable livestock management, can positively impact open-farmland specialists, such as little bustard and calandra lark, especially during extremely dry years (e.g., 2005). Ultimately, birds' responses to afforestation depend on a complex interplay between the grassland matrix and adjacent plantation edges. Conservation efforts addressing Mediterranean farmland ecosystems should consider these local factors (e.g., vegetation height, grassland heterogeneity) to preserve open-farmland birds under increasingly dry conditions.

3.5.1 Winners and losers from vegetation height changes

Our findings suggest an association with vegetation height changes and avian assemblage responses near plantations. We observed a significant increase in grassland vegetation height between the two periods, coinciding with a rise in overall farmland bird abundance, particularly ground-nesting and cereal-associated species. Reduced rainfall during the first period (2005) likely affected water availability and, subsequently, the observed vegetation growth (Derner and Schuman, 2007; Cantarel *et al*., 2013). Livestock (sheep and cattle) occurrence in the parcels remained consistent between sampling periods, though changes to grazing regimes or agricultural practices in some of the grassland parcels could also explain the observed vegetation height differences (Reino *et al*., 2010b; Beja *et al*., 2014; Ren *et al*., 2018). Our sampling design excluded sites subjected to major changes (corroborated by a lack in changes observed in landscape associated variables) and focused only on grassland parcels composed of fallow and pastures to minimise the influence of factors such as changes to agricultural practices in the grassland (Morgado *et al*., 2020) on bird responses to afforestation. Increased vegetation height positively affected the difference in abundance of woodland birds and cereal-associated species, regardless of the adjacent plantation. The latter group includes species like the corn bunting, benefiting from taller grassland vegetation,

especially farther from the plantation edge. These species typically favour tall and dense vegetation (Moreira, 1999; Delgado and Moreira, 2000) and are often ground-nesting (e.g., the zitting cisticola), benefiting from increased nest-site cover (Batáry *et al*., 2007; Bellamy *et al*., 2018) and more readily available resources (Ponce *et al*., 2018). Contrastingly, we observed a negative relationship of vegetation height to the abundance of species associated with ploughed fields, such as the tawny pipit and short-toed lark, which prefer areas with shorter vegetation (Moreira *et al*., 2007; Santana *et al*., 2017). The trend towards less heterogeneity within the agricultural matrix brought by changes implemented after the CAP reform (Ribeiro *et al*., 2014) may thus lead to negative effects on bird diversity (Reino *et al*., 2010b; Santana *et al*., 2017; Lituma *et al*., 2022) as a mix of plant species and varying vegetation heights support more food sources and nesting sites for bird species than monoculture grasslands (Fisher and Davis, 2010; Jacobs *et al*., 2012; Hovick *et al*., 2015).

3.5.2 Influence of plantation type

Adjacent plantation type influenced the effects of grassland vegetation height on farmland bird abundance. Increased vegetation height had a positive association with farmland birds' abundance near young oak and pine plantations, but a negative one when adjacent to older eucalyptus plantations. Differences in adjacent plantations' characteristics associated with growth and maturity (Reino *et al*., 2010a; 2010b; Sánchez-Oliver *et al*., 2014b), and their associated nest-predator community (Beja *et al*., 2009; Faria *et al*., 2022), as well as variations in species abundance at the regional level (Reino *et al*., 2013), could also have affected bird responses to afforestation. For instance, increased avian predator abundance (i.e., carrion crows) near eucalyptus plantations (our data; Faria *et al*., 2022) may have influenced the observed differences in bird responses compared to younger oak and pine plantations.

Species abundance of all species or all ground-nesting birds analysed together had no relationship with vegetation height, likely due to both groups encompassing various species in terms of functional habitat preferences (Delgado and Moreira, 2000; Moreira *et al*., 2007; Santana *et al*., 2017). For instance, species like the tawny pipit or short-toed lark, known to breed and occur preferably in ploughed fields (Moreira, 1999; Delgado and Moreira, 2000; Moreira *et al*., 2007), were negatively affected by increased vegetation height, whereas the zitting cisticola or corn bunting (also ground-nesters), which favour high vegetation cover (Delgado and Moreira, 2000), were positively associated with it. Overall, ground-nesting species abundance was more influenced by the adjacent plantation type, with pine and especially oak plantations being favoured over eucalyptus plantations.

3.5.3 Influence of distance to plantation edge

Our findings align with previous studies showing mixed edge responses for farmland birds (Reino *et al*., 2009; Terraube *et al*., 2016; Phifer *et al*., 2017). For instance, the tawny pipit and short-toed lark, that typically avoid edges (Sliwinsky and Koper, 2012; Besnard *et al*., 2016), are steppe specialists that favour expansive farmland areas over fragmented landscapes (Morgado *et al*., 2010; Keyel *et al*., 2013). Contrastingly, commonly widespread species known to benefit from increased plantation cover, such as the common linnet, (Reino *et al*., 2009; 2010a), strongly favoured edge proximity. Overall, steppe bird assemblage benefitted from increased vegetation height, though this was much more prevalent near the plantation edge and varied with plantation type. The likely reason is that higher predation rates in proximity to plantation edges (Kaasiku *et al*., 2022), particularly eucalyptus edges, increase the importance of adequate nest-site cover for nesting success (Homberger *et al*., 2017). It could also reflect an upsurge in invertebrate prey near plantation edges (Vasconcelos *et al*., 2018). Thus, steppe birds primarily benefited from grasslands adjacent to oak plantations, particularly in areas farther from the plantation edge. Oak plantations are generally less dense with shorter trees, creating softer edges (Reino *et al*., 2009), which are favoured by edge avoiders (Sliwinsky and Koper, 2012; Besnard *et al*., 2016). Moreover, oak plantations likely have lower predator abundance (Faria *et al*., 2022), resulting in reduced ground-nesting predation pressure in these grasslands.

Lastly, there were no major changes in the number of threatened birds, which can be attributed to the overall landscape structure stability, including plantation edge density, habitat fragmentation and land-use cover. Both sampling campaigns occurred after the implementation of the CAP reform in 2003, associated with significant land-use changes in this area (Ribeiro *et al*., 2014). Furthermore, the sampling process deliberately excluded parcels undergoing significant land-use shifts during the latter period. As such, threatened bird abundance was mainly influenced by distance to the plantation edge, and varied significantly between different plantation types. This emphasises the potential impacts of grassland habitats' fragmentation (Reino *et al*., 2009; Morgado *et al*., 2010; Pretelli *et al*., 2018; Jacoboski *et al*, 2019), especially in relation to forest plantation edges (Sánchez-Oliver *et al*., 2014a; Faria *et al*., 2022).

3.5.4 Conservation implications

Our findings highlight a complex interplay between vegetation height, plantation type and edge avoidance, impacting bird responses to afforestation. This underpins the need for

a multifaceted conservation approach to support the diverse avian species inhabiting Mediterranean farmlands under on-going climate and land-use changes. Notably, grassland vegetation height significantly influenced avian assemblage dynamics, affecting various bird guilds and species differently, highlighting the importance of grassland heterogeneity in preserving diversity and stability in bird communities (Hovick *et al*., 2015; Traba and Morales, 2019). Grazing regimes, intensity (Batáry *et al*., 2007; Reino *et al*., 2010b, Ramos *et al*. 2021), and annual climatic conditions (Conrey *et al*., 2016; Zuckerberg *et al*., 2018) should also be considered by conservation efforts which aim to support a wide range of farmland species, as they directly affect grassland biodiversity and can influence grassland structure. Maintaining a balance in vegetation height diversity can benefit ground-nesting species seeking increased nest-site cover (Erdös *et al*, 2009), and cereal-associated species that thrive in taller vegetation (Delgado and Moreira, 2000; Batáry *et al*., 2007), while also preserving open-farmland specialists preferring shorter vegetation (Delgado and Moreira, 2000). Our study also emphasises the importance of the type of forest plantations adjacent to grasslands, with oak and pine plantations having a less detrimental impact on bird abundance and diversity compared to eucalyptus. Prioritising the former is likely to better accommodate open-farmland specialists. Lastly, we emphasise the importance of grassland habitat fragmentation, associated with forest plantation edges, in shaping bird responses. Strategies to reduce predation pressures near edges (Reino *et al*., 2010a; Faria *et al*., 2022), preserve large grassland patches (Morgado *et al*., 2010; Reino *et al*., 2013) and enhance landscape connectivity (Sánchez *et al*., 2014a), can help mitigate edge effects. Preserving grassland diversity with varying vegetation heights and minimising the use of new eucalyptus in afforestation are valuable bird conservation measures for Mediterranean farmland landscapes.

3.6. Authors' contributions

João Faria: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. **Luís Reino**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Pedro Beja**: Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing. **David Gonçalves**: Supervision, Writing – review & editing. **Juan Sánchez-Oliver**: Investigation, Methodology. **Francisco Moreira**: Investigation, Writing – review & editing. **Inês Catry**: Investigation, Writing – review & editing. **Lluís Brotons**: Investigation, Writing – review & editing. **John T. Rotenberry**: Investigation, Writing – review & editing. **Rui Morgado**: Investigation, Writing – review & editing. **Stefan**

Dullinger: Investigation, Writing – review & editing. **Stefan Schindler**: Investigation, Writing – review & editing. **Joana Santana**: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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3.9. Supplementary Material

Table S3.1 – Description of guilds' composition and number of species included in each guild. Key to IUCN classification: LC – least concern; NT – near threatened; VU – vulnerable.

Guilds	no. species	description	bibliography
All species	52	All detected bird species that were not mainly migratory or aquatic.	Reino *et al*. 2009
Woodland	29	Species that usually benefit from forest plantations, requiring wooded habitats (e.g., forests, woodlots, orchards and shrubland).	Díaz *et al*. 1998
Farmland	23	Species regionally associated with arable agriculture and pastureland.	Delgado & Moreira, 2000
Ground-nesting	16	Farmland subset of ground-nesting species usually affected by nest detectability.	Vickery *et al*. 1992; Reino *et al*. 2010a
Steppe	11	Open-grassland specialists, usually of conservation concern, that may be particularly sensitive to habitat fragmentation.	Brotons *et al*., 2005; Moreira *et al*., 2005
Cereal fields	4	Grassland species grouped according to their functional associations with elements of the traditional farmland mosaic (i.e., fallow, cereal and ploughed fields)	Delgado & Moreira 2000; Moreira *et al*. 2007; Santana *et al*. 2014
Ploughed fields	5		
Fallow fields	2		
Threathened	8	Species of conservation concern, which included species classified as near threatened, vulnerable or endangered in a European context.	BirdLife International, 2021

Table S3.2 – All species % occurrence in sampled sites for both periods. **Bold** denotes species occurring in >25% of sampled sites. Selected widespread species are highlighted in grey.

species	year	% occurrence in sampled sites	Guild classification	IUCN
Alectoris rufa	**2005**	**26.32**	Farmland, ground-nesting	NT
	2014-15	5.26		
Anthus campestris	**2005**	**39.47**	Farmland, ground-nesting, steppe bird, ploughed	LC
	2014-15	7.89		
Athene noctua	2005	5.26	Farmland	LC
	2014-15	2.63		
*Bubulcus ibis**	2005	5.26	Farmland	LC
	2014-15	**36.84**		
Burhinus oedicnemus	2005	2.63	Farmland, ground-nesting, steppe bird, ploughed	LC
	2014-15	5.26		
Calandrella brachydactyla	**2005**	**60.53**	Farmland, ground-nesting, steppe bird, ploughed	LC
	2014-15	**34.21**		
Linaria cannabina	**2005**	**26.32**	Woodland	LC
	2014-15	**26.32**		
Carduelis carduelis	**2005**	**28.95**	Woodland	LC
	2014-15	**39.47**		
Carduelis chloris	2005	7.89	Woodland	LC
	2014-15	10.53		
Certhia brachydactyla	2005	2.63	Woodland	LC

	2014-15	0.00		
*Ciconia ciconia**	2005	18.42	Farmland	LC
	2014-15	**28.95**		
Circus pygargus	2005	21.05	Farmland, ground-nesting, steppe bird, cereal	LC
	2014-15	7.89		
Cisticola juncidis	2005	5.26	Farmland, ground-nesting, cereal	LC
	2014-15	**68.42**		
Clamator glandarius	2005	0.00	Woodland	VU
	2014-15	18.42		
Columba livia	2005	0.00	Woodland	LC
	2014-15	2.63		
Columba palumbus	2005	0.00	Woodland	LC
	2014-15	13.16		
Corvus corax	2005	2.63	Woodland	LC
	2014-15	2.63		
Corvus corone	2005	10.53	Woodland	LC
	2014-15	**26.32**		
Coturnix coturnix	2005	2.63	Farmland, ground-nesting, cereal	NT
	2014-15	21.05		
Cuculus canorus	2005	2.63	Woodland	LC
	2014-15	2.63		
Cyanistes caeruleus	2005	2.63	Woodland	LC
	2014-15	7.89		
Cyanopica cyanus	2005	10.53	Woodland	LC
	2014-15	15.79		
Emberiza calandra	**2005**	**63.16**	Farmland, ground-nesting, cereal	LC
	2014-15	**94.74**		
Falco naumanni	2005	5.26	Farmland, steppe bird	LC
	2014-15	10.53		
Falco tinnunculus	2005	5.26	Farmland	LC
	2014-15	7.89		
Fringilla coelebs	2005	2.63	Woodland	LC
	2014-15	5.26		
Galerida sp.	**2005**	**60.53**	Farmland, ground-nesting	LC
	2014-15	**78.95**		
Garrulus glandarius	2005	0.00	Woodland	LC
	2014-15	2.63		
Glareola pratincola	2005	2.63	Farmland, ground-nesting, steppe bird	LC
	2014-15	7.89		
Hippolais polyglotta	2005	0.00	Woodland	LC
	2014-15	2.63		
Lanius meridionalis	2005	13.16	Farmland	VU
	2014-15	23.68		
Lanius senator	2005	5.26	Woodland	NT
	2014-15	13.16		
Lullula arborea	2005	0.00	Farmland, ground-nesting	LC
	2014-15	13.16		
Melanocorypha calandra	**2005**	**57.89**	Farmland, ground-nesting, steppe bird, fallow	LC
	2014-15	**50.00**		
Oenanthe hispanica	2005	7.89	Farmland, ground-nesting, steppe bird, ploughed	LC
	2014-15	2.63		
Otis tarda	2005	2.63	Farmland, ground-nesting, steppe bird	LC
	2014-15	13.16		
Parus major	2005	2.63	Woodland	LC
	2014-15	0.00		
Passer domesticus	2005	0.00	Woodland	LC
	2014-15	10.53		
Passer hispaniolensis	2005	5.26	Woodland	LC
	2014-15	5.26		
Passer sp	2005	0.00	Woodland	LC

	2014-15	0.00		
Pica pica	2005	0.00	Woodland	LC
	2014-15	7.89		
Picus viridis	2005	2.63	Woodland	LC
	2014-15	0.00		
Pterocles orientalis	2005	2.63	Farmland, ground-nesting, steppe bird, ploughed	EN
	2014-15	0.00		
Saxicola rubicola	**2005**	**31.58**	Farmland, ground-nesting	LC
	2014-15	**31.58**		
Serinus serinus	2005	5.26	Woodland	LC
	2014-15	5.26		
Streptopelia decaocto	2005	2.63	Woodland	LC
	2014-15	13.16		
Sturnus unicolor	2005	7.89	Woodland	LC
	2014-15	5.26		
Sylvia melanocephala	2005	5.26	Woodland	LC
	2014-15	13.16		
Sylvia undata	2005	0.00	Woodland	NT
	2014-15	5.26		
Tetrax tetrax	**2005**	**31.58**	Farmland, ground-nesting, steppe bird, fallow	VU
	2014-15	**34.21**		
Turdus merula	2005	5.26	Woodland	LC
	2014-15	7.89		
Upupa epops	2005	7.89	Farmland	LC
	2014-15	**26.32**		

* Species excluded due to being cosmopolitan and with little relevance to the farmland context of the study area

Table S3.3 – Summary statistics (mean ± standard deviation [SD]; minimum [min], and maximum [max]) of variables describing local structure and landscape context in 1 km buffers around 38 transects where bird counts were performed in 2005 and 2014-2015 in southern Portugal. Temporal variation indicates differences between the second and the first period, and significant deviations from zero ($p < .05$; paired t-test) are in **bold**. AWMSI – Area Weighted Mean Shape Index; MPS – Mean Patch Size; ED – Edge Density.

	2005		2014-15		Temporal variation		Paired t-test	
Variable (unit)	**Mean ± SD**	**min-max**	**Mean ± SD**	**min-max**	**Mean ± SD**	**min – max**	***t***	***p***
Grassland structure								
Vegetation height (cm)	5.96 ± 3.55	0.64 – 14.49	30.82 ± 10.51	9.85 – 55.28	24.86 ± 10.34	0.42 – 48.22	-27.63	**2.20E-16**
Livestock occurrence (presence/parcel)	0.38 ± 0.37	0 – 1	0.30 ± 0.33	0 – 1	-0.08 ± 0.40	0 – 1	-1.05	0.36
Forest Plantation structure								
Tree height (m)	3.77 ± 4.68	0.30 - 17.30	4.30 ± 4.89	1.10 - 26.10	0.53 ± 2.78	-10.6 - 8.8	-0.96	0.34
Tree density (trees/m)	0.11 ± 0.05	0.03 - 0.22	0.11 ± 0.05	0.04 - 0-27	0.01 ± 0.03	-0.08 - 0.08	-1.17	0.24
Landscape composition								
Agricultural land-use cover (%)	0.98 ± 0.16	0.55 – 1.45	0.98 ± 0.17	0.55 – 1.45	-0.01 ± 0.04	-0.17 – 0.01	0.60	0.55
Eucalyptus plantations cover (%)	0.08 ± 0.13	0.00 – 0.48	0.08 ± 0.13	0.00 – 0.48	0 ± 0.01	-0.03 – 0.07	-0.07	0.94
Pine plantations cover (%)	0.19 ± 0.23	0.00 – 0.62	0.2 ± 0.23	0.00 – 0.62	0.01 ± 0.03	-0.01 – 0.15	-0.22	0.83
Oak plantations cover (%)	0.31 ± 0.24	0.00 – 0.70	0.32 ± 0.24	0.00 – 0.70	0.01 ± 0.05	0 – 0.24	-0.43	0.67
Shrubland cover (%)	0.06 ± 0.07	0.00 – 0.21	0.06 ± 0.07	0.00 – 0.26	0 ± 0.02	-0.06 – 0.09	0.13	0.90
Wood-pastures cover (%)	0.12 ± 0.15	0.00 – 0.45	0.12 ± 0.15	0.00 – 0.45	0 ± 0.01	-0.07 – 0	0.11	0.92
Bodies of water cover (%)	0.05 ± 0.07	0.00 – 0.25	0.08 ± 0.07	0.00 – 0.25	0 ± 0.01	0 – 0.07	-0.26	0.80
Urban areas cover (%)	0.09 ± 0.08	0.00 – 0.28	0.09 ± 0.09	0.00 – 0.28	0 ± 0.01	0 – 0.03	-0.10	0.92
Olive groves cover (%)	0.05 ± 0.08	0.00 – 0.39	0.05 ± 0.08	0.00 – 0.39	0 ± 0	-0.01 – 0	0.04	0.97
Landscape heterogeneity								
AWMSI	1.96 ± 0.37	1.22 – 3.04	1.94 ± 0.36	1.22 – 2.95	-0.02 ± 0.07	-0.25 – 0.07	0.52	0.60
MPS (ha)	89.88 ± 75.44	16.55 – 274.85	91.99 ± 75.27	19.16 – 274.85	2.11 ± 15.54	-28.66 – 88.74	-0.24	0.81
ED (km/km2)	46.41 ± 15.23	22.11 – 109.62	45.08 ± 14.56	22.11 – 101.31	-1.33 ± 3.05	-12.96 – 1.15	0.80	0.43

Table S3.4 – Average modelling results (GLMM) for each guild and species abundance. Included are the variables selected for each model with delta < 2; degrees of freedom (df) log-likelihood of each model (logLik); the resulting Akaike Information Criterion corrected for small samples (AICc); and model weights (weight).

Guilds	Variables	df	logLik	AICc	delta	weight
All species	distance; forest type; distance:forest type	7	-512.38	1039.53	0.00	0.66
	forest type	4	-516.30	1040.88	1.34	0.34
Woodland birds	distance; forest type; distance:forest type	7	-473.78	962.34	0.00	0.58
	distance; forest type; veg. height; distance:forest type	8	-473.01	963.02	0.68	0.42
Farmland birds	forest type; veg. height	5	-417.59	845.59	0.00	0.48
	forest type; veg. height; forest type:veg. height	7	-415.96	846.69	1.10	0.28
	forest type	4	-419.33	846.94	1.35	0.24
Ground-nesting birds	forest type	5	-357.73	725.87	0.00	0.72
	forest type; veg. height	6	-357.60	727.78	1.91	0.28
Steppe birds	distance; forest type; veg. height; distance:forest type; distance:veg. height	10	-309.91	641.38	0.00	0.36
	distance; forest type; veg. height; distance:veg. height	8	-312.30	641.61	0.23	0.32
	distance; veg. height; distance:veg. height	6	-314.55	641.67	0.29	0.31
Cereal related birds	distance; veg. height; distance:veg. height	6	-251.91	516.41	0.00	0.55
	distance; veg. height	5	-253.21	516.83	0.43	0.45
Fallow related birds	(Null)	3	-297.01	600.18	0.00	0.20
	distance; forest type; veg. height; distance:veg. height	8	-291.74	600.49	0.31	0.17
	distance; forest type	5	-295.07	600.55	0.37	0.17
	forest type; veg. height	6	-294.01	600.61	0.43	0.16
	distance; veg. height; distance:veg. height	6	-294.04	600.66	0.48	0.16
	veg. height;	4	-296.32	600.90	0.72	0.14
Ploughed related birds	distance; forest type; veg. height; distance:forest type	8	-172.81	362.63	0.00	0.22
	distance; forest type; veg. height; distance:forest type; distance:veg. height	9	-171.74	362.76	0.12	0.21
	distance; forest type; veg. height;	6	-175.14	362.87	0.23	0.20
	distance; forest type; veg. height; distance:veg. height	7	-174.41	363.59	0.96	0.14
	distance; veg. height;	4	-177.67	363.62	0.98	0.14
	distance; veg. height; distance:veg. height	5	-176.96	364.33	1.70	0.10
Threatened species	distance; forest type; distance:forest type	8	-216.56	450.13	0.00	0.51
	distance	4	-220.98	450.23	0.09	0.49
Species						
Ale. rufa	(Null)	3	-65.40	136.96	0.00	0.56
	veg. height	4	-65.24	138.75	1.79	0.23
	distance	4	-65.32	138.92	1.96	0.21
Ant. campestris	forest type; veg. height	5	-44.99	100.38	0.00	0.28
	distance; forest type; veg. height	6	-44.36	101.30	0.92	0.18
	veg. height;	3	-47.69	101.54	1.15	0.16
	distance; forest type; veg. height; distance:veg. height	7	-43.46	101.70	1.32	0.15
	forest type	4	-46.86	102.00	1.62	0.13
	forest type; veg. height; forest type:veg. height	7	-43.76	102.29	1.91	0.11

Cal. brachydactyla	distance; veg. height	4	-167.76	343.78	0.00	0.41
	distance; forest type; veg. height	6	-166.25	345.08	1.29	0.21
	distance	3	-169.52	345.21	1.42	0.20
	distance; veg. height; distance:veg. height	5	-167.51	345.44	1.65	0.18
Lin. cannabina	distance	3	-85.67	177.50	0.00	0.60
	(Null)	2	-87.11	178.30	0.80	0.40
Car. carduelis	(Null)	2	-121.46	247.00	0.00	0.60
	veg. height	3	-120.84	247.84	0.83	0.40
Cis. juncidis	veg. height	4	-112.18	232.62	0.00	0.35
	distance; veg. height	5	-111.13	232.68	0.06	0.34
	distance; veg. height; distance:veg. height	6	-110.14	232.86	0.23	0.31
Cor. corone	(Null)	2	-195.82	395.73	0.00	0.66
	forest type	4	-194.37	397.02	1.29	0.34
Emb. calandra	distance; veg. height; distance:veg. height	6	-221.28	455.15	0.00	0.79
	distance; veg. height	5	-223.72	457.85	2.70	0.21
Gal. lark	veg. height	3	-210.67	427.51	0.00	0.72
	forest type; veg. height	5	-209.48	429.37	1.86	0.28
Mel. calandra	distance; forest type; veg. height; distance:veg. height	7	-261.87	538.52	0.00	0.33
	forest type; veg. height	5	-264.07	538.54	0.02	0.33
	veg. height	3	-266.86	539.89	1.36	0.17
	distance; veg. height; distance:veg. height	5	-264.75	539.91	1.38	0.17
Sax. rubicola	veg. height	3	-98.13	202.43	0.00	0.44
	(Null)	2	-99.58	203.25	0.82	0.29
	distance; veg. height; distance:veg. height	5	-96.53	203.47	1.04	0.26
Tetrax tetrax	(Null)	3	-161.49	329.14	0.00	0.72
	veg. height	4	-161.40	331.07	1.93	0.28
Upu. epops	distance; veg. height; distance:veg. height	5	-37.44	85.29	0.00	0.57
	veg. height	3	-39.84	85.84	0.55	0.43

Chapter 4

Combined effects of land-use and climatic factors on farmland bird species regional distribution

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4.1. Abstract

The Mediterranean farmlands are biodiversity hotspots undergoing substantial changes due to agricultural intensification, land abandonment, and afforestation, compounded by extreme climatic conditions. These transformations alter landscape structure and impacting farmland bird species' diversity, abundance, and distribution patterns. To understand the relative and combined importance of each of these factors and their implications for conservation strategies at a regional scale, we investigated the effects of land use, land-use heterogeneity, and climatic conditions on the distribution of several farmland bird species in Southern Portugal.

Our results revealed that models incorporating both land-use and climatic predictors outperformed those using only one set of variables in predictive accuracy, with random forests being the best-performing method overall. Land-use variables, namely forest plantations and temporary farmland cover, were more influential than climatic variables in determining species distributions. Species exhibited diverse suitability niches, with preferences ranging from open grassland areas in the case of habitat specialists, to forested habitats or regions of lower precipitation and higher temperatures for generalist species. Furthermore, landscape context effects, although not majorly important in general, contributed positively to the distribution of farmland generalists.

These findings underscore the importance of considering both land-use and climatic variables in conservation strategies for farmland bird species. While climatic forecasts provide insights into general avian diversity changes, finer-scale predictions integrating landscape variables are crucial for targeting conservation efforts effectively. Monitoring land-use changes, particularly afforestation initiatives, agriculture intensification and vegetation encroachment, can aid in managing avian biodiversity in the Mediterranean basin. Overall, understanding species-specific responses to landscape changes is essential for implementing tailored conservation measures to safeguard farmland bird populations in dynamic agricultural landscapes.

Keywords: Mediterranean farmland conservation, species distribution models, open farmland specialists, land-use effects, climatic conditions

4.2. Introduction

The Mediterranean farmlands have historically served as biodiversity hotspots (Myers *et al*., 2000; Plieninger *et al*., 2014), fostering a diverse group of avian species adapted to the intricate mosaic of natural, semi-natural and extensively cultivated landscapes (Donald *et al*., 2001; Stoate *et al*., 2001; Sirami *et al*., 2010). However, decades of gradual land-use changes, driven by agricultural intensification (Donald *et al*., 2001, 2006; Vickery *et al*., 2004), land abandonment (Plieninger *et al*., 2014; Herrando *et al*., 2016), and afforestation (Reino *et al*., 2009; Tomaz *et al*., 2013), coupled with increasingly extreme climatic conditions (Barbet-Massin *et al*., 2012; Şekercioğlu *et al*., 2012; Conrey *et al*., 2016; Marcelino *et al*., 2020), are reshaping the structure of these farmlands, consequently affecting the diversity (Plieninger *et al*., 2014; Morgado *et al*., 2020), abundance (Vickery *et al*., 2004; Donald *et al*., 2006) and distribution patterns of farmland bird species (Barbet-Massin *et al*., 2012; Reino *et al*., 2013, 2018; Valladares *et al*., 2014).

Agricultural intensification is an increasingly pervasive trend across the Mediterranean region, characterized by increased levels of mechanization, use of chemical products, livestock grazing intensity, and major changes to traditional farming practices (Stoate *et al*., 2001; Donald *et al*., 2006), such as the fast and large-scale olive farming intensification seen over the last 30 years in Mediterranean farmland landscapes (Morgado *et al*., 2020, 2022). While the range of impacts may vary across different groups, farmland bird species have been particularly affected by the associated land-use changes (Vickery *et al*., 2004; Donald *et al*., 2006). Concurrently, land abandonment, often driven by environmental (Rey Benayas *et al*., 2007) or socioeconomic factors, is also on the rise (Plieninger *et al*., 2014). While its successional aspects may contribute to a passive restoration of agricultural areas into semi-natural vegetation and eventual recovery of natural ecosystems (Bowen *et al*., 2007), these landscape transformations can also represent a threat to functional farmland biodiversity, through a reduction in landscape heterogeneity and increased afforestation (Báldi and Batáry, 2011; Queiroz *et al*., 2014), particularly in landscapes of high nature value (Peco *et al*., 2012; Plieninger *et al*., 2014; Ribeiro *et al*., 2014).

Afforestation is a land-use change that gained increasing momentum globally (Hansen *et al*., 2013; Brazeiro *et al*., 2018; Jacoboski and Hartz, 2020), particularly in countries associated with higher economic development (Ewers, 2006), where it is often implemented to mitigate the impacts of climate change (García *et al*., 2020) by increasing carbon sequestration, improving soil quality and promote habitat restoration (Curtis *et al*., 2018; Holl *et al*., 2020). However, farmland biodiversity responses to afforestation in the Mediterranean region were found to be mixed (Pita *et al*., 2009; Reino *et al*., 2009;

Vasconcelos *et al*., 2019; Faria *et al*., 2024), with several bird species assemblages responding negatively to planted forests (Reino *et al*., 2009; Faria *et al*., 2024). This is because afforested areas can lead to the loss and fragmentation of habitats used by species often dependent on open grassland areas (Brotons *et al*., 2005; Reino *et al*., 2009; Pretelli *et al*., 2018). In already highly fragmented landscapes, land abandonment may provide beneficial effects from large-scale restoration of natural systems (Brunori *et al*., 2017). However, it is often large open farmlands which are subjected to fragmentation (Paulus *et al*., 2022), whether through afforestation or intensification of production (e.g., olive grove intensification with irrigated systems) (Morgado *et al*., 2022). Farmland bird species can be additionally impacted by increased predator abundance and associated nest predation risk in the fragmented grasslands remaining (Santos *et al*., 2006; Terraube *et al*., 2016; Faria *et al*., 2022).

In addition to the landscape composition, the heterogeneity of the landscape, usually representing the degree to which farmland regions are more or less fragmented by different land uses (i.e., the degree of spatial association of the farmland region) (Fahrig *et al*., 2011; Santana *et al*., 2017), can influence not only local species diversity (Báldi and Batáry, 2011; Santana *et al*., 2017) but also the ability to accurately predict species distributions at broader scales (Whittingham *et al*., 2007; Mattsson *et al*., 2013; Reino *et al*., 2013). High levels of habitat heterogeneity are often positively associated with farmland species richness and abundance (Benton *et al*., 2003; Báldi and Batáry, 2011; Fahrig *et al*., 2011). However, the cost may be the decrease of open grassland specialists, which tend to benefit from larger homogeneous landscapes (Morgado *et al*., 2010; Sliwinski and Koper, 2012), and may instead favour local-scale grassland heterogeneity, such as different grassland vegetation heights (Vickery *et al*., 2009; Báldi and Batáry, 2011; Faria *et al*., 2024). Thus, it is important to consider the effects of local-scale land-use heterogeneity on farmland birds' distribution patterns, to help understand the appropriate scale for optimal conservation strategies (Whittingham *et al*., 2007; Barbet-Massin *et al*., 2012).

Farmland bird species, adapted to the historical agricultural landscapes of the Mediterranean, have finely tuned ecological necessities, exhibiting a high sensitivity to changes in land use, fragmentation, and environmental conditions (Delgado and Moreira, 2000; Santana *et al*., 2017; Reino *et al*., 2018; Gaüzère *et al*., 2020; Faria *et al*., 2024). Recognizing this sensitivity, our research focuses on a diverse group of farmland bird species, selected for being widespread in the Mediterranean farmland region of Southern Portugal, while possessing specific and distinct habitat requirements (Moreira, 1999; Delgado and Moreira, 2000; Reino *et al*., 2009).

Employing a systematic approach to modelling the distribution of each species integrating spatial analysis and ecological modelling, we aim to untangle the effects and relative importance of different land uses, land-use heterogeneity, climatic conditions, and vegetation productivity at a regional scale. Additionally, by evaluating the local spatial association of the land uses within the studied region, we seek to better understand how farmland heterogeneity can affect the distribution ranges of species ranging from farmland generalists to open grassland specialists. Specifically, this study aims to i) analyse and compare the improvements in model accuracy and predicted ranges when including land-use predictors at the regional scale, in addition to climatic variables; ii) investigate and quantify the most relevant land-use categories and their interactions with climatic conditions to establish likely ecological niches, focusing on the potential consequences of increased afforestation cover on representative Mediterranean farmland bird species; and iii) explore how incorporating local spatial association of land-use predictors may affect the distributions of species with different sensitivities to habitat fragmentation at the regional level, and potential consequences at larger scale distributions. This will allow to better understand the main limiting factors shaping the regional distribution ranges of these species.

4.3. Methods

4.3.1 Study area

The study area comprises a large region of Southern Portugal (Alentejo), an area that includes several Natura 2000 designated sites, among which is the Castro Verde Special Protection Area (SPA), developed for steppe bird conservation under the European Union Birds Directive (Ribeiro *et al*., 2014) (**Fig. 4.1**).

The area is classified as a meso-Mediterranean bioclimatic stage (Vasconcelos *et al*., 2019), with mild winters (9 ºC [5–14 ºC] in January), hot and dry summers (24 ºC [16–32ºC] in July) and an average annual precipitation of ca. 500 mm mostly concentrated in October through March. The landscape is either flat or gently undulating, with a few low-elevation mountain ranges (ca. 100 – 650 m a.s.l.), and composed of a mosaic of the following land uses: open agricultural areas, including rainfed and irrigated annual fallows, crops and pastures; permanent crops such as olive groves and vineyards with different levels of management intensification; and agroforestry systems composed of cork and holm oak (*Quercus suber* and *Q. rotundifolia*, respectively) woodlands of varying tree density (i.e., *montados*) that are typically used for extensive livestock rearing (usually cattle or sheep) (Delgado and Moreira, 2000; Ribeiro *et al*., 2014; Santana *et al*., 2017; Morgado *et al*., 2022). Planted forests in the area are usually composed of trees of eucalyptus (*Eucalyptus sp.*), umbrella pines (*Pinus pinea*) or oaks, although the

last decades saw an increase in afforestation with umbrella pines and holm and cork oaks in the periphery of the SPA (IFD, 2001). Additionally, this region also experienced the expansion of modern olive farming, with an increase in irrigated olive groves, as well as irrigated vineyards and permanent pastures (Ribeiro *et al*., 2014; Santana *et al*., 2017; Morgado *et al*., 2022).

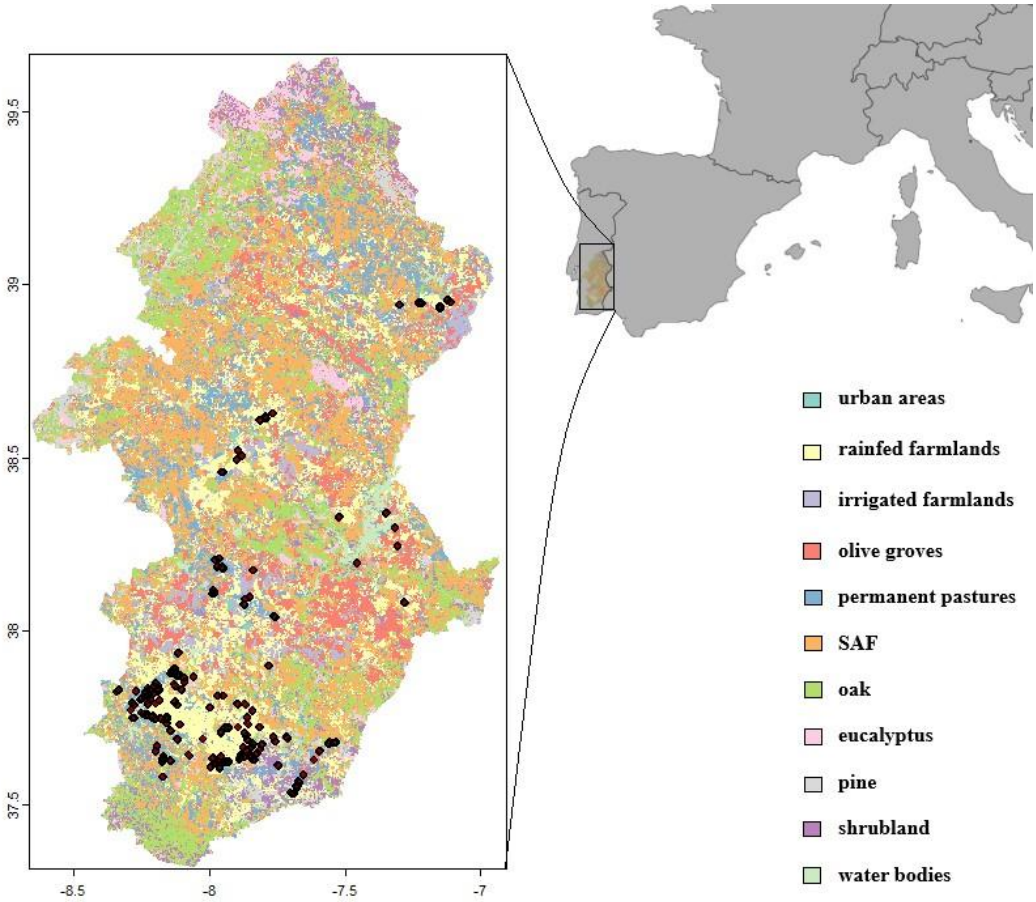

Figure 4.1 – Map of the study area with sampling point locations and all land-use categories (10 m resolution). These include urban areas; temporary traditional crops such as fallow and pastures (rainfed farmlands); temporary irrigated crops and pastures (irrigated farmlands); intensive and extensive olive groves (olive groves); permanent pastures; agroforestry systems (i.e., montado - SAF); forests of oak, eucalyptus and pine species; shrubland vegetation; and water bodies (e.g., aquifers, small rivers).

4.3.2 Presence-absence data and selected species

Sampling was carried out across 148 sites between April and June of 2014 and 2015. Sites were composed of a woody vegetation area (olive groves or plantation forests) and open habitat area (usually cereal, fallow fields and pastures). At each site, a transect of points distributed in 100-m intervals was established perpendicularly to the woody-grassland edge. At each point, bird count surveys were conducted sequentially for 10

minutes, where each bird seen or heard within 50 m from the observer was recorded. The number of points per transect varied according to the size of each area, being limited to half the length of the open grassland and woody vegetation area, to minimise the influence of other adjacent land uses (from 400 to 700 m; mean ± SD = 531 ± 101). In total, 937 points were sampled across the 148 sites. Sampling was conducted by experienced observers preferably at dawn, or at either dawn or dusk, as Mediterranean farmland birds have similar peaks of activity during these periods (Caro *et al*., 2015). To minimise double counting of individuals, birds in flight were not recorded, except in the case of song flights (e.g., calandra lark, *Melanocorypha calandra*). Additionally, extra care was taken to not count any birds flushed between counts that landed at a subsequent survey point, which was always within sight (Reino *et al*., 2009; Faria *et al*., 2024).

For detailed species distribution analyses, we selected the most widespread and ecologically relevant species, occurring in over 40% of all sampled sites across the region: corn bunting (*Emberiza calandra*), zitting cisticola (*Cisticola juncidis*), common quail (*Coturnix coturnix*), European goldfinch (*Carduelis carduelis*), little bustard (*Tetrax tetrax*), red-legged partridge (*Alectoris rufa*), calandra lark, woodpigeon (*Columba palumbus*) and Eurasian hoopoe (*Upupa epops*).

4.3.3 Land-use categories and local spatial association

Land uses were defined for the study area using a land-use cover map from 2015 (Caetano *et al*., 2018), which was then reclassified to include the ecologically relevant categories we considered. This was done by consulting orthophotos of the time (2015) and previous partial land-use mapping of the region developed by Morgado (2022). The final land-use map was converted into a raster file of 10 m resolution using ArcGIS (ver. 3.1.0) (ESRI, 2023) composed by a total of 11 land-use categories: agroforestry systems (SAF); oak, pine, and eucalyptus forests; temporary traditional crops and irrigated crops; permanent pastures; permanent cultures, such as olive groves, vineyards and other orchards; shrubland vegetation; urban areas, such as roads, industry or other human structures; and bodies of water, such as aquifers and small rivers (**Fig. 4.1**). To perform species distribution model analyses, these land-uses were transformed into a raster of the proportion of land-use cover for each category over a 500 m cell-size. The final categories selected as predictor variables, after preliminary analysis, were urban (i.e., all urban areas), forest (i.e., all forest types), farm (i.e., both rain-fed and irrigated farmland pastures), olive (i.e., both irrigated and rain-fed olive groves), pasture (i.e., permanent pastures), saf (i.e., agroforestry systems), shrubland (i.e., shrubland vegetation) and water (i.e., all bodies of water) (**Fig. S4.1**).

Local spatial association between the categorical variables was also estimated for all the study area. Specifically, we employed a local indicator of spatial association (ELSA) which is entropy-based and does not rely on spatial stationarity of global measures (Naimi *et al*., 2019). This method analyses spatial structure of the land-use variables, producing a term for each raster pixel, between 0 and 1, that summarizes the attribute distance between a location and its neighbourhood locations over a given geographical distance. Briefly, higher ELSA values indicate high spatial heterogeneity between land uses (Naimi *et al*., 2019). We created three different predictors to measure spatial association at different scales, i.e., using different distance measures of 250, 500 and 1000 m.

4.3.4 Climatic predictors

We extracted bioclimatic variables for the study region (WorldClim, 2024), which are derived from monthly temperature and rainfall values to generate variables representing trends, seasonality and extreme environmental factors for the period of 1970-2000. A total of 19 bioclimatic variables were extracted. After verifying for potential multicollinearity issues over our study area (Daoud, 2017), the five variables with lowest multicollinearity were kept as climatic predictors: average diurnal temperature range, given by the average monthly variation between minimum and maximum temperatures (m.diurnal.range); minimum temperature of the coldest month, given by the average of the minimum temperatures for the days of the coldest month (min.temp.cold.month); average temperature over the wettest quarter, given by the average temperatures during the three month-period with highest rainfall (m.temp.wet.quart); precipitation for the wettest month, given by the total precipitation for the month with highest rainfall (precip.wet.month) and precipitation for the driest month, for the month with the lowest rainfall (precip.dry.month) (**Fig. S4.1**). Additionally, we also included the Enhanced Vegetation Index (EVI) (NASA, 2024), a satellite-based measure of vegetation productivity with a 250 m resolution (Sims *et al*., 2006). As this is a biweekly measure, data was extracted for the first six months of 2015 and averaged to form a single predictor (**Fig S4.1**). All predictors were scaled with bilinear interpolation (Barbet-Massin *et al*., 2012) to match resolutions with land-use predictors, as model performance may be strongly influenced by the variable resolution (Farashi and Alizadeh-Noughani, 2018).

4.3.5 Statistical analysis

To understand the degree of spatial autocorrelation of our land uses in the study area, we developed *entrograms*, at two different distance ranges which is essentially a variogram-like plot that summarizes the spatial association within the land-use categories (Naimi *et al*., 2019). Multicollinearity of climatic predictors was analysed using a variable inflation factor function using a stepwise procedure, to exclude highly correlated predictors (Naimi *et al*., 2014).

Species distribution models (SDMs) were developed for the nine selected species with the collected presence-absence data. For each, species distributions were modelled using i) two regression methods: generalized linear models (GLM; McCullagh, 2019); multivariate adaptive regression splines (MARS; Elith *et al*., 2020); ii) two machine learning methods: Random Forests (RF; Breiman, 2001); Booster regression trees (BRT; Friedman, 2001); and iii) one recursive partitioning method (Rpart; Strobl *et al*., 2009). To evaluate the predictive performance of the SDMs for each species, we used a bootstrapping method, as well as a subsampling method, where 70% of the data was used to calibrate the model and 30% was used for evaluation. Each model was replicated three times and tested against the input data (i.e., training data). Maxent was not used, as it is less adequate with presence-absence data, only useful for relative suitability without post-processing the results (Guillera-Arroita *et al*., 2014).

The area under the curve (AUC) of the receiver operating characteristic (ROC) was the main statistic used to measure predictive performance of the models (Fielding and Bell, 1997). This is a threshold and prevalence-independent metric varying between 0-1 where a value of 0.5 implies random predictive discrimination and predictive power increases as this gets closer to one (Naimi and Araújo, 2016). Other performance metrics were also calculated for validation of AUC results (e.g., correlation and deviance).

To obtain the probability of occurrence across the study area for each species, we used the *sdm* package (Naimi and Araújo, 2016), computing three different sets of SDMs with different groups of predictors: land-use predictors (n = 11), climatic-only predictors (n = 6), and all predictors (land-use + climatic predictors; n = 17). Three sets of ensemble models were then developed, combining all 30 predicted models for each species and group of predictors, through a weighted average method based on the combination of sensitivity and specificity of each model, called the true skill statistic (TSS) (Allouche *et al*., 2006). With the resulting ensemble models, the average relative variable importance was calculated for each species, based on a Pearson correlation metric. Considering the two most important variables (on average) for each species, we

computed two-dimensional maps that effectively reflect an ecological niche for that species, with a suitability range (Naimi and Araújo, 2016).

Finally, using the resulting ensemble models of the probability of occurrence, a presence-absence threshold was calculated for each species based on TSS, to map the potential distribution range of each species across the study area (Jiménez-Valverde, 2021).

Multicollinearity was analysed using the *usdm* package (Naimi *et al*., 2014). Local-scale spatial association and entrogram analyses were performed with the *elsa* package (Naimi *et al*., 2019). All SDMs (individual and ensemble models), relative variable importance and niche characterization analyses were implemented using functions from the *sdm* package in R software (R Core Team, 2023).

4.4. Results

4.4.1 Model performance

Overall, model performance estimated from the AUC statistic obtained from a ROC plot was on average consistently superior (mean ± SD AUC = 0.71 ± 0.06) for the models which included a combination of land-use and climatic predictors, compared to models using only land-use (mean ± SD AUC = 0.68 ± 0.06) or climatic condition variables (mean ± SD AUC = 0.68 ± 0.06), although not significantly so (**Table 4.1**)**.** In terms of model methods, when considering all species, RF performed consistently better across the different predictor uses (mean ± SD AUC = 0.76 ± 0.06), and included the best-performing model, using all predictors, for the Calandra lark (AUC_{rf} = 0.85), being followed by BRT (mean ± SD AUC_{brt} = 0.70 ± 0.04). On average, GLM performed worse than other methods (mean ± SD AUC_{glm} = 0.65 ± 0.05), regardless of predictors considered, and also included the worse performing model, which included all predictors, for the common quail (AUC_{glm} = 0.58) (**Table 4.1**). In terms of species, predicted models fitted the data more adequately, on average, for the calandra lark, whether using all predictors (mean ± SD AUC_{all} = 0.80 ± 0.03) or land-use and climatic predictors separately (mean ± SD AUC = 0.78 ± 0.03, for both). Contrastingly, predicted models for the Eurasian hoopoe performed the worst, on average when considering all predictors (mean ± SD AUC_{all} = 0.65 ± 0.03), whereas for land-use and climatic predictors, the models fitted for the common quail performed less adequately (mean ± SD AUC = 0.63 ± 0.04, for both). Correlation metrics yielded similar results for species and method average (see **Table 4.1a-c**). Additionally, true skill statistic (TSS) ranged on average, from 0.30 ± 0.06 (mean ± SD), for the Eurasian hoopoe, to 0.51 ± 0.07 (mean ± SD) for the calandra lark. Overall TSS was 0.37 ± 0.09 (mean ± SD) when considering all predictors (**Table S4.1a**).

Table 4.1 – Models mean performance (per species) based on the area under the curve (AUC) of a receiver operating characteristic plot, using a test dataset generated using 30% of total data partitioned. Ensemble model performance based on threshold-based weighted averaging (using TSS as the threshold). ALL = models including all predictors; LU = models considering land-use predictors only; CLIM = models considering Climatic predictrors only. See **Table S4.1a-c** for additional performance metrics, including correlation and deviance for all models and prevalence and threshold for Ensemble models.

		Calandra lark	Common quail	Corn bunting	Eurasian hoopoe	European goldfinch	Little bustard	Red-legged partridge	Wood pigeon	Zitting cisticola
	methods	**AUC**	**AUC**	**AUC**	**AUC**	**AUC**	**AUC**	**AUC**	**AUC**	**AUC**
ALL	glm	0.76	0.58	0.7	0.61	0.64	0.71	0.72	0.65	0.65
	mars	0.81	0.65	0.71	0.66	0.68	0.74	0.73	0.65	0.68
	rpart	0.78	0.67	0.73	0.63	0.68	0.70	0.70	0.62	0.71
	brt	0.8	0.69	0.74	0.68	0.72	0.75	0.75	0.67	0.71
	rf	0.85	0.71	0.79	0.69	0.73	0.80	0.76	0.70	0.82
	EN	**0.93**	**0.87**	**0.86**	**0.89**	**0.87**	**0.90**	**0.88**	**0.87**	**0.90**
LU	glm	0.75	0.60	0.68	0.59	0.60	0.65	0.63	0.59	0.61
	mars	0.76	0.61	0.70	0.61	0.60	0.66	0.66	0.62	0.62
	rpart	0.75	0.61	0.72	0.64	0.62	0.68	0.66	0.66	0.67
	brt	0.79	0.65	0.71	0.66	0.66	0.71	0.70	0.68	0.67
	rf	0.83	0.69	0.78	0.68	0.70	0.79	0.76	0.74	0.80
	EN	**0.92**	**0.85**	**0.86**	**0.87**	**0.86**	**0.90**	**0.88**	**0.88**	**0.90**
CLIM	glm	0.65	0.57	0.58	0.58	0.59	0.60	0.71	0.57	0.63
	mars	0.75	0.65	0.62	0.66	0.64	0.70	0.74	0.63	0.65
	rpart	0.70	0.65	0.65	0.59	0.64	0.66	0.72	0.61	0.72
	brt	0.74	0.69	0.65	0.67	0.67	0.71	0.76	0.65	0.69
	rf	0.84	0.74	0.74	0.70	0.71	0.80	0.78	0.71	0.82
	EN	**0.93**	**0.86**	**0.86**	**0.89**	**0.86**	**0.90**	**0.88**	**0.87**	**0.90**

4.4.2 Variable importance and ecological niches

Overall, land-use variables (in particular, forest plantations and temporary farmland cover) were associated with higher relative variable importance compared to climatic variables (**Fig. 4.2; Fig. S4.2**). The variables most frequently showing relative importance above 25% were forest plantation cover (7 out of 9 species) and temporary farmland cover (5 out of 9 species). Others included minimum temperature of the coldest month (2 out of 9), permanent pasture cover, average diurnal temperature range, average temperature over the wettest quarter, and EVI (1 out of 9 for each). Contrastingly, the variables more frequently displaying low relative importance (below 10%) were precipitation for the driest month (9 out of 9 species), EVI (8 out of 9 species), precipitation for the wettest month (6 out of 9 species) and average diurnal temperature range (6 out of 9 species). Others included the average temperature over the wettest quarter (3) and ELSA (2) (**Fig. S4.2**)**.** In general, among the different scales of local spatial association (250 m, 500 m or 1000 m) there was not a consistently more important variable than the other, with the highest relative importance varying between species (each scale was more important for 3 different species). Additionally, their relative importance was low, usually ranging between 10-20% (**Fig. S4.2**). Entrograms of land-use categories (**Fig. S4.3**) reveal generally low land-use heterogeneity on the study area at the low and intermediate scales (250 m and 500 m, respectively), increasing logarithmically until the maximum distance calculated (3000 and 5000 m).

For all 9 species, land-use variables (i.e., cover by temporary farmland, forest plantations or permanent pastures) were always among the two variables with highest relative importance (HRI) (**Fig. 4.2**). In terms of climatic condition variables, these were included among the two HRI variables for 4 out of the 9 species. An ecological niche describing a combination of the suitability of the two most important habitats based on probability of occurrence for each species (**Fig. 4.2**), showed that calandra lark favoured high cover by temporary farmland areas and low plantation cover. The opposite was found for the wood pigeon, favouring plantations over farmland cover. The common quail favoured high temporary farmland cover, with an inverse quadratic relation to the minimum temperature of the coldest months (i.e., higher suitability on the extremes of the variable). For the corn bunting, areas of low forest plantation cover combined with high permanent pastures' cover were preferable, while a similar but less pronounced effect was found for the Eurasian hoopoe. The little bustard usually favoured low forest plantation cover in favour of large areas of temporary farmland. However, a combination of low farmland areas and forest plantation patches also appeared to be suitable. The red-legged partridge favoured areas with a high vegetation index and a minimum area

of forest cover. Similarly, the zitting cisticola also benefited from forest plantation cover, but less so with increasing mean temperature diurnal range (**Fig. 4.2**).

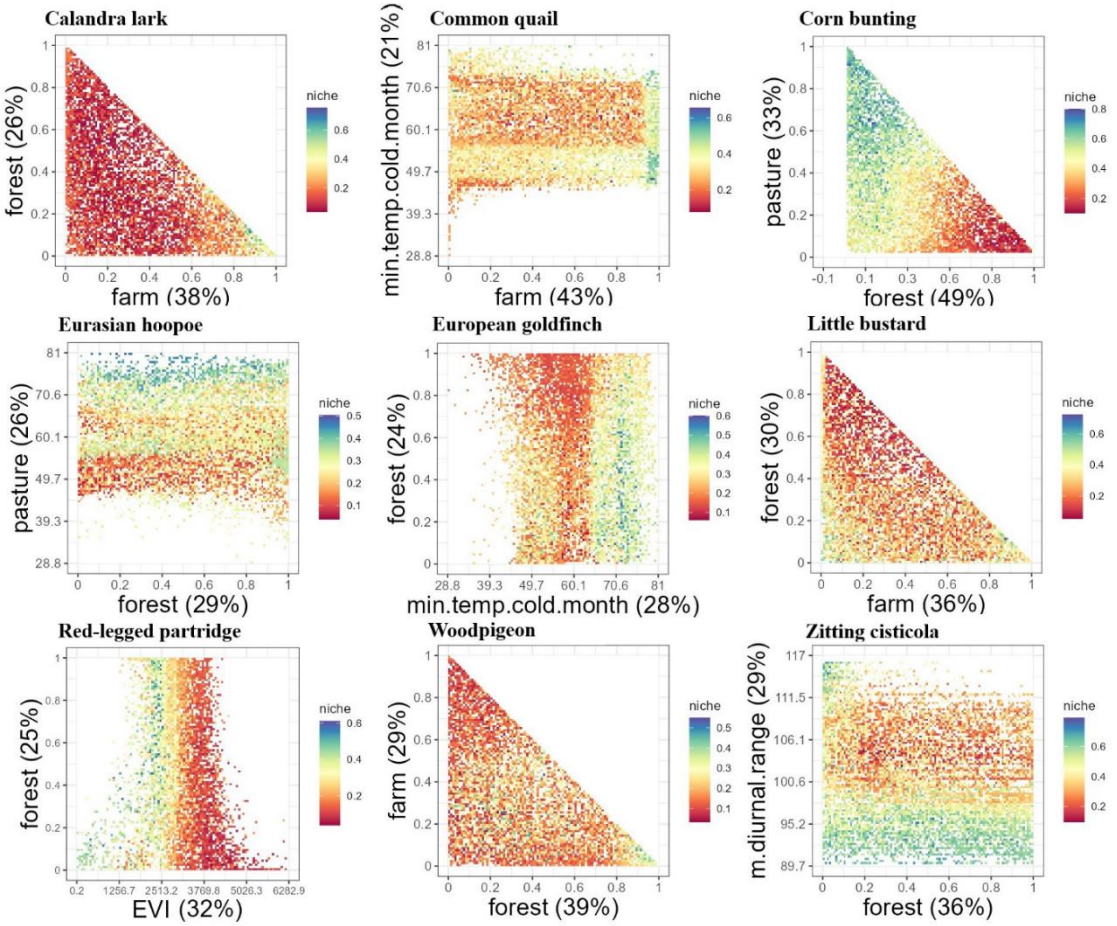

Figure 4.2 – Ecological niches based on probability of occurrence for each species in a two-dimensional environmental space (i.e., based on the two most important variables for each species, according to the 30-model average). Land-use variables (either forest, farm or pasture) were selected for all species. Climatic variables [(average minimum temperature of the coldest month (min.temp.cold.month), mean diurnal range (m.diurnal.range) and Enhanced Vegetation Index (EVI)] were selected for 4 out of 9 species.

4.4.3 Ensemble models – statistics and thresholds

Ensemble models (i.e., the combination of single models' predicted values using weighted averages based on TSS), performed similarly well with models using all predictors (mean ± SD AUC_{all} = 0.89 ± 0.02), land-use predictors (mean ± SD AUC_{LU} = 0.88 ± 0.02) and climatic predictors (mean ± SD AUC_{clim} = 0.88 ± 0.02) (**Table 4.1; Table S4.1a-c).** Considering all predictors, the best-fitted model was observed for the calandra lark (AUC_{all} = 0.93), with a prevalence (i.e., the proportion of presences in sampling points) of 0.19, while the corn bunting had the worst performing model (AUC_{all} = 0.86), with a prevalence of 0.47 (**Table S4.1**). In general, probability of occurrence for all species was more influenced by land use due to overall higher predictor importance (**Fig.**

4.2; Fig. S4.2). However, both predictor types influenced the probability of occurrence of each species, as the predicted distribution of most species using all predictors can generally be observed as a combination of both land-use and climatic predictors-only models (**Fig. 4.3a-c**).

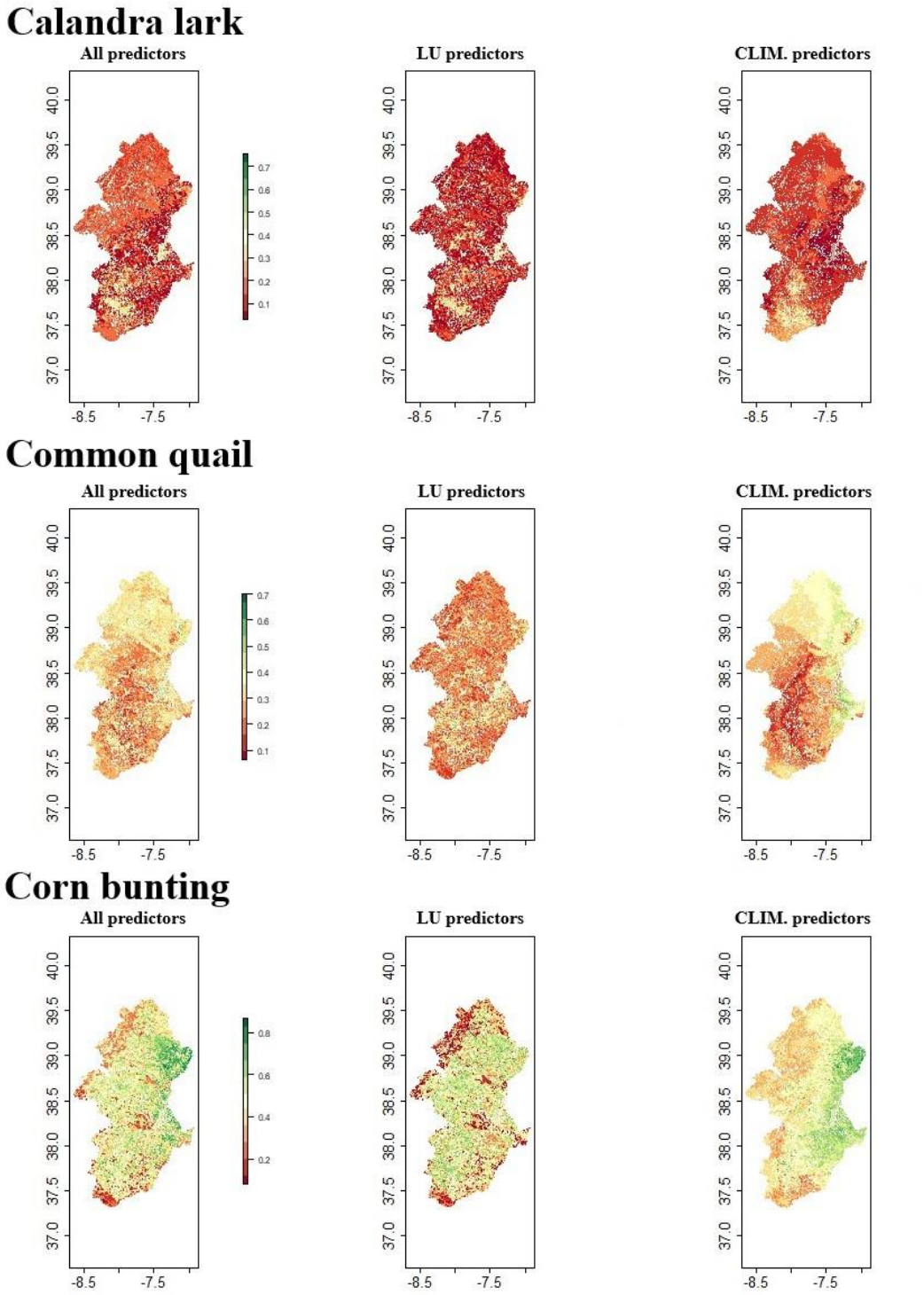

Figure 4.3a – Ensemble model of predicted species distributions for calandra lark, common quail and corn bunting based on weighted averages of models which include all predictors (left); land-use predictors (centre); and climatic predictors (right).

The calandra lark showed a generally low probability of occurrence across the region, increasing mostly in areas associated with large temporary farmland of fallow and pastures (**Fig. 4.3a; Fig. S4.1; S4.2a**), which is reflected in the presence-absence (P-A) distribution map (threshold = 0.21; **Table S4.1; Fig. S4.4a**)**.** The common quail was more prevalent, with a reasonable probability of occurrence throughout most of the region (**Fig. 4.3a**). Preferably in areas of temporary farmland and the northern area, in zones of increased precipitation and lower temperature during the wetter and colder months (**Fig. S4.1; S4.2b**). This, associated with a low threshold (0.21; **Table S4.1**), resulted in a wider distribution, according to the P-A distribution map (**Fig. S4.4b**). The corn bunting showed an overall high probability of occurrence (**Fig 4.3a**), resulting in a wide distribution based on the P-A map (threshold = 0.50; **Table S4.1; Fig. S4.4c**). It occurred preferably in areas associated with temporary farmland, away from areas densely populated by forest plantations and areas with low precipitation and low temperatures during the colder months (**Fig. S4.1; S4.2c**).

The Eurasian hoopoe displayed a generally lower probability of occurrence based on all models, but slightly higher according to the environmental variables model (**Fig 4.3b**). The resulting distribution mostly favouring the north-western and southern corners of the region (threshold = 0.13; **Table S4.1; Fig. S4.4d**) is likely influenced by a preference for high forest cover and warmer temperatures (**Fig. S4.1; S4.2d**). The European goldfinch, similarly affected by colder temperatures and high forest cover, avoided areas of low spatial heterogeneity, normally associated with high farmland cover, and areas of intermediate minimum temperatures, and intermediate to high precipitation for the region (**Fig. 4.3b; Fig. S4.1; S4.2e**), resulting in a wide distribution across most of the region (threshold = 0.20; **Table S4.1; Fig. S4.4e**). The little bustard showed a high probability of occurrence across the north-western part of the region (threshold = 0.24; **Fig 4.3b; Table S4.1; Fig. S4.4f**), driven by a strong association with either high temporary farmland cover or low farmland cover in combination with high cover of agroforestry systems (**Fig. S4.1; S4.2f**). It also favoured higher minimum temperatures during the colder months and average temperatures during months of higher precipitation (**Fig. S4.2f**).

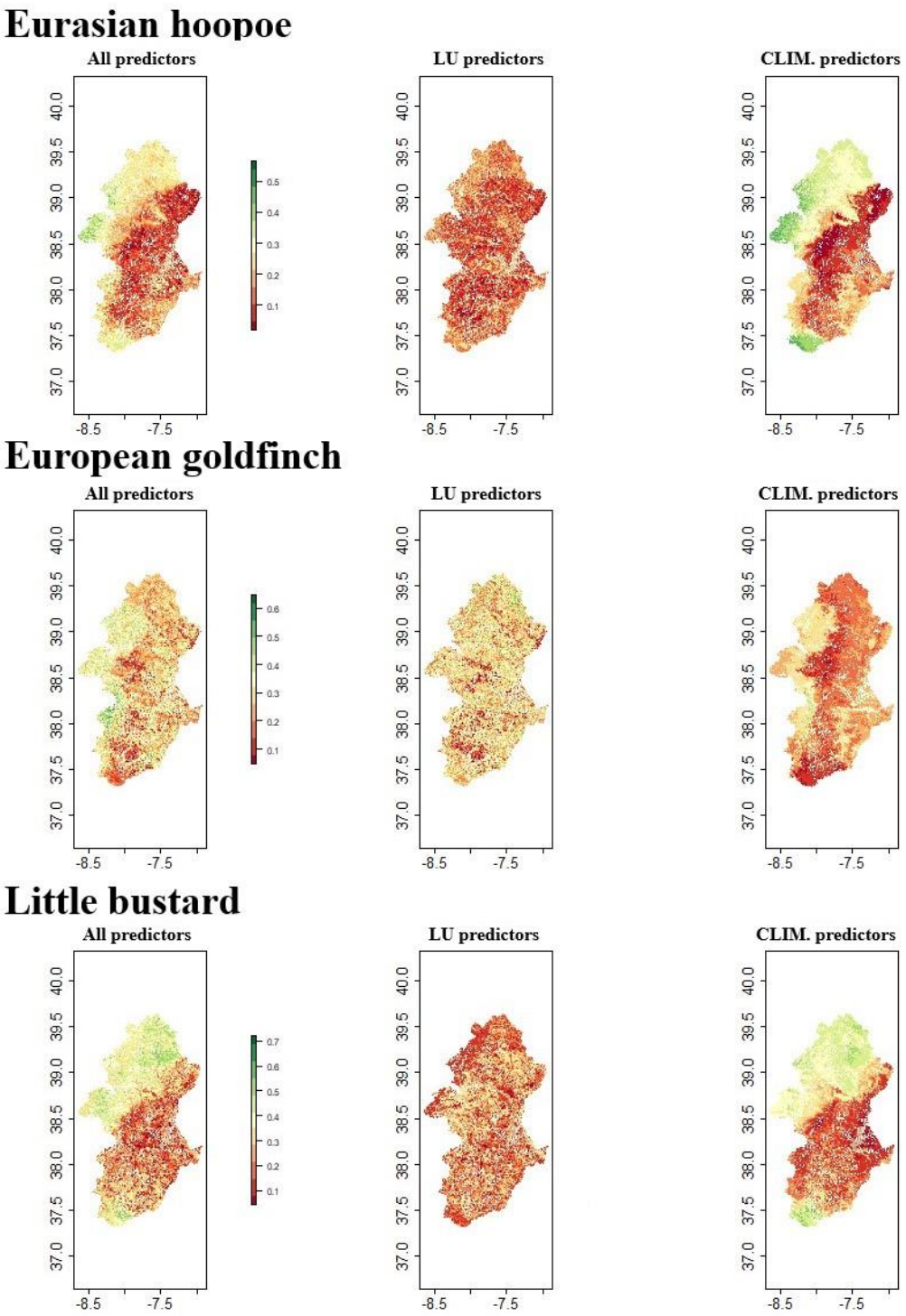

Figure 4.3b – Ensemble model of predicted species distributions for Eurasian hoopoe, European goldfinch and little bustard based on weighted averages of models which include all predictors (left); land-use predictors (centre); and climatic predictors (right).

The red-legged partridge showed an overall low probability of occurrence (**Fig. 4.3c**), resulting in a distribution mostly to the eastern part of the region (threshold = 0.17; **Table S4.1; Fig. S4.4g**). This distribution was mostly influenced by high cover of forest,

shrubland and permanent pastures, as well as a low vegetation cover index, precipitation and temperature variations (**Fig. S4.1; S4.2g**).

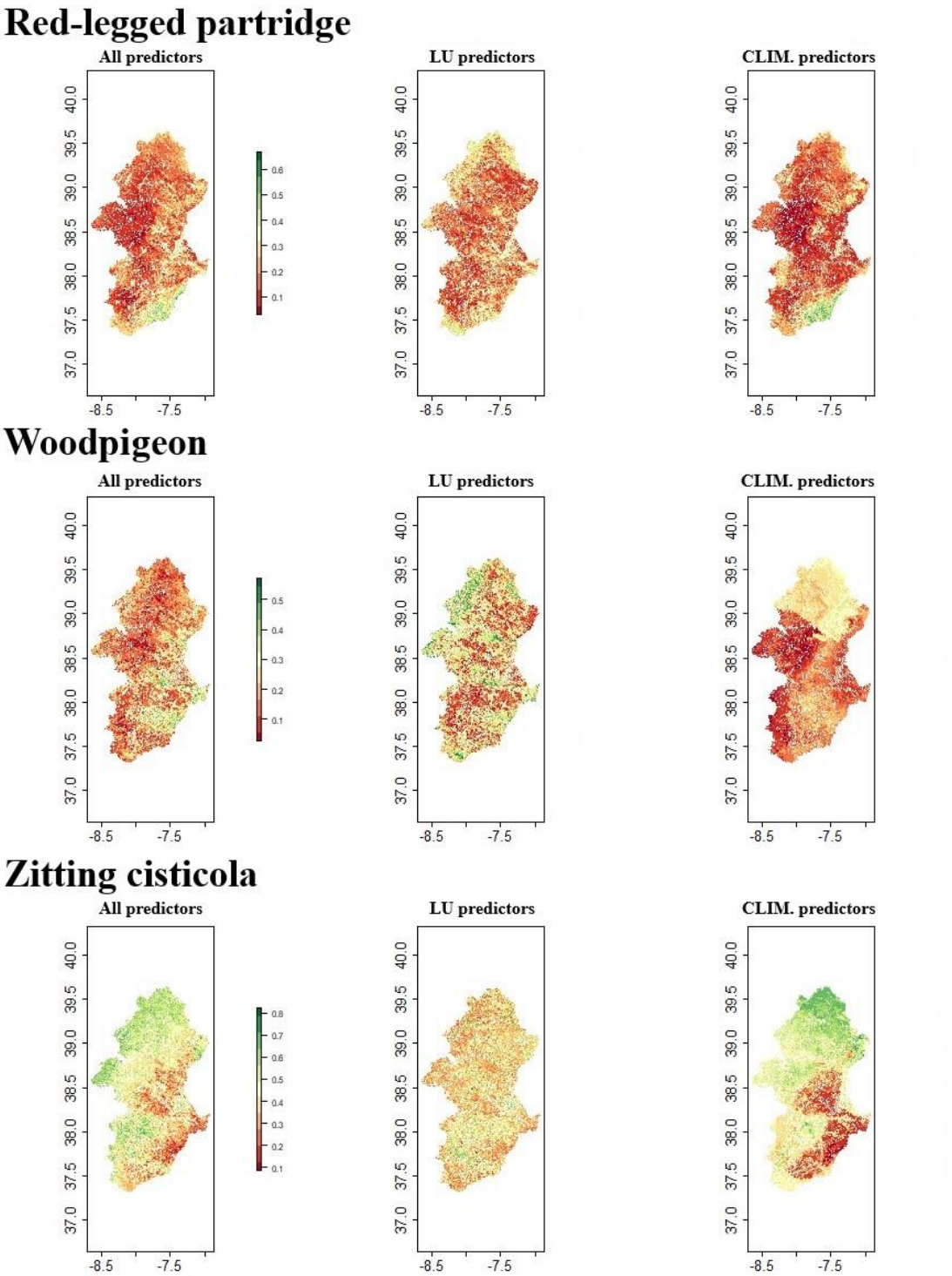

Figure 4.3c – Ensemble model of predicted species distributions for red-legged partridge, woodpigeon and zitting cisticola based on weighted averages of models which include all predictors (left); land-use predictors (centre); and climatic predictors (right).

The woodpigeon was generally predicted to be widespread, despite a low probability of occurrence, on average (threshold = 0.14; **Fig. 4.3c; Table S4.1; Fig. S4.4h**). Its distribution was mainly influenced by a combination of high forest or pasture cover and lower temperatures and higher precipitation in the colder months (**Table S4.1; Fig. S4.2h**). Finally, the zitting cisticola revealed a generally high probability of occurrence, with predicted presences distributed by most of the region, except for the southeastern (threshold = 0.37; **Fig. 4.3c; Table S4.1; Fig. S4.4i**). It appeared to favour a combination of high plantation and farmland cover in high proximity (**Fig. S4.2i**), while avoiding areas of lower minimum temperatures and lower average diurnal range (**Fig. S4.1; S4.2i**).

4.5. Discussion

4.5.1 Importance of land-use predictors on model performance and distributions

Our results indicated that, for most widespread farmland bird species in the region, a combination of land-use and climatic factors influenced their distribution, although land-use factors generally resulted in better predictive accuracy. This contrasts with other studies, in which models using climate-only variables typically resulted in increased accuracy compared to land-use variables (Thuiller *et al*., 2004; Luoto *et al*., 2007). However, these studies generally considered larger scales, where climate is assumed to be the main driver of bird distribution (Reino *et al*., 2018; Jiménez-Valverde, 2021). At the Iberian level, open habitat specialist bird species revealed severely more constrained predicted distributions when incorporating landscape variables into climate change models (Reino *et al*., 2018). Furthermore, a higher accuracy has also been found for models using a combination of both habitat and climatic variables when investigating the predicted distribution of breeding birds at a European scale (Barbet-Massin *et al*., 2012), although climatic variables were generally more informative than habitat variables at that scale. At a finer spatial resolution, land-use variables are likely to increase their importance (Luoto *et al*., 2007; Barbet-Massin *et al*., 2012) and, particularly for birds, they are expected to have the largest effects (Lee and Jetz, 2010) or greatly improve model predictive capabilities in highly changing landscapes (Reino *et al*., 2013). Indeed, understanding the habitat requirements of different species to integrate relevant categories is likely to increase predictive robustness of demographic models at the landscape scale (Keith *et al*., 2008), which will allow us to better understand the impacts of potential land-use changes.

4.5.2 Habitat suitability based on variable importance

The most important variables determining the probability of occurrence of most species were often farmland and forest plantation cover, although different species showed contrasting responses to these variables. Indeed, the habitat preferences of different bird species, along a gradient of open grasslands to forest areas, are significantly associated with population trends in the Mediterranean farmlands (Herrando *et al*., 2016). For instance, we found that the calandra lark and little bustard, species known to favour open grassland areas and low habitat fragmentation (Delgado and Moreira, 2000; Reino *et al*., 2009; Morgado *et al*., 2010) showed a higher probability of occurring in areas of higher cover of temporal farmland and low cover of planted forests.

Contrastingly, the woodpigeon which is commonly associated with areas with woody vegetation (Reino *et al*., 2009) preferred higher cover by forest plantations over farmland, corroborating the potential of these land uses to serve as potential indicators of species distribution trends (Herrando *et al*., 2016). The high relative importance found for the minimum temperature of the coldest month, associated mainly with common quail and goldfinch distributions, is in line with the importance of these climatic variables found at larger scales (Reino *et al*., 2018) regardless of the species' habitat specialization. However, we note that the majority of common quail individuals counted during surveys were likely migratory (Nadal *et al*., 2022), thus, the effects of climatic predictors for the region (e.g., temperature for the coldest month) may constitute an artifact, since at most, they could result in indirect effects to the grassland vegetation selected by this species. This could also affect the Eurasian hoopoe, though to a lesser extent, as the proportion of migratory individuals could be smaller (van Wijk *et al*., 2018) and the importance of climatic variables was lower. Despite this, both the common quail and goldfinch were generally more ubiquitous in their predicted distributions, which would explain the increased importance of climatic conditions, since contrary to what is generally accepted (Clavel *et al*., 2011), habitat generalists seem to be more constrained by climatic conditions than open grassland specialists (Reino *et al*., 2018).

The red-legged partridge and zitting cisticola, both seemed to favour proximity to forest plantation cover, although the former was constrained by areas of low to medium primary productivity, whereas the latter was more impacted by variations in daily temperatures. Both are ground-nesting species (Delgado and Moreira, 2000; Reino *et al*., 2009) which could justify the necessity for a minimum threshold of nearby forest cover (Casas *et al*., 2022), as it would result in higher resource availability to be used in nesting sites (Evans, 2004; Pita *et al*., 2009).

The zitting cisticola is usually associated with areas of tall and dense vegetation cover (Maphisa *et al*., 2017; Faria *et al*., 2024). Thus, the preference for areas with less temperature extremes is likely to reflect areas with more developed vegetation (Faria *et al*., 2024). Conversely, places with a high vegetation index could reflect intensively explored agricultural areas (e.g., olive groves) or permanent pastures, which would negatively impact the species home range selection (Borralho *et al*., 1999; Buenestado *et al*., 2008), as they are associated with pseudo-steppes and tend to select mostly areas dominated by a mosaic of crops with longer availability of field boundaries and small interspersed patches of natural vegetation (Casas *et al*., 2022).

Finally, the corn bunting and, to a lesser extent, the Eurasian hoopoe, avoided areas of high plantation cover, favouring cover by permanent crops. While this result may seem strange, since corn buntings are historically known to favour temporary rotational farmland systems over permanent pastures (Donald and Forrest, 1995), this might be a result of adaptation to years of change in agricultural practices (Ribeiro *et al*., 2014), and is in line with the knowledge that these species greatly favour taller vegetation cover, particularly in areas of the grassland more distant from the forest edges (Faria *et al*., 2024).

4.5.3 Effects of Local spatial association

At a larger scale, landscape fragmentation metrics such as increased number of patches and edge density (which indirectly reflect land-use association) can negatively impact the distribution of open grassland specialists, providing useful information to model their distribution (Reino *et al*., 2013).

Within the scope of our study area, the heterogeneity of the farmland landscape, reflected in the local spatial association metrics, was usually not the most limiting factor in species distribution, although it usually contributed between 10 to 20% of total variable importance (among 14 other variables). It was even higher for species like the hoopoe and goldfinch, which were more likely to occur in areas of higher heterogeneity. This was expected for the goldfinch, as generalist species may benefit from higher habitat heterogeneity (Benton *et al*., 2003). However, farmland species that have slowly adapted to historically homogeneous and low-intensive agricultural areas are likely to benefit from more homogeneous and less fragmented habitats (Morgado *et al*., 2010; Báldi and Batáry, 2011). While the hoopoe is not an open habitat specialist, it is usually associated with farmland areas (Faria *et al*., 2024). We suspect that, since habitat heterogeneity was generally low, with relatively high spatial association found throughout most of the region, this could reflect the preference of several farmland generalist species for farmland patches interspersed with wooded habitats (Reino *et al*., 2009).

The effects of local spatial association are thus likely to increase in importance when considering a larger scale, since we know the dispersal capabilities of birds can increase or decrease based on the degree of habitat fragmentation (Collingham and Huntley, 2000; Willis *et al*., 2009; Barbet-Massin *et al*., 2012). Additionally, because fragmentation is expected to increase due to anthropogenic activities, currently predicted distributions are likely to overestimate effective species distributions in the near future (Barbet-Massin *et al*., 2012), particularly for open grassland specialists more impacted by fragmentation (Reino *et al*., 2009; Morgado *et al*., 2010; Faria *et al*., 2024).

4.5.4 Conservation implications

Species distributions were generally more conservatively predicted using land-use variables than with climatic variables, which is in line with what was previously found at the Iberian scale (Reino *et al*., 2018), where the incorporation of landscape variables in predictive models usually resulted in less optimistic futures for the ranges of open habitat specialist species. Range shifts are likely to be much smaller compared to those predicted using climate variables only, and rarely follow a unidirectional spatial trend, as is generally found in climatic models (Barbet-Massin *et al*., 2012). Considering that open grassland specialists are likely to be more constrained by the level of intensity of agricultural management (Eglington and Pearce-Higgins, 2012), our results highlight the importance of accounting for relevant land uses to more effectively design conservation measures that prioritize species with more restricted and highly specific ranges.

Compared to natural ecosystems and temporal farmland systems, more intensively explored habitats such as permanent crops are usually prone to higher disturbance levels through agricultural activities. Thus, in cases of land abandonment, it is possible that we will observe an increase in species richness from previously intensively explored lands, as reduced soil disturbance will allow for longer-lived plants to become part of and de-simplify the available habitats (Batáry *et al*., 2010), while also potentially increasing diversity due to higher grassland heterogeneity (Hovick *et al*., 2015; Faria *et al*., 2024). However, as temporal farmland cover represented one of the main factors for the distribution of open grassland specialists, current trends in agricultural shifts towards increasingly intensive uses (Morgado *et al*., 2022) represent a major concern for these species, since the loss or alteration of natural habitats, exposure from pesticides and increased vegetation disturbance through machinery mowing and harvesting, is likely to result in extremely detrimental effects on abundance, survival and reproduction of farmland birds (Stanton *et al*., 2018).

Climatic forecasts are often used to map range shifts in bird species distributions (Huntley *et al*., 2006). However, this methodological framework based on the existence

of predictions of species distributions driven by a given pressure cannot always be easily implemented for land-use variables because of its higher complexity both in spatial and temporal dimensions (Rounsevell *et al*., 2012; Chiron *et al*., 2013). In the absence of predicted high-resolution scenarios for land-use change, current models describing species distribution may be a more readily available tool in the quantification of species' population responses to these major driving forces (Herrando *et al*., 2014). For instance, relatively inexpensive monitoring of indicators of land abandonment processes such as agriculture abandonment (i.e., the increase in spontaneous open habitats of grassland and low shrubland) and vegetation encroachment (i.e., the increase in biomass through the maturation of vegetation into woody and shrubby plants) could be effectively used to manage avian biodiversity trends in the Mediterranean basin (Herrando *et al*., 2014, 2016; Plieninger *et al*., 2014).

Overall, while understanding climatically driven spatial patterns of the predicted changes in general avian diversity may be insightful for the development of management and conservation strategies at a larger scale (Hannah *et al*., 2007), predictions at a finer scale, encompassing both high-resolution landscape and more up-to-date climatic variables, will likely be more effective in targeting key emblematic or endemic bird species of potential conservation concern (Silva *et al*., 2023, 2024).

4.6. Authors' contributions

JF: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing - original draft, Writing – review & editing. **BN**: Formal analysis, Investigation, Methodology, Writing – review & editing. **PB**: Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing. **DG**: Supervision, Writing – review & editing. **FM**: Investigation; Writing – review & editing. **RM**: Investigation; Writing – review & editing. **LB**: Supervision, Writing – review & editing. **LR**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **JS**: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing - original draft, Writing – review & editing**.**

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4.9. Supplementary Material

Table S4.1a – Models mean performance (per species) for all predictors. Statistics include AUC, Correlation (COR), True Skill Statistic (TSS) and Deviance using a test dataset generated using 30% of total data partitioned. Ensemble model performance statistics include AUC, prevalence, deviance and a threshold based weighted averaging (using TSS to determine the threshold). Complements **Table 4.1**.

species	methods	AUC	COR	TSS	Deviance	EN - AUC	EN - prevalence	EN - deviance	EN - threshold (TSS)
EmbCal	glm	0.7	0.34	0.33	1.26	0.86	0.47	1.03	0.50
	mars	0.71	0.37	0.34	1.29				
	rpart	0.73	0.41	0.38	1.33				
	brt	0.74	0.4	0.38	1.26				
	rf	0.79	0.49	0.46	1.2				
UpoEpo	glm	0.61	0.11	0.24	0.74	0.89	0.12	0.55	0.13
	mars	0.66	0.15	0.34	0.96				
	rpart	0.63	0.16	0.23	0.83				
	brt	0.68	0.2	0.32	0.7				
	rf	0.69	0.24	0.35	0.83				
ColPal	glm	0.65	0.17	0.3	0.84	0.87	0.13	0.59	0.14
	mars	0.65	0.2	0.3	1.1				
	rpart	0.62	0.16	0.23	0.95				

	brt	0.67	0.22	0.31	0.78				
	rf	0.7	0.26	0.36	0.85				
MelCal	glm	0.76	0.38	0.44	0.87	0.93	0.19	0.61	0.21
	mars	0.81	0.47	0.52	0.84				
	rpart	0.78	0.45	0.47	0.9				
	brt	0.8	0.47	0.49	0.85				
	rf	0.85	0.59	0.62	0.73				
AleRuf	glm	0.72	0.27	0.41	0.87	0.88	0.18	0.69	0.17
	mars	0.73	0.3	0.4	0.92				
	rpart	0.7	0.32	0.37	1.03				
	brt	0.75	0.34	0.43	0.85				
	rf	0.76	0.4	0.46	0.91				
TetTet	glm	0.71	0.3	0.38	0.97	0.90	0.22	0.75	0.24
	mars	0.74	0.37	0.41	0.96				
	rpart	0.7	0.35	0.36	1.05				
	brt	0.75	0.38	0.43	0.97				
	rf	0.8	0.48	0.52	0.89				
CarCar	glm	0.64	0.17	0.25	0.96	0.87	0.19	0.75	0.20
	mars	0.68	0.24	0.33	1.03				
	rpart	0.68	0.23	0.34	1.03				
	brt	0.72	0.29	0.37	0.91				
	rf	0.73	0.33	0.39	0.98				
CotCot	glm	0.58	0.13	0.18	1.01	0.87	0.20	0.77	0.20
	mars	0.65	0.26	0.28	1.03				
	rpart	0.67	0.29	0.28	1.03				
	brt	0.69	0.3	0.35	0.94				
	rf	0.71	0.36	0.38	1.01				
CisJun	glm	0.65	0.23	0.27	1.27	0.90	0.36	0.90	0.37
	mars	0.68	0.32	0.32	1.3				
	rpart	0.71	0.38	0.37	1.32				
	brt	0.71	0.35	0.33	1.21				
	rf	0.82	0.55	0.53	1.02				

Table S4.1b – Models mean performance (per species) for Land-use predictors. Statistics include AUC, Correlation (COR), True Skill Statistic (TSS) and Deviance using a test dataset generated using 30% of total data partitioned. Ensemble model performance statistics include AUC, prevalence, deviance and a threshold based weighted averaging (using TSS to determine the threshold). Complements **Table 4.1**.

species	methods	AUC	COR	TSS	Deviance	EN - AUC	EN - prevalence	EN - deviance	EN - threshold (TSS)
EmbCal	glm	0.68	0.32	0.32	1.28	0.86	0.47	1.05	0.47
	mars	0.7	0.34	0.35	1.29				
	rpart	0.72	0.39	0.38	1.31				
	brt	0.71	0.36	0.36	1.28				
	rf	0.78	0.5	0.46	1.2				

UpoEpo	glm	0.59	0.07	0.22	0.72	0.87	0.12	0.57	0.13
	mars	0.61	0.13	0.24	0.81				
	rpart	0.64	0.16	0.26	0.76				
	brt	0.66	0.19	0.29	0.69				
	rf	0.68	0.22	0.33	0.79				
ColPal	glm	0.59	0.1	0.23	0.8	0.88	0.13	0.59	0.17
	mars	0.62	0.16	0.26	0.98				
	rpart	0.66	0.22	0.27	0.82				
	brt	0.68	0.22	0.33	0.74				
	rf	0.74	0.35	0.44	0.76				
MelCal	glm	0.75	0.35	0.44	0.88	0.92	0.19	0.65	0.23
	mars	0.76	0.38	0.44	0.89				
	rpart	0.75	0.41	0.42	0.98				
	brt	0.79	0.46	0.48	0.86				
	rf	0.83	0.54	0.57	0.79				
AleRuf	glm	0.63	0.16	0.26	0.97	0.88	0.18	0.73	0.20
	mars	0.66	0.22	0.3	0.98				
	rpart	0.66	0.24	0.3	1.05				
	brt	0.7	0.29	0.34	0.92				
	rf	0.76	0.41	0.43	0.89				
TetTet	glm	0.65	0.2	0.3	0.99	0.90	0.22	0.76	0.26
	mars	0.66	0.21	0.3	1.13				
	rpart	0.68	0.27	0.34	1.09				
	brt	0.71	0.29	0.37	0.95				
	rf	0.79	0.42	0.51	0.9				
CarCar	glm	0.6	0.13	0.2	0.95	0.86	0.19	0.77	0.19
	mars	0.6	0.12	0.19	1.04				
	rpart	0.62	0.18	0.24	1.07				
	brt	0.66	0.2	0.3	0.92				
	rf	0.7	0.26	0.35	1.03				
CotCot	glm	0.6	0.16	0.21	0.97	0.85	0.20	0.80	0.20
	mars	0.61	0.17	0.22	1.03				
	rpart	0.61	0.2	0.21	1.08				
	brt	0.65	0.24	0.29	0.94				
	rf	0.69	0.32	0.36	1.02				
CisJun	glm	0.61	0.17	0.22	1.29	0.90	0.36	0.94	0.33
	mars	0.62	0.21	0.23	1.3				
	rpart	0.67	0.31	0.31	1.42				
	brt	0.67	0.3	0.28	1.23				
	rf	0.8	0.52	0.51	1.07				

Table S4.1c – Models mean performance (per species) for Climatic predictors. Statistics include AUC, Correlation (COR), True Skill Statistic (TSS) and Deviance using a test dataset generated using 30% of total data partitioned. Ensemble

model performance statistics include AUC, prevalence, deviance and a threshold based weighted averaging (using TSS to determine the threshold). Complements **Table 4.1**.

species	methods	AUC	COR	TSS	Deviance	EN - AUC	EN - prevalence	EN - deviance	EN - threshold (TSS)
EmbCal	glm	0.68	0.32	0.32	1.28	0.86	0.47	1.08	0.47
	mars	0.7	0.34	0.35	1.29				
	rpart	0.72	0.39	0.38	1.31				
	brt	0.71	0.36	0.36	1.28				
	rf	0.78	0.5	0.46	1.2				
UpoEpo	glm	0.59	0.07	0.22	0.72	0.89	0.12	0.58	0.14
	mars	0.61	0.13	0.24	0.81				
	rpart	0.64	0.16	0.26	0.76				
	brt	0.66	0.19	0.29	0.69				
	rf	0.68	0.22	0.33	0.79				
ColPal	glm	0.59	0.1	0.23	0.8	0.87	0.13	0.60	0.15
	mars	0.62	0.16	0.26	0.98				
	rpart	0.66	0.22	0.27	0.82				
	brt	0.68	0.22	0.33	0.74				
	rf	0.74	0.35	0.44	0.76				
MelCal	glm	0.75	0.35	0.44	0.88	0.93	0.19	0.67	0.24
	mars	0.76	0.38	0.44	0.89				
	rpart	0.75	0.41	0.42	0.98				
	brt	0.79	0.46	0.48	0.86				
	rf	0.83	0.54	0.57	0.79				
AleRuf	glm	0.63	0.16	0.26	0.97	0.88	0.18	0.70	0.17
	mars	0.66	0.22	0.3	0.98				
	rpart	0.66	0.24	0.3	1.05				
	brt	0.7	0.29	0.34	0.92				
	rf	0.76	0.41	0.43	0.89				
TetTet	glm	0.65	0.2	0.3	0.99	0.90	0.22	0.77	0.21
	mars	0.66	0.21	0.3	1.13				
	rpart	0.68	0.27	0.34	1.09				
	brt	0.71	0.29	0.37	0.95				
	rf	0.79	0.42	0.51	0.9				
CarCar	glm	0.6	0.13	0.2	0.95	0.86	0.19	0.77	0.20
	mars	0.6	0.12	0.19	1.04				
	rpart	0.62	0.18	0.24	1.07				
	brt	0.66	0.2	0.3	0.92				
	rf	0.7	0.26	0.35	1.03				
CotCot	glm	0.6	0.16	0.21	0.97	0.86	0.20	0.79	0.22
	mars	0.61	0.17	0.22	1.03				
	rpart	0.61	0.2	0.21	1.08				
	brt	0.65	0.24	0.29	0.94				
	rf	0.69	0.32	0.36	1.02				

	glm	0.61	0.17	0.22	1.29				
	mars	0.62	0.21	0.23	1.3				
CisJun	rpart	0.67	0.31	0.31	1.42	0.90	0.36	0.92	0.39
	brt	0.67	0.3	0.28	1.23				
	rf	0.8	0.52	0.51	1.07				

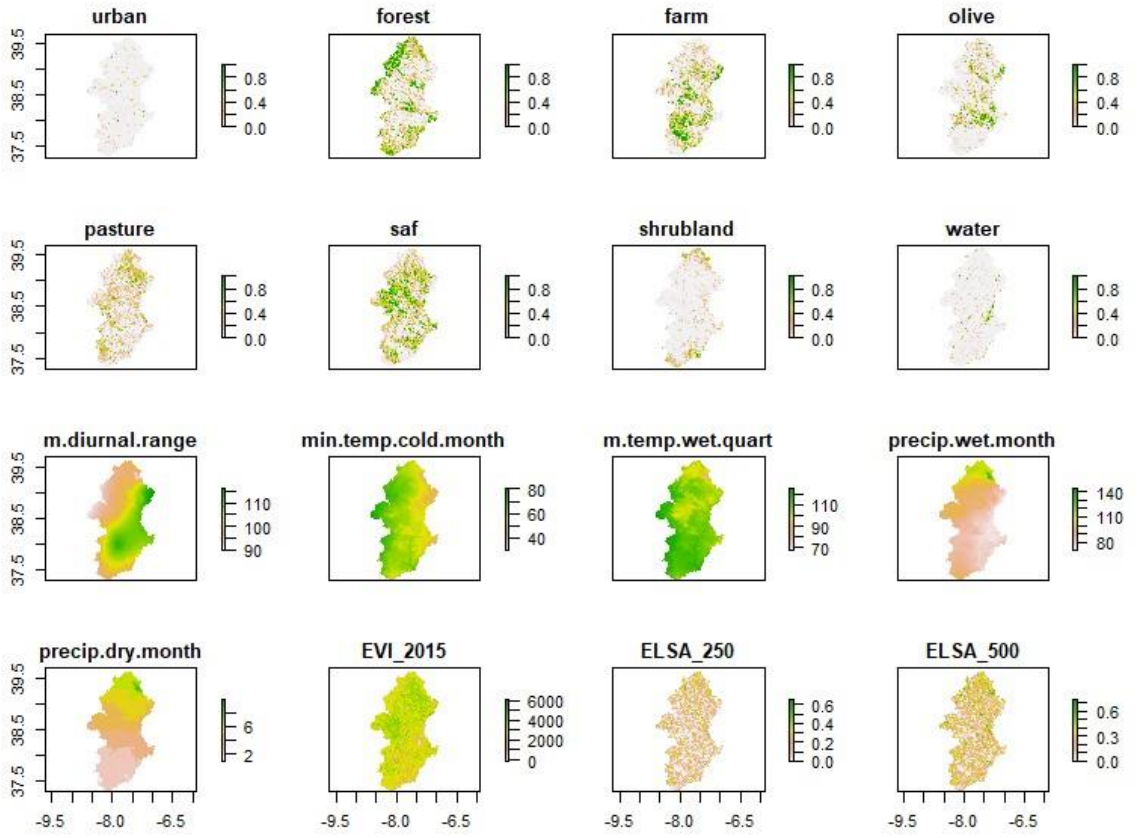

Figure S4.1 - Individual 500-m resolution raster plots of all land-use (1-8), climatic (9-14) and spatial association predictors (15-16, ELSA at 1000 m not represented).

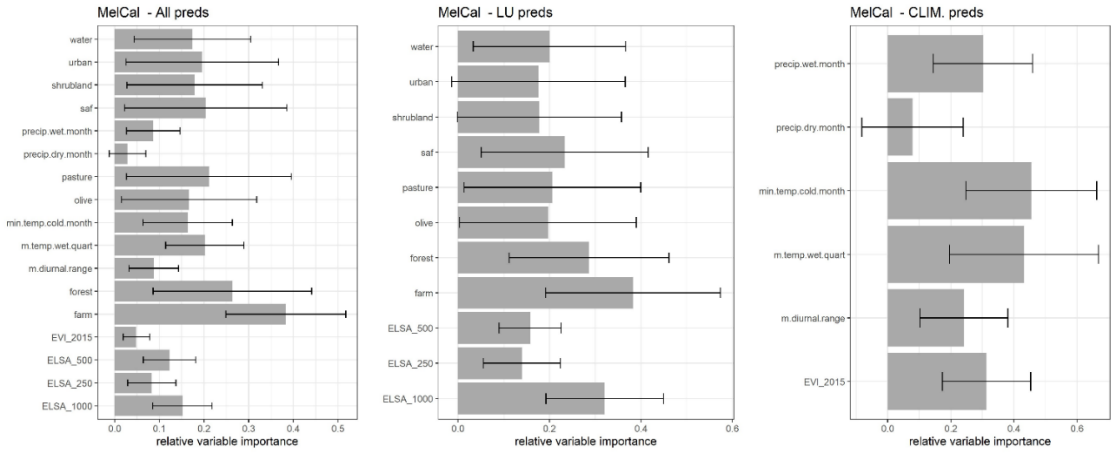

Figure S4.2a – Average variable importance obtained for Calandra lark (*Melanocorypha calandra*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

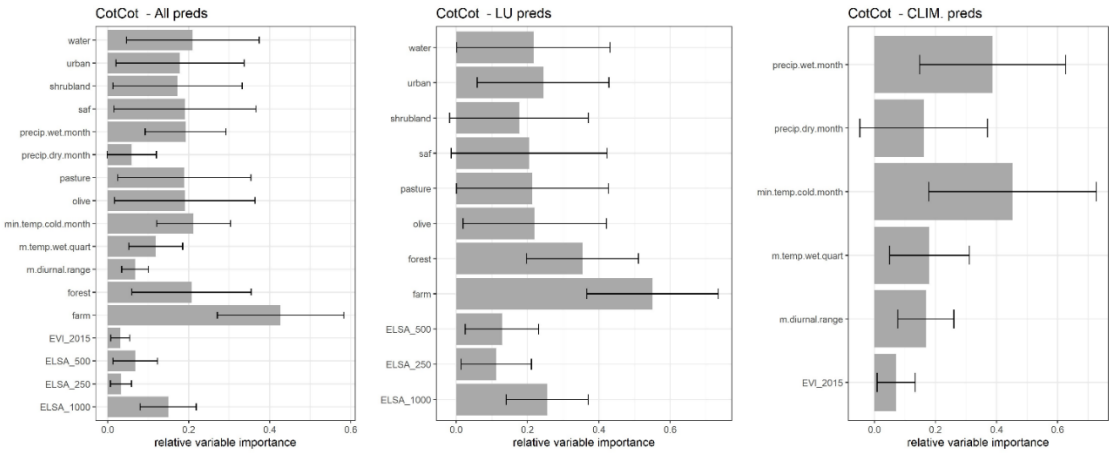

Figure S4.2b – Average variable importance obtained for Common quail (*Coturnix coturnix*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

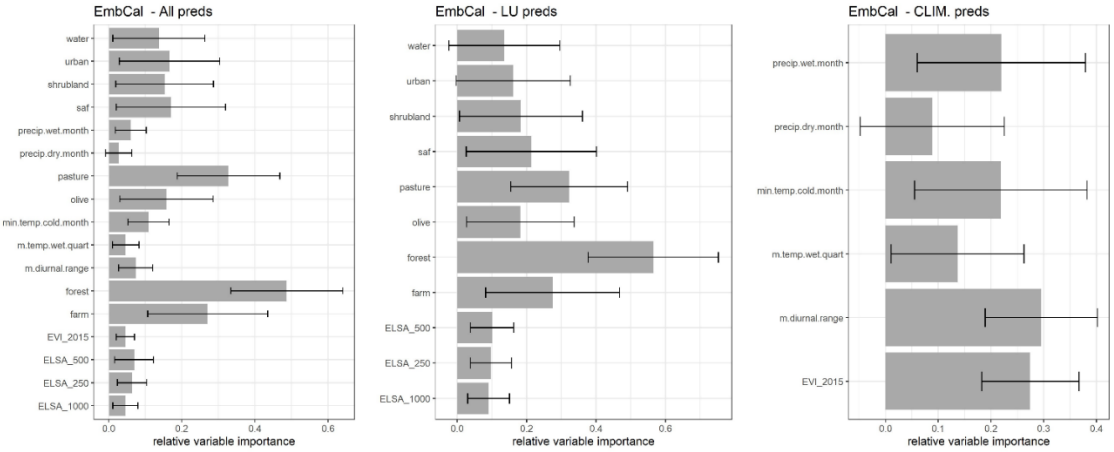

Figure S4.2c – Average variable importance obtained for corn bunting (*Emberiza calandra*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

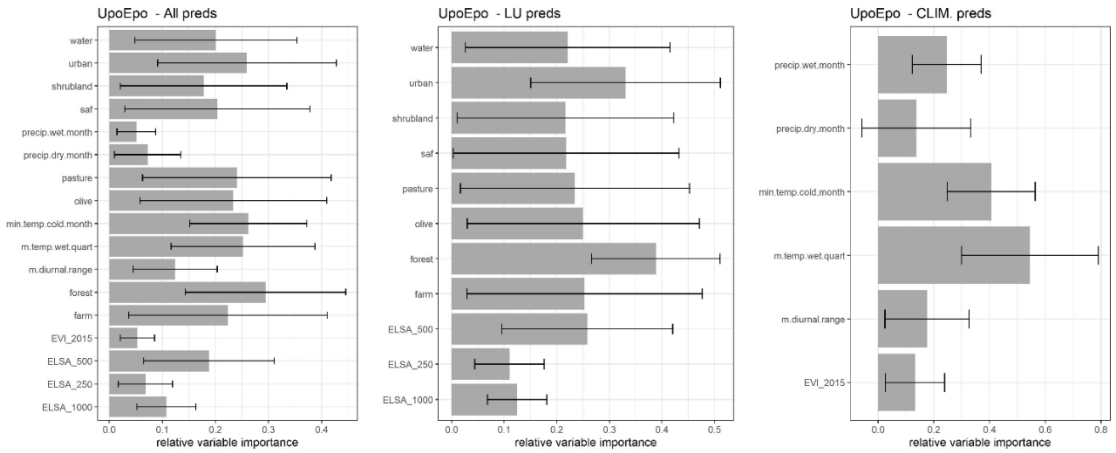

Figure S4.2d – Average variable importance obtained for Eurasian hoopoe (*Upupa epops*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

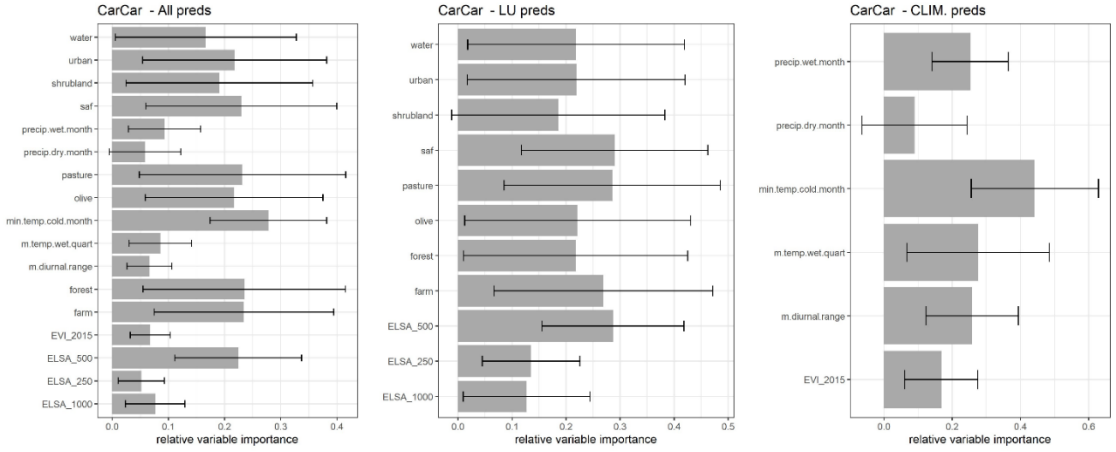

Figure S4.2e – Average variable importance obtained for European goldfinch (*Carduelis carduelis*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

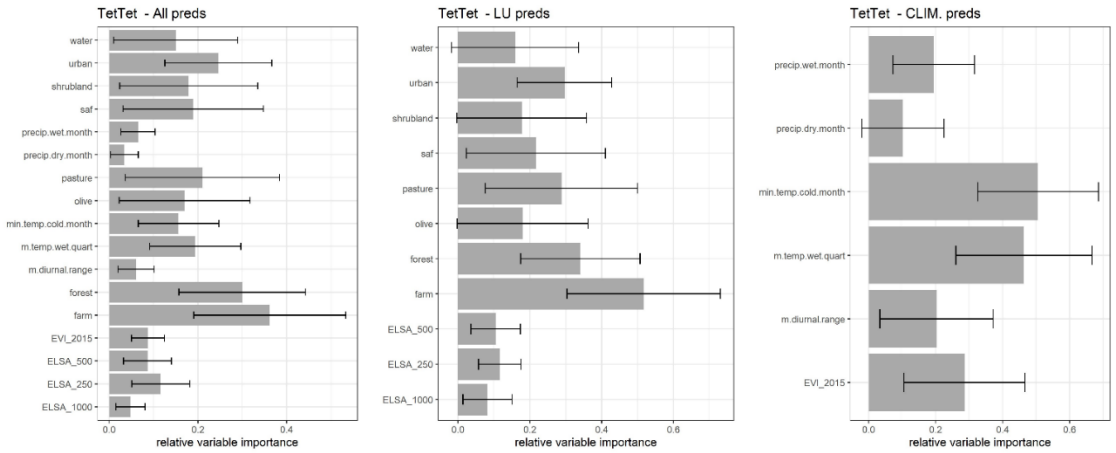

Figure S4.2f – Average variable importance obtained for little bustard (*Tetrax tetrax*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

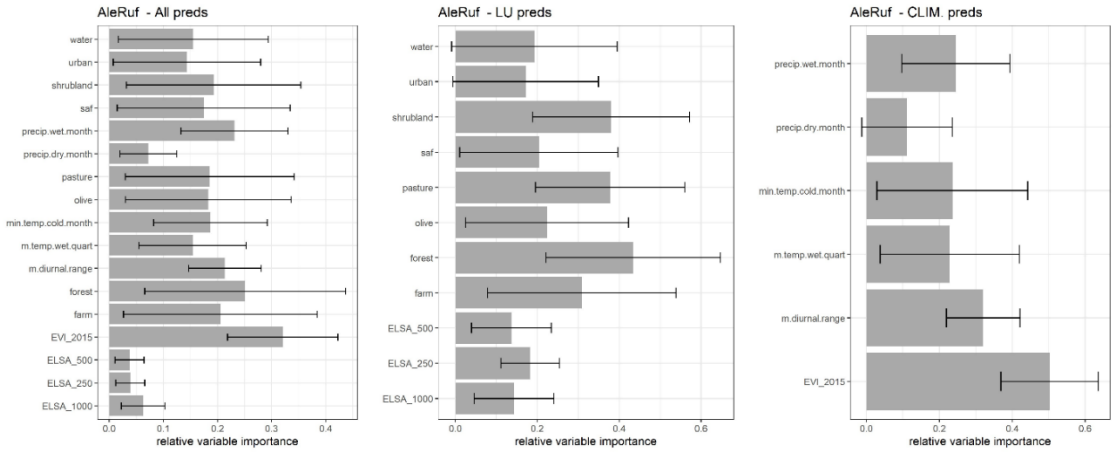

Figure S4.2g – Average variable importance obtained for red-legged partridge (*Alectoris rufa*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

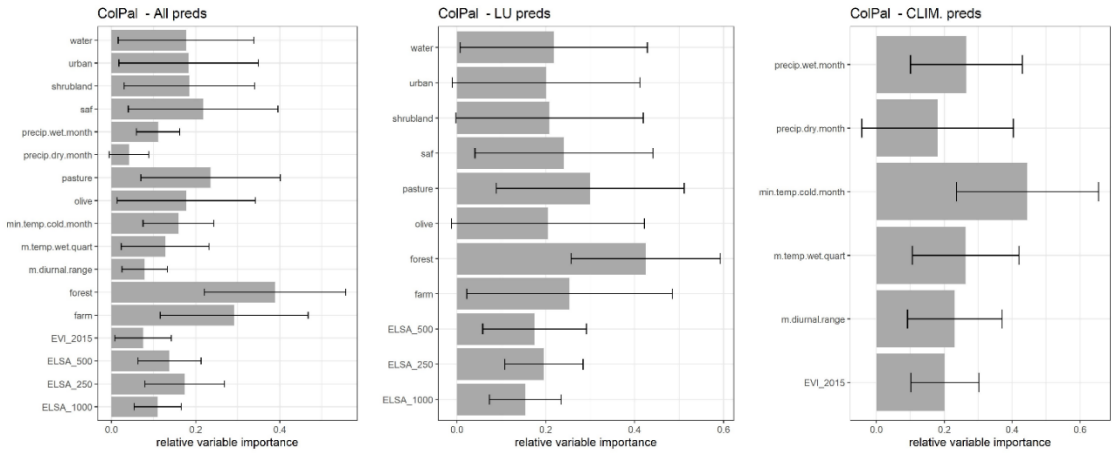

Figure S4.2h – Average variable importance obtained for wood pigeon (*Columba palumbus*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

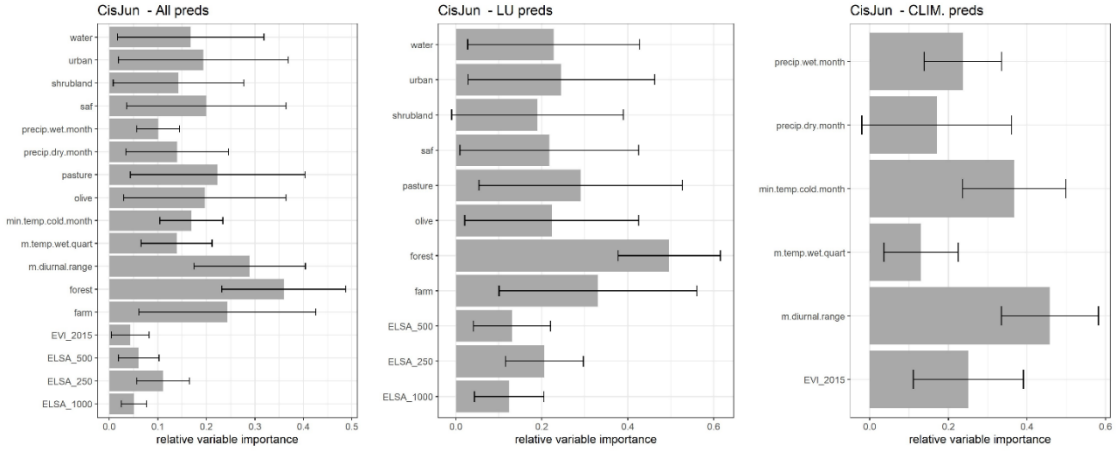

Figure S4.2i – Average variable importance obtained for zitting cisticola (*Cisticola juncidis*) species distribution models using Pearson correlation. Estimates shown for all predictors (left); land-use predictors (centre); and climatic predictors (right). Results are based on 30 total models, resulting from 5 methods replicated 6 times (three subsampling and three bootstrapping replicates).

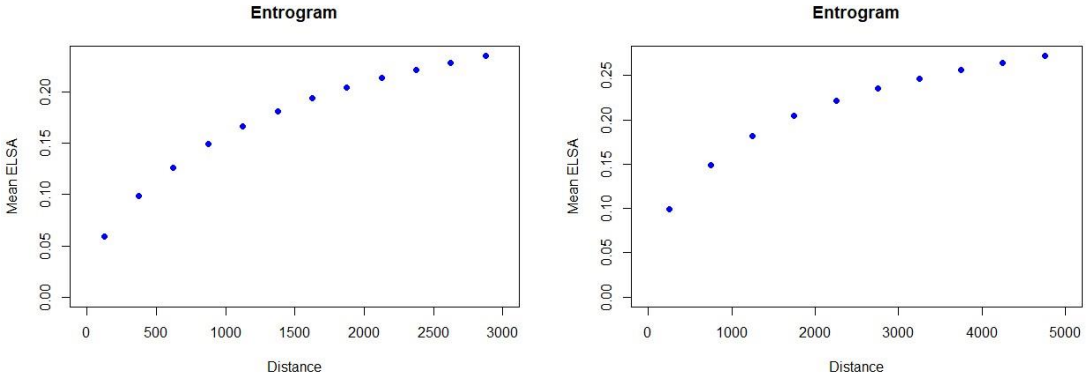

Figure S4.3 – Entrogram showing the spatial structure relations between the data within different ranges (distances). On the left, an entrogram showing a logarithmic increase of average ELSA over 250-m intervals until a 3000-m cutoff. On the right, a similar logarithmic increase of average ELSA is observed for 500-m intervals until a 5000-m cutoff.

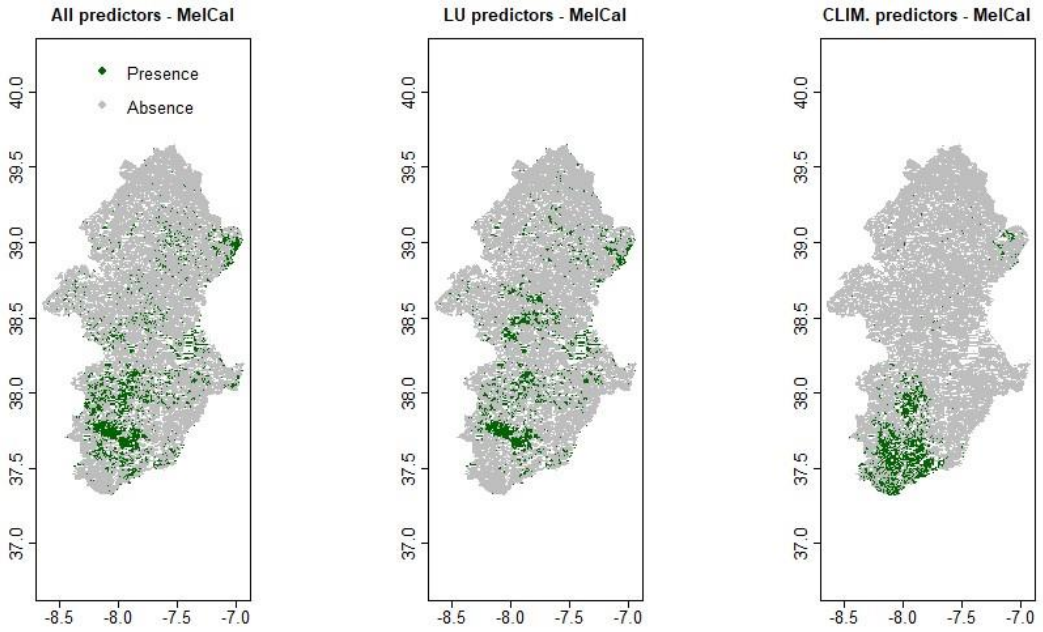

Figure S4.4a – Ensemble presence-absence SDM outputs obtained for Calandra lark (*Melanocorypha calandra*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

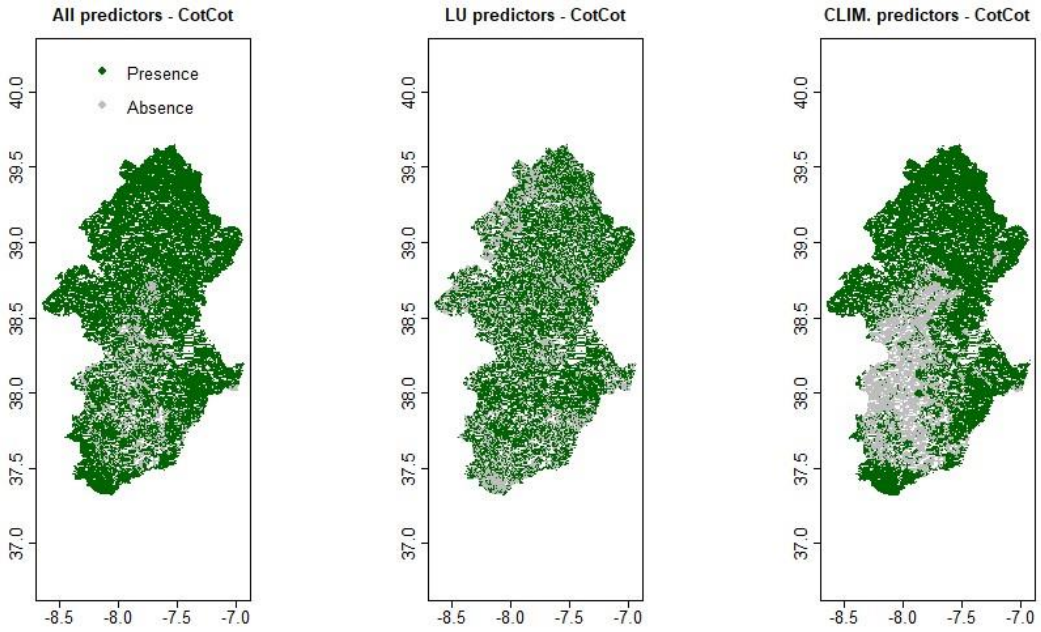

Figure S4.4b – Ensemble presence-absence SDM outputs obtained for common quail (*Coturnix coturnix*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

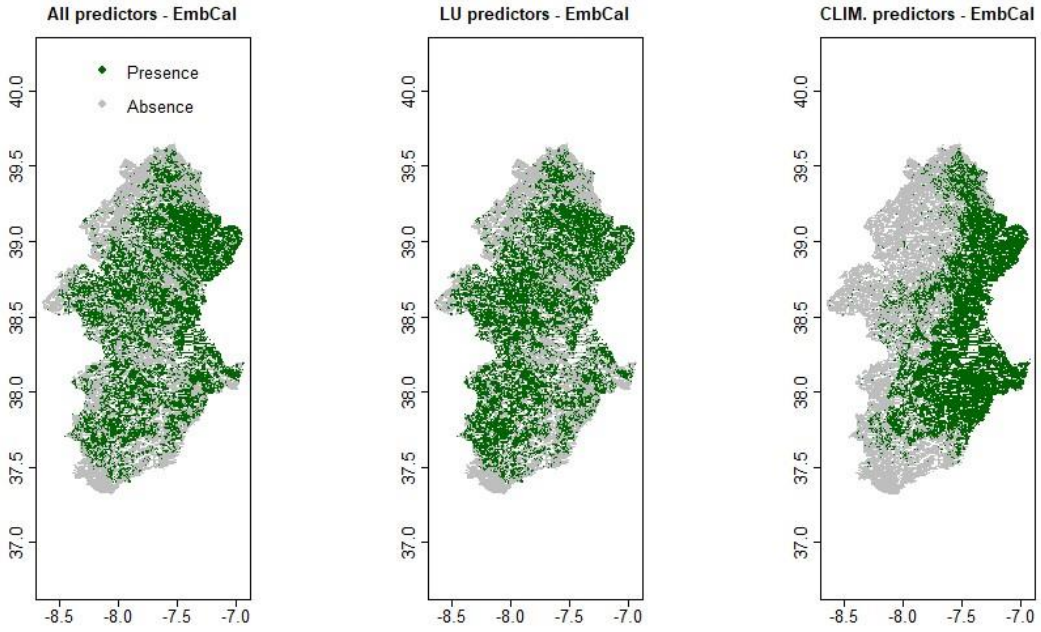

Figure S4.4c – Ensemble presence-absence SDM outputs obtained for corn bunting (*Emberiza calandra*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

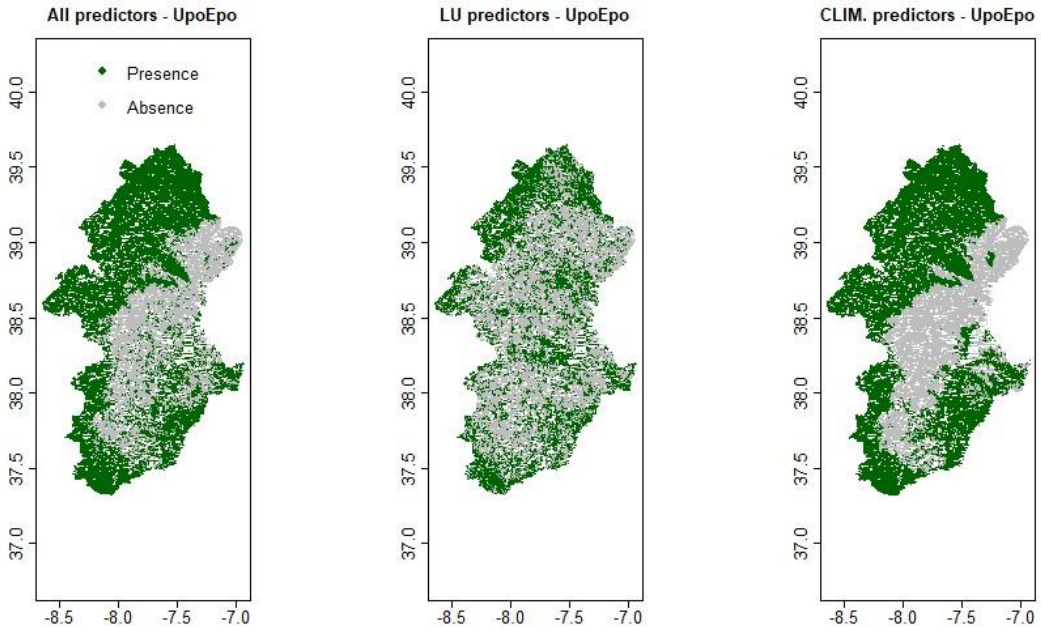

Figure S4.4d – Ensemble presence-absence SDM outputs obtained for Eurasian hoopoe (*Upupa epops*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

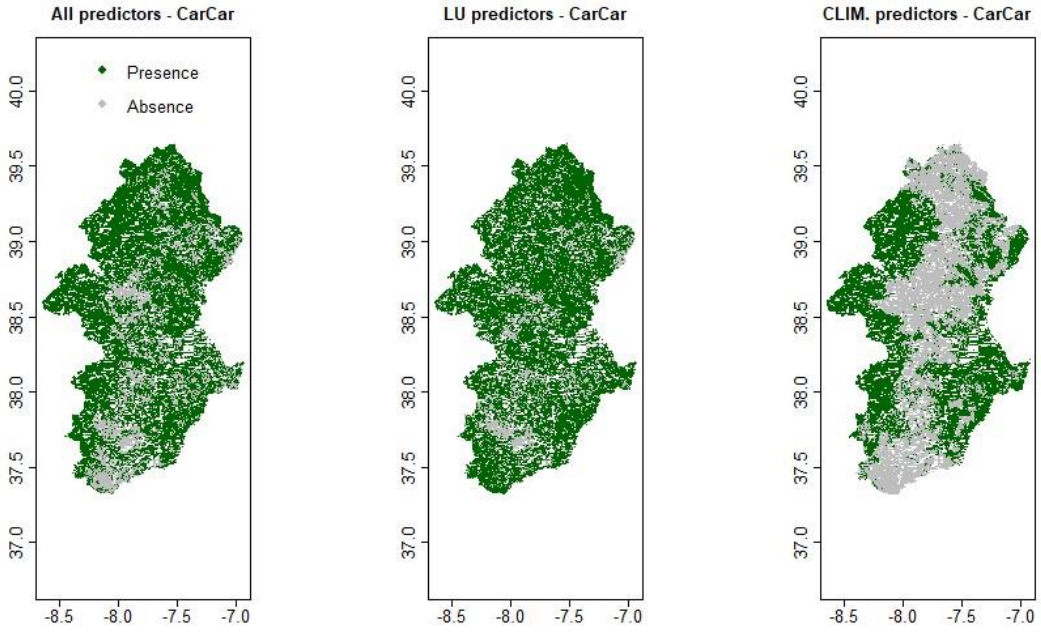

Figure S4.4e – Ensemble presence-absence SDM outputs obtained for European goldfinch (*Carduelis carduelis*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

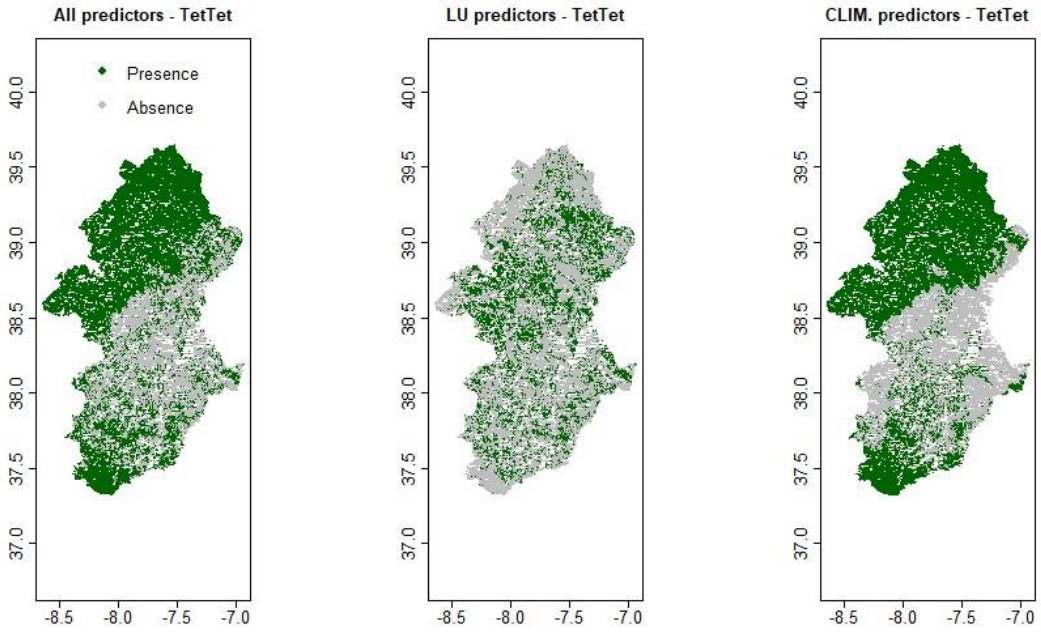

Figure S4.4f – Ensemble presence-absence SDM outputs obtained for little bustard (*Tetrax tetrax*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

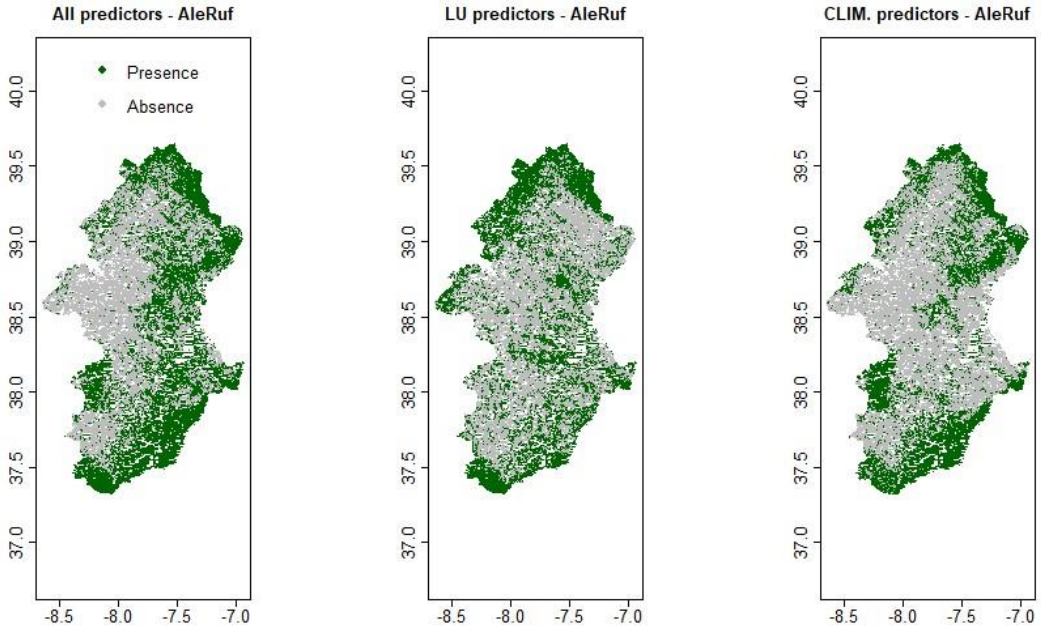

Figure S4.4g – Ensemble presence-absence SDM outputs obtained for red-legged partridge (*Alectoris rufa*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

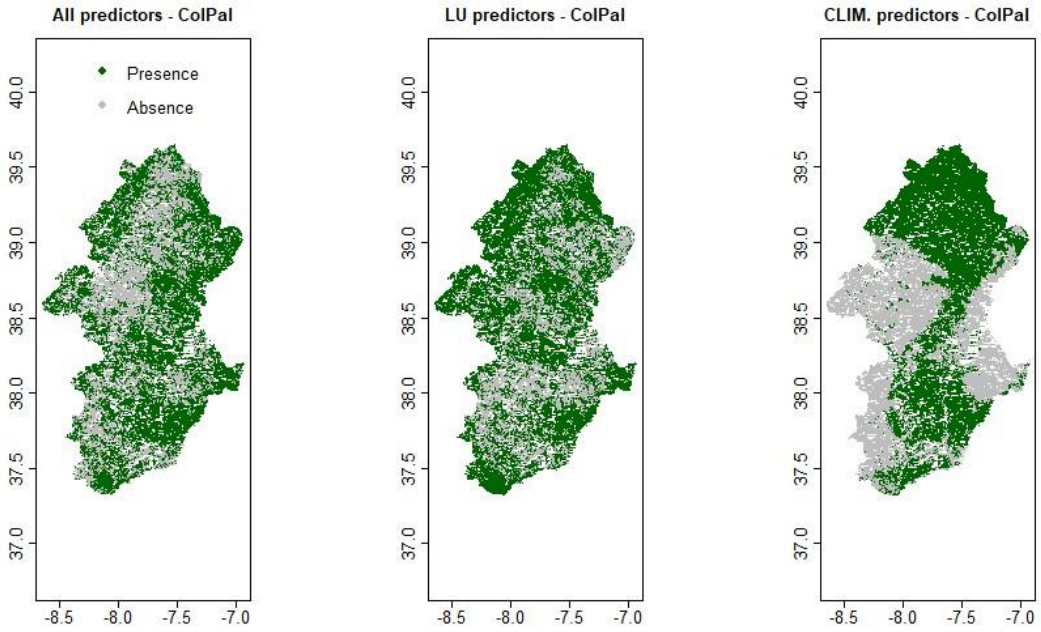

Figure S4.4h – Ensemble presence-absence SDM outputs obtained for wood pigeon (*Columba palumbus*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

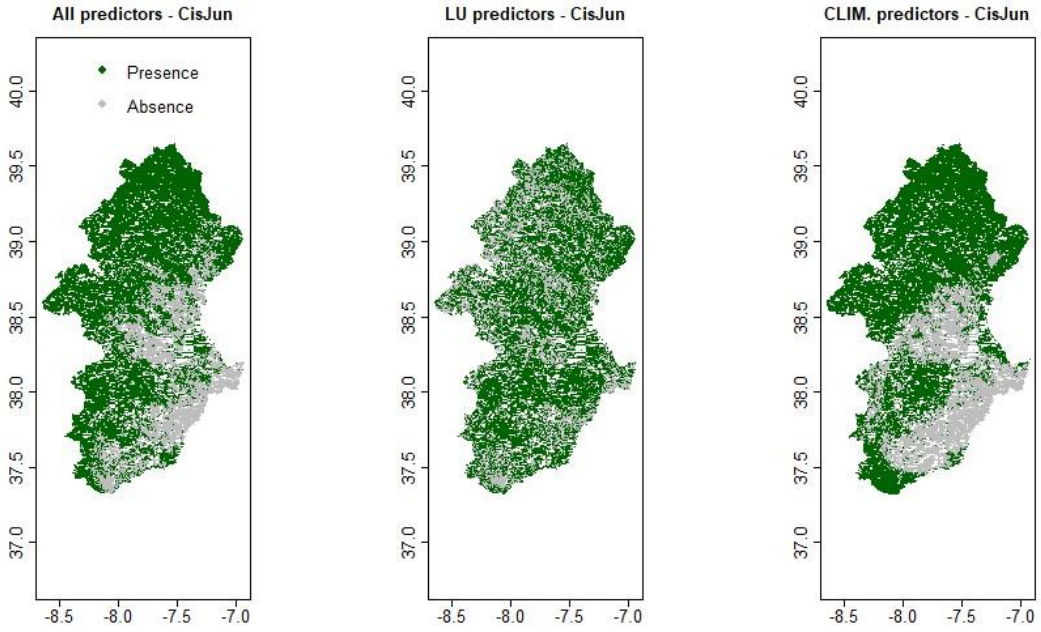

Figure S4.4i – Ensemble presence-absence SDM outputs obtained for zitting cisticola (*Cisticola juncidis*), based on TSS threshold. Presence-absence distribution estimates based on models containing all predictors (left); land-use predictors (centre); and climatic predictors (right).

Chapter 5

General Discussion

Within a context of rapidly changing Mediterranean farmland landscapes, this thesis aimed to provide a comprehensive look into the different ways in which these changes, whether human-mediated, driven by climatic conditions or an interaction of both, can affect avian communities and key bird species associated with these unique habitats. To achieve this, **Chapters 2 to 4** examined the interconnected aspects influencing different guilds and species associated with farmland habitats.

Specifically, **Chapter 2** evaluated how contrasting plantation types, of the most common tree species used in afforestation in the studied region, could affect nest predation risk in the adjacent grassland matrix, determining that there was increased predator abundance and expanded predator influence in areas associated with eucalyptus tree plantations.

Chapter 3 examined how changes in the grassland matrix could shape bird responses to these plantations, revealing that certain farmland species, usually associated with cereal fields, favoured taller grasslands. In contrast, others benefitted from the drier conditions that likely resulted in shorter vegetation height.

Finally, **Chapter 4** investigated how determinant farmland and forest plantations were, compared to other land uses and climatic variables, in influencing species distribution ranges at a regional scale, concluding that the first ones were indeed the most influencing factors for several key species, although, even at this scale, climatic conditions played an important role.

Taken together, these results shed new light on key factors influencing biodiversity within Mediterranean farmland ecosystems and on the complexities of adequately implementing management and conservation strategies that are capable of benefiting a range of farmland bird species with a diverse but specific set of habitat requirements. In the present chapter, these key findings are presented in more detail and discussed within the context of the potential risks for open farmland specialists under current agri-environmental scenarios. Conservation guidelines that could mitigate the current and future impacts of land use and climate changes in the Mediterranean farmland context are suggested, along with future research and general guidance that will be useful in granting additional insights on targeted prioritization and streamlining impact assessment.

5.1. Factors affecting Mediterranean farmland avian biodiversity

5.1.1 Afforestation and increased predator risk

Increasingly widespread afforestation in recent years (Arakwiye *et al*., 2017; Curtis *et al*., 2018; Song *et al*., 2018; Bond *et al*., 2019) is mainly driven by initiatives aiming to mitigate the impacts of climate changes (Corbera and Schroeder, 2011; Brancalion and Holl, 2020; García *et al*., 2020) through the increase in carbon sequestration, improvements to soil and habitat quality as well as reducing deforestation or forest degradation (Curtis *et al*., 2018; Holl *et al*., 2020).

However, concerns regarding afforestation have been raised by several researchers (Reino *et al*., 2009; Burrascano *et al*., 2016; Pretelli *et al*., 2018; Jacoboski *et al*., 2019) regarding its potential impacts on open farmland biodiversity through the deterioration of the quality of habitats of prominent conservation importance and even their fragmentation and loss (Shochat *et al*., 2001; Ries *et al*., 2004; Morgado *et al*., 2010; Liu *et al*., 2019; Jacoboski and Hartz, 2020).

In **Chapters 2** and **3**, we evaluated afforestation effects on a Mediterranean farmland region (Castro Verde) mostly contained within an area designated for the protection of open grassland birds (Ribeiro *et al*., 2014). These effects were examined both indirectly (through effects on nest-predation risk) and directly (through effects on bird species and guild's abundances). Regarding the former, our results were in line with other research, revealing predation rates were higher in grasslands near the edges of planted forests (Santos *et al*., 2006; Sánchez-Oliver *et al*., 2014a), but they also showed an effect of plantation type, with higher predation rates associated with grasslands adjacent to eucalyptus plantations. Additionally, predator abundance near eucalyptus forest stands was also the highest.

Observed differences between adjacent plantation types, likely reflect differences in the structure of forest plantations, as eucalyptus plantations were usually composed of taller trees and denser canopies, providing greater suitability for generalist avian predators compared to oak and pine plantations (Chalfoun *et al*., 2002; Reino *et al*., 2009). Indeed, the main predators detected were corvids, which are known generalists that occur frequently in the Mediterranean farmlands (Beja *et al*., 2014; Sánchez-Oliver *et al*., 2014a), particularly the carrion crow (Andren, 1992; Bravo *et al*., 2020). The strong correlation between identified predators in predation events captured by camera and their abundance in counts suggests that predator abundance could be a significant predictor of predation risk, but this was surprisingly not the case. In our study, we were not able to distinguish between breeding pairs and floater individuals (Erikstad *et al*., 1982; Bravo *et al*., 2020). If surveys detected mainly floaters, they would potentially have

a lesser effect on nest-predation risk, as the breeding pairs are more likely to drive predation risk, due to higher food demands, being able to depredate more effectively and potentially defend their territories from floaters (Erikstad *et al*., 1982; Bui *et al*., 2010).

The edge effects produced by eucalyptus plantations revealed a higher reach of predators into the adjacent grassland, contrasting with a lack of effects for oak and pine stands. This reinforces the detrimental effects of certain types of afforestation for open grassland specialists, as they are usually more likely to avoid predators by nesting away from plantation edges (Sliwinski and Koper, 2012), effectively favouring areas of increased predation risk (for adjacent eucalyptus plantations).

5.1.2 How grassland vegetation modulates afforestation effects

Several factors, such as tree species, edge density, and understorey vegetation can influence afforestation effects on farmland biodiversity (Santos *et al*., 2006; Reino *et al*., 2010b). Grassland vegetation height in the adjacent area is another majorly important predictor.

As examined in **Chapter 2**, nest-predation risk decreased with increasing height of vegetation, likely driven by better-concealed nests, resulting in less predator detections (Lyons *et al*., 2015; Bellamy *et al*., 2018). Additionally, vegetation was usually shorter near plantation edges, especially near eucalyptus plantations which are known to have sparse understorey vegetation (Vasconcelos *et al*., 2019) and saw the highest predator abundance (**Chapter 2**). Besides providing cover, taller vegetation is also associated with additional food and nesting resources for farmland species (Erdős *et al*., 2009; Báldi and Batáry, 2011).

In a context of agricultural land-use shifts, incentivized in part by agricultural policy reforms like the Common Agricultural Policy (CAP) (Ribeiro *et al*., 2014; Morgado *et al*., 2022), and increasingly common droughts and heat waves directly affecting grasslands (Conrey *et al*., 2016; Zuckerberg *et al*., 2018), we examined, in **Chapter 3**, how two periods with contrasting climatic conditions and vegetation height affected farmland birds' response to afforestation.

Our results revealed mixed effects of vegetation height. For instance, farmland species normally associated with more fragmented habitats and woody patches (Reino *et al*., 2010b), species associated with cereal fields, like the corn bunting, and ground-nesters like the zitting cisticola (Moreira, 1999; Delgado and Moreira, 2000), benefitted from the increased vegetation height found in the period with taller vegetation. Contrastingly, steppe specialists, such as the short-toed lark, which are usually associated with vast expanses of open grasslands and ploughed fields (Delgado and

Moreira, 2000; Santana *et al*., 2017a), were favoured by the drier period with shorter vegetation height.

These results highlight the diversity in responses of the avian farmland community, which did not follow a single universal trend. We conclude that habitat affinities of different bird species, in addition to resulting in mixed edge responses (Reino *et al*., 2009; Terraube *et al*., 2016), likely influence how vegetation height impacts their responses to afforestation, which is also affected by the nearby plantation types. For instance, the increase of ground-nesting species in the period with taller vegetation is likely due to the increased nest cover (Báldi and Batáry, 2011; Bellamy *et al*., 2018), but the potential increase in nest sites could also have led to the observed increase in corvid abundance. This is corroborated by the fact that grassland vegetation effects were not equal across all plantation types, with ground-nesting species particularly favouring taller vegetation in grassland adjacent to oak and pine plantations, over eucalyptus plantations where predator abundance was higher (**Chapter 3**). Open grassland specialists, known to avoid plantation edges (Sliwinski and Koper, 2012), primarily preferred being farther away from plantations and also favoured oak and pine plantations, likely due to the softer edges created by these plantations (Reino *et al*., 2009).

5.1.3 Impacts on the distribution of farmland avian species

Afforestation, along with other land-use changes driven by land abandonment, agricultural intensification (Donald *et al*., 2001, 2006; Vickery *et al*., 2004; Plieninger *et al*., 2014; Stanton *et al*., 2018) and evolving climatic conditions (Barbet-Massin *et al*., 2012; Conrey *et al*., 2016) also impact the distribution patterns of farmland birds (Barbet-Massin *et al*., 2012; Reino *et al*., 2013, 2018; Valladares *et al*., 2014).

In **Chapters 2** and **3,** we observed the effects of afforestation associated with increased predation risk and decreased abundances near plantation edges for several species, as well as the influence of different grassland vegetation heights, driven by climatic conditions, on the overall avian farmland community.

Chapter 4 examined how afforestation of planted forests, along with other land-use types and climatic variables, influenced the distribution of farmland species at a regional scale. We observed that forest plantation cover was a determinant factor for most farmland birds' distributions. Species such as the calandra lark, which usually prefer areas of open grassland and avoid proximity to plantation edges (Delgado and Moreira, 2000; Reino *et al*., 2009; Morgado *et al*., 2010), primarily appeared in areas of low forest plantation cover, favouring instead large grassland patches. Contrastingly, more generalist species like the woodpigeon (Herrando *et al*., 2016), occurred preferably

in areas of high plantation cover, whereas farmland ground-nesting species also favoured at least some cover by forest plantations, likely due to ease of resource availability (Casas *et al*., 2022).

The cover of temporal farmland was an important predictor for most widespread species distribution, being particularly important to grassland specialists like the little bustard and calandra lark (Morgado *et al*., 2010; Reino *et al*., 2018), which could benefit from lower nest-predation risk associated with these areas, as discussed in **Chapter 2**. Furthermore, landscape heterogeneity was an important factor in determining the probability of occurrence of most species, in particular of the hoopoe and goldfinch, which favoured larger patches of relatively similar habitat (i.e., lower heterogeneity), corroborating the idea that the expected increase in human-led landscape fragmentation causes a decrease in birds' dispersal capabilities (Collingham and Huntley, 2000; Willis *et al*., 2009), resulting in a contraction of currently predicted species distributions (Barbet-Massin *et al*., 2012). This will particularly affect open grassland specialists, as they are more sensitive to fragmentation (Reino *et al*., 2009; Morgado *et al*., 2010).

In addition to the importance of land uses, considering climatic predictors even at this scale, helped increase model predictive performance (Barbet-Massin *et al*., 2012; Reino *et al*., 2013). The distributions of zitting cisticola, common quail and European goldfinch were all highly dependent on climatic conditions. The zitting cisticola, for instance, favoured areas with more stable temperatures during the day (i.e., low diurnal range). This could also help explain why it preferred grassland areas with tall vegetation (Maphisa *et al*., 2017), as these areas are more likely to be protected from temperature extremes, making them favourable for nest placement. Minimum temperature was also a determining factor shaping the goldfinch distribution, which appears to be in line with findings that habitat generalists are more influenced by climatic conditions, whereas specialists are more directly impacted by landscape context (Reino *et al*., 2018).

Overall, it became clear that a combination of land-use and climatic predictors needs to be considered when trying to accurately predict current and future farmland birds' species distributions at a finer scale (Luoto *et al*., 2007; Barbet-Massin *et al*., 2012; Reino *et al*., 2013), with land-use predictors being particularly important for more conservatively representing the ranges of open grassland specialists (Reino *et al*., 2018).

5.2. Conservation implications

The current outlook of Mediterranean farmland bird conservation in Portugal is precarious, with key priority species designated under the European Union's Bird Directive (EU, 2009) like the great and little bustard having declined more than 50% over

the past 10 years (Alonso and Palacín, 2022; Silva *et al*., 2023, 2024), and several generalist birds associated with agricultural fields also decreasing (Alonso *et al*., 2022). This thesis provides some key insights on the factors most likely associated with these declines in species richness, abundance, and distribution range, which should be properly addressed if they are to be limited (**Table 5.1**).

Table 5.1 - Summarized management and conservation measures proposed to improve Mediterranean farmland conditions for open grassland bird species.

<table>
<tr><th>Mitigate habitat loss</th><th>Stop habitat quality deterioration</th><th>Improve grassland conditions</th></tr>
<tr><td>Shift policy focus from afforestation expansion to sustainable forest management (Chapters 2 and 3)</td><td>Provide reliable food resources in areas of higher nest-predation risk (Chapter 2)</td><td>Reduce livestock grazing on key areas for open grassland specialists (Chapters 2 and 3)</td></tr>
<tr><td>Target areas occupied by farmland generalist species (Chapters 3 and 4)</td><td>In extreme scenarios: selective predator management (Chapter 2)</td><td>Preserve areas with high vegetation heterogeneity (e.g., through selective path-burn grazing) (Chapter 3)</td></tr>
<tr><td colspan="2">When afforestation is unavoidable: focus on predominantly low biodiversity value sites; use slower-growth native species (e.g., holm and cork oak) over faster-growing exotic species which results in denser forests with taller trees (Chapters 2 and 3)</td><td>Preserve large grassland patches with high connectivity (Chapter 4)</td></tr>
<tr><td colspan="3">Restructure of agri-environment schemes to achieve higher sustainability of biodiversity (Monitoring of habitat indicators and other limiting factors) (Chapters 2 to 4)</td></tr>
</table>

5.2.1 Mitigating direct habitat loss

While there are undisputed benefits to afforestation initiatives (Curtis *et al*., 2018; Holl *et al*., 2020) that can result in an overall increase in grassland biodiversity (Burrascano *et al*., 2016; Phifer *et al*., 2017; Pretelli *et al*., 2018; Jacoboski and Hartz, 2020), **Chapters 2** to **4** showed that the implementation of these initiatives can result in detrimental effects through the loss and fragmentation of open habitats that are essential for several emblematic species, some of which of conservation concern (Brotons *et al*., 2005; Reino *et al*., 2009; Jacoboski *et al*., 2019).

In **Chapter 4** we observed how different Mediterranean farmland species distributions can be either negatively or positively impacted by increased forest plantation cover. Open grassland specialists, in particular, were usually more likely to occur in areas of low forest cover and higher cover of farmland patches, and for this group of species, these land-use predictors were more relevant than climatic conditions, overall. This

highlights the need for environmental schemes to carefully target their afforestation efforts in areas mostly occupied by farmland generalists that benefit from woody vegetation (Reino *et al*., 2009) and shift agricultural policies from afforestation expansion to sustainable forest management strategies and multifunctional farming systems driven by α- and β-diversity indicators (Santana *et al*., 2017b; Varela *et al*., 2020).

In areas where afforestation is unavoidable due to current financial incentives (Varela *et al*., 2020), predominantly low biodiversity value sites such as agriculturally intensive grasslands should be preferably considered (Graham *et al*., 2017), and favouring the use of native oak plantations over exotic monocultures of eucalyptus (Arakwiye *et al*., 2017; Phifer *et al*., 2017; Jacoboski and Hartz, 2020) will likely reduce the negative impacts of afforestation to species abundance and nest-survival (**Chapters 2** and **3**).

Furthermore, the agricultural shifts toward more intensive practices (Morgado *et al*., 2022) also directly influence the survival and distribution ranges of grassland specialists (Eglington and Pearce-Higgins, 2012; Stanton *et al*., 2018). For instance, the conversion of potential breeding habitat into permanent crops outside of Special Protection Areas (SPAs), has resulted in significant habitat loss (Silva *et al*., 2023), while large areas of agricultural abandonment leading to shrub and vegetation encroachment also affected avian biodiversity at a regional scale (Plieninger *et al*., 2014; Herrando *et al*., 2016). Thus, more sustainable agri-environment schemes must be implemented in areas critical for Mediterranean farmland birds, which can be achieved through relatively inexpensive monitoring of habitat indicators closely related to farmland biodiversity trends (Herrando *et al*., 2014, 2016; Plieninger *et al*., 2014).

Additionally, an overhaul of current agri-environmental programs implemented in Portugal is needed (Silva *et al*., 2023, 2024). By targeting the identification of limiting factors, it is possible to halt population declines and even recover depleted populations of open farmland birds of European importance (Bretagnolle *et al*., 2011; Staggenborg and Anthes, 2022).

5.2.2 Addressing deterioration of habitat quality

Along with the direct effects of habitat loss, we observed in **Chapter 2** that the negative impacts of current afforestation practices are exacerbated by a loss of habitat quality in adjacent grassland, due to increased nest predation. Because of this, open habitat specialists which usually favour breeding in areas away from plantations (Fletcher Jr, 2005; Reino *et al*., 2009; Morgado *et al*., 2010), are at an increased risk from fragmentation brought about by new plantations (Graham *et al*., 2017; Brazeiro *et al*.,

2018; Gómez-Catasús *et al*., 2018), in particular through the heavy use of fast-growing plantations with a higher density of trees developing into greater heights, resulting in harder edges (Reino *et al*., 2009, 2010a; Saccol *et al*., 2017).

As such, afforestation policies in areas with important populations of farmland bird species, should prioritize the use of holm and cork oak, as well as other native species of slower growth and, to a lesser extent, pine trees. These species, in addition to lessening the impact on local farmland biodiversity (Sánchez-Oliver *et al*., 2014b; Bellamy *et al*., 2018; Magnano *et al*., 2019; Vasconcelos *et al*., 2019), will also provide greater carbon sequestration and accumulation capabilities (García *et al*., 2020; Xiong *et al*., 2020). To directly address predator influence, provision of reliable food resources in areas of higher nest predation risk (Bravo *et al*., 2020) or the selective management of predators that disproportionally contribute to nest predation could be considered in extreme scenarios (Smith *et al*., 2010).

5.2.3 Improving and maintaining grassland conditions

Efforts to preserve diverse areas of grassland habitat harbouring open grassland specialists are also of great importance, as seen in **Chapters 2** and **3**.

Large areas of grassland patches with a high degree of heterogeneity would likely be most beneficial in preserving bird diversity (Hovick *et al*., 2015; Traba and Morales, 2019). This could be achieved using selective patch-burn grazing, keeping certain areas of taller vegetation as a refuge from nest-predators (Erdős *et al*., 2009; Arbeiter and Franke, 2018; Skagen *et al*., 2018).

Moreover, livestock grazing regimes need to be considered, as they can influence grassland vegetation structure (Reino *et al*., 2010b; Báldi and Batáry, 2011; Ramos *et al*., 2021), both directly through nest-site trampling and destruction (Beja *et al*., 2014) and also through varying grazing intensity, which can reduce grassland diversity and lead to the disappearance of most of the taller vegetation that is needed by cereal-associated species like the corn bunting (Delgado and Moreira, 2000; Santana *et al*., 2017a).

Preserving large grassland patches (Morgado *et al*., 2010; Reino *et al*., 2013), while removing small tree rows (Ellison *et al*., 2013) and preserving undisturbed vegetation corridors for grassland connectivity (Di Sacco *et al*., 2021) could help mitigating habitat fragmentation effects (**Chapter 4**).

Assuring the maintenance of areas with tall and dense vegetation will likely also help attenuate the effects of increasingly extreme climatic conditions which already affect species distributions (**Chapter 3** and **4**). This is particularly important in SPAs, where

biodiversity declines in open grassland specialists of conservation concern continue to occur (Silva *et al*., 2023).

5.3. Current limitations and future applications

Our approach in **Chapter 2** did not allow for a direct evaluation of the effects of afforestation by different plantation types on real nests' predation for different farmland species, due to the use of artificial nests for cost-effectiveness and experimental design suitability (Moore and Robinson, 2004).

Future studies could benefit from monitoring real ground-nesting predation for different functional farmland species (i.e., associated with ploughed, fallow, and cereal fields) in addition to monitoring species abundances in areas adjacent to different plantation types.

Ideally, monitoring would occur annually during the breeding period for a minimum of 10 years, which is sufficient time for significant changes to the breeding population (Silva *et al*., 2023, 2024). This period would also accommodate likely changes in the grassland vegetation height and structure and allow us to more accurately determine whether these were climatically driven, caused by livestock grazing regimes or other changes in agricultural practices, helping solve the limitations of **Chapter 3**, which was not able to determine population dynamics nor ascertain causal influence of climatic conditions on vegetation height, due to being limited to two sampling periods.

Due to the expensive and complex nature of consistently evaluating afforestation impacts on biodiversity (Varela *et al*., 2020), the monitoring of farmland birds, along with butterflies of known habitat preferences is able to output robust, relevant and likely more affordable indicators of afforestation impacts in the Mediterranean farmlands (Herrando *et al*., 2016; Vasconcelos *et al*., 2019).

In Portugal, CAP funds also need to be readjusted to decrease the current incentives for direct afforestation and conversion of temporary farmland to permanent pastures for intensive cattle grazing (Varela *et al*., 2020; Silva *et al*., 2023). Instead, more funds should be allocated for sustainable forest management (Varela *et al*., 2020) and for a better integration of sustainable and inclusive agriculture (Brunori *et al*., 2017), with consideration for biodiversity impact assessments. Additionally, direct payments should support the expansion of multifunctional farming systems like agroforestry, which is likely to greatly benefit farmland bird communities.

Since afforestation is likely to continue expanding globally, particularly in lower-income countries (Arakwiye *et al*., 2017; Song *et al*., 2018; Bond *et al*., 2019; Liu *et al*., 2019), there is a pressing need to guide all the financial and political support for the

implementation of thoroughly planned, sustainable and efficient afforestation efforts. Besides their roles in carbon sequestration, these initiatives should also strive to address deforestation and ecological restoration adjusted for the local conservation of biodiversity (Brancalion and Holl, 2020), while striving to provide ecosystem services (García *et al*., 2020).

Our results suggest that careful consideration of tree species and bird species of potential conservation concern should be prioritized over profitability generated by indiscriminate wood production (García *et al*., 2020). In addition to several global planned initiatives (Brancalion and Holl, 2020; García *et al*., 2020), large-scale multinational corporations will also play a major role in future afforestation projects through increasingly common carbon offset practices which often equate to little more than reputational enhancement efforts (i.e., greenwashing) (Abadie *et al*., 2024), and where there is no transparency or accountability on the lack of balanced outcomes (e.g., ecosystem restoration) resulting from these initiatives (Lamont *et al*., 2023).

In conclusion, there are no ‘‘one-size-fits-all’’ policy solutions for addressing the impacts of afforestation, agricultural intensification, and land abandonment on the avian biodiversity of the Mediterranean farmlands. Current management strategies and agri-environmental schemes are not sustainable nor are they capable of reversing the declining effects on emblematic open grassland species (Alonso and Palacín, 2022; Silva *et al*., 2023, 2024). In the future, agri-environmental schemes should consider low-value grassland restoration, prioritization of multifunctional farming in high nature-value farmland and sustainable plantations using native species adjusted to the local ecosystem, landscape, and land-use context, to be effective in biodiversity preservation (Plieninger *et al*., 2014; Ribeiro *et al*., 2014; Varela *et al*., 2020; Paulus *et al*., 2022).

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Appendix A: List of additional publications

Vasconcelos, S., Pina, S., Reino, L., Beja, P., Moreira, F., Sánchez-Oliver, J.S., Catry, I., Faria, J., Rotenberry J.T., & Santana, J. (2019). *Long-term consequences of agricultural policy decisions: How are forests planted under EEC regulation 2080/92 affecting biodiversity 20 years later?.* Biological conservation, 236, 393-403. https://doi.org/10.1016/j.biocon.2019.05.052.

Authors' Contributions: Joana Santana, Luís Reino, Pedro Beja, Francisco Moreira and Inês Catry designed the study. Sasha Vasconcelos, Silvia Pina collected butterfly and orthoptera data, respectively, and prepared the data files. LR, JSS-O, SV, SP, JS and João Faria selected and characterized the sampling sites. SV, SP and JS analysed the data with the assistance of PB, FM and LR. SV and SP wrote the paper with the assistance of JS, LR, PB, FM, IC and JTR. All authors have read and commented on drafts of the manuscript.

Appendix B: Published chapters (original Pdfs)

Chapter 2 - Faria, J., Sánchez-Oliver, J. S., Beja, P., Moreira, F., Catry, I., Vasconcelos, S., Pina, S., Rotenberry, J. T., Reino, L. and Santana, J. (2022). Contrasting effects of eucalyptus, pine and oak plantations on nest predation risk in Mediterranean grasslands. *Forest Ecology and Management*, 511, 120116. https://doi.org/10.1016/j.foreco.2022.120116.

Chapter 3 - Faria, J., Reino, L., Beja, P., Gonçalves, D., Sánchez-Oliver, J. S., Moreira, F., Catry, I., Rotenberry, J. T., Morgado, R., Brotons, L., Dullinger S., Schindler, S. and Santana, J. (2024). Grassland vegetation height affects bird responses to forest edges in Mediterranean open farmland. *Global Ecology and Conservation*, 50, e02818. https://doi.org/10.1016/j.gecco.2024.e02818.

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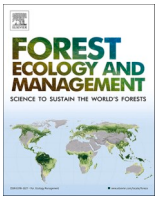

Contrasting effects of eucalyptus, pine and oak plantations on nest predation risk in Mediterranean grasslands

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A B S T R A C T

Large scale afforestation (i.e., establishment of forests on farmland, grassland and other land not previously forested) is increasingly regarded as a cost-effective option to mitigate climate change by promoting carbon sequestration. However, this strategy can have negative biodiversity impacts, potentially causing the loss and fragmentation of open habitats of conservation value, as well as edge effects that can extend well beyond forest boundaries. Mitigating impacts of afforestation programs thus requires a detailed understanding of the mechanisms whereby they affect biodiversity, particularly where new plantations are established close to areas important for open habitat species. Here, we examined how afforestation with oak, pine or eucalyptus trees, commonly planted in Mediterranean Europe, may have distinct effects on nest predation risk of grassland birds in southern Portugal. We used artificial nests with quail eggs and camera traps to: (i) identify nest predators and estimate predation risk of ground-nesting birds in grasslands adjacent to oak, pine and eucalyptus plantations across a distance gradient (0 m to 300 m) from the plantation edge; and (ii) examine how predation risk was influenced by avian predator abundance, sward height and vegetation clearing for photo-monitoring (nest-site manipulation), and their interactions with plantation type. Carrion crow was by far the main egg predator identified, followed by Montagu's harrier, raven and magpie. Overall, nest predation risk and predator abundance were higher around eucalyptus plantations, compared to either pine or oak plantations. Predation decreased with increasing sward height, but this effect was less noticeable when vegetation around nests was cleared. In pine and oak plantations, predation risk was slightly higher close to edges, and decreased with distance from the edge. Conversely, in eucalyptus plantations predation was lower close to edges, and increased with distance to edges. Distance effects around eucalyptus plantation were, however, absent in manipulated nests. Overall, results show that afforestation with different tree species has distinct impacts on predation risk of artificial nests in Mediterranean farmland. This is probably a consequence of an increasing structural complexity of the plantations, from oak to eucalyptus, driven by differences in tree growth rates and undergrowth cover. These findings suggest that farmland afforestation should favour agro-forest plantations with slow growing species (oak and pine) to mitigate negative effects on breeding grassland birds in adjacent open habitats.

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1. Introduction

Large-scale afforestation (i.e., establishment of forest on farmland, grassland and other land not previously forested) is an increasingly common land-use change worldwide (Hansen et al., 2013; Arakwiye et al., 2017; Brazeiro et al., 2018; Jacoboski and Hartz, 2020). Initially, afforestation occurred mainly in northern hemisphere countries with high income and low forest cover (Ewers, 2006), where it was promoted by schemes such as the Common Agricultural Policy (CAP) under the European Council regulation EEC 2080/92 (Burrascano et al., 2016). Recently, however, afforestation is becoming more widespread, also affecting low-income countries, mainly in the tropics (Ribas et al., 2016; Curtis et al., 2018; Song et al., 2018) and southern hemisphere (Fernandes et al., 2016; Arakwiye et al., 2017; Bond et al., 2019). This is likely to expand even more in the near future, as a result of current and planned initiatives such as Reducing Emissions from Deforestation and Forest Degradation (REDD+; Corbera and Schroeder, 2011), the Trillion Trees campaign (Brancalion and Holl, 2020), the Bonn Challenge (Laestadius et al., 2015; Bond et al., 2019; García et al., 2020), the European Green Deal (European Commission, 2019) and the United Nations' Decade on Ecosystem Restoration (2021–2030) (Brancalion and Holl, 2020). These initiatives aim to mitigate the impacts of climate change (García et al., 2020) by increasing carbon sequestration, while also improving soil quality, reducing deforestation, forest degradation and promoting habitat restoration (Loyn et al., 2007; Curtis et al., 2018; Holl et al., 2020). Afforestation policies will thus receive unprecedented financial, political and societal support in the next decade (Brancalion and Holl, 2020).

Despite their potential environmental benefits, the biodiversity consequences of afforestation schemes are often ignored or presumed to be positive with limited supporting evidence (Barcena et al., 2014; Burrascano et al., 2016; Pretelli et al., 2018; Liu et al., 2019; Varela et al., 2020). While afforestation can be neutral or beneficial to certain widespread species (Loyn et al., 2007; Reino et al., 2009; Pita et al., 2009; Phifer et al., 2017; Jacoboski and Hartz, 2020), it often leads to declines in different fauna and flora species associated with early-successional or otherwise open habitat types (Bremer and Farley, 2010; Felton et al., 2010; Morgado et al., 2010; Gries et al., 2012; Bunce et al., 2014; Vasconcelos et al., 2019). This is a case in point where afforestation involves semi-natural grasslands, i.e., extensive pastures or meadows, mainly covered by spontaneous herbaceous vegetation, which often have diverse and unique plant and animal communities (Burrascano et al., 2016; Squires et al., 2018). While afforestation can increase the overall biodiversity of these systems, concerns have been raised about its negative impacts on grassland biodiversity (Reino et al., 2009; Burrascano et al., 2016; Pretelli et al., 2018; Jacoboski et al., 2019). Moreover, there is still limited information on how to reduce impacts of forests that have been planted in the past, and how to plan and mitigate impacts of new plantations (Brancalion and Holl, 2020; Garcia et al., 2020; Varela et al., 2020).

Afforestation can have particularly serious impacts on grassland birds, mainly through habitats loss and fragmentation (Shochat et al., 2001; Reino et al., 2009; Morgado et al., 2010; Pretelli et al., 2018; Jacoboski et al., 2019; Jacoboski and Hartz, 2020), but also by increasing nest predation in surrounding open areas (Santos et al., 2006; Sánchez-Oliver et al., 2014). In fact, forest plantations can provide refuges for avian predators such as corvids and generalist mammalian predators (Santos et al., 2006; Pita et al., 2009; Reino et al., 2010b), which can also benefit from the proliferation of highly fragmented landscapes (Chalfoun et al., 2002). Corvids, in particular, are frequently identified as major predators in grasslands associated with forest plantations (Andrén, 1992; Söderström et al., 1998; Draycott et al., 2008; Aebischer et al., 2015; Madden et al., 2015). These predators may also be favoured by increases in the populations of key prey, which often thrive in more fragmented landscapes (Reino et al., 2010a; 2010b; Bátary et al., 2014; Terraube et al., 2016; Fahrig et al., 2019). This is expected to increase nest predation risk in grassland habitats surrounding planted forests, particularly at habitat edges where predator activity is often concentrated (Morris & Gilroy, 2008; Šálek et al., 2010, Cox et al., 2012).

It is likely, however, that predator impacts are not uniform across plantation types, as predator abundance and activity may differ between forests with different tree composition and development (Reino et al., 2010a). For example, previous studies found that farmland afforestation with eucalyptus may favour particularly strong increases in predator abundances, probably because it results in tall and dense plantations that likely provide avian predators with suitable nesting sites, as well as perches for roosting and hunting (Santos et al., 2006, Reino et al., 2009, 2010a). In contrast, plantations with slower growing species such as oak or pine may take more time to develop conditions for generalist predators, with shorter trees also likely to provide less favourable lookouts for avian predators. Additionally, afforestation effects on nest predation risk may be conditional on the characteristics of the adjacent swards. For instance, while taller swards of vegetation may decrease nest detectability and negatively impact nest predation risk (Beja et al., 2014; Bellamy et al., 2018), high perching sites may provide vantage points for avian predators (Rice, 1983), which could lessen the nest cover provided by taller vegetation. While one or a subset of these factors have been previously addressed, their combined effects have not been investigated (Reino et al., 2009; 2010a; Burrascano et al., 2016), thus making it difficult to have a full understanding of the mechanisms driving changes in grassland bird communities, which is crucial to minimise biodiversity impacts of afforestation schemes.

Here, we provide a case study focusing on the most common planted trees in Mediterranean Europe (oak, pine and eucalyptus), to analyse the effects of afforestation on nest predation risk in semi-natural grasslands of southern Portugal. The study area is representative of the Iberian cereal steppes, which are among the European farmland landscapes with highest conservation relevance to grassland birds (EEA, 2004; Bota et al., 2005). Nest predation risk was evaluated using a camera trap set up for predator identification, with artificial nests baited with quail (*Coturnix* spp.) eggs and placed at different distances (0–300 m) from the edge of each plantation type (oak, pine and eucalyptus) into the surround grassland matrix. We then analysed how nest predation rates varies with distance to plantations, and with the abundance of local predators and sward height. As camera traps can cause inaccuracies or potential bias in the outcomes of the experiment (Meek et al., 2016), we also considered the effects of placing a camera-trap near the nest, because this involved the removal of vegetation to clear the line of sight between the nest and cameras, and might thus affect nest detectability. Specifically, we tested the following hypotheses: (i) corvids are the main nest predators; (ii) main avian predator abundance is higher in grasslands surrounding eucalyptus plantations; (iii) predation risk is higher in grassland: (iii.a) adjacent to eucalyptus plantations compared to oak and pine plantations; (iii.b) with lower sward height due to increased nest detectability; (iii.c) and closer to plantation edges due to increased predator presence and nest detectability. Results from this study have implications for the design of policies aiming to support conservation management of current and future forest plantations on Mediterranean grasslands.

2. Methods

2.1. Study area

The study was conducted in southern Portugal, mostly within the Special Protection Area (SPA) of Castro Verde (Fig. 1) designated to protect steppe birds under the European Union Birds Directive 79/409/EEC. The climate is Mediterranean, with mild winters (averaging 9 °C [5–14 °C] in January) and hot summers (24 °C [16–32 °C] in July) and >75% of annual rainfall (500–600 mm) concentrated in October through March. The landscape is either flat or gently undulating

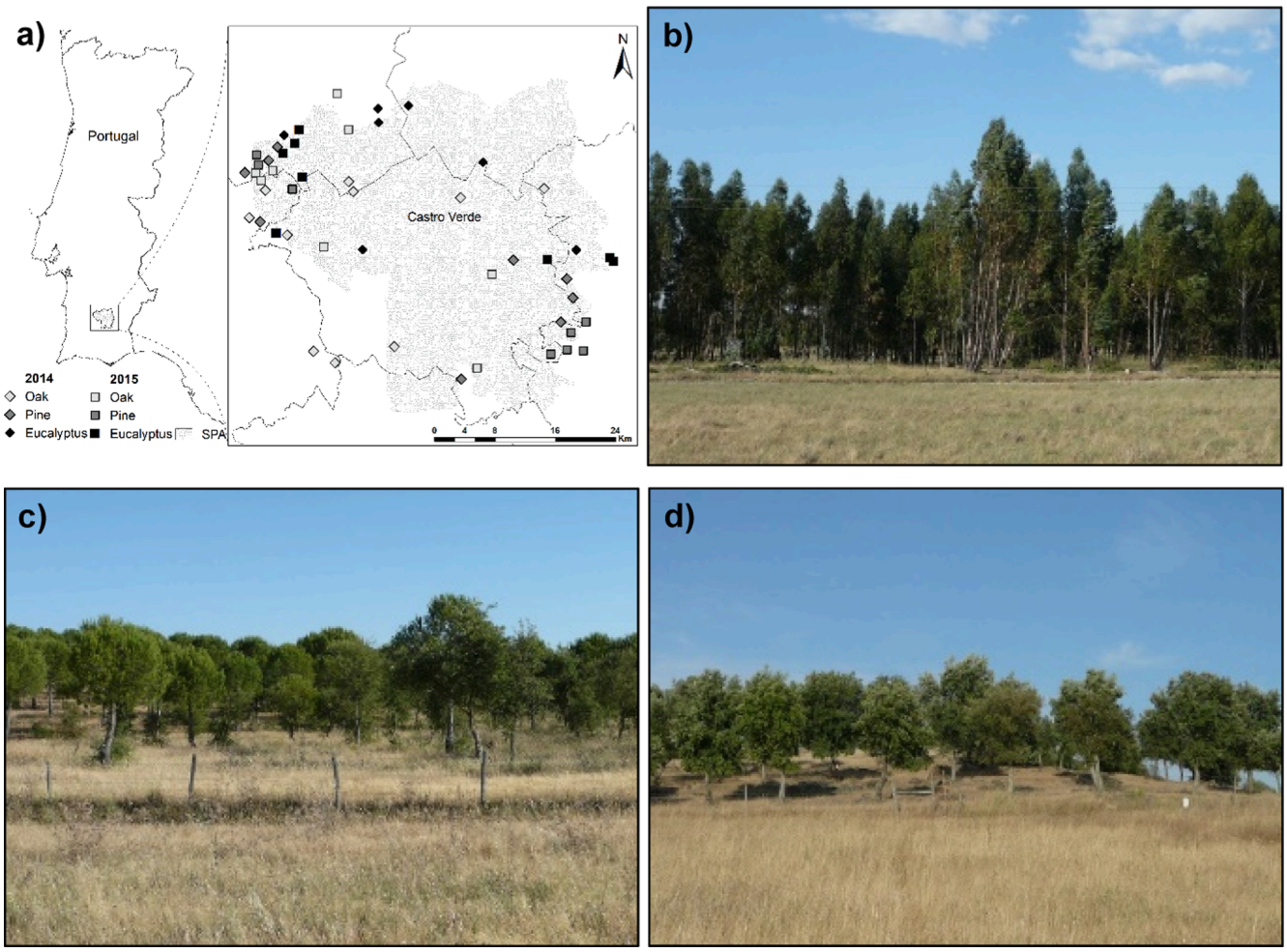

Fig. 1. a) Location of the study area in Southern Portugal, showing the Special Protection Area (SPA) of Castro Verde, and the distribution of the 51 sites sampled in 2014 (n = 26, in grey) and 2015 (n = 25, in black) across eucalyptus (n = 15), pine (n = 18) and oak (n = 18) plantations. Below, we provide examples of the b) Eucalyptus, c) Pine and d) Oak plantations and adjacent grassland (photo credits: J.S. Sánchez-Oliver).

(100–300 m a.s.l) and was traditionally dominated by either mosaics of shrubland interspersed with old fallow fields (up to 10 years) or agricultural fields cultivated with dry cereal crops in long rotations with fallows (2 to 5 years), mostly grazed by sheep at low densities (Delgado and Moreira, 2000; Moreira et al., 2007). In recent years the traditional system has shifted to a specialized production of either cattle or sheep (Ribeiro et al., 2016), with declines in cereal and fallow land, and increases in forage crops and permanent pastures (Ribeiro et al. 2014; 2016; Santana et al., 2017). Until the early 1990 s, tree cover was largely restricted to a few eucalyptus (*Eucalyptus* sp.) plantations and a few open holm and cork oak (*Quercus rotundifolia* and *Q. suber*, respectively) woodlands grazed by livestock, mainly cattle and sheep, but also horses and pigs (Delgado and Moreira, 2000; Moreira et al., 2005; Reino et al., 2009). From 1994 to 1999, following the implementation of EEC regulation 2080/92 (Institute for Forestry Development, 2001), there was an increase in afforestation with umbrella pines (*Pinus pinea*) and holm and cork oaks in the periphery of the SPA (Reino et al., 2010b). Oak plantations in the study area (Fig. 1) contain sparsely spaced trees, with understories of pastures and fallow lands with a diverse coverage of grass and forb species, broadly similar to the grassland matrix (Vasconcelos et al., 2019). Pine plantations have more closely spaced trees, while still maintaining a mix of grasses and forbs with patches of bare rocky ground (Vasconcelos et al., 2019). Contrastingly, eucalyptus plantations are usually older (50 to 70 years old), although several of these are regularly cut for wood due to their faster growth rate, thus resulting in overall taller trees and closed canopies, with very sparse herbaceous vegetation and, occasionally, dense patches of shrubs in the understory (Vasconcelos et al., 2019).

2.2. Sampling design

Sampling was carried out at 51 sites (26 in 2014 and 25 in 2015; Fig. 1). Site selection was based on sampling sites originally established in 2005 to study the effects of forest plantations on farmland birds (Reino et al., 2009). Briefly, plantations of the most common tree species were selected if the adjacent grassland parcel was at least 600 m long and wide, to allow sampling at distances up to 300 m from the nearest plantation edge. Selection was based on 1:25,000 land cover maps from 1990, updated through systematic field checking of new forest stands planted up to the beginning of 2005 (Reino et al., 2009). Of those, only sites that did not undergo considerable land use changes in 2014–2015, including, for instance, ploughing or cereal cultivation in grassland and tree harvesting in plantations, were retained. Additional sites were selected using satellite images from 2014 (GoogleEarth®), refined with field checking in 2014–2015 (Vasconcelos et al., 2019). The resulting sites consisted of a grassland parcel of fallow or pastureland, adjacent to a forest plantation stand (18 oak, 18 pine and 15 eucalyptus; Fig. 1). Only one grassland parcel per plantation was established to avoid pseudo-replication and spatial autocorrelation (Fortin and Dale, 2009; Vasconcelos et al., 2019). At each site, we established four 50-m radius sampling circles placed at 100-m intervals along a transect within the grassland parcel, perpendicular to the plantation-grassland edge

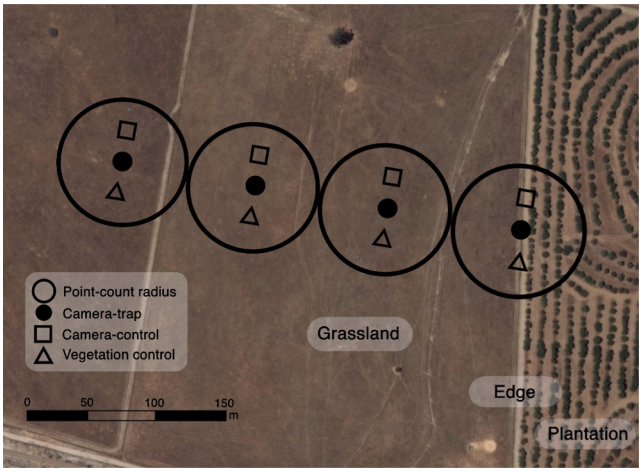

Fig. 2. Example of the spatial distribution of sampling sites in grasslands (fallow or pastureland) adjacent to forest plantations (oak, pine or eucalyptus; oak plantation in the photo), and schematic representation of the location of nests (camera-trap, camera-control and vegetation-control nests) and avian predator point-counts (50 m radius) along the 300 m long transects distributed at 100 m intervals (Image source: IFAP/ICNF, 2018).

(Fig. 2). To adequately cover grassland and edge habitats, the 50-m circles were located as follows: (i) one circle centered on the plantation-grassland edge, and (ii) three circles in grassland centered at 100, 200, and 300 m from the plantation-grassland edge (Fig. 2), as these distances appear to adequately encompass farmland bird responses to plantation edges (Reino et al., 2009; 2010a). In each site, and for each distance point, we identified the nest predators and estimated nest predation rate, sward structure and the abundance of avian predators.

2.3. Nest predators and nest predation risk

We identified nest predators and estimated nest predation risk at each site between April 17th and June 4th in 2014 and between April 7th and June 5th in 2015. This study was based on an artificial nest experiment, commonly used due to cost-effectiveness and flexibility of experimental design (Batáry and Báldi, 2004; Sánchez-Oliver et al., 2014; Huhta et al., 2015). Although the use of artificial nests has been criticised because they do not necessarily reflect predation rates on natural nests (e.g., Thompson and Burhans, 2004; Burke et al., 2004; but see Hoset and Husby, 2019), the method remains widely used to assess variation in predation risk in relation to habitats and predator communities (Batáry and Báldi, 2004; Huhta et al., 2015; Krüger et al., 2018; Bravo et al., 2020). The set-up consisted of three artificial nests placed 25-m apart, parallel to the plantation edge, in each 50-m circle (Fig. 2). The nest at the centre of the circle (hereafter camera-monitored nest) was made with herbaceous vegetation collected near the nesting area and baited with two fresh quail eggs (*Coturnix* sp.), and then monitored using an automatic camera (Scoutguard SG570-6 M; http://www.trail-camera.co.uk/scoutguard20SG570_6M.html) to identify predators and estimate predation risk. These are automatic cameras equipped with infra-red (IR) sensors and built-in IR LEDs functioning as a flash during the night, set to automatically take three sequential photos (trigger speed: 1.2 s) upon movement detection, with a 15 s delay between the following triggers. Cameras (n = 29) were placed in a metal bracket nailed to the ground (in grassland) or attached to trees (in plantation edges) and were supplied with 6 V lead acid batteries. The camera and battery set-up were stored in a camouflaged box (Herranz et al., 2002; Fig. S1a), to minimise their potential effects on the behaviour of nest predators (Meek et al., 2014; 2016). Herbaceous vegetation between the camera and the nest-site was manually trimmed or removed as needed to ensure an adequate field of view during shooting of photographs, and to avoid continuous camera-shooting due to the movement of herbs.

Since site manipulation can increase nest detectability (Suvorov et al., 2012), two types of artificial nests were used as controls to evaluate the effect of the camera (hereafter camera-control nest) and vegetation removal (hereafter vegetation-control nest) on nest predation risk (Fig. S1b-c). The camera-control nest was similar to the camera-monitored nest but without camera (Fig. S1b), while in the vegetation-control nest, the eggs were placed in a small depression in the soil and surrounding vegetation was not removed (Fig. S1c). In total, 532 artificial nests were placed and verified after seven days, 204 of which were camera-monitored, and 164 nests for each control situation (camera- and vegetation-control nests), as we were unable to place controls for the first 10 sites where nests were deployed in 2014.

Vegetation-control nests represent non-manipulated nest-sites (manipulation = 0). Since nest-predation risk between camera-monitored and camera-control nests did not significantly differ (Fisher's exact test, $F = 0.79$; $P = 0.295$), we pooled their data in a single variable describing nest-site manipulation (manipulation = 1). This variable aims to control for the effects of both camera presence and vegetation removal on nest predation risk potentially due to any increased nest detectability by avian predators.

Nests were set by two researchers (JSSO and JF), who avoided trampling the vegetation around the nests and wore rubber gloves and rubber boots to minimize potential human scent influence (Duncan et al., 2002), and to avoid potential biases due to variation in nest placement criteria. Nests position was recorded with a GPS tracker during placement and checked only once at the time of equipment removal to reduce potential observer effects and preserve nest concealment (Reino et al., 2010a; Ekanayake et al., 2015). We considered a predation event either the clear displacement or complete removal of an egg, along with beak, bite or claw marks visible on the eggshell (Reino et al., 2010a; Sánchez et al., 2014). Images obtained by camera traps for each parcel were thoroughly verified to corroborate each predation event and identify nest predators at the species level. Multiple visits by the same species to a nest were only counted once and visits to the nest-site subsequent to the predation event were disregarded. Nest predation risk was characterized as a binary variable of the different outcomes: 0 if not depredated and 1 if at least one egg was depredated (Table 1).

2.4. Sward height

Sward height was characterized as the mean height of the herbaceous vegetation, which was estimated from four measurements evenly spaced in a ca. 50-cm radius around each nest, just outside the manipulated area (Table 1); measurements were taken during nest placement (Fig. S1). This variable is uncorrelated with nest-site manipulation (Pearson's correlation coefficient = − 0.042; $P = 0.331$, Table S1), and conceptually different: sward height aims to measure the increase in nest safety from predators due to increased cover surrounding the nests, while nest-site manipulation intends to account for the impacts of manipulation on the protection normally offered by sward cover.

2.5. Avian predator abundance

Avian predators were surveyed at each site between April 1st and June 5th in 2014, and between April 11th and June 5th, 2015. Point-count surveys at each camera-monitored nest-site were performed to record all birds seen or heard during 10 min on nearly windless and rainless days (Bibby et al., 2000; Reino et al., 2009). To maximize detection probability, every point-count station was surveyed either at dawn or dusk. At each point, individual birds and flocks were identified and recorded on maps if they were < 50 m from the observer (Fig. 2). Double counting of individuals between survey points was minimized because birds flying over without landing were not counted and when

Table 1
Variables considered in analyses, with respective description and prediction according to relevant references.

Variable	Type	Description	Prediction
Parcel	Random - Categorical	The sampling site associated with each grassland parcel and adjacent plantation stand	Used to account for lack of independence among sites at different distances within each parcel (Reino et al., 2009)
Plantation type	Fixed - Categorical	The type of plantation adjacent to where nests were placed (Eucalyptus, Pine and Oak)	Steeper decreases in risk associated with Eucalyptus than Pine or Oak (Reino et al., 2009; 2010a)
Distance	Fixed - Continuous	Distance starting from the edge of the plantation and extending into the adjacent grassland (0, 100, 200 and 300 m)	Linear decrease of predation risk with increasing Distance (Reino et al., 2010a; Dodonov et al., 2017)
Predator abundance	Fixed - Discrete quantitative	Total number of individuals of the main avian predator species detected per site	Linear increase associated with higher predator abundance (Beja et al., 2014; Bravo et al., 2020)
Sward height	Fixed - Continuous	The mean height of 4 evenly spaced measures of the herbaceous vegetation surrounding the nest	Linear decrease associated with higher sward height (Bellamy et al., 2018)
Manipulation	Fixed - Binary (0/1)	The effects of camera presence and consequent removal of herbaceous vegetation to clear the camera field of view	Higher predation risk associated with Manipulated nests (Meek et al., 2014; 2016)

birds were suddenly flushed, extra care was taken to check if they landed in a potential survey point further ahead (Reino et al., 2009).

Predator abundance was defined as a discrete quantitative variable corresponding to the total number of individuals of each of the main avian predator species observed at each site, obtained by adding the counts of all four distance points together (Table 1). We grouped the four point counts because it was difficult to associate each bird with a single distance point given the short distances between consecutive points. Avian predators considered included the corvids carrion crow (*Corvus corone*), common raven (*Corvus corax*), and common magpie (*Pica pica*), and Montagu's harrier (*Circus pygargus*) (Arroyo, 1997; Terraube et al., 2010). The corvids Azure-winged magpie (*Cyanopica cooki*) and Eurasian Jay (*Garrulus glandarius*) were not considered as predators because there is, to our knowledge, no documented evidence of their nest-predation in grassland areas, likely due to their strong preference for woodland areas (Badge, 2020).

2.6. Statistical analysis

To begin, we investigated if there were noticeable differences in the total abundance of the main avian predators found across plantations. For this, we tested the relationship between predator abundance and plantation type (oak, pine and eucalyptus), using a generalized linear model (GLM) with Poisson errors and a log link function after testing for overdispersion (dispersion parameter = 1.16; $P = 0.057$; Kleiber and Zeileis, 2008).

Then, we investigated how nest predation risk varied with distance from edges (0 m,100 m, 200 m, 300 m), forest plantation type (oak, pine and eucalyptus), predator abundance, sward height, and nest-site manipulation, using generalized linear mixed models (GLMM; Bolker et al., 2008) with binomial errors and a logit link function. Interaction terms were added to test how distance effects varied with plantation type and predator abundance, and how sward height effects varied with nest site manipulation. Distance was specified as a continuous variable despite responses being estimated only at 100-m intervals, because categorisation would reduce the power of analysis by increasing the degrees of freedom (i.e., one versus three, for each term including distance), and because this specification allowed for detecting monotonic increases (or decreases) of the response variables even if only approximately linear. Detecting more complex non-linear responses (e.g. unimodal), would require a denser sampling of distances and larger sample sizes. GLMM was used to account for lack of independence among sites at different distances within each parcel, treating parcels as random effect (Zuur et al., 2009), resulting in the following candidate full model:

$$\begin{aligned} Predation \sim\ & distance + plantation + pred.abundance + sward\ height \\ & + manipulation + distance \\ & : plantation + plantation : pred.abundance + sward\ height \\ & : manipulation + (1|parcel) \end{aligned}$$

Lastly, we modelled predation risk separately for nests placed close to oak, pine and eucalyptus plantations, to examine how nest manipulation effects interacted with distance from the edge and sward height simultaneously, in different plantation types. This modelling strategy was used instead of incorporating plantation type and the interaction terms in the global model described above, due to lack of convergence. We used GLMM with binomial errors and logit link function with the same fixed and random effects described above, except plantation type, resulting in the following candidate model for each type of plantation:

$$\begin{aligned} Predation_{plantation} \sim\ & distance + pred.abundance + sward\ height \\ & + manipulation + distance \\ & : sward\ height + distance : manipulation + sward\ height \\ & : manipulation + distance : sward\ height \\ & : manipulation + (1|parcel) \end{aligned}$$

Model selection was performed by starting from a candidate full model and sequentially dropping the least significant variables and testing the effects of removing them in the model deviance with a chi-square test. We kept only variables whose removal caused significant decreases in model deviance ($P < 0.10$). If multiple variables simultaneously did not meet these criteria, we prioritized dropping the most complex interaction first.

Overdispersion tests were performed using "dispersiontest" function from the AER package (Kleiber and Zeileis, 2008). GLMM models were developed using "glmer" function, from the lme4 package (Bates et al., 2015), and model selection was performed using "drop1" function from the stats package (R Core Team 2020). All analyses were performed using R 3.6.4 software (R Core Team 2020).

3. Results

3.1. Overall patterns

Overall, the mean proportion of nests depredated was higher at the plantation edge (mean ± SE = 0.50 ± 0.04) than at any other distance point in the grassland matrix (mean ± SE = 0.43 ± 0.02; Fig. 3a, Table 2). This overall pattern was found for pine and oak plantations,

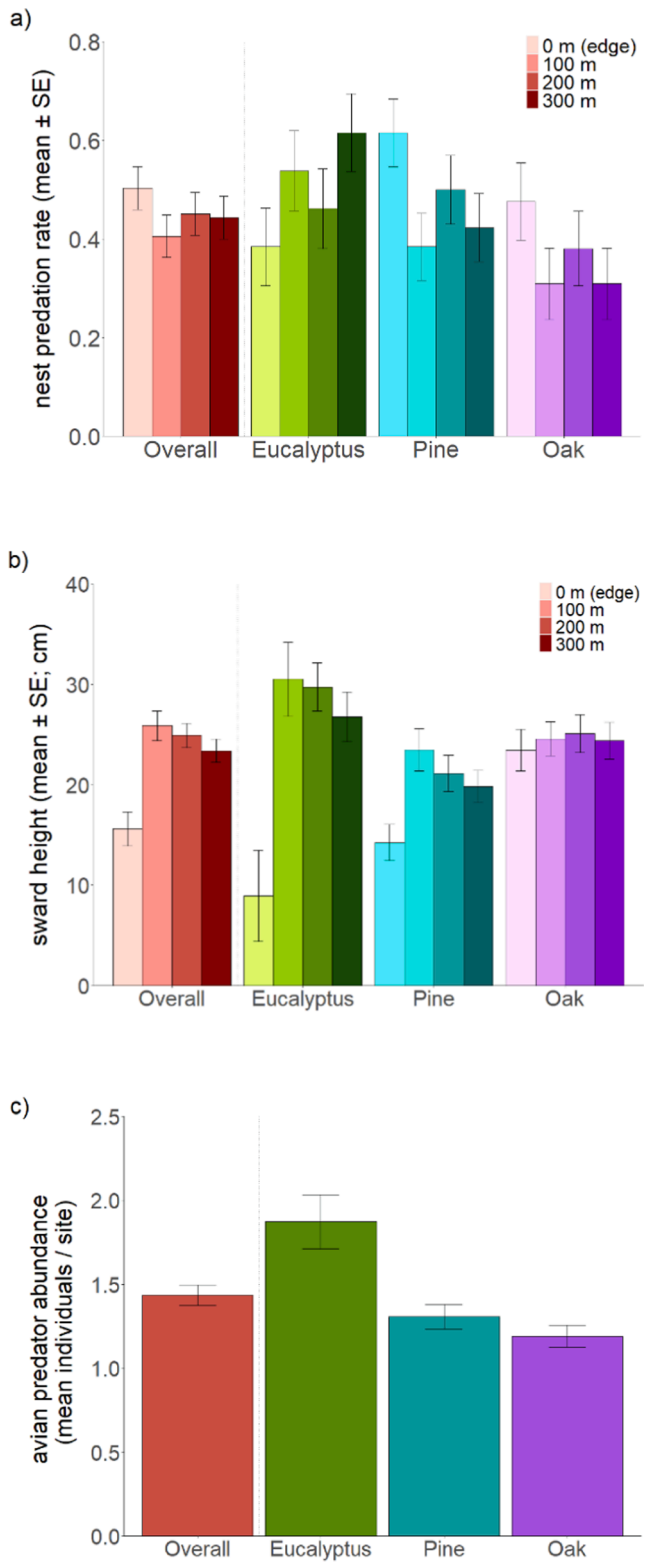

Fig. 3. Mean ± SE (before model tests) for: a) nest predation rate in relation to distance points; b) sward height (cm) surrounding the nest in relation to distance points; and c) avian predator abundance per site in relation to plantation types. Transparency scale in legend applies for each plantation colour.

but not for the eucalyptus plantations, which had lower mean predation rates at edges than farther away (Fig. 3a, Table 2).

Overall, mean sward height was higher in grassland than at plantation edges (Fig. 3b, Table 2). For different plantation types (Fig. S2), mean sward height was highest around eucalyptus but lowest at its edges. Sward in the grassland matrix near oak plantations was comparatively shorter but with similar mean sward height at the edges. Mean sward height was lowest in the grassland matrix associated with pine plantations, being particularly low at the plantation edge.

3.2. Avian predator abundance

The most abundant (mean count per site ± standard error) avian predators recorded were the carrion crow (0.63 ± 0.12) and the Montagu's harrier (0.43 ± 0.10), followed by the common raven (0.20 ± 0.08) and common magpie (0.18 ± 0.08) (Fig. 4; Table S2). The abundance of avian predators varied significantly across plantation types ($X^2 = 28.77$; $P < 0.001$), being higher near eucalyptus plantations (1.87 ± 0.16), compared to pine (1.31 ± 0.07, $Z = -2.35$; $P = 0.019$) and oak plantations (1.19 ± 0.07, $Z = -2.82$; $P = 0.005$; Fig. 3c; Table 2).

3.3. Nest predator identification

We obtained more than 770,000 photos for the 204 camera-trapped nests (up to 4000 photos/nest). Predators appeared in ca 0.35% of the photos (2153 photos, an average of 42.2 predator photos/parcel). After excluding nests trampled by cattle (18 out of 532 nests, 3.4%), nearly half (46.1%) of the camera-monitored nests were depredated (94 out of 204) by at least 13 different species, which were successfully identified in 72% of the predation events (Fig. S4; Table S3).

Carrion crow was the main nest predator (Table S3), accounting for 40.4% of depredated nests (n = 38), followed by Montagu's harrier (n = 8; 8.5%), common raven (*Corvus corax*, n = 4; 4.3%) and common magpie (n = 2; 2.1%). Mammals represented only 11.7% of total depredated nests, involving mainly cattle (*Bos taurus*, n = 4; 4.3%, excluding trampling), garden dormouse (*Eliomys quercinus*) (n = 2; 2.1%) and red fox (*Vulpes vulpes*) (n = 2; 2.1%).

3.4. Factors affecting overall nest predation rate

Nest predation rate was significantly related to all predictors, except predator abundance, including the main effects of sward height and nest-site manipulation, and the interactions between distance * plantation type and sward height * nest-site manipulation (Table 3). Nest predation increased with distance from eucalyptus plantations, but no significant distance effects were found for oak and pine plantations (Fig. 5; Table 5 & 6). Overall predation rate was lower in grasslands adjacent to oak (mean ± SE = 0.37 ± 0.04) and pine plantations (mean ± SE = 0.48 ± 0.03), than eucalyptus plantations (mean ± SE = 0.50 ± 0.04; Fig. 5, Table 2).

Manipulation significantly affected overall nest predation rate (Table 3). Nest predation rate was consistently ca. 20% lower in non-manipulated nests irrespective of plantation type, and it decreased with increasing sward height, particularly in non-manipulated nests (Fig. 5; Table 4). In manipulated nests around eucalyptus plantations there were no significant effects of distance and sward height (Fig. 5a-b).

3.5. Effects of plantation type on predation rate

There was a significant effect of distance to eucalyptus edge, which negatively interacted with manipulation ($\beta_{euc.} = -1.15$; $P_{euc.} = 0.028$).

Table 2
Description and summary statistics [mean ± SE (min–max)] describing variation between habitat type (grassland and edge) and plantation type (edge + grassland: eucalyptus, oak and pine) in predation rate, sward height and predator abundance. Predator abundance was surveyed at each sampling site without distinction between grassland and edge due to the difficulty in associating each counted bird with the correct habitat type given the short distances between survey points and bird movements between each point count.

Variable	Description	Total	Habitat type		Plantation type (Edge + Grassland)		
			Grassland	Edge	Eucalyptus	Oak	Pine
Predation rate	Presence (1) / absence (0) of nest predation per transect.	0.45 ± 0.02 (0–1)	0.43 ± 0.02 (0–1)	0.50 ± 0.04 (0–1)	0.50 ± 0.04 (0–1)	0.37 ± 0.04 (0–1)	0.48 ± 0.03 (0–1)
Sward height	Mean height of herbaceous vegetation in cm, estimated from 4 measurements taken around each nest.	22.38 ± 0.72 (0–175)	24.64 ± 0.74 (2.5–98.5)	15.60 ± 1.70 (0–175)	23.99 ± 1.82 (0–175)	24.38 ± 0.93 (0–64)	19.56 ± 0.94 (0–65)
Predator abundance	Total number of individuals of the main avian predator species in the sampling site.	2.53 ± 0.13 (0–17)	–	–	4.23 ± 0.75 (0–17)	1.33 ± 0.15 (0–3)	2.23 ± 0.22 (0–6)

Fig. 4. Camera trap photos of the main nest-predators. In order of abundance, the carrion crow (top-left), the common raven (top-right), the common magpie (bottom-left) and the Montagu's harrier (bottom-right).

Table 3
Goodness of fit tests of the predation risk for the overall generalized linear mixed model (GLMM) obtained after variable selection. For each model term we provide degrees of freedom (Df), Akaike Information Criteria (AIC) scores, Likelihood Ratio Test (LRT) outputs and significance level (*P*). **Bold** denotes $P < 0.10$.

	Df	AIC	*LRT*	*P*
NULL	NA	639.17	NA	NA
distance	0	639.17	0.00	0.999
plantation type	2	637.31	2.14	0.541
sward height	1	656.07	18.90	**<0.001**
manipulation	1	647.16	10.00	**0.002**
distance : plantation type	2	648.75	13.58	**0.001**
sward height : manipulation	1	644.05	6.89	**0.009**

Additionally, there was a positive interaction between sward height and nest-site manipulation ($\beta_{euc.} = 2.67$; $P_{euc.} = 0.0024$; Tables 5 & 6), with predation rate of non-manipulated nests increasing with distance from the plantation edge and decreasing with sward height (Fig. 5a-b).

Predation rate was significantly affected by sward height and nest-site manipulation around pine ($X^2_{pine} = 11.38$; $P < 0.001$) and oak ($X^2_{oak} = 4.21$; $P = 0.041$) plantations (Table 5b-c & 6b-c), with stronger effects for sward height (LRT = 3.75, $P = 0.053$) than for manipulation (LRT = 2.92, $P = 0.087$) around oak plantations (Table 5c). Predation risk significantly decreased with sward height around pine ($\beta_{pine} = -0.61$; $P_{pine} = 0.007$), but less so around oak plantations ($\beta_{oak} = -0.53$; $P_{oak} = 0.063$).

Manipulation affected predation rate in eucalyptus plantations by reducing the effects of the other predictors, with nest-predation rates becoming largely similar irrespective of distance to edge and sward height (Fig. 5a-b). Predation rate increased with nest-site manipulation in pine plantations ($\beta_{pine} = 0.86$; $P_{pine} = 0.02$) and weakly so in oak plantations ($\beta_{oak} = 0.74$; $P_{oak} = 0.09$) (Fig. 5c-d, Tables 5 & 6).

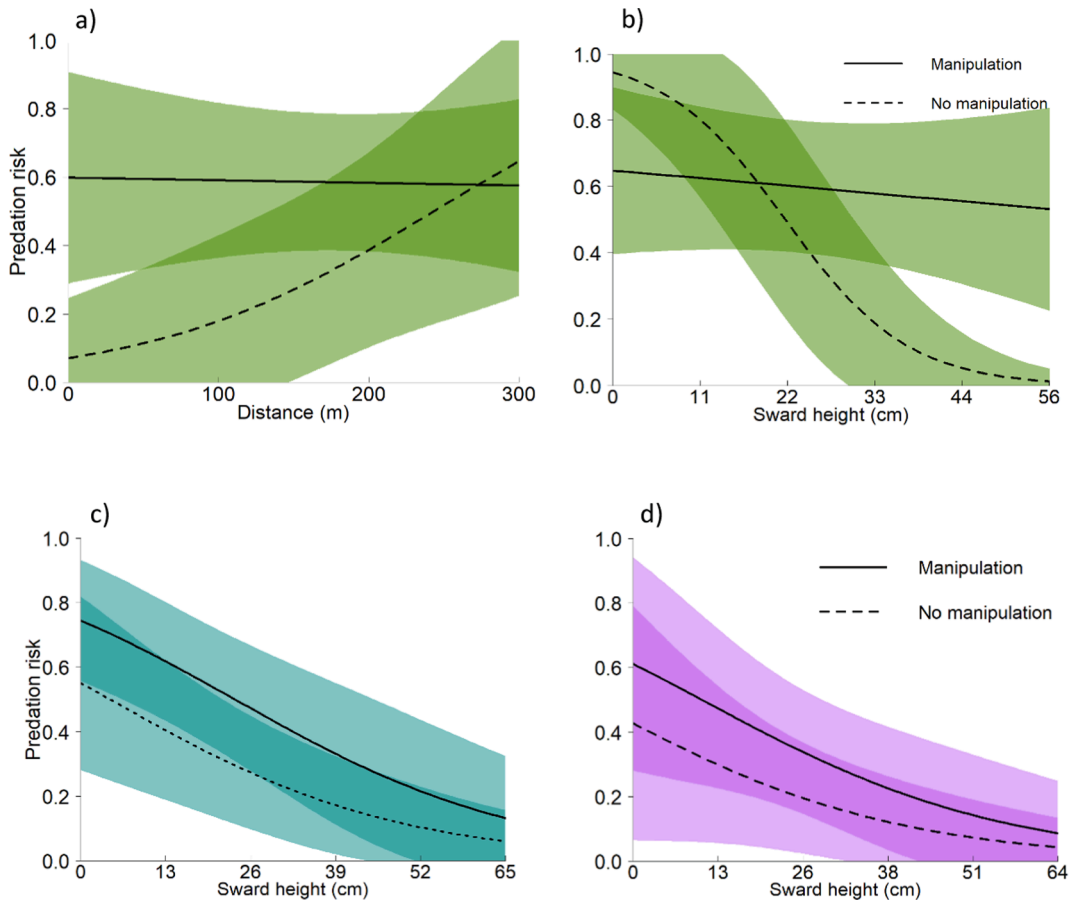

Fig. 5. Predicted nest predation risk in grassland adjacent to (a-b) eucalyptus, (c) pine, and (d) oak plantation forests, in relation to distance to grassland-plantation edge (a) and sward height (b-d). Predicted values (black line) and 95% confidence intervals (shaded area), for manipulated (filled line) and non-manipulated (dashed line) nests are represented. See also Tables 5 and 6.

Table 4
GLMM of overall predation risk with selected parameters. For each parameter we provide the coefficient estimate (β), its standard error (SE), z-value and significance level (P). **Bold** denotes $P < 0.05$.

	β	SE	Z-value	*P*
(Intercept)	−1.34	0.51	−2.59	0.010
distance	**0.56**	**0.19**	**3.02**	**0.003**
pine	0.90	0.63	1.46	0.150
oak	0.41	0.65	0.62	0.530
sward height	**−1.08**	**0.27**	**−3.99**	**<0.001**
manipulation	**0.74**	**0.24**	**3.13**	**0.002**
distance : pine	**−0.76**	**0.24**	**−3.23**	**0.001**
distance : oak	**−0.80**	**0.25**	**−3.21**	**0.001**
sward height : manipulation	**0.71**	**0.28**	**2.55**	**0.011**

Table 5
Goodness of fit tests of the predation risk GLMM for each plantation type model obtained after variable selection. For each model term we provide degrees of freedom (Df), Akaike Information Criteria (AIC) scores, Likelihood Ratio Test (LRT) outputs and significance level (P). **Bold** denotes $P < 0.10$.

	Df	AIC	*LRT*	*P*
Eucalyptus				
NULL	NA	193.79	NA	NA
distance	1	203.29	11.50	**<0.001**
sward height	1	209.92	18.12	**<0.001**
manipulation	1	198.97	7.18	**0.007**
distance : manipulation	1	197.43	5.63	**0.018**
sward height : manipulation	1	205.69	13.89	**<0.001**
Pine				
NULL	NA	246.18	NA	NA
sward height	1	251.83	7.65	**0.006**
manipulation	1	249.94	5.76	**0.016**
Oak				
NULL	NA	202.72	NA	NA
sward height	1	204.47	3.75	**0.053**
manipulation	1	203.65	2.92	**0.087**

4. Discussion

This study showed that corvids, and particularly the carrion crow, were the most important nest predators in our Mediterranean grasslands surrounding forest plantations. Specifically, we found that predator abundance was generally higher in grassland areas adjacent to eucalyptus plantations. Our study also showed that nest predation risk around eucalyptus plantations was lower near edges and increased into the grassland, contrasting with oak and pine plantations where predation risk was similar across all distances from edge, although highest at the edges. Furthermore, this study supported the idea that nest predation risk increases with decreasing sward height, likely because nests are less concealed in shorter vegetation and consequently more detectable by predators (Lyons et al., 2015; Bellamy et al., 2018). Our results provide insight for ongoing and future afforestation schemes, highlighting potentially different impacts on grassland birds depending on the type of adjacent plantation.

4.1. Predators identity and abundance

Our study supported the idea that corvids are important nest predators in Mediterranean farmland (Rodewald et al., 2011; Beja et al.,

Table 6
GLMM of predation risk for each plantation type with selected parameters. For each parameter we provide the coefficient estimate (β), its standard error (SE), z-value and significance level (P). **Bold** denotes $P < 0.05$ and **grey** denotes $P < 0.10$.

	β	SE	Z-value	*P*
Eucalyptus				
(Intercept)	−2.69	0.98	−2.76	**0.006**
distance	1.42	0.48	2.93	**0.003**
sward height	−2.73	0.84	−3.23	**0.001**
manipulation	2.45	1.01	2.43	**0.015**
distance : manipulation	−1.15	0.52	−2.19	**0.028**
sward height : manipulation	2.67	0.88	3.04	**0.002**
Pine				
(Intercept)	−0.68	0.44	−1.55	0.120
manipulation	0.86	0.36	2.38	**0.017**
sward height	−0.61	0.23	−2.71	**0.007**
Oak				
(Intercept)	−1.36	0.55	−2.11	**0.014**
manipulation	0.74	0.44	1.69	**0.090**
sward height	−0.53	0.29	−1.86	**0.063**

2014; Sánchez-Oliver et al., 2014). Carrion crows depredated almost half of the nests monitored with camera-traps, while ravens and common magpies were only responsible for a few nest losses. Of these corvid species, the carrion crow is considered the most important predator near edges of forest plantations, leading to increased predation rates (Andrén, 1992). This is corroborated by a recent camera-trap study where corvids were also the main predators, and carrion crows accounted for more than half of predation events (Bravo et al., 2020). Although less important, Montagu's harrier was also responsible for the loss of several nests, confirming the opportunistic foraging strategy of this raptor (Terraube and Arroyo 2011).

The abundance of avian predators was significantly higher around eucalyptus plantations than around pine or oak plantations, probably reflecting differences in the structure of forest plantations. Eucalyptus plantations are composed of faster growing trees with taller and denser canopies (Reino et al., 2009; Vasconcelos et al., 2019), which provide more suitable habitat for generalist predators such as corvids (Chalfoun et al., 2002; Pita et al., 2006) than pine and oak plantations. In contrast, oak and pine plantations were composed of shorter trees because of their slower growth, which are sparsely spaced with pasture understories broadly similar to the grassland matrix (Vasconcelos et al. 2019, Fig. 1), thus offering less breeding and foraging habitat for avian predators than eucalyptus plantations (Reino et al., 2009).

All the species identified as important nest predators were also the most abundant predators detected in the study area, suggesting that a higher availability of predators may lead to increased nest predation risk. However, predator abundance was not selected as a significant predictor of predation risk, nor was it significantly related to predation events (result not presented). This may be because our surveys did not differentiate between breeding pairs and floaters, as only the former was found to relate significantly to risk of predation by corvids (Erisktad et al., 1982; Bravo et al., 2020). As such, if we detected mostly floaters, it is likely that our predictor of predator abundance poorly correlates with predation risk (Bravo et al., 2020). Additionally, the most common predator, carrion crow, tended to occur very frequently near eucalyptus patches, due to their need of forest cover for breeding. But most contacts with this species during counts were mainly vocal, as the birds were persistently vocalizing through their common contact calls. This should help alleviate any potential bias that could occur due to lower detection probability around the taller and denser eucalyptus forest edges.

Our results are in line with other studies conducted in Mediterranean farmland areas that also observed a significant majority of avian predators (Reino et al., 2010a; Krüger et al., 2018; Ponce et al., 2018). However, mammal and reptile predators such as foxes, domestic dog, rats, hedgehogs or snakes may also play a role in shaping nest predation (Batáry and Báldi, 2004; Reino et al., 2010a; Beja et al., 2014; Arbeiter and Franke, 2018). Although mammals represented a small part of the total predation events detected in camera-traps in our study (ca. < 11%), we do not know the real dimension of their impacts on predation as we were unable to identify predators in ~ 30% of the depredated nests. Despite this, in the unlikely chance that all unknown events were from mammals, corvids would still dominate nest-predation events. Livestock grazing may also contribute to reduce nest survival rates (Beja et al., 2014) through nest destruction caused by livestock trampling or nest predation. In our study, trampling by cattle represented 3.4% of total nests destroyed, while 4.3% of all depredated nests were depredated by cattle. Despite their impact being low when compared to overall corvid predation (55.3%), it still represents a higher impact than several individual species. However, this is unlikely to change the main conclusions of this study, as we were primarily interested in the effects of afforestation on nest predation risk. While livestock may significantly reduce nest survival, their occurrence and abundance in grassland stands is driven by human decisions for grazing purposes independent of adjacent plantation stand composition.

4.2. Contrasting edge effects by plantation type on nest predation risk

Contrary to expectations, overall nest predation risk remained unchanged with distance to plantation edge, though there was a significant positive effect for the main distance predictor in the general model. The lack of an overall distance effect likely results from the contrasting effects of this variable for different plantation types, and should be carefully interpreted without such context, following the principle of marginality (Nelder, 1977). Indeed, we found that nest predation risk increased significantly with distance from the edge in eucalyptus plantations, but remained stable and overall lower in the grasslands adjacent to oak and pine plantations.

The increase in nest predation risk farther into the grassland around eucalyptus plantations likely occurs because these have generally taller trees that can provide a better vantage point near the plantations' edges, thus increasing nest detectability into the adjacent grassland (Rice, 1983; Eggers et al., 2008). This can also increase the likelihood of the spill-over of carrion crow (Reino et al., 2009; 2010a), as they often nest in tall trees (Santos et al., 2006) and feed in adjacent open farmland (McCollin, 1998) by adapting to their prey's habitat preferences in order to opportunistically consume them (Anderson and Burgin, 2008).

In the case of oak and pine plantations, the lack of differences in predation risk across distances may reflect the similarity between the plantation understory and the adjacent grassland, with very similar sward heights and sparse and shorter trees, especially in the case of oak plantations (Vasconcelos et al. 2019). Contrary to eucalyptus plantations, these trees would also provide less advantage in detecting prey at increasing distances into the grassland (Rice, 1983), resulting in similar predation efforts between edge and the adjacent grassland matrix.

While reduced predation risk near the plantation edge may appear to be a potential benefit of eucalyptus plantations, careful analysis actually suggests otherwise. In this study, the use of artificial nests allowed us to place them evenly along a gradient in distance from plantation edges. However, grassland birds, particularly grassland specialists such as the calandra lark (*Melanocorypha calandra*) and short-toed lark (*Calandrella brachydactyla)*, are more likely to nest farther into the grassland, as several of these species are known to be edge avoiders, placing their nests far from plantation edges (Reino et al., 2009; 2010a; Morgado et al., 2010; Pretelli et al., 2018), where plantation risk was found to be higher.

4.3. Camera trapping effects on nest predation

The effects of nest-site manipulation, consisting of camera placement and vegetation removal in front of the camera-trap to reduce the number of photos from vegetation in movement due to the wind, led to

consistently higher levels of nest predation. This likely reflects the potential of cameras to sometimes attract animals (Meek et al., 2016), thus increasing nest detection and inherent predation risk. Moreover, vegetation removal may have increased the detectability of nests by reducing the camouflage effects normally provided by the higher sward height. In our study, interaction effects between nest-site manipulation, distance to edge, and sward height were found in eucalyptus plantations. Predation risk in grasslands surrounding these plantations became unchanged by sward height and distance when nests were manipulated. In the case of pine and oak plantations, manipulation increased the overall predation risk across the entire sward height gradient. This difference could be explained by the higher number of corvids in eucalyptus plantations compared to other areas, which can lead to changes in predation rates in the adjacent area (Andrén, 1992; Lyons et al., 2015; Bellamy et al., 2018). For instance, corvids may take advantage of the higher perches of eucalyptus trees (Santos et al., 2006) to optimize their foraging abilities, extending their ability to detect nests farther into the taller swards of grassland (Rice, 1983; Eggers et al., 2008; Bellamy et al. 2018). This detection is enhanced by increased visibility due to vegetation removal in nest sites, even with higher sward height surrounding it. Overall, despite generally increasing predation risk associated with distance and sward height effects in eucalyptus plantations, nest-site manipulation did not significantly affect predator identity or nest predation risk by plantation type.

4.4. Management implications

Our results highlight a major concern in the conservation of several key species associated with Mediterranean farmland, such as calandra larks, little and great bustards (*Tetrax tetrax*), Montagu's harrier or greater short-toed larks. These species, normally associated with open habitats, are directly affected through habitat loss due to former and current plantation practices (Bremer and Farley, 2010; Morgado et al., 2010; Jacoboski and Hartz, 2020). We fear this effect may be further exacerbated by loss of habitat quality due to increased nest predation, as these open farmland species normally opt to breed at safer distances further from plantations (Fletcher, 2005; Reino et al., 2009; Morgado et al., 2010). This may lead to an asymmetrical impact by eucalyptus plantations compared to oak or pine stands, due to the observed increase in nest predation risk away from edges.

Several studies have suggested that afforestation practices worldwide should avoid areas preferred by open-habitat species of conservation concern to avoid exacerbating potentially negative consequences on them (see also: Graham et al., 2017; Brazeiro et al., 2018; Gómez-Catasús et al., 2018; Cravino & Brazeiro, 2021). Although we did not aim to assess the impacts of afforestation by plantation forests on nest predation risk, we should note that a previous study conducted in a relatively close area but without nearby plantations observed noticeably lower predation rates (0.18 ± 0.23 SD, Beja et al., 2014), compared to our observed overall predation risk (ca. 0.45). Regarding plantation type, afforestation practices that focus on eucalyptus or other fast-growing tree species could represent an increased risk for grassland bird specialists (Reino et al., 2009; 2010a; Saccol et al., 2017; Jacoboski and Hartz, 2020). In situations where these are of particular concern, afforestation policies could instead prioritise plantations with lesser impact on local biodiversity such as oak, pine, or other slower growing native species (Sánchez-Oliver et al., 2014; Bellamy et al., 2018; Magnano et al., 2019; Vasconcelos et al., 2019). These species also seem to provide an additional advantage in one of the main targets of current and future afforestation policies: greater carbon accumulation and sequestration (He et al., 2018; García et al., 2020; Xiong et al., 2020).

Moreover, efforts should be made to preserve the quality of areas of grassland habitat when these harbour grassland specialists. This could be achieved by removing small tree rows whenever possible, and the use of selective patch-burn grazing, focusing on maintaining taller swards of vegetation to provide refuge for ground-nesters and decrease predation risk (Klug et al., 2010; Ellison et al., 2013; Arbeiter and Franke, 2018; Skagen et al., 2018).

A more controversial management option (Beja et al., 2009; Treves et al., 2016; 2019) would be the culling of key predators such as the carrion crow, which seems to have a disproportionately higher predation impact compared to other predators in our and other Mediterranean grasslands (Smith et al., 2010; Phifer et al., 2017; Bond et al., 2019). However, this approach is costly, time-consuming and sometimes ineffective (Bolton et al., 2007; Madden et al., 2015), with a high likelihood of increasing dispersal and replacement rates (Marzluff and Heinrich, 1991; Bodey et al., 2009). As such, a better approach could be to understand in detail the feeding behaviour of corvids, by comparing nest predation between areas rich and poor in alternative corvid food (i.e., insects and worms) and testing the provision of alternative food sources in areas where nests may be at a higher risk (Bravo et al., 2020). We believe that careful consideration and selective implementation of these measures can economically and environmentally benefit the outcome of these afforestation schemes.

5. Conclusions

The carrion crow was the principal nest predator in our Mediterranean grassland area. Different plantation types can have different impacts on predation risk in the surrounding grasslands by providing potentially distinct advantages for predators targeting grassland bird species. Among oak, pine and eucalyptus, the latter was associated with significantly more predator presence than other plantation types. Furthermore, while its impact on predation risk was lower near edges, it seemed to extend farther into the grassland area, potentially exacerbating its negative effects on certain species. Considering these results, we advise that afforestation practices should carefully consider between the use of eucalyptus or other fast-growth species, and slower growing species such as oak and pine, particularly when targeting grassland patches with high conservation value. Finally, we suggest potential alternatives to reduce predation risk, from the less favourable culling of the main corvid predators, to focusing instead on alternative resource availability and habitat improvement, which may tie into the suggested afforestation measures. The successful consideration of these measures in ongoing and future large-scale afforestation schemes may not only reduce their impacts, but also help achieve carbon sequestration goals while keeping sustainable grassland biodiversity levels.

CRediT authorship contribution statement

João Faria: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Juan S. Sánchez-Oliver:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Pedro Beja:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing. **Francisco Moreira:** Investigation, Writing – review & editing. **Inês Catry:** Investigation, Writing – review & editing. **Sasha Vasconcelos:** Investigation, Writing – review & editing. **Sílvia Pina:** Investigation, Writing – review & editing. **John T. Rotenberry:** Investigation, Writing – review & editing. **Luís Reino:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Joana Santana:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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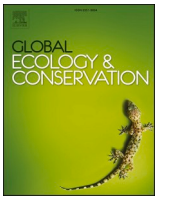

Grassland vegetation height affects bird responses to forest edges in Mediterranean open farmland

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ABSTRACT

Afforestation affects Mediterranean farmland biodiversity due to loss and fragmentation of grassland habitats. While the influence of landscape context and plantation edges on farmland bird responses to afforestation is well-documented, less is known about the influence of grassland vegetation height and how it interacts with afforestation to influence bird communities. Here, we examined how changes in grassland vegetation height affect bird responses to afforestation in a farmland region in southern Portugal, and how these are affected by plantation type and edge. This region has experienced afforestation with eucalyptus, pine and oak stands, agricultural intensification, and frequent dry periods. To capture local and landscape-level changes, we collected data in two periods (2005 and 2014–15). Grassland vegetation height varied between sampling periods, emerging as a key factor affecting changes observed. Ground-nesting and cereal-associated species increased in abundance with taller vegetation in 2014–15, while in 2005, with drier weather and shorter vegetation, the species associated with ploughed fields were

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more abundant. Vegetation height effects on bird assemblages depended on plantation type and distance to plantation edges. Farmland bird abundance, including ground-nesting and cereal crops-associated species, increased with taller vegetation, particularly near oak and pine plantations. Conversely, species associated with ploughed fields declined with taller vegetation, especially near eucalyptus plantations. Results highlight complex interactions between vegetation height, plantation type, and edge proximity shaping avian assemblages. This study supports the importance of field and landscape-level management with special focus on grassland vegetation height and landscape heterogeneity for preserving open-farmland birds in fast-changing Mediterranean farmland landscapes.

1. Introduction

Afforestation, prominently discussed for its potential in carbon reduction and sequestration (Potter et al., 2007; Lin et al., 2013), poses conservation concerns due to its transformation of natural and semi-natural ecosystems into smaller fragmented habitats (Liu et al., 2019). This is particularly concerning when open habitats of conservation significance are replaced (Reino et al., 2009; Bond et al., 2019; Jacoboski et al., 2019; Faria et al., 2022), as newly formed plantation edges reinforce fragmentation effects, potentially reducing the quality of the remaining open-habitat fragments (Ries et al., 2004; Ewers and Didham, 2007). Open farmland bird species are particularly affected by this (Brotons et al., 2005; Reino et al., 2009; Morgado et al., 2010; Pretelli et al., 2018; Jacoboski et al., 2019; Jacoboski and Hartz, 2020), experiencing increased nest predation in grasslands adjacent to these plantations (Santos et al., 2006; Sánchez-Oliver et al., 2014a; Faria et al., 2022). Afforestation effects on farmland biodiversity are influenced by various factors. Different plantations provide varying understorey vegetation and tree species composition, which influences avian community composition adjacent to open habitats, including potential predators and competitors (Reino et al., 2010a; Calviño-Cancela et al., 2012; Faria et al., 2022). Additionally, taller tree growth and higher density may amplify edge effects, modifying suitability for certain species and increasing predation pressure in the adjacent grasslands (Santos et al., 2006; Reino et al., 2010a; Faria et al., 2022).

Grassland vegetation height is thus of particular importance in the resulting grassland fragments (Moreira, 1999), as in addition to protection from nest predation (Faria et al., 2022), taller vegetation can provide adequate cover, food and nesting resources to numerous open farmland species (Batáry et al., 2007; Erdös et al., 2009). Vegetation height may be directly affected by changes to farming systems, e.g., in the context of agricultural policy reforms, such as the Common Agricultural Policy (CAP) introduced by the EU in 2003 (Ribeiro et al., 2014). The Mediterranean farmlands of southern Portugal are part of the cereal-steppes of the Iberian Peninsula, representing a High Nature Value Farmland (HNVF) system critical for the conservation of a range of open farmland birds (Suárez et al., 1997; Bota et al., 2005; Reino et al., 2009). It was mostly composed of extensively farmed traditionally mixed-rotational systems of dry cereal, fodder crops and fallow land and pastures grazed by sheep (Ribeiro et al., 2014). However, this is currently changing with the increased cultivation of intensive woody crops and the establishment of specialised livestock systems, associated with an increased cover by permanent pastures (Ribeiro et al., 2014; Ren et al., 2018; Morgado et al., 2020).

Concerns regarding the impact of extreme climatic conditions (i.e., droughts and heat waves) on grasslands have also been raised (Conrey et al., 2016; Zuckerberg et al., 2018). These result in less biomass production and changes to soil properties (Wu et al., 2022) decreasing vegetation cover (Conrey et al., 2016), and shifting grazing patterns (Li et al., 2018). Lower vegetation height, driven by droughts (Conrey et al., 2016), intensive grazing (Reino et al., 2010b; Ribeiro et al., 2014), or a combination of both, likely raises nest-detectability (Bellamy et al., 2018) and vulnerability to predators near plantation edges (Beja et al., 2014; Faria et al., 2022). Thus, farmland birds inhabiting these habitats are expected to be particularly susceptible to changes in grassland vegetation height. However, while both the effects of afforestation and (to a lesser extent) vegetation heights on bird communities have been studied, little is known about the interaction of these two factors, i.e., how variations in vegetation height may affect farmland bird responses to afforestation differentially depending on plantation type.

In this study we aimed to analyse afforestation's impact on Mediterranean open farmland bird communities in two periods (2005, 2014–15) with contrasting vegetation heights in grasslands adjacent to different plantation types. We focused on a representative area of Iberian cereal steppes that has experienced recent afforestation (Reino et al., 2010a) and has been facing increasing drought severity (García-Ruiz et al., 2011; FFMS, 2022). This area is also among the European farmland landscapes with the highest conservation relevance to farmland birds (Bota et al., 2005; EEA, 2006). Specifically, we examined: 1) variations in bird composition and local and landscape characteristics, and 2) the influence of those characteristics that changed significantly between periods on avian assemblages' responses to plantation edges and types. We hypothesise that (i) grassland vegetation is shorter in the drier period (Conrey et al., 2016); (ii) ground-nesting species, especially those associated with cereal fields, increase in abundance with taller vegetation due to the role played by vegetation cover in nest survival (Delgado and Moreira, 2000), while those specifically associated with ploughed fields decrease; and (iii) steppe birds benefit from increased vegetation height in grasslands adjacent to the softer edges of oak plantations and higher distances to the plantation edge (Reino et al., 2009; Sliwinski and Koper, 2012; Besnard et al., 2016).

2. Methods

2.1. Study area

The study was conducted in southern Portugal, mostly within the Special Protection Area (SPA) of Castro Verde. Since 1995, this

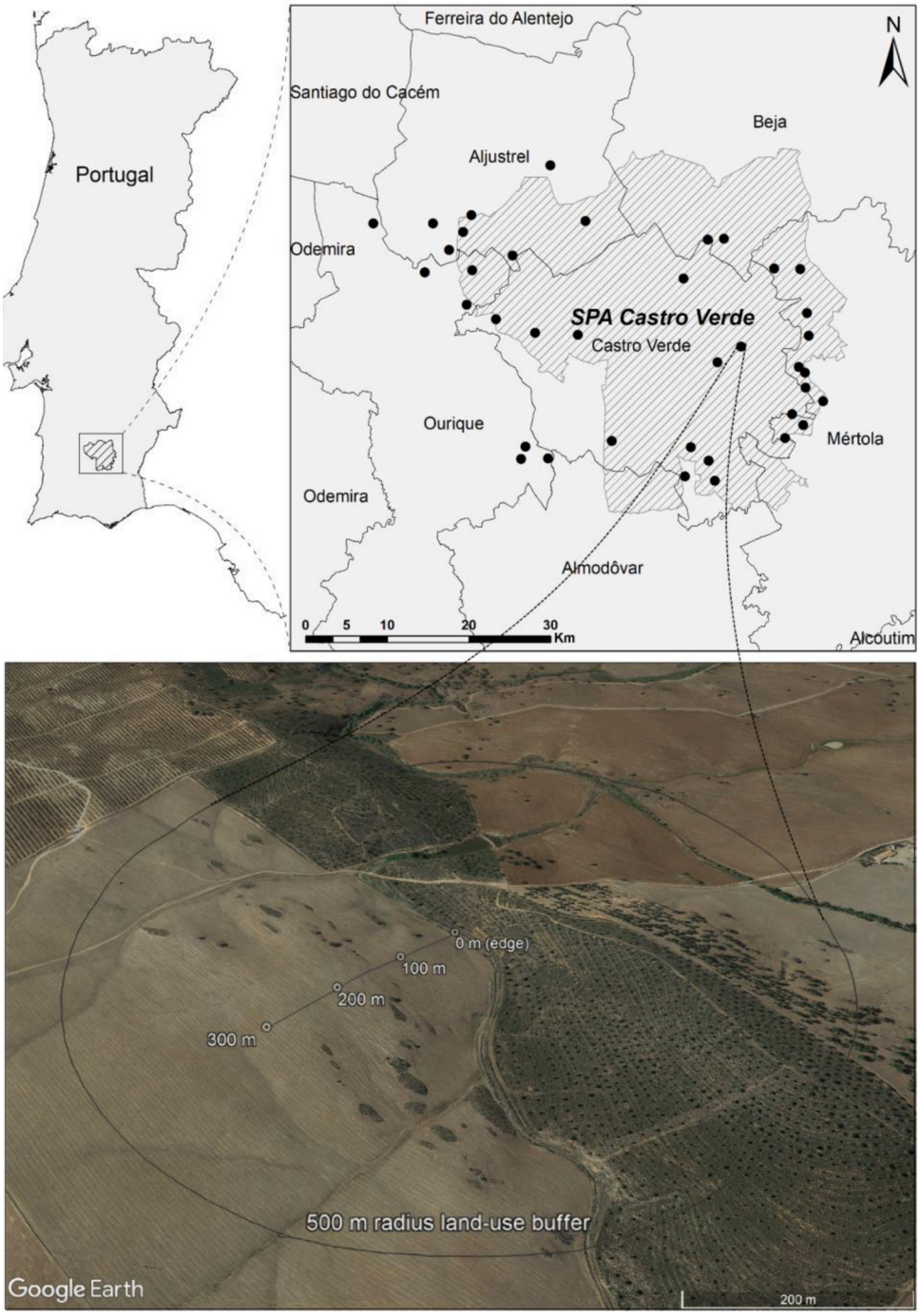

Fig. 1. Study area located in Southern Portugal, showing the Special Protection Area (SPA) of Castro Verde (Alentejo region), and the distribution of the 38 sampled sites. Below is highlighted an example of the spatial distribution of the survey points used in the grasslands (fallow or pastureland) adjacent to each forest plantations (oak, pine or eucalyptus; oak plantation in the photo). See methods section for further details.
Image source Google Earth Pro (ver. 7.3.4.857).

area has benefitted from an agri-environment scheme targeting the conservation of steppe birds under the European Union Birds Directive 2009/147/EC, through the maintenance of traditional farming systems (Ribeiro et la, 2014) (Fig. 1). The region has a Mediterranean climate, characterised by mild winters (averaging 9 ºC [5–14 ºC] in January) and hot summers (24 ºC [16–32 ºC] in July), with > 75% of annual rainfall (500–600 mm) concentrated between October and March (Moreira et al., 2005; Morgado et al., 2020). Over the past 30 years, there has been a decrease in annual rainfall (from 584 to 547 mm) and an increased number of days without rain (from 150 to 155) (FFMS, 2022).

The landscape is predominantly flat or gently undulating (100–300 m a.s.l) (Moreira et al., 2005) and consists mostly of open farmland, traditionally composed of old fallow fields (lasting up to 10 years) or agricultural fields cultivated with dry cereal crops in rotations with fallows (2 to 5 years). Historically, these farmlands were grazed by sheep at low densities (Delgado and Moreira, 2000; Santana et al., 2017). Following the implementation of the European Economic Community regulation 2080/92 in the mid to late 1990 s (Institute for Forestry Development, 2001), there was an increase in afforestation with umbrella pines (*Pinus pinea*) and holm and cork oaks (*Quercus rotundifolia* and *Q. suber*, respectively) in the periphery of the SPA (Reino et al., 2010). Until then, tree cover largely consisted of eucalyptus plantations (*Eucalyptus* sp.) and a few open-oak woodlands, grazed by livestock (Delgado and Moreira, 2000; Moreira et al., 2005; Reino et al., 2009). More recently, the traditional mixed system has shifted towards specialised production of cattle or sheep (Ribeiro et al., 2016), with declines in cereal and fallow land, and increases in forage crops and permanent pastures (Ribeiro et al., 2014, 2016; Santana et al., 2017).

2.2. Sampling design

We sampled 38 grassland parcels twice in each sampling period (2005, 2014–15), each time along 300-m transects perpendicular to the edge of one of three types of forest plantations commonly found in the region, including younger pine, and oak stands (mean age = 15.4 ± 4.9 years and 12.9 ± 5.9 years, respectively) and older eucalyptus stands (mean age = 41.8 ± 18.1 years). Grassland parcels consisted of fallow fields and pastures (i.e. rainfed cereal fields were excluded) to reduce variation unrelated to the variables tested, and due to their particular importance for steppe bird species (Delgado and Moreira, 2000; Reino et al., 2009).

Site selection was carried out prior to the 2005 sampling period, based on 1:25,000 land cover maps from 1990, updated through systematic field checking of new forest stands planted up to early 2005 (Reino et al., 2009). Each site included a grassland parcel plus an adjacent plantation, selected only if the grassland parcel was at least 600 m long and wide, to allow sampling up to 300 m from the nearest plantation edge. Additionally, only one grassland parcel per plantation was considered to avoid pseudo-replication and spatial autocorrelation (Fortin and Dale, 2009; Vasconcelos et al., 2019). For the 2014–15 sampling period, we were able to resample several of the original sites, retaining 38 sites that did not undergo major land-use changes, such as ploughing or cereal cultivation in the grassland parcel, and tree harvest or thinning in the adjacent plantations (Vasconcelos et al., 2019; Faria et al., 2022). These included grassland parcels adjacent to 8 eucalyptus, 13 pine and 17 oak plantation stands.

2.3. Bird data

Bird surveys were conducted during the breeding season in 2005 (from April 1st to May 31st), and again in either 2014 or 2015 (from April 1st to June 5th, 2014, and April 11th to June 5th, 2015). Surveys were conducted twice per sampling period. They consisted of four sequential point-counts performed at 0, 100, 200, and 300 m perpendicularly from the plantation edge, where for 10 min, each bird seen or heard within 50 m from the observer was recorded. Sampling was conducted preferably at dawn, or at either dawn or dusk in the two sampling occasions for each period, as Mediterranean farmland birds have similar peaks of activity during these periods (Caro et al., 2015). To help reduce detectability problems, surveys were only conducted on nearly windless and rainless days on mostly flat grassland parcels (Bibby et al., 2000; Reino et al., 2009) by two experienced observers (LR and RM). At each point, individual birds and flocks were identified and mapped (Fig. 1). To minimise double counting of individuals, birds in flight were not recorded, except in the case of song flights (e.g., calandra lark). Additionally, extra care was taken to not count any birds flushed between counts that landed at a subsequent survey point, which was always within sight (Reino et al., 2009). To address identification challenges in the field, crested and Thekla larks (*Galerida cristata* and *G. theklae,* respectively) and common and Spanish sparrows (*Passer domesticus* and *P. hispaniolensis,* respectively*) were categorised at the genus level.*

For each sampling period, we estimated bird abundance (i.e., the highest number of birds counted between the two surveys per distance point per site) for the overall assemblage and at a species level. To evaluate differences in responses in the bird community according to their habitat affinities, we categorised species into guilds: woodland; farmland; ground-nesting; open-farmland (steppe) specialists (Reino et al., 2009); cereal, fallow or ploughed fields (Delgado and Moreira, 2000; Santana et al., 2014); and threatened species, including near threatened, vulnerable or endangered on the IUCN European red list of birds (BirdLife International, 2022; Table A1). Species-specific analyses were carried out for the 13 most widespread bird species in either period (higher than 25% occurrence, Table A2): tawny pipit (*Anthus campestris*), red-legged partridge (*Alectoris rufa*), greater short-toed lark (*Calandrella brachydactyla*), European goldfinch (*Carduelis carduelis*), zitting cisticola (*Cisticola juncidis*), carrion crow (*Corvus corone*), corn bunting (*Emberiza calandra*), Galerida larks (*Galerida* spp.), common linnet (*Linaria cannabina*), calandra lark (*Melanocorypha calandra*), European stonechat (*Saxicola rubicola*), little bustard (*Tetrax tetrax*) and Eurasian hoopoe (*Upupa epops*).

2.4. Variable selection

Plantation structure was characterised by tree height and edge density, estimated using ground-level photographs taken at

70–100 m perpendicular to the plantation edge. A field scale was employed at the edge to determine pixel size, which was then used to calculate average tree height. Tree density was derived from the total number of trees per metre of edge captured in the photographs. Additionally, plantation type was included to account for other potential effects of different plantation characteristics, such as plantation age, vegetation structure and composition, and avian predator abundance.

For vegetation height, grassland vegetation height was estimated from the average of four measurements evenly spaced in a ca. 50-cm radius centred at each sampling point, using a 50-cm ruler. This process was repeated in both periods (Table A3). The potential influence of livestock grazing on vegetation height was also considered by recording the occurrence (presence/absence) of livestock (sheep and cattle) at each grassland parcel during counts.

Furthermore, we also considered weather conditions in the study area for both periods. Data from the nearest weather station (Beja weather station) (https:www.pordata.pt; FFMS, 2022), was used to extract three precipitation indicators: annual precipitation (annual rainfall), maximum monthly precipitation (max. precipitation) and total number rainless days. To accommodate the potential influence of the preceding year's precipitation on grassland conditions (Zuckerberg et al., 2018), annual data from 2004 and 2005 were used for the first sampling period (2005), and data from 2013 to 2015 were used for the second (2014–2015).

For landscape context, land cover maps for both periods were created within 500-m radius buffers centred on the plantation-grassland edge (Fig. 1). Images from Google Earth Pro (ver. 7.3.4.857) from 2005–2007 and 2015–2016 were used. Land-use categories were obtained from a governmental database (DGT, 2007, 2015), and included agricultural area; eucalyptus, pine, and oak plantations; shrubland; wood-pastures; water bodies; urban areas; and olive groves. These were selected to broadly reflect all land-use types within the area, with greater detail provided for plantation cover (Table A3). Landscape heterogeneity metrics (Elkie et al., 1999), including area-weighted mean shape index (AWMSI), mean patch size (MPS), and edge density (ED) were computed using the Patch Analyst plugin in ArcGIS (ver. 10.2.2; ESRI Inc, 2014).

2.5. Statistical analysis

Variation in the abundance of avian assemblages at each site (i.e., relative abundance per site, including all distance points) and local and landscape variables between periods was evaluated through individual paired t-tests or Wilcoxon rank-sum test with continuity correction, preceded by Shapiro-Wilk tests for sample normality (Hollander et al., 2013).

Table 1
Average number of birds detected per site per period (site abund 05, site abund 15) and respective differences in relative bird abundance (guilds and species) (Δabund) between periods (2005 and 2014–15) and *p*-value of the t-test; **bold** signs denote $P < 0.05$. For each guild and species, we provide model averaging (GLMM) coefficient estimates (β) for effects of vegetation height (veg. height), distance, plantation type (young oak; young pine; old eucalyptus - default level) and two-level interactions.

	site abund 05	site abund 15	Δabund	*P*-value	veg. height	distance	young oak	young pine	distance: veg. height	oak:veg. height	pine:veg. height
Bird guilds											
All species	**15.92**	**20.34**	**4.42**	**< 0.001**		1.48	2.17	2.29			
Woodland	**6.03**	**5.58**	**-0.45**	**0.017**	0.55	1.98	2.16	2.36			
Farmland	**9.84**	**14.76**	**4.92**	**< 0.001**	-0.55		0.58	0.53		0.45	0.11
Ground-nesting	**8.34**	**12.13**	**3.79**	**< 0.001**	-0.11		0.55	0.18			
Steppe	4.63	4.45	-0.18	0.301	0.15	0.24	0.16	0.08	-0.43		
Cereal related	**1.82**	**5.45**	**3.63**	**< 0.001**	0.35	0.06			0.17		
Fallow related	2.63	2.95	0.32	0.859	-0.04	0.25	0.20	-0.06	-0.29		
Ploughed related	**1.68**	**0.82**	**-0.87**	**0.002**	-0.10	-0.13	0.04	0.10	-0.08		
Threatened species	1.13	1.74	0.61	0.114		-0.13	-0.03	0.12			
Species											
Calandra lark	**2.16**	**2.29**	0.13	0.874	-0.09	0.20	0.15	-0.07	-0.23		
Carrion crow	**0.21**	**0.53**	0.32	0.433			-0.11	-0.11			
Common linnet	**0.37**	**0.37**	0	1		0.06					
Corn bunting	**1.53**	**3.68**	**2.16**	**< 0.001**	0.02	-0.07			0.19		
Eurasian hoopoe	0.08	0.29	0.21	**0.050**	-0.07	-0.05			0.06		
European goldfinch	**0.53**	**0.53**	0	0.899	0.05						
European stonechat	0.47	0.50	0.03	0.828	-0.07	-0.06			0.07		
Galerida larks (spp.)	1.32	1.95	0.63	**0.039**	-0.16		0.11	0.04			
Little bustard	0.47	0.66	0.18	0.660	0.03						
Red-legged partridge	**0.37**	**0.05**	**-0.32**	**0.012**	-0.02	0.01					
Short-toed lark	1.11	0.63	-0.47	0.053	-0.09	-0.16	0.07	0.10	-0.04		
Tawny pipit	**0.42**	**0.11**	**-0.32**	**0.005**	-0.04	-0.01	0.05	0.06	-0.04	-0.02	0.01
Zitting cisticola	**0.05**	**1.45**	**1.39**	**< 0.001**	0.23	-0.02			-0.06		

Then, we modelled how changes in guilds and species abundance between 2005 and 2014–2015 were associated with variables that differed significantly between these periods (i.e., vegetation height; see Table A3), across distances from different plantation edge types. Bird abundance differences were measured by subtracting bird counts at each distance in 2005 from those in 2014–2015 (i.e., dif. abundance = bird abund [2014,2015] – bird abund [2005]). Changes in vegetation height were estimated likewise, after being standardised (dif. height = veg height [2014,2015] – veg height [2005]). Generalised Linear Mixed Models (GLMMs) were used with a Gaussian distribution and identity link function (Bolker, 2015). To address the lack of independence among samples, transect (representing the site) was used as a random factor (Zuur et al., 2009; Santana et al., 2014).

Model selection was performed using a Multi-model Inference approach (Burnham & Anderson, 2002), generating a table of subset model combinations using standardised coefficients and ranking them based on weights derived from Akaike Information Criteria corrected for small samples (AICc). Model averaging was then conducted for models with delta AICc < 2, using partial standardized regression coefficients to estimate the relative importance of each coefficient on the final models (Cade, 2015).

All analyses were performed using R (ver. 4.2.0; R Core Team, 2022). GLMM models were developed using "glmer" function, from the lme4 package (Bates et al., 2015), and model selection and averaging were performed using "dredge" and "model.avg" functions from MuMIn package (Bartoń, 2023).

3. Results

3.1. Overall patterns

Overall bird abundance was significantly higher in the second period (Δabund, Table 1), primarily driven by an increase in farmland birds. Contrastingly, woodland birds decreased during this time (Table 1). Among farmland species, there were significant increases in ground-nesting birds (Δabund = 3.79, $p < 0.001$) and those associated with cereal fields (3.63; $p < 0.001$), while species

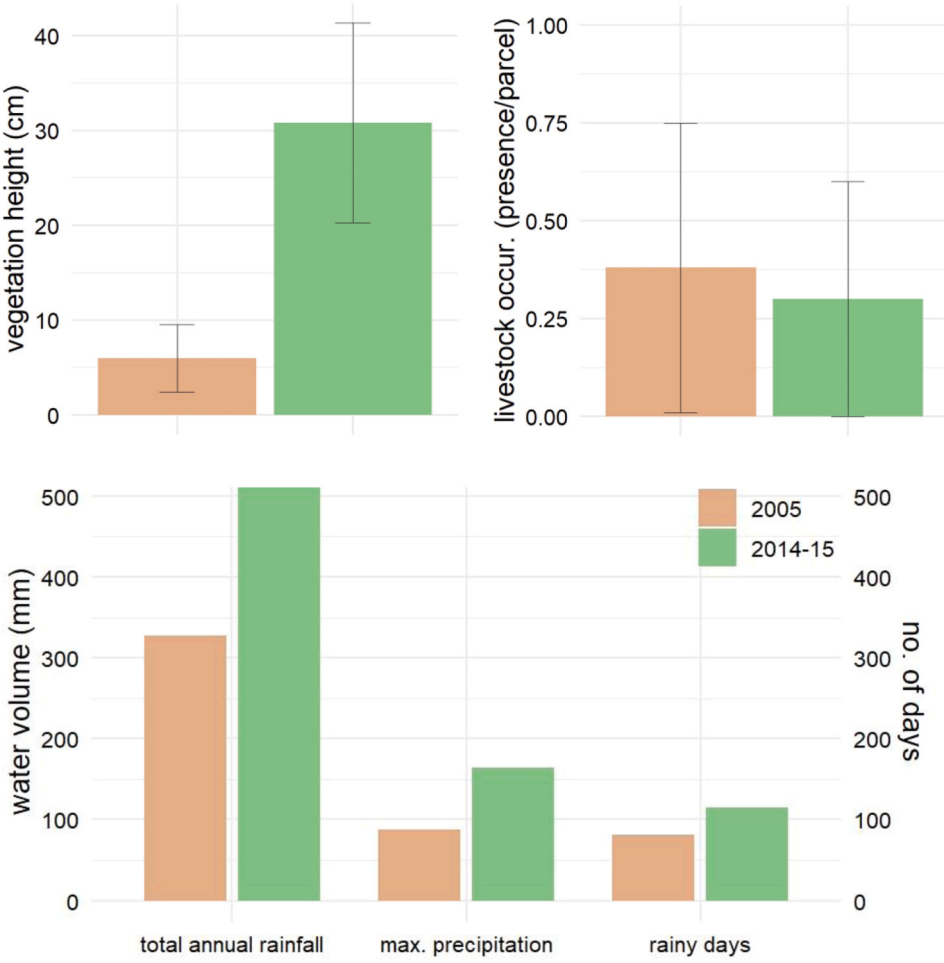

Fig. 2. Temporal changes in vegetation height, livestock occurrence and precipitation variables between periods. Full details and tests on landscape context and plantation attribute variables provided in Table A3.

associated with ploughed fields decreased. Abundance of steppe specialists, birds associated with fallow fields and threatened species remained relatively stable (Table 1).

The corn bunting, Eurasian hoopoe, *Galerida* larks and zitting cisticola were significantly more abundant in 2014–15, while the red-legged partridge and the tawny pipit were more abundant in 2005. Short-toed lark abundance decreased slightly, whereas other species remained relatively constant (Table 1).

Vegetation height was significantly higher in the second period (Fig. 2). This period (2014–15) was characterised by heightened annual rainfall, maximum precipitation, and number of rainy days. Livestock occurrence and all other variables regarding plantation attributes and landscape context remained stable between periods and were thus not included in further analyses (Fig. 2; Table A3).

3.2. Effects of vegetation height and distance from different plantation edges

As initially expected, vegetation height significantly influenced various guilds and species abundance (Table 1; Table A4). Increased vegetation height was positively related to woodland birds' abundance regardless of plantation type ($\beta_{heig} = 0.55$). However, the impact of grassland vegetation height on farmland bird abundance varied based on adjacent plantation types. Vegetation height negatively influenced farmland bird abundance near eucalyptus plantations but was associated with their abundance near oak and pine plantations ($\beta_{oak:heig} = 0.45$; $\beta_{pine:heig} = 0.11$). Ground-nesting birds slightly decreased with increasing vegetation height ($\beta_{heig} = -0.11$). Steppe birds' abundance showed a positive association with higher vegetation height near plantation edges, with this effect diminishing at greater distances ($\beta_{D:heig} = -0.43$).

Distance to the plantation edge played an important role in the overall assemblage's abundance, as well as that of woodland birds, depending on the adjacent plantation type (i.e., increased distances only had a positive effect in eucalyptus plantations) (Table 1; Table A4). It also interacted with vegetation height in several cases. For instance, species linked to fallow and ploughed fields not only decreased slightly with taller vegetation, but also exhibited a more pronounced decrease as distance to the plantation edge increased (respectively, $\beta_{D:heig} = -0.29$; $\beta_{D:heig} = -0.08$). Contrastingly, cereal crops-associated species marginally increased in abundance with greater distance to the plantation edge ($\beta_{D} = 0.06$), with larger increases where vegetation was significantly taller ($\beta_{D:heig} = 0.17$).

The abundance of farmland, ground-nesting and fallow-related species increased in certain plantation types regardless of distance, generally favouring oak plantations (respectively, $\beta_{oak} = 0.58$; $\beta_{oak} = 0.55$; and $\beta_{oak} = 0.20$). Indeed, farmland bird abundance increased with taller vegetation, primarily in grasslands adjacent to oak plantations ($\beta_{oak:heig} = 0.45$).

At the species level, vegetation height influenced the abundance of all but two (woodland) species (Table 1). Vegetation height was negatively related to red-legged partridge ($\beta_{heig} = -0.02$) and Galerida larks abundances ($\beta_{heig} = -0.16$), and positively so to goldfinch ($\beta_{heig} = 0.05$) and little bustard ($\beta_{heig} = 0.03$). For other species, the vegetation height effect was contingent on the distance to the plantation edge. The positive association of vegetation height with corn bunting abundance ($\beta_{heig} = 0.02$) increased with distance from the forest edge ($\beta_{D:heig} = 0.19$), while species like the calandra lark, experienced a negative relationship ($\beta_{heig} = -0.09$) exacerbated by distance ($\beta_{D:heig} = -0.23$). Vegetation height had an overall positive relationship with zitting cisticola ($\beta_{heig} = 0.23$), though that decreased with distance to the plantation edge ($\beta_{D:heig} = -0.06$). Contrastingly, the abundance of stonechat and hoopoe was negatively associated with increased vegetation height ($\beta_{heig} = -0.07$ in both cases), especially near wooded edges ($\beta_{D:heig} = 0.07$; 0.06) (Table 1). Linnet abundance increased solely with distance from the edge ($\beta_{D} = 0.06$). Regarding plantation type, oak plantations had a positive association with *Galerida*, calandra and short-toed larks, while eucalyptus plantations positively associated with carrion crow (β_{oak} & $\beta_{pine} = -0,11$).

4. Discussion

Our results demonstrate that forest edges may impact avian communities differently, depending on locally varying factors such as grassland vegetation height and its interactions with different adjacent plantations and proximity to edge in open-farmland Mediterranean landscapes. Specifically, farmland bird abundance was higher in the wet period (2014–15) and thrived with taller vegetation near oak and pine plantations. Cereal-field associated species benefitted from taller vegetation cover regardless of adjacent plantation type, but preferred greater distances from the forest edge. Conversely, ploughed-field associated species declined, negatively impacted by taller vegetation in 2014–15, particularly close to plantation edges. Thus, results suggest that local field management, such as a more sustainable livestock management, can positively impact open-farmland specialists, such as little bustard and calandra lark, especially during extremely dry years (e.g., 2005). Ultimately, birds' responses to afforestation depend on a complex interplay between the grassland matrix and adjacent plantation edges. Conservation efforts addressing Mediterranean farmland ecosystems should consider these local factors (e.g., vegetation height, grassland heterogeneity) to preserve open-farmland birds under increasingly dry conditions.

4.1. Winners and losers from vegetation height changes

Our findings suggest an association with vegetation height changes and avian assemblage responses near plantations. We observed a significant increase in grassland vegetation height between the two periods, coinciding with a rise in overall farmland bird abundance, particularly ground-nesting and cereal-associated species. Reduced rainfall during the first period (2005) likely affected water availability and, subsequently, the observed vegetation growth (Derner and Schuman, 2007; Cantarel et al., 2013). Livestock (sheep and cattle) occurrence in the parcels remained consistent between sampling periods, though changes to grazing regimes or agricultural practices in some of the grassland parcels could also explain the observed vegetation height differences (Reino et al., 2010b; Beja et al.,

2014; Ren et al., 2018). Our sampling design excluded sites subjected to major changes (corroborated by a lack in changes observed in landscape associated variables) and focused only on grassland parcels composed of fallow and pastures to minimise the influence of factors such as changes to agricultural practices in the grassland (Morgado et al., 2020) on bird responses to afforestation. Increased vegetation height positively affected the difference in abundance of woodland birds and cereal-associated species, regardless of the adjacent plantation. The latter group includes species like the corn bunting, benefiting from taller grassland vegetation, especially farther from the plantation edge. These species typically favour tall and dense vegetation (Moreira, 1999; Delgado and Moreira, 2000) and are often ground-nesting (e.g., the zitting cisticola), benefiting from increased nest-site cover (Batáry et al., 2007; Bellamy et al., 2018) and more readily available resources (Ponce et al., 2018). Contrastingly, we observed a negative relationship of vegetation height to the abundance of species associated with ploughed fields, such as the tawny pipit and short-toed lark, which prefer areas with shorter vegetation (Moreira et al., 2007; Santana et al., 2017). The trend towards less heterogeneity within the agricultural matrix brought by changes implemented after the CAP reform (Ribeiro et al., 2014) may thus lead to negative effects on bird diversity (Reino et al., 2010b; Santana et al., 2017; Lituma et al., 2022) as a mix of plant species and varying vegetation heights support more food sources and nesting sites for bird species than monoculture grasslands (Fisher and Davis, 2010; Jacobs et al., 2012; Hovick et al., 2015).

4.2. Influence of plantation type

Adjacent plantation type influenced the effects of grassland vegetation height on farmland bird abundance. Increased vegetation height had a positive association with farmland birds' abundance near young oak and pine plantations, but a negative one when adjacent to older eucalyptus plantations. Differences in adjacent plantations' characteristics associated with growth and maturity (Reino et al., 2010a, 2010b; Sánchez-Oliver et al., 2014b), and their associated nest-predator community (Beja et al., 2009; Faria et al., 2022), as well as variations in species abundance at the regional level (Reino et al., 2013), could also have affected bird responses to afforestation. For instance, increased avian predator abundance (i.e., carrion crows) near eucalyptus plantations (our data; Faria et al., 2022) may have influenced the observed differences in bird responses compared to younger oak and pine plantations.

Species abundance of all species or all ground-nesting birds analysed together had no relationship with vegetation height, likely due to both groups encompassing various species in terms of functional habitat preferences (Delgado and Moreira, 2000; Moreira et al., 2007; Santana et al., 2017). For instance, species like the tawny pipit or short-toed lark, known to breed and occur preferably in ploughed fields (Moreira, 1999; Delgado and Moreira, 2000; Moreira et al., 2007), were negatively affected by increased vegetation height, whereas the zitting cisticola or corn bunting (also ground-nesters), which favour high vegetation cover (Delgado and Moreira, 2000), were positively associated with it. Overall, ground-nesting species abundance was more influenced by the adjacent plantation type, with pine and especially oak plantations being favoured over eucalyptus plantations.

4.3. Influence of distance to plantation edge

Our findings align with previous studies showing mixed edge responses for farmland birds (Reino et al., 2009; Terraube et al., 2016; Phifer et al., 2017). For instance, the tawny pipit and short-toed lark, that typically avoid edges (Sliwinski and Koper, 2012; Besnard et al., 2016), are steppe specialists that favour expansive farmland areas over fragmented landscapes (Morgado et al., 2010; Keyel et al., 2013). Contrastingly, commonly widespread species known to benefit from increased plantation cover, such as the common linnet, (Reino et al., 2009, 2010a), strongly favoured edge proximity. Overall, steppe bird assemblage benefitted from increased vegetation height, though this was much more prevalent near the plantation edge and varied with plantation type. The likely reason is that higher predation rates in proximity to plantation edges (Kaasiku et al., 2022), particularly eucalyptus edges, increase the importance of adequate nest-site cover for nesting success (Homberger et al., 2017). It could also reflect an upsurge in invertebrate prey near plantation edges (Vasconcelos et al., 2018). Thus, steppe birds primarily benefited from grasslands adjacent to oak plantations, particularly in areas farther from the plantation edge. Oak plantations are generally less dense with shorter trees, creating softer edges (Reino et al., 2009), which are favoured by edge avoiders (Sliwinski and Koper, 2012; Besnard et al., 2016). Moreover, oak plantations likely have lower predator abundance (Faria et al., 2022), resulting in reduced ground-nesting predation pressure in these grasslands.

Lastly, there were no major changes in the number of threatened birds, which can be attributed to the overall landscape structure stability, including plantation edge density, habitat fragmentation and land-use cover. Both sampling campaigns occurred after the implementation of the CAP reform in 2003, associated with significant land-use changes in this area (Ribeiro et al., 2014). Furthermore, the sampling process deliberately excluded parcels undergoing significant land-use shifts during the latter period. As such, threatened bird abundance was mainly influenced by distance to the plantation edge, and varied significantly between different plantation types. This emphasises the potential impacts of grassland habitats' fragmentation (Reino et al., 2009; Morgado et al., 2010; Pretelli et al., 2018; Jacoboski et al., 2019), especially in relation to forest plantation edges (Sánchez-Oliver et al., 2014a; Faria et al., 2022).

4.4. Conservation implications

Our findings highlight a complex interplay between vegetation height, plantation type and edge avoidance, impacting bird responses to afforestation. This underpins the need for a multifaceted conservation approach to support the diverse avian species inhabiting Mediterranean farmlands under on-going climate and land-use changes. Notably, grassland vegetation height significantly influenced avian assemblage dynamics, affecting various bird guilds and species differently, highlighting the importance of grassland

heterogeneity in preserving diversity and stability in bird communities (Hovick et al., 2015; Traba and Morales, 2019). Grazing regimes, intensity (Batáry et al., 2007; Reino et al., 2010b, Ramos et a, 2021), and annual climatic conditions (Conrey et al., 2016; Zuckerberg et al., 2018) should also be considered by conservation efforts which aim to support a wide range of farmland species, as they directly affect grassland biodiversity and can influence grassland structure. Maintaining a balance in vegetation height diversity can benefit ground-nesting species seeking increased nest-site cover (Erdös et al., 2009), and cereal-associated species that thrive in taller vegetation (Delgado and Moreira, 2000; Batáry et al., 2007), while also preserving open-farmland specialists preferring shorter vegetation (Delgado and Moreira, 2000). Our study also emphasises the importance of the type of forest plantations adjacent to grasslands, with oak and pine plantations having a less detrimental impact on bird abundance and diversity compared to eucalyptus. Prioritising the former is likely to better accommodate open-farmland specialists. Lastly, we emphasise the importance of grassland habitat fragmentation, associated with forest plantation edges, in shaping bird responses. Strategies to reduce predation pressures near edges (Reino et al., 2010a; Faria et al., 2022), preserve large grassland patches (Morgado et al., 2010; Reino et al., 2013) and enhance landscape connectivity (Sánchez et al., 2014a), can help mitigate edge effects. Preserving grassland diversity with varying vegetation heights and minimising the use of new eucalyptus in afforestation are valuable bird conservation measures for Mediterranean farmland landscapes.

CRediT authorship contribution statement

Schindler Stefan: Investigation, Writing – review & editing. **Faria João:** Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. **Santana Joana:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Brotons Lluís:** Investigation, Writing – review & editing. **Dullinger Stefan:** Investigation, Writing – review & editing. **Rotenberry John T.:** Investigation, Writing – review & editing. **Morgado Rui:** Investigation, Writing – review & editing. **Moreira Francisco:** Investigation, Writing – review & editing. **Catry Inês:** Investigation, Writing – review & editing. **Gonçalves David:** Supervision, Writing – review & editing. **Sánchez-Oliver Juan:** Investigation, Methodology. **Reino Luís:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Beja Pedro:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02818.

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