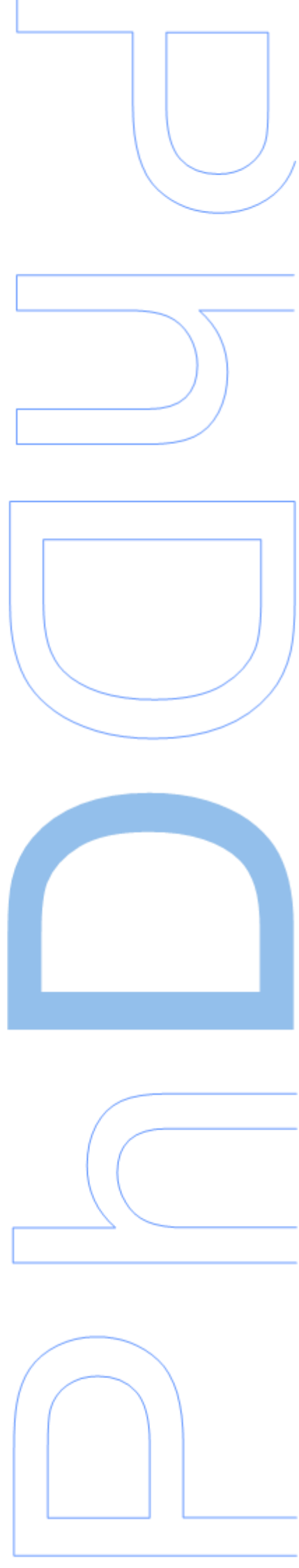


On the history of mixing: Knowledge trends on relevance, patterns and drivers of adaptive introgression

Pedro Miguel Sobreiro Horta

Tese de Doutoramento apresentada à
Faculdade de Ciências da Universidade do Porto, CIBIO-InBIO,
Biologia
2021





On the history of mixing: Knowledge trends on relevance, patterns and drivers of adaptive introgression

Pedro Miguel Sobreiro Horta

Biodiversidade, Genética e Evolução
Departamento de Biologia
2021

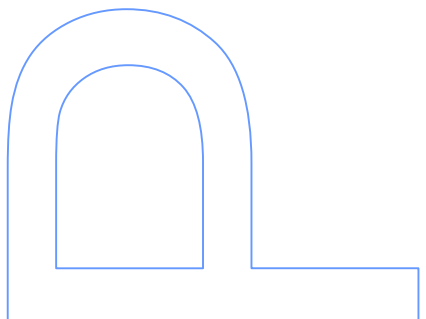
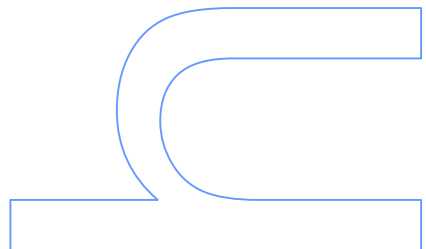
Orientador

Hugo Emanuel Vitorino Rebelo, Investigador Auxiliar, CIBIO-InBIO,
Faculdade de Ciências da Universidade do Porto

Coorientadores

Orly Razgour, Senior lecturer in Ecology, NERC Independent Research Fellow
University of Exeter

Francisco Javier Juste Ballesta, Assistant Professor, Bat Research group
Dpt. Evolutionary Ecology, Estación Biológica de Doñana, CSIC



“The proof of evolution lies in those adaptations that arise from improbable foundations.”

Stephen Jay Gould (1941–2002)

Nota Prévia

De acordo com o número 2 do Artigo 4º do Regulamento Geral dos Terceiros Ciclos de Estudos da Universidade do Porto e do Artigo 31º do D.L. 74/2006, de 24 de Março, com a nova redação introduzida pelo D.L. 230/2009, de 14 de Setembro, esta tese foi elaborada em formato de artigos científicos resultantes de um conjunto de trabalhos de investigação parcialmente submetidos para publicação em revistas internacionais indexadas e com arbitragem científica, os quais integram alguns dos seus capítulos. É importante clarificar que os referidos trabalhos foram efetuados em colaboração com outros investigadores, oportunamente identificados como coautores. O candidato desenvolveu de uma força ativa o trabalho científico em todas as fases de desenvolvimento de todos os capítulos, desde a sua conceção, obtenção de dados, análise e discussão de resultados, bem como na elaboração da sua forma final de publicação, sendo simultaneamente o seu primeiro autor e autor correspondente.

Capítulo 2 – **Horta P.**, Raposeira H., Vaz A.S., António J., Juste J., Razgour O. & Rebelo H. (submitted). What about Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception. Research Square (preprint). DOI: 10.21203/rs.3.rs-1041127/v1

Capítulo 3 – **Horta P.**, Raposeira H., Juste J., Razgour O., & Rebelo H. (final stages of submission). From Genomes to Ecology: Meta-analysis of Knowledge Trends about Introgression Mechanisms.

Capítulo 4 – **Horta P.**, Raposeira H., Juste J., Razgour O., & Rebelo H. (final stages of submission). The Other Side of the Coin: How Phylogeny Affects Species Receptivity for Introgression.

Capítulo 5 – **Horta P.**, Raposeira H., Baños A., Ibáñez C., Razgour O., Rebelo H. & Juste J. (submitted). Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats. Scientific reports. DOI: <https://doi.org/10.1038/s41598-022-15412-2>

Este trabalho foi apoiado pela Fundação para a Ciência e Tecnologia (FCT) através da atribuição de bolsa de doutoramento (SFRH/BD/117979/2016) e de um projeto de investigação (PTDC/BIA-ECO/31731/2017) tendo sido financiado por fundos nacionais do Ministério da Educação e Ciência e pelo Fundo Social Europeu através do Programa Operacional Potencial Humano (POPH) – Programa Operacional Regional Norte – Portugal 2020.



Este trabalho foi desenvolvido em:



This thesis should be cited as:

Horta, P. (2021). On the history of mixing: Knowledge trends on relevance, patterns and drivers of adaptive introgression. Ph.D. Thesis, Faculdade de Ciências da Universidade do Porto, Portugal

Agradecimentos / Acknowledgements

What is the value of knowledge? Intrinsic and structural? I tend to believe that it will be closer to the value it can bring to the world than just the satisfaction of knowing. Even because it will support in itself a great layer of subjectivity subjugated to conjunctures. Thus, if a certain knowledge can, in some way, contribute as an added value at some time and space, it will have surpassed the effort to obtain it. I take refuge in this argument to justify the pertinence of having invested all of this time in completing this work and derive some personal satisfaction from there. Absolute altruism will surely be restricted to a rare and superlative set of human beings in which I am certainly not included. On the other hand, the result of the equation between satisfaction and effort in a scientific process as long as a PhD is not fair, since the former has a positive sign fundamentally for myself, the second has a negative sign that I shared with many people who will not necessarily benefit. It was a collective effort for my personal fulfilment that can only be justified, by the altruism, professionalism (or love), that yes, for all these people. Therefore, this section, more than acknowledgements, which it will also be, is an attempt, certainly insufficient, to give them a little justice and to repay them with the exaltation of the fundamental role they played in the realization of this little piece of science.

I will start with the most important, because I should not let it stay until the end:

Helena is my wife, my traveling companion, the tender mother of our little one... who supports me, advises me, who suffers for me, who dreams with me, who walks by my side... I have not to say that this work is your work.

Benjamim was born at some point on this path. When I write these words he has only months of existence. Your light illuminates the trail for us and it is for you that we walk.

A long time ago my father asked me what I would be professionally. Not knowing the answer, I just told him I needed time to see it. I had it, he didn't. But today, at the end of this stage of my life, I believe I can finally answer him: I will be a scientist, in any case.

For so many moments my family had to do without my presence in favour of something they will eventually have, some difficulty in understanding the scope or relevance. And yet, they supported me... Thank you all. I'm sure I won't be able to compensate you all. It's yours too. I would particularly like to thank Mr. Luis, Helena's father, for having helped us so many times in the field (Montesinho, S. Mamede, Lousã, Estrela, Troia, etc.). For the patience and the effort. Thank you very much.

Hugo must remember when we knocked on his door, wanting to return to science with a vague idea that I wanted to do a PhD. I can thank him for so many practical things about this work. In fact, everything went through him. But I wanted to take this opportunity to thank you, Hugo, for having rescued me for science. Always with a positive, proactive and sharing attitude, you put me on the path of my future. Thanks for that and for the rest.

Orly was beginning her brilliant career when I came to her, with limited ability, but with the dream of being able to do something important. She has agreed since the first hour to be my co-supervisor and did not let go of my hand during the hardest times. So, many years and projects later, I hope she feels that the insistence was worth it. Her support was crucial.

At a certain point in the process, when I decided to change the course of my thesis, with Hugo's unconditional support, it became clear that I needed Javier's co-supervision. Yes, it couldn't be anyone else but Javier. Would he be willing to get on a boat in progress? He accepted me with a huge heart and always supported me scientifically and morally. An example and a friend. Thank you Javier.

For helping me on data analysis and/or for scientific discussions, I want to thank João António, Miguel Carneiro, José Melo-Ferreira and Ana Sofia Vaz. For genomics and laboratory issues thank you Sandra Afonso. For dealing with material acquisitions, thank you Sara João. For the partnership during fieldwork in Spain, thank you Jesús Noguerras. For the samples from Italy, thanks to Adriano Martinoli and Martina Spada. I would also like to thank Prof. Paulo Célio for the stays at CIBIO's facilities whenever it was necessary.

To all my friends who make life seem easier whenever it seems complicated.

Finally, I'll finish as I started. It took me some years to present an acceptable work to make me glad. Along this process we have undergone Homeric adventures, from terrible wildfires that destroyed part of our study areas (and almost took our lives), to a worldwide pandemic that hardened the development of the work and severely conditioned the born of our son and, obviously the recent arrival of Benjamim. I feel this thesis as part of you Helena, so I decided to dedicate it to him. Because in him we encompass everything: the dreams of our past and the future that is awaiting for us.

May this thesis be another small beginning...

To my son Benjamim

Abstract

Since ancient times, humans are actively confronted with genetic admixture. Despite being a natural phenomenon, observable and even experienced, it was considered dysfunctional or even relegated to categories close to perversion. Paradoxically, it was historically used for the benefits of human communities, for example, in processes such as domestication.

When evolutionists began to explore this topic, they would be also imbued with these paradoxes, seeking to justify a certain irrelevance they attributed to this phenomenon. Others went further, considering it as an imperfection of nature or even a threat for species integrity. This "purist" view of life overflowed the borders of science and was abusively used to justify discriminatory thoughts, such as biological racism, culminating in tenebrous forms of forced sterilizations, segregation and murders. On the other hand, these thoughts conditioned for long the development of scientific knowledge about the role of genetic admixture for adaptation and evolution.

At the beginning of 20th century some scientists recognized in counter-current, that phenomena such as hybridization may benefit some lineages through the sharing and incorporation of genetic material associated with well-adapted traits to new or changing environmental conditions. Called as adaptive introgression this was a target-process of controversy due to difficulties in demonstrating it unequivocally and for interfering with rooted convictions and prejudices. Almost a century later, methodological developments in genomics allowed the successive accumulation of evidence. This thesis seeks to explore how this increase in scientific evidence has shaped the trends in current knowledge about the relevance, patterns of functioning and causes of introgression, as well as to bring new perspectives on how it strikes a balance with evolutionary forces from divergence.

Introgression was deeply discussed from several perspectives. First of all, this work carried out an analysis of the current opinion of the scientific community on the importance, prevalence and consequences of introgression. From the psychobiological point of view it was addressed subjects such as, what is the capacity of scientific production to influence people's opinion, how long and under what amount of publications, as well as whether prejudices remain conditioning the opinion of scientists and people in their assessment of genetic admixture. From an operational point of view, I organized, merged and analyzed from a global viewpoint the main mechanisms and constraints on introgression operation along the tree of life. From an evolutionary perspective, it was analyzed the impact of stored divergence, reflected in phylogenetic distances, on its occurrence and potential prevalence in different taxonomic groups, discussing what structural characteristics of the organisms worked as limiting factors. Finally, from a functional point of view, it was considered through an empirical study on cryptic bats', how introgressive hybridization may establish a balance

with potential competition and how this balance can shape the relationship between closely-related species and their ecological resources.

The results obtained showed that the genomic revolution is behind most of the current evidence on introgression, helping to promote it as one of the most important topics in current science in the context of global scientific literature. This thesis highlighted the capacity and relevance of scientific publications to change public opinions, placing them on a less emotional and more factual basis, despite prejudices still remaining in the public perception about genetic miscegenation in relation to taxonomic bias. In operational terms, results from this thesis provided evidence on introgression as an evolutionary process acting in parallel with divergence, evolving and establishing in balance with it through interconnected mechanisms, whose drivers increase its complexity across the biological organization. As organisms gradually increase their genomic, physiological and behavioural complexity, divergence processes impose more constraints on introgression occurrence. Thus, simpler organisms present greater phylogenetic amplitude in the occurrence of introgression due to both smaller genomes and randomness in choosing mating partners. Alternative mechanisms to divergence allow the occurrence of introgression, impacting different axes of ecological niches, and allowing stable co-existence of closely-related species. Finally, I argue that introgression transfers to each species/lineage/breed an instrumental value, which can go far beyond its intrinsic importance. Each one can act as a genetic resource for evolutionary rescue at some point in the evolutionary process. This value is crucial and should be preserved, being particularly important under strong environmental changes, such as the current ones, resulting from anthropogenic climate change.

Keywords: Biological organization, cryptic bats species, divergence, genomic revolution, hybridization, instrumental value, introgression, knowledge trends, meta-analyses, perception, phylogeny, prejudices, structural complexity and systematic review

Resumo

Desde tempos remotos que os seres humanos são ativamente confrontados com a mistura genética. Apesar de ser um fenómeno natural, observável e até vivenciado, foi desde cedo considerado disfuncional ou mesmo relegado a categorias próximas da depravação. Paradoxalmente, a mistura genética foi historicamente utilizada para o benefício de comunidades humanas, por exemplo, em processos de domesticação.

Quando os evolucionistas começaram a explorar este tema, também eles estariam imbuídos destes paradoxos, procurando justificar uma certa irrelevância que atribuíam a este fenómeno. Outros foram ainda mais longe, considerando-o uma imperfeição da natureza ou mesmo uma ameaça à integridade das espécies. Essa visão "purista" da vida extrapolou as fronteiras da ciência e foi abusivamente utilizada para justificar pensamentos discriminatórios, como o racismo biológico, culminando em formas tenebrosas de esterilizações forçadas, segregação e assassinatos. Por outro lado, este pensamento condicionou por muito tempo o desenvolvimento do conhecimento científico sobre o papel da mistura genética para a adaptação e evolução.

No início do século 20, alguns cientistas reconheceram em contracorrente que fenómenos como a hibridização podem beneficiar algumas linhagens através da partilha e incorporação de material genético associado a características bem adaptadas a novas condições ambientais ou em mudança. Designado por introgressão adaptativa, este foi um processo alvo de polémica devido às dificuldades em demonstrá-lo de forma inequívoca e por interferir com convicções e preconceitos enraizados. Quase um século depois, os desenvolvimentos metodológicos na área da genómica permitiram acumular sucessivamente evidências sobre a introgressão. Esta tese procura explorar como esse aumento de evidências científicas moldou as tendências do conhecimento atual sobre a relevância, padrões de funcionamento e causas da introgressão, bem como trazer novas perspetivas sobre como esta estabelece um equilíbrio com as forças evolutivas da divergência.

A introgressão foi profundamente discutida sob várias perspetivas. Em primeiro lugar, este trabalho realizou uma análise à opinião atual da comunidade científica sobre a relevância, prevalência e consequências da introgressão. Do ponto de vista psicossociológico foram abordados temas como: qual a capacidade da produção científica de influenciar a opinião das pessoas, por quanto tempo e a partir de que quantidade de publicações, bem como se os preconceitos permanecem como condicionantes da opinião dos cientistas e das pessoas, na sua visão sobre a miscigenação genética. Do ponto de vista operacional, organizei, fundi e analisei, numa perspetiva global, os principais mecanismos e estrangimentos ao funcionamento da introgressão ao longo da árvore da vida. Do ponto de vista evolutivo, foi analisado o impacto da divergência acumulada, refletida nas distâncias filogenéticas, na ocorrência e na prevalência

potencial de introgressão em diferentes grupos taxonómicos, discutindo-se quais as características estruturais dos organismos que funcionam como fatores limitantes. Finalmente, do ponto de vista funcional, foi considerado através de estudos empíricos em modelos naturais de morcegos crípticos, como a hibridização introgressiva pode estabelecer um equilíbrio com a competição, e como esse equilíbrio pode moldar a relação das espécies com os seus recursos ecológicos.

Os resultados obtidos mostraram que a revolução genómica está por trás da maioria das evidências atuais de introgressão, ajudando a promovê-la como um dos tópicos mais importantes da ciência atual, no contexto da literatura científica global. Esta tese destacou a capacidade e relevância das publicações científicas para mudar a opinião pública, colocando-a numa base menos emocional e mais factual, embora o preconceito ainda permaneça na percepção pública sobre a miscigenação genética em função do preconceito taxonómico. Em termos operacionais, os resultados desta tese forneceram evidências da introgressão como sendo um processo evolutivo que atua em paralelo com a divergência, evoluindo e se estabelecendo em equilíbrio com ela por meio de mecanismos interligados, cujos drivers aumentam sua complexidade através da organização biológica. À medida que os organismos aumentam gradualmente sua complexidade genómica, fisiológica e comportamental, os processos de divergência impõem mais restrições à ocorrência de introgressão. Assim, organismos mais simples apresentam maior amplitude filogenética na ocorrência de introgressão devido à menor dimensão do genoma e à aleatoriedade na escolha dos parceiros sexuais. Mecanismos alternativos à divergência permitem a ocorrência de introgressão na sua presença, impactando de forma diferenciada os eixos dos nichos ecológicos, e permitindo a coexistência estável de espécies intimamente relacionadas. Finalmente, argumento que a introgressão adaptativa transfere para cada espécie/linhagem/raça um valor instrumental que pode ir muito além de sua importância intrínseca. Este valor é crucial e deve ser preservado, sendo particularmente importante sob fortes mudanças ambientais, como as atuais, decorrentes das alterações climáticas antropogénicas.

Palavras-chave: Complexidade estrutural, divergência, espécies crípticas, filogenia, hibridização, introgressão, meta-análises, organização biológica, padrões de conhecimento, percepção, preconceitos, revisão sistemática, revolução genómica, valor instrumental

Table of Contents

Chapter 1 – General Introduction.....	1
1.1 The importance of knowledge about Natural Gene Transfer.....	2
1.2 Introgressive hybridization process.....	3
1.3 Consequences of introgression	5
1.3.1 Evolutionary biology	5
1.3.2 Conservation biology.....	6
1.3.3 Socio-biology	8
1.4 Knowledge gaps on prevalence, functioning and outcomes of introgression.....	9
1.5 Propose of this research.....	10
1.5.1 Systematic review	11
1.5.2 Bibliometric analyses	12
1.5.3 Meta-analyses.....	12
1.5.4 Empirical studies.....	12
1.5.5 Objectives	13
1.6 Thesis outline.	14
 Chapter 2 – What about introgression? The genomic revolution is shaping scientific and public perception	 17
Abstract.....	18
2.1 Introduction.....	19
2.2 Methods.....	21
2.2.1 Approach	21
2.2.2 Systematic review	22
2.2.3 Bibliometric analysis.....	23
2.2.4 Salience analysis	23
2.2.5 Sentiment analysis	24
2.3 Results	26
2.3.1 The scope and evolution of knowledge about introgression	26
2.3.2 Perception of scientists	29

2.3.3 Public perception and sentiment	32
2.4 Discussion	36
2.4.1 The scope and evolution of knowledge about introgression	36
2.4.2 What do we think about introgression?.....	36
2.4.3 Public sentiment in response to evidence of introgression	38
2.4.4 Caveats and limitations	39
2.5 Conclusions	40
Acknowledgments	41
Supplementary Material	42
 Chapter 3 – From genomes to ecology: Meta-analysis of knowledge trends about introgression mechanisms.....	 60
Abstract.....	61
3.1 Introduction.....	62
3.2 Methods.....	66
3.2.1 Literature search	66
3.2.2 Literature review	66
3.2.3 Meta-Analysis	67
3.3 Results	68
3.3.1 Structural characteristics of organisms and introgression.....	68
3.3.2 Trends in the literature on the mechanisms of introgression.....	72
3.3.3 Environmental impacts on spatio-temporal introgression	77
3.4 Discussion	78
3.4.1 Structural characteristics of organisms that impact the function of introgression	78
3.4.2 The balance between introgression and divergence.....	80
3.4.3 Environmental impacts on spatio-temporal patterns of introgression.....	84
3.4.4 Knowledge gaps and future challenges.....	85
3.4.5 Conclusions	86
Acknowledgments	87
Supplementary Material	88
 Chapter 4 – The other side of the coin: How phylogeny affects species receptivity for introgression.....	 96
Abstract.....	97

4.1 Introduction.....	98
4.2 Methods.....	100
4.2.1 Literature search.....	100
4.2.2 Literature review	100
4.2.3 Data analysis	101
4.3 Results	102
4.3.1 Global introgression network.....	102
4.3.2 Influence of phylogenetic dissimilarity on introgression	107
4.4 Discussion	111
4.4.1 The direction of introgression	111
4.4.2 Connections between introgressed closely-related species.....	112
4.4.3 Influence of phylogenetic dissimilarity on introgression	113
4.4.4 Conclusions	115
4.5 Future challenges	111
Acknowledgments	116
Supplementary Material	117

Chapter 5 – Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats..... 126

Abstract.....	127
5.1 Introduction.....	128
5.2 Methods.....	131
5.2.1 Study area	131
5.2.2 Sampling design	131
5.2.3 Statistical analyses.....	132
5.3 Results	135
5.3.1 Testing for morphological differences between cryptic <i>Eptesicus</i> species.....	135
5.3.2 Species discrimination through classification statistics	141
5.4 Discussion	144
5.5 Conclusions	148
Acknowledgments	148
Supplementary Material	149

Chapter 6 – General Discussion 164

6.1 The relevance of knowledge about introgression	165
--	-----

6.2 Main current trends on the knowledge about introgression	165
6.3 Merging the knowledge about introgression functionality	166
6.4 Introgression during the process of divergence.....	167
6.5 The importance of evolutionary history for introgression occurrence.....	168
6.6 Evolutionary outcomes of introgression	169
6.7 Final remarks.....	170
Bibliography	175
Appendix A – Paper Proofs	208
What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception (<i>Scientific Reports</i>)	209
Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian <i>Eptesicus</i> bats (<i>Communications Biology</i>).....	276
Appendix B – Other papers arising from the PhD research.....	335
Hidden in our pockets: building of a DNA barcode library unveils the first record of <i>Myotis alcathoe</i> for Portugal	337
The InBIO Barcoding Initiative Database Portuguese Bats (Chiroptera)	339
Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators	341
MAMMALS IN PORTUGAL: a data set of terrestrial, volant and marine mammal occurrences in Portugal.....	343
Bat calls of Britain and Europe: A Guide to Species Identification – Serotine <i>Eptesicus serotinus</i> (Schreber, 1774).....	347
Bat calls of Britain and Europe: A Guide to Species Identification – Meridional serotine <i>Eptesicus isabellinus</i> (Temminck, 1840)	349
Appendix C – Papers retrieved from the systematic review	351

List of Tables

Table 5.1 - Descriptive statistics of the morphometric traits of <i>Eptesicus serotinus</i> , <i>E. isabellinus</i> and their hybrids	135
--	-----

Table 5.2 - Correct species classification rates, species overlap and hybrids contribution to species overlap obtained by two different methods of classification statistics (DFA and SVM) based on morphometric and colour traits of <i>E. isabellinus</i> and <i>E. serotinus</i> in sympatry.....	143
---	-----

Tables in Supplementary Materials

Table S2.1 - Full list of information and the total number of papers that includes each category extracted from each reviewed paper	46
--	----

Table S2.2 - Total number of papers produced by teams from specific geographic regions on case studies located in other geographical locations. 26 papers analysed more than one case study and three papers did not include a case study, resulting in a total of 388 case studies.	49
--	----

Table S3.1 - Full list of information and the total number of papers that includes each category extracted from each reviewed paper	90
--	----

Table S4.1 - Full list of information and the total number of papers that includes each category extracted from each reviewed paper	118
--	-----

Table S4.2 - Statistical results of multiple comparisons of mean based non-parametric Kruskal-Wallis test, performed to identify which taxa groups present significant differences in phylogenetic distances among species showing evidence of introgression (yellow background) with reference to Mean Difference (MD); and pairwise chi-square comparisons under IQR analyses (interquartile range analyses) comparing phylogenetic extent of introgression between taxonomic groups (grey background). Green cells represent significant differences at $P < 0.05$	124
---	-----

Table S5.1 - Statistical values of multiple comparisons of original morphometric variables according to the post-hoc Fisher's LSD test. Green cells represent significant differences ($P < 0.05$).	153
---	-----

Table S5.2 - Statistical values of multiple comparisons of dorsal and ventral original colour variables (L^* , a^* and b^*). Green cells represent significant differences ($P < 0.05$)	155
--	-----

Table S5.3 - Principal components extracted from the PCA analysis, with the respective eigenvalues, % variance explained, Cronbach's α and weight of each variable	156
--	-----

Table S5.4 - Statistical values of multiple comparisons of means orders of morphometric PCA variables. Green cells represent significant differences ($P < 0.05$)	157
Table S5.5 - Statistical values of multiple comparisons of means orders of dorsal and ventral PCA colour variables. Green cells represent significant differences ($P < 0.05$).....	157
Table C1 - Papers retrieved from the systematic review	352

List of Figures

- Figure 2.1** - Spatial networks of case studies featured in the meta-analysis (blue dots) performed by each research team with a specific host geographic location (red dots) (a). Case study locations were georeferenced based on the description of the study area provided within each paper. Circle sizes reflect the number of papers from a specific location. Arrows represent directional pathways from the team to the case study with line width representing the number of papers published by each team on the specific case study. Temporal changes in the number of published papers on introgression by methodology (b) and scientific field (c). The solid lines represent the correlation between the number of papers and time and the dashed line shows the tipping point, when the trend line started to show an exponential increase – representing the beginning of the genomic revolution in introgression studies 28
- Figure 2.2** - Multidimensional Scaling (MDS) tripartite network used to quantify the extent of connections between each scientific area, the polarity of authors' perceptions of introgression and their positive, negative and neutral biological arguments (a). Violin plots representing Altmetric Attention Score (ASS) compared to A) all research outputs scored by Altmetric.com, B) all papers of the same journal, C) all papers of the same age and D) all papers of the same age and journal (b). Standardized ranking position is represented between 0 (first position) to 100 (last position). Within them white solid lines boxplots include medians (horizontal white line) and average (white dot), boxes indicate quartiles and ranges, simultaneously 31
- Figure 2.3** - Three-dimensional plot showing temporal changes (2000 to 2019) of the estimated exposure–lag–response association between the number of papers providing evidence for introgression and the standardized polarity perception by the public ($_{st}PP$), with the average as reference and each Lag period corresponding to 4 years (a). Overall cumulative exposure–response relationships between the temporal changes (2000 to 2019) of the number of papers providing evidence for introgression and standardized polarity perception by the public ($_{st}PP$), predicted from the model with no interaction (interpreted as the average), with 95% CI (b). Lag–response relationships between the number of papers providing evidence for introgression and $_{st}PP$, with 95% CI and each Lag period corresponding to 4 years (c). 33
- Figure 2.4** - Standardized Polarity Perception ($_{st}PP$) correlation with taxonomic groups under study (a). Grey and pink bars represent public and authors' perception, respectively. Solid lines depict the relationship between their $_{st}PP$ and the different taxonomic groups under study based on the phylogenetic distance from modern Humans. Hierarchical network chord diagram with expanded

endpoints illustrating public total polarity perception and expressed emotions about introgression papers from different taxonomic groups under study (b). 35

Figure 3.1 - Bipartite network of introgression's functionality variables and taxonomic groups. (a) Representation of introgression operation across a taxonomic complexity gradient and throughout different levels of biological organization. (b) Cladogram with the potential evolutionary cleavage moments of introgression functionality. A – Prokaryotes; B – Unicellular eukaryotes, C – Multicellular eukaryotes with sex-chromosomes and D – Multicellular eukaryotes with sex-chromosomes and sexual selection. Genomics/cytology's layer (Autosomal introgression [Introq_Auto], Autosomal islands of speciation [Isl_Speciation_Auto], Nuclear introgression [Introq_NUCLEAR], Introgression on Sex-chromosomes [Introq_SEX], Cytoplasmic introgression [Introq_CYTO], Nuclear islands of speciation [Isl_Speciation_NUCLEAR], Islands of Speciation on Sex-chromosomes [Isl_Speciation_SEX], Cytoplasmic islands of speciation [Isl_Speciation_CYTO] and presence of balancing selection [Balancing_selection]); Physiology's layer (endogenous impacts on introgression [Endogenous_impacts], Haldanes's rule compliance [Haldane's_rule], female sterility [Female_sterility], male sterility [Male_sterility], exception to Haldanes's rule [No_Haldane's_rule], any sterility [No_sterility], sex-bias introgression [Sex-bias_introgression], paternal direction of introgression [Paternal_way] and maternal direction of introgression [Maternal_way]); Demography's layer (demographic disparities [Demography], any demographic disparities [No_Demography], direction of introgression from native-to-colonizers [Native-to-colonizer] and exception to native-to-colonizers direction [Native-to-colonizer]); Behaviour's layer (presence of sexual selection [sexual_selection], presence of assortative mating [Assortative_mating], presence of intra-sexual interspecific competition [Sex_competition] and absent of intra-sexual interspecific competition [No_competition]; and Ecology's layer (environmental-mediated introgression [Environment_mediated], iteration between allopatric and sympatric periods [Temporal_cycling], exogenous impacts on introgression [Exogenous_impacts], Allele surfing [allele_surfing], Any allele surfing [No_allele_surfing]. 69

Figure 3.2 - Multilayer network of introgression's functionality variables at different levels of biological organization. (a) Multilayer graphs of networks. (b) Heatmap of pairwise standardized edges' weight ($_{st}EW$) among introgressions operating variables and taxonomic groups. Acronyms of variables are available in the legend of Figure 3.1 74

Figure 4.1 - Plant bipartite introgression network between species acting as donors and receptors.104

Figure 4.2 - Animal bipartite introgression network between species acting as donors and receptors106

Figure 4.3 - Bayesian phylogenetic analyses of animal and plant species reported as promoters of introgression. Radial phylogenetic trees of animal species using the COI gene as genetic marker and plant species using ITS2 as genetic marker broken down by their introgression characteristics (a – donor taxa, receptor taxa or both; b – bidirectional, unidirectional or both; c) symmetric, asymmetric or both and d) number of connection). 109

Figure 5.1 - Wing and dentition morphometric measurements taken from *Eptesicus* bat species during field work. 131

Figure 5.2 - Colour differences between bat groups. (A) Photographic representation of hair colour of representative specimens of both parental species groups (*Eptesicus isabellinus* and *E. serotinus*) as a function of their geographical relationships. (B) Descriptive statistics of dorsal and ventral colour of *E. serotinus*, *E. isabellinus* and their hybrids. Background colour represents the mean colour of the dorsum and belly in the CIELAB colour space of each parental species and in function to their different geographical relationships and their hybrids. (C) Percentage of reflectance measured by colorimeter across the visible wavelength scale. Acronyms are available in Table 5.1..136

Figure 5.3 - Positioning of each individual in the two-dimensional space defined by the main PCA components retained and their position relative to the original morphometric variables (A). The violin plots represent *Eptesicus isabellinus* (allopatric and sympatric), *E. serotinus* (allopatric and sympatric) and Hybrids PCA scores compared to size (PC1) and shape (PC2) (B). Within violin plots white solid lines boxplots include medians (horizontal white line) and averages (white dot); boxes and vertical white lines indicate quartiles and ranges (excluding outliers), respectively. Acronyms are available in Table 5.1... 138

Figure 5.4 - Positioning of each individual in the two-dimensional space defined by the PCA main components retained and their position relative to the original dorsal colour variables (A). The violin plots represent *E. isabellinus* (allopatric and sympatric), *E. serotinus* (allopatric and sympatric) and Hybrids PCA scores compared to dorsal a^*b^* Grey-Brown (PC1 Colour) and dorsal L^* lightness (PC2 Colour) (B). Within violin plots white solid lines boxplots include medians (horizontal white line) and averages (white dot); boxes and vertical white lines indicate quartiles and ranges (excluding outliers), respectively. Acronyms are available in Table 5.1.... 140

Figures in Supplementary Materials

WebFigure 1 - PRISMA 2020 flow diagram. Adapted from: Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 2021;372:n71. doi: 10.1136/bmj.n71. For more information, visit: <http://www.prisma-statement.org/>..... 44

- Figure S2.1** - Distribution of reported introgression case studies by research team origin (top plot) and geographic location (plot from below) 48
- Figure S2.2** - Spatial distribution of reported introgression case studies by taxa. 50
- Figure S2.3** - Predictive model of temporal series projections (until 2030), performed by the Expert Modeler Method 51
- Figure S2.4** - Altmetric.com Attention Score (ASS) correlation with citation count (traditional bibliometric for research ranking) in the literature through Spearman correlation analysis. The solid blue line depicts the relationship between ASS and the number of citations with the main outlier (Green et al. 2010) (a) and without it (b)..... 52
- Figure S2.5** - Annual changes in authors' average perception of the prevalence of introgression, categorized into nine classes: very rare [-3], rare [-2], infrequent [-1], unknown [0], few cases [1], some cases [2], common [3], many cases [4] and ubiquitous [5]. The solid line depicts the relationship between the perception ranking over time 53
- Figure S2.6** - Overall cumulative exposure–response relationships between the temporal change in the number of papers providing evidence for introgression and authors' prevalence perception predicted from the model with no interaction (interpreted as the average), with 95% CI (a). Lag–response relationships between the number of introgression evidence (number of papers) and authors' perception about its prevalence, with 95% CI (b). 54
- Figure S2.7** - Three-dimensional plots showing temporal changes (from 2000 to 2019) in the estimated exposure–lag–response association between the number of published papers providing evidence for introgression and the percentage of mentions expressing negative emotions (anger, disgust, fear and sadness) of the total annual mentions expressed by the public about them, with the average as reference, and each Lag period corresponding to 4 years 55
- Figure S2.8** - Three-dimensional plots showing temporal changes (from 2000 to 2019) of the estimated exposure–lag–response association between the number of published papers providing evidence for introgression and the percentage of mentions expressing positive emotions (anticipation, joy, surprise and trust) of the total annual mentions expressed by the public about them, with the average as reference, and each Lag period corresponding to 4 years. 56
- Figure S2.9** - Overall cumulative exposure–response (left plots) and Lag–response (right plots) relationships between temporal changes (from 2000 to 2019) in the number of papers providing evidence for introgression evidences and the percentage of mentions revealing negative emotions

(Anger, Disgust, Fear and Sadness) predicted from the model with no interaction (interpreted as the average), with 95% CI..... 57

Figure S2.10 - Overall cumulative exposure–response (left plots) and Lag–response (right plots) relationships between the temporal changes (from 2000 to 2019) in the number of introgression evidences (number of papers) and the percentage of mentions revealing positive emotions (Anticipation, Joy, Surprise and Trust) predicted from the model with no interaction (interpreted as the average), with 95% CI..... 58

Figure S3.1 - Multilayer network metrics. (a) Computed multilayer-specific network properties of eigenvector centrality algorithm, which measures each node's importance depending on its connections, and (b) Page rank versatility, which quantify the importance of each one based on being adjacent to nodes with highest eigenvectors. Genomics/cytology's layer (Autosomal introgression [Introq_Auto], Autosomal islands of speciation [Isl_Speciation_Auto], Nuclear introgression [Introq_NUCLEAR], Introgression on Sex-chromosomes [Introq_SEX], Cytoplasmic introgression [Introq_CYTO], Nuclear islands of speciation [Isl_Speciation_NUCLEAR], Islands of Speciation on Sex-chromosomes [Isl_Speciation_SEX], Cytoplasmic islands of speciation [Isl_Speciation_CYTO] and presence of balancing selection [Balancing_selection]); Physiology's layer (endogenous impacts on introgression [Endogenous_impacts], Haldanes's rule compliance [Haldane's_rule], female sterility [Female_sterility], male sterility [Male_sterility], exception to Haldanes's rule [No_Haldane's_rule], any sterility [No_sterility], sex-bias introgression [Sex-bias_introgression], paternal direction of introgression [Paternal_way] and maternal direction of introgression [Maternal_way]); Demography's layer (demographic disparities [Demography], any demographic disparities [No_Demography], direction of introgression from native-to-colonizers [Native-to-colonizer] and exception to native-to-colonizers direction [Native-to-colonizer]); Behaviour's layer (presence of sexual selection [sexual_selection], presence of assortative mating [Assortative_mating], presence of intra-sexual interspecific competition [Sex_competition] and absent of intra-sexual interspecific competition [No_competition]; and Ecology's layer (environment-mediated introgression [Environment_mediated], iteration between allopatric and sympatric periods [Temporal_cycling], exogenous impacts on introgression [Exogenous_impacts], Allele surfing [allele_surfing], Any allele surfing [No_allele_surfing]..... 93

Figure S4.1 - Number of connections per taxa by taxonomic group (mean $\pm$ SD), in donor species (a), receptor species (b) and globally (c). Solid lines indicate medians; the dots represent outliers; boxes and whiskers indicate quartiles and ranges, respectively. 123

Figure S5.1 - CIELAB colour space expressing colours in three values: L^* for perceptual lightness, and a^* and b^* for the scales of the four colours of human vision: red and green, blue and yellow, respectively..... 150

Figure S5.2 - Support Vector Machine classification plots based on morphometric (on left) and colour traits (on right) for both parental species in sympatry, including hybrids on top and excluding them on the bottom. Density of probability of correct classification rate was based on Kernel statistics. Red spots regard *E. isabellinus* and the blue ones *E. serotinus*..... 162

List of Abbreviations

AAS - Altmetric Attention Score

AI – Artificial intelligence

C1-C1 - Rostral width at the canines' level

CI – Confidence interval

COI - Cytochrome c oxidase subunit I

CM3 - Canine to third molar interval

D3 MC - Metacarpals of the 3rd finger

D5 MC - Metacarpals of the 5th finger

D3 F1 - Phalanges of the 3rd finger

D5 F1 - Phalanges of the 5th finger

DFA - Discriminant function analysis

DLNMs - Distributed lag non-linear models

EBD - CSIC - Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas

EBLV-1 - European bat Lyssavirus type 1

EU – European Union

FA – Forearm

GDPR - General Data Protection Regulation

GLM - General Linear Models

HTS - High throughput sequencing

IQR - Interquartile range

ITS2 - Internal transcribed spacer

LGL - Large Graph Layout

MCCT - Maximum clade credibility tree

MCMC - Markov chain Monte Carlo

MD – Mean difference

MDS - Multi-Dimensional Scaling

MPPD - Maximum pairwise phylogenetic dissimilarity

MRCA - Most recent common ancestor

NGT – Natural Gene Transfer

PCA – Principal Component Analyses

QTL - Quantitative trait locus

RAD-seq - Restriction-site associated sequencing

SNP - Single Nucleotide Polymorphisms

SPSS - Statistical Package for the Social Sciences

_{st}EW - Standardized edges' weight

_{st}PP - Standardized Polarity Perception

SVM - Support vector machines

Tweet's ID - Individual tweet

USA – United States of America

US\$ - American dollar

Chapter 1

General Introduction

“The view generally entertained by naturalists is that species, when intercrossed, have been specially endowed with the quality of sterility, in order to prevent the confusion of all organic forms”

Charles Darwin, 1859

1.1 The importance of knowledge about Natural Gene Transfer

Natural Gene Transfer (NGT) is the natural movement of genetic material across species boundaries (Gladyshev et al., 2008) reached horizontally (from a donor lineage to a recipient not directly through the offspring), which can occur from several biological mechanisms (such as transduction by virus or transformation by free DNA on prokaryotes) (Mallet, 2005), or vertically (from parents to offspring) through reproductive processes such as hybridization (Rieseberg and Welch, 2002). In both cases, but mainly on vertical gene transfer, the process that enables successful recombination (interspecific random gene swap) is admittedly more effective when the donor and recipient lineages are relatively closely-related (Soucy et al., 2015).

Recent evidence has shown that, by mechanisms not yet clearly understood, it is not only possible the occurrence of NGT in extreme phylogenetic distances (e.g. from plants toward insects) but also that it has an evolutionary and adaptive significance along species co-evolutionary history (Xia et al., 2021). Other previous evidence had already demonstrated the possible occurrence of NGT from microorganisms towards arthropods (Wybouw et al., 2016). It is now possible to speculate that intense biological interactions (e.g. parasitism, herbivory, pollination, etc.) along co-evolutionary processes may be generators and empowering of NGT when the traits of one species exert a selective pressure on the other (Lin et al., 2007). In addition to its potential occurrence in a wide phylogenetic range, there has been an exponential increase in studies that demonstrate the occurrence of NGT in a wide variety of taxa (from virus until mammals) and biomes in all over the world (Taylor and Larson, 2019).

The current knowledge highlighted the importance of scientific development around NGT by demonstrating it as a potentially ubiquitous, transversal and universal phenomenon (Ryan et al., 2018). Yet, its critical role as a significant evolutionary force is difficult to demonstrate (Koonin et al., 2001) and susceptible to ideological, social and cultural biases against admixture (genetics and others) (Arnold, 2004). Genetic admixture from all origins represents a natural force acting against the systematic and hierarchical organization of living beings in tight taxonomic groups (Morange, 2001) as a 'breakdown of isolating mechanisms' (Mayr, 1942). However, it seems factual that this idea is a simplification of life that might be useful for humans understanding but it is keeping disconnected from the real complexity of life (Deichmann, 2017).

Although humans have been dealing with phenomena such as hybridization, probably shortly after the first domesticated animals, more than 10.000 years ago (Bekoff, 1986), apart of their own admixture with other closely-related ancient human species (Enard et al., 2018, Vernot et al., 2016, Yair, 2021), it was only in the 18th and 19th centuries that some studies began to focus on the study of reproduction and hybridization (Rieseberg and Welch, 2002). Even so, NGT continued to be underestimated, ignored or devalued for a very long time (Mallet, 2008). Even

Charles Darwin despite his disruptive vision of life, shared with his contemporaries the view that natural interspecific crossbreeding hardly should produce fertile offspring (Darwin, 1859).

It was only in the 20th century that the scientific community recognized the possibility of the occurrence of vertical NGT through hybridization (Anderson and Hubricht, 1938), starting a debate that has arrived to the present days (Chan et al., 2019; Rieseberg and Welch, 2002). Two clearly contradictory lines of thought have emerged. On the one hand, hybridization was seen as a maladaptive process (Lowe et al., 2015), a threat to species conservation (Oliveira et al., 2008), a violation of species integrity or even an imperfection of nature (Mayr, 1942). On the contrary, it may benefit some lineages through the sharing and incorporation of genes associated with well-adapted traits to new or changing environmental conditions (Arnold et al., 2012; Arnold and Kunte, 2017; Martin et al., 2006; Martin and Jiggins, 2017; Suarez-Gonzalez et al., 2018a). The permanence of this paradoxical way of understanding NGT through hybridization and its consequences for subsistence, adaptation and evolution of life on Earth, highlights a pressing need to pay closer attention to the current scientific knowledge trends about this topic (Arnold and Kunte, 2017). So, it is crucial to identify potential sociological barriers to the development of scientific progress (Paterson, 1985). Additionally, it is relevant that we can provide not only new and more powerful technical and methodological advances but also philosophical bases, in order to open new mentalities for both science and society (Laplaine et al., 2019).

More than guaranteeing survival, adaptation or expansion of some specific lineages (Arnold et al., 2012), NGT, seems to present itself as a last resort for safeguarding life in extreme environmental changes (De La Torre et al., 2014; Ng et al., 2017). This idea is based on a vision in which living beings naturally resort to admixture (genetic but also cultural), purposefully or instinctively, as a way to increase the variability of offspring and their survival (Arnold and Kunte, 2017). Theoretically, NGT presents itself as a mechanism that allows the subsistence of Life through increasing variability, even if implies, in extreme scenarios, the sacrifice of other life forms by mechanisms such as outbreeding depression and genetic swamping (Peris et al., 2017). Finally, the study of the implications of NGT for the evolution of life on Earth as an ultimate adaptive force becomes particularly pressing in a current reality subjugated to the harmful effects of extreme anthropogenic climate change (Lamichhaney et al., 2016; Quigley et al., 2019).

1.2 Introgressive hybridization process

Natural hybridization implicates successful mating between individuals from two natural and different evolutionary lineages, independently of species' definitions and concepts (Arnold, 1997). Biological or Phylogenetic Species Concepts (Mayr, 1963; Hennig, 1965), for example, have considered natural hybridization as an impracticable process - because, from the operational point

of view, species are completely isolated or because new lineages must be considered monophyletic. In their strict applications, natural hybridization is considered a “violation” of “species boundaries” that results in less fit “mongrels” (Arnold, 1997). As argued by Arnold (1997), only the moderation of the constraints of these restricted views derived from taxonomy can allow the study of this natural process, free of abstract scientific and socio-cultural pre-conceptions.

When hybridization promotes completely sterile offspring, derived from a high degree of post-breeding barriers or hybrids inviability and breakdown, its evolutionary consequences have been considered limited or circumscribed to the process of divergence (Brideau et al., 2006; Kost et al., 2016). However, the role of sterile hybrids’ within a community, in terms of behaviour and cultural heritage, such as its non-parental care efforts and/or the exploration of new niches, has been prominently ignored (Moran et al., 2019).

On other circumstances when hybridization leads to a genes’ movement between hybridizing lineages through backcrossing, we are in the presence of a process of introgression, hence **introgression** may be defined as the transmission and insertion of genetic material from one lineage to another (Anderson and Hubricht, 1938). Introgression may lead to the introduction of maladaptive genes, although they are unlikely to establish themselves in a stable way in a population due to stochastic and natural selection reasons (Seixas et al., 2018). However, introgressive hybridization was often considered neutral without phenotypic/physiological outcomes (Matosiuk et al., 2014; Minder and Widmer, 2008). Nonetheless, when introgressive hybridization has adaptive consequences, recipient lineages are facing a process of **adaptive introgression**, sharing genetic material through repeated interbreeding and incorporating alleles responsible by well-adapted traits to biophysical conditions (Jones et al., 2018; Nadachowska-Brzyska et al., 2012; Pfennig, 2021; Yair et al., 2021). Preliminary empirical experiments accumulated evidence of the relationship between natural hybridization and habitat disturbance (Anderson, 1949). These first authors found adaptive introgression to be such relevant that “must greatly exceeds the new genes produced directly by mutation” (Anderson, 1949). Therefore, hybridizing populations can jump directly to a new adaptive optimum, bypass intermediate steps in the adaptive process, as the natural selection along generations or isolated mutations (Herrig et al., 2014). This is a very important evolutionary process that enable species to a quicker adaptation to new or changing environmental conditions (Acosta and Premoli, 2018; Boratynski et al., 2014; Hamilton et al., 2013; Lewontin and Birch, 1966; Melo-Ferreira et al., 2014; Yair et al., 2021).

1.3 Consequences of introgression

1.3.1 Evolutionary biology

Introgression can potentially impact species adaptive capacity (Acosta and Premoli, 2018; Aeschbacher et al., 2017) by increasing their survival (Hejase and Liu, 2016; Norris et al., 2015), promoting range expansion (Whitney et al., 2015), leading to species divergence or driving adaptive radiation (Poelstra et al., 2018; Seehausen, 2004; Zhang et al., 2016) and also supporting evolutionary rescue (Quigley et al., 2019), whilst species maintain their taxonomic identity (Räsänen and Hendry, 2008):

✓ Increasing survival – *Anopheles* sp. case study

The two distinct populations of African malaria vector, nowadays recognized as two distinct mosquito species, *Anopheles coluzzii* and *A. gambiae* (Coetzee et al., 2013), are known to co-exist in sympatry, for example in Mali and Guinea Bissau (Norris et al., 2015; Vicente et al., 2017). Studies have shown that because of a brief breakdown in assortative mating mechanisms, it followed intense periods of introgressive hybridization (Norris et al., 2015). Introgression of adaptive genes changed the mosquito fitness landscape by providing fruitful responses to selection pressure in their backcrosses in reply to insecticide exposure, favouring these species survival (Hanemaaijer et al., 2018; Norris et al., 2015).

✓ Promoting range expansion – *Helianthus* sp. case study

Hybridization between wild North American sunflowers *Helianthus annuus* and *H. debilis* is one of the first identified examples of adaptive introgression (Heiser Jr, 1951). *H. annuus* has captured beneficial alleles from *H. debilis* ssp. *cucumerifolius* through introgressive hybridization, within the ecotone of central Texas. *H. annuus* has used them to expand southward (Whitney et al., 2015). Adaptive introgression to the new geographical conditions culminated in the formation of a stabilized hybrid species, *H. a. texanus* (Scascitelli et al., 2010). With its southern expansion *H. annus*, in its *H. a. texanus* biological form, occupied new ecological niches by combining the edaphic preferences of the *H. annuus*, preferring clay rather than sand, with the climatic adaptations to the southern latitudinal of *H. debilis* (Whitney et al., 2015).

✓ Leading to species divergence and driving adaptive radiation – *Coptodon* sp. case study

Coptodon cichlids fishes from Lake Ejagham, Cameroon, suffered a historical process of sympatric speciation through radiation. Ejagham is a small lake (only with 0.5km²) that hosts limited pressures for fishes' divergence because of its small ecological gradient (Poelstra et al., 2018). Although the colonization of the lake took place shortly after its formation (9,000 years ago) the radiation process only occurred much more recently (1,000-2,000 years ago). Recent studies have shown that during this speciation process a secondary gene flow from a nearby riverine species has started and is still ongoing (Poelstra et al., 2018). The introgression of olfactory receptor genes near the time of the first speciation coincided with a higher overall rate of interbreeding. These olfactory receivers are a key factor for mate choice in cichlids showing that their adaptive value for mating may have facilitated their current radiation process (Poelstra et al., 2018).

✓ Supporting evolutionary rescue – *Acropora* sp. case study

Corals from the Great Barrier Reef, such as *Acropora* sp., may not be able to generate and spread beneficial mutations, quickly enough to face climate change (Mao et al., 2018; Quigley et al., 2019; Stoeckl et al., 2021). However, the introgression of genes from warmer-tolerant species into the genomic background of cooler-environment species can promote fast adaptation to warmer waters and supporting corals evolutionary rescue (Quigley et al., 2019). However, recent simulations have demonstrated that even through adaptive introgression the natural process can take more than 30 generations for the introgressed adaptive genes to definitively fix in the population. On the other hand, it is unlikely to these genes spread far from northern reefs (Quigley et al., 2019).

1.3.2 Conservation biology

Introgressive hybridization is yet an enigmatic evolutionary force (Fijarczyk et al., 2018) with potential paradoxical outcomes, particularly for species conservation (Allendorf et al., 2001). On one hand, interspecific gene flow is recurrently understood as a conservation concern (Genovart, 2009; Lyu et al., 2021; O'Brien et al., 2009; Rieseberg et al., 1989), by counteracting local selective pressures and decreasing the fitness of diverging populations by introducing alleles outside their local adaptive range (Bolnick and Nosil, 2007; Maguilla et al., 2017). Thus, it has been frequently considered as a homogenizing process (Latch et al., 2006) and a conservation concern due to genetic swamping risk, which could impact negatively species long-term viability (Maguilla et al., 2017). For example, under biological invasion scenarios, introgression has been historically pointed as an important conservation threat for endemic taxa under hybridization (Scascitelli et al., 2010).

On the other hand, introgressive hybridization between wild species and their domestic variants is frequently identified also as a conservation threat (Anderson et al., 2009), whilst recent studies have demonstrated that even this process has the potential to promote adaptations of wild species to anthropogenic environments and climate change (Acosta and Premoli, 2018; De La Torre et al., 2014; Mao et al., 2018; Ng and Glor, 2011).

When introgressive hybridization leads to adaptive introgression it can impact positively species conservation through supporting evolutionary rescue (Quigley et al., 2019). However, the speed of environmental change can be a conditioning factor in the effectiveness of the natural introgression (Anderson et al., 2009). Under these conditions, such as anthropogenic climate change (Ottenburghs, 2021), assisted gene flow has been discussed (Quigley et al., 2019).

First of all, differentiating natural from human-mediated introgressive hybridization has been pointed to be essential to develop effective conservation efforts (Quigley et al., 2019). Under natural introgressive hybridization scenarios, management programs that seek to isolate a lineage (species/population/breed) from its closely-related should be actively avoided because, by aiming to preserve taxa purity or genetic integrity, paradoxically these management options can increase the risks of inbreeding depression (Liddell et al., 2021). Through genetic drift the loss of rare alleles can lead to a decrease of gene pool size (Hasselgren et al., 2021). Under theoretical impacts of extreme inbreeding, drastic decrease in the population size can result in populations' bottleneck, arising from a significant decrease of breeding individuals or even drastically increasing the death rate (Bradke et al., 2021).

Assisted gene flow (human-mediation of already natural introgression processes either by hybridization and/or selective breeding) should be considered due to its high adaptive potential (Liddell et al., 2021; Quigley et al., 2019)). Assisted gene flow should be designed through genomic architecture of admixture of genes underlying the adaptation of the targets' lineages (Li et al., 2016). When it is unclear what genes should be targeted, the genes under balancing selection should constitute the first option (Fijarczyk et al., 2018) and it should be assessed whether genetic rescue through intraspecific translocations and/or selective breeding is a viable option (Fijarczyk et al., 2018). Even so, how manageable are translocation, breeding and reseedling risks must be carefully evaluated in each management program individually (Quigley et al., 2019). After all, human-mediation of gene flow for endangered species conservation, in cases in which introgression naturally already occurs, should be considered in addition to conventional management (Quigley et al., 2019). Nevertheless, these management options should not be considered in replacement of strong mitigation measures of the threats that put at risk the conservation of targets' lineages (Liddell et al., 2021). The development of introgression conservation programs could become, in the near future, especially fruitful in cases in which

species are facing quick changes in their environmental conditions, deriving, for example, from climate change (Chan et al., 2019; Ottenburghs, 2021).

1.3.3 Socio-biology

There are a substantial number of genetics or genomics concepts extensively used in contemporary narratives and thoughts, such as race, gender, sexuality, ethnicity, and others (Bivins, 2008). However, the impact of genetics and genomics developments on society has been limited studied (Bivins, 2008). Still, biological sciences are particularly valuable for society, helping to satisfy basic human needs (Rull, 2014). Thus, it is crucial to consider that the historical background and philosophical values may promote biased judgements (Laplane et al., 2019) that scientists may also be sensitive too, as "human beings rooted in cultural contexts" (Gould, 1978). There are known paradigmatic examples of the usurpation and misrepresentation of scientific facts for socio-political purposes that go far beyond the scientific process itself (Cortes and Salgado, 2011). This is particularly true in the current context subjugated to a post-truth society, in which mistrust and misperceptions of scientific knowledge progressively stem from the extensive diffusion of distorted and biased information (Araujo, 2021).

Genetic miscegenation has historically suffered from controversies and paradoxes that make this theme particularly susceptible (Marsden et al., 2011). Crossing over scientific borders, it has served as basis for intense debate in society, from philosophy to human relations and social policies (Cortes and Salgado, 2011). Some authors have suggested that philosophical and cultural background may be behind the negative prejudices towards natural phenomena like hybridization (Paterson, 1985). In animal husbandry/agriculture, for example, the demand for pure variants, with desirable traits, is nowadays seen as development and progress (Henkel et al., 2019) and the protection of pure lineages/species remains at the forefront of conservation priorities (Biermann and Mansfield, 2014). From a social point of view, biases against genetic miscegenation were demonstrated through segregation, human forced sterilizations, homicides and lab experiments with human beings (Schoen, 2005), as well as anti-miscegenation laws, prohibiting marriage between people from different "races" (Baker, 2016).

Recent methodological developments have allowed the accumulation of evidence on the role of genetic admixture for the evolution and survival of many living organisms through introgression (Acosta and Premoli, 2018; Aeschbacher et al., 2017; Pfeifer and Kapan, 2019; Suarez-Gonzalez et al., 2018b; Whitney et al., 2015). According to the current literature this is an apparently universal natural process whose benefits are ubiquitous both in terms of geographic (Brower, 2018; Giska et al., 2019; Ma et al., 2019; Morales et al., 2018; Suarez-Gonzalez et al., 2018a) and taxonomic occurrence (Maddamsetti and Lenski, 2018; Maxwell et al., 2019; Nader et al., 2019; Paetzold et

al., 2019; Silvert et al., 2019) and transversal to the time scale (Dunn et al., 2013; Schumer et al., 2016), including in human evolutionary history (Antelope et al., 2017; Enard and Petrov, 2018). However, as empirical literature frequently refers, there are great difficulties in investigating how deeply science impacts society because data on public perception of scientific facts is hard to obtain and work with (Trochim, 2010). On the other hand, delay of scientific translation should be frequently necessary to ensure the accuracy and efficacy of new advances (Morris et al., 2011). However, it is relatively accepted by both the scientific and policy communities that a fast translation of research into practice is somehow positive (Morris et al., 2011). The ignorance is another issue at the root of stereotypes and prejudices (Matusitz, 2012), also against genetic admixture. So, high degree of communication on introgression knowledge can be efficient to society refute theories that promote taxa 'purity, like eugenics, which have historically used scientific facts from evolutionary biology to justify racism and other forms of social discrimination (Matusitz, 2012; Nshom and Croucher, 2017).

1.4 Knowledge gaps on prevalence, functioning and outcomes of introgression

The advent of high throughput sequencing (HTS) has increased the ability to detect genomic areas under introgression and, to a lesser extent, its adaptive and evolutionary consequences (Kuhlwilm et al., 2019; Ryan et al., 2018). The development of new high throughput sequencing platforms led to a subsequent reduction in sequencing costs, for example, whole genome sequencing reduced from US \$3 billion to less than US \$1,000 in 12 years (from 2000 to 2012) (Hayden, 2014). Both efficiency and accessibility of these techniques have led to a substantial increase in publications and evidences of introgression in biological systems from all over the world (Ryan et al., 2018). However, limitations on multidisciplinary, multidimensional and multiple taxa experimental methods, limit a broader understanding of its real adaptive role, mode of operation and prevalence. While understanding the general mechanisms under which introgression can contribute to adaptation requires vast characterizations and demonstrations of the process across the tree of life, understanding how scientists have been interpreting patterns and causes of potential introgression can provide a general overview of major hypothesis to test in the future.

Complex evolutionary histories of species under rapid or preliminary speciation processes and introgression can result in high levels of phylogenetic incongruences due to NGT (Ottenburghs et al., 2017). Spatio-temporal dynamics expose different lineages to different ecological forces and may lead to change in their genomic and phenotypic characteristics (Ryan et al., 2018). These differences alongside dissimilarities in mating, dispersal and competitive behaviours should influence the way how each species-pair are impacted by introgression, under what conditions and

with what consequences (Yang et al., 2018). How evolutionary history and characteristics of each taxonomic group directly impact evolutionary outcomes of introgression, as well as its extent remains deeply unknown. On the other hand, closed-related species/lineages may coexist stably during secondary contacts under antagonistic evolutionary forces, imposed for example by introgressive hybridization and competition. If genetic material can be transferred through introgressive hybridization with potential evolutionary convergence (Song et al., 2011), ecological interactions, such as competition, predation or parasitism may produce exclusion or promote morphological divergence as a response to niche-partitioning (Anderson et al., 2002). So, the effect of introgressive hybridization on the traits of introgressing lineages when facing counteracting evolutionary forces from competition is still largely unknown.

Finally, the way and the intensity in which current knowledge about the role of introgression can impact on the scientists' perceptions on the benefits of genetic admixture will help to understand how prejudices remain, evolve and condition scientific progress. Additionally, public perception on genetic miscegenation in response to this body of knowledge has not been adequately explored (Bivins, 2008). It can be essential for determining how scientific evidence can shape public opinion and emotions towards genetic miscegenation (Damasio and Carvalho, 2013) and how it can influence public beliefs and decision-making in the future. Overall, despite the very significant recent increase in knowledge about introgression, the consequences of biases and lack of knowledge on prevalence, functioning and both biological and psycho-sociological outcomes still remain particularly challenging.

1.5 Purpose of this research

Scientific progress requires systematic and replicable processes of merging data and evaluation of large amounts of scientific data to respond to the current exponential increase in the scientific production (Magalhães et al., 2017; O'Dea et al., 2021). Systematic reviews complemented with meta-analyses are nowadays a renowned approach to organize knowledge and identify its main trends. It is also very important to provide information about its gaps, advising for upcoming investigation efforts (Livoreil et al., 2017; O'Dea et al., 2021). Thus, standard protocols of systematic reviews are crucial as a guarantee against subjective decision during its execution (Shamseer et al., 2015). In parallel, meta-analyses through multidimensional approaches are particularly able and advantageous as an integrative and holistic framework to merge and analyse the trends of knowledge on biological data from standard systematic reviews (Bradley et al., 2005), potentially leading to increasing knowledge through empirical results (Shamseer et al., 2015).

On the other hand, empirical studies about cryptic species are particularly valuable for studies about introgressive hybridization because they are an extreme case among closely-related lineages since they are morphologically identical but genetically distinct (Jones, 1997). Due to their phylogenetic proximity and partial niche overlap, as well as morphological similarity and high potential for hybridization, they represent excellent case studies for the study of the effect of antagonistic evolutionary processes, such as introgressive hybridization and competition, particularly when they present sympatric or parapatric distributions (Marsteller et al., 2009; Tene Fossog et al., 2015).

I designed an approach combining an extensive systematic review and multidimensional meta-analyses to gather published evidence on introgression and to analyse the current trends on scientific knowledge. This approach was complemented with preliminary empirical studies on the Iberian cryptic *Eptesicus* bats' species focusing on the effects of introgression as a counteracting evolutionary force of competition.

1.5.1 Systematic review

Following standard review protocols (Moher et al., 2009; O'Dea et al., 2021), I carried out a systematic literature search for studies between 1900 and 2019 that interpreted introgression patterns resulting from adaptation. I used in some search engines (Falagas et al., 2008) a combination of terms relating to natural hybridization, genome, introgression and adaptation, avoiding the terms related to domestication and exotic/invasive species, thus restricting the search only to natural phenomena of genomic introgression, excluding all cases of direct or indirect human interference. Searches were exclusively done in English and were finished in November 2019.

Initial searches yielded 820 documents. From this dataset, I excluded duplications, non-original studies, theoretical essays, opinion texts, non-peer-reviewed papers, off-topic documents and non-ISI journals. After excluding reviews and book chapters, I screened individually the title and abstract of the remaining 436 empirical studies to evaluate their eligibility for the analysis, namely: 1) if introgression was pointed by the authors as the main explanation for the evolutionary processes under study, and 2) if the papers complied with the natural origin for the described introgression process. The final dataset included 358 relevant studies that were read and analysed in full.

1.5.2 Bibliometric analyses

I adopted a series of bibliometric analyses to explore the geographic scope, research areas and taxonomic groups, as well as the temporal evolution covered by the current literature. Then, I evaluated authors' perceptions on polarity, relevance and prevalence of introgression. Additionally, I made use of sentiment analysis techniques to analyse the polarity and sentiments from the public on introgression's evidence, considering the chronology of the publications and the taxonomic groups under study. I further registered information on taxa under the introgression process and noted which method has been used in each study, including the type of experiment, the type of introgression markers and whether the whole-genome sequencing was implemented or not. Finally, I registered the main characteristics of introgression in each case study and its adaptive results, both phenotypic and ecologic outcomes.

1.5.3 Meta-analyses

I regard introgression as a long-term biological interaction between two different lineages in which members of one (receptor) can gain adaptive benefits under specific environmental conditions, while those of the other taxa (donor) neither benefit nor are harmed. I performed different approaches for data-mining and organizing the knowledge with the aim of identifying its main trends. I used several statistical approaches from basic statistics of meta-data, temporal projections, Bayesian data analysis, a set of network analysis and even some approaches of artificial intelligence for compiling and analysis the data.

1.5.4 Empirical studies

Additionally to the systematic reviews, this thesis also uses biological data from empirical experiments. This section aimed to test the effect of introgressive hybridization on morphologic traits of the two cryptic Iberian *Eptesicus* bats when facing counteracting evolutionary forces from competition. First of all, bats present as ideal candidates to test antagonistic evolutionary forces as they present high rates of cryptic diversity (over 20% in the Iberian Peninsula). Secondly, although their morphological similarity, some species-pairs of cryptic species present significant genetic divergence, such as *Eptesicus serotinus* (Schreber 1774) and *E. isabellinus* (Temminck 1840), over 16% distance in the mtDNA Cytochrome b gene. This species-pair has experienced a peculiar evolutionary history that includes periods of divergence during phases of geographic isolation and periods in which they overlap within contact zones. In addition to a sympatry zone partially limited to the central Iberian mountain range, these bat species currently have a distribution marked by

bioclimatic issues. *E. serotinus* is distributed along the northern Temperate region of Iberia (colder and humid) while *E. isabellinus* mainly occurs in the southern Mediterranean area (hotter and drier) (Santos et al., 2014). Within the contact zone, they interbreed with some particularities: a) there is no evidence of mitochondrial introgression, b) nuclear markers identified a male-mediated introgression and c) ongoing directional asymmetric hybridization occurs mainly from *E. isabellinus* to *E. serotinus* (Centeno-Cuadros et al., 2019).

Morphological data from these cryptic bats were recorded during mist-net captures sessions across Iberian Peninsula. To study the effect of inter-specific responses of morphology of the *E. serotinus* and *E. isabellinus* and their hybrids, bats were clustered into five experimental groups: allopatric *E. isabellinus*, sympatric *E. isabellinus*, Hybrids (individuals classified as hybrids according to Centeno-Cuadros et al. (2019)) sympatric *E. serotinus* and allopatric *E. serotinus*. Then, I analysed how the geographic origin and hybrids' presence affect bats morphology, summarizing and comparing morphological variables and proceeding to classification statistics with and without hybrids' presence.

1.5.5 Objectives

Through systematic review and meta-analysis approaches, I started by testing the extent of attention that introgression has been receiving in scientific literature and the way how scientific community and the public perceive scientific discoveries relating to this theme. After that, I intended to analyse the current trend of knowledge about the factors that impact introgression operation with potential adaptive outcomes. Then, I analysed how evolutionary history and characteristics of each taxonomic group directly impact introgression occurrence, as well as its extent, through an investigation into how phylogenetic distance imposed by periods of divergence shapes the functioning of introgression. Finally, through an empirical approach I studied the effect of introgressive hybridization on morphologic traits of the two cryptic Iberian *Eptesicus* bats when facing counteracting potential evolutionary forces from competition.

The proposed objectives of this thesis are:

- 1 - To investigate the scope and evolution of knowledge about introgression, as well as the scientific perception and the emotions that can be triggered in the public as a reaction to the evidences of genetic miscegenation.
- 2 - To analyse the knowledge trends about the introgression mechanisms across the taxonomic complexity gradient at different levels of biological organization.

3 - To analyse how phylogenetic dissimilarity between introgressed species influence introgression occurrence and its main characteristics.

4 - To test the impact of introgressive hybridization when facing competition between parental species of cryptic *Eptesicus* species and their first-generation hybrids.

1.6 Thesis outline

The structure of this thesis obeys the constraints of a broad-spectrum approach, with an interdisciplinary nature, standing at the interface between Evolutionary Biology, Phylogeny, Genomics, Socio-biology and Psychosociology.

The second chapter seeks to organize and systematize current knowledge about introgression from a spatial and temporal point of view, as well as the taxonomic range of its known occurrence. Additionally, this chapter assesses the extent to which methodological developments derived from the genomic revolution have influenced current knowledge and attempts to analyse in context the relevance that is attributed to this topic by the scientific community. Finally, the capacity of this body of knowledge to change the psychosociological perception of the general public is analysed, as well as the impact of prejudice in the public assessment of scientific evidence.

Taking into account the high relevance given to the subject by the scientific community, the following two chapters seek understanding the current knowledge trends about the general mechanisms under which introgression can contribute to adaptation, as well as the impact of species' evolutionary history on its occurrence. Both chapters try to gather the current knowledge trends through a vast characterization and demonstration of the process across the tree of life, which can provide a general overview to test with empirical data. Precisely, the last chapter seeks to empirically test a relevant hypothesis raised in the previous results, namely how it is established the evolutionary balance between convergent forces derived from introgressive hybridization and divergent forces from competition and niche partitioning when species remain in secondary contacts.

Chapter 2 examines the scope and evolution of knowledge about introgression and what do the scientific community and general public think about it. Results show that the genomic revolution provided a remarkable increase in scientific evidence supporting beneficial effects of this phenomenon mainly for species adaptation. This amount of new evidences can influence public perception in the medium to long term despite an initially strong emotional resistance, subject to a certain degree of prejudice against genetic miscegenation.

Chapter 3 investigates into the current trend of knowledge about the factors that impact introgression occurrence and operation. Results reinforce a marked trend to consider introgression as an evolutionary process acting in parallel with divergence, evolving and establishing in balance with it. Through interconnected mechanisms its drivers increase complexity across the biological organization, from genomics, physiology, demography to behaviour, depending on species structural complexity and responding to environmental conditions.

Chapter 4 studies the influence of phylogenetic dissimilarity on introgression occurrence and patterns. Results demonstrate introgression as flexible evolutionary mechanism, which can change its direction and consequences, depending on the environment. More ancient taxonomic groups have a wider ability to promote introgression. However, regardless of the ancestry of each taxonomic group, there are promiscuous species particularly able to promote introgression, which may act as keystone species for hypothetically indirect introgression.

In **chapter 5** the main aim is to investigate the effect of introgressive hybridization on morphologic traits of the two cryptic Iberian *Eptesicus* bats facing counteracting forces from competition within contact zone. Results show a large overlap both in dentition and in wing morphology traits mainly in individuals in sympatry. Hybrids presence contributes to a fifth of this overlap, showing traits with intermediate morphometry. Introgressive hybridization is potentially contributing to species adaptation to trophic and ecological space of the sympatric zone and may respond directly to the macro ecological conditions and to local prey availability. Contrary, colours differences could result from partitioning of resources as a result of competition from roosts and microhabitats.

Chapter 6 presents the main conclusions from these studies and their implications, pointing the path for future research.

Chapter 2

What about introgression? The genomic revolution is shaping scientific and public perception

Pedro Horta, Helena Raposeira, Ana Sofia Vaz, João António, Javier Juste, Orly Razgour and Hugo Rebelo

Horta P., Raposeira H., Vaz A.S., António J., Juste J., Razgour R. & Rebelo H. (submitted). What about Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception. DOI: 10.21203/rs.3.rs-1041127/v1

Keywords: Genetic admixture, Introgression, Perception, Sentiment analysis, Systematic review

Abstract

Genetic admixture was historically perceived as a maladaptive process or even an imperfection of nature. However, through adaptive introgression, some species can share genes associated with well-adapted traits. Current scientific perceptions on the benefits of introgression can help to clarify how these paradoxes condition scientific progress and influence public beliefs and decision-making. We carried out a systematic review and bibliometric analysis using artificial intelligence on introgression evidence. The genomic revolution provided an exponential growing of evidence predominately interpreted as beneficial for species adaptation. We show that this remarkable increase on publications influences public perception in the medium-long term. Despite an initially emotional response, peoples' final opinion tends to incorporate science-based evidence, although prejudices seem to influence peoples' polarity opinion. We argue that developing the knowledge on introgression will allow to scientifically refute theories that promote genetic "purity", used to justify racism and other forms of discrimination.

2.1 Introduction

Introgression can be a key evolutionary mechanism allowing species to incorporate portions of the genome of another species through vertical gene transfer (Anderson and Hubricht, 1938, Arnold and Kunte, 2017). Through repeated interbreeding a species can receive genes from another species, eventually resulting in fitness changes (Cahill *et al.* 2015, Djogbénou *et al.* 2008, Enciso-Romero *et al.* 2017, Gagnaire *et al.* 2009) - a natural evolutionary phenomenon known as adaptive introgression (Pfennig, 2021). Methodological developments through High-Throughput Sequencing and bioinformatics approaches led to an increase in the scientific evidence for the spread of introgression (Pfeifer and Kapan, 2019, Taylor and Larson, 2019) across different geographic areas (Brower, 2018, Giska *et al.* 2019, Ma *et al.* 2019, Morales *et al.* 2018, Suarez-Gonzalez *et al.* 2018b) and taxonomic groups (Maddamsetti and Lenski, 2018, Maxwell *et al.* 2019, Nader *et al.* 2019, Paetzold *et al.* 2019, Silvert *et al.* 2019). It is not always the case that introgressed populations have an adaptive advantage derived from introgression (Harris and Nielsen, 2016). However, when it does occur, they can potentially jump to a new adaptive optimum, thus surpassing intermediate evolutionary steps (Ballerini *et al.* 2012).

Several studies recognise introgression as beneficial for species fitness (Acosta and Premoli, 2018, Aeschbacher *et al.* 2017, Hohmann and Koch, 2017, Horn *et al.* 2018, Lehnert *et al.* 2019, Ma *et al.* 2019, Paun *et al.* 2016, Semenov *et al.* 2018). Possible reasons for the benefit of introgression are the potential for promoting individual survival (Hejase and Liu, 2016, Norris *et al.* 2015), range expansion (Whitney *et al.* 2015), species divergence (Morales *et al.* 2017), evolutionary rescue (Quigley *et al.* 2019) and adaptive radiation (Poelstra *et al.* 2018, Zhang *et al.* 2016). Additionally, there is multiple evidence of advanced-generation hybrids whose backcrosses exhibit adaptive traits beyond the ancestral phenotypic range (DiBattista *et al.* 2016, Salazar *et al.* 2008, Scascitelli *et al.* 2010), sometimes leading to hybrid speciation (Aleksic *et al.* 2018, Brower, 2018). This is a strong argument to support that gene flow between sympatric lineages (species, population, breeds, etc.) may represent an adaptive strategy for survival under extreme environmental conditions (Hamlin and Arnold, 2012, Martin *et al.* 2016, Martin *et al.* 2006, Suarez-Gonzalez *et al.* 2018a).

On the other hand, introgression has been historically understood as a homogenizing process (Latch *et al.* 2006, Oliveira *et al.* 2008), which can influence the long-term viability of species through genetic swamping (Maguilla *et al.* 2017). Some scientists argue that interspecific gene flow may counteract local selection pressures, decreasing the fitness of diverging populations by introducing alleles from outside the local adaptive range (outbreeding depression; Bolnick and Nosil, 2007, García-Ramos and Kirkpatrick, 1997, Maguilla *et al.* 2017). Moreover, other scientists

considered natural hybridization as a violation of species integrity, a maladaptive process or an unexpected imperfection of Nature (Llopart *et al.* 2014, Lowe *et al.* 2015).

These contrasting views reveal a controversy over the merits of introgression. In fact, a number of studies have already suggested that philosophical and cultural background may be behind the negative prejudices of the scientific community towards natural hybridization (Arnold *et al.* 2012). Paterson (1985) highlights such prejudice even in terms of semantics noticing how appreciative are “words such as “pure”, “purebred”, “thoroughbred” and how pejoratives are those like “mongrel”, “bastard”, “half-breed” or “hybrid” with the role of ‘protecting the integrity of species’. Assessing scientific perception of the benefits of genetic admixture through introgression is important for better understanding which factors, beyond scientific evidence, condition scientific progress. Bias in perceptions of the merits of genetic miscegenation directly or indirectly influences fields like conservation biology (Biermann and Mansfield, 2014, Chan *et al.* 2019, Genovart, 2008), animal husbandry/agriculture (Henkel *et al.* 2019), human relations and social policies (Bethencourt, 2013, Baker, 2016, Fredrickson, 2002).

In animal husbandry and agricultural production the demand for pure variants, with the most desirable traits, is nowadays seen as development and progress (Henkel *et al.* 2019). Paradoxically, although the promotion of genetic variation is a key conservation goal (Chan *et al.* 2019), the protection of pure lineages/species remains at the forefront of conservation priorities (Biermann and Mansfield, 2014, Genovart, 2008). From a social point of view, biases against genetic miscegenation were historically manifested through policies promoting forced sterilizations, segregation, direct medical killings and lab experiments in human beings (Schoen, 2005), as well as anti-miscegenation laws, prohibiting marriage between people from different “races” (Baker, 2016).

Understanding both scientific and public perception of the evidence for introgression is essential for determining how the evidence can shape public opinion and emotions towards genetic miscegenation (Damasio and Carvalho, 2013) and how it can influence decision makers (politicians, conservationists, lobbyists, human rights organizations, etc.).

However, inferences of perception patterns about scientific facts are nowadays particularly hard to obtain due to the growing amount of scientific publications and the huge number of opinions derived therefrom that circulate in official documents and conventional and social media. Conventional approaches for obtaining scientific data about perceptions, such as social surveys, can be costly and time-consuming, especially when targeting large audiences and broad spatial and temporal coverages. These approaches can also be difficult to implement because they assume an active process with strong subjectivity bias, namely due to perceivers’ experience, motivation and how they are feeling when processing the information (Sacks and Gary, 2012,

Dange, 2016). This is particularly evident in the phenomenon of "perceptual defence", whereby perceivers only see what they expect to see to support their own beliefs (Christianson *et al.* 2017).

To help overcome these limitations, artificial Intelligence (AI) tools, and specifically deep learning techniques, have been increasingly adopted to analyse large amounts of online data (Yang *et al.* 2019). Deep learning relies on mathematical algorithms endowing machines with intelligent behaviour to learn patterns and adapt such learning processes to new data. By doing so, deep learning algorithms gain the ability to automatically process and identify similarities between patterns of digital information, such as texts or images (Yang *et al.* 2019). In the case of textual data, sentiment analysis has become a promising technique to analyse the polarity of written sentences or words as positive, negative or neutral (Ainin *et al.* 2020). When supported by robust data and adequate meaning, sentiment analysis can serve as a proxy to verbal behaviour, attitudes, and emotions, which are useful for understanding the perceptions and opinions of writers about different topics (Ainin *et al.* 2020).

Here, we aim to understand the extent to which introgression has been receiving attention in scientific literature and the way the scientific community and the public perceive scientific discoveries relating to introgression. Specifically, we aim to answer the following questions: (1) What is the scope and evolution of knowledge about introgression? (2) What do the scientific community and general public think about introgression? (3) Which sentiments can be triggered in the public as a reaction to evidence of adaptive introgression? Based on our findings we suggest avenues for fostering progress of introgression and adjust its course in Evolutionary Biology.

2.2 Methods

2.2.1 Approach

To answer our research questions, we first carried out a systematic review to retrieve all published scientific literature on introgression and respective bibliographic meta-data. Then, we adopted a series of bibliometric analyses to understand the taxonomic coverage, geographic patterns, and temporal evolution of the retrieved literature. Additionally, we used salience analysis grounded on citation indices and attention scores, to understand the popularity level of the different studies among the scientific community and the public. Finally, we analysed the prevalence, polarity and relevance of introgression based on the perceptions from the authors of those studies, as well as the sentiment of the public towards this body of knowledge.

2.2.2 Systematic review

Following standard PRISMA systematic review protocols (Moher *et al.* 2009, O'Dea *et al.* 2021, Page *et al.* 2020), we carried out a systematic literature search for studies that explored the adaptive and evolutionary potential of natural introgression. We used ISI Web of Knowledge, Scopus, Google and Google Scholar, as the main search engines (Falagas *et al.* 2008). We used a combination of search terms relating to natural hybridization, genome, introgression and adaptation, avoiding the ones related to domestication and exotic/invasive species, with the aim of restricting the search only to natural phenomena of genomic introgression with potential adaptive outcomes, excluding all processes under direct or indirect human interference (breeding manipulations, genetic manipulation, invasive species scenarios, etc.). The selection of keywords was based on a review of previous keywords from a list of reference papers, and under a participatory approach with a team of scientists specialised in evolutionary processes. The final list of keywords included the most common and unambiguous words to reach the largest number of publications on the subject (see search details in Supplementary materials for the full list of keywords). The timespan of our search was 1900-2019. Searches were carried out in November 2019 and were restricted to English.

Our initial search yielded 820 documents. After removing duplicates from the dataset, we excluded non-original studies, theoretical essays, opinion pieces, non-peer-reviewed papers, off-topic documents and non-indexed papers. Then we checked their reference list to search for other publications that included the terms under study (i.e. snow-ball effect). Finally, after excluding all reviews and book chapters, we screened the title and abstract of the remaining 436 articles individually to evaluate their eligibility for the analysis, namely: 1) if the papers complied with the natural origin for the introgression process and 2) if introgression was pointed by the authors as the main explanation for the biological processes under study. The final dataset included 358 relevant studies (WebFigure 1; Supplementary materials). All papers were analysed in full only by the first author.

We extracted bibliographic information from the 358 studies. Each study was then reviewed to extract information on authors' initial perception about introgression and the temporal epoch and spatial location of the introgression phenomena reported in the study. We noted information on the taxa undergoing the introgression process. Finally, we reviewed which main method was considered in the publication, including the type of experiment, the type of introgression markers and whether whole-genome sequencing was performed or not. Detailed information about the variables extracted is available in table S2.1.

2.2.3 Bibliometric analysis

✓ *Geographic and taxonomic patterns in the published literature*

To investigate the associations between the geographical origin of researchers, the location of their case studies and the targeted taxonomic group, we used a spatial bipartite association network built using the GeoLayout 0.9.2.2. plugin from Gephi (<https://gephi.org/>) (scale of 20.000). We identified the main regions of origin of the introgression scientific study and the most important case studies based on their node weight (number of papers). Based on the betweenness centrality metric, we placed particular attention on nodes representing case studies that were studied by several teams. This approach measures the influence of a case study over the flow of the scientific information used to find the ones that serve as a bridge between research teams (Ulrik and Faster, 2001).

✓ *Temporal changes in publication, methods and research areas*

Temporal changes in the number of published papers were tested through General Linear Models (GLM) with temporal series projections (until 2030) by the Expert Modeler Methods available on IBM SPSS Statistics software (v. 22; SPSS Inc, Chicago, IL). This approach was complemented with a linear regression, assessed through the coefficient of determination, between the number of published papers and time as a function of the methods used and research areas. We defined as the tipping point the temporal moment when the exponential trend lines ceased to show a reduced slope (Maroco, 2010).

2.2.4 Salience analysis

We searched in June 2020 each paper title in Altmetric Explorer, the web-based platform available through Altmetric.com which allows to browse and report the attention data that each paper has been receiving through online media (others include mainstream media mentions, peer reviews and citations to research in policy documents) (Tahamtan and Bornmann, 2020). Data included citations count and Altmetric Attention Score (AAS) (global and in context) recorded for each one of the 358 papers included in the review, including their geographical breakdown and temporal trends (Tahamtan and Bornmann, 2020). To determine the scientific relevance currently attributed to introgression, measured from the attention it is given, first we examined if paper AAS correlate with citation count (a traditional bibliometric indicator for research systems) (Okubo 1997) using Spearman correlation analysis. We then analysed AAS and compared: 1) all papers

published in the same year and journal, 2) all papers published in the same year, 3) all papers published in the same journal and 4) all research outputs scored by Altmetric.com (28,900,000 outputs).

2.2.5 Sentiment analysis

✓ *Perceptions of scientists*

We obtained the data on the perceptions of scientists directly from the systematic review, namely the scientific area of the study, the authors' polarity opinion about introgression and the arguments used to justify it. We performed a Multi-Dimensional Scaling (MDS) tripartite network analysis with Gephi ThirdParties Plugins v. 0.9.2, to quantify the extent of known connections between these variables. The final layout represents the distance between nodes based on the similarities of their attributes, namely their connections' weight and connected nodes' identity. We chose the network metrics "node weight", "edges weight" and "node degree" to describe the main characteristics of the perception network (Algorithmics Group, 2009). Node weight, symbolised by node size, represents the total number of papers from each scientific area with similar authors' perception about introgression. Edge weight, symbolised by edge thickness, represents the total number of papers on which a connected pattern between two opinion characteristics simultaneously occurs. Node degree measures the number of relationships between nodes. Nodes with high degree have many connections, suggesting that they may possess strong supporting arguments. All metrics were obtained directly from Gephi platform (Algorithmics Group, 2009).

We performed a temporal analysis of authors' perceptions of natural introgression in relation to changes in the amount of scientific evidence over time. We applied a distributed-lag model that is a dynamic model in which the effect of an x on y regression occurs over time, and not all at once. This modelling framework is useful to analyse variable associations in time series data even if data are non-linear and/or with delayed effects (DLNMs-distributed lag non-linear models) (Gasparrini, 2011). This approach is based on 'cross-basis', defined by a bi-dimensional space of functions that describe simultaneously the temporal relationship across the space of a predictor and the delay of its occurrence (Gasparrini, 2011). Thus, DLNMs analysis relies on a combination of these two sets of functions specifying the relationship between the dimensions of the number of scientific evidence and time lags, allowing to establish an immediate or delayed cause and effect relationship in the response variable (e.g. authors' prevalence perception – from "Very rare" to "Ubiquitous"). All DLNM analyses were executed in the dlnm R package (Gasparrini, 2011).

✓ *Public perceptions*

We considered the target public as a group of people broader than the scientific community, who show their interest in introgression through citation, reference, opinion and/or comment. We analysed 11,650 mentions by the public of the 358 introgression papers. The mentions, over multiple websites and different online platforms were mainly downloaded from Altmetric.com. Regarding twitter's mentions (from the social media network Twitter), the data exported from Altmetric.com only included the tweet's ID for an individual tweet. We obtained access to Twitter's Developer Portal, and taking this information into a Twitter API, we got access to each message. Finally, we used Postman software (<https://www.postman.com/>) to get the link from Twitter API and the Power BI Desktop software (<https://powerbi.microsoft.com/>) to get the final published tweets table of each introgression paper. Our approach complies with the Terms of Use and Developer Policy of the platform. All information extracted was anonymous or threatened as confidential in respect to the General Data Protection Regulation (GDPR) from EU Regulation 2016/679. To perform the sentiment analysis based on lexicons, we uploaded each paper's mentions table into the syuzhet R package (Jockers, 2015). This package measures polarity (Positive, Negative or Neutral) and identifies eight different emotions, when present, for each message. It follows the basic emotion theory proposed by Plutchik (Plutchik, 1962): Anger, Anticipation, Disgust, Joy, Fear, Sadness, Surprise and Trust.

We standardized the differences between Positive and Negative mentions of each paper using the following formula:

$$stPP = \frac{Pos - Neg}{TotalMentions}$$

Where:

“*stPP*” represents the Standardized Polarity Perception,

“Pos” represents the total number of positive mentions,

“Neg” represents the total number of negative mentions,

“TotalMentions” represents the total mentions obtained by an individual paper.

We then performed a temporal analysis of public polarity perception (*stPP*) of introgression as a function of temporal changes in the number of scientific evidence of its occurrence through DLNMs analysis. Lastly, we followed the same approach to analyse the temporal changes in public emotions that introgression studies raise in public opinion as a function of temporal changes in the amount of scientific evidence for its occurrence.

Finally, to understand whether public opinion and the emotions that a scientific paper about introgression elicits are conditioned by the taxonomic group under study, we established the relationship between global polarity perceptions and public emotions for each taxonomic group

under study. To illustrate this relationship, a chord diagram was produced using the Circlize R package (Gu, et al. 2014). This diagram was complemented with a linear regression, assessed through the coefficient of determination, between the standardized polarity perception of the public and scientists for each taxonomic group under study in each paper as a function of the phylogenetic distance from humans (Maroco, 2010).

2.3 Results

2.3.1 The scope and evolution of knowledge about introgression

Our systematic review showed that introgression studies were mainly carried out by researchers from North America (>50%) (Especially USA – with 167 published works) and Europe (>30%), with the remaining regions showing very few research teams working on introgression (Figure S2.1). The scientific knowledge covered case studies from multiple geographic areas: North America (28% of all case studies), Europe (19%), Africa (12%), Asia (9%), South America (8%), Central America (7%), Oceania (4%), Eurasia (4%), global (3%), Pacific Ocean (2%), Atlantic Ocean (1%) and Indian Ocean (1%) (Figure 2.1a).

The spatial bipartite association network showed a geographical proximity between case studies and research teams of 56.7%, meaning that most studies were performed by teams from the same geographical region (Figure 2.1a, table S2.2). There was also a strong association between the taxa studied and the geographic origin of the research teams (Figure S2.2). In North America, plants represented almost half of all studies (48%), especially angiosperms (38%). In Central and South America, invertebrates were the most represented taxa (43% and 48%, respectively), followed by birds (24%) and angiosperms (26%). Similarly, in Africa invertebrates represented 58% of all studies, followed by fish (21%). In Europe, like in North America, angiosperms were the most represented taxa (33%), but most studies focused on animals (63%). In Asia, mammals (36%), followed by fish (22%), were the most represented taxa, whereas in Oceania and Pacific islands all taxa had similar representation (angiosperms: 20%, birds: 20%, mammals: 16%, reptiles: 12% and insects: 12%) (Figure S2.2).

Globally, introgression has been demonstrated in a wide range of taxa since Bacteria (1%), Protists (<1%), Fungi (3%) and Plants (27%) until Animals (69%). Mammals were the most studied taxonomic groups with 34% of all studies, followed by angiosperms (84% of plant studies) and insects (27% of all animals). Yeast represented 67% of studies of introgression in Fungi.

We observed only a few studies published during the 20th century, with the highest prevalence in the 1990s, which saw an increase in published evidence for introgression, particularly from botanical controlled experimental studies involving the use of quantitative trait locus (QTL). A slight increase in the number of publications between 2000 and 2012 was observed alongside the rising of Methodological developments from the Human Genome project (<https://www.genome.gov/>).

The increased publication rate from 2012 was accompanied by a methodological revolution due to the generalization of genomic approaches, mainly through the advent of high throughput sequencing (HTS) and the use of Whole-Genome Sequencing and Single Nucleotide Polymorphisms (SNPs). These techniques proved to be effective in detecting cost-efficient way genomic areas under introgression and their adaptive value. Increasing in an exponential way through time (GLM_SNPs [family="poisson"]: $R^2=0.80$, $p<0.05$, GLM_Whole-Genome [family="poisson"]: $R^2=0.76$, $p<0.05$), these techniques also contributed significantly to an exponential growth of introgression knowledge, which is evident by the cumulative number of published papers over time (GLM_Total Number of Papers [family="poisson"]: $R^2=0.94$, $p<0.05$) (Figure 2.1b).

This growth pattern was evident in the different scientific fields (Anthropology, Phylogeny/Genealogy, Plant Sciences, etc.), and particularly in Evolutionary Biology. Bioinformatics was also identified as an emerging important field that became prevalent since 2016 (Figure 2.1c) (Pfeifer and Kapan, 2019).

The genomic revolution in introgression studies began in 2012, when the annual average of published papers increased from 1.9 ± 3.1 (1966-2011) to 34.5 ± 10.1 (2012-2019), equating to an average annual increase of 1824.14% of papers ($X^2_1= 97.37$, $p<0.01$). Temporal series projections, following the current publication growth rates, demonstrated an annual publication rate reaching 130 papers/year in 2030 (95% CI: 100-155) (Figure S2.3).

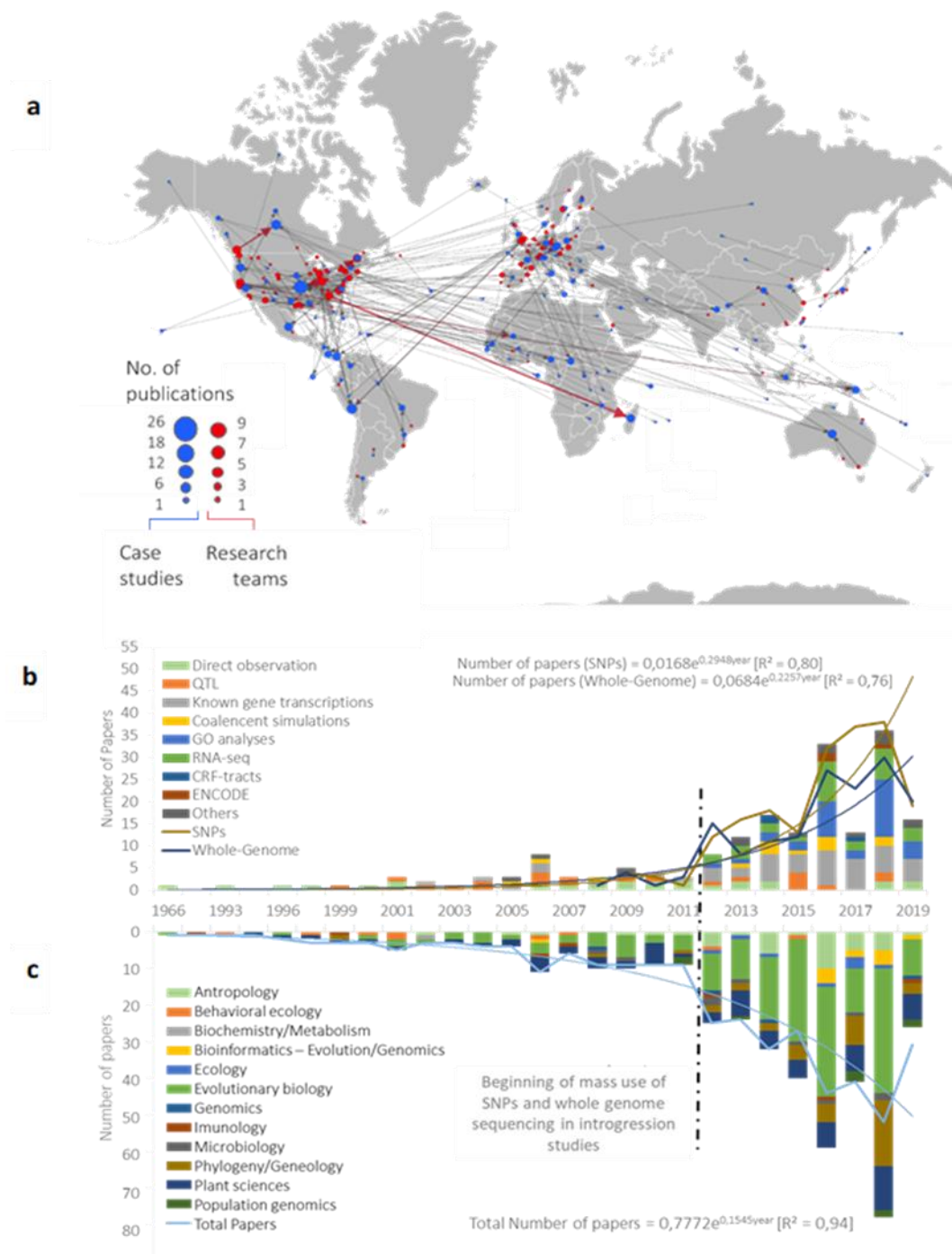


Figure 2.1 - Spatial networks of case studies featured in the meta-analysis (blue dots) performed by each research team with a specific host geographic location (red dots) (a). Case study locations were georeferenced based on the description of the study area provided within each paper. Circle sizes reflect the number of papers from a specific location. Arrows represent directional pathways from the team to the case study with line width representing the number of papers published by each team on the specific case study. Temporal changes in the number of published papers on introgression by methodology (b) and scientific field (c). The solid lines represent the correlation between the number of papers and time and the dashed line shows the tipping point, when the trend line started to show an exponential increase – representing the beginning of the genomic revolution in introgression studies.

2.3.2 Perceptions of scientists

Our results showed that 12 different scientific areas have been exploring introgression. The authors of 78% of the studies (N=280 papers) presented a scientifically grounded opinion about this topic. The argument polarity results show that the great majority of the authors had a positive opinion on introgression (node weight = 164). These results are mainly supported by authors' perceptions about the positivity of the impact of introgression on species' "adaptation to changing/new environmental conditions" (edges' weight = 143), a result influenced by studies in the scientific areas of Plant Sciences (edges' weight = 51) and Anthropology (edges' weight = 30). However, most of the studies were carried out in Evolutionary Biology (node weight = 140), where authors presented the greatest number of biological arguments to support the sense of the polarity of their opinions (node degree = 45), which were mainly positive (edges' weight = 67) (Figure 2.2a). Negative arguments were derived mainly from Evolutionary Biology (edges' weight = 9.0), Plant Sciences (edges' weight = 6.0) and Anthropology (edges' weight = 4.0). The main negative argument presented is that introgression may "act against speciation" (Figure 2.2a).

The total number of positive and negative arguments was similar (N = 24 and N = 20, respectively) even though in the total number of mentions, the latter were significantly lower (N = 296 and N = 78, respectively). Authors who presented mixed arguments (positive and negative) tended to use the greatest number of biological arguments (node degree = 56, betweenness = 1113.37) (Figure 2.2a).

Analysing the interest of the scientific community in the topic, we found a strong relationship between Altmetric.com scores and the traditional citation metrics (GLM [family="poisson"]: $R^2=0.72$, $p<0.05$) (Figure S2.4). The position of introgression papers in relation to the Altmetric.com score when analysed in comparison with all papers published in the same year, in the same journal, in both simultaneously and, especially, when analysed in relation to all published literature, revealed a bimodal distribution (Figure 2.2b). Although some studies have received little attention, a quarter of the papers were within the top 5% of the most cited and commented papers globally.

There was no clear relationship between the temporal increase in the number of papers providing evidence for introgression and authors' prevailing perception (GLM [family="Gaussian"]: $R^2=0.04$, NS) (Figure S2.5). The overall cumulative exposure–response relationships based on DMNL models revealed a slightly positive impact of the amount of evidence on author's perception about the prevalence of introgression (DLMN: $R^2=0.08$, NS) from "unknown" (0) to "few cases" (1) after a rate of 20 paper/year (95% CI: infrequent [-1] – common [2]) (Figure S2.6).

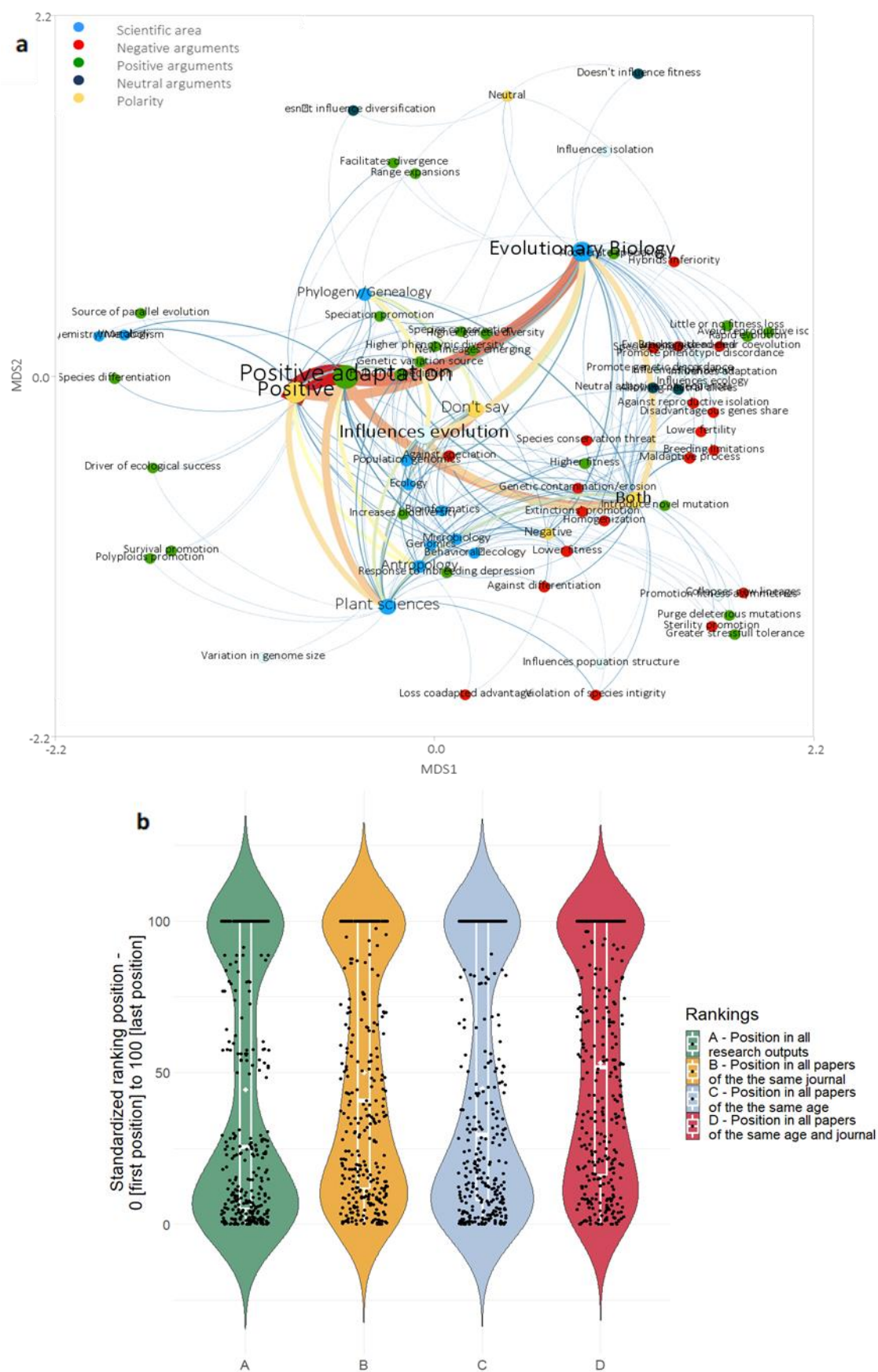


Figure 2.2 – Multi-Dimensional Scaling (MDS) tripartite network used to quantify the extent of connections between each scientific area, the polarity of authors' perceptions of introgression and their positive, negative and neutral biological arguments (**a**). Violin plots representing Altmetric Attention Score (ASS) compared to A) all research outputs scored by Altmetric.com, B) all papers of the same journal, C) all papers of the same age and D) all papers of the same age and journal (**b**). Standardized ranking position is represented between 0 (first position) to 100 (last position). Within them white solid lines boxplots include medians (horizontal white line) and average (white dot), boxes indicate quartiles and ranges, simultaneously.

2.3.3 Public perception and sentiment

A total of 14,214 mentions were recorded between 2000 and 2019 (including shares). Of these, 11,650 mentions were of introgression papers expressing some kind of opinion (polarity, emotions or both). The source of the vast majority of mentions was Social Media (N=11,628) followed by News and Blogs (N= 2,193) from traditional on-line newspapers. Academic sources were infrequently mentioned (N=145). Policy and Patents documents showed limited interest in the topic (N=24).

The overall cumulative exposure–response relationships, summing up the contributions for the 20 years of lag considered in the analysis, showed a tendency for scientific publications to have just a slightly positive impact on public opinion of introgression with polarity perception reaching 0.1 after a rate of 20 papers/year (95% CI: - 0.2 – 0.2) (Figure 2.3b). However, this impact does not seem to be immediate and presents a reversal of trend (from negative to positive) approximately following a delay of 7 years (Figure 2.3c). A temporal analysis showed that the increase in the amount of evidence for introgression has nearly no immediate impact on public polarity perception (Figure 2.3a). It occurs with a delay that promotes a high positive effect of scientific publications on the positivity of public opinion, increasing exponentially with high number of papers. However, there is almost no effect on public opinion from a reduced number of annually published papers, even after considering the delay (Figure 2.3).

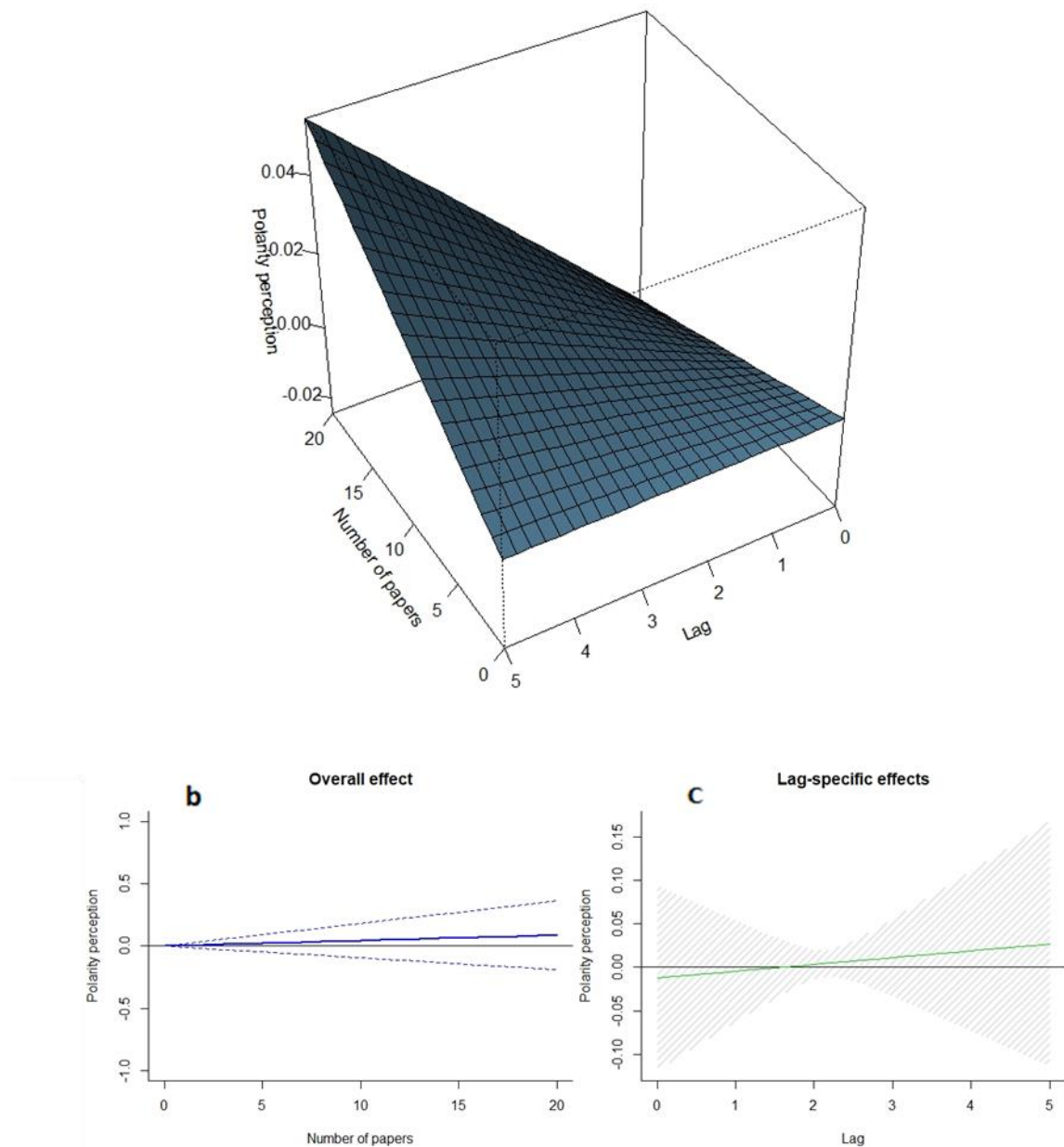


Figure 2.3 - Three-dimensional plot showing temporal changes (2000 to 2019) of the estimated exposure–lag–response association between the number of papers providing evidence for introgression and the standardized polarity perception by the public ($stPP$), with the average as reference and each Lag period corresponding to 4 years (a). Overall cumulative exposure–response relationships between the temporal changes (2000 to 2019) of the number of papers providing evidence for introgression and standardized polarity perception by the public ($stPP$), predicted from the model with no interaction (interpreted as the average), with 95% CI (b). Lag–response relationships between the number of papers providing evidence for introgression and $stPP$, with 95% CI and each Lag period corresponding to 4 years (c).

The publication of a large number of scientific papers had an immediate emotional public response (both negative and positive). After that, people's emotions began to immediately and exponentially diminish over time (Figures S7, S8, S9 and S10). Of the 9,867 mentions recorded that expressed some kind of emotions, with positive emotions being more frequent than negative ones (especially trust (N=1958 mentions), followed by anticipation (N=1,581 mentions) and surprise (N=1,314 mention). Anger (N=825 mentions) was the least evoked emotion by the papers. In contrast, fear (N=1,111 mentions) and disgust (N = 960 mentions) were the most often expressed negative emotions (Figure 2.4b).

This disparity between positive and negative emotions explained the greater number of mentions by expressing a global positive polarity about introgression (N=4,179 mentions). However, often the interest in the topic was not accompanied by a clear position on the orientation of the opinion, so neutral mentions were slightly higher than positive mentions (N=4,440 mentions, Figure 2.4b). On the other hand, there was a disparity in the attention given by the public when comparing the mentions about papers on vertebrates (N=8,850 mentions - including Humans - the majority of mentions [N=4,654]) with all the other taxonomic groups (Figure 2.4b).

The distribution of mentions by the different emotions and directions of polarity that the papers raise in the public followed the same pattern as their total number (more positive than negative) (Figure 2.4b). However, in all taxonomic groups and in the global studies about introgression, scientists held more positive opinions about introgression than the general public ($F(1, 10) = 54.260$, $p < 0.05$) (Figure 2.4a). Finally, contrary to what happens within the scientific community (GLM [family="poisson"]: $R^2=0.13$, NS), the polarity of public opinion (although always positive) has a positive correlation with the phylogenetic distance from modern human beings (GLM [family="poisson"]: $R^2=0.86$, $p < 0.05$). In other words, the more distant from humans the phenomenon occurs, the more people consider introgression to be positive (Figure 2.4a).

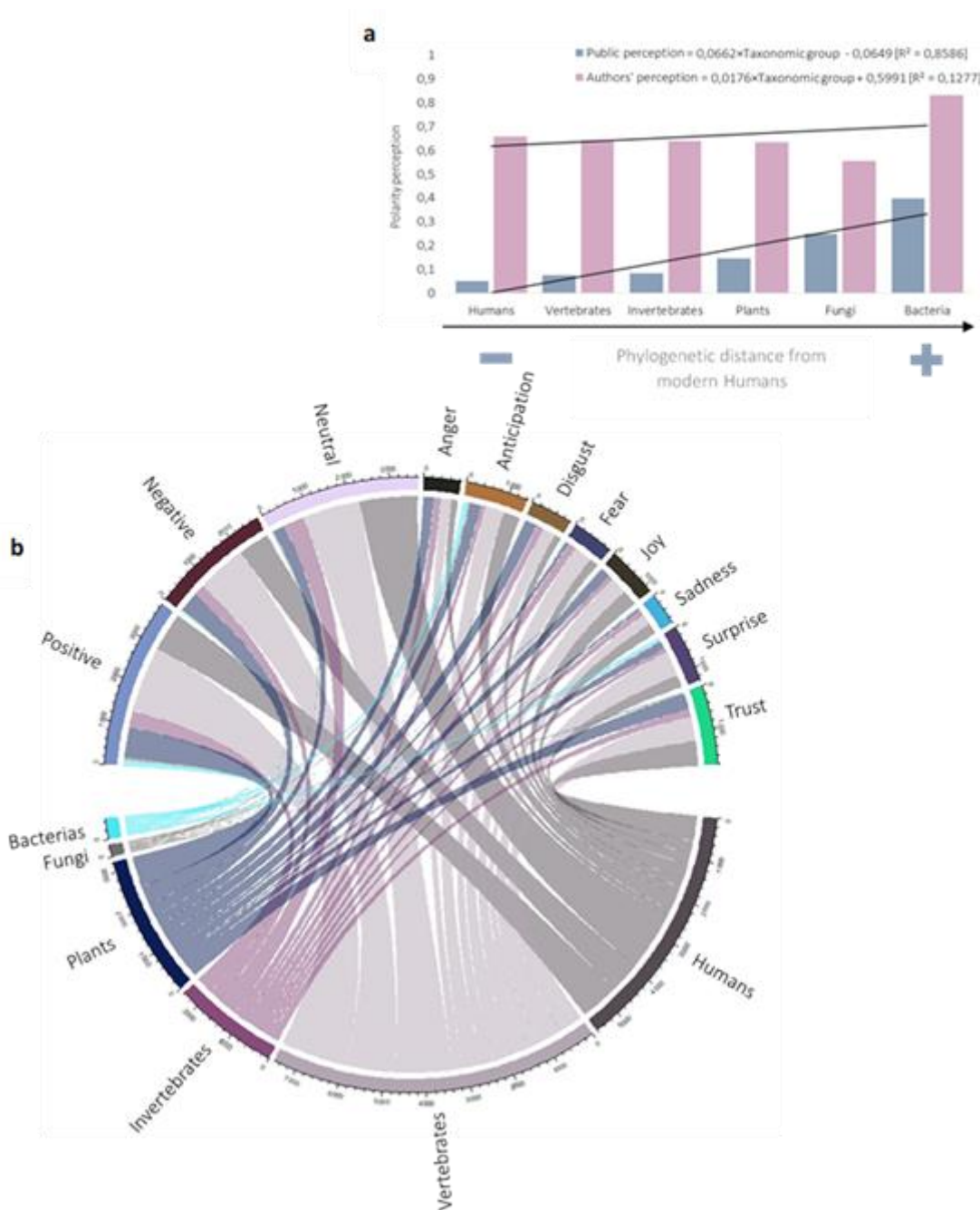


Figure 2.4 - Standardized Polarity Perception ($stPP$) correlation with taxonomic groups under study (a). Grey and pink bars represent public and authors' perception, respectively. Solid lines depict the relationship between their $stPP$ and the different taxonomic groups under study based on the phylogenetic distance from modern Humans. Hierarchical network chord diagram with expanded endpoints illustrating public total polarity perception and expressed emotions about introgression papers from different taxonomic groups under study (b).

2.4 Discussion

2.4.1 The scope and evolution of knowledge about introgression

The geographical scope of taxa under study is widespread, despite a slight tendency for geographical proximity between case studies and research teams. This shows that there have been no major geographical biases in introgression studies. Scientific interest in introgression has been increasing over the past two decades. However, since 2012 the number of papers published per year began to increase exponentially. This turning point marks the beginning of the genomic revolution in introgression studies. Most likely, it occurred in response to the increased use of whole genome sequencing and reduced representation genome sequencing methods, such as restriction-site associated sequencing (RADseq), and the development of new high throughput sequencing platforms and the subsequent reduction in sequencing costs (Hayden, 2014). The cost per sequenced genome was dropped from US \$3 billion to less than US \$1,000 from 2000 to 2012 (Hayden, 2014). These methodological and sequencing advances have enabled the scientific community to compare the genomes of a large number of individuals, thus increasing the probability of identifying shared genomic regions under selection (Kuhlwilm *et al.* 2019, Ryan *et al.* 2018). Our temporal series models predicted that this trend will continue through the next decade (Figure S2.3, Supplementary material) in response to the growing interest in the topic and the widespread use and development of these genomic analysis tools and sequencing platforms.

2.4.2 What do we think about introgression?

Introgression has received considerable attention from both the scientific community and the public, with high average rankings compared to the total current scientific literature. Several papers ranked within the top 5% most cited and commented papers globally.

Despite the exponential increase in scientific evidence since 2012, the genomic revolution does not seem to have changed authors' perception of the prevalence of introgression in nature, being frequently underestimated with authors citing difficulties in demonstrating its presence (Reid *et al.* 2012). In terms of polarity in the opinions of the scientific community about introgression, the total number of positive and negative arguments is rather balanced. However, positive arguments are clearly most mentioned among scientists. Authors' perception of whether the impact of introgression on species was positive is mainly based on potentially beneficial outcomes for "species adaptation to changing/new environmental conditions" (Acosta and Premoli, 2018, Boratynski *et al.* 2014, Hamilton *et al.* 2013, Lewontin and Birch, 1966, Melo-Ferreira *et al.* 2014). The main negative argument put forward by scientists is that introgression may have negative impacts because it "acts against speciation" (Naisbit *et al.* 2003, Payseur *et al.* 2004).

The source of public opinion about introgression studies was dominated by social media (and mainly Twitter), followed at great distance by traditional on-line newspapers. Academic media sources and policy documents infrequently refer to introgression papers, showing limited interest in the topic. This seems to indicate that there is a much greater interest among the general public in the subject than the importance given to it by traditional media and institutions both in terms of dissemination and socio-political orientations.

The increased number of papers providing scientific evidence for introgression led to marked increase in positive public opinion, however, only following a seven year delay. There was either no initial response or even an initial negative impact on people's perception. Empirical literature refers to the difficulties of investigating research phases impacting on society (Trochim, 2010). On some occasions, delay of scientific translation should be necessary to ensure the accuracy and efficacy of new evidence or advances (Morris et al. 2011). However, it is relatively accepted by both the scientific community and policy that quick translation of research into practice is somehow positive (Morris et al. 2011). Nevertheless, the research translation process is known to undergo long periods of time-lag (Kilbourne et al. 2020, Morris et al. 2011).

Our results demonstrate that only the annual publication of a sufficiently large number of papers providing evidence for introgression influences public perception of its merits and consequently of genetic miscegenation. This trend of increase in positive opinions is probably to accentuate in the future if the number of publications on the topic will continue to increase exponentially up to at least 2030, as we have predicted.

For all taxonomic groups, and overall in studies of introgression, there is a significant disparity between the opinions of scientists and the general public, whereby scientists hold more positive opinions. This disparity between the opinions of scientists and the public follows the trend of other studies on public perception about scientifically controversial topics, such as the origin of climate change and the risks of nuclear power (Taylor et al. 2014).

There is a taxonomic bias revealed by the great disparity in the attention given by the public to papers on vertebrates (mainly on humans) compared to all other taxonomic groups (Troudet et al. 2017). Regardless, papers referring to all taxonomic groups frequently receive positive opinions from the public, mostly eliciting positive emotions (primarily anticipation and trust). The polarity of public opinion (although always positive) positively relates to the phylogenetic distance from human beings, whereby the more distant the taxa are from humans, the more people consider introgression as positive. This pattern can be explained by different degrees of bias in the perception about genetic miscegenation according to taxonomy once societal inclinations strongly correlate with taxonomic bias (Troudet et al. 2017). Groups phylogenetically closer to human beings are the target of greater attention and importance whereas they are simultaneously the target of higher degrees of prejudice (Troudet et al. 2017). Bias has the potential to inappropriately influence

the scientific process (Fanelli et al. 2017) because “scientists are human beings rooted in cultural contexts” (Gould, 1978). However, the scientific method usually shield scientists from the consequences of their own cultural biases (Lewis et al. 2011).

2.4.3 Public sentiment in response to evidence of introgression

Scientific work in psychology has pointed to the relevance of emotions in addition to cognition in public perception and decision-making (Kahneman, 2011, Stanovich and West, 2008a). The publication of a large amount of scientific evidence for introgression has an immediate increasing effect on the emotional public response (both negative and positive). People's emotions rise immediately and diminish exponentially over time, showing an intense, but temporary, emotional cascade. The first reaction responds to an intuitive mode of thought that is fast, involves limited judgement, and is driven by emotions. It is later replaced by an analytical mode of thought (based on evidence), which is more rational, slower, involving more effort and deliberate reasoning (Kahneman and Frederick, 2002). This replacement over time can help explain the increase in positive polarity in the medium-long term. Time-lag helps to clarify this change in the mode of thought, from instinctive to analytical (Whitmarsh, 2011), once emotion based reactions decrease over time (Taylor et al. 2014).

The overall cumulative exposure–response relationships of all sentiments expressed by public mentions about introgression papers, summing up the contributions for the 20 years of lag considered and analysing their balance with the increase of scientific evidence published over time, show just a slightly positive impact on the expression of all positive emotions (mainly anticipation and joy). According to the probabilistic sequence of events involved in the development of an emotion, anticipation responds to stimulus events like “novelty” promoting the behaviour of examining and the effect of exploration whereas joy explains the pride of achievement (Izard, 2007). This means that the increase in evidence outweighs the potential negative effect of time on people's positive emotional response, allowing them to experience the urge to learn more about the benefits of genetic miscegenation and taking from there the pride of discovery. However, the same trend happened for two negative emotions (disgust and fear). Disgust is a response to a “gruesome object” and promotes rejection whereas fear explains flight for safety in response to an “obstacle” and stimulates destructive feelings (Izard, 2007). Despite occurring to a lesser extent compared to positive emotions, paradoxically, the increase in evidence, by offsetting the negative effect of time, raises a slight increase in some people in the identification of genetic miscegenation as being susceptible to repugnance. It stimulates looking at it as an obstacle to their safety and boosting reactions of rejection and destructive opinions.

In contrast, the increasing number of papers over time influences negatively public emotions of sadness and anger. Sadness responds to stimulus events like a "life-changing loss" promoting the effect of reintegration, whereas anger explains the frustration in response to blocked goals (Izard, 2007). In both cases, the increase in evidence complements the effect of time in decreasing such reactions to genetic miscegenation.

The individual proximity to the facts under evaluation, derived from personal experience or shared by mimicry, conditions the emotions that are expressed. For example, social groups that have experienced the effects of extreme weather events (e.g. wildfires or severe droughts) tend to experience higher levels of anger, sadness and fear when confronted with climate change issues (Loureiro and Alló, 2020). In contrast, groups that have never been confronted with the consequences of nuclear accidents tend to have higher levels of trust in nuclear energy (Loureiro and Alló, 2020).

On the other hand, studies show that ignorance is at the root of stereotypes and prejudice (Matusitz, 2012) and that these influence negative emotions like disgust and fear (Dasgupta et al. 2009), which can only be countered by high degree of communication (Matusitz, 2012, Nshom and Croucher, 2017). However, the emotions also vary according to the signal of potential threat. For example, disgust increases bias against homosexuality, but anger did not. Instead, anger increased bias against ethnic minorities (e.g. Arabs) in western societies, but disgust did not (Dasgupta et al. 2009). In this context, genetic miscegenation is more susceptible to prejudice derived from disgust than anger.

Overall, public interest in introgression leads to an immediate rise of different emotional reactions that increase with increasing number of scientific evidence on the topic. Immediately after that emotional response, a cascade of divergent opinions spreads by emotional contagion and mimicry among social groups (Ferrara and Yang, 2015, Sonnby-Borgström et al. 2003) due to different social norms and circumstances of the common identities they share within (Pagel, 2012). However, negative emotions are potentially oversized because reactions to negative news tend to be stronger (Soroka et al. 2019).

2.4.4 Caveats and limitations

The impact of scientific developments on society is often difficult to measure mainly because data on perception of scientific facts are hard to obtain and work with. Using algorithms like those employed by Altmetric.com, it is possible to compile and organise all information available online about a set of papers retrieved from a systematic search of a scientific subject. When analysing such a large amount of data, the relevance of subjectivity decreases when the intention is to find general trends. Still, even approaches designed to mimic and replace the human brain still have important limitations. In sentiment analysis, for example, there are still limitations in

the interpretation of forms of literary expression, such as irony or sarcasm (Sykora et al. 2020). However, recent studies showed that the percentage of sarcastic and ironic content in social media is normally very low (Sykora et al. 2020). In traditional media and official documents their use should be even lower. So, in large datasets, sarcasm, irony and even the use of humour may be much less of a concern than was previously thought (Puschmann and Powell, 2018). Given that these expressions are probably rare in the dataset covered in our study, this is unlikely to influence the results of the general trends.

We assume that written mentions are behaviours that reflect the opinions or attitudes of the writer. Yet, opinion is usually associated with a certain degree of subjective judgment (Sacks and Gary, 2012). On the other hand, the subjectivity of individual judgment is also subject to conflicts with social norms, political and cultural contexts (Dange, 2016). In other words, we could see a change in social behaviour (such as the proportional increase in positive mentions about introgression) due to a potential change in social norms (e.g. greater tolerance or acceptance/appreciation of genetic miscegenation) derived from the increase in the number of scientific evidence, but it may still not mean that beliefs and/or mentalities are in fact being changed (Schultz et al. 2007). Therefore, it seems probably that the publication of a large amount of scientific evidence in the medium-long term has promoted a change in opinion polarity about introgression and consequently about genetic miscegenation after undergoing an initial emotional response and a certain degree of rejection. However, whether this can promote an effective change in people's mentality and beliefs will require further studies.

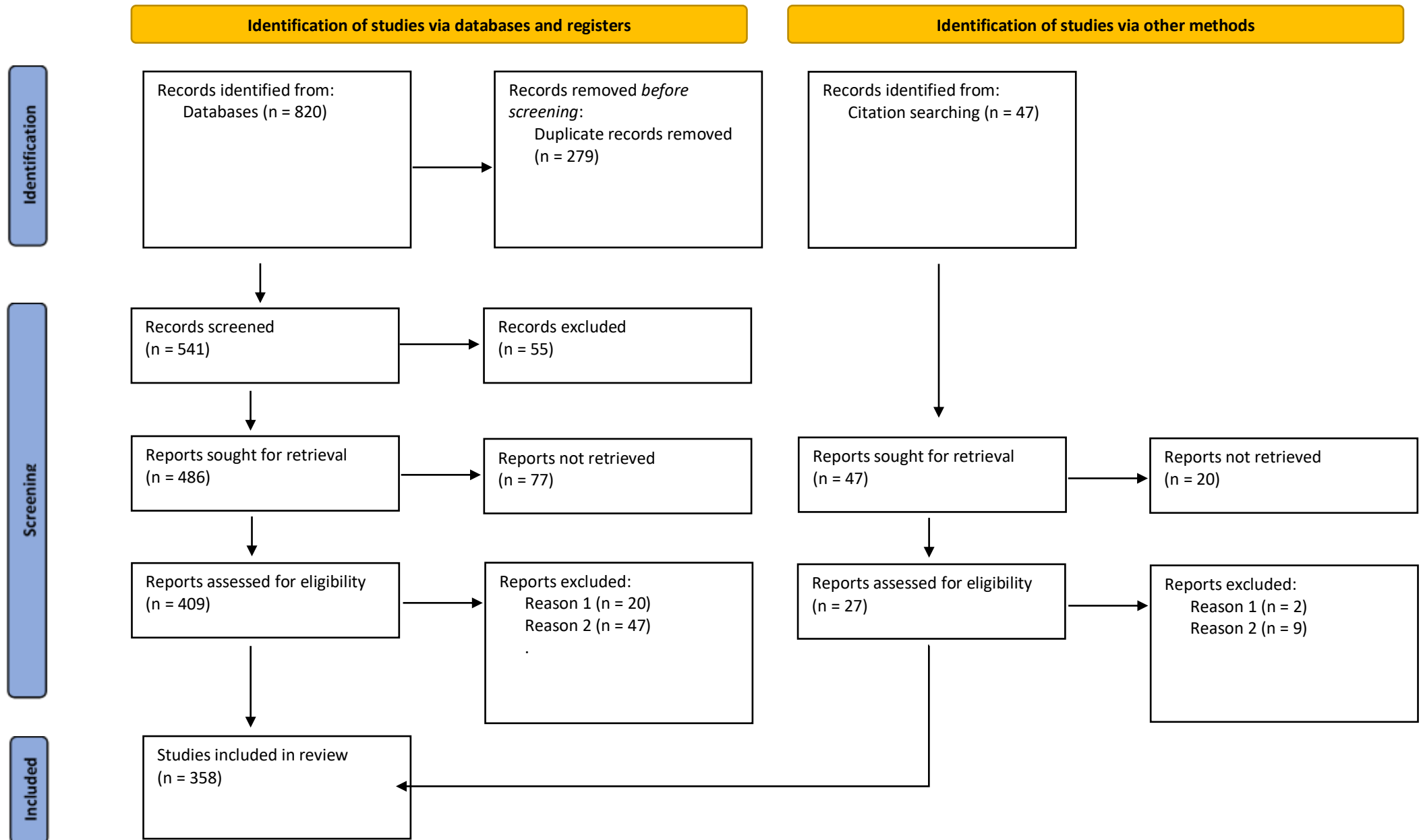
2.5 Conclusions

We show that the genomic revolution provided mounting evidence for introgression, which is mainly understood by the scientific community as particularly beneficial for species ability to adapt to changing or new environmental conditions. Scientific evidence suggests that introgression, or even genetic miscegenation, from a scientific point of view, represents a key natural evolutionary process. The exponential increase in scientific evidence for the beneficial effects of genetic miscegenation led to more positive public perception of the topic in the medium-long term. Therefore, we argue that continuing the development of knowledge on introgression will allow Evolutionary Biology to scientifically refute eugenics and other evolutionary theories that promote taxa 'purity'. In the past, these ideas were employed to justify racism and other forms of discrimination. However, in light of current scientific evidence, only bias in perception appears to stand in the way of accepting the fundamental role that genetic miscegenation plays for life.

Acknowledgments

PH and HRa were funded by the Portuguese Foundation for Science and Technology (FCT) with a PhD grant (SFRH/BD/117979/2016 and SFRH/BD/124367/2016, respectively). HRe was also funded by FCT (DL57/2016/EEC2018/07). OR was funded through a Natural Environment Research Council Independent Research Fellowship (NE/M018660/1). ASV was supported by FCT through Stimulus of Scientific Employment, Individual Support (reference 2020.01175.CEECIND). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017. We also thank the company Altmetric.com for approving our project and granting us free access to Altmetric.com explorer and its information.

Supplementary Material



WebFigure 1 - PRISMA 2020 flow diagram. *Adapted from:* Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 2021;372:n71. doi: 10.1136/bmj.n71. For more information, visit: <http://www.prisma-statement.org/>

Search details

We used the following search string for on-line databases:

“Topic=(*hybrid** AND *adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest** NOT *exotic*)
OR Topic=(*adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest** NOT *exotic*)”

We defined some keywords as strict retention criteria: *Adapt** (all terms related to adaptation, adaptive, etc.), *Introgress** (all terms related to introgression, introgressive, etc) and *Genom** (all terms related to genome, genomics, etc.). We also used as non-strict retention criterion for the term *hybrid** (all terms related to hybrids, hybridization, etc.) that could be present together with the previous ones or not. We excluded all breeding contacts between taxa under direct human interference (breeding manipulations between species that do not naturally interbreed, genetic manipulation, invasive species scenarios, etc.). We used the following keywords as strict exclusion criteria: *Invas** (all terms related to invasion, invasive species, etc.), *Exotic* and *Domest** (all terms related to domestic species, domestication, etc.).

We defined the expression “*Adaptive Introgression*” as a keyword used as strict retention criteria searching for relevance grey literature through Google and Google scholar.

Table S2.1 - Full list of information and the total number of papers that includes each category extracted from each reviewed paper.

Categories of information	Variables extracted	Classes used	Number of papers
Bibliographic information	✓ Authors		358
	✓ Year		
	✓ Title		358
	✓ Journal		358
	✓ Research area		358
	✓ Type of publication		358
	✓ Location of author's institution		358
Authors' initial perception about introgression	✓ Polarity	Positive	351
		Negative	
		Both	
		Neutral	
	✓ Why positive?		250
	✓ Why negative?		
	✓ Why neutral?		78
	✓ Prevalence		129
		Very rare [-3]	135
		Rare [-2]	
		Infrequent [-1]	
		Unknown [0]	
		Few cases [1]	
		Some cases [2]	
		Common [3]	
	✓ Semantics	Many cases [4]	
		Ubiquitous [5]	
		Hybrid* terms used	358
		Hybrid* terms not used	
Taxa under study	✓ Main taxonomic group	Animal	355
		Plant	
		Fungi	
		Protists	
		Bacteria	
	✓ Families		
	✓ Species pairs		

			355
			355
Time and space of introgressions' case studies	✓ Epoch	Ancient	355
		Recent	
		Both	
	✓ Continent		355
	✓ Approximated location		355
Methods used	✓ Type of experiment	In-situ	351
		Ex-situ	
		Both	
	✓ Type of introgression markers	Quantitative Trait Locus	347
		Microsatellites	
		Mitochondrial DNA	
		Ribosomal DNA	
		Single-Nucleotide Polymorphisms	
		AFLP	
		PCR amplification	
		Electrophoresis (DGGE)	
	✓ Whole-genome sequencing	Karyotypes	347
	✓ Reference genome	Performed	
		Not performed	165
		Available	
		Not available	

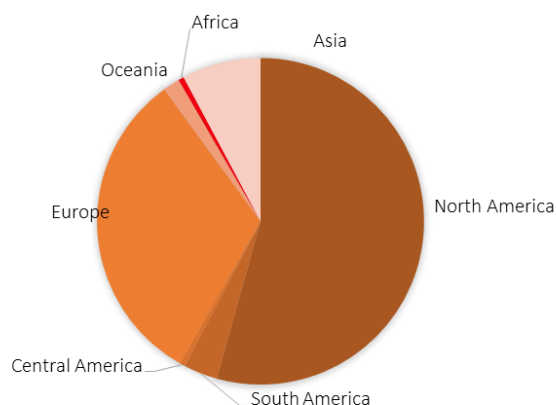
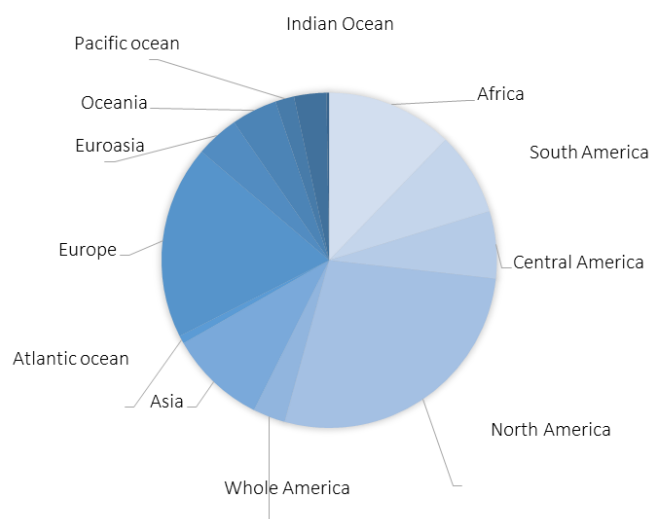
Research teams'
originCase studies'
distribution

Figure S2.1 - Distribution of reported introgression case studies by research team origin (top plot) and geographic location (plot from below).

Table S2.2 - Total number of papers produced by teams from specific geographic regions on case studies located in other geographical locations. 26 papers analysed more than one case study and three papers did not include a case study, resulting in a total of 388 case studies.

Research Team	North America	South America	Central America	Europe	Oceania	Africa	Asia	N _{br} of case study
Case Study								
North America	93%	0%	0%	6%	0%	0%	1%	104
South America	27%	46%	4%	23%	0%	0%	0%	26
Central America	62%	10%	5%	24%	0%	0%	0%	21
Europe	19%	0%	0%	81%	0%	0%	0%	73
Oceania	41%	0%	0%	29%	29%	0%	0%	17
Africa	55%	0%	0%	40%	0%	4%	0%	47
Asia	10%	0%	0%	14%	0%	0%	76%	58
Indian Ocean	0%	0%	0%	67%	0%	0%	33%	3
Atlantic ocean	50%	0%	0%	50%	0%	0%	0%	2
Pacific ocean	57%	0%	0%	29%	0%	0%	14%	7
Whole world	91%	0%	0%	9%	0%	0%	0%	11
Whole America	50%	0%	0%	50%	0%	0%	0%	4
Eurasia	53%	0%	0%	27%	0%	0%	20%	15
N _{br} of papers per research team	195	14	2	120	5	2	50	388

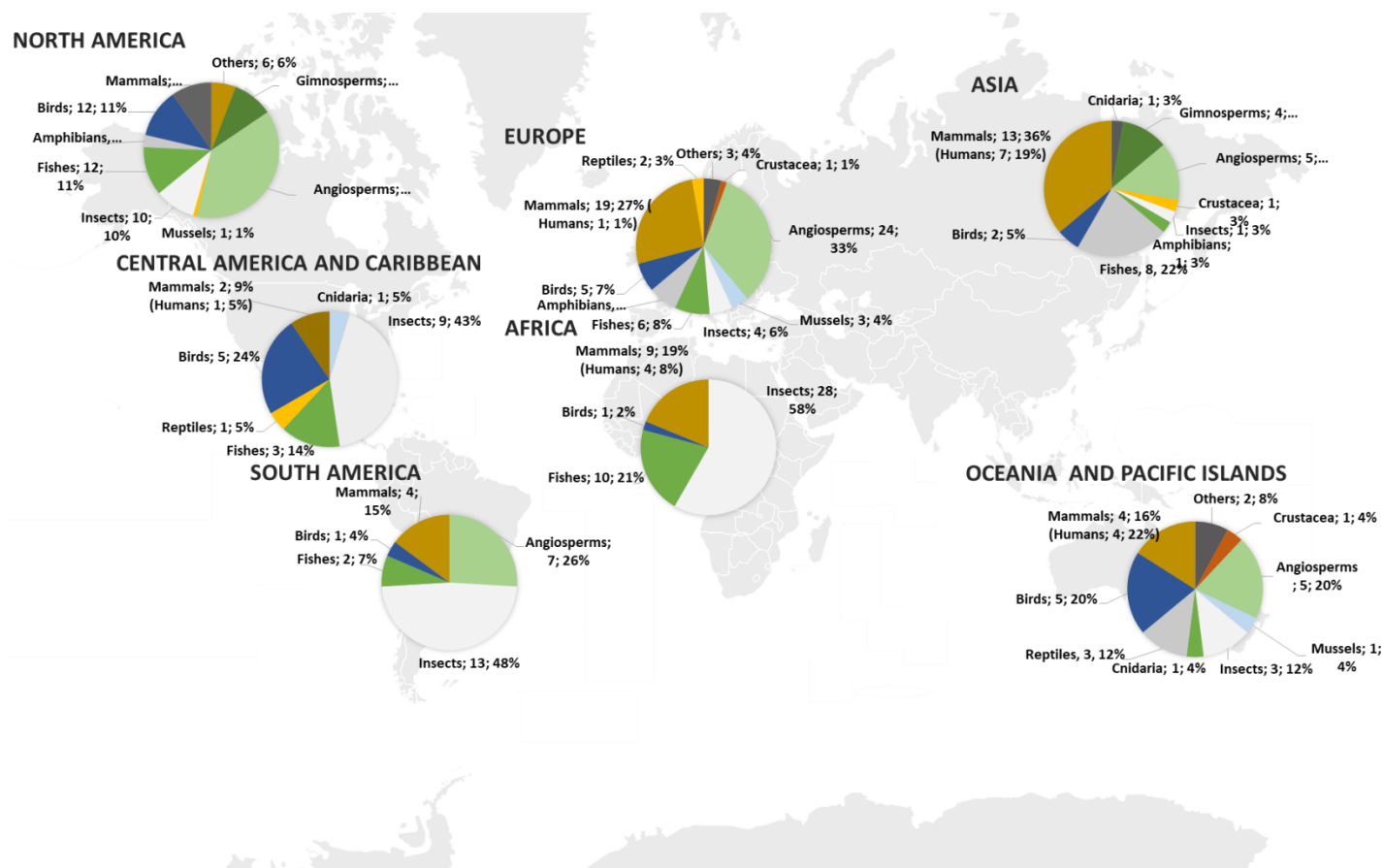


Figure S2.2 - Spatial distribution of reported introgression case studies by taxa.

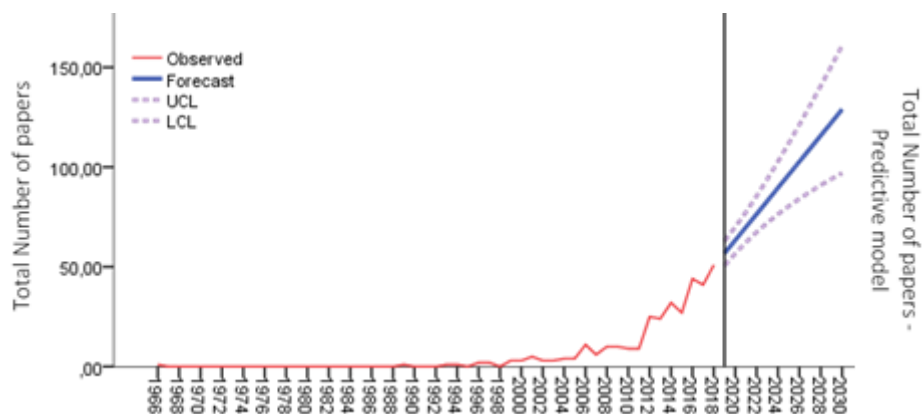


Figure S2.3 - Predictive model of temporal series projections (until 2030), performed by the Expert Modeler Method.

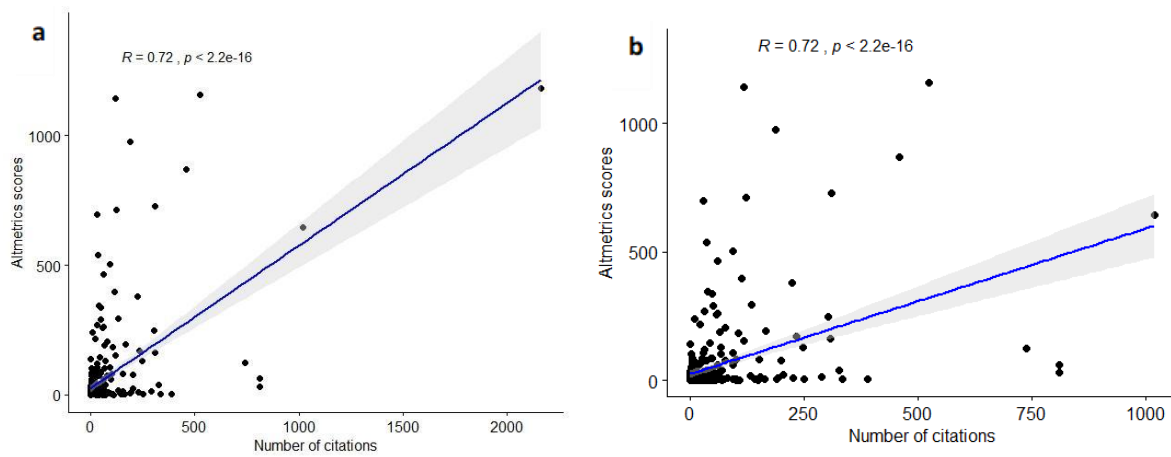


Figure S2.4 - Altimetric.com Attention Score (ASS) correlation with citation count (traditional bibliometric for research ranking) in the literature through Spearman correlation analysis. The solid blue line depicts the relationship between ASS and the number of citations with the main outlier (Green *et al.* 2010) (a) and without it (b).

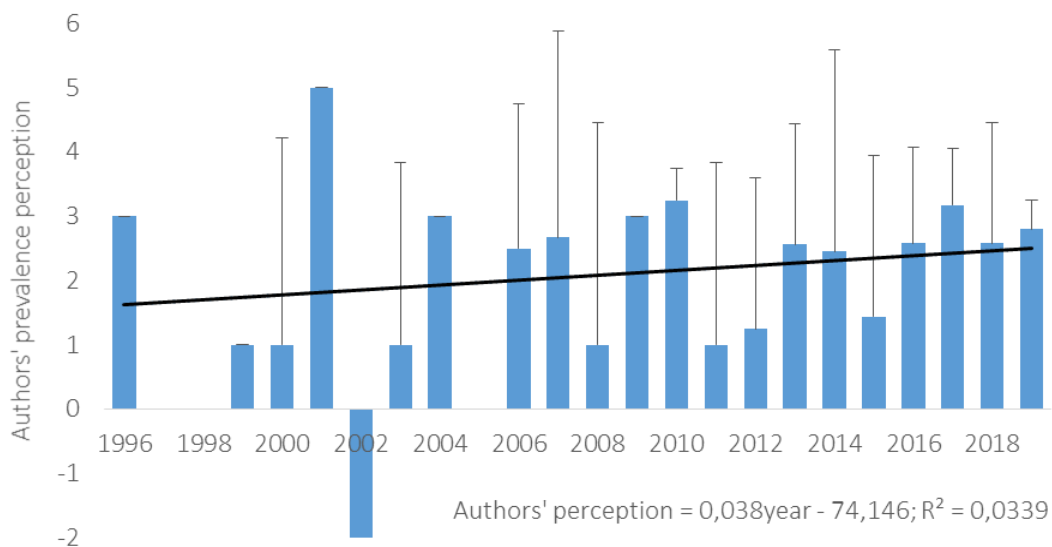


Figure S2.5 - Annual changes in authors' average perception of the prevalence of introgression, categorized into nine classes: very rare [-3], rare [-2], infrequent [-1], unknown [0], few cases [1], some cases [2], common [3], many cases [4] and ubiquitous [5]. The solid line depicts the relationship between the perception ranking over time.

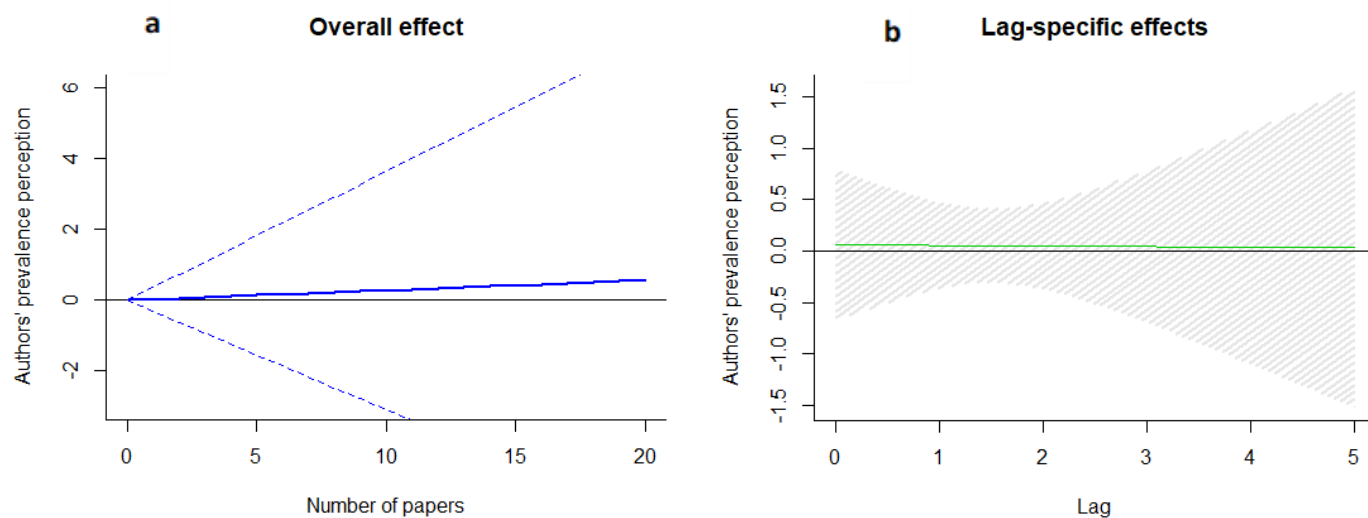


Figure S2.6 - Overall cumulative exposure–response relationships between the temporal change in the number of papers providing evidence for introgression and authors' prevalence perception predicted from the model with no interaction (interpreted as the average), with 95% CI (**a**). Lag–response relationships between the number of introgression evidence (number of papers) and authors' perception about its prevalence, with 95% CI (**b**).

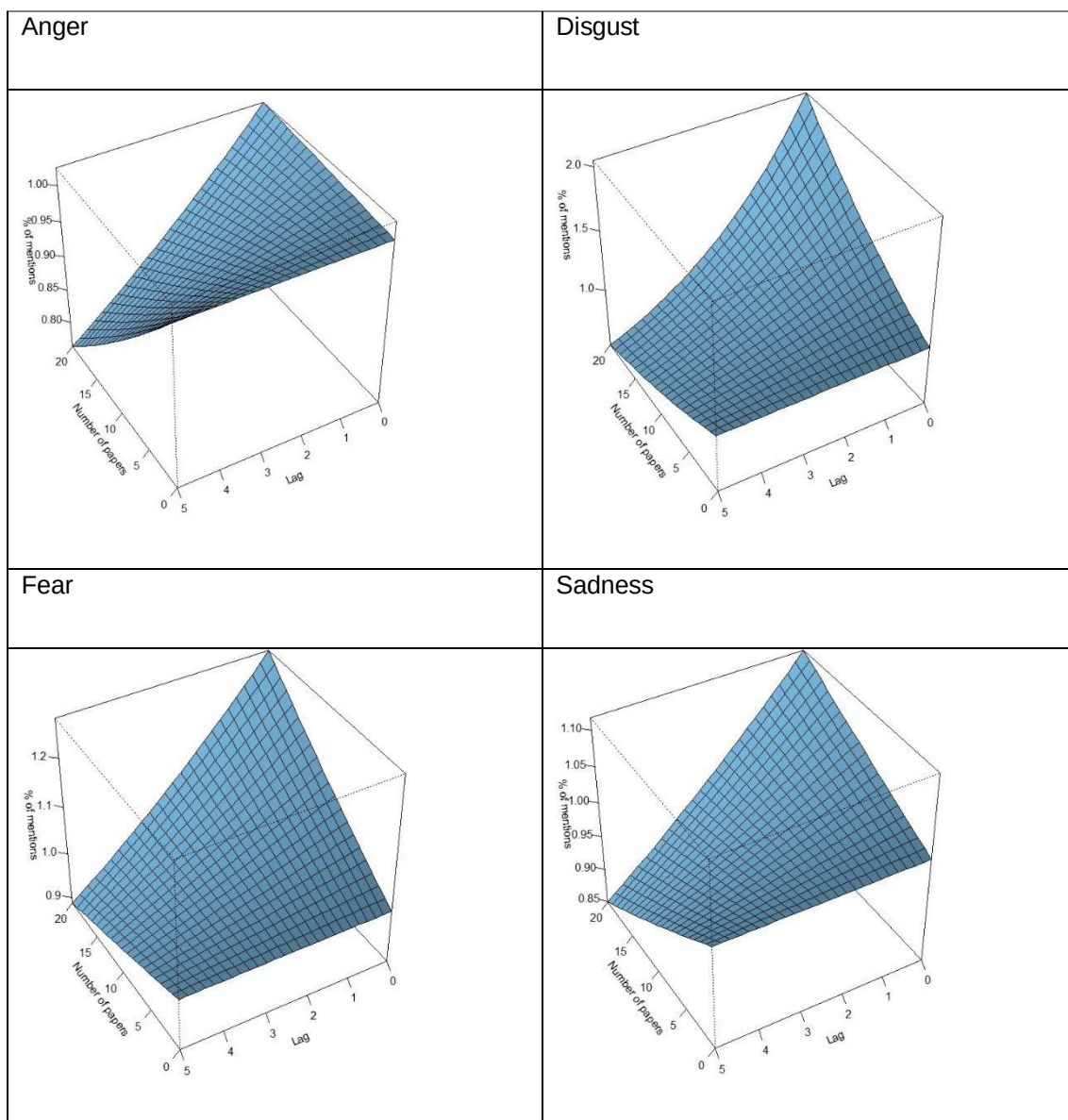


Figure S2.7 - Three-dimensional plots showing temporal changes (from 2000 to 2019) in the estimated exposure–lag–response association between the number of published papers providing evidence for introgression and the percentage of mentions expressing negative emotions (anger, disgust, fear and sadness) of the total annual mentions expressed by the public about them, with the average as reference, and each Lag period corresponding to 4 years.

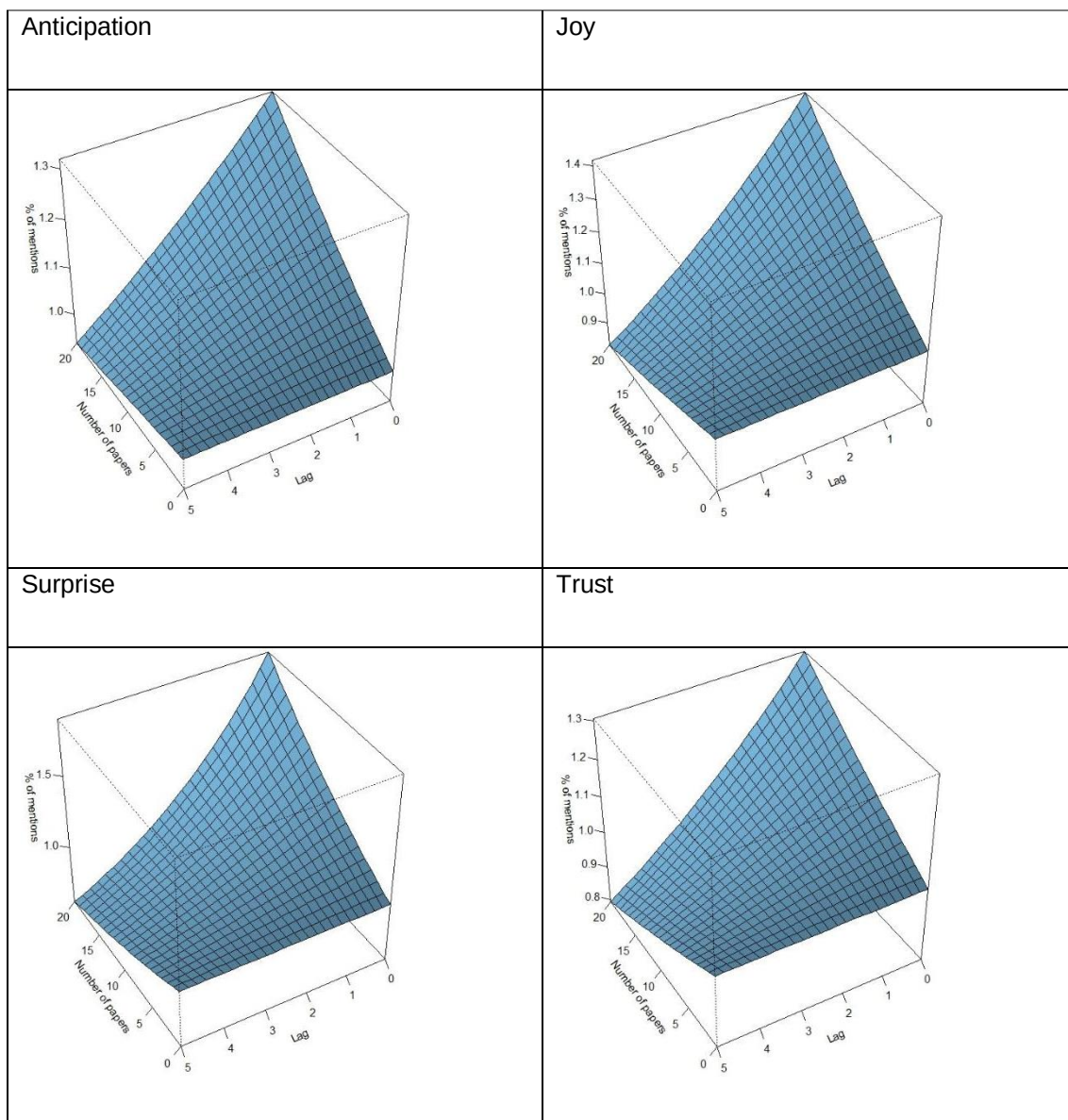


Figure S2.8 - Three-dimensional plots showing temporal changes (from 2000 to 2019) of the estimated exposure–lag–response association between the number of published papers providing evidence for introgression and the percentage of mentions expressing positive emotions (anticipation, joy, surprise and trust) of the total annual mentions expressed by the public about them, with the average as reference, and each Lag period corresponding to 4 years.

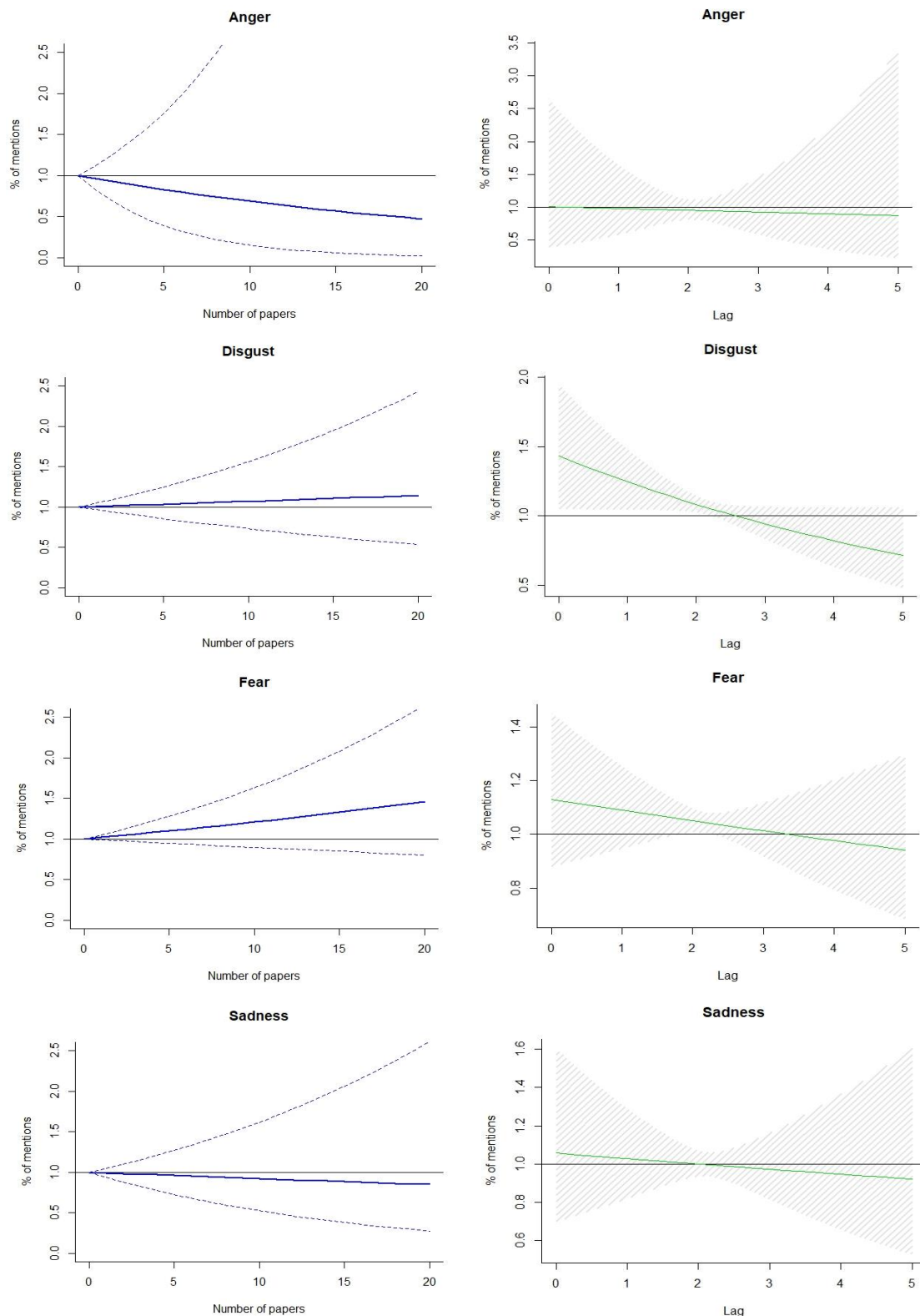


Figure S2.9. Overall cumulative exposure–response (left plots) and Lag–response (right plots) relationships between temporal changes (from 2000 to 2019) in the number of papers providing evidence for introgression evidences and the percentage of mentions revealing negative emotions (Anger, Disgust, Fear and Sadness) predicted from the model with no interaction (interpreted as the average), with 95% CI.

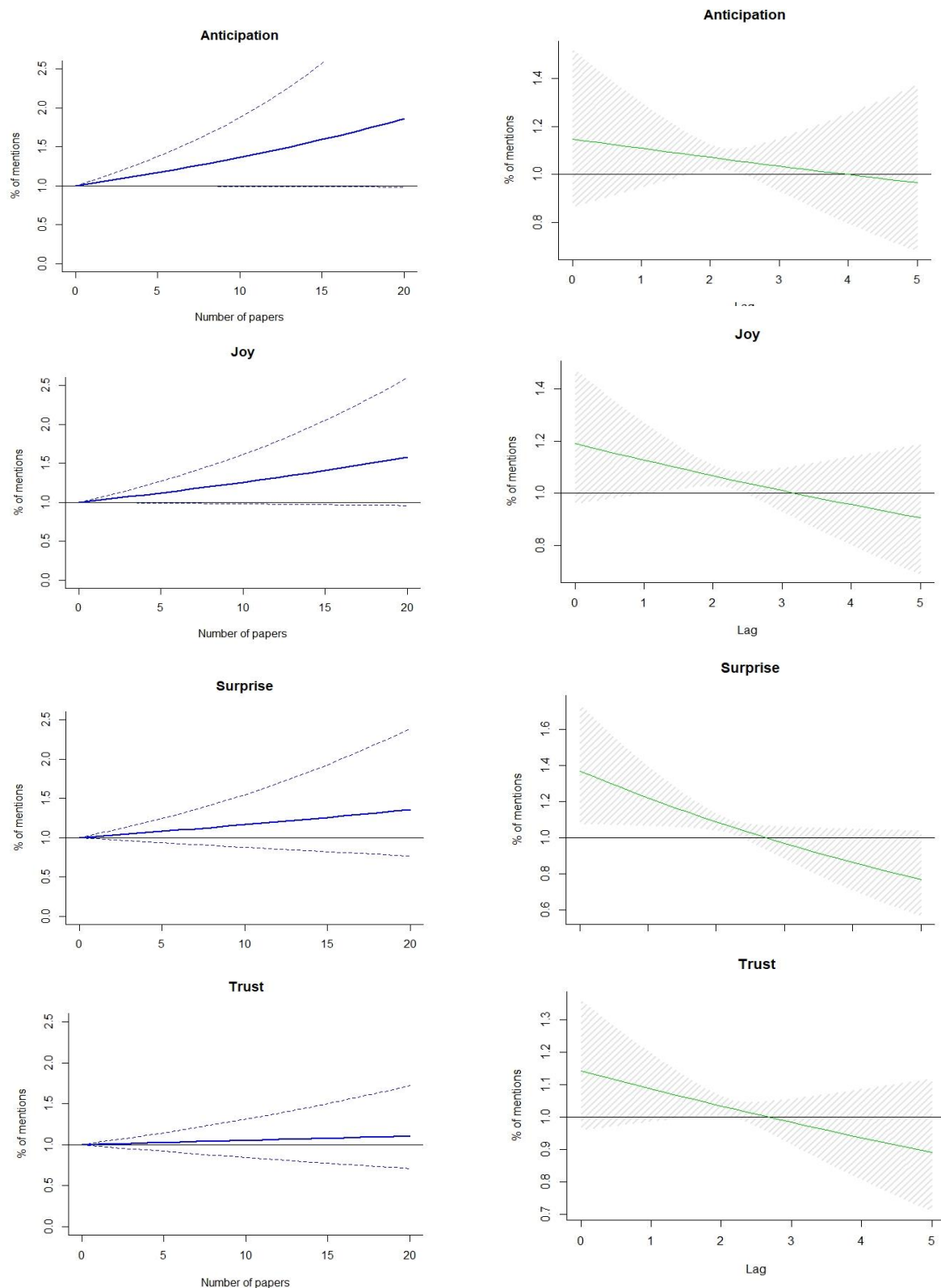


Figure S10 - Overall cumulative exposure-response (left plots) and Lag-response (right plots) relationships between the temporal changes (from 2000 to 2019) in the number of introgression evidences (number of papers) and the percentage of mentions revealing positive emotions (Anticipation, Joy, Surprise and Trust) predicted from the model with no interaction (interpreted as the average), with 95% CI.

Chapter 3

From Genomes to Ecology: Meta-analysis of Knowledge Trends about Introgression Mechanisms

Pedro Horta, Helena Raposeira, Javier Juste, Orly Razgour and Hugo Rebelo

Horta P., Raposeira H., Juste J., Razgour O., & Rebelo H.. From Genomes to Ecology: Meta-analysis of Knowledge Trends about Introgression Mechanisms. *Final stages of submission*

Keywords: Biological organization, Introgression mechanisms; Knowledge trends; Meta-analyses, Structural complexity

Abstract

Natural hybridization has historically been a controversial topic, subject to disagreement regarding its consequences. However, a recent proliferation of evidence demonstrate that introgression may enable some closely-related species to share and incorporate alleles associated with traits adapted to new environmental conditions. Understanding how introgression can lead to adaptation and evolution, will require an investigation into essential mechanisms behind introgression. On the other hand, merging the knowledge on the general mechanisms from which scientists have been interpreting patterns and causes of introgression, across the tree of life, can provide a general overview of the major hypothesis to test with empirical data.

We carried out a systematic review and multidimensional meta-analysis, showing the presence of introgression is a function of the structural complexity of organisms. While in prokaryotes introgression operates fundamentally into genomes, for eukaryotic species it is driven by cytonuclear interactions. In multicellular eukaryotic species with heteromorphic sex-chromosomes introgression is subject to genomic pressures over breeding physiology and conditioned by demography. In more recently evolved and complex eukaryotes species, sexual behaviours condition the occurrence, direction, extent and functionality of introgression.

Our results demonstrate that introgression may act in balance with species divergence. Through interconnected mechanisms with divergent, e.g. assortative mating *versus* sexual selection, introgression increases in complexity across the levels of biological organization, from genomics to behaviour. We also demonstrate that environmental conditions promote and propel introgression, which, in turn affects species and their relationship with their environment, independently of species' structural complexity. We argue that the balance between divergent processes and introgression makes speciation a flexible process mediated by environmental changes, a common pattern shaping the paths of evolution across the entire tree of life.

3.1 Introduction

Repeated interbreeding can result in closely-related species sharing genetic material through introgression (Arnold, 2004; Hedrick, 2013; Hoffmann and Sgrò, 2011; Powell et al., 1999; Rieseberg et al., 2007; Seehausen, 2004). Introgression has been historically regarded as a homogenizing process (Latch et al., 2006; Oliveira et al., 2008) that counteracts local selection pressures, decreasing the fitness of diverging populations by introducing alleles outside the local adaptive range (Bolnick and Nosil, 2007; García-Ramos and Kirkpatrick, 1997; Maguilla et al., 2017). Consequently, it was considered of conservation concern due to the risk of genetic swamping, which could impact species' long-term survival (Maguilla et al., 2017). Following this rationale, some authors considered introgression as either a damage to species integrity, a maladaptive procedure or an unexpected misfortune of nature (Llopart et al., 2014).

Conversely, recent evidence has demonstrated that introgressed alleles can be responsible for traits that are adapted to novel conditions (Jones et al., 2018; Lexer et al., 2004; Nadachowska-Brzyska et al., 2012). This phenomenon, known as adaptive introgression, is recognized as the main evolutionary outcome of natural hybridization, which leads to faster adaptation than *de novo* mutations (Anderson and Hubricht, 1938). Hence, introgression has been shown to impact species' adaptive capacity, contributing to species' evolutionary jumps, allowing them bypassing intermediate steps of evolution (Acosta and Premoli, 2018; Aeschbacher et al., 2017).

Standing genetic variation is likely to lead to faster evolution through the fixation of more and more recessive alleles (Lai et al., 2019). Thus, faster adaptation can occur when this standing genetic variation comes from other species that are better adapted to the environmental conditions (Lai et al., 2019). This mechanism can increase species survival (Liu et al., 2015; Norris et al., 2015), promoting their range expansion (Aleksic et al., 2018) and even supporting evolutionary rescue (Aeschbacher et al., 2017). On the other hand, it seems to have the ability to lead to species' divergence (Alexander et al., 2017; Antelope et al., 2017), for example, by promoting speciation (Arcella et al., 2015; Arnold et al., 2012).

Historically, since the publication of the first theoretical essays on introgression, the role of introgressed alleles was subject of controversy because introgressed alleles can be found in parts of the genome that are under selection or neutral regions, and may contribute to adaptations, have no impacts or be eliminated for being pejorative (introgression suppression) (Seixas et al., 2018). Introgression can be impacted by random processes like genetic drift (Gompert et al., 2013; Wade and Goodnight, 2006), which can eliminate maladaptive alleles in a few generations or keep others with propensity to persist as neutral and dependent on demography (Harris and Nielsen, 2016). Introgression is considered neutral when introgressed alleles have no phenotypic/physiological

consequences that could affect the fitness of the receptor lineage. Otherwise, it is considered maladaptive if it has negative adaptive outcomes (Matosiuk et al., 2014; Minder and Widmer, 2008). Contrary to the historical assumption that introgression should have neutral impacts (Leigh Van, 1976; Maguilla et al., 2017; Räsänen and Hendry, 2008), recent evidence supports that beneficial alleles introgress more easily than neutral ones (Harrison and Larson, 2014) by mechanisms that seem to be universal (Pease et al., 2016). This evidence led to adaptive introgression being increasingly documented as a major adaptive driving force (Pfeifer and Kapan, 2019).

Being initially rare, beneficial introgressed alleles can be favoured, for example by balancing selection (Nadachowska-Brzyska et al., 2012), and quickly establish in the receptor species through selective sweeps (Bay and Ruegg, 2017; Kuhlwilm et al., 2019; Otto and Barton, 2001). On the other hand, unlike new mutations, which starts with a prevalence of $1/2N$, the introgressed alleles may have a higher “initial” prevalence, depending on hybridization rates. Thus, high initial prevalence of introgressed alleles can also enhance their fixation. After settling in a stable way, these alleles can act as an important source of novel genetic and phenotypic variation (Baldassarre et al., 2014; Cahill et al., 2015). Just a single introgressed gene can have the potential to promote variation and consequently to have a large ecological impact (Bouck et al., 2007; Bradshaw and Schemske, 2003).

The advent of high-throughput sequencing approaches resulted in an exponential growth of scientific evidence documenting the occurrence of introgression and, to a lesser extent, its adaptive and evolutionary consequences (Taylor and Larson, 2019). There are many areas of knowledge that have been dedicated to the study of introgression, from genetics and microbiology to behaviour and anthropology. Great attention has been paid to some case studies that helped to clarify the functioning of introgression in the particular circumstances in which they occur (Taylor and Larson, 2019). From the global set of literature, introgression stands out as an extremely complex process that acts on all organisms regardless of their structural complexity, including bacteria (Palmer et al., 2010), protists (Nader et al., 2019), fungi (Dunn et al., 2013), plants, from bryophytes (James et al., 2008) to angiosperms (Taylor et al., 2009), and animals, both invertebrates (Norris et al., 2015) and vertebrates (Liu et al., 2015). With drivers working in response to several environmental pressures, both natural (Matosiuk et al., 2014) or anthropogenic (Pardo-Diaz et al., 2012), introgression can act potentially at different levels of biological organization. Some studies have looked at the genomic mechanisms through which introgression occurs (Morales et al., 2018). Others focused on the physiological restraints it can cause (Storchová et al., 2004). There are also examples of important constraints on introgression functionality due to demographic disparities (Ray and Excoffier, 2009) and the impact of reproductive behaviours on the patterns it presents (McDonald et al., 2001).

Understanding how introgression can contribute to species adaptations and evolution will require an investigation into the current knowledge trends on introgression patterns and causes. It will require a vast characterization and demonstration of the introgression process across the tree of life and in all its biological dimensions, in particular in cases where it leads to fitness changes (Pfennig, 2021). This can be also important to provide a general overview of major hypothesis to test with empirical data.

Systematic reviews complemented with meta-analyses are commonly used for merging data and evaluating large amounts of scientific information. They can also result in new ways of organizing knowledge and identifying its main trends and provide information on gaps in the literature, advising future investigation efforts (Livoreil et al., 2017; O'Dea et al., 2021). Standard protocols of systematic reviews allow for reproducibility and guard against subjective decision making during the review process (Shamseer et al., 2015). Meta-analyses through multidimensional approaches provide an integrative and holistic framework to merge biological data from standard systematic reviews (Bradley et al., 2005). They can help to extend the understanding of the functionality of drivers of natural biological processes at different levels of biological organization.

We carried out a systematic review and meta-analysis to analyse the current trend of knowledge about the factors that impact introgression with potential adaptive outcomes. We addressed two main questions: 1) What are the main structural characteristics of organisms that is conditional for the occurrence of introgression? and 2) What are the main current knowledge trends about mechanisms of introgression at different levels of biological organization?

Clarifying these objectives could bring us new open-spectrum views about how introgression can lead to adaptation and how it can shape the evolution. Finally, it can provide major hypothesis to test through empirical studies about the mechanisms behind the balance between introgression and divergence.

GLOSSARY

Adaptive introgression

The natural transfer of genetic material by interspecific breeding and backcrossing of hybrids with parental species followed by selection on introgressed alleles (de Lafontaine et al., 2015; Song et al., 2011).

Assortative mating

A mating behaviour by which individuals show higher preference for mating with individuals with similar phenotypes and genotypes than expected under a random mating pattern (Herbers, 2010).

Balancing selection

A set of selective pressures which actively allow the maintenance of multiple alleles in the population gene pool at greater frequencies than expected based on the effects of genetic drift alone (King, 2006).

Biological organization

The hierarchical organization of complex biological structures and systems (Mazzocchi, 2008).

Genetic drift

Changes in the frequency of an existing allele in the genetic pool of a population as a result of the random sampling of organisms (Bolnick et al., 2011).

Genetic recombination

Genetic exchange between different taxa which leads to new combinations of traits that differ from those found in the parental species (Martinsen et al., 2001).

Genetic swamping

Gene flow from most abundant species toward species with smaller population size that can lead to outbreeding depression due to the replacement of local genotypes (Todesco et al., 2016).

Genomic introgression

Distribution of introgressed alleles in across the genome (Gompert and Buerkle, 2009).

Geographic introgression

Geographic distribution of alleles across a hybrid zone (Payseur et al., 2004).

Haldane's rule

Heterozygous sex shows greater hybrids fitness reduction (Haldane, 1922).

Natural hybridization

Secondary breeding contact between two populations that have evolved separately over a period of time but under natural conditions (Neri et al., 2017).

Selective sweep

Genetic process through which a new allele that increases the fitness of the individual increases in frequency in a population and becomes fixed (frequency of 1) due to natural selection (Bay and Ruegg, 2017; Kuhlilm et al., 2019).

Sexual selection

Breeding behaviour favouring mating partners with adaptive advantage (higher fitness), independently of their species (Parrett and Knell, 2018)

Transgressive segregation

Extreme phenotypic traits outside the original phenotypic range of parental species produce by introgression and leading to hybrid speciation (Nichols et al., 2015; Rieseberg et al., 2003).

3.2 Methods

3.2.1 Literature search

We carried out a systematic literature search for studies that interpreted introgression patterns as resulting from adaptation. Following the standard PRISMA review protocols (Moher et al., 2009; O'Dea et al., 2021), we used ISI Web of Knowledge, Scopus, Google and Google Scholar, as the search engines (Falagas et al., 2008). We selected a set of search terms related to natural hybridization, genomics, introgression and adaptation, purposefully avoiding terms associated with direct or indirect human intervention (breeding or genetic manipulation, invasive species scenarios, etc.), such as domestication and invasive scenarios, limiting the search to natural genomic introgression with potential adaptive consequences. The keywords were selected from a list of keywords in reference papers, and through the consultation of a team of scientists' expert in evolutionary processes. With the aim to obtain the largest number of publications on the topic, the final set of selected keywords included the most common and unambiguous terms and expressions (see Supplementary Material for search details). The searches covered a period between 1900 and 2019 and were restricted to English.

Our searches produced 820 publications. From this dataset, we removed duplicates. After that we excluded theoretical essays, opinion texts, non-peer-reviewed papers, off-topic documents and non-ISI journals. Then we checked the reference list of the remaining publications looking for others that included the terms under study and that were not counted in the initial search. From this global set of publications we excluded all reviews and book chapters. Both the title and abstract of the remaining 436 articles were then read to assess their relevance for the study, based on: 1) if the introgression process was the result of natural processes, and 2) if introgression was pointed by the authors as the most plausible explanation behind the observed biological processes. The final dataset comprised 358 studies (WebFigure1 - Supplementary materials). All papers were analysed in full by the first author.

3.2.2 Literature review

We extracted bibliographic information from the 358 studies, including the temporal period and spatial location of the introgression phenomena reported in each study, the taxa undergoing the introgression process, and the main study methods (type of experiment, type of introgression markers and whether whole-genome sequencing was performed). Finally we recorded the main sub-mechanisms of introgression referred to in each study and the adaptive outcomes, both phenotypic and ecological. Detailed information about the variables extracted is available in Table S3.1. It is important to consider that it is not always certain that alleles/traits are in fact adaptively

introgressed. Therefore, we based this conclusion on the authors' interpretation as stated in the conclusions of the study and on described evidence of shared genes and/or traits that have potentially adaptive outcomes.

3.2.3 Meta-Analysis

We performed a multilayer analysis through an open-source multilayer network visualization and analysis platform MuxViz (<http://muxviz.net/>). MuxViz is an approach for representing a large variety of complex systems, such as biological structures, at different levels of biological organization, using empirical genetic, neuronal and transportation networks (De Domenico et al., 2014). Multilayer graphs of networks can be visualized by creating a relationship between two or more extracted variables, as nodes, incorporating them into different levels (layers) (De Domenico et al., 2014). These relationships occur when two characteristics of a case study (two variables extracted) are simultaneously described into the same paper which, depending on whether they are interdependent or not, can be directed or not directed. Here, the graph layers were designed to represent different levels of biological organization:

- Layer 1) Genomics/cytology - Location of introgression/islands of differentiation in the genome/cell;
- Layer 2) Physiology - Physiological constraints on introgression patterns;
- Layer 3) Behaviour - Behavioural impact on introgression patterns;
- Layer 4) Demography – The impacts of demography on the direction and amount/patterns of introgression;
- Layer 5) Ecology - Ecological influences on spatial-temporal introgression patterns.

We used the Large Graph Layout (LGL) algorithm at two-dimension with multiplex node arrangement and the interception as the template method, where all nodes can be connected to each other (intra and inter-layer connection) (De Domenico et al., 2014). For computing multilayer-specific network properties we perform an eigenvector centrality algorithm to analyse eigenvector versatility through the multilayer extension, which measures each node's importance depending on its connections within and across layers (De Domenico et al., 2014).

Node size was represented by the logarithm PageRank centrality and versatility that rank case studies' characteristics (see Supplementary material) to quantify the importance of each node in the network, by correlation with eigenvector metrics (De Domenico et al., 2015). Edges weight, symbolised by edges' thickness, represents the total number of papers in which a connected pattern between two nodes was described. These relationships were computed as standardized edges' weight ($_{st}EW$):

$$stEW = \begin{cases} (\frac{\alpha \times 100}{\beta})/100, & \text{if } \beta \geq \gamma \\ (\frac{\alpha \times 100}{\gamma})/100, & \text{if } \gamma \geq \beta \end{cases}$$

Where:

α represents the total Edges' Weight measured by the total number of papers that simultaneously described two introgression variables;

β represents the total number of papers that describe one of the variables;

γ represents the total number of papers that describe the second variable.

3.3 Results

3.3.1 Structural characteristics of organisms and introgression

Introgression is a natural process apparently conditioned by the structural complexity of organisms mainly at the genomic or behavioural level. Our results point to three mainly characteristics that seem to condition the way of functioning and the complexity of introgression: the functional and structural complexity of the eukaryotic cell, the presence of sex chromosomes and the development of behavioural mechanisms of sexual selection. Thus, across the taxonomic complexity gradient, introgression gradually becomes operational in higher layers of biological organization. Genomics/cytology covers almost half of the total connections between the taxonomic groups and introgression claims (46.7 ± 30.17 %). Physiology comprises one fifth of connections (20.1 ± 16.88), followed by demographic aspects (6.3 ± 6.69 %). Behaviour represented just 3.5 ± 5.81 % of total connections (Figure 3.1).

Figure 3.1 - Bipartite network of introgression's functionality variables and taxonomic groups. **(a)** Representation of introgression operation across a taxonomic complexity gradient and throughout different levels of biological organization. **(b)** Cladogram with the potential evolutionary cleavage moments of introgression functionality. A – Prokaryotes; B – Unicellular eukaryotes, C – Multicellular eukaryotes with sex-chromosomes and D – Multicellular eukaryotes with sex-chromosomes and sexual selection.

Genomics/cytology's layer (Autosomal introgression [Introq_Auto], Autosomal islands of speciation [Isl_Speciation_Auto], Nuclear introgression [Introq_NUCLEAR], Introgression on Sex-chromosomes [Introq_SEX], Cytoplasmic introgression [Introq_CYTO], Nuclear islands of speciation [Isl_Speciation_NUCLEAR], Islands of Speciation on Sex-chromosomes [Isl_Speciation_SEX], Cytoplasmic islands of speciation [Isl_Speciation_CYTO] and presence of balancing selection [Balancing_selection]);

Physiology's layer (endogenous impacts on introgression [Endogenous_impacts], Haldanes's rule compliance [Haldane's_rule], female sterility [Female_sterility], male sterility [Male_sterility], exception to Haldanes's rule [No_Haldane's_rule], any sterility [No_sterility], sex-bias introgression [Sex-bias_introgression], paternal direction of introgression [Paternal_way] and maternal direction of introgression [Maternal_way]);

Demography's layer (demographic disparities [Demography], any demographic disparities [No_Demography], direction of introgression from native-to-colonizers [Native-to-colonizer] and exception to native-to-colonizers direction [Native-to-colonizer]);

Behaviour's layer (presence of sexual selection [sexual_selection], presence of assortative mating [Assortative_mating], presence of intra-sexual interspecific competition [Sex_competition] and absent of intra-sexual interspecific competition [No_competition]; and

Ecology's layer (environmental-mediated introgression [Environment_mediated], iteration between allopatric and sympatric periods [Temporal_cycling], exogenous impacts on introgression [Exogenous_impacts], Allele surfing [allele_surfing], Any allele surfing [No_allele_surfing].

In evolutionarily older and less complex organisms, namely in prokaryotes, introgression was expressed fundamentally at the level of the genome, representing the only layer present in the majority of prokaryote networks (e.g. percentage of Bacilli's connections = 100%; $_{st}EW=0.11$). For older single-celled eukaryotic species, genomics/cytology represented $73.3 \pm 25.3\%$ of all connections with their introgression characteristics. However, unlike prokaryotes, for this group, introgression had a clearer expression at the level of cytology, for example in the location of the islands of introgression (nucleus *versus* cytoplasm) (Figure 3.1). In multicellular eukaryotic species with heteromorphic sex chromosomes, their dioecious sexual reproduction increased the complexity of introgression at the physiological level. For these more complex eukaryotes, physiology layer even matched the importance of the genomics/cytology in terms of the percentage of connections ($21.5 \pm 18.3\%$, $_{st}EW_{[physiology]}=0.07$; $23.0 \pm 19.5\%$, $_{st}EW_{[genomics/cytology]}=0.08$). Physiology strongly impacted the functionality of introgression in crustaceans (44.4% , $_{st}EW= 0.15$), mussels (24.0% , $_{st}EW= 0.10$) and gymnosperms (17.7% , $_{st}EW= 0.05$). In these more ancient multicellular eukaryotes with heteromorphic sex-chromosomes, introgression also increased its complexity at the demographic level. Once reproduction becomes stochastic in contact zones, demographic asymmetries become a fundamental mechanism for promoting introgression from the most abundant to the least abundant species. Gymnosperms are probably the most prominent example of this (20.6% , $_{st}EW= 0.13$). In more recent and complex eukaryotes species (genomically, physiologically but also behaviourally), introgression increased its complexity at the level of sexual behaviour (Figure 3.1). Eukaryotes with mating preferences were the only ones whose behaviour strongly impacts their receptivity to introgression ($8.4 \pm 6.4\%$, $_{st}EW= 0.15$). Birds and reptiles stood out for the importance of sexual behaviours for their expression of introgression (12.1% , $_{st}EW= 0.21$ and 21.5% , $_{st}EW= 0.33$, respectively).

At the ecological level, spatio-temporal environmental impacted on the operation of introgression showed very strong connections between the taxonomic groups and their introgression characteristics ($23.4 \pm 24.95\%$). Ecology strongly impacted species regardless of their taxonomic complexity, from single-celled eukaryotes ($15.0 \pm 22.4\%$, $_{st}EW=0.06$), older eukaryotes with sex-linked chromosomes and stochastic breeding choices ($45.5 \pm 39.2\%$, $_{st}EW=0.22$) to eukaryotes with sexual selection ($20.1 \pm 8.2\%$, $_{st}EW=0.18$) (Figure 3.1).

3.3.2 Trends in the literature on the mechanisms of introgression

✓ *Introgression in eukaryotic species*

We found evidence of introgression with adaptive outcomes in both cytoDNA and nDNA, exclusively or simultaneously ($_{st}EW=0.43$, $N= 31$ papers) (Figure 3.2) albeit a number of cases of cytonuclear incompatibilities reported (Gagnaire et al., 2013). However, many reported cases showed lower levels (or even none) of cytoplasmic introgression, particularly when compared to nuclear introgression (Brown et al., 2019; Carling and Brumfield, 2008; Hulsey et al., 2013; Morales et al., 2017). Our results showed that nuclear introgression is not only the most frequently reported location of introgressed genes into genomes of the eukaryotes, but also the most prevalent introgression characteristic among all published studies (Eigenvector=1.00, PageRank=0.98, $N=144$ paper) (Figure 3.2). However, we found no association between the timing of introgression (ancient *versus* current events) and the genomic location of introgression (CytoDNA *versus* nDNA) ($X^2_1= 3.46$; $P>0.05$). Balancing selection was more prevalent in introgression studies (Eigenvector=0.11, PageRank=0.26, $N=32$ papers) than genetic drift ($X^2_1= 13.23$; $p<0.01$), impacting mainly in nuclear introgression ($_{st}EW=0.50$, $N= 18$ papers) (Figure 3.2).

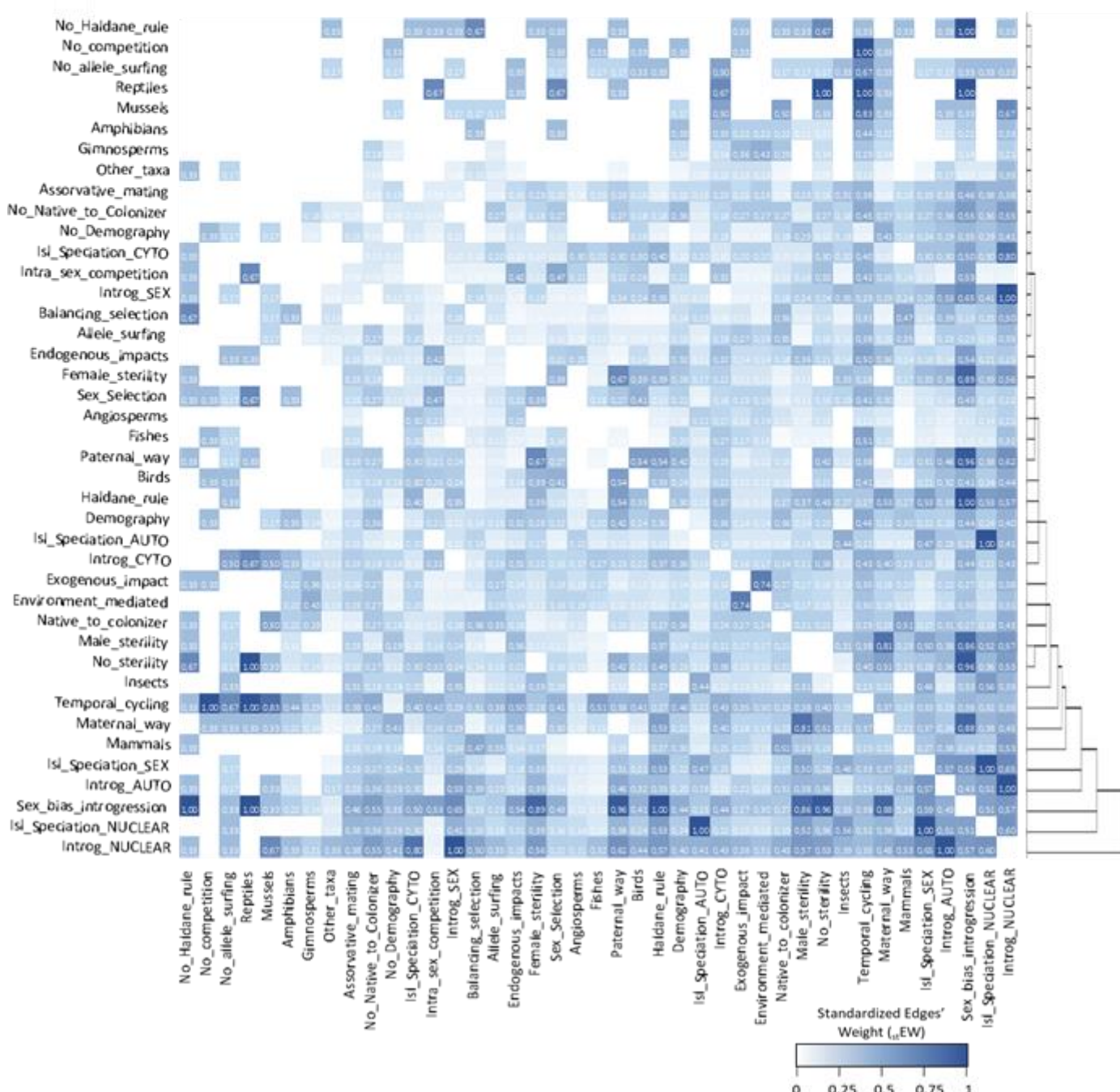


Figure 3.2 - Multilayer network of introgression's functionality variables at different levels of biological organization. **(a)** Multilayer graphs of networks. **(b)** Heatmap of pairwise standardized edges' weight ($_{st}EW$) among introgressions operating variables and taxonomic groups. Acronyms of variables are available in the legend of Figure 3.1.

✓ *Introgression in species with sex chromosomes*

Our results demonstrated that there are less reported cases of introgression in cytoDNA (Eigenvector=0.40, PageRank=0.34, N=72 paper), than into autosomes (Eigenvector=0.90, PageRank=0.74, N=84 papers) (Carling and Brumfield, 2008). However, they were both much more commonly reported than those in sex-linked chromosomes (Eigenvector=0.21, PageRank=0.24, N=17 papers). Introgression in sex chromosomes was never simultaneously described with cytoDNA introgression, occurring frequently in parallel with autosomal introgression ($_{st}EW=0.53$, N=9 papers) (Figure 3.2). Species with heteromorphic sex chromosomes, in particular mammals, showed lower rates of introgression in sex-linked chromosomes compared to autosomes [$X^2_2=19.14$; $p<0.01$]).

Several studies, covering numerous taxa, identified simultaneously islands of speciation in sex-linked chromosomes, where they are preferably located, and autosomal introgression ($_{st}EW=0.57$, N=36 papers; Figure 3.2). Nevertheless, there were important exceptions in the genomic location of islands of speciation (Autosomes: Eigenvector=0.37, PageRank=0.34, N=32). Only one paper provided evidence for either cytoplasmic or autosomal islands of speciation and genetic drift ($_{st}EW=0.13$).

We found evidence for islands of speciation in sex-linked chromosomes alongside some degree of sex sterility/unviability in 28 papers ($_{st}EW=0.51$), which was particularly high comparing to non-sterility cases ($_{st}EW=0.28$, N=13 papers) ($X^2_1=4.23$; $p<0.05$). Both, islands of speciation in sex-linked chromosomes and sterility/unviability affect preferentially the heterogametic sex ($_{st}EW=0.53$, N=16 papers and $_{st}EW=0.60$, N=18 papers, respectively) compared to the homogametic sex ($_{st}EW=0.00$, no papers and $_{st}EW=0.33$, two papers, respectively) (Figure 3.2).

In line with Haldane's rule (Eigenvector=0.40, PageRank=0.34, N=30 papers), according to which the sex with heteromorphic sex-chromosomes shows greater hybrid fitness reduction (Haldane, 1922; Kulmuni and Pamilo, 2014), the heterogametic sex showed greater hybrids fitness reduction through either increasing sterility (completely or partially) or even their unviability (Kulmuni and Pamilo, 2014). A significantly higher number of cases complied with Haldane's rule than those that did not [$X^2_1=20.48$; $p<0.01$]). The applicability of Haldane's rule seems to stem indirectly from the presence of islands of speciation in the sex chromosomes ($_{st}EW=0.53$, N=16). However, in several cases that corroborate with Haldane's rule sterility or unviability was not reported ($_{st}EW=0.43$, N=13 papers), or papers provided evidence that islands of speciation do not always result in sterility or unviability ($_{st}EW=0.28$, N=13).

Sex-biased sterility/unviability ($_{st}EW_{[males]}=0.86$, N=36 papers and $_{st}EW_{[females]}=0.89$, N=16 papers) and also endogenous impacts on reproductive cells and/or secondary sexual characteristics ($_{st}EW=0.54$, N=15 papers) can both promote sex-biased introgression (Walsh et al.,

2016). Sex-biased introgression is one of the most important introgression characteristic among all published studies (Eigenvector=0.59, PageRank=1.00, N=95; Figure 3.2). Our results showed that the largest number of papers in compliance with Haldane's rule ($_{st}EW=1.00$, N=30) were a fundamental outcome of the presence of islands of speciation in sex-linked chromosomes ($_{st}EW=0.59$, N=37). On the other hand, high co-occurrence with cases of introgression in sex-linked chromosomes revealed that Haldane's rule also contributed to introducing sex-bias in the introgression process ($_{st}EW=0.65$, N=11 papers), which likely did not occur through directly promoting sex-biased sterility (or even total unviability) ($_{st}EW=0.24$, N=4 papers).

Our results also showed high connectivity between sex-biased introgression and exceptions to Haldane's rule ($_{st}EW=1.00$, N=3 papers) and even cases of absence of sterility/unviability ($_{st}EW=0.96$, N=45 papers). Female-mediated introgression (Eigenvector=0.46, PageRank=0.64, N=65 papers), strongly connected with sex-biased introgression ($_{st}EW=0.88$, N=57 papers), was common among introgression case studies due to some degree of males sterility/unviability ($_{st}EW=0.81$, N=34 papers) in cases where they are the heterogametic sex (particularly in mammals [$_{st}EW=0.22$, N=14 papers] and insects [$_{st}EW=0.21$, N=13 papers]), following the assumptions of Haldane's rule ($_{st}EW=0.53$, N=16 papers). Despite male-mediated introgression being significantly less reported (Eigenvector=0.18, PageRank=0.30, N=26 papers) ($X^2_1=15.87$; $p<0.01$), it follows the same pattern as a result of sex-biased introgression ($_{st}EW=0.96$, N=25 papers). It is closely related to high levels of female sterility/unviability ($_{st}EW=0.67$, N=12 papers) in rarer cases in which they are the heterogametic sex (particularly in birds [$_{st}EW=0.54$, N=14 papers]).

✓ *Introgression in species under sexual selection*

Demographic asymmetries can play an important role in patterns of introgression in species complexes where a certain degree of stochasticity occurs during mating selection between two introgressing species (Eigenvector=0.27, PageRank=0.71, N=50 papers). In those cases, introgression tends to be directed towards the less abundant species. This direction is significantly more frequent (Eigenvector=0.08, PageRank=0.19, N=17 papers) ($X^2_1=15.28$; $p<0.01$). In line with this pattern, which is often connected to demography or stochastic mate choices ($_{st}EW=0.36$, N=18 papers), we found that the asymmetric direction of introgression from native-to-colonizer species is one of the most cited introgression pattern (Eigenvector=0.28, PageRank=0.68, N=70 papers). Native-to-colonizers direction is much more frequently reported than the rarer examples of the reverse directional introgression from colonizer-to-native species (Eigenvector=0.07, PageRank=0.22, N=11 papers) (Figure 3.2).

Balancing selection processes seem to be strictly related to this native-to-colonizer demographic pattern ($_{st}EW=0.36$, N=13 papers). This direction of introgression is a pattern that

seems to affect mainly older taxa (e.g. $_{st}EW_{[Mussels]}=0.50$, $N=3$ papers; $_{st}EW_{[Gymnosperms]}=0.29$, $N=4$ papers). However, high values of simultaneity between balancing selection and the direction of introgression from native-to-colonizer mammals species ($_{st}EW=0.51$, $N=36$ papers) suggests the influence of other phenomena than demographic asymmetries in species abundances. We found a possible relationship between examples of some degree of random mate choice and the opposite direction of introgression from colonizers-to-native species ($_{st}EW=0.36$, $N=4$ papers) (Figure 3.2).

Sexual selection, defined as a breeding behaviour favouring mating partners with fitness advantage independent of their species (Eigenvector=0.19, PageRank=0.77, $N=37$ papers), showed less reported cases of co-occurrence with demographic asymmetries ($_{st}EW=0.22$, $N=8$ papers). Sexual selection influences the occurrence of sex-biased introgression ($_{st}EW=0.43$, $N=16$ papers), preferably by impacting female or male breeding choices, depending on whether introgression is female or male-mediated ($_{st}EW=0.30$, $N=11$ papers and $_{st}EW=0.27$, $N=7$ papers, respectively). It was more prevalent than assortative mating, which is an opposite breeding force in conspecific direction (Eigenvector=0.06, PageRank=0.16, $N=13$ papers) ($X^2_1= 10.58$; $p<0.01$). However, there are important examples of the occurrence of assortative mating at the same time as introgression occurs (Eigenvector=0.06, PageRank=0.13, $N=13$ papers). It could happen even in cases where sexual selection appears as an important force determining the direction of introgression ($_{st}EW=0.15$, $N=2$ papers) (Figure 3.2).

Intra-sexual interspecific competition (Eigenvector=0.12, PageRank=0.77, $N=19$ papers) is another mating behaviour that contributed to directional introgression, with high levels of co-occurrence with sexual selection ($_{st}EW=0.47$, $N=9$ papers). Intra-sexual competition occurs more often than not ($X^2_1= 10.23$; $p<0.01$), being strongly connected with patterns of sex-biased introgression ($_{st}EW=0.53$, $N=10$ papers). Our results showed co-occurrence between this type of competition and endogenous factors that impact the direction of introgression ($_{st}EW=0.42$, $N=8$ papers) (Figure 3.2).

3.3.3 Environmental impacts on spatio-temporal introgression

Exogenous factors exert strong influences over introgression (Eigenvector=0.26, PageRank=0.68, $N=57$ papers) mainly through natural environmental conditions ($_{st}EW=0.74$, $N=40$ papers) despite the very relevant examples of introgression in response to anthropogenic impacts ($X^2_1= 17.36$; $p<0.01$). Spatio-temporal fluctuations in environmental conditions may impact the historical direction and extent of introgression and can result in introgressed species alternating periods of divergence and convergence ($_{st}EW=0.35$, $N=19$ papers). This historical iteration between divergence and introgression was one of the most relevant described patterns between

introgression case studies (Eigenvector=0.40, PageRank=0.57, N=117 papers) (Figure 3.2) (Staubach et al., 2012).

Regarding the geographical extent of introgression, there are still few empirical examples of introgressed alleles outside contact zones through allele surfing (Eigenvector=0.11, PageRank=0.27, N=26 papers). However, we identified some examples of expansion of introgression by alleles surfing ($_{st}EW=0.81$, N=21 papers) (Figure 3.2).

3.4 Discussion

Introgression is a very complex evolutionary process, which drives functionality at different levels of biological organization. Our study demonstrates that the complexity of processes of introgression increases across the taxonomic complexity gradient, from bacteria to mammals. We identify three key characteristics that impact the functioning of introgression: the eukaryotic cell, the presence of sex chromosomes and sexual selection.

Our results reinforce that introgression acts in parallel with divergence, leading to evolution through counteracting forces. Associated drivers increase its complexity across the biological organization through interconnected mechanisms, from genomics, cytology, physiology, demography to behaviour, depending on the species' structural complexity.

Adaptation to environmental conditions is a crucial target of the process of introgression. Therefore, all the described mechanisms are mediated by exogenous conditions regardless of the degree of the organisms' complexity and the level of biological organization in which they operate. The general patterns that stand out from our results highlight that the consequences of introgression transcend how organisms operate at the cellular, physiological, demographic or behavioural levels, affecting them even in their relationship with other organisms and the environment that surrounds them.

3.4.1 Structural characteristics of organisms that impact the function of introgression

Introgression represents an important source of genetic variation including for single-celled prokaryotic organisms, which provides adaptive advantages, such as resistance to antibiotics (McAshan et al., 1999; Palmer et al., 2010). In prokaryote species, introgression operates fundamentally by genetic recombination through chromosomal conjugative mobilization (McAshan et al., 1999). However, plasmids comprise a substantial fraction of the auxiliary genome, being responsible for much of their natural gene transfer (Palmer et al., 2010). For 1 to 1.5 billion years following the origin of life, introgression may have contributed to colonization of new habitats and

adaptation to abrupt changes in environmental conditions, typical of these primordial geological ages (Brooke, 2014). Selective genomic processes enhance the fixation of introgressed alleles in the gene pool of receptor species through selection, an opposing random process that may cause rare alleles to disappear in a few generations through genetic drift.

For eukaryotic species, introgression is driven by cyto-nuclear discordance, differences in recombination rates and selection within the cell (Burton and Barreto, 2012; Derr et al., 2012; Matosiuk et al., 2014). By bypassing these limitations, introgression can establish at the cellular level into autosomes in regions not strictly connected to cytoDNA and/or not resistant to recombination. In multicellular eukaryotic species with heteromorphic sex chromosomes, while introgression occurs mainly in the autosomes, islands of differentiation are fundamentally present in sex-linked chromosomes. Sex chromosomes are involved in specific functions in reproduction that exert pressures over breeding physiology. Thus, introgression in sex chromosomes can sometime have negative consequences like sex-biased sterility or even unviability (Storchová et al., 2004). However, sex-biased introgression allows organisms to bypass these physiological constraints.

Discrepancies in demography, such as great differences on parental species abundances, lead to mating with individuals of the most abundant species. In extreme cases it could even lead to the disappearance of the rarest species through genetic swamping (Todesco et al., 2016). However, introgression through establishing asymmetrical and directionally toward the less abundant species, allows species to incorporate the traits of the more abundant species. This process allows the rarer species to adapt to the environment, overcoming the constraints of genetic swamping and outbreeding depression.

In more recently evolved and complex eukaryotes species, sexual behaviours, such as non-random mating, can lead to assortative mating, whereby individuals tend to seek conspecific mating partners, reducing the occurrence of introgression (Hume et al., 2018). However, when the choice of breeding partners is not random, the tendency is to favour the fittest, independently of the species, through sexual selection (Parrett and Knell, 2018). This behaviour allows the less fit species to adapt and thrive by incorporating the traits that allowed its sister species to become more fit, bypassing restrictions resulting from assortative mating.

If structural complexity of current organisms (from bacteria to mammals) has occurred in parallel to the evolution of organism on Earth across the evolutionary history (from the most primitive living beings to current ones), the evolution of the complexity of the process of introgression appear to be marked by three main cleavage moments: the origin of eukaryotic cell, the origin of sex-linked chromosomes and the origin of sexual selection.

3.4.2 The balance between introgression and divergence

The increase in structural complexity of organisms throughout their evolutionary history of divergence seems to have brought new challenges to the occurrence and functioning of the process of introgression. Therefore, introgression acting in parallel with divergence, should evolved through counteracting forces and mechanisms.

✓ Balancing selection *versus* genetic drift

How introgressed genes are established in the genomes of the receptor taxa is still debated. These genes may be under negative pressure from stochastic mechanisms, such as genetic drift, which can impact particularly in natural systems with small populations, in which sexual selection is weak or absent (Gompert et al., 2013). However, balancing selection favours introgression by acting against the selection for conspecific breeding partners (assortative mating) or self-fertilization. Balancing selection is responsible for the decrease of stochastic loss of new/rare alleles, enabling them to establish in the recipient genome (While et al., 2015). Nevertheless, not all balancing selection mechanisms are likely to promote introgression (see While et al. (2015) for further discussion). Genes affected, for example, by negative frequency-dependent selection have higher migration rate that may contribute to a more efficient and easier establishment of the introgression process in the gene pool of the receptor species (Brennan et al., 2013).

✓ Autosomal introgression *versus* cyto-nuclear discordance

Cyto-nuclear discordance resulting from introgression, can impact species' fitness, leading to lower fertility and/or diseases or even promoting hybrids collapse (Burton and Barreto, 2012; Derr et al., 2012; Matosiuk et al., 2014). Despite some reported cases of cytonuclear incompatibilities (Gagnaire et al., 2013), evidence of introgression in both cytoDNA and nDNA in co-introgression indicates that individuals with the nuclear genome of one species (in full or in part) and the cytogenome of another (in full or in part) are frequently viable, and able to backcross (Pujolar et al., 2014; Sarver et al., 2017).

The location of introgression in the genome of eukaryotes is associated with cytonuclear discordances (Morales et al., 2018), as well as other impacts on physiology, demography and mating behaviours of complex organisms (Beckman et al., 2018; Di Candia and Routman, 2007; Fraisse et al., 2016; Herrig et al., 2014; Li et al., 2016; Massey, 2017; Seixas et al., 2018). The majority of reported introgression cases occur at the nuclear level (Hulsey et al., 2013), although some authors consider that organelle genomes introgress more easily and more frequently than the nuclear genomes (Giannoulis et al., 2019; Hawkins et al., 2016; Wade and Goodnight, 2006; Willis et al., 2012). However, nuclear introgression is responsible for cyto-nuclear discordance only under

a narrow range of conditions (Bonnet et al., 2017), while cytoplasmic genome selection may lead to strong discordance, mainly in biological systems with short dispersal capacity (Brower, 2018).

Within the nucleus, differentiation in allopatry acts particularly at autosomes centers. Instead, sympatry leads to extended introgression into chromosome ends, with greater recombination rates and selective pressures. CytoDNA introgression can occur, without promoting discordance, mainly if it is unconnected to nDNA regions responsible to interspecific incompatibilities (Di Candia and Routman, 2007). CytoDNA single-parent inheritance also reinforces the importance of sex-biased dispersal (Kulikova et al., 2004) for its introgression, impacting on cytonuclear gene interactions (Feder et al., 2005; Llopart et al., 2014). Nevertheless, after a period of isolation, cytonuclear interactions may evolve separately (Herrig et al., 2014). Therefore, disequilibrium between cytoDNA and autosomal haplotypes (Oliver et al., 2002), can minimize the likelihood of cytoDNA introgression (Herrig et al., 2014), making nDNA introgression with no cytoDNA gene flow a common phenomenon among introgression case studies.

✓ Autosomal introgression *versus* islands of differentiation in sex-linked chromosomes

Nuclear asymmetric introgression, favouring autosomes (Carling and Brumfield, 2008), means sex chromosomes become the candidate for storing islands of speciation (Runemark et al., 2018). Thus, islands of speciation in sex chromosomes and autosomal introgression are not mutually exclusive (Cruickshank and Hahn, 2014). These are two genomic processes probably in balance between the divergent selection and genetic homogenizing forces (Minder and Widmer, 2008). Differences in recombination rates in sex chromosomes (Wadsworth et al., 2015) (with positive association to introgressed regions (Gante et al., 2016; Ravinet et al., 2018)) help to explain this genomic balance (Wadsworth et al., 2015). Sex chromosomes have particular characteristics, such as morphological and genetic differentiation between the sexual chromosomes X and Y or Z and W or restrictions to recombination (Storchová et al., 2004). These characteristics together with the fundamental role they play in sexual reproduction (e.g. formation of gametes) make them particularly resistant to mechanisms of introgressions in species with dioecious sexual reproduction. Limitations on DNA repair in genes with organellic function (Runemark et al., 2018) and demographic aspects derived from the single-parent inheritance of sex chromosomes (in the heterogametic sex), (e.g. sex-biased dispersal) (Kulikova et al., 2004), can explain the rarity or even absence of introgression in sex chromosomes (Cahill et al., 2015) (a similar process that happens with haplodiploids species like ants and bees; Ghenu et al., 2018). On the other hand, sex chromosomes demonstrate higher adaptive evolution capacity than autosomes, probably because of the higher gene densities and because the existence of only one copy of a compatible allele is not likely to prevent individual incompatibility (Muirhead and Presgraves, 2016). Exceptions in the

genomic location of islands of speciation (incidental islands) (Sun et al., 2012) are probably present at high levels of gene flow and do not impact breeding isolation, being frequently discerned by random processes like genetic drift (Nosil et al., 2012).

✓ Sex-biased introgression *versus* physiological constrains

Islands of speciation in sex-linked chromosomes are rarer than introgression regions (Gante et al., 2016; Nosil et al., 2012) (often expand over just few hundred of kilobases, though sometimes up to several megabases) (Gagnaire et al., 2013), and mainly comprise loci affecting breeding isolation (Nosil et al., 2012; Suarez-Gonzalez et al., 2018). These may act like breeding barriers, being related to temporal and behavioural isolation (Wadsworth et al., 2015), namely effecting individuals' sex-biased sterility/unviability (Dopman et al., 2005). This asymmetry occurs due to their faster evolution and meiotic drive (Sun et al., 2012). Both islands of speciation in sex-linked chromosomes and sterility/unviability affect preferentially the heterogametic sex. This pattern is in line with the Haldane's rule, according to which the sex with heteromorphic sex-chromosomes shows greater hybrid fitness reduction (Haldane, 1922; Kulmuni and Pamilo, 2014). Physiologic outcomes deriving from Haldane's rule are frequently responsible for promoting asymmetric patterns of sex-biased introgression (Sackton et al., 2011), commonly mediated by females, especially in cases of homogametic males with some level of postzygotic breakdown. Examples of simultaneous occurrence between sex-biased introgression and exceptions to Haldane's rule are probably related to demographic and/or behavioural traits, such as positive selective heterosis in a single sex (uniparental introgression) (Beresford et al., 2017; Kim et al., 2018). Moreover, the sex with the higher dispersal rate usually presents higher levels of gene flow with conspecific populations outside the contact zone (Kulikova et al., 2004; Li et al., 2016; Massey, 2017; Morales et al., 2018). On the other hand, though rarely identified, islands of differentiation and/or introgression in sex-linked chromosomes can also express other endogenous impacts on reproductive cells and on secondary sexual characteristics, which can also lead to a decrease of hybrid and backcross fitness (Walsh et al., 2016).

✓ Directional introgression *versus* genetic swamping

Stochastic processes, such as colonisations, extinctions and bottlenecks, can impact species' survival (Vaillant et al., 2013) when species are simultaneously under extreme demographic discrepancies and the absence of (or weak) sexual selection (Sotola et al., 2019). When parental species differ in their abundance, stochasticity over the choice of mating partners means breeding is directed towards the most abundant species, leading to the disappearance of the rarer species in

just a few generations through genetic swamping (Lexer et al., 2010). However, because gene flow occurs from the most abundant species toward the species with smaller population size (Lexer et al., 2010), breeding stochasticity when together with discrepancies in parental species abundances can promote directional introgression (Kim et al., 2018; Takahashi et al., 2017).

This scenario arises particularly during species' expansion (Currat et al., 2008; Excoffier et al., 2008). Native species, more abundant and better-adapted to local ecological conditions, can quickly introduce adaptive alleles into the genome of the colonizer species, which become more prevalent in the expanding population and help species establishment in the new environment (Garcia-Elfring et al., 2017). Examples of the relationship between random mate choice and the opposite direction of introgression, from colonizers-to-native, arise from cases where stochasticity is not the main driver. Selection processes appear to be closely related to these demographic asymmetric patterns (native-to-colonizer or colonizer-to-native) because they can allow the establishment of introgressed alleles in the genetic pool of receptor species independently of the disproportionality in the abundances (Fijarczyk et al., 2018).

✓ Sexual selection *versus* assortative mating

The process of how individuals find and select their breeding partners plays a key role in determining the patterns of divergence and introgression. Assortative mating positively impacts divergent evolution by promoting mate choice toward conspecific partners, representing an opposite force to introgression. However, there are examples of introgression occurring simultaneously with strong assortative mating (Lexer et al., 2010; Mavárez et al., 2006; Ng et al., 2017; Poelstra et al., 2018; Salazar et al., 2008). It can be explained through introgression of specific alleles responsible for traits used for mate recognition in species with preferences for conspecific mates. These alleles are potentially mediators of introgression of neighbour-genes responsible for other characteristics that are indirect targets of introgression (Mavárez et al., 2006; Salazar et al., 2010).

There are other organisms that through sexual selection favour mates with higher fitness, regardless of which species they belong to, which influences the direction and extent of introgression (Sotola et al., 2019; Mao et al., 2014; Salazar et al., 2010). Sexual promiscuously is an important factor in this context (Baldassarre et al., 2014), which under strong sexual selection contributes to the spread of new non-existing traits via selective sweeps (Bay and Ruegg, 2017). Under expansion scenarios, sexual selection is expected to be directed towards native species, which are better adapted to local environmental conditions, and therefore could represent an adaptive advantage for the colonizing species. Paradoxically, environmental changes in contact zones can favour the characteristics of colonizer species' opening the path for expansion. Such

characteristics can be the target of sexual selection by native species, allowing them to adapt to the environmental changes and directing introgression.

Other mating behaviours under selective processes, such as differential parental care and sociality, may also favour asymmetric directional introgression (Sullivan et al., 2016; Trigo et al., 2014). Intra-sexual interspecific competition can mediate introgression, promoting the passing of genes from the species with greater competitive capacity (larger size, stronger bite, earlier flowering, etc.) to the other species, thus further contributing for asymmetric directional introgression. Intra-sexual interspecific competition was thought to occur only under weak or absent sexual selection (While et al., 2015), however we show that the two mating behaviours are non-mutually exclusive and even complementary.

3.4.3 Environmental impacts on spatio-temporal patterns of introgression

Adaptation to environmental conditions is the fundamental target of introgression, being simultaneously its main facilitator. Climatic fluctuations are frequently regarded as one of the main mediators (Grant and Grant, 2016) of the iteration between periods of divergence and convergence through introgression (Pauquet et al., 2018; Pfennig, 2007; Staubach et al., 2012). Divergence was frequently assumed to occur mainly through phases of allopatry (Baiz et al., 2019; Renaut et al., 2013; Slager et al., 2020). However, differences in the prevalence of recombination may contribute to explaining cases of divergence in the presence of gene flow (Wadsworth et al., 2015).

Local environmental conditions of each geographic region across the historical evolution of two divergent lineages, help to explain spatial discrepancies in the characteristics of introgression between different contact zones (Stuckas et al., 2009). Although natural environmental factors influence introgression, there are also examples of species responses to anthropogenic impacts (e.g. response to antibiotics (McAshan et al., 1999), pesticides (Song et al., 2011), deforestation (Alexander et al., 2017) or climate change (De La Torre et al., 2014; Quigley et al., 2019). Changes in altitude (Huerta-Sánchez et al., 2014), pollinators (Wang et al., 2013), pathogens exposure (Jagoda et al., 2018), ultraviolet-light (Ding et al., 2013) and temperature (Suarez-Gonzalez et al., 2016), can modulate the strength of ecological post-breeding barriers (Reidenbach et al., 2012) and promote variation in hybrid and backcross fitness through introgression (Kingston et al., 2017). Independently of its extent and historical context, introgression mediated by environmental conditions helps species to expand their ranges into new ecological regions (Aleksic et al., 2018) and can allow them to adapt to environmental changes (De La Torre et al., 2014; Quigley et al., 2019), both outside of their original realised niche. Allele surfing enables species to spread introgressed alleles throughout the whole species' range (Sarver et al., 2017), increasing the geographical extent of introgression beyond the boundaries of sympatric zones. In our study we

have found examples of this phenomena, for example, in insects that can spread introgressed alleles over 400 km (Norris et al., 2015) and mammals more than 2000 km from the contact zone in just a few generations (Matosiuk et al., 2014).

3.4.4 Knowledge gaps and future challenges

The advent of high-throughput sequencing approaches led to the proliferation of empirical examples of allele sharing between different taxa, in addition to enabling the identification of the process leading to its establishment (e.g. introgression or incomplete lineage sorting). However, several knowledge gaps about introgression remain. Islands of differentiation on sex-linked chromosomes during introgression processes should impact the reproductive performance of heterogametic sex, not only by directly promoting sterility (or even complete unviability) but also by causing some endogenous physiological changes in reproductive cells and/or secondary sexual characteristics (Walsh et al., 2016), which was seldom analysed. The characteristics and functions of islands of differentiation outside of sex-linked chromosomes can be considered as “incidental” by random processes. However, how genetic drift influences the occurrence of “incidental” islands of differentiation and their relevance for introgression remains largely unknown.

Another knowledge gap involves the connection between breeding behaviours (sexual selection, intra-sexual interspecific mating competition, parental care, etc.) and the genetic drivers of introgression. Due to sexual selection, colonizing species can favour mate choice with native species because of their better-adapted traits to the local environmental conditions. In this case, introgression could represent an advantage for the colonizing species. However, there are few examples detecting relationships between sexual selection and introgression from native-to-colonizer species. Finally, despite a few interesting examples, there is still little evidence of geographic expansion of introgressed alleles beyond contact zones. Allele surfing was rarely tested and just proved circumstantially. Nonetheless, it is essential to clarify the real spatial extent of introgression.

3.4.5 Conclusions

We show that introgression is a natural process operating at different levels of biological organization, whose complexity increases across the gradient of taxonomic complexity. Our results support that introgression acts in parallel with divergence, evolving and establishing in balance through interconnected mechanisms. Adaptation to environmental conditions is a fundamental target of the process of introgression that is simultaneously mediated by environmental conditions regardless of the degree of the organisms' complexity. These patterns suggest that the impacts of

introgression transcend the basic operation of organisms, affecting even their relationship with the environment. Finally, we argue that the balance between divergence and converge forces, such as introgression, makes speciation as a flexible process. They represent two path of the evolutionary process that can alternate or co-occur but that are equal in relevance. Their balance established at all levels of the biological organization and it is mediated by environmental changes, across the entire tree of life.

Acknowledgments

PH and HRa were funded by the Portuguese Foundation for Science and Technology (FCT) with a PhD grant (SFRH/BD/117979/2016 and SFRH/BD/124367/2016, respectively). HRe was also funded by FCT (DL57/2016/EEC2018/07). OR was funded through a Natural Environment Research Council Independent Research Fellowship (NE/M018660/1). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017.

Supplementary Material

Search details

We used the following search string for on-line databases:

“Topic=(*hybrid** AND *adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest** NOT *exotic*)
OR Topic=(*adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest** NOT *exotic*)”

We defined some keywords as strict retention criteria: *Adapt** (all terms related to adaptation, adaptive, etc.), *Introgress** (all terms related to introgression, introgressive, etc.) and *Genom** (all terms related to genome, genomics, etc.). We also used as non-strict retention criterion for the term *hybrid** (all terms related to hybrids, hybridization, etc.) that could be present together with the previous ones or not. We excluded all breeding contacts between taxa under direct human interference (breeding manipulations between species that do not naturally interbreed, genetic manipulation, invasive species scenarios, etc.). We used the following keywords as strict exclusion criteria: *Invas** (all terms related to invasion, invasive species, etc.), *Exotic* and *Domest** (all terms related to domestic species, domestication, etc.).

We defined the expression “*Adaptive Introgression*” as a keyword used as strict retention criteria searching for relevance grey literature through Google and Google scholar. We extracted 43 different variables grouped into seven categories: 1) Paper bibliometric information; 2) Type of publication; 3) Taxa under study; 4) Epoch and location of the introgressions case studies; 5) Methods used; 6) Sub-mechanisms of introgression and 7) Outcomes.

Table S3.1 - Full list of information and the total number of papers that includes each category extracted from each reviewed paper.

Categories of information	Variables extracted	Classes used	Number of papers
Bibliographic information	✓ Authors		358
	✓ Year		358
	✓ Title		358
	✓ Journal		358
	✓ Research area		358
	✓ Type of publication		358
	✓ Location of first author's institution		358
Authors' initial perception about introgression	✓ Polarity	Positive, Negative, Both, Neutral.	351
	✓ Why positive?		250
	✓ Why negative?		78
	✓ Why neutral?		129
	✓ Prevalence	Very rare [-3], Rare [-2], Infrequent [-1], Unknown [0], Few cases [1], Some cases [2], Common [3], Many cases [4], Ubiquitous [5].	135
	✓ Semantics	Hybrid* terms used, Hybrid* terms not used.	358
Taxa under study	✓ Main taxonomic group	Animal, Plant, Fungi, Protists, Bacteria.	355
	✓ Families		355
	✓ Species pairs		355
Time and space of introgressions' case studies	✓ Epoch	Ancient, Recent, Both.	355

	✓ Continent		355
	✓ Approximated location		355
Methods used	✓ Type of experiment	In-situ, Ex-situ, Both.	351
	✓ Type of introgression markers	Quantitative Trait Locus, Microsatellites, Mitochondrial DNA, Ribosomal DNA, Single-Nucleotide, Polymorphisms, AFLP, PCR amplification, Electrophoresis (DGGE), Karyotypes.	347
	✓ Whole-genome sequencing	Performed, Not performed.	347
	✓ Reference genome	Available, Not available.	165
	✓ Cyto-nuclear location of islands of differentiation	Cytoplasm (mitochondria, ribosome, chloroplast), Nucleus; Both. Sex-linked chromosomes,	87
	✓ Nuclear location of islands of differentiation	Autosomes, Both. Cytoplasm (mitochondria, ribosome, chloroplast), Nucleus;	83
Sub-mechanisms	✓ Cyto-nuclear location of introgression	Both. Sex-linked chromosomes, Autosomes,	182
	✓ Nuclear location of introgression	Both. Yes,	91
	✓ Sex-biased introgression	No. Yes,	96
	✓ Haldane's rule	No. Maternal,	34
	✓ Maternal vs paternal way	Paternal. Yes,	91
	✓ Sexual selection impacts	No. Yes,	51

	✓ Assortative mating preferences	No.	
	✓ Intra-sex interspecific competition	Yes,	12
	✓ Balancing selection	No.	
		Yes (Multiallelic, transespecific polymorphisms, etc.),	22
		No (Genetic drift).	40
	✓ Demographic impacts	Yes,	
		No.	
	✓ Symmetry	Symmetric,	
		Asymmetric.	67
	✓ Direction	Unidirectional,	
		Bidirectional.	276
	✓ Donor species		
	✓ Receptor species		259
	✓ Native-to-colonizer	Yes,	
		No.	259
	✓ Endogenous impacts	Yes (Baculum format, flowering time, sexual characters, etc.),	259
		No.	81
		Yes (temperature, topography, pesticides, etc.),	28
	✓ Exogenous impacts	No.	
		Yes,	
		No.	64
	✓ Climate-mediated introgression	Yes,	
	✓ Allele surfing	No.	
			53
			32
Outcomes	✓ Phenotypic traits shared		230
	✓ Physiologic system		230
	✓ Polarity	Positive,	230
		Negative,	
		Neutral.	
	✓ Adaptive outcomes		230

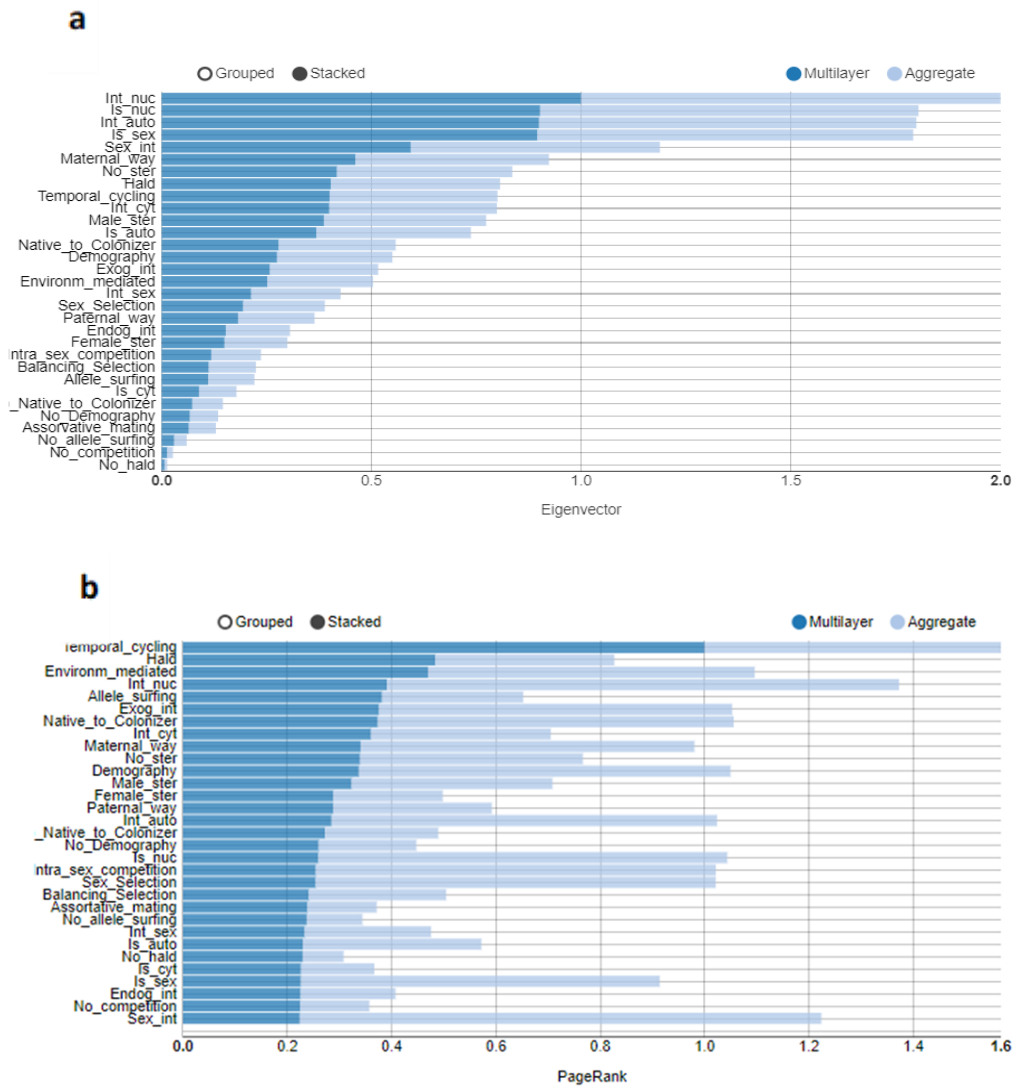


Figure S3.1 - Multilayer network metrics. **(a)** Computed multilayer-specific network properties of eigenvector centrality algorithm, which measures each node's importance depending on its connections, and **(b)** Page rank versatility, which quantify the importance of each one based on being adjacent to nodes with highest eigenvectors. *Genomics/cytology's layer* (Autosomal introgression [Introg_Auto], Autosomal islands of speciation [Isl_Speciation_Auto], Nuclear introgression [Introg_NUCLEAR], Introgression on Sex-chromosomes [Introg_SEX], Cytoplasmic introgression [Introg_CYTO], Nuclear islands of speciation [Isl_Speciation_NUCLEAR], Islands of Speciation on Sex-chromosomes [Isl_Speciation_SEX], Cytoplasmic islands of speciation [Isl_Speciation_CYTO] and presence of balancing selection [Balancing_selection]); *Physiology's layer* (endogenous impacts on introgression [Endogenous_impacts], Haldanes's rule compliance [Haldane's_rule], female sterility [Female_sterility], male sterility [Male_sterility], exception to Haldanes's rule [No_Haldane's_rule], any sterility [No_sterility], sex-bias introgression [Sex-bias_introgression], paternal direction of introgression [Paternal_way] and maternal direction of introgression [Maternal_way]); *Demography's layer* (demographic disparities [Demography], any demographic disparities [No_Demography], direction of introgression from native-to-colonizers [Native-to-colonizer] and exception to native-to-colonizers direction [Native-to-colonizer]); *Behaviour's layer* (presence of sexual selection [sexual selection], presence of

assortative mating [Assortative_mating], presence of intra-sexual interspecific competition [Sex_competition] and absent of intra-sexual interspecific competition [No_competition]; and *Ecology's layer* (environmental-mediated introgression [Environment_mediated], iteration between allopatric and sympatric periods [Temporal_cycling], exogenous impacts on introgression [Exogenous_impacts], Allele surfing [allele_surfing], Any allele surfing [No_allele_surfing].

Chapter 4

The other side of the coin: How phylogeny affects species receptivity for introgression

Pedro Horta, Helena Raposeira, Javier Juste, Orly Razgour, and Hugo Rebelo

Horta P., Raposeira H., Juste J., Razgour O., & Rebelo H.. The Other Side of the Coin: How Phylogeny Affects Species Receptivity for Introgression. *Final stages of submission*

Keywords: Bidirectional asymmetry, Donor species; Instrumental value, Introgression, Keystone species, Meta-analyses, Phylogeny, Receptor species

Abstract

Interbreeding across evolutionary history frequently results in phylogenetic incongruences due to natural gene transfer. Several recent studies have focused on the resulting problems when reconstructing phylogenetic trees, particularly in species going through microevolution or secondary contacts during the early stages of the macroevolution process. However, the effect of species' phylogeny on their ability to promote allele share through introgression, as well as its influence on mechanisms through which it occurs, remain fundamentally unknown. We carried out a systematic review and meta-analysis to compile a global introgression network between currently known donor and receptor species. Through assessing their phylogenetic dissimilarity, we studied the influence of species evolutionary history on introgression occurrence and patterns when it was demonstrated impacts on species fitness. Our results shown that asymmetric bidirectional introgression is a commonplace among literature, overflowing introgression as a flexible evolutionary mechanism, which can change its intensity but also its direction and consequences, depending on the environmental conditions. More ancient taxonomic groups have a natural ability to promote introgression with higher phylogenetic distance thus with higher probability for this phenomenon to occur. In contrast, for the most recent taxonomic groups, introgression seems to be restricted to phylogenetically closer species, probability conditioned by genetic and behaviour constraints. In both cases there are important species acting simultaneously as specialist donors and receptors, which working as connectors stand out as keystone species for potential indirect introgression. We argue that adaptive introgression provides species a fundamental instrumental value as a genetic resource for evolution that should be preserve and that go far beyond the intrinsic value of its own existence or its contribution to ecosystems.

4.1 Introduction

Phylogeny is a particularly relevant tool for measuring biodiversity, assessing conservation priorities and quantifying the evolution of taxa (Mace et al. 2003), apart from providing an effective representation of evolutionary relationships (Bonizzoni et al., 2017). However, complex evolutionary histories of species under rapid or preliminary speciation processes and introgression can result in high levels of phylogenetic incongruences. It makes phylogeny particularly hard to represent by traditional bifurcating trees because species may be artificially grouped (Ottenburghs Jente et al. 2017a).

Introgression is a movement of genetic material between different lineages resulting from interbreeding (Abbott et al. 2013). It represents one of the main evolutionary forces, which can strongly impact co-evolution and speciation (Xia et al. 2021). Being historically understood as a homogenizing process, it can be thought acting against divergence (Latch et al. 2006, Oliveira et al. 2008). However, adaptive introgression is a natural process that, unlike neutral introgression, promotes the establishment of alleles into genomes of closely-related lineages, through backcrossing, which are responsible for important fitness benefits (Aleksic et al. 2018, Alexander et al. 2017, Brower 2018, Cahill et al. 2015, Djogbénou et al. 2008, Gagnaire et al. 2009), whilst species maintain their taxonomic identity (Räsänen and Hendry, 2008). Thus, adaptive introgression can enable species to accelerate their evolutionary processes through subsequent spread of traits adapted to new environmental conditions (Acosta and Premoli 2018, Aeschbacher et al. 2017).

Redundantly, environmental conditions from both natural and anthropogenic origin (such as altitude (Huerta-Sánchez et al. 2014), temperature (Suarez-Gonzalez et al. 2016), pathogens exposition (Jagoda et al. 2018), exposure to pesticides (Song et al. 2011) and climate change (De La Torre et al. 2014, Quigley et al. 2019) may modulate the strength of ecological post-breeding barriers, and promote variability in hybrids and backcross fitness being the main drivers of introgression (Kingston et al. 2017, Reidenbach et al. 2012). Spatially, individuals carrying new introgressed alleles can expand their range beyond contact zone. Through backcrossing and allele surfing, these introgressed alleles can rapidly spread throughout the whole species' range (Sarver et al. 2017). Introgression can thus favour species adaptation and evolution far beyond sympatric areas, where hybridization occurs, depending on their species' dispersal capacity (Sarver et al. 2017). Spatio-temporal dynamics, such as environmental change and hybrid zones movements, expose introgressed species to different ecological forces and may lead to changes in the characteristics of introgression over their evolutionary history (Ryan et al. 2018).

Introgression trends are subject to strong influences from the evolutionary history of each species-pairs and from the phenotypes that it has shaped over time. Genomic and phenotypic

characteristics, alongside differences in mating, dispersal and competitive behaviours, should influence the way each species-pairs are impacted by introgression, under what conditions and with what characteristics. Environmental conditions are one of the main mediators of historical iterations between periods of speciation (during allopatric phases) and introgression (during periods of sympatry) (Pauquet et al. 2018, Pfennig 2007). Allopatry is frequently assumed to promote phylogenetic divergence (Baiz et al. 2019, Renaut et al. 2013, Seixas et al. 2018). Consequently the accumulation of post-breeding barriers (genetic, physiologic, behavioral, ecological, etc.) can severely condition inter-species breeding episodes (Reidenbach et al. 2012). So, throughout closely-related species' evolutionary history the increase of phylogenetic distances can potentially impact introgression prevalence and magnitude. As isolation increases, the occurrence of introgression should decrease over time as species accumulate genetic and phenotypic differences during each period of allopatry (Kronforst et al. 2013). Therefore, in cases where there is a temporal iteration between periods of isolation and secondary contact, the interval of time that a species remains isolated from the others (within each phase of divergence) should represent an important factor affecting patterns of introgression during the following periods of sympatry, impacting its functioning, intensity, symmetry and/or direction (Trigo et al. 2013).

Closely-related lineages have been tested for both the relative contributions of interspecific gene flow and incomplete lineage sorting during their evolutionary history (Meyer et al. 2017). Several recent studies have focused on the effects of introgression on their phylogeny (Cavender-Bares et al. 2015, McCluskey and Postlethwait 2015, Paetzold et al. 2019, Reid et al. 2012). However, the opposite effect of phylogeny over species receptivity to introgression remains largely unknown. Understand how evolutionary history and characteristics of each taxonomic group directly impact evolutionary outcomes of introgression, as well as its extent, it will require an investigation on how phylogenetic distance imposed by periods of divergence shapes the occurrence and functioning of introgression.

We used systematic review and meta-analyses approaches to: 1) generate a global introgression network according to the current state of knowledge, analysing the direction and connections between donors and receptors species of adapted alleles based on their taxonomy; and 2) analyse how phylogenetic dissimilarity between introgressing species influences introgression's occurrence and mechanisms.

4.2 Methods

4.2.1 Literature search

An extensive review of literature on introgression was carried out following standard PRISMA review protocols (Moher et al. 2009, O'Dea et al. 2021) to ascertain the current knowledge pattern about its phylogenetic extent. Clarivate Analytic's Web of Science e, Scopus, Google and Google Scholar were explored to discover the extent of literature published from 1900 to 2019 (Falagas et al. 2008). Literature was searched against various keywords related to introgression, hybridization, genome and adaptation restricting the search only to natural phenomena of genomic introgression with potential adaptive outcomes, excluding all processes under direct or indirect human interference (breeding manipulations, genetic manipulation, invasive species scenarios, etc.). The selection of the search terms was based on a review of previous keywords from a list of reference papers, and under a participatory approach with a team of scientists specialised in evolutionary biology. The final list of keywords included the most common and unambiguous words to reach the largest number of publications on the subject (see Supplementary material for the string code and search details). All review process was restricted to English and was performed in full by our first author. The searches finished in November 2019.

Initial searches resulted in 820 documents. From this dataset, we excluded duplications, non-original studies, theoretical essays, opinion texts, non-peer-reviewed papers, off-topic documents and non-ISI journals. Then we checked the reference list of the remaining papers to search for other papers that included the selected keywords. After excluding the reviews and book chapters, we read and analysed the title and abstract of the remaining 436 empirical studies individually. We evaluated their eligibility for the analysis according two main criteria: 1) if introgression was pointed by the authors as the main explanation for the evolutionary processes under study, and 2) if the papers complied with the natural origin for the described introgression process. The final dataset comprised 358 relevant studies (WebFigure1; Supplementary materials – Chapter 2).

4.2.2 Literature review

Each of the 358 studies was reviewed to extract information such as the temporal epoch and spatial location of the introgression case studies. We further recorded information on species under introgression and the main method that was considered in the publication, including the type of experiment, the type of introgression markers and whether whole-genome sequencing was performed or not. Finally, we registered the main operating details of introgression referred in each study and the phenotypic and ecological outcomes. Detailed information about the variables extracted are available in Table S4.1. It is important to take into account that it was not possible in

all cases to be certain that alleles/traits are adaptively introgressed. So, we assumed the authors' conclusions stated at each study and on described patterns of all introgression studies evidence of shared genes and/or traits that have potentially adaptive outcomes.

4.2.3 Data analyses

We regard introgression as a long-term biological interaction between two different taxa in which members of one (receptor) gain adaptive benefits under specific environmental conditions, while those of the other taxa (donor) neither benefit nor are harmed. The direction of introgression within each species pair was visualized by assembling a bipartite network using the R package BIPARTITE (Dormann et al., 2008). The relative abundance and overlap of reported cases of introgression were analysed in the form of a quantitative bipartite network using the number of papers reporting the connection between a donor and a receptor taxon as a proxy for interaction prevalence based on the published literature.

To analyse how phylogenetic proximity influences the introgression network and its patterns and characteristics, we performed a Bayesian evolutionary analyses for animals and plants (that represent more than 95% of all reported cases) following the protocol defined by Drummond and Bouckaert (2015). We used the COI gene and ITS2 gene as genetic markers, both useful for phylogenetic analyses in animals and plants, respectively. We extracted specific .fasta files directly from Genbank (<https://www.ncbi.nlm.nih.gov/genbank/>) and BOLD (<https://www.boldsystems.org/>) online databases, using the R packages SEQINR (Charif and Lobry, 2007). Multiple sequence alignment was constructed on GENEIOUS Prime (<https://www.geneious.com/>) with the default parameters and automatic determination of sequence's direction. We then re-aligned sequences using MUSCLE alignment with eight iterations. Sequences that could not be aligned were removed. Alignments were carefully edited by eye introducing gaps where necessary (Felix, 2021).

We generated Bayesian phylogenetic trees in BEAST (<https://beast.community/>) (Drummond and Rambaut 2007). All analyses were performed with relaxed clock log normal and Yule tree model calibrated with the known most recent common ancestor (MRCA) between *Homo sapiens* and *Pan*, here used as calibration species pair based on fossil records and the consensus estimate of the date of the MRCA between humans and chimpanzees (5–7 Mya of divergence - $M = 1.78$, $S = 0.085$, which specified a distribution centred around 6 million years with a standard deviation of 0.5 million years) (Drummond and Bouckaert 2015). We performed the analyses with a Markov chain Monte Carlo (MCMC) chain length of 108 iterations, sampling every 1000 steps. Sample size and estimated parameter were checked using Tracer 1.7.1 (Rambaut et al. 2018). These parameters were summarised using the TreeAnnotator software (Drummond and Rambaut 2007),

taking the set of trees that was retrieved from BEAST and finding the best-supported one (MCCT - maximum clade credibility tree), selected from the last 5% (501) of the trees sampled across the MCMC (Drummond and Bouckaert 2015). The final annotated phylogenetic trees were generated with the ggtree R package (Yu et al. 2017), with heatmap of associated matrix (both numerical – number of connected species, and categorical – symmetry, direction and donor *versus* receptor species) created by gheatmap (Perry 2019) and ggnewscale R packages (Campitelli 2020).

We tested for validation of both assumptions for multivariate normal distribution and homogeneity of variance-covariance of the pairwise phylogenetic distance matrix directly extracted from R software (Maroco, 2010). Even after transformation (log10, ln, arcsen, etc.), the assumptions could not be assumed. So, in order to assess whether phylogenetic distance significantly affects the taxa groups, we performed a non-parametric Kruskal-Wallis test on the pairwise phylogenetic distance matrix to identify in which taxa groups the differences were significant. Multiple comparisons of means by the post-hoc Fisher's LSD test complemented the analyses (Maroco, 2010).

We performed an interquartile range analyses (IQR analyses) based on pairwise chi-square comparisons to analyse the phylogenetic extent of introgression between taxonomic groups. Finally, differences on phylogenetic distance between taxa according to their introgression's mechanisms and characteristics were assessed through Wilcoxon-Mann-Whitney tests. All analyses were performed with a type I error probability (α) of 0.05 (Maroco, 2010).

4.3 Results

4.3.1 Global introgression network

Our results show that 76.9% of all studies have analysed the direction of introgression (N=276 papers). Asymmetric introgression is a common pattern that emerges from the literature, representing 91.2% (N=249 papers) of the papers that looked into the direction of introgression. Only 7.8% of these studies found that introgression was symmetric (N=22 papers), and only two cases demonstrated the existence of both symmetrical and asymmetric introgression in the same species pair (although in different historical sympatric periods). Although asymmetric introgression is a common *phenomena* across all taxa, we only found limited support for extreme asymmetry in the form of unidirectional introgression (6.9%, N=19 papers).

Studies considered in our work have identified 244 species-pairs sharing alleles through introgression (211 donors taxa and 212 receptors), mostly angiosperms (N=60 species pairs), mammals (N=46 species pairs) and fishes (N=34 species) (Figure 4.1 and 4.2). Both donor and receptor species show similar average levels of connectance (number of connections per taxa) (donors = 1.16 ± 0.46 connections/taxa; receptors = 1.15 ± 0.47 connections/taxa). Unicellular

organisms show greater connectance, probably due to their higher potential for genetic recombination (essentially Ascomycetes [1.60 ± 1.341 connection/taxa], Bacilli [1.50 ± 1.000 connection/taxa] and Yeasts [1.43 ± 0.786 connection/taxa]). In plants, Gymnosperms (1.28 ± 0.458 connection/taxa), and in animals, Invertebrates (mainly Insects [1.29 ± 0.682 connection/taxa] and Crustacea [1.25 ± 0.462 connection/taxa]) also show higher levels of connectance, likely for the same reason (Figure S4.1).

Within multicellular organisms, 13 genera (or genus complexes) have higher mean connectance compared to the global mean (comprising a total of 131 taxa – 30.9% of total): Plants - *Picea* ($N=1.64 \pm 0.504$ connection/taxa), *Helianthus* ($N=1.64 \pm 0.504$ connection/taxa), *Ilex* (1.33 ± 0.816 connection/taxa), *Iris* (1.33 ± 0.516 connection/taxa) and *Senecio* (1.33 ± 0.816 connection/taxa); Animals - *Pocillopora* (1.33 ± 0.577 connection/taxa), *Anopheles* (1.56 ± 0.527 connection/taxa), *Heliconius* (1.56 ± 1.333 connection/taxa), *Papilio* (1.50 ± 0.577 connection/taxa), *Rhagoletis* (1.33 ± 0.557 connection/taxa), *Mytilus* (1.33 ± 0.557 connection/taxa), Cichlidae genus complex (1.33 ± 0.488 connection/taxa), *Cyprinodon* (1.33 ± 0.557 connection/taxa), *Anas* (1.33 ± 0.557 connection/taxa), *Myotis* (1.29 ± 0.488 connection/taxa), *Lepus* (1.57 ± 0.788 connection/taxa), *Mus* (1.33 ± 0.577 connection/taxa) and *Homo* (1.60 ± 1.342 connection/taxa) (Figure 4.1 and 4.2). In contrast, the majority of cases (268 taxa - 67.1% of total multicellular taxa identified) show lower levels of connectance ($\approx N=1$ connection/taxa).

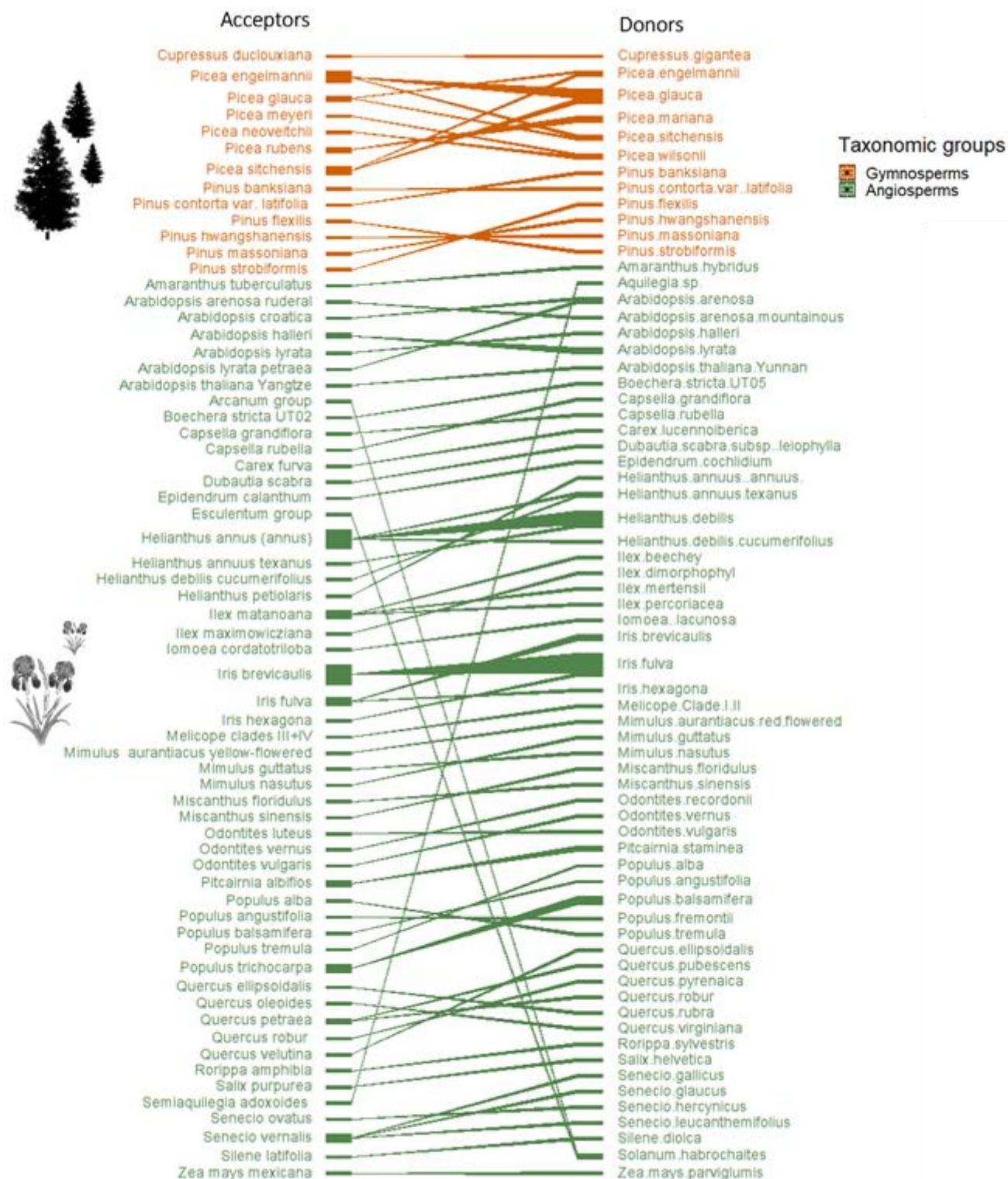


Figure 4.1 - Plant bipartite introgression network between species acting as donors and receptors.

We identified 17 outlier donor species with particularly high connectance values that donated alleles to several taxa, up to five connections per taxa, include the angiosperms *Helianthus annuus texanus*, *Helianthus debilis* and *Iris fulva*, the insects *Heliconius melpomene*, *Anopheles coluzzii* (gambie M), *Anopheles gambiae* (S) and *Papilio canadensis*, the fish *Boulengerochromis microlepis*, *Coptodon* sp. 'Mamfé', *Cyphotilapiini* sp., *Sarotherodon galilaeus*, the bird *Anas platyrhynchos*, and the mammals *Lepus timidus*, *Mus (musculus) domesticus*, *Mus musculus*, *Myotis alcathoe*, and *Myotis mystacinus* (Figure 4.1 and 4.2).

Similarly, we identified 11 specialist receptor species that received alleles from several taxa, up to five connections per taxa, include the gymnosperms *Picea engelmannii* and *Picea glauca*, the angiosperms *Helianthus annus (annus)*, *Ilex matanoana*, *Iris fulva*, *Quercus petraea* and *Senecio vernalis*, the fishes *Boulengerochromis microlepis* and the mammals *Homo sapiens*, *Mus (musculus) domesticus* and *Myotis brandtii* (Figure 4.1 and 4.2). Species like *Iris fulva*, *Boulengerochromis microlepis* and *Mus (musculus) domesticus* that are simultaneously specialist donors and receptors can maybe act as transmitters of alleles between species that do not directly introgress with each other (Figure 4.1 and 4.2).

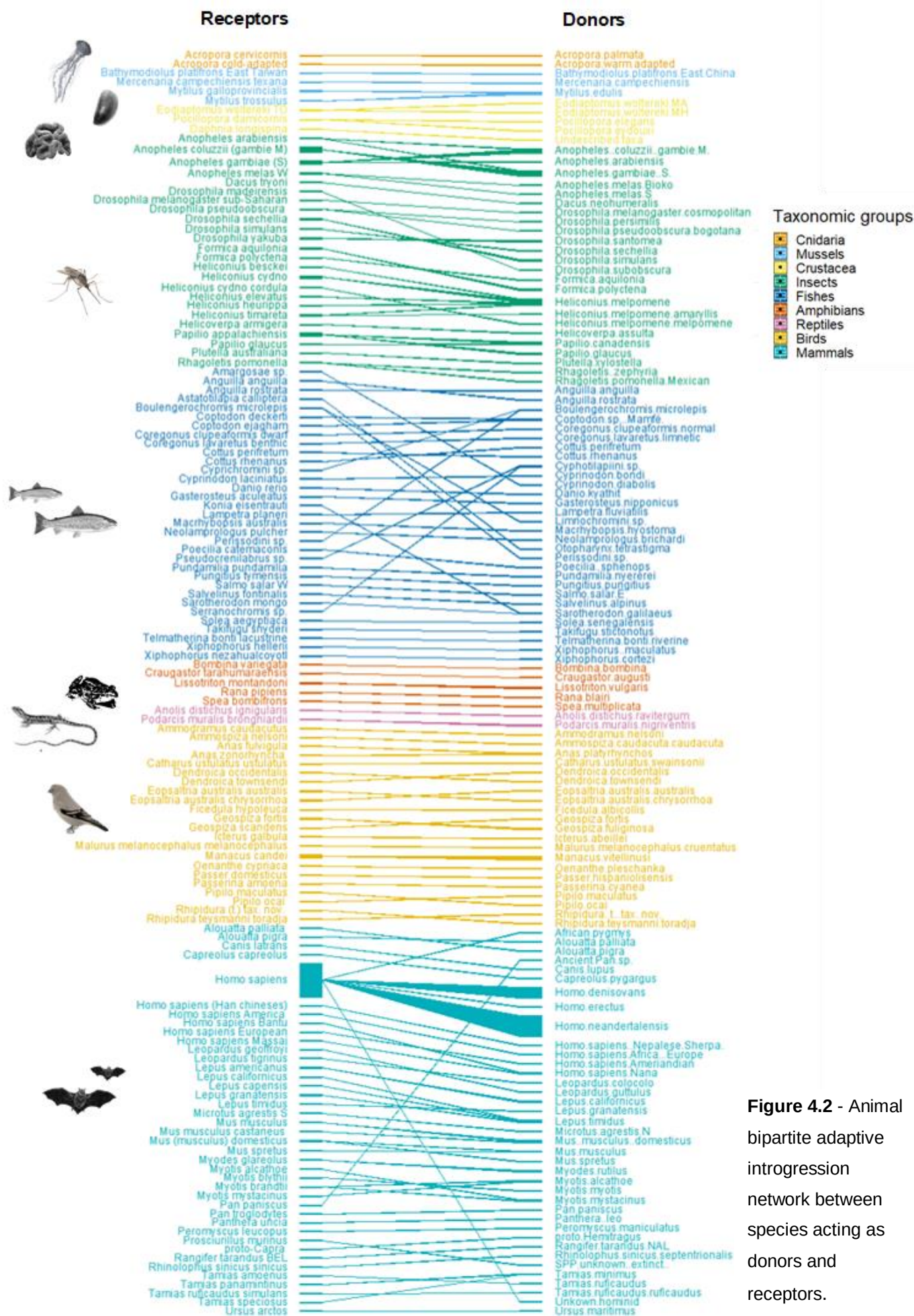


Figure 4.2 - Animal bipartite adaptive introgression network between species acting as donors and receptors.

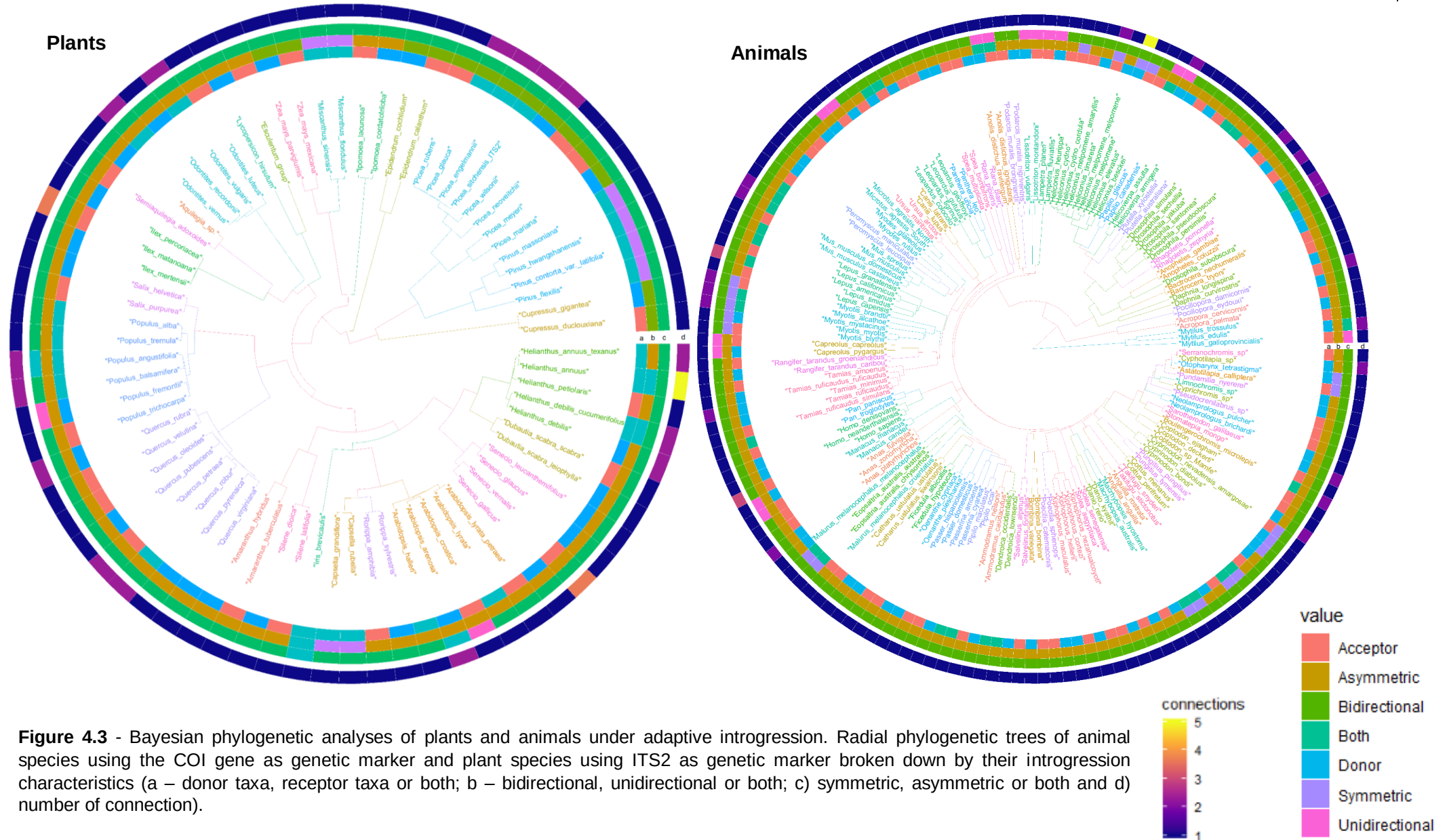
4.3.2 Influence of phylogenetic dissimilarity on introgression

Our results demonstrate that phylogenetic dissimilarity influences differently the occurrence of introgression over each taxonomic group ($X^2_{kw} (11) = 53.53$; $p < 0.01$). In terms of maximum pairwise phylogenetic dissimilarity (MPPD) and the range of phylogenetic distance (IQR), gymnosperms show a remarkable capacity of introgression between phylogenetically distant species (MPPD = 26.57% and IQR = 0.26), significantly higher than any other taxonomic group (Figure 2b). Other groups able to introgress with distant species include Crustacea (MPPD=23.06%, IQR=0.23) and Mollusca (MPPD=22.48%, IQR=0.05). Among Chordata, Amphibians and Reptiles show the highest capacity to introgress between species with wider phylogenetic distance (MPPD=15.59%, IQR=0.11 and 13.74%, IQR=0.9). In contrast, angiosperms (MPPD=3.17%, IQR=0.02), insects (MPPD=3.63%, IQR=0.03), birds (MPPD=3.24%, IQR=0.02) and mammals (MPPD=4.57%, IQR=0.03) appear to be able to introgress only with phylogenetically closer species (Figure 4.3, 4.4 and table S5.1).

Multiple comparisons of means revealed that, following the same pattern, Mussels ($19.91 \pm 2.95\%$) and Crustacea ($11.53 \pm 16.31\%$) promote introgression between individuals with a higher phylogenetic mean distance. Among Chordata, both Amphibians ($10.91 \pm 8.44\%$) and Reptiles ($10.74 \pm 10.37\%$) showed the highest phylogenetic mean distance (Table S5.1). Gymnosperms (mean= $10.61 \pm 12.29\%$; median= 3.48%) are a particular case because it mainly occurs with closer related species (in terms of median they are even comparable to angiosperms), despite being able to adaptively introgress with phylogenetically very distant species. In contrast, angiosperms ($3.52 \pm 4.58\%$), insects ($2.25 \pm 2.12\%$), birds ($3.51 \pm 4.35\%$) and mammals ($3.90 \pm 3.97\%$) seem to be only able to introgress with phylogenetically closer species (Figure 4.3, 4.4 and Table S5.1).

Reported case studies demonstrating introgression impacted by demographic disparities in the abundance of both parental species and/or stochasticity on breeding partner choice, show higher phylogenetic distance than in cases where there were no demographic or stochastic influences ($U=123.0$; $W=178.0$; $p=0.031$) (Figure 4.3 and 4.4). Similarly, patterns of directional introgression from native to colonizing species show higher phylogenetic distance scores than cases on which this pattern is absent ($U=140.0$; $W=195.0$; $p=0.001$) (Figure 4.3 and 4.4). On the other hand, species pairs with cytoplasmic introgression show a tendency towards marginally higher phylogenetic distance scores than species with nuclear introgression ($U=2253.5$; $W=7609.5$; $p=0.076$) (Figure 4.3 and 4.4). Islands of speciation located on cytoplasmic genome also showed slightly significantly higher phylogenetic distance scores than the others with nuclear islands of speciation ($U=34.5$; $W=1259.5$; $p=0.067$) (Figure 4.3 and 4.4). Finally, our results demonstrated an absence of significant difference between cytoplasmic introgression in relation to introgression

timing (ancient *versus* current events - $X^2_1 = 3.46$; NS). On the contrary, there are evidences of a significantly higher prevalence of cytoplasmic introgression in the most ancient taxonomic groups (Gymnosperms, Crustacea, Mollusca) compared to the most recent ones (Angiosperms, Birds and Mammals) ($X^2_1 = 5.82$; $p < 0.05$).



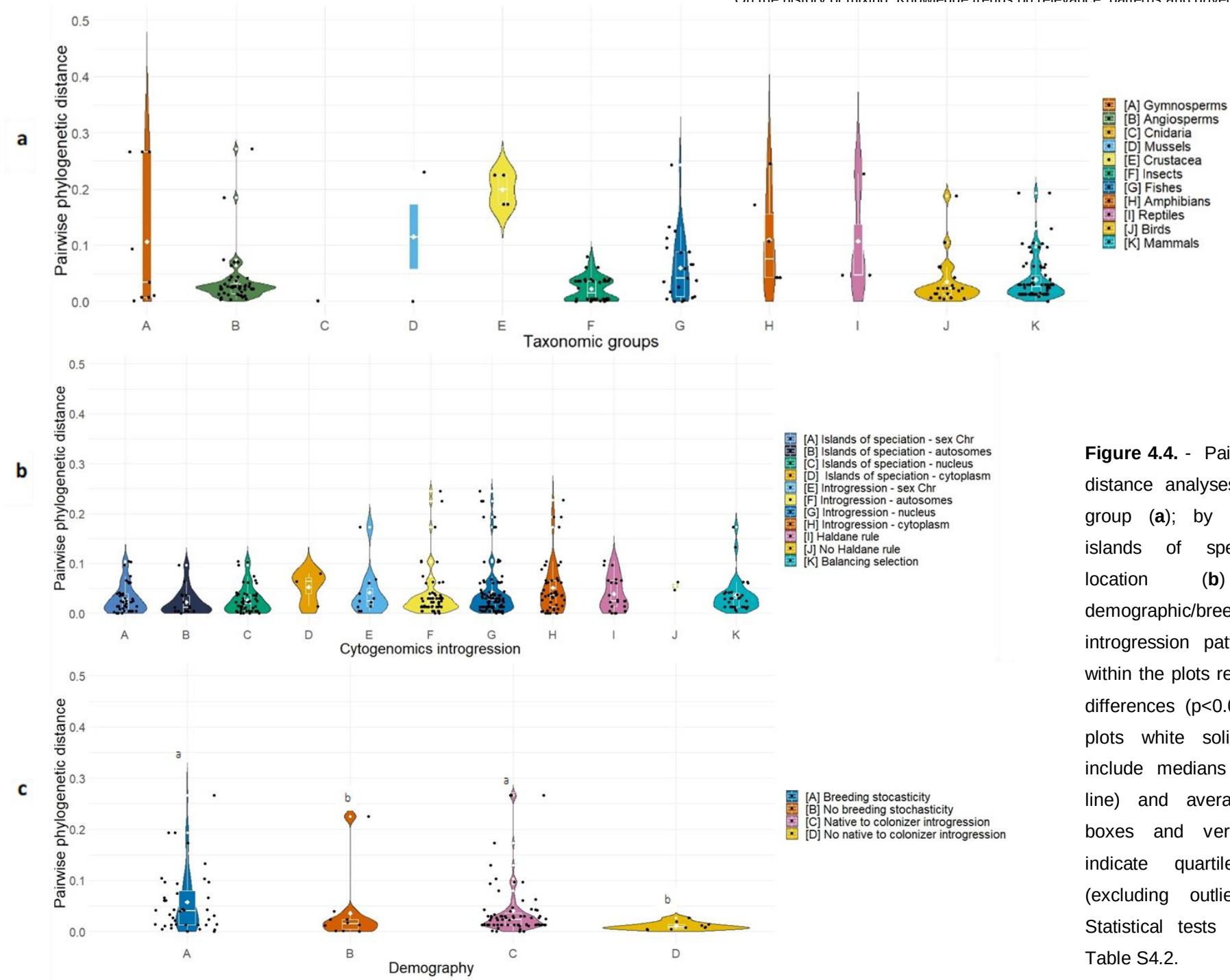


Figure 4.4. - Pairwise phylogenetic distance analyses - by taxonomic group (a); by introgression and islands of speciation genomic location (b) and by demographic/breeding stochasticity introgression patterns (c). Letters within the plots represent significant differences ($p < 0.05$). Within violin plots white solid lines boxplots include medians (horizontal white line) and averages (white dot); boxes and vertical white lines indicate quartiles and ranges (excluding outliers), respectively. Statistical tests are presented in Table S4.2.

4.4 Discussion

Our findings demonstrate that the value of a species is not only related to the intrinsic value of its own existence or its contribution to nature's benefits. Each species carries its own priceless instrumental value derived from the role as potential allele donor (direct or potentially indirect) through introgression to a set of potential closely-related species. When a species becomes extinct, a link in the global introgression network is lost, which may represent the end of this genetic resource of fundamental variability that may be essential for the evolutionary process of other species. In theory, an extinction may trigger a long-term cascade of extinctions due to the inability of other potential receptor species to make evolutionary leaps in response to environmental change. Thus, each species can be seen as a fundamental genetic resource for evolution over space and time, particularly relevant in historical moments marked by extreme changes in the environment, such as those resulting from current anthropogenic climate change.

Moreover, we also found that asymmetric bidirectional patterns overflow as commonplace among introgression cases studies revealing it as a flexible evolutionary mechanism, which can change its intensity, direction and outcomes, depending on the environmental conditions at a given historical moment in the evolutionary process. In here we show for the first time that ancient evolutionary taxonomic groups have a natural ability to promote introgression with higher phylogenetic distant species, thus providing a wider range of possibilities (number of species, population, lineages, etc.) for introgression to occur. In contrast, for the most recent taxonomic groups, introgression seems to be restricted to phylogenetically closer species. In both cases there are important species that act simultaneously as specialist donors and receptors, while working as connectors, stand out as keystone species for potential indirect introgression.

4.4.1 The direction of introgression

One of the noteworthy results we got was that bidirectional asymmetric introgression (directional gene flow preferably from one species to another with adaptive consequences) is common among the great majority of introgressing species pairs may be as a consequence of the genomic and phenotypic characteristics of the involved species (Sullivan et al. 2016, Trigo et al. 2014). Differences in ploidy level and endogenous traits, which are partially responsible for some degree of postzygotic isolation, in part caused by genomic islands of speciation, should be at the root of this pattern (Emms et al. 1996). Behaviours, such as sex-biased dispersal rates, differential sexual selection and intra-sexual interspecific competition, are also likely to promote sex-biased introgression, and promote these asymmetries (Emms et al. 1996).

Demographic differences between hybridizing species, differences in sex-dispersal rates and hybrid zone movements, associated with strong environmental impacts on natural selection, particularly climatic, are also responsible for asymmetry in introgression (Meier et al. 2017). Nevertheless, it cannot be excluded that the high proportion of studies identifying asymmetric introgression may be the result of methodological limitations, namely the limitations of study designs that looked for introgression in just one direction and the widely used genetic differentiation test that only detects asymmetric gene flow (Ottenburghs J. et al. 2017b). However, the limited support for extreme asymmetry in the form of unidirectional introgression seems to point for introgression as a flexible mechanism that can change its intensity, direction and consequences, depending on the environmental conditions. For example, Suarez-Gonzalez et al. (2018) show that asymmetric introgression can reverse the historical direction in poplar trees (*Populus trichocarpa* into *P. balsamifera*) as a response to climate change, contributing with beneficial disease resistant genes. There are cases of asymmetric introgression favouring one or the other species depending on the habitat (Sung et al. 2018) and in more extreme scenarios, introgression can be adaptively beneficial in one direction and harmful or benign in the opposite direction (Suarez-Gonzalez et al. 2016, Suarez-Gonzalez et al. 2018).

4.4.2 Connections between introgressed closely-related species

From the taxonomic groups in which introgression was studied, the majority of cases were identified in the angiosperms, mammals and fishes. Globally, older taxa with less complex physiology appear to have the capacity to introgress with a greater number of closely-related taxa showing weaker barriers to interspecific gene flow. Single-celled organisms are in the forefront of this pattern, probably due to their larger potential for genetic recombination (Palmer et al. 2010). But, even within multicellular organisms, gymnosperms and invertebrates, such as insects and crustacea, stand out for the same reason.

Genera in which introgression occurred in taxa pairs that are either undergoing the first steps of macroevolution or belong to a species complex that went through adaptive radiation, have particularly high connectance in terms of number of taxa they adaptively introgress with. However, the majority of taxa has lower connectance (around one per taxa) mainly because of their more advanced stages of evolutionary divergence.

Along the evolutionary history repeated periods of iterations of genetic isolation and secondary contacts, occurring frequently (Lee and Coop 2017) in a complex and/or reticulated way (Slager et al. 2020). Nevertheless, the magnitude of introgression probably decreases over the time due to the accumulation of genetic differentiation in each cycle of allopatry (Kronforst et al. 2013). We found that the time and type of divergence, responsible for different levels of genetic,

physiological and behavioural changes (Trigo et al. 2013), appear to be determining factors for the number of species able to mutually share their genes through introgression (Stuckas et al. 2009). Yet, a number of species seem to act as major donors or receptors of genes from other species. A possible hypothesis behind these specialist donor and receptor species can be the result of these particular outlier species being tested against a larger number of species. Despite these methodological limitations, species like *Iris fulva*, *Boulengerochromis microlepis* and *Mus (musculus) domesticus* being simultaneously specialist donors and receptors act as connectors and stand out as potential keystone introgression species. Acting as an introgression bridge between third-party species that do not hybridize directly with each other, they can potentially promote indirect natural introgression. If the presence of indirect introgression is confirmed, it will indicate a much higher extent and taxonomic reach than currently known.

4.4.3 Influence of phylogenetic dissimilarity on introgression

Differences in phylogenetic dissimilarity among species through the accumulation of genetic and physiological variations during allopatric divergence, seem to influence differently the occurrence of introgression over each taxonomic group. Gymnosperms, Crustacea and Mollusca show a remarkable capacity of introgression between phylogenetically distant plant or invertebrate species, respectively. Among Chordata, amphibians and reptiles showed the highest capacity of introgression between species with greater phylogenetic distance. In contrast, angiosperms, birds and mammals seem to be available to introgress only with phylogenetically closer species.

The most ancient species tend to have smaller genomes, thus less likely to generate genetic incompatibilities, and more permeable to recombination (Blommaert 2020). Cases of cytoplasmic introgression showed significantly higher phylogenetic distance scores than nuclear introgression cases. Introgressions' events on cytogenome are known to reflect ancient reticulate events (Malhotra and Thorpe 2000, Thorpe et al. 2010), showing higher prevalence among more ancient taxonomic groups, with consequences in the wider phylogenetic extent in which it may occur.

Other explanations for the higher extent of introgression among ancient taxa derived from mating strategies under high rates of stochasticity and weak or even non-sexual selection. Indeed, the way how individuals find and select their breeding partners plays a key role determining the patterns of introgression, for example the extent and direction for which species it occurs (Vaillant et al. 2013). Stochastic processes on mating partner choices, frequently impacted by demographic differences in parental species abundances (Lepais et al. 2009), help species undergo introgression in the absence/weak specialized sexual selection (Sotola et al. 2019), (here understood as a specialized breeding behaviour to find and select mating partners with adaptive advantages independently of their species) (Parrett and Knell 2018). For example, anemophilous gymnosperms disperse their

gametes by the wind, with fertilization being random or at least involving limited mating partners' selection (Wang Xiao-Quan and Ran 2014). In the ocean, Crustacea and Mollusca use a similar strategy via sea currents (Baur 1998). In both cases, when they are in heterospecific communities this mating strategy increases substantially the probability of interspecific crossbreeding and introgression. Directional introgression from native (more abundant) to colonizing species (less abundant) is a recurrent consequence of breeding stochasticity and demographic disparities between introgressing species abundances (Hawkins et al. 2016). As a result, the most ancient taxonomic groups tend to promote introgression impacted by demographic disparities or breeding stochasticity. Both introgression patterns showed significantly higher phylogenetic distance scores than the others without any particular pattern of directional introgression.

On the other hand, zoophilic angiosperms have developed reproductive strategies through specialized vectors (pollinators), capable of successfully finding even rare individuals as similar as possible to the original plant species (even over considerable distances) (Tylianakis Jason 2013). Other recent taxonomic groups in evolutionary terms, such as mammals and birds, have a higher tendency to develop reproductive behaviours that allow them to actively select sexual partners (frequently through assortative mating) (Jiang et al. 2013, Wang Daiping et al. 2019) compared to older groups, like amphibians and reptiles (Olsson and Madsen 2001). The development of assortative mating, makes individuals to seek conspecific mating partners, which can strictly condition the occurrence of introgression (Xue et al. 2014).

Zoophilia and assortative mating are both breeding behaviours that appear to limit introgression to species with closer phylogenetic distances. Thus, our results seem to reinforce the importance of breeding behaviours like zoophilia or assortative mating as limiting the phylogenetic amplitude of introgression. It can also have important consequences for the occurrence of directional introgression related to demographic phenomena (expansion, colonization, establishment, etc.).

We argue that in past geological eras introgression it must have been more prevalent and operating at higher phylogenetic amplitude due to the high rates of breeding strategies based on a certain degree of randomness in the choice of sexual partners and demographic disparities between introgressing species, alongside a tendency for the species to have smaller genomes. In the ancient past, it must have been an even more relevant source of genetic variation, adaptability and accelerated speciation through direct or potentially indirect mechanisms. Thus, we propose that introgression may have decreased progressively as living beings become genomically, physiologically and behaviourally more complex.

4.4.4 Conclusions

Any taxonomic entities hold in themselves an intrinsic value, for what they are, or as an end. However, they can also demonstrate an instrumental value as a way to achieve a desired or valued end (Sandler, 2012). On the one hand, the instrumental value of a species/lineage is derivative from the value of the end. On the other hand, species' instrumental value is conditioned by its effectiveness to achieve that end in comparison to other alternatives (Sandler, 2012). We conclude that introgression provides species, additionally to their intrinsic value, a fundamental instrumental value as a genetic resource for adaptation and evolution across space and time, which can go far beyond their alternatives, such as mutations. Thus, the conservation efforts should not only be considered by species threat or by the value they present to ecosystems. It must be actively considered by the fact that each species/lineage contains a unique genetic heritage that at some point of the evolutionary history may serve as a natural genetic bank available through introgression. Theoretically it may avoid a cascade of extinctions, for example in times of rapid environmental changes, such as the current anthropogenic climate change.

4.5 Future challenges

A particular issue that arises directly from our results is the lack of evidence for indirect natural introgression based on the literature reviewed. This remains one of the greatest challenges for understanding the true extent and taxonomic reach of introgression. Keystone introgression species that work like an introgression bridge between third-party species and their network of introgression interactions, should be the first candidates to be tested for the presence of indirect natural introgression.

Our results also indicate that species ancientness (both in terms of genome and behaviour) impacts the phylogenetic extent to which introgression can occur. We propose that the frequency and the taxonomic amplitude of introgression in past geological eras represented an even more relevant source of genetic variation, adaptability and accelerated speciation, that has decreased gradually as organisms became genomically, physiologically and behaviourally more complex. Testing this assumption requires extensive paleogenomic analyses of natural communities from past geological eras and novel statistical approaches to model the global introgression probability.

Acknowledgments

PH and HRa were funded by the Portuguese Foundation for Science and Technology (FCT) with a PhD grant (SFRH/BD/117979/2016 and SFRH/BD/124367/2016, respectively). HRe was also funded by FCT (DL57/2016/EEC2018/07). OR was funded through a Natural Environment Research Council Independent Research Fellowship (NE/M018660/1). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017.

Supplementary Material

Search details

We used the following search string for on-line databases:

“Topic=(*hybrid** AND *adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest** NOT *exotic*) OR Topic=(*adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest** NOT *exotic*)”

We defined some keywords as strict retention criteria: *Adapt** (all terms related to adaptation, adaptive, etc.), *Introgress** (all terms related to introgression, introgressive, etc) and *Genom** (all terms related to genome, genomics, etc.). We also used as non-strict retention criterion for the term *hybrid** (all terms related to hybrids, hybridization, etc.) that could be present together with the previous ones or not. We excluded all breeding contacts between taxa under direct human interference (breeding manipulations between species that do not naturally interbreed, genetic manipulation, invasive species scenarios, etc.). We used the following keywords as strict exclusion criteria: *Invas** (all terms related to invasion, invasive species, etc.), *Exotic* and *Domest** (all terms related to domestic species, domestication, etc.).

We defined the expression “*Adaptive Introgression*” as a keyword used as strict retention criteria searching for relevance grey literature through Google and Google scholar. We extracted 43 different variables grouped into seven categories: 1) Paper bibliometric information; 2) Type of publication; 3) Taxa under study; 4) Epoch and location of the introgressions case studies; 5) Methods used; 6) Sub-mechanisms of introgression and 7) Outcomes.

Table S4.1 - Full list of information and the total number of papers that includes each category extracted from each reviewed paper.

Categories of information	Variables extracted	Classes used	Number of papers
Bibliographic information	✓ Authors		358
	✓ Year		358
	✓ Title		358
	✓ Journal		358
	✓ Research area		358
	✓ Type of publication		358
	✓ Location of first author's institution		358
			358

Authors' initial perception about introgression	✓ Polarity	Positive,	351
		Negative,	
		Both,	
		Neutral.	
	✓ Why positive?		250
	✓ Why negative?		
	✓ Why neutral?		78
	✓ Prevalence		129
		Very rare [-3],	135
		Rare [-2],	
		Infrequent [-1],	
		Unknown [0],	
		Few cases [1],	
		Some cases [2],	
		Common [3],	
	✓ Semantics	Many cases [4],	
		Ubiquitous [5].	
		Hybrid* terms used,	358
		Hybrid* terms not used.	
Taxa under study	✓ Main taxonomic group	Animal,	355
		Plant,	
		Fungi,	
		Protists,	
		Bacteria.	
	✓ Families		355
	✓ Species pairs		355
Time and space of introgressions'	✓ Epoch	Ancient,	355
		Recent,	

case studies		Both.	
	✓ Continent		355
	✓ Approximated location		355
Methods used	✓ Type of experiment	In-situ,	351
		Ex-situ,	
		Both.	
	✓ Type of introgression markers	Quantitative Trait Locus,	347
		Microsatellites,	
		Mitochondrial DNA,	
		Ribosomal DNA,	
		Single-Nucleotide,	
		Polymorphisms,	
		AFLP,	
		PCR amplification,	
		Electrophoresis (DGGE),	
	✓ Whole-genome sequencing	Karyotypes.	
		Performed,	347
	✓ Reference genome	Not performed.	
		Available,	165
		Not available.	
Sub-mechanisms	✓ Cyto-nuclear location of islands of differentiation	Cytoplasm (mitochondria, ribosome, chloroplast),	87
		Nucleus;	
		Both.	
	✓ Nuclear location of islands of differentiation	Sex-linked chromosomes, Autosomes,	83
	✓ Cyto-nuclear location of introgression	Both.	
		Cytoplasm (mitochondria,	

	ribosome, chloroplast),	182
	Nucleus;	
✓ Nuclear location of introgression	Both.	
	Sex-linked chromosomes,	
	Autosomes,	91
✓ Sex-biased introgression	Both.	
	Yes,	
✓ Haldane's rule	No.	96
	Yes,	
✓ Maternal vs paternal way	No.	34
	Maternal,	
✓ Sexual selection impacts	Paternal.	91
	Yes,	
✓ Assortative mating preferences	No.	51
✓ Intra-sex interspecific competition	Yes,	
✓ Balancing selection	No.	12
	Yes,	
	No.	22
✓ Demographic impacts	Yes (Multiallelic, transespecific polymorphisms, etc.),	40
	No (Genetic drift).	
✓ Symmetry	Yes,	
	No.	
✓ Direction	Symmetric,	67
	Asymmetric.	
✓ Donor species	Unidirectional,	
✓ Receptor species	Bidirectional.	276
✓ Native-to-colonizer		
✓ Endogenous impacts		

		259
✓ Exogenous impacts	Yes,	
	No.	259
	Yes (Baculum format, flowering time, sexual characters, etc.),	259
✓ Climate-mediated introgression	No.	81
	Yes (temperature, topography, pesticides, etc.),	28
✓ Allele surfing	No.	
	Yes,	
	No.	
	Yes,	64
	No.	
		53
		32
Outcomes	✓ Phenotypic traits shared	230
	✓ Physiologic system	230
	✓ Polarity	
	Positive,	230
	Negative,	
	Neutral.	
	✓ Adaptive outcomes	230

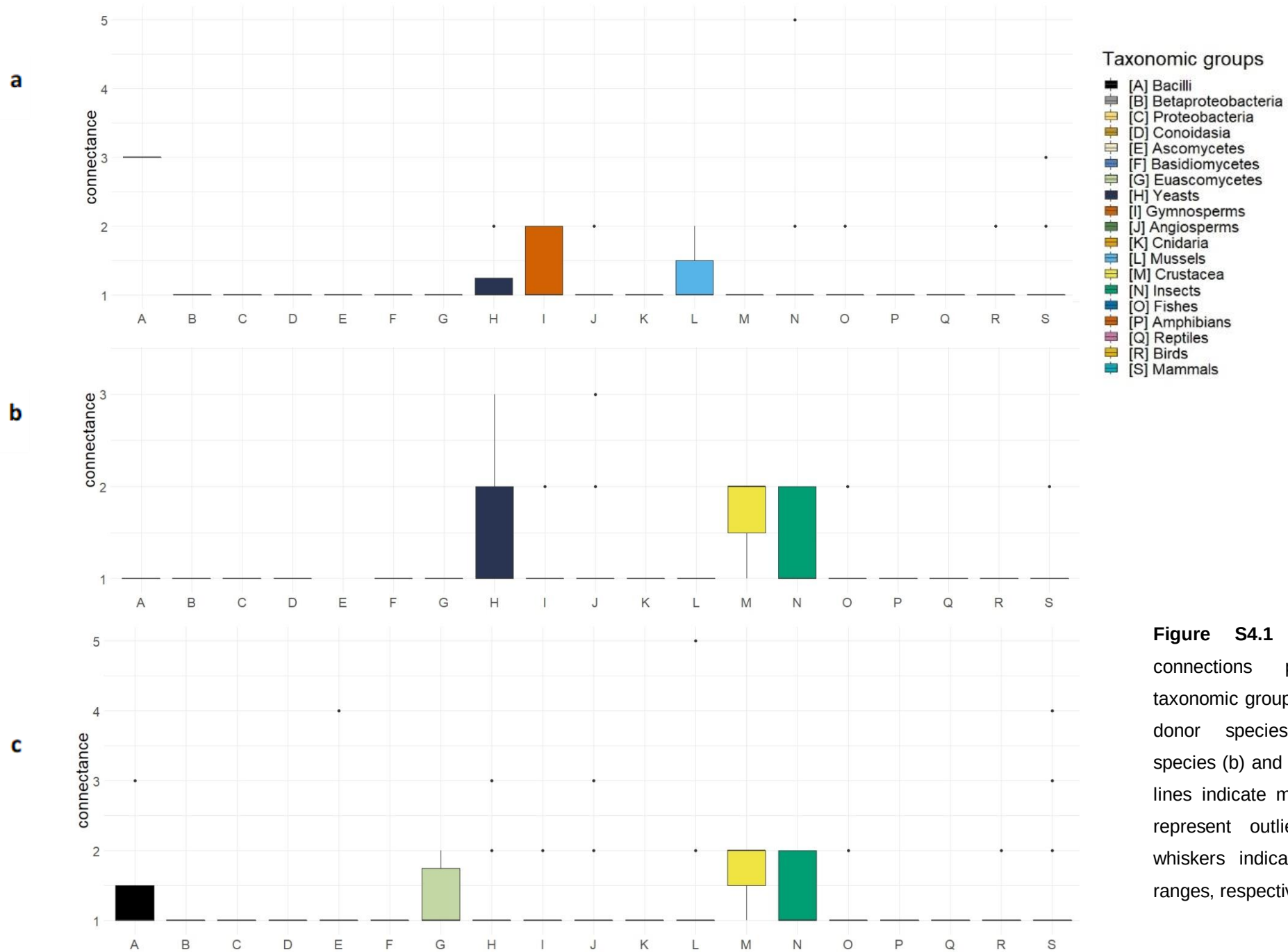


Figure S4.1 - Number of connections per taxa by taxonomic group (mean $\pm$ SD), in donor species (a), receptor species (b) and globally (c). Solid lines indicate medians; the dots represent outliers; boxes and whiskers indicate quartiles and ranges, respectively.

Table S4.2 - Statistical results of multiple comparisons of mean based non-parametric Kruskal-Wallis test, performed to identify which taxa groups present significant differences in phylogenetic distances among species showing evidence of introgression (yellow background) with reference to Mean Difference (MD); and pairwise chi-square comparisons under IQR analyses (interquartile range analyses) comparing phylogenetic extent of introgression between taxonomic groups (grey background). Green cells represent significant differences at $P < 0.05$.

	Gymnosperms	Angiosperms	Crustacea	Mussels	Insects	Fishes	Amphibians	Reptiles	Birds	Mammals
Gymnosperms		MD=-23.90 NS	MD=-11.97 NS	MD=86.28 $p=0.001$	MD=44.97 $p=0.044$	MD=-0.41 NS	MD=57.44 NS	MD=57.44 $p=0.046$	MD=-28.67 NS	MD=-16.08 NS
Angiosperms	$X^2_1=19.17$ $p<0.01$		MD=11.92 NS	MD=110.17 $p<0.01$	MD=-22.28 NS	MD=23.48 NS	MD=81.34 $p=0.002$	MD=81.34 $p<0.01$	MD=-4.78 NS	MD=-7.80 NS
Crustacea	$X^2_1=4.70$ $p<0.05$	$X^2_1=5.74$ $p<0.05$		MD=98.25 $p=0.001$	MD=34.00 NS	MD=11.56 NS	MD=69.42 $p=0.049$	MD=69.42 $p=0.031$	MD=-16.70 NS	MD=-4.11 NS
Mussels	$X^2_1=12.50$ $p<0.01$	$X^2_1=0.08$ NS	$X^2_1=1.76$ NS		MD=-132.25 $p<0.01$	MD=86.69 $p<0.01$	MD=-28.83 NS	MD=-28.83 NS	MD=-114.95 $p<0.01$	MD=-102.36 $p<0.01$
Insects	$X^2_1=16.13$ $p<0.01$	$X^2_1=0.03$ NS	$X^2_1=3.69$ NS	$X^2_1=0.11$ NS		MD=45.56 $p=0.007$	MD=103.42 $p<0.01$	MD=103.42 $p<0.01$	MD=17.30 NS	MD=29.89 $p=0.017$
Fishes	$X^2_1=8.51$ $p<0.01$	$X^2_1=2.66$ NS	$X^2_1=0.37$ NS	$X^2_1=0.23$ NS	$X^2_1=1.23$ NS		MD=57.86 $p=0.041$	MD=57.86 $p=0.018$	MD=-28.12 NS	MD=-15.67 NS
Amphibians	$X^2_1=4.92$ $p<0.05$	$X^2_1=5.51$ $p<0.05$	$X^2_1=0.02$ NS	$X^2_1=1.61$ NS	$X^2_1=3.49$ NS	$X^2_1=0.30$ NS		MD=0.00 NS	MD=-86.12 $p=0.003$	MD=-73.53 $p=0.005$
Reptiles	$X^2_1=7.17$ $p<0.01$	$X^2_1=3.57$ NS	$X^2_1=0.12$ NS	$X^2_1=0.58$ NS	$X^2_1=1.91$ NS	$X^2_1=0.00$ NS	$X^2_1=0.08$ NS		MD=-86.12 $p=0.001$	MD=-73.53 $p=0.001$
Birds	$X^2_1=18.60$ $p<0.01$	$X^2_1=0.15$ NS	$X^2_1=5.33$ $p<0.05$	$X^2_1=0.61$ NS	$X^2_1=0.00$ NS	$X^2_1=2.35$ NS	$X^2_1=5.10$ $p<0.05$	$X^2_1=3.22$ NS		MD=12.59 NS
Mammals	$X^2_1=15.95$ $p<0.01$	$X^2_1=0.04$ NS	$X^2_1=3.58$ NS	$X^2_1=0.09$ NS	$X^2_1=0.13$ NS	$X^2_1=1.10$ NS	$X^2_1=3.38$ NS	$X^2_1=1.83$ NS	$X^2_1=0.01$ NS	

Chapter 5

Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats

Pedro Horta, Helena Raposeira, Adrián Baños, Carlos Ibáñez, Orly Razgour, Hugo Rebelo and Javier Juste

Horta P., Raposeira H., Baños A., Ibáñez C., Razgour O., Rebelo H. & Juste J. (submitted). Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats. Scientific Reports. DOI: <https://doi.org/10.1038/s41598-022-15412-2>

Keywords: Allopatry, cryptic species, *Eptesicus isabellinus*, *Eptesicus serotinus*, hybrids, Introgressive hybridization, niche partitioning, morphology, sympatry

Abstract

Cryptic species that coexist in sympatry are likely to simultaneously experience strong competition and hybridization. The first phenomenon would lead to character displacement, whereas the second can potentially promote morphological similarity through introgression. The main goal of this work was to investigate the effect of introgressive hybridization on the morphology of cryptic Iberian *Eptesicus* bats when facing counteracting evolutionary forces from interspecific competition. We found substantial overlap both in dentition and in wing morphology traits, though mainly in individuals in sympatry. The presence of hybrids contributes to a fifth of this overlap, with hybrids showing traits with intermediate morphometry. Thus, introgressive hybridization may contribute to species adaptation to trophic and ecological space responding directly to the macro-habitats characteristics of the sympatric zone and to local prey availability. On the other hand, fur shade tended to be browner and brighter in hybrids than parental species. Colour differences could result from partitioning of resources as an adaptation to environmental factors such as roost and microhabitats. We argue that a balance between introgressive hybridization and niche partitioning shapes species interactions with the environment through affecting morphological traits under selection.

5.1 Introduction

The evolutionary history of species under preliminary stages of macroevolution moves through complex forces, leading to incongruities in phylogenetic inferences and species classification (Ottenburghs et al., 2017). Divergence is frequently discussed as involving mainly stages of allopatry (Baiz et al., 2019; Renaut et al., 2013; Slager et al., 2020). However, historical environmental fluctuations (Grant and Grant, 2016) mediate iterations between periods of allopatry and sympatry (Pauquet et al., 2018; Pfennig, 2007; Staubach et al., 2012). When past allopatry was not sufficient to eliminate or significantly reduce niche overlap, closely-related species may coexist stably during secondary contacts under antagonistic evolutionary forces, imposed for example by hybridization and niche partitioning (Schluter, 2000). On one hand, under sympatry, genetic material can be transferred through introgressive hybridization with potential evolutionary convergence (Song et al., 2011). On the other hand, ecological interactions, such as competition, predation or parasitism may produce exclusion or promote divergence as a response (Anderson et al., 2002).

When hybridization between lineages presents adaptive advantages in relation to the parental lines resulting in increased fitness, the genetic pools will face a process of adaptive introgression. This has been described as the main evolutionary response in natural hybridization (Anderson and Hubricht, 1938; Dunn et al., 2013; Gramlich et al., 2018; Ma et al., 2010; Mavárez et al., 2006). Introgressed alleles potentially associated to well-adapted traits (Aleksic et al., 2018; Alexander et al., 2017; Brower, 2013; Cahill et al., 2015; Djogbénou et al., 2008; Enciso-Romero et al., 2017; Gagnaire et al., 2009) are introduced into the gene pool of the recipient species by backcrossing and fixed by natural selection (de Lafontaine et al., 2015; Song et al., 2011). Therefore, introgressed species can jump directly to new adaptive optimum, bypassing intermediate steps (Cahill et al., 2015; Dasmahapatra et al., 2012). By allowing closely-related species to share particularly beneficial traits, adaptive introgression is sometimes understood as a homogenizing process promoting evolutionary convergence (Latch et al., 2006; Oliveira et al., 2008).

Recent studies have shown important phenotypic expression of adaptive introgression in morphological traits of many taxa. Introgressed morphological traits were reported to promote dehydration/water-loss resistance to warmer or colder climates in plants, for example by increasing number or size of leaves, branches or roots under desert conditions (Gramlich et al., 2018). Moreover, changes in body width,

head shape or eye size were shown to promote higher fitness in some fishes (Nichols et al., 2015), while larger heads with stronger bite and larger testes promoted better sexual performance in reptiles (Yang et al., 2018). Introgression of morpho-physiological traits also promotes higher fitness in some rodents in environments with lower precipitation and temperatures (Boratyński et al., 2011). Ancient events of adaptive introgression have even allowed humans to adapt to island environments by decreasing their size (Mondal et al., 2016). Colour change through adaptive introgression was reported in insects (Dasmahapatra et al., 2012; Enciso-Romero et al., 2017), mammals (Jones et al., 2018; Melo-Ferreira et al., 2014) and fishes (Meier et al., 2017; Mims et al., 2010). Colour change is frequently associated with increasing mating performance (Salazar et al., 2010; Yang et al., 2018), better mimicry capacity (Naisbit et al., 2003; Zhang et al., 2016), higher success in escaping predators (Zhang et al., 2013) and in exploring new habitats (Mims et al., 2010) and as responses, for example, to climate change (Giska et al., 2019; Jones et al., 2018; Melo-Ferreira et al., 2014; Zhang et al., 2013).

As an opposite evolutionary force, competition may lead species or lineages to avoid each other and to occupy a narrower and differentiated optima and set of conditions. If this effect is durable and prevalent enough, then it may lead to a species-specific divergent trait displacement due to a differential exploitation of resources (Melville, 2002; Pfennig and Pfennig, 2010).

Competition has been reported to drive divergence in phenological traits, like changing floral shape of angiosperms in response to altitudinal gradients (Kooyers et al., 2017), and to promote functional and biomechanical differences in jaw closure of salamanders (Adams and Rohlf, 2000). Moreover, competition has been shown to play a role in beak size divergence and larynx morphology in birds, both relevant traits for diet adaptations, and song characteristics, thus influencing sexual selection and species recognition (Grant and Grant, 2006). Head morphology and size divergence were also described as being the result of competition in spadefoot toads, in response to omnivore or carnivore diet (Pfennig and Murphy, 2000).

Despite the relevance of morphological traits for species adaptive capacity and individual fitness, the impact of hybridization on morphological traits when occurring in sympatry or parapatry remains largely unknown. Cryptic species are an extreme case among closely-related taxa for being morphologically identical but genetically distinct (Jones, 1997). Due to their phylogenetic proximity and partial niche overlap, as well as morphological similarity and high potential for hybridization, they represent excellent case studies for the effect of antagonistic evolutionary processes on morphological trait

displacement, particularly when associated with sympatric or parapatric distributions (Marsteller et al., 2009; Tene Fossog et al., 2015).

Notably, in the Iberian Peninsula, over 20% of known bats species show cryptic diversity (Ibáñez et al., 2006; Juste et al., 2004). Some of the cryptic species pairs exhibit high genetic divergence, such as *Eptesicus serotinus* (Schreber 1774) and *E. isabellinus* (Temminck 1840), which show over 16% divergence in the mtDNA Cytochrome b gene (Ibáñez et al., 2006). A comparative recent study supports a more pronounced and geographically structured intraspecific genetic variation within *E. isabellinus* (Centeno-Cuadros et al., 2019). This species has experienced a rapid post-glacial expansion earlier, heading northwards until occupying its current range. *E. serotinus* is thought to have expanded southwards from Central Europe, likely arriving later than *E. isabellinus* to the ecotone of central Iberia where both species meet (Centeno-Cuadros et al., 2019). Currently, *E. serotinus* is distributed along the Atlantic region of Iberia (colder and wetter) while *E. isabellinus* mainly occurs in the Mediterranean region (hotter and drier) (Santos et al., 2014). Across their ranges, the two species geographically avoid each other, indicating that interspecific competition likely shaped their broad-scale distributions (Novella-Fernandez et al. 2021). With a vast allopatric distribution, the species share a restricted contact zone, where they interbreed (Centeno-Cuadros et al., 2019). Although nuclear markers identified a male-mediated hybridization, there is no evidence of mitochondrial introgression, contrary to what is known for other *Eptesicus* (Neubaum et al., 2007). Moreover, ongoing hybridization is asymmetric, occurring mainly from *E. isabellinus* to *E. serotinus* (28% hybrids in *E. serotinus* colonies and 2.7% in *E. isabellinus* colonies) (Centeno-Cuadros et al., 2019).

This study aims to understand the effect of this introgressive hybridization on morphological traits of the two cryptic Iberian *Eptesicus* bats in face of counteracting evolutionary forces from interspecific competition. We addressed three main objectives: 1) Test for morphological differences between cryptic *Eptesicus* species; 2) Determine the influence of sympatry and allopatry on patterns of morphological variation (wing, dentition and colour traits); 3) Assess the efficiency of classification statistics on species identification even in the presence of hybrids.

Clarifying these objectives could elucidate how potential natural gene transfer through introgression can allow recipient bat species to incorporate into its genome alleles responsible for the presence of novel morphological traits.

5.2 Methods

5.2.1 Study area

We searched for *Eptesicus* bat colonies between 1998 and 2014 along a North–South gradient across the Iberian Peninsula, including allopatric areas of only *E. serotinus* in the north, a central region of sympatric zone and allopatric areas of *E. isabellinus* in the south. Field sampling methods were described in previous publications (Centeno-Cuadros et al., 2019; Santos et al., 2014) as well as the location of all sampled colonies (Centeno-Cuadros et al., 2019). The methods were performed in accordance with relevant guidelines and regulations and approved by the Ethical committee at the EBD- CSIC (Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas) that granted protocol approval.

5.2.2 Sampling design

Wing membrane biopsies (3 mm) were collected according to Worthington-Wilmer and Barratt (1996) from all captured bats. The samples were kept in 96% ethanol at -20°C until processed in the laboratory for molecular analysis to confirm species identification (see Centeno-Cuadros et al., 2019 for laboratory procedures).

Wing morphology variables were measured with a calliper and included the lengths of the forearm (FA), metacarpals of the III and V fingers and the first phalanges of the same fingers, as well as the length of the upper dental series (canine to third molar - CM3) and the rostral width measured at the canines' level (C1-C1) (Figure 5.1).



Figure 5.1 - Wing and dentition morphometric measurements taken from *Eptesicus* bat species during field work.

Coat colour was quantified by measuring the reflectance through a High Resolution Colorimeter (Spectrophotometer CM-2600d/2500d, Konica, Minolta). Two measurements were obtained for dorsal and ventral colours from each bat. Each measurement was the average of three light flashes' reflectance. Reflectance was measured at a wavelength band from 350 to 740 nm and was decomposed according to the colour space defined by CIELAB colour space, which included three parameters, L^* , a^* and b^* . L^* represents perceptual lightness, and a^* and b^* a four colours' scale, from red to green and blue to yellow, respectively (Figure S5.1) (Illumination, 2004).

To study the effect of interspecific responses of *E. serotinus* and *E. isabellinus* and their hybrids, bats were clustered into five experimental groups: allopatric *E. isabellinus*, sympatric *E. isabellinus*, hybrids (individuals classified as hybrids by Centeno-Cuadros et al. (2019) based on genetic data, using a conservative criteria), sympatric *E. serotinus* and allopatric *E. serotinus*. We assumed that both species were geographically isolated from each other and the respective hybrids within the allopatric groups. On the contrary, in the sympatric groups, each species co-existed with the other species and their hybrids. The geographic classifications of each experimental group were based on previous studies (Ibáñez et al., 2006; Santos et al., 2014; Centeno-Cuadros et al. 2019).

5.2.3 Statistical analyses

✓ The effect of geographic origin and hybrids presence on bat morphometry

We used General Linear Models to assess whether geographic relationships significantly affected the morphometry and/or the colour of the studied bats. We performed a non-parametric MANOVA (Maroco, 2007) on the morphological variables because homogeneity of variance could not be assumed according to the Box's M tests (Morphometry: Box's $M=133.73$; $F_{(84, 16828.68)}=1.393$; ns; Colour: Box's $M=215.69$; $F_{(63, 1824.12)}=2.480$; ns) even after trying several data transformations ($\log_{10}$, $\ln$, arcsen, etc.). We performed a Kruskal-Wallis test to identify which morphometric traits and colour variables were significantly different, followed by multiple comparisons by the post-hoc Fisher's LSD test to check for differences between groups (Maroco, 2010).

✓ *Summarizing and comparing morphological variables*

The original morphometric space of the wing and dentition variables was summarized into its main components by a principal component analysis (PCA) with the symmetrical normalization method (Maroco, 2010). The eigenvalue rule greater than 1 was used as criterion for components' retention alongside the scree-plot. We analysed the internal consistency of each component through Cronbach's alpha (Maroco, 2010).

After the validation of both assumptions for multivariate normal distribution and homogeneity of variance-covariance ($M=13.98$; $F_{(12, 7934.55)}=1.104$, $p=0.352$), we performed a MANOVA over the PCA's axes to evaluate the relationship of the five experimental groups with morphometric traits. When the MANOVA detected significant effects, we performed an ANOVA for each component (PC1 and PC2), followed by multiple comparison through Tukey's HSD post-hoc test. Again, according to the Box's M tests, even after transformation, the homogeneity of covariance could not be assumed (Box's $M=30.41$; $F_{(12, 2323.67)}=2.250$; ns) for retained colour's PCA. In order to assess whether geographic origin affected colour variables, we performed a non-parametric MANOVA (Maroco, 2010), followed by the tests described above (Maroco, 2010). We carried out all analyses with $\alpha=0.05$ in SPSS Statistics software (v. 22; SPSS Inc, Chicago, IL), producing all visualizations through "ggplot2" R package (Wickham, 2016).

✓ *Classification statistics with and without hybrids' presence*

We used two classification algorithms to classify both species in sympatry according to the morphological variables: discriminant function analysis (DFA - quadratic with cross-validation) and the support vector machines (SVM - with a machine learning approach).

The morphometric matrices fulfils the assumptions of normal distribution and homogeneity of variance so we proceeded with parametric analyses (Morphometry with hybrids: Box's $M=38.33$; $F_{(28, 32463.13)}=1.267$; $p=0.157$; Morphometry without hybrids: Box's $M=11.10$; $F_{(10, 5819.66)}=0.996$; $p=0.444$).

The data were firstly included in two stepwise discriminant analyses with the method of Wilks' Λ used to identify which of the morphological and colour variables under study can better discriminate both parental species with and without the presence of hybrids. Again, homogeneity of the variance-covariance matrices could not

be assumed for the colour variables (Colour with hybrids: Box's $M=37.65$, $F_{(10, 11071.13)}=3.474$, ns; Colour without hybrids: Box's $M=38.06$, $F_{(10, 4588.83)}=3.414$, ns). Still, we proceeded with analysis because the discriminant analysis is robust to violation of assumptions when (i) the size of the smallest group (sympatric *E. serotinus*) is greater than the number of variables in the study and (ii) the means of the groups are not proportional to their variances (Stevens 1986). Finally, we used Classification Statistics to obtain the classification functions and to assign species identification according to morphometric traits and/or colour variables. All DFA analyses were carried out with $\alpha=0.05$.

In addition, a support-vector machine (SVM) algorithm was performed using the principal components extracted from each PCA (morphometry and colour), through “tidyverse” (performing data manipulation) (Wickham et al., (2019), “kernlab” (Karatzoglou et al., 2004) and “e1071” R packages (Meyer et al., 2012) (performing calculations and producing visualizations). The kernel functions of the support vector machines used a radial basis function with a gamma parameter ranging from 0.1, 1, 10, 100 and 1000. For each value of gamma, the SVM was reinitialised 20-times to increase the chance of obtaining an optimal classifier (Redgwell et al., 2009; Sáez et al., 2019). For Classification Statistics the algorithm of the SVM was trained for every target case in the dataset (each species) (Redgwell et al., 2009). All classifiers were then combined and categorised for each morphological trait as either belonging to a specific class, or not. Each bat was considered as classified correctly only if a single support vector machine classified it and if validated by molecular identification.

✓ *Quantification of the impact of the hybrids on the external morphological traits overlap between species*

We repeated the entire statistical procedure after extracting from the dataset all individuals classified as hybrids in Centeno-Cuadros et al. (2019). We compared the classification performance of both algorithms in the sympatric population with hybrids *versus* the same population after excluding them. This approach made it possible to calculate the contribution of hybrids to the overlap of morphological traits with their cryptic parental species.

5.3 Results

5.3.1 Testing for morphological differences between cryptic *Eptesicus* species

Our results showed significant differences of both morphometric and colour variables along the experimental groups. Morphometric differences occurred for the variables FA, D3 MC, D5 MC, D5 F1, C1-C1 and CM3 but not for the variable D3 F1 (Table 5.1). For coat colour, we found significant differences between the groups in the variables L* dorsal, a* dorsal, b* dorsal, a* ventral and b* ventral, but not for the variable L* ventral (Figure 5.2).

Table 5.1 - Descriptive statistics of the morphometric traits of *Eptesicus serotinus*, *E. isabellinus* and their hybrids.

	Wing					Dentition	
	FA	D3 MC	D3 F1	D5 MC	D5 F1	C1-C1	CM3
<i>E. isabellinus</i> allopatric (Eisa allo; n=31 individuals)	51.6 49.9 – 55.7	47.1 44.0 – 52.0	17.8 12.2 – 19.8	44.1 41.3 – 48.0	10.9 10.0 – 12.0	6.7 6.3 – 7.2	7.2 6.8 – 7.7
<i>E. isabellinus</i> sympatric (Eisa sym; n=33 individuals)	51.6 48.6 – 54.3	46.1 42.6 – 48.6	18.0 16.5 – 20.5	43.0 40.1 – 48.5	11.3 10.2 – 12.6	6.9 6.3 – 7.4	7.2 6.5 – 8.4
<i>Hybrids</i> (n=8 individuals)	52.6 49.7 – 53.7	46.8 42.7 – 47.7	18.8 16.8 – 19.1	43.4 39.9 – 45.9	12.0 11.0 – 13.3	6.7 6.5 – 6.9	7.4 7.1 – 7.5
<i>E. serotinus</i> sympatric (Eser sym; n=19 individuals)	52.8 49.7 – 55.2	47.5 44.7 – 49.7	17.8 16.8 – 20.4	44.5 40.5 – 47.2	11.7 9.9 – 13.1	6.9 6.6 – 7.5	7.6 7.3 – 8.5
<i>E. serotinus</i> allopatric (Eser allo; n=35 individuals)	52.6 48.8 – 56.1	49.0 41.4 – 51.6	18.0 13.2 – 19.5	46.5 41.6 – 49.6	11.3 10.0 – 12.5	6.9 6.6 – 7.5	7.7 7.4 – 8.7
$\chi^2_{KS} (4)$	13.302	38.271	1.698	25.234	12.244	15.300	64.410
<i>p</i> -value	0.010	<0.001	ns	<0.001	0.016	0.004	<0.001

Medians are shown above
range

A**B**

	Dorsal mean colour			Ventral mean colour		
	L*	a*	b*	L*	a*	b*
<i>E. isabellinus</i> allopatric (n= 6 individuals) *	40.4 ± 2.18	5.4 ± 0.61	15.2 ± 1.29	51.3 ± 2.74	5.2 ± 0.94	17.8 ± 1.70
<i>E. isabellinus</i> sympatric (n= 39 individuals) **	38.4 ± 3.77	6.1 ± 1.16	17.1 ± 4.81	52.0 ± 4.73	5.3 ± 0.97	18.2 ± 2.43
Hybrids (n=7 individuals)	37.4 ± 7.06	6.8 ± 1.66	19.1 ± 5.74	51.9 ± 4.20	5.5 ± 0.78	19.4 ± 2.42
<i>E. serotinus</i> sympatric (n= 17 individuals) ***	32.9 ± 6.74	7.3 ± 2.13	21.1 ± 8.50	48.3 ± 5.03	5.6 ± 0.84	19.2 ± 3.67
<i>E. serotinus</i> allopatric (n= 11 individuals) ****	33.6 ± 5.14	3.8 ± 0.50	10.9 ± 2.35	50.3 ± 6.97	3.4 ± 0.40	13.9 ± 1.72
$X^2_{KS} (4)$	17.309	32.975	28.697	6.986	26.736	23.125
p-value	0.002	<0.001	<0.001	ns	<0.001	<0.001

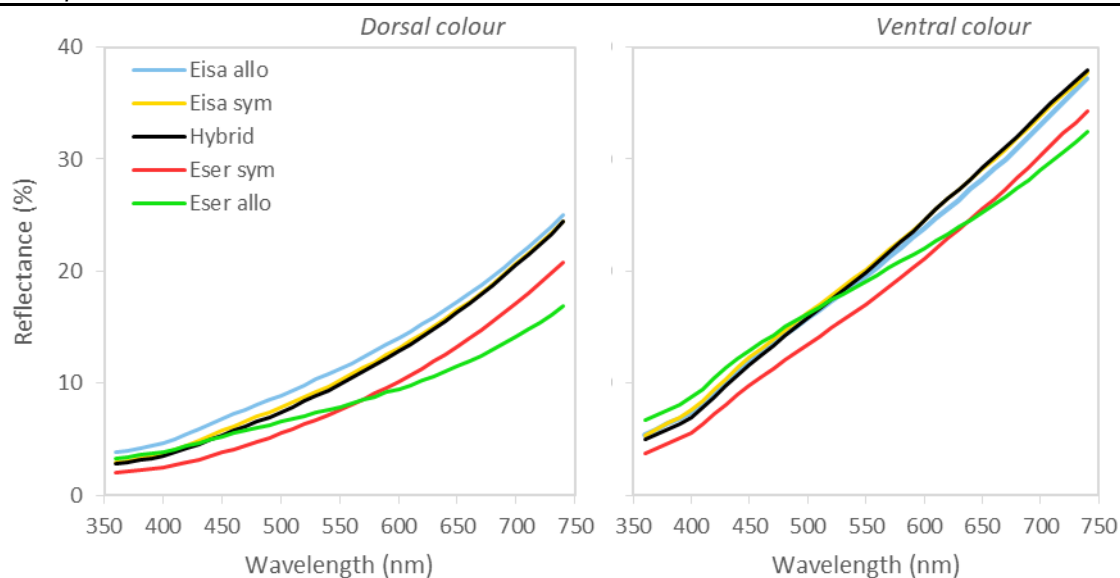
C

Figure 5.2 - Colour differences between bat groups. **(A)** Photographic representation of hair colour of representative specimens of both parental species groups (*Eptesicus isabellinus* and *E. serotinus*) as a function of their geographical relationships. **(B)** Descriptive statistics of dorsal and ventral colour of *E. serotinus*, *E. isabellinus* and their hybrids. Background colour represents the mean colour of the dorsum and belly in the CIELAB colour space of each parental species and in function to their different geographical relationships and their hybrids. **(C)** Percentage of reflectance measured by colorimeter across the visible wavelength scale. Acronyms are available in Table 5.1.

The information between both morphometric and colour variables was summarized in two main orthogonal components, explaining respectively 59.8% and 83.4% of the total variance of the original morphometric and colour variables (Table S5.2). The first morphometric component was associated with bats' "Size", whereby generally, the weight of all variables was very high and positive. The second morphometric component essentially summarized the wing "Shape", namely the metacarpals and first phalanges proportion. Additionally, the inversely proportional relationship between the length of the first phalanges and the dentition variables, mainly CM3, had a very high and negative score in this second component (Table S5.2). Despite an evident overlap, the two-dimensional PCA map showed that *E. serotinus* is generally larger in both wing and dentition (Table S5.3), particularly in the allopatric zone with respect to *E. isabellinus*. In sympatry there was a greater overlap between both species despite maintaining the same pattern (Figure 5.3).

E. isabellinus both in allopatry and sympatry showed a greater proportion between first phalanges and both metacarpals (e.g. smaller ratio of length of both metacarpals to first phalange), revealing an inversely proportional relationship between the length of the first phalanges and both dentition variables (larger phalanges and smaller C1-C1 and mainly CM3) (Figure 5.3). In contrast, *E. serotinus* revealed, in both sympatry and allopatry, to have substantially smaller first phalanges relative to metacarpals, as well as to both dentition variables (mainly CM3) (Figure 5.3).

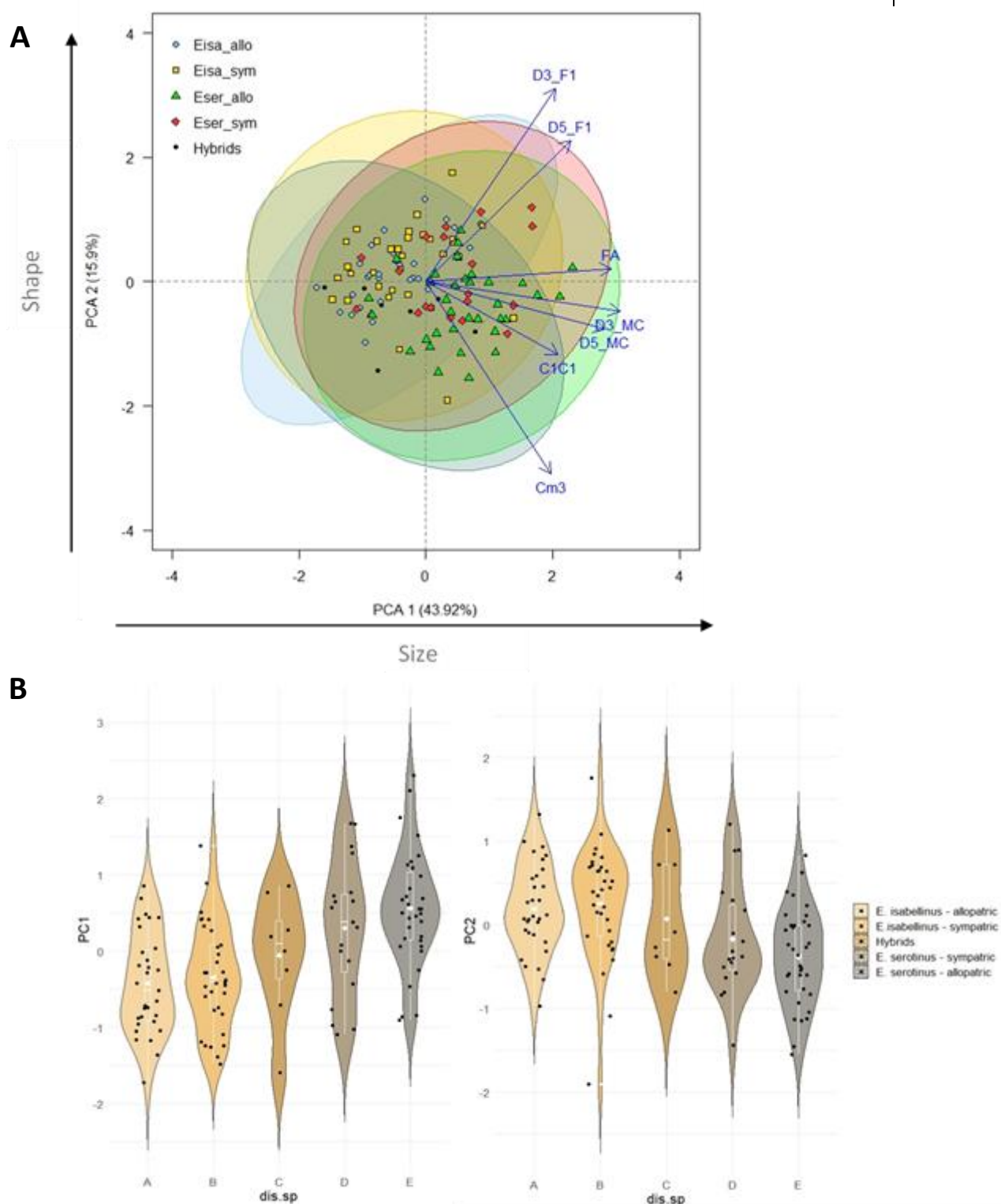
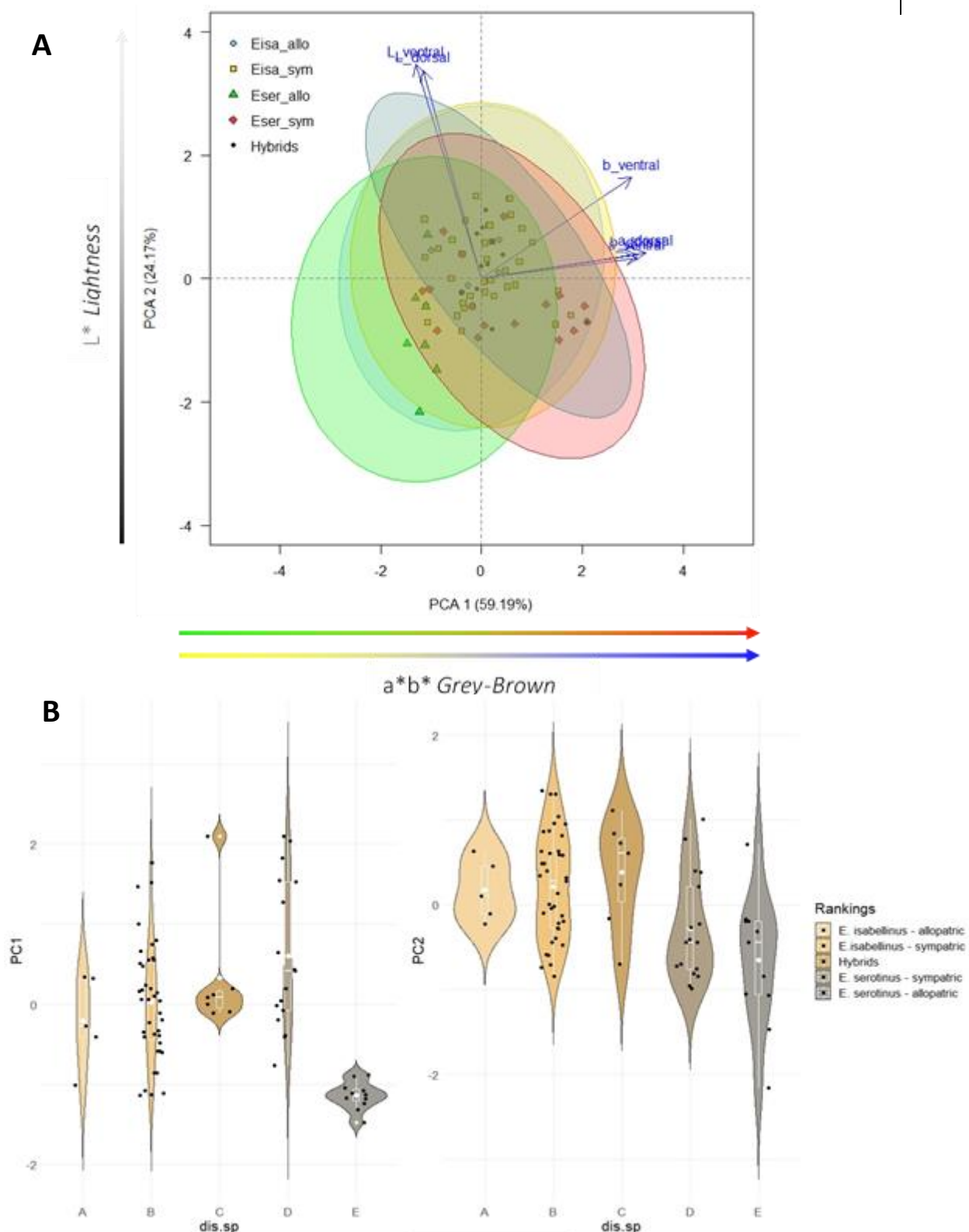


Figure 5.3 - Positioning of each individual in the two-dimensional space defined by the main PCA components retained and their position relative to the original morphometric variables (**A**). The violin plots represent *Eptesicus isabellinus* (allopatric and sympatric), *E. serotinus* (allopatric and sympatric) and Hybrids PCA scores compared to size (PC1) and shape (PC2) (**B**). Within violin plots white solid lines boxplots include medians (horizontal white line) and averages (white dot); boxes and vertical white lines indicate quartiles and ranges (excluding outliers), respectively. Acronyms are available in Table 5.1.

The first colour component of the PCA was associated with a range of colours from grey to brown, named as "a*b* Grey-Brown scale", while the second component essentially summarized the "L*Brightness" (Table S5.2). Despite an evident overlap, it was possible to characterize allopatric *E. serotinus* as being darker and greyer by showing a combination of higher black, green and yellow components in both dorsal and ventral colourations (Figure 5.4). All the remaining groups varied mainly along the brown pallet by having higher values for red and blue. Sympatric *E. serotinus* was in the other extreme of that Grey-Brown colour pallet, being the brownest group (Table S5.4). Likewise, sympatric *E. serotinus* shared the darkest position with allopatric *E. serotinus*, into brightness scale ("L* brightness"). Allopatric *E. isabellinus* was the brightest group. In sympatry, once again, *E. isabellinus* showed brightest colour patterns. The ventral colour was always brighter than the dorsal one in all experimental groups due to its higher L* values, showing even more subtle colour differences between groups (Figure 5.2).



✓ *Sympatry versus Allopatry – influence on morphology*

There were no significant differences in the bats' size and shape between allopatric and sympatric groups within each species (except in metacarpals). However, all morphological variables differed significantly between allopatric groups. Regarding morphometric variables (D5 MC, D5 F1 and C1C1), especially for bats' "shape", these significant differences disappear in sympatry (a detailed description of the morphometric comparisons is available in Supplementary material).

Regarding the colour variables, all experimental groups differed significantly from allopatric *E. serotinus* in the $a^* b^*$ Grey-Brown scale, which were the only individuals in the grey range of the colour pallet. In terms of brightness, allopatric *E. serotinus* was only not significantly different from individuals of the same species when in sympatry (bats were equally dark, though in sympatry they tended to be significantly browner). In sympatry, both species also differed significantly, however, contrary to the morphometric variables, this difference was slightly greater than that found between species in allopatry.

✓ *Hybrids versus Parental species – impact of hybridization on morphology*

Hybrids did not differ significantly from the other groups of allopatry/sympatry in wing size (except for metacarpals), showing intermediate wing morphometric values relative to both parental species. Hybrids differed significantly in the dentition between the two species, even in comparison with both sympatric groups with which they coexist (e.g. CM3). Nonetheless, hybrids showed consistently intermediate phenotypes in both dentition and wing size, as well as wing shape (a detailed description of the morphometric comparisons between hybrids and parental species is available in the Supplementary material).

Hybrids showed the brightest pelage colour (both in their dorsal and ventral coat), although not significantly different from *E. isabellinus* in both groups (sympatry and allopatry) (Figure 5.3; Table S5.5). On the other hand, hybrids were significantly browner than allopatric *E. serotinus* and they were also the brownest group together with sympatric *E. serotinus* (Table S5.5).

5.3.2 Species discrimination through classification statistics

✓ *Stepwise DFA with and without hybrids*

The morphometric stepwise DFA generated one discriminant function mainly defined by D3_MC and CM3 ($\Lambda=0.579$, $\chi^2_{(7)} = 53.773$, $p<0.001$). The percentage of individuals classified correctly in the presence of hybrids was 81.7%. After hybrids removing, discriminant analysis generated also one discriminant function, with FA, D3_MC, D5_MC (marginally significant [$F=3.450$, $p=0.069$]) and CM3 as statistically significant variables ($\Lambda=0.632$, $\chi^2_{(4)}=21.073$, $p<0.001$). The results of Classification Statistics showed that the total percentage of individuals classified correctly increased to 84.0% after hybrids removing.

The colour stepwise DFA generated also only one discriminant function, with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant variables ($\Lambda=0.842$, $\chi^2_{(4)}=10.115$, $p=0.039$). The percentage of individuals classified correctly in the presence of hybrids was 71.4%. After removing the hybrids, the colour discriminant analysis generated also one discriminant function, once again with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant ($\Lambda=0.762$, $\chi^2_{(4)}=14.114$, $p=0.007$). The results of Classification Statistics showed that the total percentage of individuals classified correctly increased to 78.6% after hybrids removing.

✓ *Support Vector Machine with and without hybrids*

SVM generated one discriminant function based on morphometric PC1 and PC2 as predictors' variables that summarized all morphometric traits. After simulations, the results of Classification Statistics showed that the percentage of individuals classified correctly in the presence of hybrids was 75.0%. Without hybrids, SVM generated also one discriminant function. The percentage of individuals classified correctly increased to 76.9% after removing hybrids.

Based on colour PC1 and PC2 as predictors' variables, SVM generated also one discriminant function. After simulations, the results of Classification Statistics showed that the percentage of individuals classified correctly in the presence of hybrids was 68.3%. After hybrids removing, the colour SVM also generated one discriminant function. The results of Classification Statistics showed that the total percentage of individuals classified correctly increased to 76.8% after removing hybrids (detail description is available in Supplementary Material).

Finally, both species showed a statistically significant differential behaviour in relation to the correct classification rate for both classification methods tested (χ^2_{kw}

(1)=10.678, $p=0.01$, $N=16$) and *E. isabellinus* individuals were significantly classified correctly than the individuals of *E. serotinus* ($F=15.976$; $p=0.001$) (Table 5.2).

Table 5.2 - Correct species classification rates, species overlap and hybrids contribution to species overlap obtained by two different methods of classification statistics (DFA and SVM) based on morphometric and colour traits of *E. isabellinus* and *E. serotinus* in sympatry.

	DFA	SVM
	Morphometry	
<i>E. isabellinus</i> correct classification rate	84.5%	78.9%
<i>E. serotinus</i> correct classification rate	78.3%	72.3%
<i>E. isabellinus</i> correct classification rate without hybrids presence	96.0%	83.9%
<i>E. serotinus</i> correct classification rate without hybrids presence	66.7%	66.7%
Global correct classification rate	81.7%	75.0%
Global correct classification rate without hybrids presence	84.0%	76.9%
Overlap in sympatry	18.3%	25.0%
Hybrids contribution to species overlap	13.6%	7.6%
	Colour	
	DFA	SVM
<i>E. isabellinus</i> correct classification rate	92.3%	92.3%
<i>E. serotinus</i> correct classification rate	37.5%	29.2%
<i>E. isabellinus</i> correct classification rate without hybrids presence	92.3%	77.1%
<i>E. serotinus</i> correct classification rate without hybrids presence	47.1%	75.0%
Global correct classification rate	71.4%	68.3%
Global correct classification without hybrids presence	78.6%	76.8%
Overlap in sympatry	28.6%	31.7%
Hybrids contribution to species overlap	25.2%	26.8%

✓ *General impact of introgressive hybridization on classification success*

Based on the two tested algorithms and the two sets of traits (morphometry and colour), the overlap between the two parental species was around $25.9 \pm 5.76\%$. The contribution of hybrids to overlap among parental species was significantly higher for colour ($26.0 \pm 1.13\%$) than morphometry ($10.6 \pm 4.24\%$) ($F=24.602$; $p=0.038$). Overall, hybrids contributed on average $18.3 \pm 9.25\%$ to traits overlapping between their parental species (Table 5.2).

5.4 Discussion

Differences in morphology have been commonly used to differentiate taxa undergoing preliminary steps of macroevolution. However, as predicted by the particular challenges posed by the similarity of cryptic species, overlap in all morphological variables was the most evident pattern. Yet, for the two species of Iberian *Eptesicus* the differences in size and shape were strikingly larger when comparing allopatric populations than when comparing populations in sympatry. Still, the high overlap in all morphological traits meant that no single variable could be used as a diagnostic characteristic to distinguish the two species. Even so, the analyses of the external morphological traits (wing and dentition) confirmed that *E. serotinus* is slightly, but significantly, larger and darker than *E. isabellinus*. Although allopatric *E. serotinus* bats showed a greyer coat, the remaining four groups were distributed along the brown pallet, with sympatric groups showing the brownest coat. Molecularly confirmed hybrids showed intermediate morphometric values between both parental species in terms of size and shape, particularly when compared to allopatric populations. Hybrids were significantly browner than allopatric *E. serotinus*, showing the brightest coats of all, significantly brighter than both allopatric and sympatric *E. isabellinus*. Thus, alongside a probable process of adaptation to the local environmental conditions in the sympatric zone, bidirectional introgression (even if asymmetrical) can lead to convergence in size and shape, increasing morphological overlap among parental species (Grant and Grant, 2016). Hybrids, distributed along a sympatric zone, show intermediate values in morphometric traits (both in size and shape), while differences between both parental species in morphometry decreased significantly in sympatry. Therefore, it is probable that hybridization and introgression affect the morphology of the parental species through backcrossing (Boratyński et al., 2011; Gramlich et al., 2018; Nichols et al., 2015; Yang et al., 2018).

External traits are priority targets for natural selection as they directly impact the fitness of individuals and the ecological niche in which they occur (Ochoa-López et al., 2020). According to Grant and Grant (2016), it is possible to make genetic inferences grounded in two morphological aspects, size and shape, due to the narrow connection between introgressed alleles and species morphology. This fact is based on high frequency of heritable variation and polygenic origin of external traits (Grant and Grant, 1994). This relationship is supported by evidence from genes that were identified as regulating the development of vertebrate' size and shape (Abzhanov et al., 2006;

Abzhanov et al., 2004; Mallarino et al., 2011). There is considerable amount of evidence that supports the influence of introgression on morphometry impacting both size and shape (Boratyński et al., 2011; Nichols et al., 2015; vonHoldt et al., 2016; Yang et al., 2018). Adaptive introgression consequences seem plastic enough to be able to promote divergent adaptations in response to the particularities of environmental conditions (Gramlich et al., 2018). For example, introgression events promoted size reduction in ancient humans, allowing them to adapt to insular environments (Mondal et al., 2016), while on the other hand they enabled carnivores to obtain larger prey by increasing their body size (vonHoldt et al., 2016).

Introgression of bat morphological traits should respond to the circumstances in which they co-occur within the sympatric zone. Introgression in *Eptesicus* dentition and wing morphology, for example, could impact their trophic space, being connected to their diet, as well as their ecological niches, responding directly to the macro-habitat characteristics of the sympatric zone and to local prey availability. With increasing dentition size, *E. isabellinus* is more able to capture larger prey, while the smaller dentition of *E. serotinus* makes it more efficient in capturing smaller prey (Santana et al., 2011). On the other hand, increased wing size and shape changes (namely decreasing the proportion between first phalanges and metacarpals) may have enabled *E. isabellinus* to become more efficient in exploring more open habitats (Kalcounis and Brigham, 1995) and disperse over longer distances (Muijres, et al., 2011). In contrast, decreased wing length and shape changes (namely increasing the proportion between first phalanges and metacarpals) may have rendered *E. serotinus* more prone to explore close habitats than those used in allopatry (Kalcounis and Brigham, 1995).

Mammals are not frequently colourful being mostly colour-blind to the red-green spectrum because they tend to be crepuscular or nocturnal (Bradley and Mundy, 2008). Bats are an extreme example of it. Under low-light conditions, dichromatic vision seems to be advantageous over colour vision because the reduced number of colour-sensitive cones in the retina means they focus on more light-sensitive rods, thus improving their visual acuity (Müller and Peichl, 2005). Similar to other nocturnal mammals, bats are commonly shades of black, grey or brown, with only small colour differences between species (Winter et al., 2003). Thus, the differences found in bat colours are substantially smaller than morphometric ones. Still, contrary to the patterns found in morphometry, colour characteristics of hybrids are in the extreme of the brown colour palette. In parallel, they are also consistently the brightest ones. Still, the differences in colour parameters of both parental species seem slightly greater in sympatry.

Colour patterns have been linked to communication and physiological processes, such as thermoregulation (Caro, 2005). However, most bats use vocal and olfactory cues rather than visual signals to perceive the environment and for social interactions (Chaverri et al., 2018). On the other hand, brighter colours cannot affect mating recognition without the development of tri- or tetra-chromatic vision (Caro, 2005). Bat colouration is most probably the result of adaptation to a nocturnal niche, likely associated with concealment from predators (Caro, 2005). So, bats colouration should reflect environmental pressures, for example, from the roosts that they occupy. Different colour patterns can be expected in species occupying different types of roosts because roost conditions differ in their visual environment (e.g. luminance and colour spectrum), as well as in their level of exposure to twilight or diurnal predators (Caro, 2005).

The two Iberian *Eptesicus* species do not share roosts, despite their colonial behaviour with nursery colonies comprising up to 300 animals (Dietz et al., 2009), and their tendency to share roosts with other species (Martinoli et al., 2020). This suggests that these two bats may compete actively for the best spots when in sympatry. *E. serotinus* colonies are mainly associated with buildings in Central Europe (Dinger, 1991), while in the Mediterranean region, they also roost in crevices of cliffs and at the entrance of caves (Dietz et al., 2009). *E. isabellinus*, instead, seems to prefer crevices (cliffs or bridges) and tree hollows in date palms in North Africa (Kowalski and Rzebik-Kowalska, 1991).

Resource partitioning and geographic avoidance have been described for several pairs of cryptic bat species across Europe (Nicholls and Racey, 2006, Novella-Fernandez et al., 2020, Novella-Fernandez et al., 2021). Cryptic species can exploit different microhabitats and roosts to avoid competition when sharing the same sympatric area (Novella-Fernandez et al., 2020), and this may be the case for the Iberian *Eptesicus* in sympatry. Therefore, roost-mediated coevolution could be one plausible hypothesis to explain the different colour patterns in the bats. The light environment of nocturnal niches can be dominated by yellow-green wavelengths, for example in more closed foraging spots, which coincides with the spectral sensitivity of bats (Galván et al., 2020). Therefore, the natural pressure of nocturnal light conditions occurring over the various microhabitats that are explored by each species in sympatry may have interacted with diurnal light conditions in roosts to favour the pelage colour differences in *Eptesicus*. Thus, any possible differences promoted by the interactions between the two cryptic bats in sympatry through potential competition for roosts and microhabitats will not only have consequences for their colour and their discrimination,

but fundamentally for their interactions with predators and the environment (Wang et al., 2005).

The extent of morphological overlap between the two cryptic bats was around 26%. The presence of hybrids contributes substantially to a fifth of the total traits overlap. Even so, classification statistics showed high differentiation rate between the two parental species in sympatry, particularly for *E. isabellinus*, with higher correct identification rates for morphometric traits, which were more distinct than colour. Discriminant functions showed D3_MC and CM3 are the main variables discriminating between the species. However, only CM3 showed limited overlap between them with values below 7.3 cm found only in *E. isabellinus*, whereas values above 8.4 cm only in *E. serotinus*. Therefore CM3 is the only measure that can be used to confidently distinguish between the two species.

Morphological diversity is a critical facet of evolution and adaptation (Anderson et al., 2009). However, morphology is also extremely important for field identification, particularly for endangered species. Accurate field identification is particularly important for *Eptesicus* species because they are hosts of different lineages of the European bat Lyssavirus type 1 (EBLV-1), the most common rabies related virus found in European bats (Vázquez-Moron et al., 2011, Mingo-Casas et al., 2018). Moreover, using morphological traits for cryptic species identification in sympatry, instead of molecular approaches that are frequently used for *in-situ* identification, could be particularly useful due to the reduced associated costs.

✓ *Caveats and limitations*

We classified individuals as hybrids following Centeno-Cuadros et al. (2019) and applying the conservative criteria proposed by Burgarella et al. (2009) to the microsatellite genotypes to guarantee there were no misclassifications. On the other hand, this approach does not allow us to exclude the possibility of the presence of other possible hybrids in the other sympatric groups. In addition, the lab methodology used to detect hybrids does not detect the presence of second generation and later hybrids, as well as backcrosses. These potential overlooked hybrids may be falsely inflating the overlap between morphological characteristics of the two sibling bat species. Despite this, we still obtained high values of correct identifications in the classification statistics, which indicates that the proportion of undetected hybrids was low.

5.5 Conclusions

We demonstrated that cryptic Iberian *Eptesicus* species can coexist during secondary contacts under antagonistic evolutionary forces, imposed simultaneously by introgressive hybridization and potential niche-partitioning. This balance may be driven by the partitioning of resources along two niche axes, microhabitats and roosts. The situation may be different in other niche axes, such as trophic resources, prey characteristics and macro-habitats, which are under adaptive pressure from local conditions. Divergence due to niche differentiation and introgressive hybridization should impact on different aspects of morphology (Abrams, 1986). The latter seems to have a greater effect on the divergence of bat pelage colour. Instead, introgression seems to act as a homogenising force over morphometric traits, such as wing and dentition shape and size. Finally, we argue that a balance between introgressive hybridization and interspecific competition, beyond mediating species divergence, shapes their interactions with the environment by impacting morphological traits under selection.

Acknowledgments

PH and HRa were funded by the Portuguese Foundation for Science and Technology (FCT) with a PhD grant (SFRH/BD/117979/2016 and SFRH/BD/124367/2016, respectively). HRe was also funded by FCT (DL57/2016/EEC2018/07). OR was funded through a Natural Environment Research Council Independent Research Fellowship (NE/M018660/1). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017.

Supplementary Material

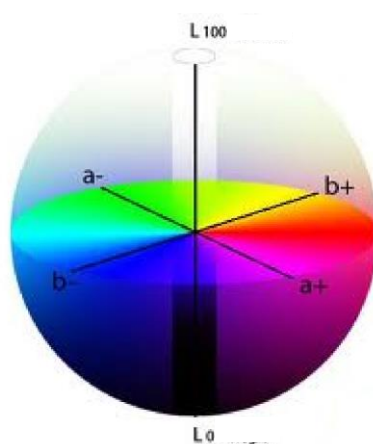


Figure S5.1 - CIELAB colour space expressing colours in three values: L^* for perceptual lightness, and a^* and b^* for the scales of the four colours of human vision: red and green, blue and yellow, respectively.

Multiple comparisons of morphometric variables

✓ *Allopatry versus sympatry*

Within each species there were no differences in forearm (FA) length between allopatric and sympatric groups, though both groups of both species differed significantly from the others of its sibling. Nevertheless, FA differences between the two species in allopatry was slightly higher than that found in sympatry.

Allopatric and sympatric groups differed significantly in the variable D3 MC within each species. The same also occurred between sympatric groups of species, as well as between their allopatric groups. Differences between both species in allopatry was also slightly higher than that found in sympatry. Multiple comparison in D5 MC followed the same pattern. Allopatric and sympatric groups differed significantly within each species. However, there were no significant differences between species in the sympatric area, only between individuals of allopatric regions.

For phalange measures, such as D5 F1, all groups differed from allopatric *E. isabellinus* due to its lowest length, except from individuals living in sympatry with *E. serotinus*. Therefore, in allopatry both species differed significantly in the size of the first phalanges, while in sympatry there were no significant differences.

There were no differences in the dentition variable CM3 within species between allopatric and sympatric groups. However, both groups of both species differed significantly from the other species. In this case, differences in CM3 between both species in allopatry was essentially similar than that found in sympatry.

Finally, the results demonstrated statistically significant differences in C1-C1 variable between allopatric *E. isabellinus* and both groups of *E. serotinus* (sympatric and allopatric). However, in that case, under sympatry there was no significant differences between both species unlike what happens in allopatry.

From a multivariate point of view, there were no significant differences in the bats' size between allopatric and sympatric groups within each species. However, both groups of both species differed significantly from the other species' groups. Nevertheless, size differences between both species in allopatry was slightly higher than that found in sympatry. Regarding the shape component (PC2 morphology), there were no significant differences within each species when in the presence or absence of its sibling. No significant differences were found among individuals of the two species when they were in sympatry, while in allopatry the differences in the bats' shape were

clearly significant. For allopatric *E. serotinus* the shape component stood out as substantially different, making it significantly different even from the sympatric *E. serotinus* group.

✓ *Hybrids versus parental species*

The FA length of hybrids did not differ significantly between groups, with both parental species showing intermediate values. *E. serotinus* had the longer average length of FA (both allopatric and sympatric, in this order) followed by the hybrids and *E. isabellinus* (sympatric and allopatric).

Regarding the metacarpals, hybrids only differed significantly from allopatric *E. serotinus*, having significantly lower D3 MC and D5 MC. Allopatric *E. serotinus* had the longest metacarpals and hybrids showed the lowest values in both finger (D3 and D5). Sympatric groups revealed intermediate values between the respective allopatric groups of each species and the hybrids (Table 5.1). The exception was sympatric *E. isabellinus* group that shared the lowest values with hybrids in the metacarpals of the fifth finger.

In contrast, hybrids had the longest first phalanges although they did not differ from the rest of the groups. Both sympatric groups had higher values than the respective allopatric groups and intermediate between them and the hybrids (Table 5.1).

Hybrids showed intermediate values of CM3 between both parental species, with significantly higher values than both *E. isabellinus* groups. *E. serotinus* had the longest CM3 (mainly allopatric *E. serotinus*), followed by the hybrids and *E. isabellinus* (sympatric and allopatric) (Table 5.1). Regarding C1-C1, hybrids showed the lowest values alongside the allopatric *E. isabellinus*, which was the only group from which hybrids did not significantly differ (Table S1). In the multivariate analysis, hybrids showed intermediated phenotypes in dentition, wing sizes (PC1 morphology) and the metacarpals and first phalanges proportion, as well as between the length of the first phalanges and the dentition (mainly CM3) (PC2 morphology).

Table S5.1 - Statistical values of multiple comparisons of original morphometric variables according to the post-hoc Fisher's LSD test. Green cells represent significant differences ($P < 0.05$).

Fisher's LSD

		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
		FA				
Eisa_all			0.826	0.451	0.008	0.006
Eisa_sy		0.026		0.535	0.013	0.010
Hybrid	D3 MC	0.524	0.670		0.253	0.317
Eser_sy		0.249	0.003	0.219		0.752
Eser_all		0.000	0.000	0.005	0.005	
		D5 MC				
Eisa_all			0.047	0.513	0.891	0.001
Eisa_sy		0.085		0.771	0.066	0.000
Hybrid	D5 F1	0.011	0.080		0.483	0.029
Eser_sy		0.004	0.132	0.375		0.008
Eser_all		0.036	0.721	0.110	0.220	
		CM3				
Eisa_all			0.254	0.000	0.000	0.000
Eisa_sy		0.019		0.002	0.000	0.000
Hybrid	C1-C1	0.572	0.040		0.171	0.059
Eser_sy		0.003	0.301	0.009		0.563
Eser_all		0.004	0.593	0.017	0.554	

Multiple comparisons of colour variables

All groups differed significantly from allopatric *E. serotinus* in the a^* b^* Grey-Brown scale (PC1 colour), being the only one in the grey space of the colour pallet. In terms of lightness (PC2 colour), allopatric *E. serotinus* was only not significantly different from individuals of the same species when in sympatry (they were equally dark although in sympatry they tended to be significantly browner). In sympatry both species also differed significantly, however, contrary to the morphometric variables, this difference was slightly higher than that found between species in allopatry. According to colour multivariate analyses, hybrids were browner than *E. serotinus* in allopatry and lighter than it both in sympatry and allopatry (Table S5.5). For L^* Lightness component (PC2 colour), hybrids demonstrated the lightest colour patterns (both in their dorsal and ventral coat) despite being not significantly different from both *E. isabellinus* groups (sympatric or allopatric) (Figure 5.3 and Table S5.5).

Table S5.2 - Statistical values of multiple comparisons of dorsal and ventral original colour variables (L^* , a^* and b^*). Green cells represent significant differences ($P < 0.05$).

Fisher's LSD

		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
L* dorsal						
Eisa_all		0.423	0.318		0.004	0.015
Eisa_sy			0.618		0.000	0.006
Hybrid					0.045	0.120
Eser_sy						0.692
Eser_all						
b* dorsal						
Eisa_all		0.474	0.240		0.043	0.152
Eisa_sy		0.286		0.395	0.018	0.002
Hybrid	a^*	0.077	0.194		0.435	0.003
Eser_sy	dorsal	0.010	0.005	0.501		0.000
Eser_all		0.045	0.000	0.000	0.000	
b* ventral						
Eisa_all		0.747	0.311	0.298		0.007
Eisa_sy		0.938		0.283	0.196	0.000
Hybrid	a^*	0.581	0.486		0.885	0.000
Eser_sy	ventral	0.390	0.170	0.799		0.000
Eser_all		0.000	0.000	0.000	0.000	

Table S5.3 - Principal components extracted from the PCA analysis, with the respective eigenvalues, % variance explained, Cronbach's α and weight of each variable.

Morphometric variables	Morphometry		Colour	
	PC1 (Size)	PC2 (Shape)	PC1 (a*b* Grey-Brown)	PC2 (L* lightness)
FA	0.973	-0.071	-	-
D3 MC	1.020	-0.159	-	-
D3 F1	0.679	1.035	-	-
D5 MC	0.939	-0.253	-	-
D5 F1	0.759	0.757	-	-
C1-C1	0.693	-0.390	-	-
CM3	0.656	-1.030	-	-
L* dorsal	-	-	-0.387	1.125
a* dorsal	-	-	1.084	0.139
b* dorsal	-	-	1.032	0.128
L* ventral	-	-	-0.436	1.157
a* ventral	-	-	1.028	0.114
b* ventral	-	-	0.989	0.546
<i>Eigenvalue</i>	3.315	1.245	3.552	1.450
Variance explained	43.92%	15.90%	59.19%	24.17%
Cronbach's α	0.815	0.230	0.862	0.373

Table S5.4 - Statistical values of multiple comparisons of means orders of morphometric PCA variables. Green cells represent significant differences ($P < 0.05$).

Tukey's LSD

		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
		PC1 Size				
Eisa_all			0.992	0.715	0.009	0.000
Eisa_sy		0.994		0.860	0.024	0.000
Hybrid	PC2	0.987	0.940		0.781	0.214
Eser_sy	Shape	0.267	0.124	0.889		0.732
Eser_all		0.002	0.000	0.328	0.727	

Table S5.5 - Statistical values of multiple comparisons of means orders of dorsal and ventral PCA colour variables. Green cells represent significant differences ($P < 0.05$).

Fisher's LSD

			Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
			PC1 a*b* Grey-Brown				
Eisa_all				0.505	0.214	0.033	0.021
Eisa_sy			0.883		0.315	0.008	0.000
Hybrid	PC2	L*	0.578	0.532		0.409	0.000
Eser_sy	Lightness		0.164	0.008	0.023		0.000
Eser_all			0.018	0.000	0.001	0.133	

Detail description of classification analyses

Species discrimination through classification statistics

✓ Stepwise DFA with and without hybrids

The morphometric stepwise DFA generated one discriminant function, retaining all variables as statistically significant (D3_F1 only marginally [$F=3.643$, $p=0.058$]). A single discriminant function was defined mainly by D3_MC and CM3. This function discriminated the two species ($\Lambda=0.579$, $\chi^2_{(7)} = 53.773$, $p<0.001$). The results of Classification Statistics showed that 49 out of 58 *E. isabellinus* individuals (84.5%) and 36 out of 46 *E. serotinus* individuals (78.3%) were classified correctly. The percentage of individuals classified correctly by stepwise DFA to morphometric variables in the presence of hybrids was 81.7%.

The morphometric stepwise discriminant analysis after hybrids removing generated also one discriminant function, with FA, D3_MC, D5_MC (marginally significant [$F=3.450$, $p=0.069$]) and CM3 as statistically significant variables. A single discriminant function was defined mainly by D3_MC and CM3. This function discriminated the two species ($\Lambda=0.632$, $\chi^2_{(4)}=21.073$, $p<0.001$). The results of Classification Statistics showed that 30 out of 32 *E. isabellinus* individuals (96.0%) and 12 out of 18 *E. serotinus* individuals (66.7%) were classified correctly. The total percentage of individuals classified correctly by stepwise DFA of morphometric variables increased to 84.0% after hybrids removing.

The colour stepwise DFA generated also only one discriminant function, with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant variables. A single discriminant function was defined mainly by dorsal colour scales (a*_dorsal, L*_dorsal and b*_dorsal - in this decreasing order of influence). This function discriminated the two species ($\Lambda=0.842$, $\chi^2_{(4)}=10.115$, $p=0.039$). The results of Classification Statistics showed that 36 out of 39 *E. isabellinus* individuals (92.3%), but only 9 out of 24 *E. serotinus* individuals (37.5%) were classified correctly. The percentage of individuals classified correctly by stepwise DFA to colour variables in the presence of hybrids was 71.4%.

After removing hybrids the colour stepwise discriminant analysis generated also one discriminant function, once again with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant variables. A single discriminant function was

defined mainly by variable L^*_{dorsal} . This function discriminated the two species ($\Lambda=0.762$, $\chi^2_{(4)}=14.114$, $p=0.007$). The results of Classification Statistics showed that 36 out of 39 *E. isabellinus* individuals (92.3%), but only 8 out of 17 *E. serotinus* individuals (47.1%) were classified correctly. The total percentage of individuals classified correctly by stepwise DFA of colour variables increased to 78.6% after hybrids removing.

✓ Support Vector Machine with and without hybrids

SVM generated one discriminant function based on morphometric PC1 and PC2 as predictors' variables that summarized all morphometric traits. Once composed of only two variables, a single classification function was defined similarly by PC1 and PC2 in the same direction. After simulations, the results of Classification Statistics showed that 45 of 57 individuals of *E. isabellinus* (78.9%) and 34 of 47 individuals from *E. serotinus* (72.3%) were classified correctly (Figure S5.2). The percentage of individuals classified correctly by SVM of morphometric variables in the presence of hybrids was 75.0%.

Without hybrids, SVM generated one discriminant function based on morphometric PC1 and PC2 as predictors' variables that summarized all morphometric traits. Once composed of only two variables, a single classification function was defined especially by PC1. After simulations, the results of Classification Statistics showed that 26 of 31 individuals of *E. isabellinus* (83.9%) and 14 of 21 individuals from *E. serotinus* (66.7%) were classified correctly (Figure S5.2). The percentage of individuals classified correctly by SVM to summarized morphometric variables increased to 76.9% after removing hybrids.

SVM generated also one discriminant function based on colour PC1 and PC2 as predictors' variables that summarized all colour variables. Composed by only two variables, a single classification function was defined mainly by PC1. After simulations, the results of Classification Statistics showed that 36 of 39 individuals of *E. isabellinus* (92.3%) and only 7 of 24 individuals from *E. serotinus* (29.2%) were classified correctly (Figure S5.2). The percentage of individuals classified correctly by SVM of colour variables in the presence of hybrids was 68.3%.

Without hybrids, the colour SVM generated one discriminant function based on PC1 and PC2 as predictors' variables that summarized all colour variables. Once composed by only two variables, a single classification function is defined similarly by

PC1 and PC 2 in opposite directions. The results of Classification Statistics showed that 37 of 48 individuals of *E. isabellinus* (77.1%) and only 2 of 8 individuals from *E. serotinus* (75.0%) were classified correctly (Figure S5.2). The percentage of individuals classified correctly by SVM of summarized colour variables increased to 76.8% after removing hybrids.

Discriminant and classification functions

✓ *Stepwise DFA with hybrids*

Morphometry

Discriminant function (eigenvalue=0.726):

$$\text{Species} = 0.183 (\text{FA}) + 0.692 (\text{D3_MC}) - 0.468 (\text{D3_F1}) - 0.259 (\text{D5_MC}) - 0.359 (\text{D5_F1}) + 0.271 (\text{C1_C1}) + 0.837 (\text{CM3}).$$

Classification functions:

$$\begin{aligned} E. \text{ isabellinus} = & 16.760 (\text{FA}) + 6.148 (\text{D3_MC}) - 4.801 (\text{D3_F1}) - 3.999 \\ & (\text{D5_MC}) - 6.861 (\text{D5_F1}) + 31.608 (\text{C1_C1}) + 25.371 (\text{CM3}) + 600.300 \end{aligned}$$

$$\begin{aligned} E. \text{ serotinus} = & 16.948 (\text{FA}) + 6.790 (\text{D3_MC}) - 5.576 (\text{D3_F1}) - 4.214 (\text{D5_MC}) \\ & - 6.077 (\text{D5_F1}) + 30.035 (\text{C1_C1}) + 29.193 (\text{CM3}) + 643.292 \end{aligned}$$

Colour

Discriminant function (eigenvalue=0.187):

$$\text{Species} = 0.686 (\text{L}^*_{\text{dorsal}}) - 0.825 (\text{a}^*_{\text{dorsal}}) + 0.571 (\text{b}^*_{\text{dorsal}}) + 0.111 (\text{L}^*_{\text{ventral}}).$$

Classification functions:

$$\begin{aligned} E. \text{ isabellinus} = & 2.094 (\text{L}^*_{\text{dorsal}}) + 13.092 (\text{a}^*_{\text{dorsal}}) - 0.840 (\text{b}^*_{\text{dorsal}}) + \\ & 2.243 (\text{L}^*_{\text{ventral}}) - 131.706 \end{aligned}$$

$$\begin{aligned} E. \text{ serotinus} = & 1.979 (\text{L}^*_{\text{dorsal}}) + 13.568 (\text{a}^*_{\text{dorsal}}) - 0.922 (\text{b}^*_{\text{dorsal}}) + \\ & 2.223 (\text{L}^*_{\text{ventral}}) - 128.605 \end{aligned}$$

✓ *Support Vector Machine with hybrids*

Morphometry

SVM function:

$$\text{Species} = - 4.59 (\text{PC1_morphometry}) - 4.08 (\text{PC2_morphometry}) + 0.02.$$

Colour

SVM function:

$$\text{Species} = -4.39 (\text{PC1_colour}) - 0.28 (\text{PC2_colour}) - 0.42.$$

✓ *Stepwise DFA without hybrids*

Morphometry

Discriminant function (eigenvalue=0.581):

$$\text{Species} = 0.026 (\text{FA}) + 0.501 (\text{D3_MC}) - 0.148 (\text{D5_MC}) + 0.815 (\text{CM3}).$$

Classification functions:

$$E. \text{ isabellinus} = 21.383 (\text{FA}) + 6.178 (\text{D3_MC}) - 1.729 (\text{D5_MC}) + 34.384 (\text{CM3}) - 780.827$$

$$E. \text{ serotinus} = 21.412 (\text{FA}) + 6.696 (\text{D3_MC}) - 1.850 (\text{D5_MC}) + 38.063 (\text{CM3}) - 829.241$$

Colour

Discriminant function (eigenvalue=0.312):

$$\text{Species} = 0.830 (\text{L}^*_{\text{dorsal}}) - 0.395 (\text{a}^*_{\text{dorsal}}) + 0.395 (\text{b}^*_{\text{dorsal}}) + 0.182 (\text{L}^*_{\text{ventral}}).$$

Classification functions:

$$E. \text{ isabellinus} = 2.258 (\text{L}^*_{\text{dorsal}}) + 12.308 (\text{a}^*_{\text{dorsal}}) - 0.786 (\text{b}^*_{\text{dorsal}}) + 2.193 (\text{L}^*_{\text{ventral}}) - 131.525$$

$$E. \text{ serotinus} = 2.054 (\text{L}^*_{\text{dorsal}}) + 12.619 (\text{a}^*_{\text{dorsal}}) - 0.851 (\text{b}^*_{\text{dorsal}}) + 2.148 (\text{L}^*_{\text{ventral}}) - 123.650$$

✓ *Support Vector Machine without hybrids*

Morphometry

SVM function:

$$\text{Species} = -57.49 (\text{PC1_morphometry}) - + 25.91 (\text{PC2_morphometry}) - 2.97.$$

Colour

SVM function:

$$\text{Species} = -4.44 (\text{PC1_colour}) + 3.29 (\text{PC2_colour}) - 0.51.$$

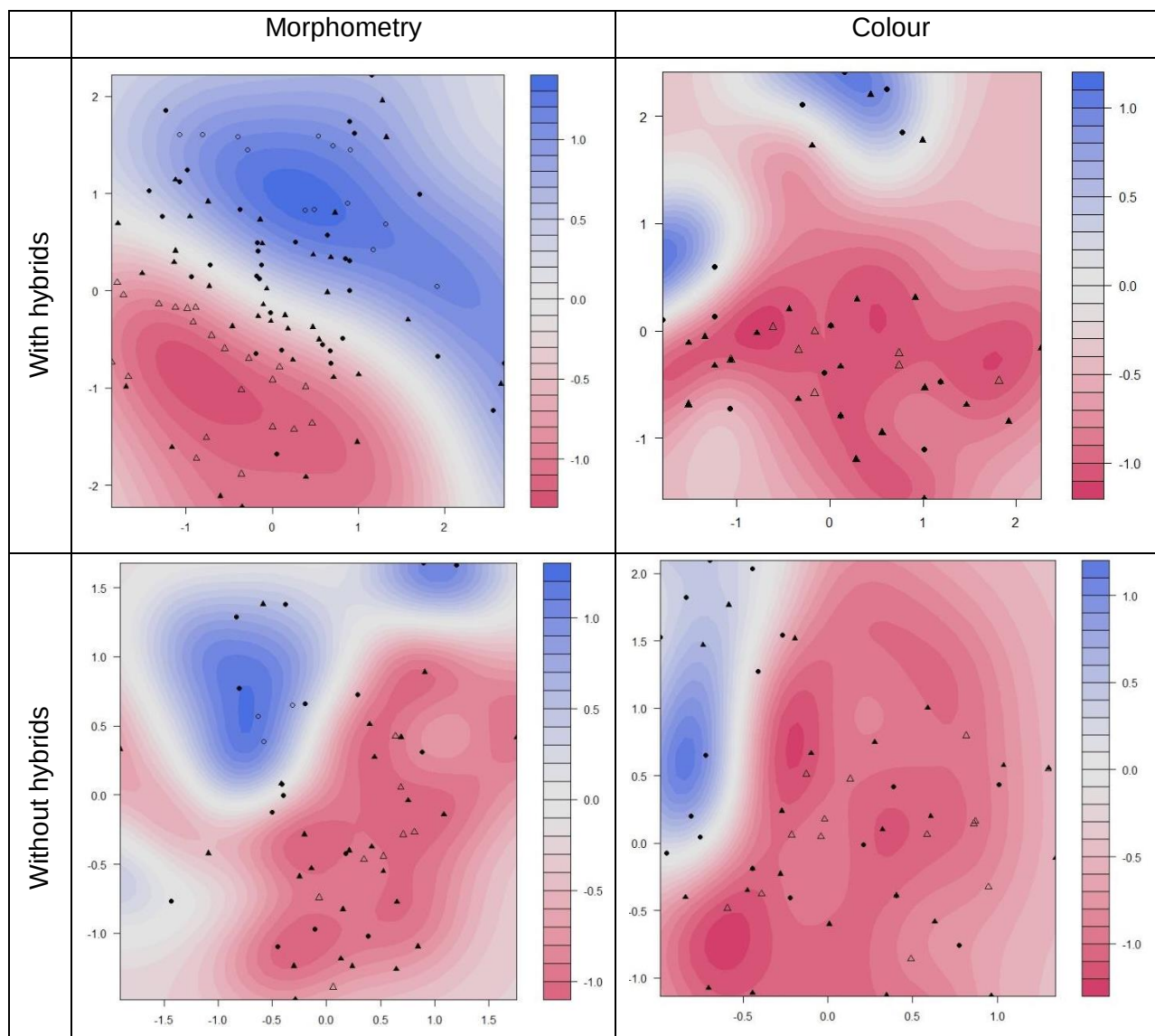


Figure S5.2 - Support Vector Machine classification plots based on morphometric (on left) and colour traits (on right) for both parental species in sympatry, including hybrids on top and excluding them on the bottom. Density of probability of correct classification rate was based on Kernel statistics. Red spots regard *E. isabellinus* and the blue ones *E. serotinus*.

Chapter 6

General Discussion

“Given so much time, the ‘impossible’ becomes possible, the possible probable, and the probable virtually certain”

George Wald, 1954

6.1 The relevance of knowledge about introgression

The great relevance of studying introgression is linked to structural issues related to the mechanisms behind the evolutionary processes and it is often underlying the genetic admixture influencing the divergence process (Gompert et al., 2013; Lazic et al., 2021). Moreover, its importance is also related to methodological issues, as introgression presents structural features (genomics and others) useful to test new approaches, both laboratorial (Sankararaman, 2020) and bioinformatics (Forsythe et al., 2020). Novelty on the study on introgression are also related to conjectural circumstances, for instance the adaptation of organisms to the current climate change (Leroy et al., 2017; Mao et al., 2018; Quigley et al., 2019; Ryan et al., 2018) or the capacity of other, which represents a threat to human health, to adapt to the technological development, such as the resistance of malaria mosquito to insecticides (Fouet et al., 2018; Norris et al., 2015) or the ability of some bacteria to transfer resistance to antibiotics (Mallet et al., 2016; Palmer et al., 2010).

Finally, this topic has underlying psycho-social, historical and ideological issues (Arnold, 2004). The polarization of opinion on genetic admixture directly and paradoxically influences the path of technological progress (in areas such as agriculture or cattle husbandry (Henkel et al., 2019)) and the development of genetic rescue through assisted interbreeding as a management program for biodiversity conservation (Chan et al., 2019; Quigley et al., 2019). Yet, scientific facts inherent to adaptive introgression give rise to an intense theoretical and philosophical debate on prejudices against admixture (genetic, cultural or social) (Paterson, 1985), which can potentially be at the root of some forms of discrimination (e.g. biological racism) (Fredrickson, 2002). It occurs particularly when these discrimination thoughts have an underlying the idea of "safeguarding the integrity" (Mayr, 1942; O'Brien et al., 2009) of "superior" human groups (Cortes and Salgado, 2011). Social relevance of studying introgression is based on its potential capacity to justify with a scientific narrative the humans' freedoms and guarantees (Plakhotniuk et al., 2021) that lead to active strategies to promote a global social progress towards a compromising and anti-discriminatory society (Iheduru-Anderson and Wahi, 2021; Markey et al., 2012; Razack, 1999).

6.2 Main current trends on the knowledge about introgression

Introgression is currently a topic under intense debate among the scientific community. While some authors reinforce, for example, the potential of adaptive introgression for species conservation (Quilodr  n et al., 2020) under climate change (Quigley et al., 2019), others argue that the potential increase of introgression as a response to climate change (Todesco et al., 2016) has the potential to threaten species diversity (Owens and Samuk, 2020). An assessment of the

scientific relevance of this topic compared to all current scientific literature, both in terms of citations and attention scores, revealed introgression as a particularly important topic for current science. A quarter of its papers are nowadays within the top 5% of the most cited and commented papers in the world.

From anthropology (Mondal et al., 2016; Silvert et al., 2019; Vernot et al., 2016) to microbiology (Leducq et al., 2017; Sun et al., 2012), passing through phylogeny (Ceballos et al., 2019; Stryjewski and Sorenson, 2017) or behavioural sciences (Pfennig, 2007; While et al., 2015), there has been a significant increase in research teams and publications on the theme (de Lafontaine et al., 2015; Moran et al., 2021; Racimo et al., 2017), especially after 2012. Methodological developments in genomics, which gradually became widely used (Hayden, 2014), are at the root of this exponential increase (Moran et al., 2021). More advanced techniques than those used previously, increased the researchers' ability to detect regions of the genome under recombination as well as, although less frequently, their phenotypic outcomes (Kuhlwilm et al., 2019; Ryan et al., 2018).

Though the research teams are mostly concentrated in North America and Western Europe, evidence of the current or past introgression occurrence (Moran et al., 2021) are widely spatially dispersed across the globe, in all major biomes (Clarkson et al., 2014; de Lafontaine and Bousquet, 2017; Ghenu et al., 2018; Mao et al., 2018; Ryan et al., 2018). There are many biological arguments used by the authors to justify the polarity of their opinions on this evolutionary phenomenon. Despite being very similar in number, the arguments that tend to consider its effect to be beneficial are significantly more mentioned than the negative ones. So, when introgression can lead to an effective change in species fitness, there is a tendency in the scientific community to consider it as positive for enhancing adaptation to new or changing environmental conditions (Bahbahani et al., 2018; Gittelman et al., 2016; Lewontin and Birch, 1966).

6.3 Merging the knowledge about introgression functionality

The characterization and demonstration of the process of introgression across the tree of life regarding the general mechanisms under which it can contribute to adaptation are crucial in providing new insights for empirical studies.

Introgression may express itself on genomic, physiology, reproductive behaviour and at demographical levels. Many studies have looked at the genomic mechanisms through which adaptive introgression occurs (Brower, 2018; Ferreira et al., 2021; Gagnaire et al., 2013; Matosiuk et al., 2014; Pujolar et al., 2014; Sarver et al., 2017). Other authors focused on physiological constraints that introgression can cause, namely on endogenous traits that may act like breeding barriers, impacting on its adaptive capacity (Dopman et al., 2005; While et al., 2015). Some authors

also demonstrated the importance of reproductive behaviours on introgression patterns (McDonald et al., 2001; While et al., 2015; Yang et al., 2018). Finally, there are also important patterns of introgression derived from demographic disparities (Meier et al., 2017; Ray and Excoffier, 2009). This thesis demonstrated that the main drivers of introgression increase its complexity across the biological organization, from genomics, physiology, demography to behaviour, through a taxonomic complexity gradient. The increase in the structural complexity of organisms throughout their evolutionary history has consecutively brought new challenges to the occurrence and functioning of the introgression process. It was highlighted as a general overview that introgression acts in parallel with divergence, evolving and establishing in balance through interconnected mechanisms (Pauquet et al., 2018; Pfennig, 2007; Staubach et al., 2012). For example, constraints caused by cyto-nuclear discordance (Bonnet et al., 2017; Brower, 2018; Morales et al., 2018) or by the presence of islands of differentiation in sex-linked chromosomes (Runemark et al., 2018) can be circumvented by mechanisms of autosomal introgression. Others, such as genetic drift (Gompert et al., 2013; Wade and Goodnight, 2006) or physiological constraints (Kulmuni and Pamilo, 2014) can be overcome through selection and sex-biased introgression, respectively. Finally, risks derived from genetic swamping (Todesco et al., 2016) or constraints promoted by behaviours such as assortative mating (Ng et al., 2017; Poelstra et al., 2018; Salazar et al., 2008) can be mitigated by directional introgression and sexual selection, respectively. Finally, it was shown that adaptation to environmental conditions is the ultimate target of the introgression process that is simultaneously mediated by environmental conditions (Bahbahani et al., 2018; Ferreira et al., 2021), regardless of the degree of the organisms' complexity.

6.4 Introgression during the process of divergence

Divergence was frequently assumed to occur mainly through phases of allopatry (Baiz et al., 2019; Renaut et al., 2013; Slager et al., 2020). However, differences in recombination prevalence may contribute to explain cases of divergence in the presence of gene flow (Wadsworth et al., 2015). There are remarkable examples not only of the co-existence of both phenomena (Aguirre-Liguori et al., 2019; Wadsworth et al., 2015) but also of the potential that introgression presents as an enhancer of divergence (Morales et al., 2017), not only through hybrid speciation (Comeault, 2018; Nolte and Tautz, 2010; Schumer et al., 2013) but also as a potential promoter of adaptive radiation (Poelstra et al., 2018; Zhang et al., 2016). The balance that is established in the way both phenomena work can explain the possibility of co-occurrence of introgression and divergence, but the knowledge on the consequences for the evolution of two distinct lineages is still on its first steps (Lind-Riehl and Gailing, 2017). The results of this work demonstrated that cryptic Iberian bats species (*Eptesicus serotinus* (Schreber 1774) and *E. isabellinus* (Temminck 1840)) can coexist

during secondary contacts under antagonistic evolutionary forces, imposed simultaneously by introgressive hybridization and competition. This balance should be driven from partitioning of resources, microhabitats and roosts, eventually sufficient for stable coexistence (Novella-Fernandez et al., 2020). On the contrary, introgressive hybridization should lead these species to an evolutionary convergence, as an adaptation process to ecological condition of the contact zone such as trophic resources (preys availability) and macro-habitats (vonHoldt et al., 2016). Divergence due to niche differentiation and introgression impact different aspects of morphology over different directions. While the former can have an effect on the divergence of bats' pelage colour, introgression seems to act as a homogenising force over morphometric traits, such as wing and dentition on both shape and size. These conclusions suggested that there is a balance between introgressive hybridization and interspecific competition that mediates species divergence shaping their interactions with the environment.

6.5 The importance of evolutionary history for introgression occurrence

There seems to be no consensus regarding the prevalence of introgression in nature when it leads to a change in the fitness of introgressing species. Opinions range from "Very rare" (Weetman et al., 2014) to "Ubiquitous" (Ghenu et al., 2018; Ryan et al., 2018). On average the authors tend to consider introgression only as an evolutionary phenomenon that occurs in "Few cases". Interestingly, the increase in the number of scientific evidence does not seem to have changed the authors' perception of introgression prevalence despite its occurrence has been described in a wide variety of organisms, from prokaryotic, unicellular and multicellular eukaryotic species (Brand et al., 2013; Caseys et al., 2012; Ravinet et al., 2018). Even so, most of the scientific evidence has been confirmed in animals, especially in mammals (including humans) contrary to the idea of some authors that it would be eventually more frequent in plants (de Lafontaine et al., 2015).

In this thesis it was found that both time and type of divergence, responsible for different levels of genetic, physiological and behavioural changes (Trigo et al., 2013), appear to be determining factors for the number of species able to mutually share their genes through introgression. Species going through microevolution (Palmer and Kronforst, 2015; Richards and Martin, 2017) or secondary contacts during preliminary stages of macroevolution (Leroy et al., 2017; Ward and Baxter, 2018) have shown greater connectance in terms of number of taxa they adaptively introgress with. On the contrary, the majority of taxa, has lower connectance (around one per taxa) mainly because of their more advanced stages of macroevolution. The interval of time that a species remains isolated from the others (within each phase of divergence) represents

another important factor affecting the occurrence and the patterns of introgression (Nosil et al., 2012) during the following periods of sympatry, impacting its intensity, symmetry and/or direction.

More ancient taxonomic groups have a natural ability to promote introgression with other groups with higher phylogenetic distance thus with higher probability for this phenomenon to occur. On the one hand, the most ancient species tend to have smaller genomes, thus less likely to generate genetic incompatibilities, being more permeable to recombination (Blommaert, 2020). Secondly, the mating strategies under high rates of stochasticity and weak or even non-sexual selection are additional explanations for the higher potential extent of introgression (Kim et al., 2018; Takahashi and Takata, 2000) among ancient taxonomic groups, such as Gymnosperms, Crustacea or Mollusca (Baur, 1998; Wang and Ran, 2014) in contrast to Angiosperms, Birds or Mammals (Jiang et al., 2013; Tylianakis Jason, 2013; Wang et al., 2019).

6.6 Evolutionary outcomes of introgression

Many mechanisms behind evolution are far from being completely understood. It seems consensual that despite being non-linear, the evolutionary process does not inevitably culminate in divergence (Garrick et al., 2020). Phenomena such as the fusion of once divergent lineages (Garrick et al., 2014) or the increase of speciation through theoretically converging evolutionary forces, such as introgressive hybridization (Comeault, 2018; Morales et al., 2017; Seehausen, 2004), are prominent examples of its complexity. As previously argued, a number of evolutionary processes that initially seemed impossible are not only possible but probable, and even eventually certain, if we give them the necessary time to occur (Wald, 1954). Even processes identified as “rare” can have very wide impacts on evolutionary history. For example, even if first-generation hybrids show high levels of post-zygotic breakdown or a marked reduction in fitness compared to their parental species, this does not necessarily indicate that the same will occur with their backcrosses and/or that these factors may change if environmental circumstances quickly change (Arnold and Hodges, 1995).

Any natural phenomenon seems negligible from an evolutionary point of view (Wald, 1954). Its relevance is that it changes according to the spatial-temporal dynamics of environmental conditions. For example, even if two species meet in a geographically very limited contact zone, the impact of adaptive introgression can reach far across the range of occurrence of both species by phenomenon such as allele surfing (Matosiuk et al., 2014; Norris et al., 2015; Sarver et al., 2017). In terms of phylogeny, even if introgression is restricted to closely-related species, the occurrence of particularly “promiscuous” species increases the potential evolutionary reach of introgression (Dasmahapatra et al., 2012). Acting as an introgression bridge between third-party species that do

not hybridize directly with each other, these specialists' donor and receptor species may promote potential indirect introgression, which could vastly increase the reach of introgressed alleles.

Although introgression has been analysed in this work as a product of vertical gene transfer via hybridization, the occurrence of similar adaptive processes via horizontal gene transfer, from a theoretical point of view, is not only possible but also probable or eventually certain in a wide range of species (Xia et al., 2021). Recent evidence demonstrated the occurrence of horizontal gene transfer with adaptive outcomes in extreme phylogenetic distances, from plants toward insects (Xia et al., 2021). Thus, intense biological interactions (e.g. parasitism, herbivory, pollination, etc.) along co-evolutionary processes may also be generators and empowering of allele sharing when the traits of one species exert a selective pressure on the other (Lin et al., 2007). This new evidence points to the fact that adaptive beneficial outcomes derived from natural gene transfer (both horizontal or vertical) occur through diverse paths (Enard and Petrov, 2018) and in a much wider phylogenetic range than is normally considered (Soucy et al., 2015), and therefore, they may have a truly primordial evolutionary relevance (Yair et al., 2021).

6.7 Final remarks

The ability of introgressed alleles to be transcribed into proteins and promote an effective change in phenotypes has not always been possible to clarify in literature (Moran et al., 2021). Despite several methodological approaches and hypotheses tested on the systematic review about introgression from this thesis, it would be possible to widen the scope of the results by analysing deeply the data regarding introgression outcomes, both phenotypic and ecological. This remains an important issue, especially since it is the phenotypes that potentially affect species fitness and that are under the direct impact of natural selection. Compiling the current knowledge about the physiological systems most affected by introgression and in what respects, taking into account the taxonomic group and the polarity of its consequences, represents a fundamental step towards understanding its real capacity to affect the fitness of recipient lineages. On the other hand, it will be only possible to consider integrating introgression into conservation plans for endangered species conservation if we understand in depth its consequences for the relationship of recipient lineages with the environmental conditions (Quigley et al., 2019).

The results of this study provided general overviews of major hypotheses to test with empirical data. There are several knowledge gaps about introgression operation that still remain open. From a genomic point of view, the impact of islands of speciation into the sex-linked chromosomes on the reproductive performance of heterogametic sex, not only by directly promoting sterility (or even total inviability) was seldom analysed (Walsh et al., 2016). The occurrence islands of speciation outside of sex chromosomes can be considered as "incidental" by

random processes (Sun et al., 2012). However, their impacts on introgression are still unknown. Another caveat regards the connection between breeding behaviours (sexual selection, intra-sexual interspecific mating competition, parental care, etc.) and the genetic drivers of introgression. There are a few examples detecting relationships between sexual selection and the direction of introgression from native-to-colonizer species, which should represent an adaptive strategy for colonizer species, to promote better-adapted traits to the local environmental conditions. Finally, there are interesting examples, but still little evidence of geographic expansion of introgressed alleles beyond contact zones, for example through allele surfing (Matosiuk et al., 2014; Norris et al., 2015; Sarver et al., 2017). Nonetheless, it seems essential to clarify the real spatial extent of introgression. One of the most interesting challenges that emerge from the results of this work is related to the potential occurrence of indirect introgression. Clarifying this point is really important to understand the true extent and taxonomic reach of introgression via vertical gene transfer. On the other hand, the results of this work indicate that it is plausible that in past geological eras introgression should represent an even more relevant source of genetic variation, adaptability and accelerated speciation. It should have decreased gradually as organisms became genomically, physiologically and behaviorally more complex. Testing this assumption requires extensive paleogenomic analyses of natural communities from past geological eras.

Cryptic bat species represent excellent case studies for empirical studies on introgression, as demonstrated in this work, due to their phylogenetic proximity and partial niche overlap, as well as morphological similarity and high potential for hybridization (Jones, 1997). It is particularly interesting the study of the introgression process of cryptic bats species as an adaptive strategy to fast environmental changes, particularly to climate change. However, much work remains to be done on the drivers that condition its expression (genomic, physiological, demographic and behavioral). Questions such as the direction, extent and prevalence of introgression remain to be clarified, as well as the identification of multiple signatures of species-specific positive selection, affecting genes related to adaptive traits outside the original phenotypic range of both parental species. In parallel, it is important to understand how landscape features act as promoters or barriers of introgressed allele surfing, helping to clarify the spatial extent of introgression. Finally, cryptic bat species can represent the first options to test on a practical point of view how to implement assisted gene flow, designed through genomic architecture of admixture of genes, underlying the adaptation to climate change. Designing a network of ecological corridors, considering optimum ecological conditions for introgression occurrence and spatial patterns of future gene flow, can contribute to minimize the impact of ongoing climate change on species.

In another perspective, this thesis demonstrated that the annual publication of a large number of papers on introgression is capable of influencing the public perception of genetic admixture in the medium-long term. If, on the one hand, it is proven that promoting investigation of this topic has

significant social influence, making it possible to transform emotional reactions into opinions based on scientific facts, on the other hand, its ability to shape the beliefs and mentalities of different social groups remains uncertain. Furthermore, it was clear that issues of phylogenetic distance influence public opinion on a topic such as genetic miscegenation, which is why it is at the root of many forms of discrimination and prejudice. This is another conclusion that needs further studies in the future helping to clarify the psycho-sociological processes behind phenomena such as biological racism.

In conclusion, this work has made a contribution to clarify the amplitude and relevance of genetic admixture for life by organizing, merging and analysing the current knowledge trends on introgression. Corroborating previous assumptions, it emphasized that introgression occurrence was demonstrated whenever sought (Maxwell et al., 2019; Vicente et al., 2017), and probably being the rule in nature more than the exception (Brennan et al., 2013). A methodological revolution in genomics is behind most of the current evidence (Kuhlwilm et al., 2019). These new advances boosted the scientific community's capacity and interest in exploring introgression. They helped to promote this topic as one of the most important in current science, taking into account the scope of publications in the context of the global scientific literature. The multidisciplinary nature of the study on introgression, as well as the transverse nature of its consequences, explains the public's interest in this topic. This work highlighted the capacity and importance of scientific publications to change public opinion, placing it on a less emotional and more factual basis. In this aspect, the high number of publications and the delay of scientific translation are two preponderant factors. However, different degrees of bias still remain in the public perception about genetic miscegenation (Matusitz, 2012; Nshom and Croucher, 2017), which can only be countered by a high degree of scientific communication (Iyengar and Massey, 2019).

Concluding, introgression overflowed as a preponderant mechanism for the evolution of many species complexes, particularly those found in primordial phases of macroevolution or under microevolution processes. According to the main current knowledge patterns, introgression seems an evolutionary process acting in parallel with divergence, evolving and establishing in balance with it. Through interconnected mechanisms its drivers increase its complexity across the biological organization, depending on species structural complexity. As organisms gradually increase their genomic, physiological and behavioural complexity, more constraints on divergence processes for the occurrence of introgression. Alternative mechanisms promoting divergence allow the co-occurrence of introgression albeit in the presence of divergence processes. Even so, it was demonstrated that simpler organisms present greater phylogenetic amplitude in the occurrence of introgression. Both the reduced size of the genome and the randomness in choosing a sexual partner seem to underlie this pattern. The results of the empirical studies identified a case study of

cryptic bats in which counteracting evolutionary forces currently co-exist (introgressive hybridization and competition), impacting different axes of ecological niches.

Finally, the taxonomic and geographic prevalence of introgression and its demonstrated (or potential) adaptive and evolutionary relevance, current or past, allow to support the idea that introgression can transfer to each species/lineage/breed a fundamental instrumental value, which can go far beyond its intrinsic value. Each one can act as a genetic resource for evolutionary rescue at some point of the evolutionary process. This value is crucial and should be preserve, being particularly important under strong environmental changes, as the current ones, resulting from anthropogenic climate change.

Bibliography

- Abbott, R., Albach, D., Ansell, S., Arntzen, W., Baird, S.J.E, Bierne, N. Boughman, J., Brelsford, A., Buerkle, C.A., Buggs, R., Butlin, R.K., Dieckmann, U., Eroukhmanoff, F., Grill, A., Cahan, S.H., Hermansen, J.S., Hewitt, G., Hudson, A.G., Jiggins, C., Jones, J., Keller, B., Marczewski, T., Mallet, J., Martinez-Rodriguez, P., Möst, M., Mullen, S., Nichols, R., Nolte, A.W., Parisod, C., Pfennig, K., Rice, A.M., Ritchie, M.G., Seifert, B., Smadja, C.M., Stelkens, R., Szymura, J.M., Väinölä, R., Wolf, J.B.W., and Zinner, D (2013). Hybridization and speciation. *Journal of Evolutionary Biology* 26, 229-246.
- Abrams, P.A. (1986). Character displacement and niche shift analyzed using consumer-resource models of competition. *Theoretical population biology* 29, 107-160.
- Abzhanov, A., Kuo, W.P., Hartmann, C., Grant, B.R., Grant, P.R., and Tabin, C.J. (2006). The calmodulin pathway and evolution of elongated beak morphology in Darwin's finches. *Nature* 442, 563-567.
- Abzhanov, A., Protas, M., Grant, B.R., Grant, P.R., and Tabin, C.J. (2004). Bmp4 and morphological variation of beaks in Darwin's finches. *Science (New York, NY)* 305, 1462-1465.
- Acosta, M.C., and Premoli, A.C. (2018). Understanding the extensive hybridization in South American *Nothofagus* through karyotype analysis. *Botanical Journal of the Linnean Society* 188, 74-86.*
- Adams, D.C., and Rohlf, F.J. (2000). Ecological character displacement in *Plethodon*: Biomechanical differences found from a geometric morphometric study. *Proceedings of the National Academy of Sciences* 97, 4106-4111.
- Aeschbacher, S., Selby, J.P., Willis, J.H., and Coop, G. (2017). Population-genomic inference of the strength and timing of selection against gene flow. *Proceedings of the National Academy of Sciences of the United States of America* 114, 7061-7066.*
- Aguirre-Liguori, J.A., Gaut, B.S., Jaramillo-Correa, J.P., Tenaillon, M.I., Montes-Hernández, S., García-Oliva, F., Hearne, S.J., and Eguiarte, L.E. (2019). Divergence with gene flow is driven by local adaptation to temperature and soil phosphorus concentration in teosinte subspecies (*Zea mays parviglumis* and *Zea mays mexicana*). *Molecular ecology* 28, 2814-2830.*
- Ainin, S., Feizollah, A., Anuar, N.B., and Abdullah, N.A. (2020). Sentiment analyses of multilingual tweets on halal tourism. *Tourism Management Perspectives* 34: 8.
- Akkuratov, E.E., Gelfand, M.S., and Khrameeva, E.E. (2018). Neanderthal and Denisovan ancestry in Papuans: A functional study. *Journal of Bioinformatics and Computational Biology* 16: 12.*
- Aleksic, J.M., Skondric, S., and Lakusic, D. (2018). Comparative phylogeography of capitulate *Campanula* species from the Balkans, with description of a new species, *C.-daucoides*. *Plant Systematics and Evolution* 304, 549-575.*

- Alexander, A.M., Su, Y.C., Oliveros, C.H., Olson, K.V., Travers, S.L., and Brown, R.M. (2017). Genomic data reveals potential for hybridization, introgression, and incomplete lineage sorting to confound phylogenetic relationships in an adaptive radiation of narrow-mouth frogs. *Evolution; international journal of organic evolution* 71, 475-488.*
- Algorithmics Group (2009). MDSJ: Java Library for Multidimensional Scaling (Version 0.2). Available at <http://www.inf.uni-konstanz.de/algo/software/mdsj/>. University of Konstanz.
- Allendorf, F.W., Leary, R.F., Spruell, P., and Wenburg, J.K. (2001). The problems with hybrids: setting conservation guidelines. *Trends in ecology & evolution* 16, 613-622.
- Anderson, E. (1949). *Introgressive hybridization* (New York: J. Wiley).
- Anderson, E., and Hubricht, L. (1938). Hybridization in *Tradescantia*. III. The evidence for introgressive hybridization. *American Journal of Botany* 25, 396-402.
- Anderson, R.P., Peterson, A.T., and Gómez-Laverde, M. (2002). Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98, 3-16.
- Anderson, T.M., vonHoldt, B.M., Candille, S.I., Musiani, M., Greco, C., Stahler, D.R., Smith, D.W., Padhukasahasram, B., Randi, E., Leonard, J.A., Bustamante, C.D., Ostrander, E.A., Tang, H., Wayne, R.K., and Barsh G.S. (2009). Molecular and evolutionary history of melanism in North American gray wolves. *Science (New York, NY)* 323, 1339-1343.*
- Antelope, C.X., Marnetto, D., Casey, F., and Huerta-Sanchez, E. (2017). Leveraging Multiple Populations across Time Helps Define Accurate Models of Human Evolution: A Reanalysis of the Lactase Persistence Adaptation. *Human Biology* 89, 81-97.*
- Araujo, C.A.A. (2021). Post-truth as central challenge for the contemporary information science. *EM QUESTAO* 27, 13-29.
- Arcella, T., Hood, G.R., Powell, T.H.Q., Sim, S.B., Yee, W.L., Schwarz, D., Egan, S.P., Goughnour, R.B., Smith, J.J., and Feder, J.L. (2015). Hybridization and the spread of the apple maggot fly, *Rhagoletis pomonella* (Diptera: Tephritidae), in the northwestern United States. *Evol Appl* 8, 834-846.*
- Arnold, M.L. (1992). Natural Hybridization as an Evolutionary Process. *Annual Review of Ecology and Systematics* 23, 237-261.
- Arnold, M.L. and Hodges, S.A. (1995). Are natural hybrids fit or unfit relative to their parents? *Trends in ecology & evolution* 10, 67-71.
- Arnold, M.L. (1997). *Natural hybridization and evolution* (Oxford: Oxford University Press).
- Arnold, M.L. (2004). Transfer and Origin of Adaptations through Natural Hybridization: Were Anderson and Stebbins Right? *The Plant Cell* 16, 562-570.

- Arnold, M.L., Ballerini, E.S., Brothers, A.N., Hamlin, J.A.P., Ishibashi, C.D.A., and Zuellig, M.P. (2012). The genomics of natural selection and adaptation: Christmas past, present and future (?). *Plant Ecology & Diversity* 5, 451-456.*
- Arnold, M.L., and Kunte, K. (2017). Adaptive Genetic Exchange: A Tangled History of Admixture and Evolutionary Innovation. *Trends in ecology & evolution* 32, 601-611.
- Bahbahani, H., Afana, A., and Wragg, D. (2018). Genomic signatures of adaptive introgression and environmental adaptation in the Sheko cattle of southwest Ethiopia. *PloS one* 13, 14.
- Baiz, M.D., Tucker, P.K., and Cortés-Ortiz, L. (2019). Multiple forms of selection shape reproductive isolation in a primate hybrid zone. *Molecular ecology* 28, 1056-1069.*
- Baker, N. (2016). Eugenics and Racial Hygiene: The Connections between the United States and Germany. Student Theses, Papers and Projects (History). 67. <https://digitalcommons.wou.edu/his/67>
- Baldassarre, D.T., White, T.A., Karubian, J., and Webster, M.S. (2014). Genomic and morphological analysis of a semipermeable avian hybrid zone suggests asymmetrical introgression of sexual signal. *Evolution; international journal of organic evolution* 68, 2644-2657.*
- Ballerini ES, Brothers AN, Tang SX, Knapp SJ, Bouck A, Taylor SJ, Arnold ML, Martin NH (2012). QTL mapping reveals the genetic architecture of loci affecting pre- and post-zygotic isolating barriers in Louisiana Iris. *Bmc Plant Biology* 12: 12.*
- Baur, B. (1998). Sperm competition in molluscs. *Sperm competition and sexual selection*. 1st edition. Academic Press.
- Bay, R.A., and Rugg, K. (2017). Genomic islands of divergence or opportunities for introgression? *Proceedings of the Royal Society B-Biological Sciences* 284, 9.*
- Beckman, E.J., Benham, P.M., Cheviron, Z.A., and Witt, C.C. (2018). Detecting introgression despite phylogenetic uncertainty: The case of the South American siskins. *Molecular ecology* 27, 4350-4367.*
- Bekoff, M. (1986). Olsen, S. J. *Origins of the Domestic Dog: The Fossil Record*. Univ. Arizona Press, Tucson. *Journal of Mammalogy* 67, 218-219.
- Beresford, J., Elias, M., Pluckrose, L., Sundstrom, L., Butlin, R.K., Pamilo, P., and Kulmuni, J. (2017). Widespread hybridization within mound-building wood ants in Southern Finland results in cytonuclear mismatches and potential for sex-specific hybrid breakdown. *Molecular ecology* 26, 4013-4026.*
- Bethencourt, F. (2013). *Racisms – From the Crusades to the Twentieth Century*. Princeton University Press.
- Biermann, C., and Mansfield, B. (2014). Biodiversity, Purity, and Death: Conservation Biology as Biopolitics. *Environment and Planning D: Society and Space* 32, 257-273.

- Bivins, R. (2008). Hybrid Vigour? Genes, Genomics, and History. *Genomics, society, and policy* 4, 12-22.
- Blommaert, J. (2020). Genome size evolution: Towards new model systems for old questions. *Proceedings of the Royal Society B* 287, 20201441.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., and Vasseur, D.A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution* 26, 183-192.
- Bolnick, D.I., and Nosil, P. (2007). Natural selection in populations subject to a migration load. *Evolution; international journal of organic evolution* 61, 2229-2243.
- Bonizzoni, P., Carrieri, A.P., Della Vedova, G., Rizzi, R., and Trucco, G. (2017). Species-Driven Persistent Phylogeny. *Fundamenta Informaticae* 154, 47-63.
- Bonnet, T., Leblois, R., Rousset, F., and Crochet, P.A. (2017). A reassessment of explanations for discordant introgressions of mitochondrial and nuclear genomes. *Evolution; international journal of organic evolution* 71, 2140-2158.*
- Boratyński, Z., Alves, P.C., Berto, S., Koskela, E., Mappes, T., and Melo-Ferreira, J. (2011). Introgression of mitochondrial DNA among *Myodes* voles: consequences for energetics? *BMC Evolutionary Biology* 11, 355.*
- Boratynski, Z., Melo-Ferreira, J., Alves, P.C., Berto, S., Koskela, E., Pentikainen, O.T., Tarroso, P., Ylilauri, M., and Mappes, T. (2014). Molecular and ecological signs of mitochondrial adaptation: consequences for introgression? *Heredity* 113, 277-286.*
- Bouck, A., Wessler, S.R., and Arnold, M.L. (2007). QTL analysis of floral traits in Louisiana iris hybrids. *Evolution; international journal of organic evolution* 61, 2308-2319.*
- Bradke, D.R., Altobelli, J.T., Russell, A.L., Jaeger, C.P., and Moore, J.A. (2021). Low Bottleneck Detection in Long-Lived Species despite Lost Genetic Diversity: A Case Study of Tuatara and Eastern Massasauga Rattlesnakes. *Journal of Heredity* 112, 346-356.
- Bradley, B.J., and Mundy, N.I. (2008). The primate palette: The evolution of primate coloration. *Evolutionary Anthropology Issues News and Reviews* 17, 97-111.
- Bradley, R., Greene, J., Russ, E., Dutra, L., and Westen, D. (2005). A multidimensional meta-analysis of psychotherapy for PTSD. *The American journal of psychiatry* 162, 214-227.
- Bradshaw, H.D., and Schemske, D.W. (2003). Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* 426, 176-178.
- Brand, C.L., Kingan, S.B., Wu, L.J., and Garrigan, D. (2013). A Selective Sweep across Species Boundaries in *Drosophila*. *Molecular Biology and Evolution* 30, 2177-2186.
- Brennan, A.C., Harris, S.A., and Hiscock, S.J. (2013). The population genetics of sporophytic self-incompatibility in three hybridizing *Senecio* (Asteraceae) species with constrating population histories. *Evolution; international journal of organic evolution* 67, 1347-1367.

- Brideau, N.J., Flores, H.A., Wang, J., Maheshwari, S., Wang, X., and Barbash, D.A. (2006). Two Dobzhansky-Muller genes interact to cause hybrid lethality in *Drosophila*. *Science* (New York, NY) 314, 1292-1295.
- Brooke, J.L. (2014). *Climate change and the course of global history: a rough journey*. Cambridge University Press.
- Brower, A.V.Z. (2013). Introgression of wing pattern alleles and speciation via homoploid hybridization in *Heliconius* butterflies: a review of evidence from the genome. *Proceedings of the Royal Society B-Biological Sciences* 280, 9.
- Brower, A.V.Z. (2018). Alternative facts: a reconsideration of putatively natural interspecific hybrid specimens in the genus *Heliconius* (Lepidoptera: Nymphalidae). *Zootaxa* 4499, 1-87.*
- Brown, A.P., McGowan, K.L., Schwarzkopf, E.J., Greenway, R., Rodriguez, L.A., Tobler, M., and Kelley, J.L. (2019). Local ancestry analysis reveals genomic convergence in extremophile fishes. *Philosophical transactions of the Royal Society of London Series B, Biological sciences* 374, 20180240.*
- Burgarella, C., Lorenzo, Z., Jabbour-Zahab, R., Lumaret, R., Guichoux, E., Petit, R.J., Soto, Á., and Gil, L. (2009). Detection of hybrids in nature: application to oaks (*Quercus suber* and *Q. ilex*). *Heredity* 102, 442-452.
- Burton, R.S., and Barreto, F.S. (2012). A disproportionate role for mtDNA in Dobzhansky-Muller incompatibilities? *Molecular ecology* 21, 4942-4957.
- Cahill, J.A., Stirling, I., Kistler, L., Salamzade, R., Ersmark, E., Fulton, T.L., Stiller, M., Green, R.E., and Shapiro, B. (2015). Genomic evidence of geographically widespread effect of gene flow from polar bears into brown bears. *Molecular ecology* 24, 1205-1217.*
- Campitelli, E. (2020). Ggnewscale: Multiple Fill and Colour Scales in "Ggplot2". R package version 0.4 1.
- Carling, M.D., and Brumfield, R.T. (2008). Haldane's rule in an avian system: using cline theory and divergence population genetics to test for differential introgression of mitochondrial, autosomal, and se-linked loci across the *Passerina* bunting hybrids zone. *Evolution; international journal of organic evolution* 62, 2600-2615.*
- Caro, T. (2005). The Adaptive Significance of Coloration in Mammals. *BioScience* 55, 125-136.
- Caseys, C., Glauser, G., Stolting, K.N., Christe, C., Albrechtsen, B.R., and Lexer, C. (2012). Effects of interspecific recombination on functional traits in trees revealed by metabolomics and genotyping-by-sequencing. *Plant Ecology & Diversity* 5, 457-471.*
- Cavender-Bares J, Gonzalez-Rodriguez A, Eaton DAR, Hipp AAL, Beulke A, Manos PS. (2015). Phylogeny and biogeography of the American live oaks (*Quercus* subsection *Virentes*): a genomic and population genetics approach. *Molecular Ecology* 24, 3668-3687.*

- Ceballos, S.G., Roesti, M., Matschiner, M., Fernandez, D.A., Damerau, M., Hanel, R., and Salzburger, W. (2019). Phylogenomics of an extra-Antarctic notothenioid radiation reveals a previously unrecognized lineage and diffuse species boundaries. *Bmc Evolutionary Biology* 19, 14.*
- Centeno-Cuadros, A., Razgour, O., García-Mudarra, J.L., Mingo-Casas, P., Sandonís, V., Redondo, A., Ibáñez, C., de Paz, O., Martínez-Alós, S., Pérez Suarez, G., Echevarría, J.E., and Juste, J. (2019). Comparative phylogeography and asymmetric hybridization between cryptic bat species. *Journal of Zoological Systematics and Evolutionary Research* 57, 1004-1018.
- Chan, W.Y., Hoffmann, A.A., and van Oppen, M.J.H. (2019). Hybridization as a conservation management tool. *Conservation Letters* 12, e12652.
- Charif, D., Lobry, J. (2007). SeqinR 1.0-2: a contributed package to the R project for statistical computing devoted to biological sequences retrieval and analysis. In Bastolla U, Porto M, Roman H, Vendruscolo M (eds.), *Structural approaches to sequence evolution: Molecules, networks, populations, series Biological and Medical Physics, Biomedical Engineering*, 207-232. Springer Verlag, New York.
- Chaverri, G., Ancillotto, L., and Russo, D. (2018). Social communication in bats. *Biological Reviews* 93, 1938-1954.
- Clarkson, C.S., Weetman, D., Essandoh, J., Yawson, A.E., Maslen, G., Manske, M., Field, S.G., Webster, M., Antao, T., MacInnis, B., Kwiatkowski, D., and Donnelly, M.J. (2014). Adaptive introgression between *Anopheles* sibling species eliminates a major genomic island but not reproductive isolation. *Nature Communications* 5, 10.*
- Coetzee, M., Hunt, R.H., Wilkerson, R., Della Torre, A., Coulibaly, M.B., and Besansky, N.J. (2013). *Anopheles coluzzii* and *Anopheles amharicus*, new members of the *Anopheles gambiae* complex. *Zootaxa* 3619, 246-274.
- Comeault, A.A. (2018). The genomic and ecological context of hybridization affects the probability that symmetrical incompatibilities drive hybrid speciation. *Ecology and Evolution* 8, 2926-2937.
- Cortes, F.V., and Salgado, J.E.L. (2011). Eugenics. A historical analysis and a possible proposal. *Acta Bioethica* 17, 189-197.
- Christianson, K., Zhou, P.Y., Palmer, C., and Raizen, A. (2017). Effects of context and individual differences on the processing of taboo words. *Acta Psychologica* 178: 73-86.
- Cruickshank, T.E., and Hahn, M.W. (2014). Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. *Molecular ecology* 23, 3133-3157.
- Currat, M., Ruedi, M., Petit, R.J., and Excoffier, L. (2008). The hidden side of invasions: massive introgression by local genes. *Evolution; international journal of organic evolution* 62, 1908-1920.

- Damasio, A., and Carvalho, G.B. (2013). The nature of feelings: evolutionary and neurobiological origins. *Nature reviews Neuroscience* 14, 143-152.
- Dange, J. (2016). Perception, passion and obsession: The three elements of theory of success. *International Journal of Advanced Education and Research*. 7: 01-03.
- Darwin, C. (1859). *On the origin of species by means of natural selection or the preservation of favored races in the struggle for life*. J. Murray, London.
- Dasgupta, N., Desteno, D., Williams, L.A., and Hunsinger, M. (2009). Fanning the flames of prejudice: the influence of specific incidental emotions on implicit prejudice. *Emotion* (Washington, DC) 9: 585-591.
- Dasmahapatra, K.K., Walters, J.R., Briscoe, A.D., Davey, J.W., Whibley, A., Nadeau, N.J., Zimin, A.V., Hughes, D.S.T., Ferguson, L.C., Martin, S.H., et al. (2012). Butterfly genome reveals promiscuous exchange of mimicry adaptations among species. *Nature* 487, 94-98.*
- De Domenico, M., Porter, M.A., and Arenas, A. (2014). MuxViz: a tool for multilayer analysis and visualization of networks. *Journal of Complex Networks* 3, 159-176.
- De Domenico, M., Solé-Ribalta, A., Omodei, E., Gómez, S., and Arenas, A. (2015). Ranking in interconnected multilayer networks reveals versatile nodes. *Nature Communications* 6, 6868.
- De La Torre, A.R., Wang, T.L., Jaquish, B., and Aitken, S.N. (2014). Adaptation and exogenous selection in a *Picea glauca* x *Picea engelmannii* hybrid zone: implications for forest management under climate change. *New Phytologist* 201, 687-699.*
- de Lafontaine, G., and Bousquet, J. (2017). Asymmetry matters: A genomic assessment of directional biases in gene flow between hybridizing spruces. *Ecology and Evolution* 7, 3883-3893.*
- de Lafontaine, G., Prunier, J., Gerardi, S., and Bousquet, J. (2015). Tracking the progression of speciation: variable patterns of introgression across the genome provide insights on the species delimitation between progenitor-derivative spruces (*Picea mariana* x *P. rubens*). *Molecular ecology* 24, 5229-5247.*
- Deichmann, U. (2017). Hierarchy, determinism, and specificity in theories of development and evolution. *History and philosophy of the life sciences* 39, 33.
- Derr, J.N., Hedrick, P.W., Halbert, N.D., Plough, L., Dobson, L.K., King, J., Duncan, C., Hunter, D.L., Cohen, N.D., and Hedgecock, D. (2012). Phenotypic effects of cattle mitochondrial DNA in American bison. *Conservation biology: the journal of the Society for Conservation Biology* 26, 1130-1136.
- DiBattista, J.D., Whitney, J., Craig, M.T., Hobbs, J.P.A., Rocha, L.A., Feldheim, K.A., Berumen, M.L., and Bowen, B.W. (2016). Surgeons and suture zones: Hybridization among four surgeonfish species in the Indo-Pacific with variable evolutionary outcomes. *Molecular Phylogenetics and Evolution* 101: 203-215.*

- Di Candia, M.R., and Routman, E.J. (2007). Cytonuclear discordance across a leopard frog contact zone. *Molecular phylogenetics and evolution* 45, 564-575.*
- Dietz, C., Von Helvesen, O., and Nill, D. (2009) Bats of Britain, Europe and Northwest Africa. A&C Black Publishers Ltd. 320-333.
- Ding, Q., Hu, Y., Xu, S., Wang, J., and Jin, L. (2013). Neanderthal Introgression at Chromosome 3p21.31 Was Under Positive Natural Selection in East Asians. *Molecular Biology and Evolution* 31, 683-695.*
- Dinger G. (1991). Winternachweise von Breitflügelfledermaus (*Eptesicus serotinus*) in Kirchen. *Nyctalus* (N.F.). 7, 614-616.
- Djogbénou, L., Chandre, F., Berthomieu, A., Dabiré, R., Koffi, A., Alout, H., and Weill, M. (2008). Evidence of introgression of the ace-1(R) mutation and of the ace-1 duplication in West African *Anopheles gambiae* s. s. *PloS one* 3: e2172.*
- Dopman, E.B., Pérez, L., Bogdanowicz, S.M., and Harrison, R.G. (2005). Consequences of reproductive barriers for genealogical discordance in the European corn borer. *Proceedings of the National Academy of Sciences of the United States of America* 102, 14706-14711.
- Dormann, C.F., Gruber, B., and Fruend, J. (2008). Introducing the bipartite Package: Analysing Ecological Networks. *R News*, 8(2), 8-11.
- Drummond, A.J., and Bouckaert, R.R. (2015). Bayesian evolutionary analysis with BEAST. Cambridge University Press.
- Drummond, A.J., and Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7, 1-8.
- Dunn, B., Paulish, T., Stanbery, A., Piotrowski, J., Koniges, G., Kroll, E., Louis, E.J., Liti, G., Sherlock, G., and Rosenzweig, F. (2013). Recurrent Rearrangement during Adaptive Evolution in an Interspecific Yeast Hybrid Suggests a Model for Rapid Introgression. *Plos Genetics* 9, 16.*
- Emms, S.K., Hodges, S.A., and Arnold, M.L. (1996). Pollen-tube competition, siring success, and consistent asymmetric hybridization in Louisiana Irises. *Evolution* 50, 2201-2206.*
- Enard, D., and Petrov, D.A. (2018). Evidence that RNA Viruses Drove Adaptive Introgression between Neanderthals and Modern Humans. *Cell* 175, 360.*
- Enciso-Romero, J., Pardo-Diaz, C., Martin, S.H., Arias, C.F., Linares, M., McMillan, W.O., Jiggins, C.D., and Salazar, C. (2017). Evolution of novel mimicry rings facilitated by adaptive introgression in tropical butterflies. *Molecular ecology* 26: 5160-5172.*
- Epstein, S. (1994). Integration of the cognitive and the psychodynamic unconscious. *The American psychologist* 49: 709-724.
- Epifanio, J., and Nielsen, J. (2000). The role of hybridization in the distribution, conservation and management of aquatic species. *Reviews in Fish Biology and Fisheries* 10, 245-251.

- Excoffier, L., Foll, M., and Petit, R.J. (2008). Genetic Consequences of Range Expansions. *Annual Review of Ecology, Evolution, and Systematics* 40, 481-501.
- Falagas, M.E., Pitsouni, E.I., Malietzis, G.A., and Pappas, G. (2008). Comparison of PubMed, Scopus, Web of Science, and Google Scholar: strengths and weaknesses. *The FASEB Journal* 22, 338-342.
- Fanelli, D., Costas, R., and Ioannidis, J.P.A. (2017). Meta-assessment of bias in science. *Proceedings of the National Academy of Sciences* 114: 3714-3719.
- Feder, J.L., Xie, X.F., Rull, J., Velez, S., Forbes, A., Leung, B., Dambroski, H., Filchak, K.E., and Aluja, M. (2005). Mayr, Dobzhansky, and Bush and the complexities of sympatric speciation in *Rhagoletis*. *Proceedings of the National Academy of Sciences of the United States of America* 102, 6573-6580.*
- Felix, B. (2021). Sequence Similarity Search, Multiple Sequence Alignment, Model Selection, Distance Matrix and Phylogeny Reconstruction. Protocol Exchange. <https://doi.org/10.1038/protex.2013.065>
- Ferreira, M.S., Jones, M.R., Callahan, C.M., Farelo, L., Tolesa, Z., Suchentrunk, F., Boursot, P., Mills, L.S., Alves, P.C., Good, J.M., and Melo-Ferreira, J. (2021). The Legacy of Recurrent Introgression during the Radiation of Hares. *Systematic Biology* 70, 593-607.
- Ferrara, E., and Yang, Z. (2015). Measuring Emotional Contagion in Social Media. *PloS one* 10: e0142390.
- Fijarczyk, A., Dudek, K., Niedzicka, M., and Babik, W. (2018). Balancing selection and introgression of newt immune-response genes. *Proceedings of the Royal Society B-Biological Sciences* 285, 9.*
- Forsythe, E.S., Sloan, D.B., and Beilstein, M.A. (2020). Divergence-Based Introgression Polarization. *Genome Biology and Evolution* 12, 463-478.
- Fouet, C., Atkinson, P., and Kamdem, C. (2018). Human Interventions: Driving Forces of Mosquito Evolution. *Trends in Parasitology* 34, 127-139.*
- Fraisse, C., Belkhir, K., Welch, J.J., and Bierne, N. (2016). Local interspecies introgression is the main cause of extreme levels of intraspecific differentiation in mussels. *Molecular ecology* 25, 269-286.
- Fredrickson, G.M. (2002). *Racism - A Short History*, REV - Revised edn (Princeton University Press).
- Gagnaire, P.A., Albert, V., Jonsson, B., and Bernatchez, L. (2009). Natural selection influences AFLP intraspecific genetic variability and introgression patterns in Atlantic eels. *Molecular ecology* 18: 1678-1691.*
- Gagnaire, P.A., Pavey, S.A., Normandeau, E., and Bernatchez, L. (2013). The genetic architecture of reproductive isolation during speciation-with-gene-flow in Lake Whitefish species pairs

assessed by RAD sequencing. *Evolution; international journal of organic evolution* 67, 2483-2497.*

- Galván, I., Vargas-Mena, J.C., and Rodríguez-Herrera, B. (2020). Tent-roosting may have driven the evolution of yellow skin coloration in Stenodermatinae bats. *Journal of Zoological Systematics and Evolutionary Research* 58, 519-527.
- Gante, H.F., Matschiner, M., Malmstrom, M., Jakobsen, K.S., Jentoft, S., and Salzburger, W. (2016). Genomics of speciation and introgression in Princess cichlid fishes from Lake Tanganyika. *Molecular ecology* 25, 6143-6161.*
- Garcia-Elfring, A., Barrett, R.D.H., Combs, M., Davies, T.J., Munshi-South, J., and Millien, V. (2017). Admixture on the northern front: population genomics of range expansion in the white-footed mouse (*Peromyscus leucopus*) and secondary contact with the deer mouse (*Peromyscus maniculatus*). *Heredity* 119, 447-458.*
- García-Ramos, G., and Kirkpatrick, M. (1997). Genetic models of adaptation and gene flow in peripheral populations. *Evolution; international journal of organic evolution* 51: 21-28.
- Garrick, R.C., Benavides, E., Russello, M.A., Hyseni, C., Edwards, D.L., Gibbs, J.P., Tapia, W., Ciofi, C., and Caccone, A. (2014). Lineage fusion in Galapagos giant tortoises. *Molecular ecology* 23, 5276-5290.
- Garrick, R.C., Hyseni, C., and Arantes, I.C. (2020). Efficient summary statistics for detecting lineage fusion from phylogeographic datasets. *Journal of biogeography* 47, 2129-2140.
- Gasparrini, A. (2011). Distributed Lag Linear and Non-Linear Models in R: The Package dlnm. *Journal of statistical software* 43: 1-20.
- Genovart, M. (2009). Natural hybridization and conservation. *Biodiversity and Conservation* 18, 1435-1439.
- Ghenu, A.H., Blanckaert, A., Butlin, R.K., Kulmuni, J., and Bank, C. (2018). Conflict between heterozygote advantage and hybrid incompatibility in haplodiploids (and sex chromosomes). *Molecular ecology* 27, 3935-3949.*
- Giannoulis, T., Plageras, D., Stamatis, C., Chatzivagia, E., Tsipourlianos, A., Birtsas, P., Billinis, C., Suchentrunk, F., and Mamuris, Z. (2019). Islands and hybrid zones: combining the knowledge from "Natural Laboratories" to explain phylogeographic patterns of the European brown hare. *Bmc Evolutionary Biology* 19, 17.*
- Giska, I., Farelo, L., Pimenta, J., Seixas, F.A., Ferreira, M.S., Marques, J.P., Miranda, I., Letty, J., Jenny, H., Hackländer, K., Magnussen, E., and Melo-Ferreira, J. (2019). Introgression drives repeated evolution of winter coat color polymorphism in hares. *Proceedings of the National Academy of Sciences of the United States of America* 116, 24150-24156.*

- Gittelman, R.M., Schraiber, J.G., Vernot, B., Mikacenic, C., Wurfel, M.M., and Akey, J.M. (2016). Archaic Hominin Admixture Facilitated Adaptation to Out-of-Africa Environments. *Current Biology* 26, 3375-3382.*
- Gladyshev, E.A., Meselson, M., and Arkhipova, I.R. (2008). Massive horizontal gene transfer in bdelloid rotifers. *Science (New York, NY)* 320, 1210-1213.
- Gompert, Z. and Buerkle, C.A. (2009). A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular ecology* 18, 1207-1224.
- Gompert, Z., Lucas, L.K., Nice, C.C., and Buerkle, C.A. (2013). Genome divergence and the genetic architecture of barriers to gene flow between *Lycaeides idas* and *L. melissa*. *Evolution; international journal of organic evolution* 67, 2498-2514.*
- Gould, S.J. (1978). Morton's ranking of races by cranial capacity. Unconscious manipulation of data may be a scientific norm. *Science* 200, 503-509.
- Gramlich, S., Wagner, N.D., and Horandl, E. (2018). RAD-seq reveals genetic structure of the F-2-generation of natural willow hybrids (*Salix L.*) and a great potential for interspecific introgression. *Bmc Plant Biology* 18, 12.*
- Grant, P.R., and Grant, B.R. (1994). Phenotypic and genetic effects of hybridization in Darwin's Finches. *Evolution; international journal of organic evolution* 48, 297-316.
- Grant, P.R., and Grant, B.R. (2016). Introgressive hybridization and natural selection in Darwin's finches. *Biological Journal of the Linnean Society* 117, 812-822.*
- Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.Y., et al. (2010). A Draft Sequence of the Neandertal Genome. *Science* 328: 710-722.*
- Gu, Z., Gu, L., Eils, R., Schlesner, M., and Brors, B. (2014). Circlize implements and enhances circular visualization in R. *Bioinformatics*, 30: 2811-2812.
- Haldane, J.B.S. (1922). Sex ratio and unisexual sterility in hybrid animals. *Journal of Genetics* 12, 101-109.
- Hamilton, J.A., Lexer, C., and Aitken, S.N. (2013). Genomic and phenotypic architecture of a spruce hybrid zone (*Picea sitchensis* P. *glauca*). *Molecular ecology* 22, 827-841.*
- Hamlin, J.A.P., and Arnold, M.L. (2014). Determining population structure and hybridization for two iris species. *Ecology and Evolution* 4: 743-755.*
- Hanemaaijer, M.J., Collier, T.C., Chang, A., Shott, C.C., Houston, P.D., Schmidt, H., Main, B.J., Cornel, A.J., Lee, Y., and Lanzaro, G.C. (2018). The fate of genes that cross species boundaries after a major hybridization event in a natural mosquito population. *Molecular ecology* 27, 4978-4990.*
- Harris, K., and Nielsen, R. (2016). The Genetic Cost of Neanderthal Introgression. *Genetics* 203, 881-891.*

- Harrison, R.G., and Larson, E.L. (2014). Hybridization, Introgression, and the Nature of Species Boundaries. *Journal of Heredity* 105, 795-809.
- Hasselgren, M., Dussex, N., von Seth, J., Angerbjorn, A., Olsen, R.A., Dalen, L., and Noren, K. (2021). Genomic and fitness consequences of inbreeding in an endangered carnivore. *Molecular ecology* 30, 2790-2799.
- Hawkins, M.T.R., Leonard, J.A., Helgen, K.M., McDonough, M.M., Rockwood, L.L., and Maldonado, J.E. (2016). Evolutionary history of endemic Sulawesi squirrels constructed from UCEs and mitogenomes sequenced from museum specimens. *Bmc Evolutionary Biology* 16, 16.*
- Hayden, E.C. (2014). Technology: The \$1,000 genome. *Nature* 507, 294-295.
- Hedrick, P.W. (2013). Adaptive introgression in animals: examples and comparison to new mutation and standing variation as sources of adaptive variation. *Molecular ecology* 22, 4606-4618.
- Heiser Jr, C.B. (1951). Hybridization in the annual sunflowers: *Helianthus annuus* × *H. debilis* var. *cucumerifolius*. *Evolution; international journal of organic evolution*, 42-51.
- Hejase, H.A., and Liu, K.J. (2016). Mapping the genomic architecture of adaptive traits with interspecific introgressive origin: a coalescent-based approach. *Bmc Genomics* 17, 17.*
- Henkel, J., Saif, R., Jagannathan, V., Schmocker, C., Zeindler, F., Bangerter, E., Herren, U., Posantzis, D., Bulut, Z., Ammann, P., et al. (2019). Selection signatures in goats reveal copy number variants underlying breed-defining coat color phenotypes. *PLOS Genetics* 15, e1008536.
- Hennig, W. (1965). Phylogenetic systematics. *Annual review of entomology* 10, 97-116.
- Herbers, J.M. (2010). Evolution: Fundamentals. In *Encyclopedia of Animal Behavior*, M.D. Breed, and J. Moore, eds. (Oxford: Academic Press), 670-678.
- Herrig, D.K., Modrick, A.J., Brud, E., and Llopart, A. (2014). Introgression in the *Drosophila* subobscura – *D. madeirensis* sister species: Evidence of gene flow in nuclear genes despite mitochondrial differentiation. *Evolution; international journal of organic evolution* 68, 705-719.*
- Hoffmann, A.A., and Sgrò, C.M. (2011). Climate change and evolutionary adaptation. *Nature* 470, 479-485.
- Hohmann, N., and Koch, M.A. (2017). An *Arabidopsis* introgression zone studied at high spatio-temporal resolution: interglacial and multiple genetic contact exemplified using whole nuclear and plastid genomes. *Bmc Genomics* 18: 18.*
- Horn, R.L., Marques, A.J.D., Manseau, M., Golding, B., Klutsch, C.F.C., Abraham, K., and Wilson, P.J. (2018). Parallel evolution of site-specific changes in divergent caribou lineages. *Ecology and Evolution* 8: 6053-6064.*
- Huerta-Sánchez, E., Jin, X., Asan, Bianba, Z., Peter, B.M., Vinckenbosch, N., Liang, Y., Yi, X., He, M., Somel, M., et al. (2014). Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature* 512, 194-197.*

- Hulsey, C.D., Keck, B.P., Alamillo, H., and O'Meara, B.C. (2013). Mitochondrial genome primers for Lake Malawi cichlids. *Molecular Ecology Resources* 13, 347-353.*
- Hume, J.B., Recknagel, H., Bean, C.W., Adams, C.E., and Mable, B.K. (2018). RADseq and mate choice assays reveal unidirectional gene flow among three lamprey ecotypes despite weak assortative mating: Insights into the formation and stability of multiple ecotypes in sympatry. *Molecular ecology* 27, 4572-4590.*
- Iheduru-Anderson, K.C., and Wahi, M.M. (2021). Rejecting the myth of equal opportunity: an agenda to eliminate racism in nursing education in the United States. *BMC Nursing* 20.
- Ibáñez, C., García-Mudarra, J.L., Ruedi, M., Stadelmann, B., and Juste, J. (2006). The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterologica* 8, 277-297.
- Illumination, I.C.o. (2004). A colour appearance model for colour management systems: CIECAM02. Technical Report No CIE 159.
- Iyengar, S., and Massey, D.S. (2019). Scientific communication in a post-truth society. *Proceedings of the National Academy of Sciences* 116, 7656.
- Izard, C.E. (2007). Basic Emotions, Natural Kinds, Emotion Schemas, and a New Paradigm. *Perspectives on Psychological Science* 2: 260-280.
- Jagoda, E., Lawson, D.J., Wall, J.D., Lambert, D., Muller, C., Westaway, M., Leavesley, M., Capellini, T.D., Lahr, M.M., Gerbault, P., Thomas, M.G., Migliano, A.B., Willerslev, E., Metspalu, M., and Pagani, L. (2018). Disentangling Immediate Adaptive Introgression from Selection on Standing Introgressed Variation in Humans. *Molecular Biology and Evolution* 35, 623-630.*
- James, K.E., Schneider, H., Ansell, S.W., Evers, M., Robba, L., Uszynski, G., Pedersen, N., Newton, A.E., Russell, S.J., Vogel, J.C., and Kilian, A. (2008). Diversity Arrays Technology (DArT) for Pan-Genomic Evolutionary Studies of Non-Model Organisms. *PloS one* 3, 11.*
- Jiang, Y., Bolnick, D.I., and Kirkpatrick, M. (2013). Assortative mating in animals. *The American Naturalist* 181, E125-138.
- Jockers, M.L. (2015). Syuzhet: Extract Sentiment and Plot Arcs from Text. <https://github.com/mjockers/syuzhet>.
- Jones, G. (1997). Acoustic signals and speciation: the roles of natural and sexual selection in the evolution of cryptic species. *Advances in the Study of Behaviour* 26, 317-354.
- Jones, M.R., Mills, L.S., Alves, P.C., Callahan, C.M., Alves, J.M., Lafferty, D.J.R., Jiggins, F.M., Jensen, J.D., Melo-Ferreira, J., and Good, J.M. (2018). Adaptive introgression underlies polymorphic seasonal camouflage in snowshoe hares. *Science* 360, 1355-1358.*
- Juste, J., Ibáñez, C., Muñoz, J., Trujillo, D., Benda, P., Karataş, A., and Ruedi, M. (2004). Mitochondrial phylogeography of the long-eared bats (*Plecotus*) in the Mediterranean Palaearctic and Atlantic Islands. *Molecular phylogenetics and evolution* 31, 1114-1126.

- Kahneman, D. (2011). *Thinking, fast and slow*. Macmillan.
- Kahneman, D., and Frederick, S. (2002). Representativeness revisited: Attribute substitution in intuitive judgment. In *Heuristics and biases: The psychology of intuitive judgment* (New York, NY, US). Cambridge University Press.
- Kalcounis, M.C., and Brigham, R.M. (1995). Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology* 73, 89-95.
- Karatzoglou A, Smola A, Hornik K, Zeileis A (2004). “kernlab – An S4 Package for Kernel Methods in R.” *Journal of Statistical Software*, 11(9), 1–20.
- Kilbourne, A.M., Glasgow, R.E., Chambers, D.A. (2020). What Can Implementation Science Do for You? Key Success Stories from the Field. *Journal of General Internal Medicine* 35: 783-787.
- Kim, B.Y., Huber, C.D., and Lohmueller, K.E. (2018). Deleterious variation shapes the genomic landscape of introgression. *PLOS Genetics* 14, e1007741.*
- King, Robert C., William D. Stansfield, and Pamela Khipple Mulligan. (2006). *A dictionary of genetics*. Oxford, Oxford University Press.
- Kingston, S.E., Parchman, T.L., Gompert, Z., Buerkle, C.A., and Braun, M.J. (2017). Heterogeneity and concordance in locus-specific differentiation and introgression between species of towhees. *Journal of Evolutionary Biology* 30, 474-485.*
- Koenig, D., Hagmann, J., Li, R., Bemm, F., Slotte, T., Neuffer, B., Wright, S.I., and Weigel, D. (2019). Long-term balancing selection drives evolution of immunity genes in *Capsella*. *eLife* 8.*
- Koonin, E.V., Makarova, K.S., and Aravind, L. (2001). Horizontal Gene Transfer in Prokaryotes: Quantification and Classification. *Annual Review of Microbiology* 55, 709-742.
- Kooyers, N.J., James, B., and Blackman, B.K. (2017). Competition drives trait evolution and character displacement between *Mimulus* species along an environmental gradient. *Evolution; international journal of organic evolution* 71, 1205-1221.
- Kost, S., Heckel, D.G., Yoshido, A., Marec, F., and Groot, A.T. (2016). A Z-linked sterility locus causes sexual abstinence in hybrid females and facilitates speciation in *Spodoptera frugiperda*. *Evolution; international journal of organic evolution* 70, 1418-1427.
- Kowalski, K., and Rzebik-Kowalska, B. (1991). *Mammals of algeria*. Wroclaw: Polish Academy of Science.
- Kronforst, M.R., Hansen, M.E.B., Crawford, N.G., Gallant, J.R., Zhang, W., Kulathinal, R.J., Kapan, D.D., and Mullen, S.P. (2013). Hybridization Reveals the Evolving Genomic Architecture of Speciation. *Cell Reports* 5, 666-677.*
- Kuhlwilm, M., Han, S., Sousa, V.C., Excoffier, L., and Marques-Bonet, T. (2019). Ancient admixture from an extinct ape lineage into bonobos. *Nature Ecology & Evolution* 3, 957-965.*

- Kulikova, I.V., Zhuravlev, Y.N., and McCracken, K.G. (2004). Asymmetric hybridization and sex-biased gene flow between Eastern Spot-billed Ducks (*Anas zonorhyncha*) and Mallards (*A. platyrhynchos*) in the Russian Far East. *The Auk* *121*, 930-949.*
- Kulmuni, J., and Pamilo, P. (2014). Introgression in hybrid ants is favored in females but selected against in males. *Proceedings of the National Academy of Sciences of the United States of America* *111*, 12805-12810.*
- Lai, Yu-Ting, Carol K. L. Yeung, Kevin E. Omland, Er-Li Pang, Yu Hao, Ben-Yang Liao, Hui-Fen Cao, Bo-Wen Zhang, Chia-Fen Yeh, Chih-Ming Hung, Hsin-Yi Hung, Ming-Yu Yang, Wei Liang, Yu-Cheng Hsu, Cheng-Te Yao, Lu Dong, Kui Lin, and Shou-Hsien Li. (2019). Standing genetic variation as the predominant source for adaptation of a songbird. *Proceedings of the National Academy of Sciences*, *116*: 2152.
- Lamichhaney, S., Han, F., Berglund, J., Wang, C., Almén, M.S., Webster, M.T., Grant, B.R., Grant, P.R., and Andersson, L. (2016). A beak size locus in Darwin's finches facilitated character displacement during a drought. *Science (New York, NY)* *352*, 470-474.*
- Laplane, L., Mantovani, P., Adolphs, R., Chang, H., Mantovani, A., McFall-Ngai, M., Rovelli, C., Sober, E., and Pradeu, T. (2019). Opinion: Why science needs philosophy. *Proceedings of the National Academy of Sciences* *116*, 3948.
- Latch, E.K., Harveson, L.A., King, J.S., Hobson, M.D., and Rhodes JR., O.E. (2006). Assessing Hybridization in Wildlife Populations Using Molecular Markers: A Case Study in Wild Turkeys. *The Journal of Wildlife Management* *70*, 485-492.
- Lazic, D., Hipp, A.L., Carlson, J.E., and Gailing, O. (2021). Use of Genomic Resources to Assess Adaptive Divergence and Introgression in Oaks. *Forests* *12*.
- Leducq, J.B., Henault, M., Charron, G., Nielly-Thibault, L., Terrat, Y., Fiumera, H.L., Shapiro, B.J., and Landry, C.R. (2017). Mitochondrial Recombination and Introgression during Speciation by Hybridization. *Molecular Biology and Evolution* *34*, 1947-1959.*
- Lee, K.M., and Coop, G. (2017). Distinguishing Among Modes of Convergent Adaptation Using Population Genomic Data. *Genetics* *207*, 1591-1619.*
- Lehnert, S.J., Bentzen, P., Kess, T., Lien, S., Horne, J.B., Clément, M., and Bradbury, I.R. (2019). Chromosome polymorphisms track trans-Atlantic divergence and secondary contact in Atlantic salmon. *Molecular ecology* *28*: 2074-2087.*
- Leigh Van, V. (1976). Ecological Species, Multispecies, and Oaks. *Taxon* *25*, 233-239.
- Lepais, O., Petit, R., Guichoux, E., Lavabre, J., Alberto, F., Kremer, A., and Gerber, S. (2009). Species relative abundance and direction of introgression in oaks. *Molecular Ecology* *18*, 2228-2242.

- Leroy, T., Roux, C., Villate, L., Bodenes, C., Romiguier, J., Paiva, J.A.P., Dossat, C., Aury, J.M., Plomion, C., and Kremer, A. (2017). Extensive recent secondary contacts between four European white oak species. *New Phytologist* 214, 865-878.*
- Lewontin, R.C., and Birch, L.C. (1966). Hybridization as a source of variation to new environments. *Evolution; international journal of organic evolution* 20, 315-336.*
- Lexer, C., Heinze, B., Alia, R., and Rieseberg, L.H. (2004). Hybrid zones as a tool for identifying adaptive genetic variation in outbreeding forest trees: lessons from wild annual sunflowers (*Helianthus* spp.). *Forest Ecology and Management* 197, 49-64.*
- Lexer, C., Joseph, J.A., van Loo, M., Barbara, T., Heinze, B., Bartha, D., Castiglione, S., Fay, M.F., and Buerkle, C.A. (2010). Genomic Admixture Analysis in European *Populus* spp. Reveals Unexpected Patterns of Reproductive Isolation and Mating. *Genetics* 186, 699-U391.*
- Lewis, J.E., Degusta, D., Meyer, M.R., Monge, J.M., Mann, A.E., and Holloway, R.L. (2011). The mismeasure of science: Stephen Jay Gould *versus* Samuel George Morton on skulls and bias. *PLoS biology* 9: e1001071.
- Li, G., Davis, B.W., Eizirik, E., and Murphy, W.J. (2016). Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae). *Genome Res* 26, 1-11.*
- Liddell, E., Sunnucks, P., and Cook, C.N. (2021). To mix or not to mix gene pools for threatened species management? Few studies use genetic data to examine the risks of both actions, but failing to do so leads disproportionately to recommendations for separate management. *Biological conservation* 256.
- Lin, Z., Nei, M., and Ma, H. (2007). The origins and early evolution of DNA mismatch repair genes—multiple horizontal gene transfers and co-evolution. *Nucleic acids research* 35, 7591-7603.
- Lind-Riehl, J.F., and Gailing, O. (2017). Adaptive Variation and Introgression of a CONSTANS-Like Gene in North American Red Oaks. *Forests* 8, 12.*
- Liu, K.J., Steinberg, E., Yozzo, A., Song, Y., Kohn, M.H., and Nakhleh, L. (2015). Interspecific introgressive origin of genomic diversity in the house mouse. *Proceedings of the National Academy of Sciences of the United States of America* 112, 196-201.*
- Livoreil, B., Glanville, J., Haddaway, N.R., Bayliss, H., Bethel, A., de Lachapelle, F.F., Robalino, S., Savilaakso, S., Zhou, W., Petrokofsky, G., *et al.* (2017). Systematic searching for environmental evidence using multiple tools and sources. *Environmental Evidence* 6, 23.
- Llopart, A., Herrig, D., Brud, E., and Stecklein, Z. (2014). Sequential adaptive introgression of the mitochondrial genome in *Drosophila yakuba* and *Drosophila santomea*. *Molecular ecology* 23, 1124-1136.*
- Loureiro, M.L., and Alló, M. (2020). Sensing climate change and energy issues: Sentiment and emotion analysis with social media in the U.K. and Spain. *Energy Policy* 143: 111490.

- Lowe, W.H., Muhlfeld, C.C., and Allendorf, F.W. (2015). Spatial sorting promotes the spread of maladaptive hybridization. *Trends in ecology & evolution* 30: 456-462.
- Lyu, R., He, J., Luo, Y.K., Lin, L.L., Yao, M., Cheng, J., Xie, L., Pei, L.Y., Yan, S.X., and Li, L.Q. (2021). Natural Hybrid Origin of the Controversial "Species" *Clematis x pinnata* (Ranunculaceae) Based on Multidisciplinary Evidence. *Frontiers in plant science* 12.
- Ma, F., Zhao, C., Milne, R., Ji, M., Chen, L., and Liu, J. (2010). Enhanced drought-tolerance in the homoploid hybrid species *Pinus densata*: implication for its habitat divergence from two progenitors. *New Phytologist* 185, 204-216.*
- Ma, Y., Wang, J., Hu, Q., Li, J., Sun, Y., Zhang, L., Abbott, R.J., Liu, J., and Mao, K. (2019). Ancient introgression drives adaptation to cooler and drier mountain habitats in a cypress species complex. *Communications biology* 2, 213.*
- Mace, G.M., Gittleman, J.L., and Purvis, A. (2003). Preserving the Tree of Life. *Science* 300, 1707-1709.
- Maddamsetti, R., and Lenski, R.E. (2018). Analysis of bacterial genomes from an evolution experiment with horizontal gene transfer shows that recombination can sometimes overwhelm selection. *Plos Genetics* 14, 30.*
- Magalhães, J., Hartz, Z., Antunes, A., and Maria do Rosário, O.M. (2017). An Overview of the Open Science in Times of Big Data and Innovation to Global Health. *International Journal of Innovation* 5, 270-288.
- Maguilla, E., Escudero, M., Hipp, A.L., and Luceno, M. (2017). Allopatric speciation despite historical gene flow: Divergence and hybridization in *Carex furva* and *C.lucennoiberica* (Cyperaceae) inferred from plastid and nuclear RAD-seq data. *Molecular ecology* 26, 5646-5662.*
- Mallarino, R., Grant, P.R., Grant, B.R., Herrel, A., Kuo, W.P., and Abzhanov, A. (2011). Two developmental modules establish 3D beak-shape variation in Darwin's finches. *Proceedings of the National Academy of Sciences of the United States of America* 108, 4057-4062.
- Malhotra, A., and Thorpe, R.S. (2000). A phylogeny of the *Trimeresurus* group of pit vipers: new evidence from a mitochondrial gene tree. *Molecular Phylogenetics and Evolution* 16, 199-211.
- Mallet, J. (2005). Hybridization as an invasion of the genome. *Trends in ecology & evolution* 20, 229-237.
- Mallet, J. (2008). Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical transactions of the Royal Society of London Series B, Biological sciences* 363, 2971-2986.
- Mallet, J., Besansky, N., and Hahn, M.W. (2016). How reticulated are species? *Bioessays* 38, 140-149.

- Mao, X.G., Zhu, G.J., Zhang, L.B., Zhang, S.Y., and Rossiter, S.J. (2014). Differential introgression among loci across a hybrid zone of the intermediate horseshoe bat (*Rhinolophus affinis*). *Bmc Evolutionary Biology* 14, 13.*
- Mao, Y.F., Economo, E.P., and Satoh, N. (2018). The Roles of Introgression and Climate Change in the Rise to Dominance of *Acropora* Corals. *Current Biology* 28, 3373.*
- Markey, K., Tilki, M., and Taylor, G. (2012). Strategies to surmount the potential barriers to providing anti-discriminatory care in Irish healthcare settings. *Contemporary Nurse* 40, 269-276.
- Maroco, J. (2010). *Análise estatística com utilização do SPSS*. 3ª Edição. Edições Silabo.
- Marsden, C.D., Lee, Y., Nieman, C.C., Sanford, M.R., Dinis, J., Martins, C., Rodrigues, A., Cornel, A.J., and Lanzaro, G.C. (2011). Asymmetric introgression between the M and S forms of the malaria vector, *Anopheles gambiae*, maintains divergence despite extensive hybridization. *Molecular ecology* 20, 4983-4994.
- Marsteller, S., Adams, D.C., Collyer, M.L., and Condon, M. (2009). Six cryptic species on a single species of host plant: morphometric evidence for possible reproductive character displacement. *Ecological Entomology* 34, 66-73.
- Martin, C.H., Crawford, J.E., Turner, B.J., and Simons, L.H. (2016). Diabolical survival in Death Valley: recent pupfish colonization, gene flow and genetic assimilation in the smallest species range on earth. *Proceedings of the Royal Society B-Biological Sciences* 283: 10.*
- Martin, N.H., Bouck, A.C., and Arnold, M.L. (2006). Detecting adaptive trait introgression between *Iris fulva* and *I. brevicaulis* in highly selective field conditions. *Genetics* 172, 2481-2489.*
- Martin, S.H., and Jiggins, C.D. (2017). Interpreting the genomic landscape of introgression. *Current Opinion in Genetics & Development* 47, 69-74.
- Martinoli, A., Mazzamuto, M.V., and Spada, M. (2020). Serotine *Eptesicus serotinus* (Schreber, 1774). *Handbook of the Mammals of Europe*, 1-17.
- Martinsen, G.D., Whitham, T.G., Turek, R.J., and Keim, P. (2001). Hybrid populations selectively filter gene introgression between species. *Evolution; international journal of organic evolution* 55, 1325-1335.*
- Massey, S.E. (2017). Strong Amerindian Mitonuclear Discordance in Puerto Rican Genomes Suggests Amerindian Mitochondrial Benefit. *Annals of Human Genetics* 81, 59-77.*
- Matosiuk, M., Sheremetyeva, I.N., Sheremetyev, I.S., Saveljev, A.P., and Borkowska, A. (2014). Evolutionary neutrality of mtDNA introgression: evidence from complete mitogenome analysis in roe deer. *Journal of Evolutionary Biology* 27, 2483-2494.*
- Matusitz, J. (2012). Relationship between knowledge, stereotyping, and prejudice in interethnic communication. *PASOS Revista de Turismo y Patrimonio Cultural* 10, 89-98.

- Mavárez, J., Salazar, C.A., Bermingham, E., Salcedo, C., Jiggins, C.D., and Linares, M. (2006). Speciation by hybridization in *Heliconius* butterflies. *Nature* 441, 868-871.*
- Maxwell, C.S., Mattox, K., Turissini, D.A., Teixeira, M.M., Barker, B.M., and Matute, D.R. (2019). Gene exchange between two divergent species of the fungal human pathogen, *Coccidioides*. *Evolution; international journal of organic evolution* 73, 42-58.*
- Mayr, E. (1942). *Systematics and the Origin of Species.*, (Columbia University Press: New York, NY, USA).
- Mayr, E. (1963). *Animal species and evolution* (Harvard University Press).
- Mazzocchi, F. (2008). Complexity in biology. Exceeding the limits of reductionism and determinism using complexity theory. *EMBO Rep* 9, 10-14.
- McAshan, S.K., Vergin, K.L., Giovannoni, S.J., and Thaler, D.S. (1999). Interspecies recombination between enterococci: genetic and phenotypic diversity of vancomycin-resistant transconjugants. *Microbial drug resistance* (Larchmont, NY) 5, 101-112.*
- McCluskey, B.M., and Postlethwait, J.H. (2015). Phylogeny of Zebrafish, a "Model Species," within *Danio*, a "Model Genus". *Molecular Biology and Evolution* 32, 635-652.*
- McDonald, D.B., Clay, R.P., Brumfield, R.T., and Braun, M.J. (2001). Sexual selection on plumage and behavior in an avian hybrid zone: experimental tests of male-male interactions. *Evolution; international journal of organic evolution* 55, 1443-1451.*
- Meier, J.I., Sousa, V.C., Marques, D.A., Selz, O.M., Wagner, C.E., Excoffier, L., and Seehausen, O. (2017). Demographic modelling with whole-genome data reveals parallel origin of similar *Pundamilia* cichlid species after hybridization. *Molecular ecology* 26, 123-141.*
- Melo-Ferreira, J., Seixas, F.A., Cheng, E., Mills, L.S., and Alves, P.C. (2014). The hidden history of the snowshoe hare, *Lepus americanus*: extensive mitochondrial DNA introgression inferred from multilocus genetic variation. *Molecular ecology* 23, 4617-4630.*
- Melville, J. (2002). Competition and character displacement in two species of scincid lizards. *Ecology letters* 5, 386-393.
- Meyer, B.S., Matschiner, M., and Salzburger, W. (2017). Disentangling Incomplete Lineage Sorting and Introgression to Refine Species-Tree Estimates for Lake Tanganyika Cichlid Fishes. *Systematic Biology* 66, 531-550.*
- Meyer D, Dimitriadou E, Hornik K, Weingessel A, Leisch F (2012). e1071: Misc Functions of the Department of Statistics, Probability Theory Group (Formerly: E1071), TU Wien. <https://cran.r-project.org/web/packages/e1071/index.html>.
- Mims, M.C., Hulsey, C.D., Fitzpatrick, B.M., and Streelman, J.T. (2010). Geography disentangles introgression from ancestral polymorphism in Lake Malawi cichlids. *Molecular ecology* 19, 940-951.*

- Minder, A.M., and Widmer, A. (2008). A population genomic analysis of species boundaries: neutral processes, adaptive divergence and introgression between two hybridizing plant species. *Molecular ecology* 17, 1552-1563.*
- Mingo-Casas P, Sandoni's V, Obo'n E, Berciano JM, Vazquez-Moron S, Juste J, and Echevarría, J.E. (2018) First cases of European bat lyssavirus type 1 in Iberian serotine bats: Implications for the molecular epidemiology of bat rabies in Europe. *PLoS Negl Trop Dis* 12(4): e0006290.
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., and The, P.G. (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *PLOS Medicine* 6, e1000097.
- Mondal, M., Casals, F., Xu, T., Dall'Olio, G.M., Pybus, M., Netea, M.G., Comas, D., Laayouni, H., Li, Q., Majumder, P.P., and Bertranpetit J. (2016). Genomic analysis of Andamanese provides insights into ancient human migration into Asia and adaptation. *Nature Genetics* 48, 1066-1070.*
- Morales, H.E., Pavlova, A., Amos, N., Major, R., Kilian, A., Greening, C., and Sunnucks, P. (2018). Concordant divergence of mitogenomes and a mitonuclear gene cluster in bird lineages inhabiting different climates. *Nature Ecology & Evolution* 2, 1258-1267.*
- Morales, H.E., Sunnucks, P., Joseph, L., and Pavlova, A. (2017). Perpendicular axes of differentiation generated by mitochondrial introgression. *Molecular ecology* 26, 3241-3255.*
- Moran, B.M., Payne, C., Langdon, Q., Powell, D.L., Brandvain, Y., and Schumer, M. (2021). The genomic consequences of hybridization. *eLife* 10.
- Moran, P.A., Hunt, J., Mitchell, C., Ritchie, M.G., and Bailey, N.W. (2019). Behavioural mechanisms of sexual isolation involving multiple modalities and their inheritance. *Journal of Evolutionary Biology* 32, 243-258.
- Morange, M. (2001). *The misunderstood gene*. Cambridge: Harvard University Press.
- Morris, Z.S., Wooding, S., and Grant, J. (2011). The answer is 17 years, what is the question: understanding time lags in translational research. *Journal of the Royal Society of Medicine* 104, 510-520.
- Muirhead, C.A., and Presgraves, D.C. (2016). Hybrid Incompatibilities, Local Adaptation, and the Genomic Distribution of Natural Introgression between Species. *American Naturalist* 187, 249-261.*
- Muijres F.T., Johansson L.C., Winter Y. and Anders H. (2011). Comparative aerodynamic performance of flapping flight in two bat species using time-resolved wake visualization. *J. R. Soc. Interface*. 81418–1428.
- Müller, B., and Peichl, L. (2005). Retinal Cone Photoreceptors in Microchiropteran Bats. *Investigative Ophthalmology & Visual Science* 46, 2259-2259.

- Nadachowska-Brzyska, K., Zieliński, P., Radwan, J., and Babik, W. (2012). Interspecific hybridization increases MHC class II diversity in two sister species of newts. *Molecular ecology* 21, 887-906.*
- Nader, J.L., Mathers, T.C., Ward, B.J., Pachebat, J.A., Swain, M.T., Robinson, G., Chalmers, R.M., Hunter, P.R., van Oosterhout, C., and Tyler, K.M. (2019). Evolutionary genomics of anthroponosis in *Cryptosporidium*. *Nature microbiology* 4, 826-836.*
- Naisbit, R.E., Jiggins, C.D., and Mallet, J. (2003). Mimicry: developmental genes that contribute to speciation. *Evolution & Development* 5: 269-280.*
- Neri, J., Wendt, T., and Palma-Silva, C. (2017). Natural hybridization and genetic and morphological variation between two epiphytic bromeliads. *AoB PLANTS* 10.
- Neubaum, M.A., Douglas, M.R., Douglas, M.E., and O'Shea, T.J. (2007). Molecular Ecology of the Big Brown Bat (*Eptesicus fuscus*): Genetic and Natural History Variation in a Hybrid Zone. *Journal of Mammalogy* 88, 1230-1238.
- Ng, J., and Glor, R.E. (2011). Genetic differentiation among populations of a Hispaniolan trunk anole that exhibit geographical variation in dewlap colour. *Molecular ecology* 20, 4302-4317.*
- Ng, N.S.R., Wilton, P.R., Prawiradilaga, D.M., Tay, Y.C., Indrawan, M., Garg, K.M., and Rheindt, F.E. (2017). The effects of Pleistocene climate change on biotic differentiation in a montane songbird Glade from Wallacea. *Molecular phylogenetics and evolution* 114, 353-366.*
- Nicholls, B., and Racey, P. (2006). Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Ecography* 29, 697-708.
- Nichols, P., Genner, M.J., van Oosterhout, C., Smith, A., Parsons, P., Sungani, H., Swanstrom, J., and Joyce, D.A. (2015). Secondary contact seeds phenotypic novelty in cichlid fishes. *Proceedings of the Royal Society B-Biological Sciences* 282, 8.*
- Nolte, A.W., and Tautz, D. (2010). Understanding the onset of hybrid speciation. *Trends in Genetics* 26, 54-58.
- Norris, L.C., Main, B.J., Lee, Y., Collier, T.C., Fofana, A., Cornel, A.J., and Lanzaro, G.C. (2015). Adaptive introgression in an African malaria mosquito coincident with the increased usage of insecticide-treated bed nets. *Proceedings of the National Academy of Sciences of the United States of America* 112, 815-820.*
- Nosil, P., Parchman, T.L., Feder, J.L., and Gompert, Z. (2012). Do highly divergent loci reside in genomic regions affecting reproductive isolation? A test using next-generation sequence data in *Timema* stick insects. *Bmc Evolutionary Biology* 12, 12.*
- Novella-Fernandez, R., Ibañez, C., Juste, J., Clare, E.L., Doncaster, C.P., and Razgour, O. (2020). Trophic resource partitioning drives fine-scale coexistence in cryptic bat species. *Ecology and evolution* 10, 14122-14136.

- Novella-Fernandez, R., Juste, J., Ibáñez, C., Rebelo, H., Russo, D., Alberdi, A., Kiefer, A., Graham, L., Paul, H., Doncaster, C. P., & Razgour, O. (2021). Broad-scale patterns of geographic avoidance between species emerge in the absence of fine-scale mechanisms of coexistence. *Diversity and Distributions*, 27, 1606–1618.
- Nshom, E., and Croucher, S. (2017). Perceived threat and prejudice towards immigrants in Finland: A study among early, middle, and late Finnish adolescents. *Journal of International and Intercultural Communication* 10, 309-323.
- Ochoa-López, S., Damián, X., Rebollo, R., Fornoni, J., Domínguez, C.A., and Boege, K. (2020). Ontogenetic changes in the targets of natural selection in three plant defenses. *New Phytologist* 226, 1480-1491.
- O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., Gurevitch, J., Page, M.J., Stewart, G., Moher, D., et al. (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews* n/a.
- O'Brien, J., Devillard, S., Say, L., Vanthomme, H., Léger, F., Ruetten, S., and Pontier, D. (2009). Preserving genetic integrity in a hybridising world: are European Wildcats (*Felis silvestris silvestris*) in eastern France distinct from sympatric feral domestic cats? *Biodiversity and Conservation* 18, 2351-2360.
- Oliveira, R., Godinho, R., Randi, E., and Alves, P.C. (2008). Hybridization *versus* conservation: are domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*) in Iberian Peninsula? *Philosophical transactions of the Royal Society of London Series B, Biological sciences* 363, 2953-2961.
- Oliver, P., Castro, J.A., Picornell, A., Ramon, M.M., Solé, E., Balanyà, J., Serra, L., Latorre, A., and Moya, A. (2002). Linkage disequilibria between mtDNA haplotypes and chromosomal arrangements in a natural population of *Drosophila subobscura*. *Heredity* 89, 133-138.
- Olsson, M., and Madsen, T. (2001). Promiscuity in Sand Lizards (*Lacerta agilis*) and Adder Snakes (*Vipera berus*): Causes and Consequences. *Journal of Heredity* 92, 190-197.
- Okubo, Y. (1997). *Bibliometric Indicators and Analysis of Research Systems: Methods and Examples*. OECD Science, Technology and Industry Working Papers. No. 1997/01. OECD Publishing, Paris.
- Ottenburghs, J. (2021). The genic view of hybridization in the Anthropocene. *Evolutionary Applications* 14, 2342-2360.
- Ottenburghs, J., Megens, H.J., Kraus, R.H.S., van Hooft, P., van Wieren, S.E., Crooijmans, R., Ydenberg, R.C., Groenen, M.A.M., and Prins, H.H.T. (2017). A history of hybrids? Genomic patterns of introgression in the True Geese. *Bmc Evolutionary Biology* 17, 14.*

- Otto, S.P., and Barton, N.H. (2001). Selection for recombination in small populations. *Evolution; international journal of organic evolution* 55, 1921-1931
- Owens, G.L., and Samuk, K. (2020). Adaptive introgression during environmental change can weaken reproductive isolation. *Nature climate change* 10, 58.
- Paetzold, C., Wood, K.R., Eaton, D.A.R., Wagner, W.L., and Appelhans, M.S. (2019). Phylogeny of Hawaiian Melicope (Rutaceae): RAD-seq Resolves Species Relationships and Reveals Ancient Introgression. *Frontiers in plant science* 10, 1074.*
- Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, A.E., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P., and Moher, D. (2021). The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ: British Medical Journal* 372, n71.
- Page, M.J., Moher, D., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, A.E., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P., and McKenzie, J.E. (2021). PRISMA 2020 explanation and elaboration: updated guidance and exemplars for reporting systematic reviews. *BMJ: British Medical Journal* 372: n160.
- Page, M. (2012). *Wired for culture. The Natural History of Human Cooperation*. New York: Penguin Press.
- Palmer, D.H., and Kronforst, M.R. (2015). Divergence and gene flow among Darwin's finches: A genome-wide view of adaptive radiation driven by interspecies allele sharing. *Bioessays* 37, 968-974.
- Palmer, K.L., Kos, V.N., and Gilmore, M.S. (2010). Horizontal gene transfer and the genomics of enterococcal antibiotic resistance. *Current opinion in microbiology* 13, 632-639.
- Pardo-Diaz, C., Salazar, C., Baxter, S.W., Merot, C., Figueiredo-Ready, W., Joron, M., McMillan, W.O., and Jiggins, C.D. (2012). Adaptive Introgression across Species Boundaries in *Heliconius* Butterflies. *Plos Genetics* 8, 13.*
- Parrett, J.M., and Knell, R.J. (2018). The effect of sexual selection on adaptation and extinction under increasing temperatures. *Proceedings Biological sciences* 285.
- Paterson 1985 in Arnold M 1997. *Natural hybridization and evolution*. Oxford University Press.
- Paun, O., Turner, B., Trucchi, E., Munzinger, J., Chase, M.W., and Samuel, R. (2016). Processes Driving the Adaptive Radiation of a Tropical Tree (*Diospyros*, Ebenaceae) in New Caledonia, a Biodiversity Hotspot. *Systematic Biology* 65: 212-227.*

- Pauquet, G., Salzburger, W., and Egger, B. (2018). The puzzling phylogeography of the haplochromine cichlid fish *Astatotilapia burtoni*. *Ecology and Evolution* 8, 5637-5648.*
- Pavlova, A., Amos, J.N., Joseph, L., Loynes, K., Austin, J.J., Keogh, J.S., Stone, G.N., Nicholls, J.A., and Sunnucks, P. (2013). Perched at the mito-nuclear crossroads: divergent mitochondrial lineages correlate with environment in the face of ongoing nuclear gene flow in an Australian bird. *Evolution; international journal of organic evolution* 67, 3412-3428.
- Payseur, B.A., Krenz, J.G., and Nachman, M.W. (2004). Differential patterns of introgression across the X chromosome in a hybrid zone between two species of house mice. *Evolution; international journal of organic evolution* 58, 2064-2078.*
- Pease, J.B., Haak, D.C., Hahn, M.W., and Moyle, L.C. (2016). Phylogenomics Reveals Three Sources of Adaptive Variation during a Rapid Radiation. *PLoS biology* 14, 24.*
- Peris, D., Arias, A., Orlić, S., Belloch, C., Pérez-Través, L., Querol, A., and Barrio, E. (2017). Mitochondrial introgression suggests extensive ancestral hybridization events among *Saccharomyces* species. *Molecular phylogenetics and evolution* 108, 49-60.*
- Perry, M. (2019). Heatmaps: Flexible heatmaps for functional genomics and sequence features. R package version 1, 2020.2010.
- Pfeifer, B., and Kapan, D.D. (2019). Estimates of introgression as a function of pairwise distances. *BMC bioinformatics* 20, 207.*
- Pfennig, D.W., and Murphy, P.J. (2000). Character Displacement in Polyphenic Tadpoles. *Evolution; international journal of organic evolution* 54, 1738-1749.
- Pfennig, D. W., and Pfennig, K. S. (2010). Character Displacement and the Origins of Diversity. *The American Naturalist* 176, S26-S44.
- Pfennig, K.S. (2007). Facultative Mate Choice Drives Adaptive Hybridization. *Science (New York, NY)* 318, 965-967.*
- Pfennig, K.S. (2021). Biased Hybridization and Its Impact on Adaptive Introgression. *Trends in ecology & evolution* 36, 488-497.
- Plakhotniuk, N., Koruts, U., and Doroshenko, E. (2021). Constitutional restrictions on human rights and freedoms in the development of liberal democracy in Europe. *Access to justice in Eastern Europe* 129-143.
- Plutchik, R. (1962). *The emotions: facts, theories, and a new model*. New York: Random House.
- Poelstra, J.W., Richards, E.J., and Martin, C.H. (2018). Speciation in sympatry with ongoing secondary gene flow and a potential olfactory trigger in a radiation of Cameroon cichlids. *Molecular ecology* 27, 4270-4288.*
- Powell, J.R., Petrarca, V., della Torre, A., Caccone, A., and Coluzzi, M. (1999). Population structure, speciation, and introgression in the *Anopheles gambiae* complex. *Parassitologia* 41, 101-113.

- Pujolar, J.M., Jacobsen, M.W., Als, T.D., Frydenberg, J., Munch, K., Jonsson, B., Jian, J.B., Cheng, L., Maes, G.E., Bernatchez, L., and Hansen M.M. (2014). Genome-wide single-generation signatures of local selection in the panmictic European eel. *Molecular ecology* 23, 2514-2528.*
- Puschmann, C., and Powell, A. (2018). Turning Words Into Consumer Preferences: How Sentiment Analysis Is Framed in Research and the News Media. *Social Media + Society* 4: 2056305118797724.
- Quigley, K.M., Bay, L.K., and van Oppen, M.J.H. (2019). The active spread of adaptive variation for reef resilience. *Ecology and Evolution* 9, 11122-11135.*
- Quilodr  n, C.S., Montoya-Burgos, J.I., and Currat, M. (2020). Harmonizing hybridization dissonance in conservation. *Communications biology* 3, 391.
- Racimo, F., Gokhman, D., Fumagalli, M., Ko, A., Hansen, T., Moltke, I., Albrechtsen, A., Carmel, L., Huerta-Sanchez, E., and Nielsen, R. (2017). Archaic Adaptive Introgression in TBX15/WARS2. *Molecular Biology and Evolution* 34, 509-524.*
- Rambaut, A., Drummond, A., Xie, D., Baele, G., and Suchard, M. (2018). Copyedited by: YS Manuscript category: Software for Systematics and Evolution Software for Systematics and Evolution Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Systematic Biology* 67, 2.
- R  s  nen, K., and Hendry, A.P. (2008). Disentangling interactions between adaptive divergence and gene flow when ecology drives diversification. *Ecology letters* 11, 624-636.
- Ravinet, M., Yoshida, K., Shigenobu, S., Toyoda, A., Fujiyama, A., and Kitano, J. (2018). The genomic landscape at a late stage of stickleback speciation: High genomic divergence interspersed by small localized regions of introgression. *Plos Genetics* 14, 32.*
- Ray, N., and Excoffier, L. (2009). Inferring Past Demography Using Spatially Explicit Population Genetic Models. *Human Biology* 81, 141-157.*
- Razack, N. (1999). Anti-discriminatory practice: Pedagogical struggles and challenges. *British Journal of Social Work* 29, 231-250.
- Redgwell, R.D., Szewczak, J.M., Jones, G., and Parsons, S. (2009). Classification of Echolocation Calls from 14 Species of Bat by Support Vector Machines and Ensembles of Neural Networks. *Algorithms* 2, 907-924.
- Reid, N., Demboski, J.R., and Sullivan, J. (2012). Phylogeny Estimation of the Radiation of Western North American Chipmunks (*Tamias*) in the Face of Introgression Using Reproductive Protein Genes. *Systematic Biology* 61: 44-62.*
- Reidenbach, K.R., Neafsey, D.E., Costantini, C., Sagnon, N., Simard, F., Ragland, G.J., Egan, S.P., Feder, J.L., Muskavitch, M.A.T., and Besansky, N.J. (2012). Patterns of Genomic Differentiation between Ecologically Differentiated M and S Forms of *Anopheles gambiae* in West and Central Africa. *Genome Biology and Evolution* 4, 1202-1212.*

- Renaut, S., Grassa, C.J., Yeaman, S., Moyers, B.T., Lai, Z., Kane, N.C., Bowers, J.E., Burke, J.M., and Rieseberg, L.H. (2013). Genomic islands of divergence are not affected by geography of speciation in sunflowers. *Nature Communications* 4, 8.*
- Richards, E.J., and Martin, C.H. (2017). Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic adaptive radiation of trophic specialist pupfishes. *Plos Genetics* 13, 35.
- Rieseberg, L.H., Kim, S.-C., Randell, R.A., Whitney, K.D., Gross, B.L., Lexer, C., and Clay, K. (2007). Hybridization and the colonization of novel habitats by annual sunflowers. *Genetica* 129, 149-165.*
- Rieseberg, L.H., Raymond, O., Rosenthal, D.M., Lai, Z., Livingstone, K., Nakazato, T., Durphy, J.L., Schwarzbach, A.E., Donovan, L.A., and Lexer, C. (2003). Major Ecological Transitions in Wild Sunflowers Facilitated by Hybridization. *Science (New York, NY)* 301, 1211-1216.*
- Rieseberg, L.H., and Welch, M.E. (2002). Chapter 18 - Gene Transfer through Introgressive Hybridization: History, Evolutionary Significance, and Phylogenetic Consequences. In *Horizontal Gene Transfer (Second Edition)*, M. Syvanen, and C.I. Kado, eds. (London: Academic Press), 199-216.
- Rieseberg, L.H., Zona, S., Abernomb, L., and Martin, T.D. (1989). Hybridization in the island endemic, Catalina mahogany. *Conservation Biology* 3, 52-58.
- Rull, V. (2014). The most important application of science: As scientists have to justify research funding with potential social benefits, they may well add education to the list. *EMBO Rep* 15, 919-922.
- Runemark, A., Trier, C.N., Eroukmanoff, F., Hermansen, J.S., Matschiner, M., Ravinet, M., Elgvin, T.O., and Saetre, G.P. (2018). Variation and constraints in hybrid genome formation. *Nature Ecology & Evolution* 2, 549-556.*
- Ryan, S.F., Deines, J.M., Scriber, J.M., Pfrender, M.E., Jones, S.E., Emrich, S.J., and Hellmann, J.J. (2018). Climate-mediated hybrid zone movement revealed with genomics, museum collection, and simulation modeling. *Proceedings of the National Academy of Sciences of the United States of America* 115, E2284-E2291.*
- Sackton, T.B., Montenegro, H., Hartl, D.L., and Lemos, B. (2011). Interspecific Y chromosome introgressions disrupt testis-specific gene expression and male reproductive phenotypes in *Drosophila*. *Proceedings of the National Academy of Sciences* 108, 17046-17051.*
- Sáez, J.A., Galar, M., and Krawczyk, B. (2019). Addressing the Overlapping Data Problem in Classification Using the One-vs-One Decomposition Strategy. *IEEE Access* 7, 83396-83411.
- Saks, A., and Gary, J. (2012). Perception, Attribution, and Judgment of Others. *Organizational Behaviour: Understanding and Managing Life at Work* 7.

- Salazar, C., Baxter, S.W., Pardo-Diaz, C., Wu, G., Surridge, A., Linares, M., Bermingham, E., and Jiggins, C.D. (2010). Genetic Evidence for Hybrid Trait Speciation in *Heliconius* Butterflies. *PLOS Genetics* 6, e1000930.*
- Salazar, C., Jiggins, C.D., Taylor, J.E., Kronforst, M.R., and Linares, M. (2008). Gene flow and the genealogical history of *Heliconius heurippa*. *Bmc Evolutionary Biology* 8, 13.*
- Sandler, R. (2012). Intrinsic value. Ecology, and Conservation. *Nature Educational Knowledge* 3.
- Sankararaman, S. (2020). Methods for detecting introgressed archaic sequences. *Current opinion in genetics & development* 62, 85-90.
- Santana, S.E., Strait, S., and Dumont, E.R. (2011). The better to eat you with: functional correlates of tooth structure in bats. *Functional Ecology* 25, 839-847.
- Santos, H., Juste, J., Ibáñez, C., Palmeirim, J.M., Godinho, R., Amorim, F., Alves, P., Costa, H., de Paz, O., Pérez-Suarez, G., et al. (2014). Influences of ecology and biogeography on shaping the distributions of cryptic species: three bat tales in Iberia. *Biological Journal of the Linnean Society* 112, 150-162.
- Sarver, B.A.J., Demboski, J.R., Good, J.M., Forshee, N., Hunter, S.S., and Sullivan, J. (2017). Comparative Phylogenomic Assessment of Mitochondrial Introgression among Several Species of Chipmunks (*Tamias*). *Genome Biology and Evolution* 9, 7-19.*
- Scascitelli, M., Whitney, K.D., Randell, R.A., King, M., Buerkle, C.A., and Rieseberg, L.H. (2010). Genome scan of hybridizing sunflowers from Texas (*Helianthus annuus* and *H. debilis*) reveals asymmetric patterns of introgression and small islands of genomic differentiation. *Molecular ecology* 19, 521-541.*
- Schluter, D. (2000). Ecological Character Displacement in Adaptive Radiation. *The American Naturalist* 156, S4-S16.
- Schreber J. (1774). *Die Säugthiere in Abbildungen nach der Natur, mit Beschreibungen*. Erlangen - Expedition des Schreber'schen säugthier- und des Esper'schen Schmetterlingswerkes. Ernst Mayr Library of the MCZ, Harvard University, pp 1774 –1855.
- Schoen, J. (2005). *Choice & coercion: Birth control, sterilization, and abortion in public health and welfare* (Univ of North Carolina Press).
- Schultz, P.W., Nolan, J.M., Cialdini, R.B., Goldstein, N.J., and Griskevicius, V. (2007). The Constructive, Destructive, and Reconstructive Power of Social Norms. *Psychological Science* 18: 429-434.
- Schumer, M., Cui, R.F., Boussau, B., Walter, R., Rosenthal, G., and Andolfatto, P. (2013). An evaluation of the hybrid speciation hypothesis for *Xiphophorus clemenciae* on whole genome sequences. *Evolution; international journal of organic evolution* 67, 1155-1168.*
- Schumer, M., Cui, R.F., Powell, D.L., Rosenthal, G.G., and Andolfatto, P. (2016). Ancient hybridization and genomic stabilization in a swordtail fish. *Molecular ecology* 25, 2661-2679.*

- Seehausen, O. (2004). Hybridization and adaptive radiation. *Trends in ecology & evolution* 19, 198-207.
- Seixas, F.A., Boursot, P., and Melo-Ferreira, J. (2018). The genomic impact of historical hybridization with massive mitochondrial DNA introgression. *Genome Biology* 19, 91.*
- Semenov, G.A., Koblik, E.A., Red'kin, Y.A., and Badyaev, A.V. (2018). Extensive phenotypic diversification coexists with little genetic divergence and a lack of population structure in the White Wagtail subspecies complex (*Motacilla alba*). *Journal of Evolutionary Biology* 31: 1093-1108.*
- Shamseer, L., Moher, D., Clarke, M., Gherzi, D., Liberati, A., Petticrew, M., Shekelle, P., and Stewart, L.A. (2015). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015: elaboration and explanation. *BMJ: British Medical Journal* 349, g7647.
- Silvert, M., Quintana-Murci, L., and Rotival, M. (2019). Impact and Evolutionary Determinants of Neanderthal Introgression on Transcriptional and Post-Transcriptional Regulation. *American journal of human genetics* 104, 1241-1250.*
- Slager, D.L., Epperly, K.L., Ha, R.R., Rohwer, S., Wood, C., Van Hemert, C., and Klicka, J. (2020). Cryptic and extensive hybridization between ancient lineages of American crows. *Molecular ecology* 29, 956-969.*
- Song, Y., Endepols, S., Klemann, N., Richter, D., Matuschka, F.-R., Shih, C.-H., Nachman, Michael W., and Kohn, Michael H. (2011). Adaptive Introgression of Anticoagulant Rodent Poison Resistance by Hybridization between Old World Mice. *Current Biology* 21, 1296-1301.*
- Sonnby-Borgström, M., Jönsson, P., and Svensson, O. (2003). Emotional Empathy as Related to Mimicry Reactions at Different Levels of Information Processing. *Journal of Nonverbal Behavior* 27: 3-23.
- Soroka, S., Fournier, P., and Nir, L. (2019). Cross-national evidence of a negativity bias in psychophysiological reactions to news. *Proceedings of the National Academy of Sciences* 116: 18888.
- Sotola, V., Ruppel, D.S., Bonner, T.H., Nice, C.C., and Martin, N.H. (2019). Asymmetric introgression between fishes in the Red River basin of Texas is associated with variation in water quality. *Ecology and Evolution* 9, 2083-2095.*
- Soucy, S.M., Huang, J., and Gogarten, J.P. (2015). Horizontal gene transfer: building the web of life. *Nature Reviews Genetics* 16, 472-482.
- Stanovich, K.E., and West, R.F. (2008). On the relative independence of thinking biases and cognitive ability. *Journal of personality and social psychology* 94: 672-695.

- Staubach, F., Lorenc, A., Messer, P.W., Tang, K., Petrov, D.A., and Tautz, D. (2012). Genome patterns of selection and introgression of haplotypes in natural populations of the house mouse (*Mus musculus*). *PLoS Genet* 8, e1002891.*
- Stoeckl, N., Condie, S., and Anthony, K. (2021). Assessing changes to ecosystem service values at large geographic scale: A case study for Australia's Great Barrier Reef. *Ecosystem services* 51.
- Storchová, R., Gregorová, S., Buckiová, D., Kyselová, V., Divina, P., and Forejt, J. (2004). Genetic analysis of X-linked hybrid sterility in the house mouse. *Mammalian Genome* 15, 515-524.*
- Stryjewski, K.F., and Sorenson, M.D. (2017). Mosaic genome evolution in a recent and rapid avian radiation. *Nature Ecology & Evolution* 1, 1912.*
- Stuckas, H., Stoof, K., Quesada, H., and Tiedemann, R. (2009). Evolutionary implications of discordant clines across the Baltic *Mytilus* hybrid zone (*Mytilus edulis* and *Mytilus trossulus*). *Heredity* 103, 146-156.*
- Suarez-Gonzalez, A., Hefer, C.A., Christe, C., Corea, O., Lexer, C., Cronk, Q.C.B., and Douglas, C.J. (2016). Genomic and functional approaches reveal a case of adaptive introgression from *Populus balsamifera* (balsam poplar) in *P. trichocarpa* (black cottonwood). *Molecular ecology* 25, 2427-2442.*
- Suarez-Gonzalez, A., Hefer, C.A., Lexer, C., Cronk, Q.C.B., and Douglas, C.J. (2018a). Scale and direction of adaptive introgression between black cottonwood (*Populus trichocarpa*) and balsam poplar (*P.balsamifera*). *Molecular ecology* 27, 1667-1680.*
- Suarez-Gonzalez, A., Hefer, C.A., Lexer, C., Douglas, C.J., and Cronk, Q.C.B. (2018b). Introgression from *Populus balsamifera* underlies adaptively significant variation and range boundaries in *P.trichocarpa*. *New Phytologist* 217, 416-427.*
- Sullivan, A.R., Owusu, S.A., Weber, J.A., Hipp, A.L., and Gailing, O. (2016). Hybridization and divergence in multi-species oak (*Quercus*) communities. *Botanical Journal of the Linnean Society* 181, 99-114.*
- Sun, Y., Corcoran, P., Menkis, A., Whittle, C.A., Andersson, S.G.E., and Johannesson, H. (2012). Large-Scale Introgression Shapes the Evolution of the Mating-Type Chromosomes of the Filamentous Ascomycete *Neurospora tetrasperma*. *Plos Genetics* 8, 19.*
- Sung, C.J., Bell, K.L., Nice, C.C., and Martin, N.H. (2018). Integrating Bayesian genomic cline analyses and association mapping of morphological and ecological traits to dissect reproductive isolation and introgression in a Louisiana Iris hybrid zone. *Molecular Ecology* 27, 959-978.*
- Sykora, M., Elayan, S., and Jackson, T.W. (2020). A qualitative analysis of sarcasm, irony and related #hashtags on Twitter. *Big Data & Society* 7: 2053951720972735.
- Tahamtan, I., and Bornmann, L. (2020). Altmetrics and societal impact measurements: Match or mismatch? A literature review. *El profesional de la información* 29: e290102.

- Takahashi, H., and Takata, K. (2000). Multiple lineages of the mitochondrial DNA introgression from *Pungitius pungitius* (L.) to *Pungitius tymensis* (Nikolsky). *Canadian Journal of Fisheries and Aquatic Sciences* 57, 1814-1833.*
- Takahashi, H., Toyoda, A., Yamazaki, T., Narita, S., Mashiko, T., and Yamazaki, Y. (2017). Asymmetric hybridization and introgression between sibling species of the pufferfish *Takifugu* that have undergone explosive speciation. *Marine Biology* 164, 11.*
- Taylor AL, Dessai S, Bruine de Bruin W (2014). Public perception of climate risk and adaptation in the UK: A review of the literature. *Climate Risk Management* 4-5: 1-16.*
- Taylor, S.A., and Larson, E.L. (2019). Insights from genomes into the evolutionary importance and prevalence of hybridization in nature. *Nature Ecology & Evolution* 3, 170-177.
- Taylor, S.J., Arnold, M., and Martin, N.H. (2009). The genetic architecture of reproductive isolation in *Luisiana Irises*: Hybrid fitness in nature. *Evolution; international journal of organic evolution* 63, 2581-2594.*
- Temminck C.J. (1840). *Monographies de Mammologie, ou description de quelques genres de Mammifères, dont les espèces ont été observées dans les différents Musées de l'Europe* 2(302):26–70.
- Tene Fossog, B., Ayala, D., Acevedo, P., Kengne, P., Ngomo Abeso Mebuy, I., Makanga, B., Magnus, J., Awono-Ambene, P., Njiokou, F., and Pombi, M. (2015). Habitat segregation and ecological character displacement in cryptic African malaria mosquitoes. *Evololuitonary Applycations* 8, 326-345.
- Thorpe, R.S., Surget-Groba, Y., and Johansson, H. (2010). Genetic tests for ecological and allopatric speciation in anoles on an island archipelago. *PLOS Genetics* 6, e1000929.
- Todesco, M., Pascual, M.A., Owens, G.L., Ostevik, K.L., Moyers, B.T., Hübner, S., Heredia, S.M., Hahn, M.A., Caseys, C., Bock, D.G., et al. (2016). Hybridization and extinction. *Evolutionary Applications* 9, 892-908.
- Trigo, T.C., Schneider, A., de Oliveira, T.G., Lehugeur, L.M., Silveira, L., Freitas, T.R.O., and Eizirik, E. (2013). Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat. *Current Biology* 23, 2528-2533.*
- Trigo, T.C., Tirelli, F.P., de Freitas, T.R.O., and Eizirik, E. (2014). Comparative Assessment of Genetic and Morphological Variation at an Extensive Hybrid Zone between Two Wild Cats in Southern Brazil. *PloS one* 9, 15.*
- Trochim, W. (2010). Translation Won't Happen Without Dissemination and Implementation: Some Measurement and Evaluation Issues. 3rd Annual Conference on the Science of Dissemination and Implementation Bethesda, MD.
- Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., and Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports* 7: 9132.

- Turissini, D.A., and Matute, D.R. (2017). Fine scale mapping of genomic introgressions within the *Drosophila yakuba* clade. *Plos Genetics* 13, 40.*
- Tylanakis Jason, M. (2013). The Global Plight of Pollinators. *Science* 339, 1532-1533.
- Ulrik, B., and Faster, A. (2001). Algorithm for Betweenness Centrality. *Journal of Mathematical Sociology* 25(2): 163-177.
- Vaillant, J.J., Bock, D.G., Haffner, G.D., and Cristescu, M.E. (2013). Speciation patterns and processes in the zooplankton of the ancient lakes of Sulawesi Island, Indonesia. *Ecology and Evolution* 3, 3083-3094.*
- Vázquez-Moron, S., Juste, J., Ibáñez, C., Berciano, J.M., and Echevarria, J.E. (2011). Phylogeny of European bat Lyssavirus 1 in *Eptesicus isabellinus* bats, Spain. *Emerg Infect Dis* 17, 520-523.
- Vernot, B., Tucci, S., Kelso, J., Schraiber, J.G., Wolf, A.B., Gittelman, R.M., Dannemann, M., Grote, S., McCoy, R.C., Norton, H., et al. (2016). Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals. *Science* 352, 235-239.*
- Vicente, J.L., Clarkson, C.S., Caputo, B., Gomes, B., Pombi, M., Sousa, C.A., Antao, T., Dinis, J., Botta, G., Mancini, E., et al. (2017). Massive introgression drives species radiation at the range limit of *Anopheles gambiae*. *Scientific Reports* 7, 13.*
- vonHoldt, B.M., Kays, R., Pollinger, J.P., and Wayne, R.K. (2016). Admixture mapping identifies introgressed genomic regions in North American canids. *Molecular ecology* 25, 2443-2453.*
- Wade, M.J., and Goodnight, C.J. (2006). Cyto-nuclear epistasis: Two-locus random genetic drift in hermaphroditic and dioecious species. *Evolution; international journal of organic evolution* 60, 643-659.*
- Wadsworth, C.B., Li, X., and Dopman, E.B. (2015). A recombination suppressor contributes to ecological speciation in *OSTRINIA* moths. *Heredity* 114, 593-600.*
- Wald, G. (1954). The origin of life. *Scientific American* 191, 44-53.
- Walsh, J., Shriver, W.G., Olsen, B.J., and Kovach, A.I. (2016). Differential introgression and the maintenance of species boundaries in an advanced generation avian hybrid zone. *Bmc Evolutionary Biology* 16, 18.*
- Wang, D., Forstmeier, W., Valcu, M., Dingemanse, N.J., Bulla, M., Both, C., Duckworth, R.A., Kiere, L.M., Karell, P., Albrecht, T., et al. (2019). Scrutinizing assortative mating in birds. *PLoS biology* 17, e3000156.
- Wang, H.Y., Hsieh, C.H., Huang, C.G., Kong, S.W., Chang, H.C., Lee, H.H., Wang, W.K., Chen, S.L., Tzeng, H.Y., and Wu, W.J. (2013). Genetic and physiological data suggest demographic and adaptive responses in complex interactions between populations of figs (*Ficus pumila*) and their pollinating wasps (*Wiebesia pumilae*). *Molecular ecology* 22, 3814-3832.*
- Wang, X.-Q., and Ran, J.-H. (2014). Evolution and biogeography of gymnosperms. *Molecular phylogenetics and evolution* 75, 24-40.

- Wang, Z.I., Zhang, D.Y., and Wang, G. (2005). Does spatial structure facilitate coexistence of identical competitors? *Ecological Modelling* 181, 17-23.
- Ward, C.M., and Baxter, S.W. (2018). Assessing Genomic Admixture between Cryptic *Plutella* Moth Species following Secondary Contact. *Genome Biol Evol* 10, 2973-2985.*
- Weetman, D., Steen, K., Rippon, E.J., Mawejje, H.D., Donnelly, M.J., and Wilding, C.S. (2014). Contemporary gene flow between wild *An. gambiae* s.s. and *An. arabiensis*. *Parasites & Vectors* 7, 9.
- While, G.M., Michaelides, S., Heathcote, R.J.P., MacGregor, H.E.A., Zajac, N., Beninde, J., Carazo, P., Pérez i de Lanuza, G., Sacchi, R., Zuffi, M.A.L., Horváthová, T., Fresnillo, B., Schulte, U, Veith, M., Hochkirch, A., and Uller, T. (2015). Sexual selection drives asymmetric introgression in wall lizards. *Ecology letters* 18, 1366-1375.*
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686.
- Whitney, K.D., Broman, K.W., Kane, N.C., Hovick, S.M., Randell, R.A., and Rieseberg, L.H. (2015). Quantitative trait locus mapping identifies candidate alleles involved in adaptive introgression and range expansion in a wild sunflower. *Molecular ecology* 24, 2194-2211.*
- Willis, S.C., Macrander, J., Farias, I.P., and Orti, G. (2012). Simultaneous delimitation of species and quantification of interspecific hybridization in Amazonian peacock cichlids (genus *cichla*) using multi-locus data. *Bmc Evolutionary Biology* 12, 24.*
- Winter, Y., López, J., and von Helversen, O. (2003). Ultraviolet vision in a bat. *Nature* 425, 612-614.
- Worthington-Wilmer, J., & Barratt, E. (1996). A non-lethal method of tissue sampling for genetic studies of chiropterans. *Bat Research News*, 37(1), 1-4.
- Wybouw, N., Pauchet, Y., Heckel, D.G., and Van Leeuwen, T. (2016). Horizontal Gene Transfer Contributes to the Evolution of Arthropod Herbivory. *Genome Biology Evolution* 8, 1785-1801.
- Xia, J., Guo, Z., Yang, Z., Han, H., Wang, S., Xu, H., Yang, X., Yang, F., Wu, Q., Xie, W., et al. (2021). Whitefly hijacks a plant detoxification gene that neutralizes plant toxins. *Cell* 184, 1693-1705.e1617.
- Xue, H.J., Li, W.Z., and Yang, X.K. (2014). Assortative mating between two sympatric closely-related specialists: inferred from molecular phylogenetic analysis and behavioral data. *Scientific Reports* 4, 5436.
- Yair, S., Lee, K.M., and Coop, G. (2021). The timing of human adaptation from Neanderthal introgression. *Genetics* 218.
- Yang, C.H., Li, Y.D., Liu, C., and Yuan, X.R. (2019). Deep learning-based viewpoint recommendation in volume visualization. *Journal of visualization* 22: 991-1003.

- Yang, W.Z., While, G.M., Laakkonen, H., Sacchi, R., Zuffi, M.A.L., Scali, S., Salvi, D., and Uller, T. (2018). Genomic evidence for asymmetric introgression by sexual selection in the common wall lizard. *Molecular ecology* 27, 4213-4224.*
- Yu, G., Smith, D.K., Zhu, H., Guan, Y., and Lam, T.T.Y. (2017). ggtree: an r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* 8, 28-36.
- Zhang, W., Dasmahapatra, K.K., Mallet, J., Moreira, G.R.P., and Kronforst, M.R. (2016). Genome-wide introgression among distantly related *Heliconius* butterfly species. *Genome Biology* 17, 15.*
- Zhang, W., Kunte, K., and Kronforst, M.R. (2013). Genome-Wide Characterization of Adaptation and Speciation in Tiger Swallowtail Butterflies Using De Novo Transcriptome Assemblies. *Genome Biology and Evolution* 5, 1233-1245.*

*Papers included in the systematic review and analysed through meta-analysis in Chapters 2, 3 and 4 (195 of 358 papers).

Appendix A

Paper Proofs

What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception

Horta P., Raposeira H., Vaz A.S., António J., Juste J., Razgour O. & Rebelo H. (submitted). What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception. *Scientific reports*. DOI: 10.21203/rs.3.rs-1041127/v1

De: Scientific Reports

Enviado: 11 de novembro de 2021 12:38

Para: pedro.horta@cibio.up.pt

Assunto: Scientific Reports - Receipt of Manuscript 'What about Adaptive...'

Ref: Submission ID c85dfd9d-c754-4caf-bc74-899519e4ba9a

Dear Dr Horta,

Thank you for submitting your manuscript to Scientific Reports.

Your manuscript is now at our initial Quality Check stage, where we look for adherence to the journal's submission guidelines, including any relevant editorial and publishing policies. If there are any points that need to be addressed prior to progressing we will send you a detailed email. Otherwise, your manuscript will proceed into peer review.

You can check on the status of your submission at any time by using the link below and logging in with the account you created for this submission:

https://researcher.nature.com/your-submissions?utm_source=submissions&utm_medium=email&utm_campaign=confirmation-email&journal_id=41598

Kind regards,

Peer Review Advisors
Scientific Reports

Springer Nature offers an open access support service to make it easier for our authors to discover and apply for APC funding. For further information please visit <http://www.springernature.com/gp/open-research/funding>



Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception

Pedro Horta (✉ pedro.horta@cibio.up.pt)

CIBIO/InBIO University of Porto <https://orcid.org/0000-0003-0715-8559>

Helena Raposeira

CIBIO/InBIO University of Porto

Ana Sofia Vaz

CIBIO/InBIO University of Porto

João António

Portuguese Catholic University <https://orcid.org/0000-0001-5142-4258>

Javier Juste

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas

Orly Razgour

University of Southampton <https://orcid.org/0000-0003-3186-0313>

Hugo Rebelo

CIBIO/InBIO University of Porto

Article

Keywords: Adaptive introgression, Genetic miscegenation, Perception, Sentiment analysis, Systematic review

Posted Date: November 11th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-1041127/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

1 **What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific**
2 **and Public Perception**

3
4
5 **ABSTRACT**

6 Genetic miscegenation was historically perceived as a maladaptive process or even an
7 imperfection of nature. However, through adaptive introgression, some species can
8 share genes associated with well-adapted traits. Current scientific perceptions on the
9 benefits of adaptive introgression can help to clarify how these paradoxes condition
10 scientific progress and influence public beliefs and decision-making. We carried out a
11 systematic review and bibliometric analysis using artificial intelligence on adaptive
12 introgression evidence. The genomic revolution provided an exponential growing of
13 evidence predominately interpreted as beneficial for species adaptation. We show that
14 this remarkable increase on publications influences public perception in the medium-
15 long term. Despite an initially emotional response, peoples' final opinion tends to
16 incorporate science-based evidence, although prejudices seem to influence peoples'
17 polarity opinion. We argue that developing the knowledge on adaptive introgression
18 will allow to scientifically refute theories that promote genetic "purity", used to justify
19 racism and other forms of discrimination.

20
21 **KEYWORDS**

22 Adaptive introgression, Genetic miscegenation, Perception, Sentiment analysis,
23 Systematic review

24

25 **1 | INTRODUCTION**

26 Introgression can be a key evolutionary mechanism allowing species to incorporate
 27 portions of the genome of another species through vertical gene transfer (Anderson
 28 and Hubricht, 1938, Arnold and Kunte, 2017). Through repeated interbreeding a
 29 species can receive genes from another species, eventually resulting in fitness changes
 30 (Cahill *et al.* 2015, Djogbénou *et al.* 2008, Enciso-Romero *et al.* 2017, Gagnaire *et al.*
 31 2009) - a natural evolutionary phenomenon known as adaptive introgression (Pfennig,
 32 2021). Methodological developments through High-Throughput Sequencing and
 33 bioinformatics approaches led to an increase in the scientific evidence for the spread
 34 of adaptive introgression (Pfeifer and Kapan, 2019, Taylor and Larson, 2019) across
 35 different geographic areas (Brower, 2018, Giska *et al.* 2019, Ma *et al.* 2019, Morales *et*
 36 *al.* 2018, Suarez-Gonzalez *et al.* 2018b) and taxonomic groups (Maddamsetti and
 37 Lenski, 2018, Maxwell *et al.* 2019, Nader *et al.* 2019, Paetzold *et al.* 2019, Silvert *et al.*
 38 2019). It is not always the case that introgressed populations have an adaptive
 39 advantage derived from introgression (Harris and Nielsen, 2016). However, when it
 40 does occur, they can potentially jump to a new adaptive optimum, thus surpassing
 41 intermediate evolutionary steps (Ballerini *et al.* 2012).

42 Several studies recognise adaptive introgression as beneficial for species fitness
 43 (Acosta and Premoli, 2018, Aeschbacher *et al.* 2017, Hohmann and Koch, 2017, Horn *et*
 44 *al.* 2018, Lehnert *et al.* 2019, Ma *et al.* 2019, Paun *et al.* 2016, Semenov *et al.* 2018).

45 Possible reasons for the benefit of introgression are the potential of adaptive
 46 introgression for promoting individual survival (Hejase and Liu, 2016, Norris *et al.*
 47 2015), range expansion (Whitney *et al.* 2015), species divergence (Morales *et al.* 2017),
 48 evolutionary rescue (Quigley *et al.* 2019) and adaptive radiation (Poelstra *et al.* 2018,

49 Zhang *et al.* 2016). Additionally, there is multiple evidence of advanced-generation
 50 hybrids whose backcrosses exhibit adaptive traits beyond the ancestral phenotypic
 51 range (DiBattista *et al.* 2016, Salazar *et al.* 2008, Scascitelli *et al.* 2010), sometimes
 52 leading to hybrid speciation (Aleksic *et al.* 2018, Brower, 2018). This is a strong
 53 argument to support that gene flow between sympatric lineages (species, population,
 54 breeds, etc.) may represent an adaptive strategy for survival under extreme
 55 environmental conditions (Hamlin and Arnold, 2012, Martin *et al.* 2016, Martin *et al.*
 56 2006, Suarez-Gonzalez *et al.* 2018a).
 57 On the other hand, introgression has been historically understood as a homogenizing
 58 process (Latch *et al.* 2006, Oliveira *et al.* 2008), which can influence the long-term
 59 viability of species through genetic swamping (Maguilla *et al.* 2017). Some scientists
 60 argue that interspecific gene flow may counteract local selection pressures, decreasing
 61 the fitness of diverging populations by introducing alleles from outside the local
 62 adaptive range (outbreeding depression; Bolnick and Nosil, 2007, García-Ramos and
 63 Kirkpatrick, 1997, Maguilla *et al.* 2017). Moreover, other scientists considered natural
 64 hybridization as a violation of species integrity, a maladaptive process or an
 65 unexpected imperfection of Nature (Llopart *et al.* 2014, Lowe *et al.* 2015).
 66 These contrasting views reveal a controversy over the merits of adaptive introgression.
 67 In fact, a number of studies have already suggested that philosophical and cultural
 68 background may be behind the negative prejudices of the scientific community
 69 towards natural hybridization (Arnold *et al.* 2012). Paterson (1985) highlights such
 70 prejudice even in terms of semantics noticing how appreciative are “words such as
 71 “pure”, “purebred”, “thoroughbred” and how pejorative are those like “mongrel”,
 72 “bastard”, “half-breed” or “hybrid” with the role of ‘protecting the integrity of

species". Assessing scientific perception of the benefits of genetic miscegenation through adaptive introgression is important for better understanding which factors, beyond scientific evidence, condition scientific progress. Bias in perceptions of the merits of genetic miscegenation directly or indirectly influences fields like conservation biology (Biermann and Mansfield, 2014, Chan *et al.* 2019, Genovart, 2008), animal husbandry/agriculture (Henkel *et al.* 2019), human relations and social policies (Bethencourt, 2013, Baker, 2016, Fredrickson, 2002).

In animal husbandry and agricultural production the demand for pure variants, with the most desirable traits, is nowadays seen as development and progress (Henkel *et al.* 2019). Paradoxically, although the promotion of genetic variation is a key conservation goal (Chan *et al.* 2019), the protection of pure lineages/species remains at the forefront of conservation priorities (Biermann and Mansfield, 2014, Genovart, 2008).

From a social point of view, biases against genetic miscegenation were historically manifested through policies promoting forced sterilizations, segregation, direct medical killings and lab experiments in human beings (Schoen, 2005), as well as anti-miscegenation laws, prohibiting marriage between people from different "races" (Baker, 2016).

Understanding both scientific and public perception of the evidence for adaptive introgression is essential for determining how the evidence can shape public opinion and emotions towards genetic miscegenation (Damasio and Carvalho, 2013) and how it can influence decision makers (politicians, conservationists, lobbyists, human rights organizations, etc.).

However, inferences of perception patterns about scientific facts are nowadays particularly hard to obtain due to the growing amount of scientific publications and the

97 huge number of opinions derived therefrom that circulate in official documents and
98 conventional and social media. Conventional approaches for obtaining scientific data
99 about perceptions, such as social surveys, can be costly and time-consuming, especially
100 when targeting large audiences and broad spatial and temporal coverages. These
101 approaches can also be difficult to implement because they assume an active process
102 with strong subjectivity bias, namely due to perceivers' experience, motivation and
103 how they are feeling when processing the information (Sacks and Gary, 2012, Dange,
104 2016). This is particularly evident in the phenomenon of "perceptual defence",
105 whereby perceivers only see what they expect to see to support their own beliefs
106 (Christianson *et al.* 2017).

107 To help overcome these limitations, artificial Intelligence (AI) tools, and specifically
108 deep learning techniques, have been increasingly adopted to analyse large amounts of
109 online data (Yang *et al.* 2019). Deep learning relies on mathematical algorithms
110 endowing machines with intelligent behaviour to learn patterns and adapt such
111 learning processes to new data. By doing so, deep learning algorithms gain the ability
112 to automatically process and identify similarities between patterns of digital
113 information, such as texts or images (Yang *et al.* 2019). In the case of textual data,
114 sentiment analysis has become a promising technique to analyse the polarity of
115 written sentences or words as positive, negative or neutral (Ainin *et al.* 2020). When
116 supported by robust data and adequate meaning, sentiment analysis can serve as a
117 proxy to verbal behaviour, attitudes, and emotions, which are useful for understanding
118 the perceptions and opinions of writers about different topics (Ainin *et al.* 2020).

119 Here, we aim to understand the extent to which adaptive introgression has been
120 receiving attention in scientific literature and the way the scientific community and the

public perceive scientific discoveries relating to adaptive introgression. Specifically, we aim to answer the following questions: (1) What is the scope and evolution of knowledge about adaptive introgression? (2) What do the scientific community and general public think about adaptive introgression? (3) Which sentiments can be triggered in the public as a reaction to evidence of adaptive introgression? Based on our findings we suggest avenues for fostering progress of adaptive introgression and adjust its course in Evolutionary Biology.

2 | METHODS

2.1 | APPROACH

To answer our research questions, we first carried out a systematic review to retrieve all published scientific literature on adaptive introgression and respective bibliographic meta-data. Then, we adopted a series of bibliometric analyses to understand the taxonomic coverage, geographic patterns, and temporal evolution of the retrieved literature. Additionally, we used salience analysis grounded on citation indices and attention scores, to understand the popularity level of the different studies among the scientific community and the public. Finally, we analysed the prevalence, polarity and relevance of adaptive introgression based on the perceptions from the authors of those studies, as well as the sentiment of the public towards this body of knowledge.

2.2 | SYSTEMATIC REVIEW

Following standard PRISMA systematic review protocols (Moher *et al.* 2009, O'Dea *et al.* 2021, Page *et al.* 2020), we carried out a systematic literature search for studies that explored the adaptive and evolutionary potential of natural introgression. We used ISI Web of Knowledge, Scopus, Google and Google Scholar, as the main search engines (Falagas *et al.* 2008). We used a combination of search terms relating to

145 natural hybridization, genome, introgression and adaptation, avoiding the ones related
146 to domestication and exotic/invasive species, with the aim of restricting the search
147 only to natural phenomena of genomic introgression with potential adaptive
148 outcomes, excluding all processes under direct or indirect human interference
149 (breeding manipulations, genetic manipulation, invasive species scenarios, etc.). The
150 selection of keywords was based on a review of previous keywords from a list of
151 reference papers, and under a participatory approach with a team of scientists
152 specialised in evolutionary processes. The final list of keywords included the most
153 common and unambiguous words to reach the largest number of publications on the
154 subject (see search details in supplemental materials for the full list of keywords). The
155 timespan of our search was 1900-2019. Searches were carried out in November 2019
156 and were restricted to English.

157 Our initial search yielded 820 documents. After removing duplicates from the dataset,
158 we excluded non-original studies, theoretical essays, opinion pieces, non-peer-
159 reviewed papers, off-topic documents and non-indexed papers. Then we checked their
160 reference list to search for other publications that included the terms under study (i.e.
161 snow-ball effect). Finally, after excluding all reviews and book chapters, we screened
162 the title and abstract of the remaining 436 articles individually to evaluate their
163 eligibility for the analysis, namely: 1) if the papers complied with the natural origin for
164 the adaptive introgression process and 2) if adaptive introgression was pointed by the
165 authors as the main explanation for the biological processes under study. The final
166 dataset included 358 relevant studies (webfigure 1; Supplemental materials). All
167 papers were analysed in full only by the first author.

We extracted bibliographic information from the 358 studies. Each study was then reviewed to extract information on authors' initial perception about introgression and the temporal epoch and spatial location of the introgression phenomena reported in the study. We noted information on the taxa undergoing the introgression process. Finally, we reviewed which main method was considered in the publication, including the type of experiment, the type of introgression markers and whether whole-genome sequencing was performed or not. Detailed information about the variables extracted is available in table S1.

2.3 | BIBLIOMETRIC ANALYSIS

Geographic and taxonomic patterns in the published literature

To investigate the associations between the geographical origin of researchers, the location of their case studies and the targeted taxonomic group, we used a spatial bipartite association network built using the GeoLayout 0.9.2.2. plugin from Gephi (<https://gephi.org/>) (scale of 20.000). We identified the main regions of origin of the introgression scientific study and the most important case studies based on their node weight (number of papers). Based on the betweenness centrality metric, we placed particular attention on nodes representing case studies that were studied by several teams. This approach measures the influence of a case study over the flow of the scientific information used to find the ones that serve as a bridge between research teams (Ulrik and Faster, 2001).

Temporal changes in publication, methods and research areas

Temporal changes in the number of published papers were tested through General Linear Models (GLM) with temporal series projections (until 2030) by the Expert Modeler Methods available on IBM SPSS Statistics software (v. 22; SPSS Inc, Chicago,

192 IL). This approach was complemented with a linear regression, assessed through the
 193 coefficient of determination, between the number of published papers and time as a
 194 function of the methods used and research areas. We defined as the tipping point the
 195 temporal moment when the exponential trend lines ceased to show a reduced slope
 196 (Maroco, 2010).

197 **2.4 | SALIENCE ANALYSIS**

198 We searched in June 2020 each paper title in Altmetric Explorer, the web-based
 199 platform available through Altmetric.com which allows to browse and report the
 200 attention data that each paper has been receiving through online media (others
 201 include mainstream media mentions, peer reviews and citations to research in policy
 202 documents) (Tahamtan and Bornmann, 2020). Data included citations count and
 203 Altmetric Attention Score (AAS) (global and in context) recorded for each one of the
 204 358 papers included in the review, including their geographical breakdown and
 205 temporal trends (Tahamtan and Bornmann, 2020). To determine the scientific
 206 relevance currently attributed to adaptive introgression, measured from the attention
 207 it is given, first we examined if paper AAS correlate with citation count (a traditional
 208 bibliometric indicator for research systems) (Okubo 1997) using Spearman correlation
 209 analysis. We then analysed AAS and compared: 1) all papers published in the same
 210 year and journal, 2) all papers published in the same year, 3) all papers published in
 211 the same journal and 4) all research outputs scored by Altmetric.com (28,900,000
 212 outputs).

213 **2.5 | SENTIMENT ANALYSIS**

214 *Perceptions of scientists*

215 We obtained the data on the perceptions of scientists directly from the systematic
216 review, namely the scientific area of the study, the authors' polarity opinion about
217 adaptive introgression and the arguments used to justify it. We performed a Multi-
218 Dimensional Scaling (MDS) tripartite network analysis with Gephi ThirdParties Plugins
219 v. 0.9.2, to quantify the extent of known connections between these variables. The
220 final layout represents the distance between nodes based on the similarities of their
221 attributes, namely their connections' weight and connected nodes' identity. We chose
222 the network metrics "node weight", "edges weight" and "node degree" to describe the
223 main characteristics of the perception network (Algorithmics Group, 2009). Node
224 weight, symbolised by node size, represents the total number of papers from each
225 scientific area with similar authors' perception about adaptive introgression. Edge
226 weight, symbolised by edge thickness, represents the total number of papers on which
227 a connected pattern between two opinion characteristics simultaneously occurs. Node
228 degree measures the number of relationships between nodes. Nodes with high degree
229 have many connections, suggesting that they may possess strong supporting
230 arguments. All metrics were obtained directly from Gephi platform (Algorithmics
231 Group, 2009).

232 We performed a temporal analysis of authors' perceptions of natural adaptive
233 introgression in relation to changes in the amount of scientific evidence over time. We
234 applied a distributed-lag model that is a dynamic model in which the effect of an x on y
235 regression occurs over time, and not all at once. This modelling framework is useful to
236 analyse variable associations in time series data even if data are non-linear and/or with
237 delayed effects (DLNMs-distributed lag non-linear models) (Gasparrini, 2011). This
238 approach is based on 'cross-basis', defined by a bi-dimensional space of functions that

239 describe simultaneously the temporal relationship across the space of a predictor and
240 the delay of its occurrence (Gasparrini, 2011). Thus, DLNMs analysis relies on a
241 combination of these two sets of functions specifying the relationship between the
242 dimensions of the number of scientific evidence and time lags, allowing to establish an
243 immediate or delayed cause and effect relationship in the response variable (e.g.
244 authors' prevalence perception – from "Very rare" to "Ubiquitous"). All DLNM analyses
245 were executed in the *dlm* R package (Gasparrini, 2011).

246 *Public perceptions*

247 We considered the target public as a group of people broader than the scientific
248 community, who show their interest in adaptive introgression through citation,
249 reference, opinion and/or comment. We analysed 11,650 mentions by the public of
250 the 358 adaptive introgression papers. The mentions, over multiple websites and
251 different online platforms were mainly downloaded from Altmetric.com. Regarding
252 twitter's mentions (from the social media network Twitter), the data exported from
253 Altmetric.com only included the tweet's ID for an individual tweet. We obtained access
254 to Twitter's Developer Portal, and taking this information into a Twitter API, we got
255 access to each message. Finally, we used Postman software
256 (<https://www.postman.com/>) to get the link from Twitter API and the Power BI
257 Desktop software (<https://powerbi.microsoft.com/>) to get the final published tweets
258 table of each adaptive introgression paper. Our approach complies with the Terms of
259 Use and Developer Policy of the platform. All information extracted was anonymous or
260 threatened as confidential in respect to the General Data Protection Regulation (GDPR)
261 from EU Regulation 2016/679. To perform the sentiment analysis based on lexicons,
262 we uploaded each paper's mentions table into the *syuzhet* R package (Jockers, 2015).

263 This package measures polarity (Positive, Negative or Neutral) and identifies eight
 264 different emotions, when present, for each message. It follows the basic emotion
 265 theory proposed by Plutchik (Plutchik, 1962): Anger, Anticipation, Disgust, Joy, Fear,
 266 Sadness, Surprise and Trust.

267 We standardized the differences between Positive and Negative mentions of each
 268 paper using the following formula:

$$269 \quad stPP = \frac{Pos - Neg}{TotalMentions}$$

270 Where:

271 “stPP” represents the Standardized Polarity Perception,

272 “Pos” represents the total number of positive mentions,

273 “Neg” represents the total number of negative mentions,

274 “TotalMentions” represents the total mentions obtained by an individual paper.

275 We then performed a temporal analysis of public polarity perception (stPP) of adaptive
 276 introgression as a function of temporal changes in the number of scientific evidence of
 277 its occurrence through DLNMs analysis. Lastly, we followed the same approach to
 278 analyse the temporal changes in public emotions that adaptive introgression studies
 279 raise in public opinion as a function of temporal changes in the amount of scientific
 280 evidence for its occurrence.

281 Finally, to understand whether public opinion and the emotions that a scientific paper
 282 about adaptive introgression elicits are conditioned by the taxonomic group under
 283 study, we established the relationship between global polarity perceptions and public
 284 emotions for each taxonomic group under study. To illustrate this relationship, a chord
 285 diagram was produced using the Circlize R package (Gu, *et al.* 2014). This diagram was
 286 complemented with a linear regression, assessed through the coefficient of

determination, between the standardized polarity perception of the public and scientists for each taxonomic group under study in each paper as a function of the phylogenetic distance from humans (Maroco, 2010).

3 | RESULTS

3.1 | The scope and evolution of knowledge about adaptive introgression

Our systematic review showed that adaptive introgression studies were mainly carried out by researchers from North America (>50%) (Especially USA – with 167 published works) and Europe (>30%), with the remaining regions showing very few research teams working on adaptive introgression (figure S1). The scientific knowledge covered case studies from multiple geographic areas: North America (28% of all case studies), Europe (19%), Africa (12%), Asia (9%), South America (8%), Central America (7%), Oceania (4%), Eurasia (4%), global (3%), Pacific Ocean (2%), Atlantic Ocean (1%) and Indian Ocean (1%) (figure 1a).

The spatial bipartite association network showed a geographical proximity between case studies and research teams of 56.7%, meaning that most studies were performed by teams from the same geographical region (figure 1a, table S2). There was also a strong association between the taxa studied and the geographic origin of the research teams (figure S2). In North America, plants represented almost half of all studies (48%), especially angiosperms (38%). In Central and South America, invertebrates were the most represented taxa (43% and 48%, respectively), followed by birds (24%) and angiosperms (26%). Similarly, in Africa invertebrates represented 58% of all studies, followed by fish (21%). In Europe, like in North America, angiosperms were the most represented taxa (33%), but most studies focused on animals (63%). In Asia, mammals (36%), followed by fish (22%), were the most represented taxa, whereas in Oceania

311 and Pacific islands all taxa had similar representation (angiosperms: 20%, birds: 20%,
 312 mammals: 16%, reptiles: 12% and insects: 12%) (figure S2).
 313 Globally, adaptive introgression has been demonstrated in a wide range of taxa since
 314 Bacteria (1%), Protists (<1%), Fungi (3%) and Plants (27%) until Animals (69%).
 315 Mammals were the most studied taxonomic groups with 34% of all studies, followed
 316 by angiosperms (84% of plant studies) and insects (27% of all animals). Yeast
 317 represented 67% of studies of adaptive introgression in Fungi.

318

319 *Temporal evolution of the adaptive introgression literature*

320 We observed only a few studies published during the 20th century, with the highest
 321 prevalence in the 1990s, which saw an increase in published evidence for adaptive
 322 introgression, particularly from botanical controlled experimental studies involving the
 323 use of quantitative trait locus (QTL). A slight increase in the number of publications
 324 between 2000 and 2012 was observed alongside the rising of Methodological
 325 developments from the Human Genome project (<https://www.genome.gov/>).
 326 The increased publication rate from 2012 was accompanied by a methodological
 327 revolution due to the generalization of genomic approaches, mainly through the
 328 advent of high throughput sequencing (HTS) and the use of Whole-Genome
 329 Sequencing and Single Nucleotide Polymorphisms (SNPs). These techniques proved to
 330 be effective in detecting cost-efficient way genomic areas under introgression and
 331 their adaptive value. Increasing in an exponential way through time (GLM_SNPs
 332 [family="poisson"]: $R^2=0.80$, $p<0.05$, GLM_Whole-Genome [family="poisson"]:
 333 $R^2=0.76$, $p<0.05$), these techniques also contributed significantly to an exponential
 334 growth of adaptive introgression knowledge, which is evident by the cumulative

number of published papers over time (GLM_Total Number of Papers
[family="poisson"]: $R^2=0.94$, $p<0.05$) (figure 1b).
This growth pattern was evident in the different scientific fields (Anthropology,
Phylogeny/Genealogy, Plant Sciences, etc.), and particularly in Evolutionary Biology.
Bioinformatics was also identified as an emerging important field that became
prevalent since 2016 (figure 1c) (Pfeifer and Kapan, 2019).
The genomic revolution in adaptive introgression studies began in 2012, when the
annual average of published papers increased from 1.9 ± 3.1 (1966-2011) to $34.5 \pm$
 10.1 (2012-2019), equating to an average annual increase of 1824.14% of papers ($X^2_1=$
 97.37 , $p<0.01$). Temporal series projections, following the current publication growth
rates, demonstrated an annual publication rate reaching 130 papers/year in 2030 (95%
CI: 100-155) (figure S3).

3.2 | Perceptions of scientists

Our results showed that 12 different scientific areas have been exploring adaptive
introgression. The authors of 78% of the studies (N=280 papers) presented a
scientifically grounded opinion about this topic. The argument polarity results show
that the great majority of the authors had a positive opinion on adaptive introgression
(node weight = 164). These results are mainly supported by authors' perceptions about
the positivity of the impact of introgression on species' "adaptation to changing/new
environmental conditions" (edges' weight = 143), a result influenced by studies in the
scientific areas of Plant Sciences (edges' weight = 51) and Anthropology (edges' weight
= 30). However, most of the studies were carried out in Evolutionary Biology (node
weight = 140), where authors presented the greatest number of biological arguments
to support the sense of the polarity of their opinions (node degree = 45), which were

359 mainly positive (edges' weight = 67) (figure 2a). Negative arguments were derived
 360 mainly from Evolutionary Biology (edges' weight = 9.0), Plant Sciences (edges' weight =
 361 6.0) and Anthropology (edges' weight = 4.0). The main negative argument presented
 362 is that introgression may "act against speciation" (figure 2a).
 363 The total number of positive and negative arguments was similar (N = 24 and N = 20,
 364 respectively) even though in the total number of mentions, the latter were significantly
 365 lower (N = 296 and N = 78, respectively). Authors who presented mixed arguments
 366 (positive and negative) tended to use the greatest number of biological arguments
 367 (node degree = 56, betweenness = 1113.37) (figure 2a).
 368 Analysing the interest of the scientific community in the topic, we found a strong
 369 relationship between Altmetric.com scores and the traditional citation metrics (GLM
 370 [family="poisson"]: $R^2=0.72$, $p<0.05$) (figure S4). The position of adaptive introgression
 371 papers in relation to the Altmetric.com score when analysed in comparison with all
 372 papers published in the same year, in the same journal, in both simultaneously and,
 373 especially, when analysed in relation to all published literature, revealed a bimodal
 374 distribution (figure 2b). Although some studies have received little attention, a quarter
 375 of the papers were within the top 5% of the most cited and commented papers
 376 globally.
 377 There was no clear relationship between the temporal increase in the number of
 378 papers providing evidence for adaptive introgression and authors' prevailing
 379 perception (GLM [family="Gaussian"]: $R^2=0.04$, NS) (figure S5). The overall cumulative
 380 exposure-response relationships based on DMNL models revealed a slightly positive
 381 impact of the amount of evidence on author's perception about the prevalence of

adaptive introgression (DLMN: $R^2=0.08$, NS) from “unknown” (0) to “few cases” (1) after a rate of 20 paper/year (95% CI: infrequent [-1] – common [2]) (figure S6).

3.3 | Public perception and sentiment

A total of 14,214 mentions were recorded between 2000 and 2019 (including shares). Of these, 11,650 mentions were of adaptive introgression papers expressing some kind of opinion (polarity, emotions or both). The source of the vast majority of mentions was Social Media (N=11,628) followed by News and Blogs (N= 2,193) from traditional on-line newspapers. Academic sources were infrequently mentioned (N=145). Policy and Patents documents showed limited interest in the topic (N=24). The overall cumulative exposure–response relationships, summing up the contributions for the 20 years of lag considered in the analysis, showed a tendency for scientific publications to have just a slightly positive impact on public opinion of adaptive introgression with polarity perception reaching 0.1 after a rate of 20 papers/year (95% CI: - 0.2 – 0.2) (figure 3b). However, this impact does not seem to be immediate and presents a reversal of trend (from negative to positive) approximately following a delay of 7 years (figure 3c). A temporal analysis showed that the increase in the amount of evidence for adaptive introgression has nearly no immediate impact on public polarity perception (figure 3a). It occurs with a delay that promotes a high positive effect of scientific publications on the positivity of public opinion, increasing exponentially with high number of papers. However, there is almost no effect on public opinion from a reduced number of annually published papers, even after considering the delay (figure 3).

The publication of a large number of scientific papers had an immediate emotional public response (both negative and positive). After that, people's emotions began to

406 immediately and exponentially diminish over time (figures S7, S8, S9 and S10). Of the
 407 9,867 mentions recorded that expressed some kind of emotions, with positive
 408 emotions being more frequent than negative ones (especially trust (N=1958 mentions),
 409 followed by anticipation (N=1,581 mentions) and surprise (N=1,314 mention). Anger
 410 (N=825 mentions) was the least evoked emotion by the papers. In contrast, fear
 411 (N=1,111 mentions) and disgust (N = 960 mentions) were the most often expressed
 412 negative emotions (figure 4b).
 413 This disparity between positive and negative emotions explained the greater number
 414 of mentions by expressing a global positive polarity about adaptive introgression
 415 (N=4,179 mentions). However, often the interest in the topic was not accompanied by
 416 a clear position on the orientation of the opinion, so neutral mentions were slightly
 417 higher than positive mentions (N=4,440 mentions, figure 4b). On the other hand, there
 418 was a disparity in the attention given by the public when comparing the mentions
 419 about papers on vertebrates (N=8,850 mentions - including Humans - the majority of
 420 mentions [N=4,654]) with all the other taxonomic groups (figure 4b).
 421 The distribution of mentions by the different emotions and directions of polarity that
 422 the papers raise in the public followed the same pattern as their total number (more
 423 positive than negative) (figure 4b). However, in all taxonomic groups and in the global
 424 studies about adaptive introgression, scientists held more positive opinions about
 425 adaptive introgression than the general public ($F_{(1, 10)} = 54.260$, $p < 0.05$) (figure 4a).
 426 Finally, contrary to what happens within the scientific community (GLM
 427 [family="poisson"]: $R^2 = 0.13$, NS), the polarity of public opinion (although always
 428 positive) has a positive correlation with the phylogenetic distance from modern human
 429 beings (GLM [family="poisson"]: $R^2 = 0.86$, $p < 0.05$). In other words, the more distant

430 from humans the phenomenon occurs, the more people consider adaptive
431 introgression to be positive (figure 4a).

432 **4 | DISCUSSION**

433 **4.1 | Scope and evolution of knowledge about adaptive introgression**

434 The geographical scope of taxa under study is widespread, despite a slight tendency
435 for geographical proximity between case studies and research teams. This shows that
436 there have been no major geographical biases in adaptive introgression studies.

437 Scientific interest in adaptive introgression has been increasing over the past two
438 decades. However, since 2012 the number of papers published per year began to
439 increase exponentially. This turning point marks the beginning of the genomic
440 revolution in adaptive introgression studies. Most likely, it occurred in response to the
441 increased use of whole genome sequencing and reduced representation genome
442 sequencing methods, such as restriction-site associated sequencing (RADseq), and the
443 development of new high throughput sequencing platforms and the subsequent
444 reduction in sequencing costs (Hayden, 2014). The cost per sequenced genome was
445 dropped from US \$3 billion to less than US \$1,000 from 2000 to 2012 (Hayden, 2014).
446 These methodological and sequencing advances have enabled the scientific
447 community to compare the genomes of a large number of individuals, thus increasing
448 the probability of identifying shared genomic regions under selection (Kuhlwilm *et al.*
449 2019, Ryan *et al.* 2018). Our temporal series models predicted that this trend will
450 continue through the next decade (figure S3, Supplemental material) in response to
451 the growing interest in the topic and the widespread use and development of these
452 genomic analysis tools and sequencing platforms.

453 **4.2 | What do we think about adaptive introgression?**

454 Adaptive introgression has received considerable attention from both the scientific
455 community and the public, with high average rankings compared to the total current
456 scientific literature. Several papers ranked within the top 5% most cited and
457 commented papers globally.

458 Despite the exponential increase in scientific evidence since 2012, the genomic
459 revolution does not seem to have changed authors' perception of the prevalence of
460 adaptive introgression in nature, being frequently underestimated with authors citing
461 difficulties in demonstrating its presence (Reid *et al.* 2012). In terms of polarity in the
462 opinions of the scientific community about adaptive introgression, the total number of
463 positive and negative arguments is rather balanced. However, positive arguments are
464 clearly most mentioned among scientists. Authors' perception of whether the impact
465 of introgression on species was positive is mainly based on potentially beneficial
466 outcomes for "species adaptation to changing/new environmental conditions" (Acosta
467 and Premoli, 2018, Boratynski *et al.* 2014, Hamilton *et al.* 2013, Lewontin and Birch,
468 1966, Melo-Ferreira *et al.* 2014). The main negative argument put forward by scientists
469 is that adaptive introgression may have negative impacts because it "acts against
470 speciation" (Naisbit *et al.* 2003, Payseur *et al.* 2004).

471 The source of public opinion about adaptive introgression studies was dominated by
472 social media (and mainly Twitter), followed at great distance by traditional on-line
473 newspapers. Academic media sources and policy documents infrequently refer to
474 adaptive introgression papers, showing limited interest in the topic. This seems to
475 indicate that there is a much greater interest among the general public in the subject
476 than the importance given to it by traditional media and institutions both in terms of
477 dissemination and socio-political orientations.

478 The increased number of papers providing scientific evidence for adaptive
479 introgression led to marked increase in positive public opinion, however, only
480 following a seven year delay. There was either no initial response or even an initial
481 negative impact on people's perception. Empirical literature refers to the difficulties of
482 investigating research phases impacting on society (Trochim, 2010). On some
483 occasions, delay of scientific translation should be necessary to ensure the accuracy
484 and efficacy of new evidence or advances (Morris *et al.* 2011). However, it is relatively
485 accepted by both the scientific community and policy that quick translation of research
486 into practice is somehow positive (Morris *et al.* 2011). Nevertheless, the research
487 translation process is known to undergo long periods of time-lag (Kilbourne *et al.* 2020,
488 Morris *et al.* 2011).

489 Our results demonstrate that only the annual publication of a sufficiently large number
490 of papers providing evidence for adaptive introgression influences public perception of
491 its merits and consequently of genetic miscegenation. This trend of increase in positive
492 opinions is probably to accentuate in the future if the number of publications on the
493 topic will continue to increase exponentially up to at least 2030, as we have predicted.

494 For all taxonomic groups, and overall in studies of adaptive introgression, there is a
495 significant disparity between the opinions of scientists and the general public, whereby
496 scientists hold more positive opinions. This disparity between the opinions of scientists
497 and the public follows the trend of other studies on public perception about
498 scientifically controversial topics, such as the origin of climate change and the risks of
499 nuclear power (Taylor *et al.* 2014).

500 There is a taxonomic bias revealed by the great disparity in the attention given by the
501 public to papers on vertebrates (mainly on humans) compared to all other taxonomic

groups (Troudet *et al.* 2017). Regardless, papers referring to all taxonomic groups frequently receive positive opinions from the public, mostly eliciting positive emotions (primarily anticipation and trust). The polarity of public opinion (although always positive) positively relates to the phylogenetic distance from human beings, whereby the more distant the taxa are from humans, the more people consider adaptive introgression as positive. This pattern can be explained by different degrees of bias in the perception about genetic miscegenation according to taxonomy once societal inclinations strongly correlate with taxonomic bias (Troudet *et al.* 2017). Groups phylogenetically closer to human beings are the target of greater attention and importance whereas they are simultaneously the target of higher degrees of prejudice (Troudet *et al.* 2017). Bias has the potential to inappropriately influence the scientific process (Fanelli *et al.* 2017) because “scientists are human beings rooted in cultural contexts” (Gould, 1978). However, the scientific method usually shield scientists from the consequences of their own cultural biases (Lewis *et al.* 2011).

4.3 | Public sentiment in response to evidence of adaptive introgression

Scientific work in psychology has pointed to the relevance of emotions in addition to cognition in public perception and decision-making (Kahneman, 2011, Stanovich and West, 2008a). The publication of a large amount of scientific evidence for adaptive introgression has an immediate increasing effect on the emotional public response (both negative and positive). People's emotions rise immediately and diminish exponentially over time, showing an intense, but temporary, emotional cascade. The first reaction responds to an intuitive mode of thought that is fast, involves limited judgement, and is driven by emotions. It is later replaced by an analytical mode of thought (based on evidence), which is more rational, slower, involving more effort and

526 deliberate reasoning (Kahneman and Frederick, 2002). This replacement over time can
527 help explain the increase in positive polarity in the medium-long term. Time-lag helps
528 to clarify this change in the mode of thought, from instinctive to analytical (Whitmarsh,
529 2011), once emotion based reactions decrease over time (Taylor *et al.* 2014).

530 The overall cumulative exposure–response relationships of all sentiments expressed by
531 public mentions about adaptive introgression papers, summing up the contributions
532 for the 20 years of lag considered and analysing their balance with the increase of
533 scientific evidence published over time, show just a slightly positive impact on the
534 expression of all positive emotions (mainly anticipation and joy). According to the
535 probabilistic sequence of events involved in the development of an emotion,
536 anticipation responds to stimulus events like "novelty" promoting the behaviour of
537 examining and the effect of exploration whereas joy explains the pride of achievement
538 (Izard, 2007). This means that the increase in evidence outweighs the potential
539 negative effect of time on people's positive emotional response, allowing them to
540 experience the urge to learn more about the benefits of genetic miscegenation and
541 taking from there the pride of discovery.

542 However, the same trend happened for two negative emotions (disgust and fear).
543 Disgust is a response to a "gruesome object" and promotes rejection whereas fear
544 explains flight for safety in response to an "obstacle" and stimulates destructive
545 feelings (Izard, 2007). Despite occurring to a lesser extent compared to positive
546 emotions, paradoxically, the increase in evidence, by offsetting the negative effect of
547 time, raises a slight increase in some people in the identification of genetic
548 miscegenation as being susceptible to repugnance. It stimulates looking at it as an
549 obstacle to their safety and boosting reactions of rejection and destructive opinions.

550 In contrast, the increasing number of papers over time influences negatively public
551 emotions of sadness and anger. Sadness responds to stimulus events like a "life-
552 changing loss" promoting the effect of reintegration, whereas anger explains the
553 frustration in response to blocked goals (Izard, 2007). In both cases, the increase in
554 evidence complements the effect of time in decreasing such reactions to genetic
555 miscegenation.

556 The individual proximity to the facts under evaluation, derived from personal
557 experience or shared by mimicry, conditions the emotions that are expressed. For
558 example, social groups that have experienced the effects of extreme weather events
559 (e.g. wildfires or severe droughts) tend to experience higher levels of anger, sadness
560 and fear when confronted with climate change issues (Loureiro and Alló, 2020). In
561 contrast, groups that have never been confronted with the consequences of nuclear
562 accidents tend to have higher levels of trust in nuclear energy (Loureiro and Alló,
563 2020).

564 On the other hand, studies show that ignorance is at the root of stereotypes and
565 prejudice (Matusitz, 2012) and that these influence negative emotions like disgust and
566 fear (Dasgupta *et al.* 2009), which can only be countered by high degree of
567 communication (Matusitz, 2012, Nshom and Croucher, 2017). However, the emotions
568 also vary according to the signal of potential threat. For example, disgust increases bias
569 against homosexuality, but anger did not. Instead, anger increased bias against ethnic
570 minorities (e.g. Arabs) in western societies, but disgust did not (Dasgupta *et al.* 2009).

571 In this context, genetic miscegenation is more susceptible to prejudice derived from
572 disgust than anger.

Overall, public interest in adaptive introgression leads to an immediate rise of different emotional reactions that increase with increasing number of scientific evidence on the topic. Immediately after that emotional response, a cascade of divergent opinions spreads by emotional contagion and mimicry among social groups (Ferrara and Yang, 2015, Sonnby-Borgström *et al.* 2003) due to different social norms and circumstances of the common identities they share within (Pagel, 2012). However, negative emotions are potentially oversized because reactions to negative news tend to be stronger (Soroka *et al.* 2019).

4.4 | Caveats and limitations

The impact of scientific developments on society is often difficult to measure mainly because data on perception of scientific facts are hard to obtain and work with. Using algorithms like those employed by Altmetric.com, it is possible to compile and organise all information available online about a set of papers retrieved from a systematic search of a scientific subject. When analysing such a large amount of data, the relevance of subjectivity decreases when the intention is to find general trends. Still, even approaches designed to mimic and replace the human brain still have important limitations. In sentiment analysis, for example, there are still limitations in the interpretation of forms of literary expression, such as irony or sarcasm (Sykora *et al.* 2020). However, recent studies showed that the percentage of sarcastic and ironic content in social media is normally very low (Sykora *et al.* 2020). In traditional media and official documents their use should be even lower. So, in large datasets, sarcasm, irony and even the use of humour may be much less of a concern than was previously thought (Puschmann and Powell, 2018). Given that these expressions are probably

596 rare in the dataset covered in our study, this is unlikely to influence the results of the
597 general trends.

598 We assume that written mentions are behaviours that reflect the opinions or attitudes
599 of the writer. Yet, opinion is usually associated with a certain degree of subjective
600 judgment (Sacks and Gary, 2012). On the other hand, the subjectivity of individual
601 judgment is also subject to conflicts with social norms, political and cultural contexts
602 (Dange, 2016). In other words, we could see a change in social behaviour (such as the
603 proportional increase in positive mentions about adaptive introgression) due to a
604 potential change in social norms (e.g. greater tolerance or acceptance/appreciation of
605 genetic miscegenation) derived from the increase in the number of scientific evidence,
606 but it may still not mean that beliefs and/or mentalities are in fact being changed
607 (Schultz *et al.* 2007). Therefore, it seems probably that the publication of a large
608 amount of scientific evidence in the medium-long term has promoted a change in
609 opinion polarity about adaptive introgression and consequently about genetic
610 miscegenation after undergoing an initial emotional response and a certain degree of
611 rejection. However, whether this can promote an effective change in people's
612 mentality and beliefs will require further studies.

613 **4.5 | CONCLUSIONS**

614 We show that the genomic revolution provided mounting evidence for adaptive
615 introgression, which is mainly understood by the scientific community as particularly
616 beneficial for species ability to adapt to changing or new environmental conditions.
617 Scientific evidence suggests that adaptive introgression, or even genetic
618 miscegenation, from a scientific point of view, represents a key natural evolutionary
619 process. The exponential increase in scientific evidence for the beneficial effects of

620 genetic miscegenation led to more positive public perception of the topic in the
 621 medium-long term. Therefore, we argue that continuing the development of
 622 knowledge on adaptive introgression will allow Evolutionary Biology to scientifically
 623 refute eugenics and other evolutionary theories that promote taxa 'purity'. In the past,
 624 these ideas were employed to justify racism and other forms of discrimination.
 625 However, in light of current scientific evidence, only bias in perception appears to
 626 stand in the way of accepting the fundamental role that genetic miscegenation plays
 627 for life.

628

629 **REFERENCES**

- 630 Acosta MC, Premoli AC 2018. Understanding the extensive hybridization in South
 631 American *Nothofagus* through karyotype analysis. *Botanical Journal of the Linnean*
 632 *Society* 188: 74-86.
- 633 Aeschbacher S, Selby JP, Willis JH, Coop G 2017. Population-genomic inference of the
 634 strength and timing of selection against gene flow. *Proceedings of the National*
 635 *Academy of Sciences of the United States of America* 114: 7061-7066.
- 636 Ainin S, Feizollah A, Anuar NB, Abdullah NA 2020. Sentiment analyses of multilingual
 637 tweets on halal tourism. *Tourism Management Perspectives* 34: 8.
- 638 Akkuratov EE, Gelfand MS, Khrameeva EE 2018. Neanderthal and Denisovan ancestry in
 639 Papuans: A functional study. *Journal of Bioinformatics and Computational Biology*
 640 16: 12.
- 641 Aleksic JM, Skondric S, Lakusic D 2018. Comparative phylogeography of capitulate
 642 *Campanula* species from the Balkans, with description of a new species, *C-*
 643 *daucoides*. *Plant Systematics and Evolution* 304: 549-575.
- 644 Algorithmics Group 2009. MDSJ: Java Library for Multidimensional Scaling (Version 0.2).
 645 Available at <http://www.inf.uni-konstanz.de/algo/software/mdsj/>. University of
 646 Konstanz.

- 647 Anderson E, Hubricht L 1938. Hybridization in *Tradescantia*. III. The evidence for
648 introgressive hybridization. *American Journal of Botany* 25: 396-402.
- 649 Arnold ML, Ballerini ES, Brothers AN, Hamlin JAP, Ishibashi CDA, Zuellig MP 2012. The
650 genomics of natural selection and adaptation: Christmas past, present and
651 future(?). *Plant Ecology & Diversity* 5: 451-456.
- 652 Arnold ML, Kunte K 2017. Adaptive Genetic Exchange: A Tangled History of Admixture
653 and Evolutionary Innovation. *Trends in ecology & evolution* 32: 601-611.
- 654 Baker N 2016. Eugenics and Racial Hygiene: The Connections between the United States
655 and Germany". Student Theses, Papers and Projects (History). 67.
656 <http://digitalcommons.wou.edu/his/67>.
- 657 Ballerini ES, Brothers AN, Tang SX, Knapp SJ, Bouck A, Taylor SJ, Arnold ML, Martin NH
658 2012. QTL mapping reveals the genetic architecture of loci affecting pre- and post-
659 zygotic isolating barriers in Louisiana Iris. *Bmc Plant Biology* 12: 12.
- 660 Bethencourt F 2013. Racisms – From the Crusades to the Twentieth Century. Princeton
661 University Press.
- 662 Biermann C, Mansfield B 2014. Biodiversity, Purity, and Death: Conservation Biology as
663 Biopolitics. *Environment and Planning D: Society and Space* 32: 257-273.
- 664 Bolnick DI, Nosil P 2007. Natural selection in populations subject to a migration load.
665 *Evolution; international journal of organic evolution* 61: 2229-2243.
- 666 Boratynski Z, Melo-Ferreira J, Alves PC, Berto S, Koskela E, Pentikainen OT, Tarroso P,
667 Ylilauri M, Mappes T 2014. Molecular and ecological signs of mitochondrial
668 adaptation: consequences for introgression? *Heredity* 113: 277-286.
- 669 Brower AVZ 2018. Alternative facts: a reconsideration of putatively natural interspecific
670 hybrid specimens in the genus *Heliconius* (Lepidoptera: Nymphalidae). *Zootaxa*
671 4499: 1-87.
- 672 Cahill JA, Stirling I, Kistler L, Salamzade R, Ersmark E, Fulton TL, Stiller M, Green RE,
673 Shapiro B 2015. Genomic evidence of geographically widespread effect of gene flow
674 from polar bears into brown bears. *Molecular ecology* 24: 1205-1217.
- 675 Chan WY, Hoffmann AA, van Oppen MJH. 2019. Hybridization as a conservation
676 management tool. *Conservation Letters* 12: e12652.
- 677 Christianson K, Zhou PY, Palmer C, and Raizen A 2017. Effects of context and individual
678 differences on the processing of taboo words. *Acta Psychologica* 178: 73-86.

- 679 Dange J 2016. Perception, passion and obsession: The three elements of theory of
680 success. *International Journal of Advanced Education and Research*. 7: 01-03.
- 681 Damasio A, Carvalho GB 2013. The nature of feelings: evolutionary and neurobiological
682 origins. *Nature reviews Neuroscience* 14: 143-152.
- 683 Dasgupta N, Desteno D, Williams LA, Hunsinger M 2009. Fanning the flames of prejudice:
684 the influence of specific incidental emotions on implicit prejudice. *Emotion*
685 (Washington, DC) 9: 585-591.
- 686 DiBattista JD, Whitney J, Craig MT, Hobbs JPA, Rocha LA, Feldheim KA, Berumen ML,
687 Bowen BW 2016. Surgeons and suture zones: Hybridization among four surgeonfish
688 species in the Indo-Pacific with variable evolutionary outcomes. *Molecular*
689 *Phylogenetics and Evolution* 101: 203-215.
- 690 Djogbénou L, Chandre F, Berthomieu A, Dabiré R, Koffi A, Alout H, Weill M 2008.
691 Evidence of introgression of the ace-1(R) mutation and of the ace-1 duplication in
692 West African *Anopheles gambiae* s. s. *PloS one* 3: e2172.
- 693 Enciso-Romero J, Pardo-Díaz C, Martín SH, Arias CF, Linares M, McMillan WO, Jiggins CD,
694 Salazar C 2017. Evolution of novel mimicry rings facilitated by adaptive introgression
695 in tropical butterflies. *Molecular ecology* 26: 5160-5172.
- 696 Epstein S 1994. Integration of the cognitive and the psychodynamic unconscious. *The*
697 *American psychologist* 49: 709-724.
- 698 Falagas ME, Pitsouni EI, Malietzis GA, Pappas G 2008. Comparison of PubMed, Scopus,
699 Web of Science, and Google Scholar: strengths and weaknesses. *The FASEB Journal*
700 22: 338-342.
- 701 Fanelli D, Costas R, Ioannidis JPA 2017. Meta-assessment of bias in science. *Proceedings*
702 *of the National Academy of Sciences* 114: 3714-3719.
- 703 Ferrara E, Yang Z 2015. Measuring Emotional Contagion in Social Media. *PloS one* 10:
704 e0142390.
- 705 Fredrickson GM 2002. *Racism - A Short History*, REV - Revised edn. Princeton University
706 Press.
- 707 Gagnaire PA, Albert V, Jonsson B, Bernatchez L 2009. Natural selection influences AFLP
708 intraspecific genetic variability and introgression patterns in Atlantic eels. *Molecular*
709 *ecology* 18: 1678-1691.

- 710 García-Ramos G, Kirkpatrick M 1997. Genetic models of adaptation and gene flow in
711 peripheral populations. *Evolution; international journal of organic evolution* 51: 21-
712 28.
- 713 Gasparrini A 2011. Distributed Lag Linear and Non-Linear Models in R: The Package
714 dlnm. *Journal of statistical software* 43: 1-20.
- 715 Genovart M 2008. Natural hybridization and conservation. *Biodiversity and*
716 *Conservation* 18: 1435.
- 717 Giska I, Farelo L, Pimenta J, Seixas FA, Ferreira MS, Marques JP, Miranda I, Letty J, Jenny,
718 H, Hackländer K, Magnussen E, Melo-Ferreira J 2019. Introgression drives repeated
719 evolution of winter coat color polymorphism in hares. *Proceedings of the National*
720 *Academy of Sciences of the United States of America* 116: 24150-24156.
- 721 Gould SJ 1978. Morton's ranking of races by cranial capacity. Unconscious manipulation
722 of data may be a scientific norm. *Science (New York, NY)* 200: 503-509.
- 723 Green RE, Krause J, Briggs AW, Maricic T, Stenzel U, Kircher M, Patterson ., Li H, Zhai W,
724 Fritz MHY, et al. 2010. A Draft Sequence of the Neandertal Genome. *Science (New*
725 *York, NY)* 328: 710-722.
- 726 Gu Z, Gu L, Eils R, Schlesner M, Brors B 2014. Circlize implements and enhances circular
727 visualization in R. *Bioinformatics*, 30: 2811-2812.
- 728 Hamilton JA, Lexer C, Aitken SN 2013. Genomic and phenotypic architecture of a spruce
729 hybrid zone (*Picea sitchensis* P. *glauca*). *Molecular ecology* 22: 827-841.
- 730 Hamlin JAP, Arnold ML 2014. Determining population structure and hybridization for
731 two iris species. *Ecology and Evolution* 4: 743-755.
- 732 Harris K, Nielsen R 2016. The Genetic Cost of Neanderthal Introgression. *Genetics* 203:
733 881-891.
- 734 Hayden EC 2014. Technology: The \$1,000 genome. *Nature* 507: 294-295.
- 735 Hejase HA, Liu KJ 2016. Mapping the genomic architecture of adaptive traits with
736 interspecific introgressive origin: a coalescent-based approach. *Bmc Genomics* 17:
737 17.
- 738 Henkel J, Saif R, Jagannathan V, Schmocker C, Zeindler F, Bangerter E, Herren U,
739 Posantzis D, Bulut Z, Ammann P, Drögemüller C, Flury C, Leeb T 2019. Selection
740 signatures in goats reveal copy number variants underlying breed-defining coat
741 color phenotypes. *PLOS Genetics* 15: e1008536.

- 742 Hohmann N, Koch MA 2017. An Arabidopsis introgression zone studied at high spatio-
 743 temporal resolution: interglacial and multiple genetic contact exemplified using
 744 whole nuclear and plastid genomes. *Bmc Genomics* 18: 18.
- 745 Horn RL, Marques AJD, Manseau M, Golding B, Klutsch CFC, Abraham K, Wilson PJ 2018.
 746 Parallel evolution of site-specific changes in divergent caribou lineages. *Ecology and*
 747 *Evolution* 8: 6053-6064.
- 748 Izard CE 2007. Basic Emotions, Natural Kinds, Emotion Schemas, and a New Paradigm.
 749 *Perspectives on Psychological Science* 2: 260-280.
- 750 Jockers ML 2015. Syuzhet: Extract Sentiment and Plot Arcs from Text.
 751 <https://github.com/mjockers/syuzhet>.
- 752 Kahneman D 2011. Thinking, fast and slow. Macmillan.
- 753 Kahneman D, Frederick S 2002. Representativeness revisited: Attribute substitution in
 754 intuitive judgment. In *Heuristics and biases: The psychology of intuitive judgment*
 755 (New York, NY, US). Cambridge University Press.
- 756 Kilbourne AM, Glasgow RE, Chambers DA 2020. What Can Implementation Science Do
 757 for You? Key Success Stories from the Field. *Journal of General Internal Medicine*
 758 35: 783-787.
- 759 Kuhlwilm M, Han S, Sousa VC, Excoffier L, Marques-Bonet T 2019. Ancient admixture
 760 from an extinct ape lineage into bonobos. *Nature Ecology & Evolution* 3: 957-965.
- 761 Latch EK, Harveson LA, King JS, Hobson MD, Rhodes JR 2006. Assessing Hybridization in
 762 Wildlife Populations Using Molecular Markers: A Case Study in Wild Turkeys. *The*
 763 *Journal of Wildlife Management* 70: 485-492.
- 764 Lehnert SJ, Bentzen P, Kess T, Lien S, Horne JB, Clément M, Bradbury IR 2019.
 765 Chromosome polymorphisms track trans-Atlantic divergence and secondary
 766 contact in Atlantic salmon. *Molecular ecology* 28: 2074-2087.
- 767 Lewis JE, Degusta D, Meyer MR, Monge JM, Mann AE, Holloway RL 2011. The
 768 mismeasure of science: Stephen Jay Gould versus Samuel George Morton on skulls
 769 and bias. *PLoS biology* 9: e1001071.
- 770 Lewontin RC, Birch LC 1966. Hybridization as a source of variation for adaptation to new
 771 environments. *Evolution; international journal of organic evolution* 20: 315-336.

- 772 Llopart A, Herrig D, Brud E, Stecklein Z 2014. Sequential adaptive introgression of the
773 mitochondrial genome in *Drosophila yakuba* and *Drosophila santomea*. *Molecular*
774 *ecology* 23: 1124-1136.
- 775 Loureiro ML, Alló M 2020. Sensing climate change and energy issues: Sentiment and
776 emotion analysis with social media in the U.K. and Spain. *Energy Policy* 143: 111490.
- 777 Lowe WH, Muhlfeld CC, Allendorf FW 2015. Spatial sorting promotes the spread of
778 maladaptive hybridization. *Trends in ecology & evolution* 30: 456-462.
- 779 Ma Y, Wang J, Hu Q, Li J, Sun Y, Zhang L, Abbott RJ, Liu J, Mao K 2019. Ancient
780 introgression drives adaptation to cooler and drier mountain habitats in a cypress
781 species complex. *Communications biology* 2: 213.
- 782 Maddamsetti R, Lenski RE 2018. Analysis of bacterial genomes from an evolution
783 experiment with horizontal gene transfer shows that recombination can sometimes
784 overwhelm selection. *Plos Genetics* 14: 30.
- 785 Maguilla E, Escudero M, Hipp AL, Luceno M 2017. Allopatric speciation despite historical
786 gene flow: Divergence and hybridization in *Carex furva* and *C. lucennoiberica*
787 (Cyperaceae) inferred from plastid and nuclear RAD-seq data. *Molecular ecology* 26:
788 5646-5662.
- 789 Maroco J. 2010. *Análise estatística com utilização do SPSS. 3ª edição. Edições Silabo.*
- 790 Martin CH, Crawford JE, Turner BJ, Simons LH 2016. Diabolical survival in Death Valley:
791 recent pupfish colonization, gene flow and genetic assimilation in the smallest
792 species range on earth. *Proceedings of the Royal Society B-Biological Sciences* 283:
793 10.
- 794 Martin NH, Bouck AC, Arnold ML (2006). Detecting adaptive trait introgression between
795 *Iris fulva* and *I. brevicaulis* in highly selective field conditions. *Genetics* 172: 2481-
796 2489.
- 797 Matusitz J 2012. Relationship between knowledge, stereotyping, and prejudice in
798 interethnic communication. *PASOS Revista de Turismo y Patrimonio Cultural* 10: 89-
799 98.
- 800 Maxwell CS, Mattox K, Turissini DA, Teixeira MM, Barker BM, Matute DR 2019. Gene
801 exchange between two divergent species of the fungal human pathogen,
802 *Coccidioides*. *Evolution; international journal of organic evolution* 73: 42-58.

- 803 Melo-Ferreira J, Seixas FA, Cheng E, Mills LS, Alves PC 2014. The hidden history of the
804 snowshoe hare, *Lepus americanus*: extensive mitochondrial DNA introgression
805 inferred from multilocus genetic variation. *Molecular ecology* 23: 4617-4630.
- 806 Moher D, Liberati A, Tetzlaff J, Altman DG, The PG 2009. Preferred Reporting Items for
807 Systematic Reviews and Meta-Analyses: The PRISMA Statement. *PLOS Medicine* 6:
808 e1000097.
- 809 Morales HE, Pavlova A, Amos N, Major R, Kilian A, Greening C, Sunnucks P 2018.
810 Concordant divergence of mitogenomes and a mitonuclear gene cluster in bird
811 lineages inhabiting different climates. *Nature Ecology & Evolution* 2: 1258-1267.
- 812 Morales HE, Sunnucks P, Joseph L, Pavlova A 2017. Perpendicular axes of differentiation
813 generated by mitochondrial introgression. *Molecular ecology* 26: 3241-3255.
- 814 Morris ZS, Wooding S, Grant J 2011. The answer is 17 years, what is the question:
815 understanding time lags in translational research. *Journal of the Royal Society of*
816 *Medicine* 104: 510-520.
- 817 Nader JL, Mathers TC, Ward BJ, Pachebat JA, Swain MT, Robinson G, Chalmers RM,
818 Hunter PR, van Oosterhout C, Tyler KM 2019. Evolutionary genomics of
819 anthroponosis in *Cryptosporidium*. *Nature microbiology* 4: 826-836.
- 820 Naisbit RE, Jiggins CD, Mallet J 2003. Mimicry: developmental genes that contribute to
821 speciation. *Evolution & Development* 5: 269-280.
- 822 Norris LC, Main BJ, Lee Y, Collier TC, Fofana A, Cornel AJ, Lanzaro GC 2015. Adaptive
823 introgression in an African malaria mosquito coincident with the increased usage of
824 insecticide-treated bed nets. *Proceedings of the National Academy of Sciences of*
825 *the United States of America* 112: 815-820.
- 826 Nshom E, Croucher S 2017. Perceived threat and prejudice towards immigrants in
827 Finland: A study among early, middle, and late Finnish adolescents. *Journal of*
828 *International and Intercultural Communication* 10: 309-323.
- 829 O'Dea RE, Lagisz M, Jennions MD, Koricheva J, Noble DWA, Parker TH, Gurevitch J, Page
830 MJ, Stewart G, Moher D, Nakagawa S 2021. Preferred reporting items for systematic
831 reviews and meta-analyses in ecology and evolutionary biology: a PRISMA
832 extension. *Biological Reviews* n/a.
- 833 Oliveira R, Godinho R, Randi E, Alves PC 2008. Hybridization versus conservation: are
834 domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*)

- 835 in Iberian Peninsula? *Philosophical transactions of the Royal Society of London*
 836 *Series B, Biological sciences* 363: 2953-2961.
- 837 Okubo Y 1997. *Bibliometric Indicators and Analysis of Research Systems: Methods and*
 838 *Examples*. OECD Science, Technology and Industry Working Papers. No. 1997/01.
 839 OECD Publishing, Paris.
- 840 Paetzold C, Wood KR, Eaton DAR, Wagner WL, Appelhans MS 2019. Phylogeny of
 841 Hawaiian Melicope (Rutaceae): RAD-seq Resolves Species Relationships and Reveals
 842 Ancient Introgression. *Frontiers in plant science* 10: 1074.
- 843 Page MJ, Moher D, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, Shamseer L,
 844 Tetzlaff JM, Akl AE, Brennan SE, Chou R, Glanville J, Grimshaw JM, Hróbjartsson A,
 845 Lalu MM, Li T, Loder EW, Mayo-Wilson E, McDonald S, McGuinness LA, Stewart LA,
 846 Thomas J, Tricco AC, Welch VA, Whiting P, McKenzie JE 2021. PRISMA 2020
 847 explanation and elaboration: updated guidance and exemplars for reporting
 848 systematic reviews. *BMJ* 372: n160.
- 849 Pagel M 2012. *Wired for culture. The Natural History of Human Cooperation*. New York:
 850 Penguin Press.
- 851 Paterson 1985 in Arnold M 1997. *Natural hybridization and evolution*. Oxford University
 852 Press.
- 853 Paun O, Turner B, Trucchi E, Munzinger J, Chase MW, Samuel R 2016. Processes Driving
 854 the Adaptive Radiation of a Tropical Tree (Diospyros, Ebenaceae) in New Caledonia,
 855 a Biodiversity Hotspot. *Systematic Biology* 65: 212-227.
- 856 Payseur BA, Krenz JG, Nachman MW 2004. Differential patterns of introgression across
 857 the X chromosome in a hybrid zone between two species of house mice. *Evolution;*
 858 *international journal of organic evolution* 58: 2064-2078.
- 859 Pfeifer B, Kapan DD 2019. Estimates of introgression as a function of pairwise distances.
 860 *BMC bioinformatics* 20: 207.
- 861 Pfennig KS 2021. Biased Hybridization and Its Impact on Adaptive Introgression. *Trends*
 862 *in ecology & evolution* 36: 488-497.
- 863 Plutchik R 1962. *The emotions: facts, theories, and a new model*. New York: Random
 864 House.

- 865 Poelstra JW, Richards EJ, Martin CH 2018. Speciation in sympatry with ongoing
866 secondary gene flow and a potential olfactory trigger in a radiation of Cameroon
867 cichlids. *Molecular ecology* 27: 4270-4288.
- 868 Puschmann C, Powell A 2018. Turning Words Into Consumer Preferences: How
869 Sentiment Analysis Is Framed in Research and the News Media. *Social Media +*
870 *Society* 4: 2056305118797724.
- 871 Quigley KM, Bay LK, van Oppen MJH 2019. The active spread of adaptive variation for
872 reef resilience. *Ecology and Evolution* 9: 11122-11135.
- 873 Reid N, Demboski JR, Sullivan J 2012. Phylogeny Estimation of the Radiation of Western
874 North American Chipmunks (*Tamias*) in the Face of Introgression Using
875 Reproductive Protein Genes. *Systematic Biology* 61: 44-62.
- 876 Ryan SF, Deines JM, Scriber JM, Pfrender ME, Jones SE, Emrich SJ, Hellmann JJ 2018.
877 Climate-mediated hybrid zone movement revealed with genomics, museum
878 collection, and simulation modeling. *Proceedings of the National Academy of*
879 *Sciences of the United States of America* 115: E2284-E2291.
- 880 Saks A, Gary J 2012. Perception, Attribution, and Judgment of Others. *Organizational*
881 *Behaviour: Understanding and Managing Life at Work* 7.
- 882 Salazar C, Jiggins CD, Taylor JE, Kronforst MR, Linares M 2008. Gene flow and the
883 genealogical history of *Heliconius heurippa*. *Bmc Evolutionary Biology* 8: 13.
- 884 Scascitelli M, Whitney KD, Randell RA, King M, Buerkle CA, Rieseberg LH (2010). Genome
885 scan of hybridizing sunflowers from Texas (*Helianthus annuus* and *H. debilis*) reveals
886 asymmetric patterns of introgression and small islands of genomic differentiation.
887 *Molecular ecology* 19: 521-541.
- 888 Schoen J 2005. Choice & coercion: Birth control, sterilization, and abortion in public
889 health and welfare. University of North Carolina Press.
- 890 Schultz PW, Nolan JM, Cialdini RB, Goldstein NJ, Griskevicius V 2007. The Constructive,
891 Destructive, and Reconstructive Power of Social Norms. *Psychological Science* 18:
892 429-434.
- 893 Semenov GA, Koblik EA, Red'kin YA, Badyaev AV 2018. Extensive phenotypic
894 diversification coexists with little genetic divergence and a lack of population
895 structure in the White Wagtail subspecies complex (*Motacilla alba*). *Journal of*
896 *Evolutionary Biology* 31: 1093-1108.

- 897 Silvert, M, Quintana-Murci L, Rotival M 2019. Impact and Evolutionary Determinants of
898 Neanderthal Introgression on Transcriptional and Post-Transcriptional Regulation.
899 American journal of human genetics *104*: 1241-1250.
- 900 Sonnby-Borgström M, Jönsson P, Svensson O 2003. Emotional Empathy as Related to
901 Mimicry Reactions at Different Levels of Information Processing. Journal of
902 Nonverbal Behavior *27*: 3-23.
- 903 Soroka S, Fournier P, Nir L 2019. Cross-national evidence of a negativity bias in
904 psychophysiological reactions to news. Proceedings of the National Academy of
905 Sciences *116*: 18888.
- 906 Suarez-Gonzalez A, Hefer CA, Lexer C, Cronk QCB, Douglas CJ 2018a. Scale and direction
907 of adaptive introgression between black cottonwood (*Populus trichocarpa*) and
908 balsam poplar (*P.balsamifera*). Molecular ecology *27*: 1667-1680.
- 909 Suarez-Gonzalez A, Hefer CA, Lexer C, Douglas CJ, Cronk QCB 2018b. Introgression from
910 *Populus balsamifera* underlies adaptively significant variation and range boundaries
911 in *P.trichocarpa*. New Phytologist *217*: 416-427.
- 912 Stanovich KE, West RF 2008. On the relative independence of thinking biases and
913 cognitive ability. Journal of personality and social psychology *94*: 672-695.
- 914 Sykora M, Elayan S, Jackson TW 2020. A qualitative analysis of sarcasm, irony and related
915 #hashtags on Twitter. Big Data & Society *7*: 2053951720972735.
- 916 Tahamtan I, Bornmann L 2020. Altmetrics and societal impact measurements: Match or
917 mismatch? A literature review. El profesional de la información *29*: e290102.
- 918 Taylor AL, Dessai S, Bruine de Bruin W 2014. Public perception of climate risk and
919 adaptation in the UK: A review of the literature. Climate Risk Management *4-5*: 1-
920 16.
- 921 Taylor SA, Larson EL 2019. Insights from genomes into the evolutionary importance and
922 prevalence of hybridization in nature. Nature Ecology & Evolution *3*: 170-177.
- 923 Trochim W. 2010. Translation Won't Happen Without Dissemination and
924 Implementation: Some Measurement and Evaluation Issues. 3rd Annual Conference
925 on the Science of Dissemination and Implementation Bethesda, MD.
- 926 Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F 2017. Taxonomic bias in
927 biodiversity data and societal preferences. Scientific Reports *7*: 9132.

- 928 Ulrik B, Faster A 2001. Algorithm for Betweenness Centrality. *Journal of Mathematical*
929 *Sociology* 25(2): 163-177.
- 930 Whitmarsh L (2011). Scepticism and uncertainty about climate change: Dimensions,
931 determinants and change over time. *Global Environmental Change* 21: 690-700.
- 932 Whitney KD, Broman KW, Kane NC, Hovick SM, Randell RA, Rieseberg, LH 2015.
933 Quantitative trait locus mapping identifies candidate alleles involved in adaptive
934 introgression and range expansion in a wild sunflower. *Molecular ecology* 24: 2194-
935 2211.
- 936 Yang CH, Li YD, Liu C, Yuan XR 2019. Deep learning-based viewpoint recommendation in
937 volume visualization. *Journal of visualization* 22: 991-1003.
- 938 Zhang W, Dasmahapatra KK, Mallet J, Moreira GRP, Kronforst MR 2016. Genome-wide
939 introgression among distantly related *Heliconius* butterfly species. *Genome Biology*
940 17: 15.

FIGURES

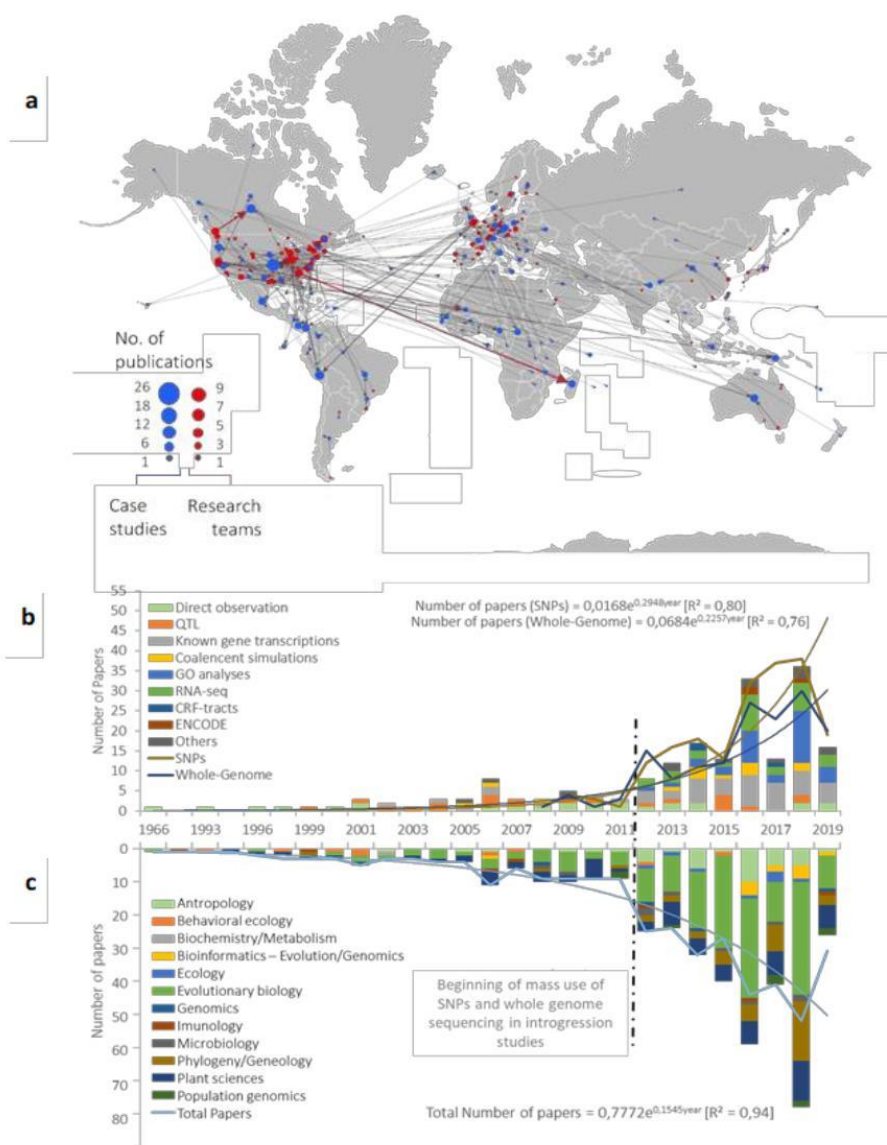


Figure 1. Spatial networks of case studies featured in the meta-analysis (blue dots) performed by each research team with a specific host geographic location (red dots) (a). Case study locations were georeferenced based on the description of the study area provided within each paper. Circle sizes reflect the number of papers from a specific location. Arrows represent directional pathways from the team to the case study with line width representing the number of papers published by each team on the specific case study. Temporal changes in the number of published papers on

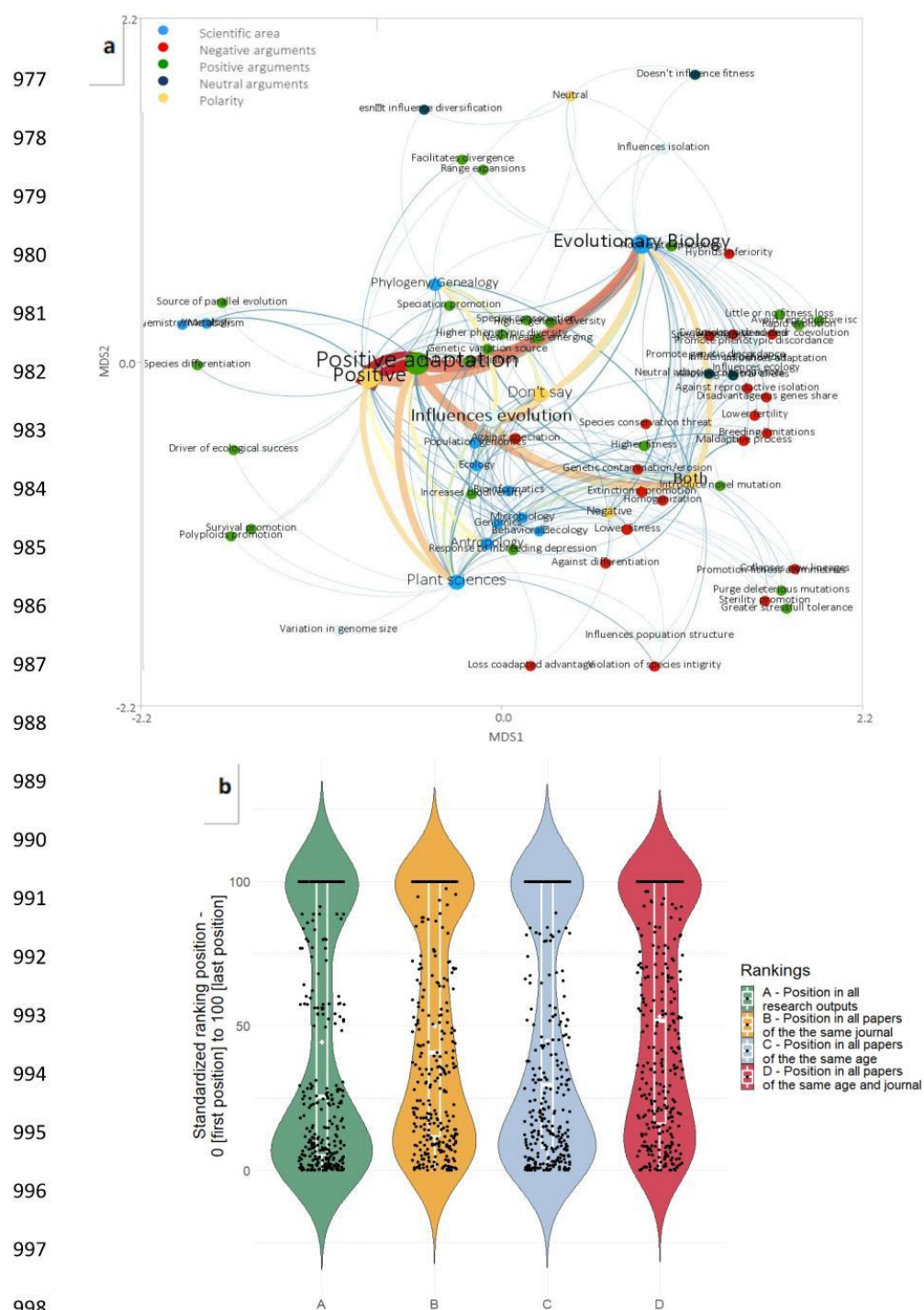
968 adaptive introgression by methodology **(b)** and scientific field **(c)**. The solid lines
969 represent the correlation between the number of papers and time and the dashed line
970 shows the tipping point, when the trend line started to show an exponential increase –
971 representing the beginning of the genomic revolution in adaptive introgression
972 studies.

973

974

975

976



1001 **Figure 2.** Multidimensional Scaling (MDS) tripartite network used to quantify the
1002 extent of connections between each scientific area, the polarity of authors'
1003 perceptions of adaptive introgression and their positive, negative and neutral
1004 biological arguments **(a)**. Violin plots representing Altmetric Attention Score (ASS)
1005 compared to A) all research outputs scored by Altmetric.com, B) all papers of the same
1006 journal, C) all papers of the same age and D) all papers of the same age and journal **(b)**.
1007 Standardized ranking position is represented between 0 (first position) to 100 (last
1008 position). Within them white solid lines boxplots include medians (horizontal white
1009 line) and average (white dot), boxes indicate quartiles and ranges, simultaneously.

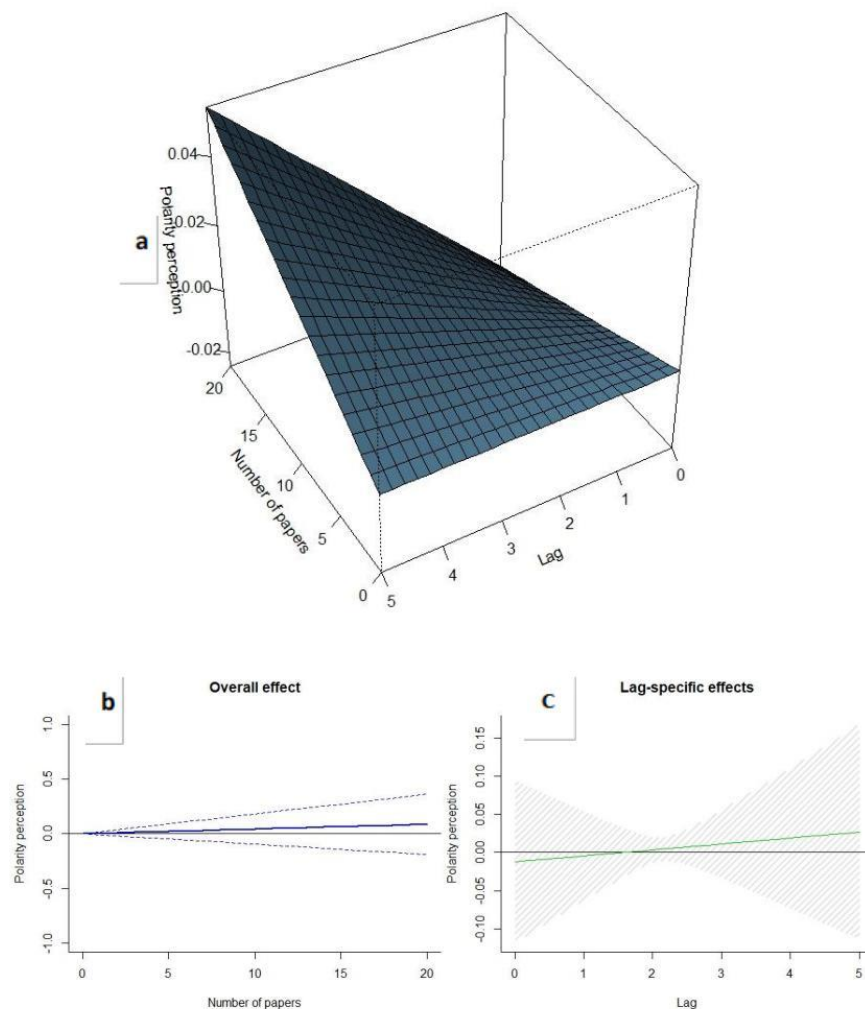


Figure 3. Three-dimensional plot showing temporal changes (2000 to 2019) of the estimated exposure–lag–response association between the number of papers providing evidence for adaptive introgression and the standardized polarity perception by the public (stPP), with the average as reference and each Lag period corresponding to 4 years (a). Overall cumulative exposure–response relationships between the temporal changes (2000 to 2019) of the number of papers providing evidence for adaptive introgression and standardized polarity perception by the public (stPP), predicted from the model with no interaction (interpreted as the average), with 95% CI (b). Lag–response relationships between the number of papers providing evidence for adaptive introgression and stPP, with 95% CI and each Lag period corresponding to 4 years (c).

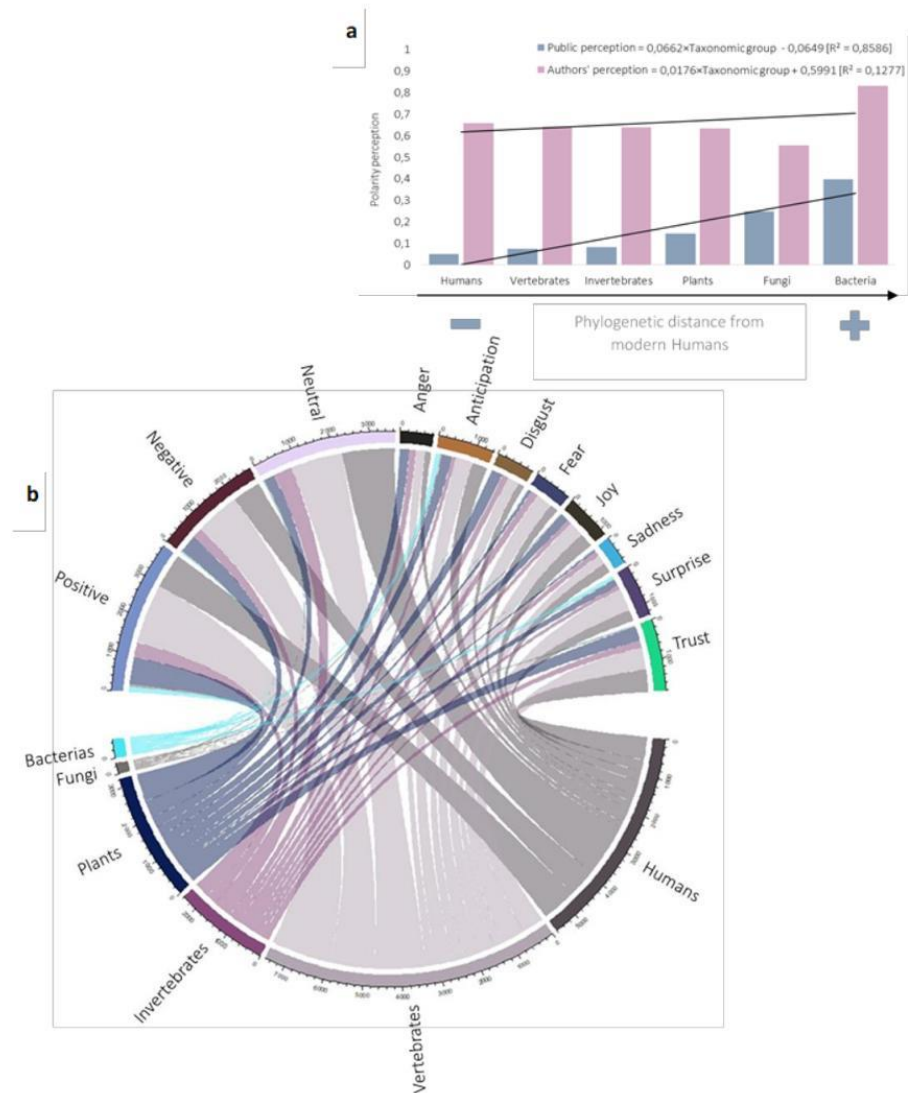


Figure 4. Standardized Polarity Perception (stPP) correlation with taxonomic groups under study (a). Grey and pink bars represent public and authors' perception, respectively. Solid lines depict the relationship between their stPP and the different taxonomic groups under study based on the phylogenetic distance from modern Humans. Hierarchical network chord diagram with expanded endpoints illustrating public total polarity perception and expressed emotions about adaptive introgression papers from different taxonomic groups under study (b).

1

2

3

4

Supplemental materials

5

6

7

8

What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific

9

and Public Perception

10

11

12

13

14

15

16

17

18

19

20

21

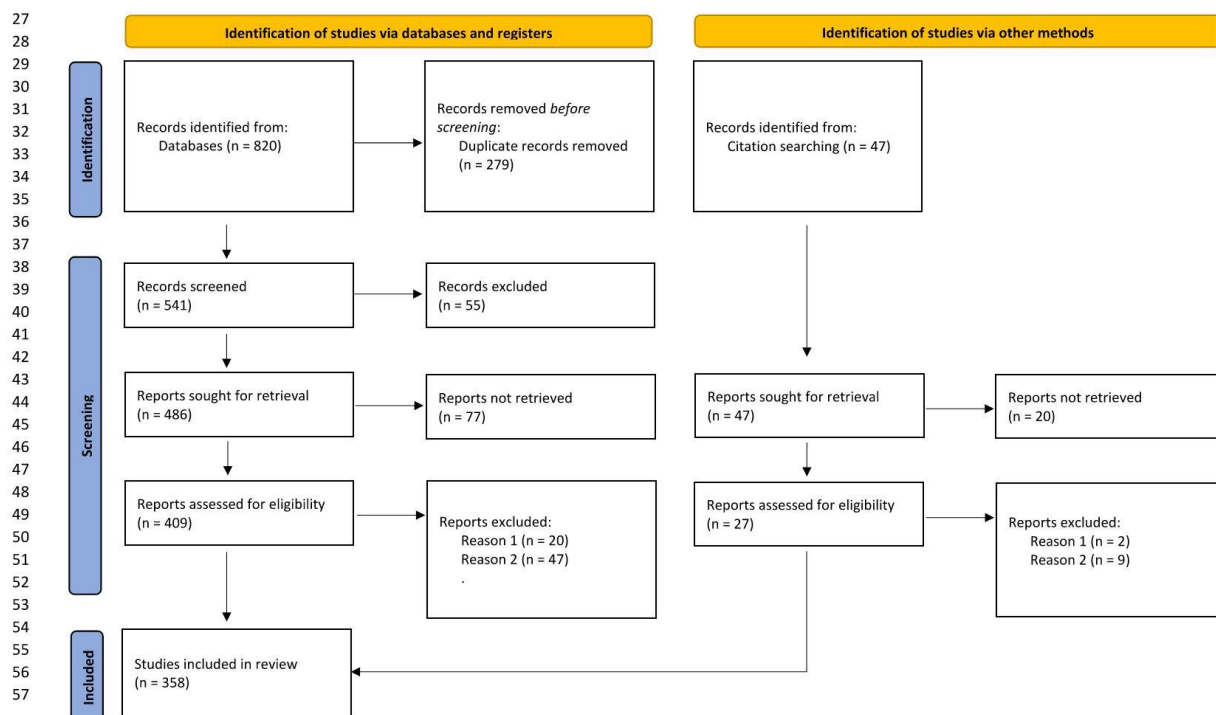
22

23

24

25

26



1

WebFigure 1. PRISMA 2020 flow diagram. Adapted from: Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, et al. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 2021;372:n71. doi: 10.1136/bmj.n71. For more information, visit: <http://www.prisma-statement.org/>

2

62 Search details

63 We used the following search string for on-line databases:

64 “Topic=(*hybrid** AND *adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest**
65 NOT *exotic*) OR Topic=(*adapt** AND *introgress** AND *genom** NOT *invas** NOT *domest**
66 NOT *exotic*)”

67 We defined some keywords as strict retention criteria: *Adapt** (all terms related to
68 adaptation, adaptive, etc.), *Introgress** (all terms related to introgression,
69 introgressive, etc) and *Genom** (all terms related to genome, genomics, etc.). We also
70 used as non-strict retention criterion for the term *hybrid** (all terms related to hybrids,
71 hybridization, etc.) that could be present together with the previous ones or not. We
72 excluded all breeding contacts between taxa under direct human interference
73 (breeding manipulations between species that do not naturally interbreed, genetic
74 manipulation, invasive species scenarios, etc.). We used the following keywords as
75 strict exclusion criteria: *Invas** (all terms related to invasion, invasive species, etc.),
76 *Exotic* and *Domest** (all terms related to domestic species, domestication, etc.).
77 We defined the expression “*Adaptive Introgression*” as a keyword used as strict
78 retention criteria searching for relevance grey literature through Google and Google
79 scholar.

80

81 **Table S1.** Full list of information and the total number of papers that includes each

82 category extracted from each reviewed paper.

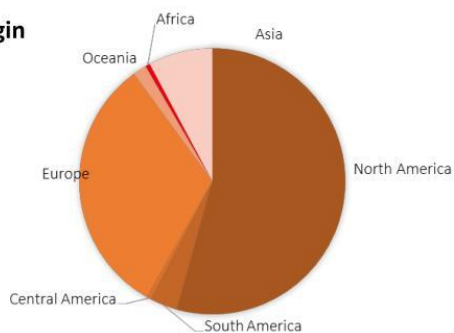
Categories of information	Variables extracted	Classes used	Number of papers
Bibliographic information	✓ Authors		358
	✓ Year		358
	✓ Title		358
	✓ Journal		358
	✓ Research area		358
	✓ Type of publication		358
	✓ Location of author's institution		358
Authors' initial perception about introgression	✓ Polarity	Positive Negative Both Neutral	351
	✓ Why positive?		250
	✓ Why negative?		78
	✓ Why neutral?		129
	✓ Prevalence	Very rare [-3] Rare [-2] Infrequent [-1] Unknown [0] Few cases [1] Some cases [2] Common [3] Many cases [4] Ubiquitous [5]	135
	✓ Semantics	Hybrid* terms used Hybrid* terms not used	358
Taxa under study	✓ Main taxonomic group	Animal Plant Fungi Protists Bacteria	355
	✓ Families		355
	✓ Species pairs		355
Time and space of introgressions' case studies	✓ Epoch	Ancient Recent Both	355
	✓ Continent		355
	✓ Approximated location		355
Methods used	✓ Type of experiment	In-situ Ex-situ	351

✓ Type of introgression markers	Both	
	Quantitative Trait Locus	347
	Microsatellites	
	Mitochondrial DNA	
	Ribosomal DNA	
	Single-Nucleotide	
	Polymorphisms	
	AFLP	
	PCR amplification	
	Electrophoresis (DGGE)	
✓ Whole-genome sequencing	Karyotypes	347
✓ Reference genome	Performed	
	Not performed	165
	Available	
	Not available	

83

84

**Research
teams' origin**



**Case studies'
distribution**

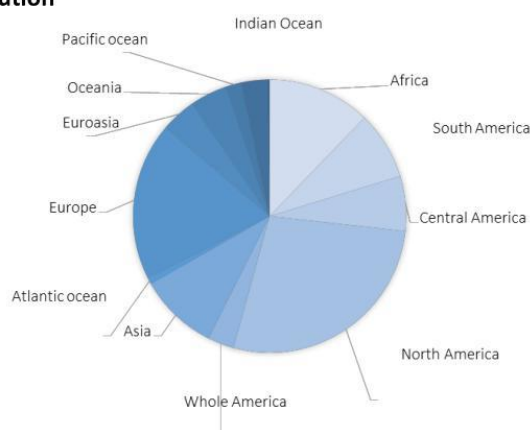
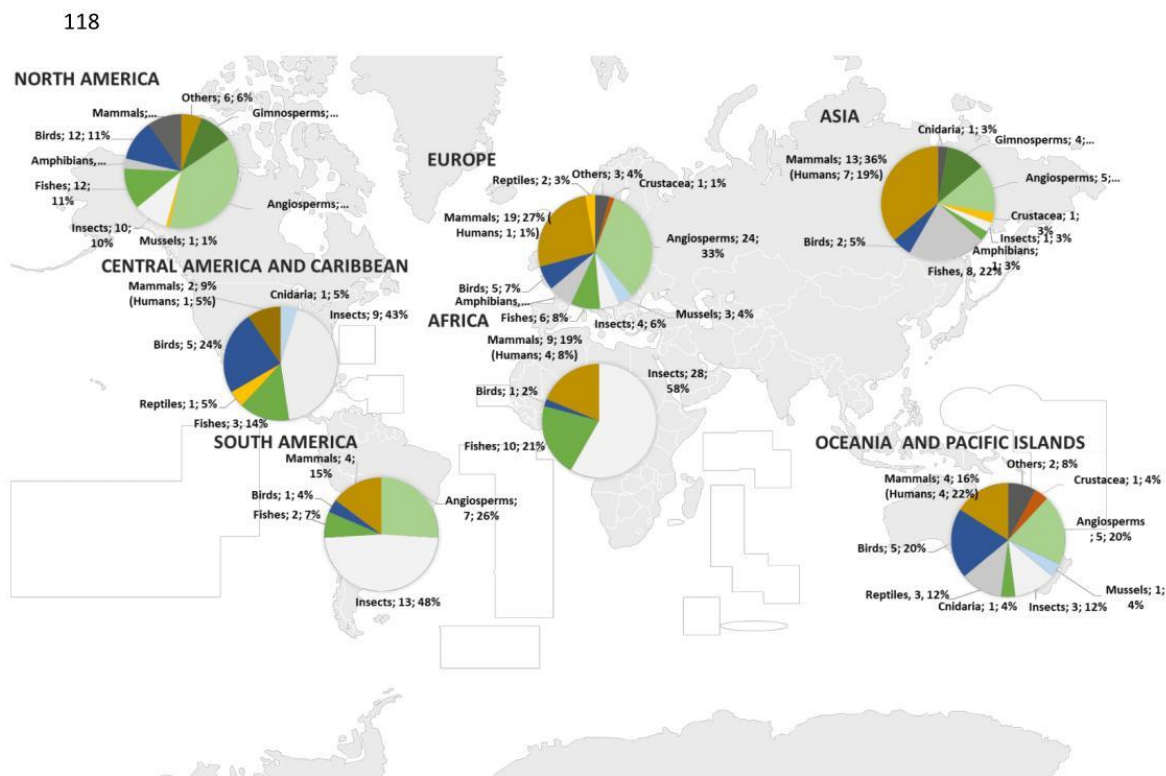


Figure S1. Distribution of reported adaptive introgression case studies by research team origin (top plot) and geographic location (plot from below).

Table S2. Total number of papers produced by teams from specific geographic regions on case studies located in other geographical locations. 26 papers analysed more than one case study and three papers did not include a case study, resulting in a total of 388 case studies.

Research Team	North America	South America	Central America	Europe	Oceania	Africa	Asia	N _{br} of case study
Case Study								
North America	93%	0%	0%	6%	0%	0%	1%	104
South America	27%	46%	4%	23%	0%	0%	0%	26
Central America	62%	10%	5%	24%	0%	0%	0%	21
Europe	19%	0%	0%	81%	0%	0%	0%	73
Oceania	41%	0%	0%	29%	29%	0%	0%	17
Africa	55%	0%	0%	40%	0%	4%	0%	47
Asia	10%	0%	0%	14%	0%	0%	76%	58
Indian Ocean	0%	0%	0%	67%	0%	0%	33%	3
Atlantic ocean	50%	0%	0%	50%	0%	0%	0%	2
Pacific ocean	57%	0%	0%	29%	0%	0%	14%	7
Whole world	91%	0%	0%	9%	0%	0%	0%	11
Whole America	50%	0%	0%	50%	0%	0%	0%	4
Eurasia	53%	0%	0%	27%	0%	0%	20%	15
N _{br} of papers per research team	195	14	2	120	5	2	50	388



119

120 **Figure S2.** Spatial distribution of reported adaptive introgression case studies by taxa.

121

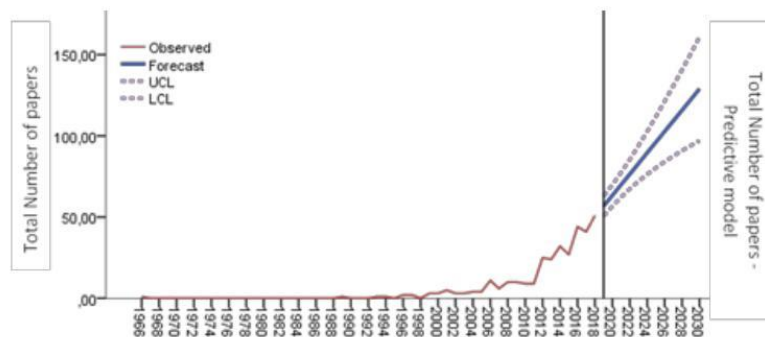


Figure S3. Predictive model of temporal series projections (until 2030), performed by the Expert Modeler Method.

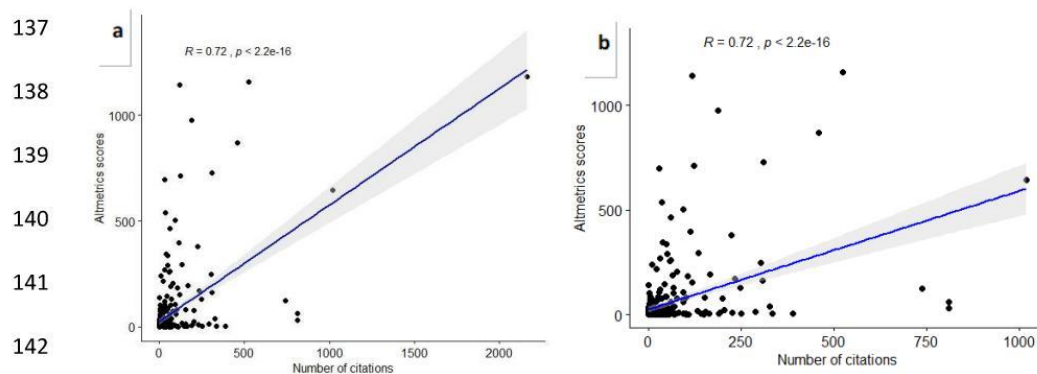
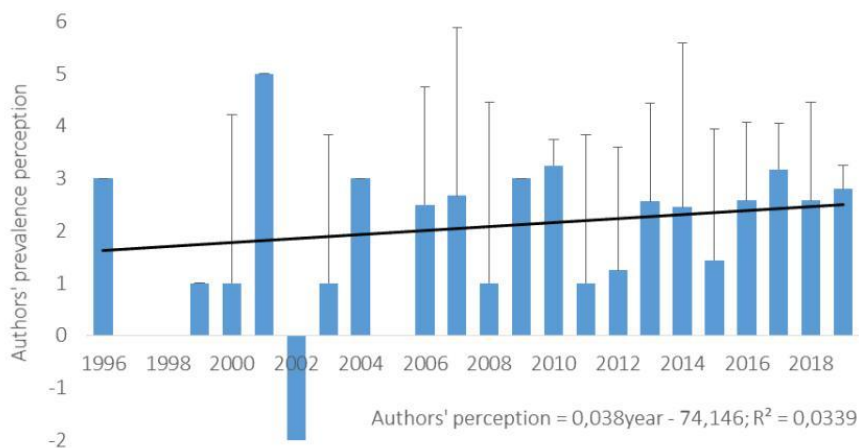


Figure S4. Altmetric.com Attention Score (ASS) correlation with citation count (traditional bibliometric for research ranking) in the literature through Spearman correlation analysis. The solid blue line depicts the relationship between ASS and the number of citations with the main outlier (Green *et al.* 2010) (a) and without it (b).



149

150

151 **Figure S5.** Annual changes in authors' average perception of the prevalence of
 152 adaptive introgression, categorized into nine classes: very rare [-3], rare [-2],
 153 infrequent [-1], unknown [0], few cases [1], some cases [2], common [3], many cases
 154 [4] and ubiquitous [5]. The solid line depicts the relationship between the perception
 155 ranking over time.

156

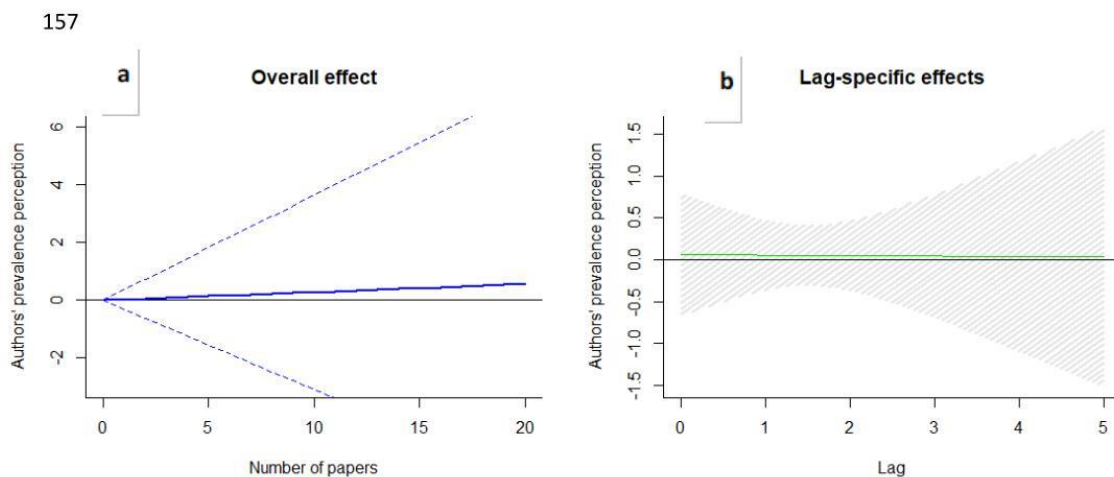
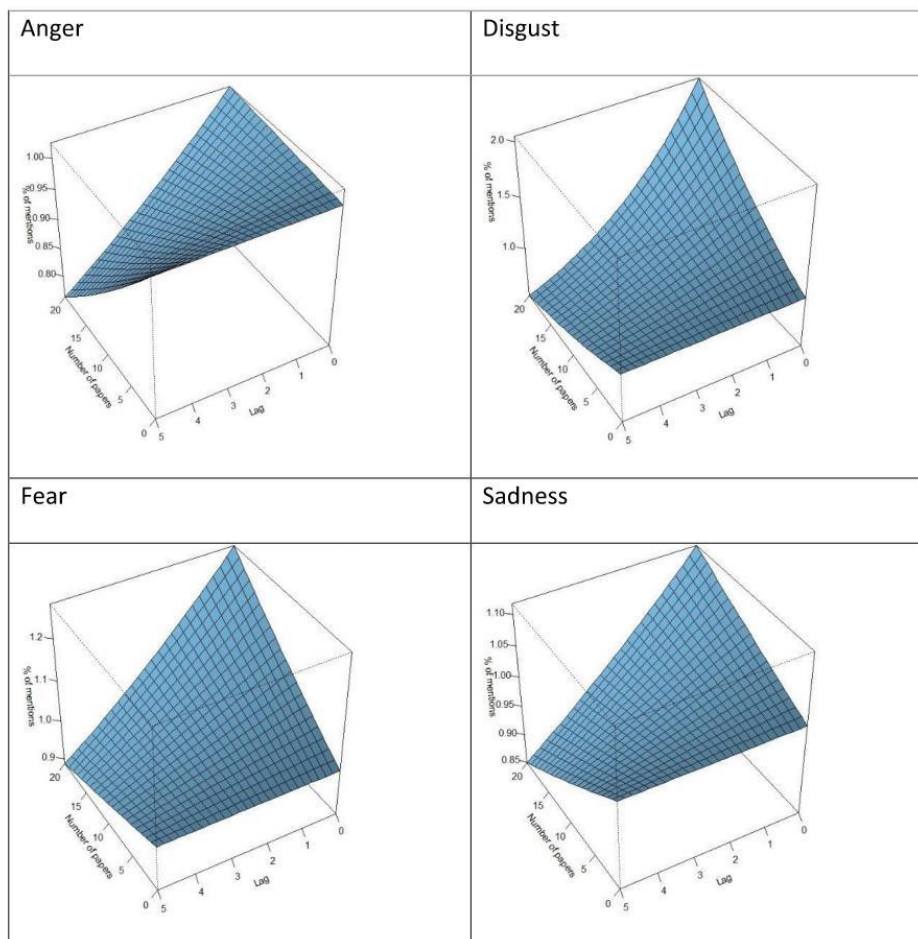


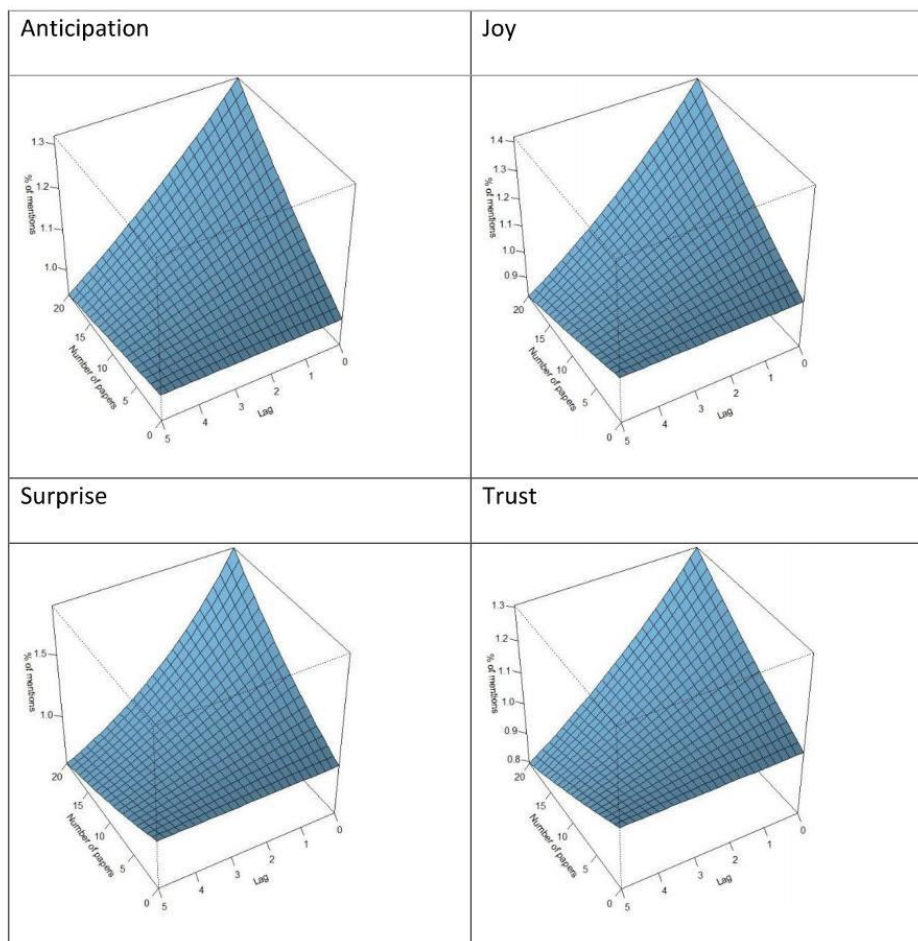
Figure S6. Overall cumulative exposure–response relationships between the temporal change in the number of papers providing evidence for adaptive introgression and authors' prevalence perception predicted from the model with no interaction (interpreted as the average), with 95% CI (**a**). Lag–response relationships between the number of adaptive introgression evidence (number of papers) and authors' perception about its prevalence, with 95% CI (**b**).



172

173 **Figure S7.** Three-dimensional plots showing temporal changes (from 2000 to 2019) in
 174 the estimated exposure–lag–response association between the number of published
 175 papers providing evidence for adaptive introgression and the percentage of mentions
 176 expressing negative emotions (anger, disgust, fear and sadness) of the total annual
 177 mentions expressed by the public about them, with the average as reference, and each
 178 Lag period corresponding to 4 years.

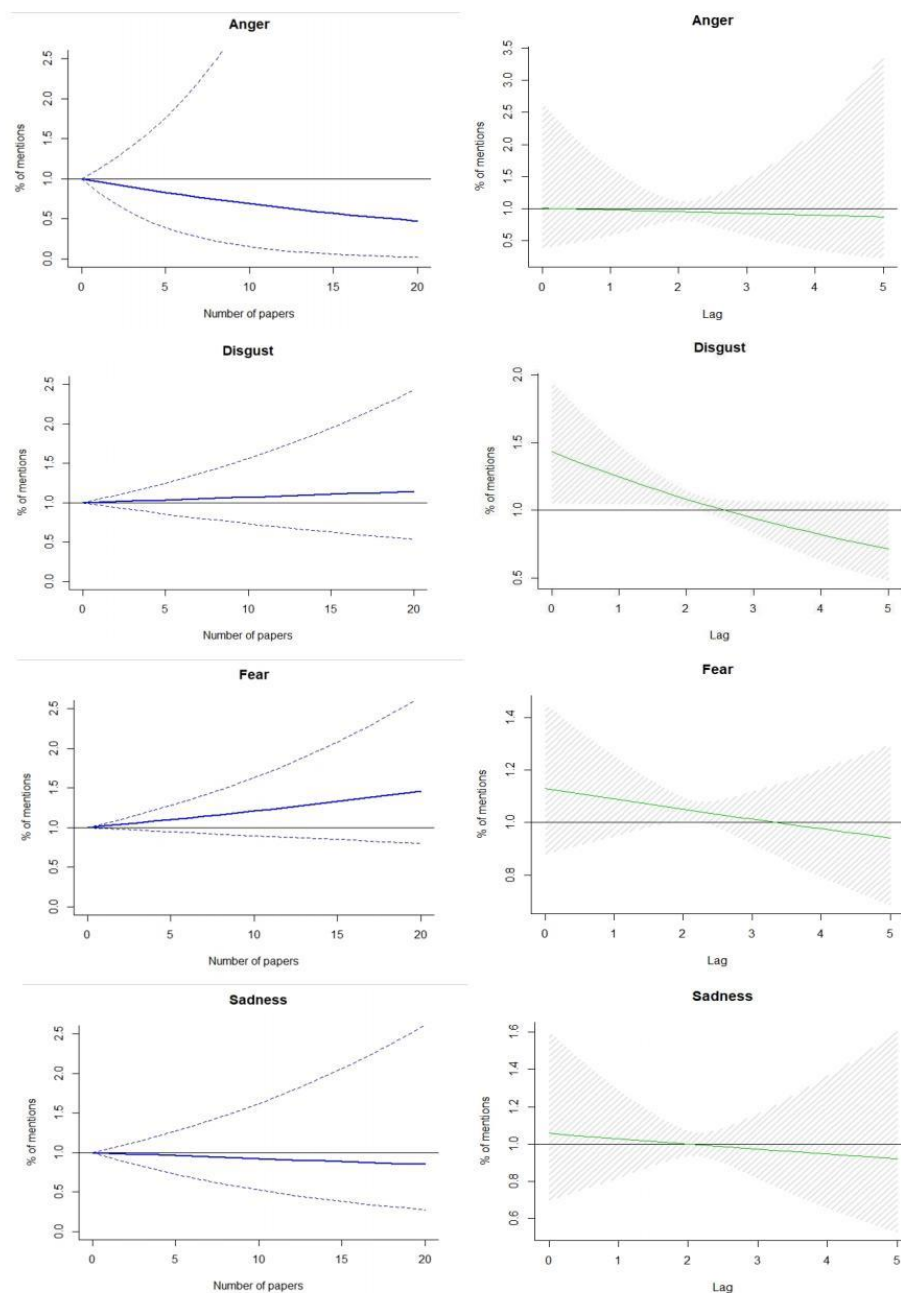
179



180

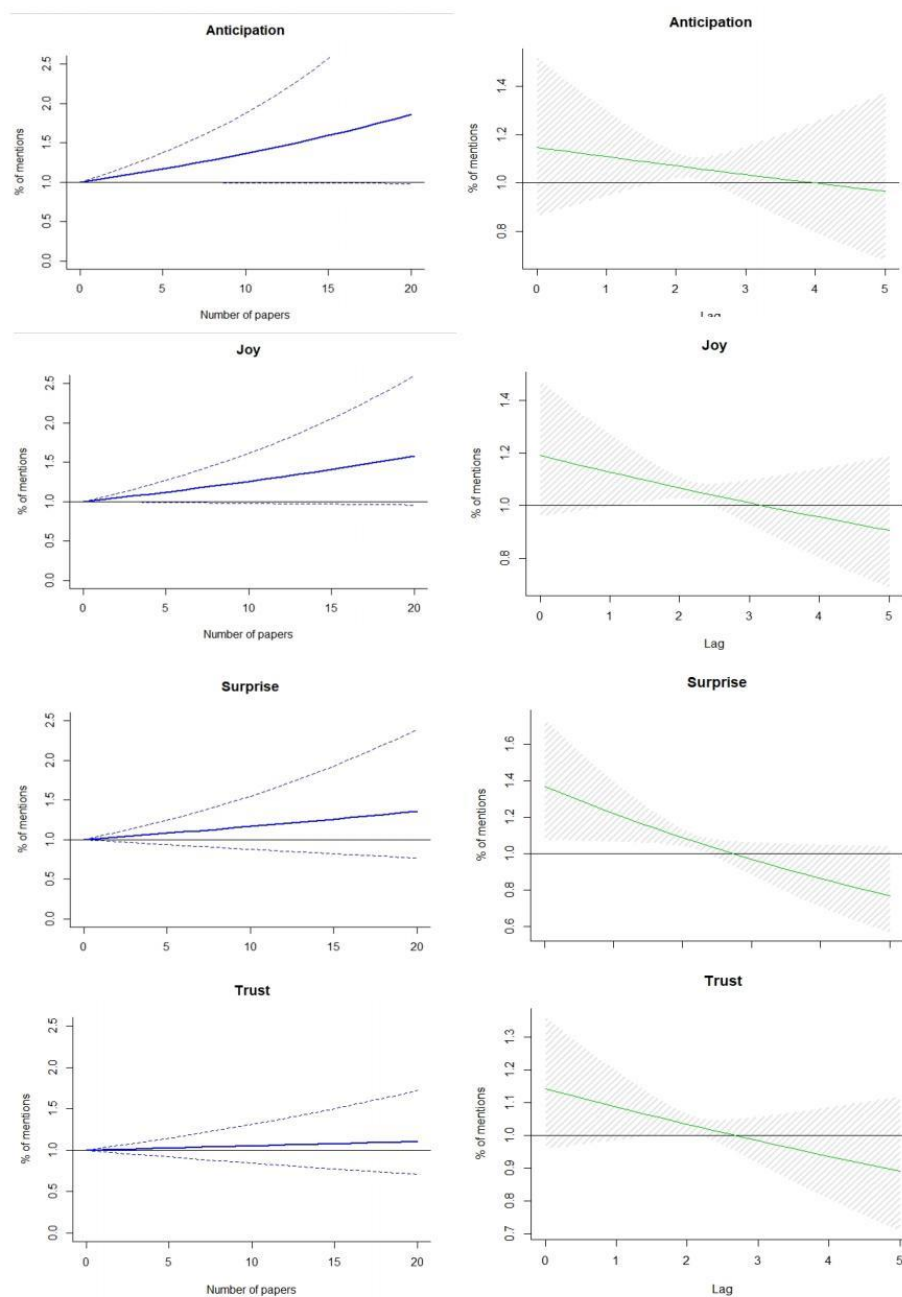
181 **Figure S8.** Three-dimensional plots showing temporal changes (from 2000 to 2019) of
 182 the estimated exposure–lag–response association between the number of published
 183 papers providing evidence for adaptive introgression and the percentage of mentions
 184 expressing positive emotions (anticipation, joy, surprise and trust) of the total annual
 185 mentions expressed by the public about them, with the average as reference, and each
 186 Lag period corresponding to 4 years.

187



188 **Figure S9.** Overall cumulative exposure-response (left plots) and Lag-response (right
 189 plots) relationships between temporal changes (from 2000 to 2019) in the number of
 190 papers providing evidence for adaptive introgression evidences and the percentage of

191 mentions revealing negative emotions (Anger, Disgust, Fear and Sadness) predicted
192 from the model with no interaction (interpreted as the average), with 95% CI.
193



194 **Figure S10.** Overall cumulative exposure–response (left plots) and Lag–response (right
 195 plots) relationships between the temporal changes (from 2000 to 2019) in the number
 196 of adaptive introgression evidences (number of papers) and the percentage of

- 197 mentions revealing positive emotions (Anticipation, Joy, Surprise and Trust) predicted
- 198 from the model with no interaction (interpreted as the average), with 95% CI.

Editorial Board
Scientific Reports,
11. November 2021

Dear Editors,

We are pleased to submit the manuscript entitled “***What about adaptive introgression? The genomic revolution is shaping scientific and public perception***” for consideration for publication as an Article in *Scientific Reports*. We believe that our paper merits consideration for publication in *Scientific Reports* and will have broad appeal due to its interdisciplinary nature, standing at the interface between Evolutionary Biology, Genomics, Socio-biology and Psychosociology. In this paper, we show for the first time that scientific developments on evolutionary biology regarding to adaptive introgression have the capacity to impact and change the scientific and public perception of genetic miscegenation following an initial emotional response.

Evolutionary sciences are particularly valuable for society. Still, it is critical that the historical background and philosophical knowledge may promote prejudice free judgements that evolutionists may also be sensitive too, as “human beings rooted in cultural contexts”. However, there are known paradigmatic examples of the usurpation and misrepresentation of scientific facts for socio-political purposes that go far beyond the scientific process itself. Genetic miscegenation has historically suffered from controversies and paradoxes that make this theme particularly susceptible. This is particularly true in a current context subjugated to a post-truth society, in which mistrust and misperceptions of scientific facts progressively stem from the extensive diffusion of distorted and biased information.

To elucidate the role that scientific knowledge and methodological developments, like the genomic revolution, play in evolutionary biology and society, regarding miscegenation, we first carried out a systematic review of the 358 published scientific articles on adaptive introgression and respective bibliographic meta-data. Then, we adopted a series of bibliometric analyses to understand the taxonomic coverage, geographic and methodological patterns, and temporal evolution of the retrieved literature. Additionally, we used salience analysis grounded in citation indices and attention scores, to understand the popularity level of the different studies among the scientific community and the public. Finally, through artificial intelligence (AI) we analysed the prevalence, polarity and relevance of adaptive introgression based on the perceptions from the authors of those studies, as well as the sentiment of the public towards this body of knowledge.

The genomic revolution speared an exponential growth of evidence for adaptive introgression across the world, showing that it is likely present in all biological systems. Our results indicate that the scientific literature recognises adaptive introgression, and even genetic miscegenation, as a crucial natural evolutionary process. The opinion of the majority of the

scientific community about adaptive introgression tended to be positive, mainly in terms of its contribution to evolution and adaptation of organisms to different environmental conditions.

The increase in scientific evidence for the presence of adaptive introgression impacts public opinion but only after a medium-long delay and high rates of publications per year. However, public opinion on adaptive introgression changes according to the studied taxonomic group. Public perceptions are more positive when the taxa studied were more phylogenetically distant from human beings. Therefore, prejudices still seem to influence people's attitudes towards genetic miscegenation.

These results suggest new avenues for fostering the progress of the knowledge on adaptive introgression and adjust its course in evolutionary biology. Specifically, the need to further explore the real prevalence of adaptive introgression and its impacts on species adaptation and evolution, and to uncover the capacity of this scientific knowledge to promote effective changes in people's attitudes and beliefs. We argue that gaining more knowledge and understanding of adaptive introgression will allow Evolutionary Sciences to scientifically refute eugenics and other theories that promote taxa 'purity'.

All authors agree with the conclusions and show no conflict of interests and the manuscript is not being considered for publication anywhere else. In order to comply with the assumptions of the Double-blind peer review guidelines I describe below the authors' affiliation and the acknowledgments section of the work.

Thank you for your consideration of this manuscript.

Yours sincerely,

Pedro Horta

Pedro Horta^{1,2,3,9*} & Helena Raposeira^{1,2,3,9} & Ana Sofia Vaz^{1,9} & João António⁴ & Javier Juste^{5,6} &

Orly Razgour⁷ & Hugo Rebelo^{1,8,9}

¹CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal

²Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal

³OII – Observatório Inovação Investigação, Seia, Portugal

⁴Universidade Católica Portuguesa, CIEP, Lisboa, Portugal

⁵Departamento de Ecología Evolutiva, Estación Biológica de Doñana (CSIC), Sevilla, Spain, Avda. Américo Vespucio 26, 41092 Sevilla, Spain

⁶CIBER de Epidemiología y Salud Pública, CIBERESP, Madrid, Spain

⁷Biosciences, University of Exeter, Exeter, UK (O.Razgour@exeter.ac.uk)

⁸CIBIO/InBio, Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa, Portugal

⁹BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal

*Corresponding author: pedro.horta@cibio.up.pt

ACKNOWLEDGMENTS

PH and HRa were funded by the Portuguese Foundation for Science and Technology (FCT) with a PhD grant (SFRH/BD/117979/2016 and SFRH/BD/124367/2016, respectively). HRe was also funded by FCT (DL57/2016/EEC2018/07). OR was funded through a Natural Environment Research Council Independent Research Fellowship (NE/M018660/1). ASV was supported by FCT through Stimulus of Scientific Employment, Individual Support (reference 2020.01175.CEECIND). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017. We also thank the company Altmetric.com for approving our project and granting us free access to Altmetric.com explorer and its information.

Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats

Horta P., Raposeira H., Baños A., Ibáñez C., Razgour O., Rebelo H. & Juste J. (submitted). Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats. *Communications Biology*.

De: commsbio@nature.com
Enviado: 11 de novembro de 2021 09:20
Para: pedro.horta@cibio.up.pt
Assunto: COMMSBIO-21-3147 Approved MS Receive

Dear [author information removed for double blind peer review]

Thank you for uploading your manuscript files to Communications Biology. We have successfully received your files and your manuscript has been assigned the tracking number COMMSBIO-21-3147. Please quote this tracking number in the subject line of any correspondence.

Your manuscript is now at our initial Quality Check stage where we check for adherence to the journal's submission guidelines, including any relevant editorial and publishing policies, prior to approval of your submission. This is to ensure that we have all the information needed to process your paper. If there are any points that need to be addressed, you will receive a detailed email shortly. Once your manuscript has been approved you will receive another email confirmation.

If you are submitting the final version of your manuscript before acceptance, you may experience a longer delay of several days to approximately 1 week. This is due to more extensive Quality Check procedures for this stage. Please note that you have successfully submitted your files and we will contact you as soon as the Quality Check stage is complete.

Best Regards,

Manuscript Administration
 Communications Biology
 4 Crinan Street
 London N1 9XW
 Manuscript Administration
 One New York Plaza, Suite 4500
 New York, NY 10004
 E-mail: commsbio@nature.com

This email has been sent through the Springer Nature Tracking System NY-610A-NPG&MTS

Confidentiality Statement:

This e-mail is confidential and subject to copyright. Any unauthorised use or disclosure of its contents is prohibited. If you have received this email in error please notify our Manuscript Tracking System Helpdesk team at <http://platformsupport.nature.com>.

Details of the confidentiality and pre-publicity policy may be found here <http://www.nature.com/authors/policies/confidentiality.html>

[Privacy Policy](#) | [Update Profile](#)

1 **Counteracting forces of introgressive hybridization and interspecific competition**
2 **shape the morphological traits of cryptic Iberian *Eptesicus* bats**

3

4 **ABSTRACT**

5 Cryptic species that coexist in sympatry are likely to simultaneously experience strong
6 competition and hybridization. The first phenomenon would lead to character
7 displacement, whereas the second can potentially promote morphological similarity
8 through adaptive introgression. The main goal of this work was to investigate the
9 effect of introgressive hybridization on the morphology of cryptic Iberian *Eptesicus*
10 bats when facing counteracting evolutionary forces from interspecific competition. We
11 found substantial overlap both in dentition and in wing morphology traits, though
12 mainly in individuals in sympatry. The presence of hybrids contributes to a fifth of this
13 overlap, with hybrids showing traits with intermediate morphometry. Thus,
14 introgressive hybridization may contribute to species adaptation to trophic and
15 ecological space responding directly to the macro-habitats characteristics of the
16 sympatric zone and to local prey availability. On the other hand, fur shade tended to
17 be browner and brighter in hybrids than parental species. Colour differences could
18 result from partitioning of resources as an adaptation to environmental factors such as
19 roost and microhabitats. We argue that a balance between adaptive introgression and
20 niche partitioning shapes species interactions with the environment through affecting
21 morphological traits under selection.

22 **KEYWORDS**

23 Adaptive introgression; Allopatry; Cryptic species; *Eptesicus isabellinus*; *Eptesicus*
24 *serotinus*; Hybrids; Niche partitioning; Morphology; Sympatry

25 **1 | INTRODUCTION**

26 The evolutionary history of species under preliminary stages of macroevolution moves
27 through complex forces, leading to incongruities in phylogenetic inferences and
28 species classification (Ottenburghs et al., 2017). Divergence is frequently discussed as
29 involving mainly stages of allopatry (Baiz et al., 2019; Renaut et al., 2013; Slager et al.,
30 2020). However, historical environmental fluctuations (Grant and Grant, 2016)
31 mediate iterations between periods of allopatry and sympatry (Pauquet et al., 2018;
32 Pfennig, 2007; Staubach et al., 2012). When past allopatry was not sufficient to
33 eliminate or significantly reduce niche overlap, closely-related species may coexist
34 stably during secondary contacts under antagonistic evolutionary forces, imposed for
35 example by hybridization and niche partitioning (Schluter, 2000). On one hand, under
36 sympatry, genetic material can be transferred through introgressive hybridization with
37 potential evolutionary convergence (Song et al., 2011). On the other hand, ecological
38 interactions, such as competition, predation or parasitism may produce exclusion or
39 promote divergence as a response (Anderson et al., 2002).

40 When hybridization between lineages presents adaptive advantages in relation to the
41 parental lines resulting in increased fitness, the genetic pools will face a process of
42 adaptive introgression. This has been described as the main evolutionary response in
43 natural hybridization (Anderson and Hubricht, 1938; Dunn et al., 2013; Gramlich et al.,
44 2018; Ma et al., 2010; Mavárez et al., 2006). Introgressed alleles potentially associated
45 to well-adapted traits (Aleksic et al., 2018; Alexander et al., 2017; Brower, 2013; Cahill
46 et al., 2015; Djogbénou et al., 2008; Enciso-Romero et al., 2017; Gagnaire et al., 2009)
47 are introduced into the gene pool of the recipient species by backcrossing and fixed by
48 natural selection (de Lafontaine et al., 2015; Song et al., 2011). Therefore, introgressed

species can jump directly to new adaptive optimum, bypassing intermediate steps (Cahill et al., 2015; Dasmahapatra et al., 2012). By allowing closely-related species to share particularly beneficial traits, adaptive introgression is sometimes understood as a homogenizing process promoting evolutionary convergence (Latch et al., 2006; Oliveira et al., 2008).

Recent studies have shown important phenotypic expression of adaptive introgression in morphological traits of many taxa. Introgressed morphological traits were reported to promote dehydration/water-loss resistance to warmer or colder climates in plants, for example by increasing number or size of leaves, branches or roots under desert conditions (Gramlich et al., 2018). Moreover, changes in body width, head shape or eye size were shown to promote higher fitness in some fishes (Nichols et al., 2015), while larger heads with stronger bite and larger testes promoted better sexual performance in reptiles (Yang et al., 2018). Introgression of morpho-physiological traits also promotes higher fitness in some rodents in environments with lower precipitation and temperatures (Boratyński et al., 2011). Ancient events of adaptive introgression have even allowed humans to adapt to island environments by decreasing their size (Mondal et al., 2016). Colour change through adaptive introgression was reported in insects (Dasmahapatra et al., 2012; Enciso-Romero et al., 2017), mammals (Jones et al., 2018; Melo-Ferreira et al., 2014) and fishes (Meier et al., 2017; Mims et al., 2010). Colour change is frequently associated with increasing mating performance (Salazar et al., 2010; Yang et al., 2018), better mimicry capacity (Naisbit et al., 2003; Zhang et al., 2016), higher success in escaping predators (Zhang et al., 2013) and in exploring new habitats (Mims et al., 2010) and as responses, for example, to climate change (Giska et al., 2019; Jones et al., 2018; Melo-Ferreira et al., 2014; Zhang et al., 2013).

73 As an opposite evolutionary force, competition may lead species or lineages to avoid
74 each other and to occupy a narrower and differentiated optima and set of conditions.
75 If this effect is durable and prevalent enough, then it may lead to a species-specific
76 divergent trait displacement due to a differential exploitation of resources (Melville,
77 2002; Pfennig and Pfennig, 2010).

78 Competition has been reported to drive divergence in phenological traits, like changing
79 floral shape of angiosperms in response to altitudinal gradients (Kooyers et al., 2017),
80 and to promote functional and biomechanical differences in jaw closure of
81 salamanders (Adams and Rohlf, 2000). Moreover, competition has been shown to play
82 a role in beak size divergence and larynx morphology in birds, both relevant traits for
83 diet adaptations, and song characteristics, thus influencing sexual selection and
84 species recognition (Grant and Grant, 2006). Head morphology and size divergence
85 were also described as being the result of competition in spadefoot toads, in response
86 to omnivore or carnivore diet (Pfennig and Murphy, 2000).

87 Despite the relevance of morphological traits for species adaptive capacity and
88 individual fitness, the impact of hybridization on morphological traits when occurring
89 in sympatry or parapatry remains largely unknown. Cryptic species are an extreme
90 case among closely-related taxa for being morphologically identical but genetically
91 distinct (Jones, 1997). Due to their phylogenetic proximity and partial niche overlap, as
92 well as morphological similarity and high potential for hybridization, they represent
93 excellent case studies for the effect of antagonistic evolutionary processes on
94 morphological trait displacement, particularly when associated with sympatric or
95 parapatric distributions (Marsteller et al., 2009; Tene Fossog et al., 2015).

96 Notably, in the Iberian Peninsula, over 20% of known bats species show cryptic
 97 diversity (Ibáñez et al., 2006; Juste et al., 2004). Some of the cryptic species pairs
 98 exhibit high genetic divergence, such as *Eptesicus serotinus* (Schreber 1774) and *E.*
 99 *isabellinus* (Temminck 1840), which show over 16% divergence in the mtDNA
 100 Cytochrome b gene (Ibáñez et al., 2006). A comparative recent study supports a more
 101 pronounced and geographically structured intraspecific genetic variation within *E.*
 102 *isabellinus* (Centeno-Cuadros et al., 2019). This species has experienced a rapid post-
 103 glacial expansion earlier, heading northwards until occupying its current range. *E.*
 104 *serotinus* is thought to have expanded southwards from Central Europe, likely arriving
 105 later than *E. isabellinus* to the ecotone of central Iberia where both species meet
 106 (Centeno-Cuadros et al., 2019). Currently, *E. serotinus* is distributed along the Atlantic
 107 region of Iberia (colder and wetter) while *E. isabellinus* mainly occurs in the
 108 Mediterranean region (hotter and drier) (Santos et al., 2014). Across their ranges, the
 109 two species geographically avoid each other, indicating that interspecific competition
 110 likely shaped their broad-scale distributions (Novella-Fernandez et al. 2021). With a
 111 vast allopatric distribution, the species share a restricted contact zone, where they
 112 interbreed (Centeno-Cuadros et al., 2019). Although nuclear markers identified a male-
 113 mediated hybridization, there is no evidence of mitochondrial introgression, contrary
 114 to what is known for other *Eptesicus* (Neubaum et al., 2007). Moreover, ongoing
 115 hybridization is asymmetric, occurring mainly from *E. isabellinus* to *E. serotinus* (28%
 116 hybrids in *E. serotinus* colonies and 2.7% in *E. isabellinus* colonies) (Centeno-Cuadros et
 117 al., 2019).
 118 This study aims to understand the effect of this introgressive hybridization on
 119 morphological traits of the two cryptic Iberian *Eptesicus* bats in face of counteracting

120 evolutionary forces from interspecific competition. We addressed three main
121 objectives: 1) Test for morphological differences between cryptic *Eptesicus* species; 2)
122 Determine the influence of sympatry and allopatry on patterns of morphological
123 variation (wing, dentition and colour traits); 3) Assess the efficiency of classification
124 statistics on species identification even in the presence of hybrids. Clarifying these
125 objectives could elucidate how potential natural gene transfer through introgression
126 can allow recipient bat species to incorporate into its genome alleles responsible for
127 the presence of novel morphological traits.

128

129 **2 | METHODS**

130 **2.1 | STUDY AREA**

131 We searched for *Eptesicus* bat colonies between 1998 and 2014 along a North–South
132 gradient across the Iberian Peninsula, including allopatric areas of only *E. serotinus* in
133 the north, a central region of sympatric zone and allopatric areas of *E. isabellinus* in the
134 south. Field sampling methods were described in previous publications (Centeno-
135 Cuadros et al., 2019; Santos et al., 2014) as well as the location of all sampled colonies
136 (Centeno-Cuadros et al., 2019). The methods were performed in accordance with
137 relevant guidelines and regulations and approved by the Ethical committee at the EBD-
138 CSIC (Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas)
139 that granted protocol approval.

140

141 **2.2 | SAMPLING DESIGN**

142 Wing membrane biopsies (3 mm) were collected according to Worthington-Wilmer
143 and Barratt (1996) from all captured bats. The samples were kept in 96% ethanol at

144 –20°C until processed in the laboratory for molecular analysis to confirm species
 145 identification (see Centeno-Cuadros et al., 2019 for laboratory procedures).
 146 Wing morphology variables were measured with a calliper and included the lengths of
 147 the forearm (FA), metacarpals of the III and V fingers and the first phalanges of the
 148 same fingers, as well as the length of the upper dental series (canine to third molar -
 149 CM3) and the rostral width measured at the canines' level (C1-C1) (Figure 1).
 150 Coat colour was quantified by measuring the reflectance through a High Resolution
 151 Colorimeter (Spectrophotometer CM-2600d/2500d, Konica, Minolta). Two
 152 measurements were obtained for dorsal and ventral colours from each bat. Each
 153 measurement was the average of three light flashes' reflectance. Reflectance was
 154 measured at a wavelength band from 350 to 740 nm and was decomposed according
 155 to the colour space defined by CIELAB colour space, which included three parameters,
 156 L*, a* and b*. L* represents perceptual lightness, and a* and b* a four colours' scale,
 157 from red to green and blue to yellow, respectively (Figure S1) (Illumination, 2004).
 158 To study the effect of interspecific responses of *E. serotinus* and *E. isabellinus* and their
 159 hybrids, bats were clustered into five experimental groups: allopatric *E. isabellinus*,
 160 sympatric *E. isabellinus*, hybrids (individuals classified as hybrids by Centeno-Cuadros
 161 et al. (2019) based on genetic data, using a conservative criteria), sympatric *E.*
 162 *serotinus* and allopatric *E. serotinus*. We assumed that both species were
 163 geographically isolated from each other and the respective hybrids within the
 164 allopatric groups. On the contrary, in the sympatric groups, each species co-existed
 165 with the other species and their hybrids. The geographic classifications of each
 166 experimental group were based on previous studies (Ibáñez et al., 2006; Santos et al.,
 167 2014; Centeno-Cuadros et al. 2019).

168

169 **2.3 | STATISTICAL ANALYSES**170 *The effect of geographic origin and hybrids presence on bat morphometry*

171 We used General Linear Models to assess whether geographic relationships
 172 significantly affected the morphometry and/or the colour of the studied bats. We
 173 performed a non-parametric MANOVA (Maroco, 2007) on the morphological variables
 174 because homogeneity of variance could not be assumed according to the Box's M tests
 175 (Morphometry: Box's $M=133.73$; $F_{(84, 16828.68)}=1.393$; ns; Colour: Box's $M=215.69$; $F_{(63, 1824.12)}=2.480$; ns) even after trying several data transformations ($\log_{10}$, $\ln$, $\arcsin$, etc.).
 176
 177 We performed a Kruskal-Wallis test to identify which morphometric traits and colour
 178 variables were significantly different, followed by multiple comparisons by the post-
 179 hoc Fisher's LSD test to check for differences between groups (Maroco, 2010).

180

181 *Summarizing and comparing morphological variables*

182 The original morphometric space of the wing and dentition variables was summarized
 183 into its main components by a principal component analysis (PCA) with the
 184 symmetrical normalization method (Maroco, 2010). The eigenvalue rule greater than 1
 185 was used as criterion for components' retention alongside the scree-plot. We analysed
 186 the internal consistency of each component through Cronbach's alpha (Maroco, 2010).
 187 After the validation of both assumptions for multivariate normal distribution and
 188 homogeneity of variance-covariance ($M=13.98$; $F_{(12, 7934.55)}=1.104$, $p=0.352$), we
 189 performed a MANOVA over the PCA's axes to evaluate the relationship of the five
 190 experimental groups with morphometric traits. When the MANOVA detected
 191 significant effects, we performed an ANOVA for each component (PC1 and PC2),

192 followed by multiple comparison through Tukey's HSD post-hoc test. Again, according
 193 to the Box's M tests, even after transformation, the homogeneity of covariance could
 194 not be assumed (Box's $M=30.41$; $F_{(12, 2323.67)}=2.250$; ns) for retained colour's PCA. In
 195 order to assess whether geographic origin affected colour variables, we performed a
 196 non-parametric MANOVA (Maroco, 2010), followed by the tests described above
 197 (Maroco, 2010). We carried out all analyses with $\alpha=0.05$ in SPSS Statistics software (v.
 198 22; SPSS Inc, Chicago, IL), producing all visualizations through "ggplot2" R package
 199 (Wickham, 2016).

200

201 *Classification statistics with and without hybrids' presence*

202 We used two classification algorithms to classify both species in sympatry according to
 203 the morphological variables: discriminant function analysis (DFA - quadratic with
 204 cross-validation) and the support vector machines (SVM - with a machine learning
 205 approach).

206 The morphometric matrices fulfils the assumptions of normal distribution and
 207 homogeneity of variance so we proceeded with parametric analyses (Morphometry
 208 with hybrids: Box's $M=38.33$; $F_{(28, 32463.13)}=1.267$; $p=0.157$; Morphometry without
 209 hybrids: Box's $M=11.10$; $F_{(10, 5819.66)}=0.996$; $p=0.444$).

210 The data were firstly included in two stepwise discriminant analyses with the method
 211 of Wilks' Λ used to identify which of the morphological and colour variables under
 212 study can better discriminate both parental species with and without the presence of
 213 hybrids. Again, homogeneity of the variance-covariance matrices could not be
 214 assumed for the colour variables (Colour with hybrids: Box's $M=37.65$, $F_{(10, 11071.13)}=3.474$, ns; Colour without hybrids: Box's $M=38.06$, $F_{(10, 4588.83)}=3.414$, ns). Still,

216 we proceeded with analysis because the discriminant analysis is robust to violation of
 217 assumptions when (i) the size of the smallest group (sympatric *E. serotinus*) is greater
 218 than the number of variables in the study and (ii) the means of the groups are not
 219 proportional to their variances (Stevens 1986). Finally, we used Classification Statistics
 220 to obtain the classification functions and to assign species identification according to
 221 morphometric traits and/or colour variables. All DFA analyses were carried out with
 222 $\alpha=0.05$.
 223 In addition, a support-vector machine (SVM) algorithm was performed using the
 224 principal components extracted from each PCA (morphometry and colour), through
 225 “tidyverse” (performing data manipulation) (Wickham et al., (2019), “kernlab”
 226 (Karatzoglou et al., 2004) and “e1071” R packages (Meyer et al., 2012) (performing
 227 calculations and producing visualizations). The kernel functions of the support vector
 228 machines used a radial basis function with a gamma parameter ranging from 0.1, 1, 10,
 229 100 and 1000. For each value of gamma, the SVM was reinitialised 20-times to
 230 increase the chance of obtaining an optimal classifier (Redgwell et al., 2009; Sáez et al.,
 231 2019). For Classification Statistics the algorithm of the SVM was trained for every
 232 target case in the dataset (each species) (Redgwell et al., 2009). All classifiers were
 233 then combined and categorised for each morphological trait as either belonging to a
 234 specific class, or not. Each bat was considered as classified correctly only if a single
 235 support vector machine classified it and if validated by molecular identification.

236

237 *Quantification of the impact of the hybrids on the external morphological traits overlap*
 238 *between species*

We repeated the entire statistical procedure after extracting from the dataset all individuals classified as hybrids in Centeno-Cuadros et al. (2019). We compared the classification performance of both algorithms in the sympatric population with hybrids versus the same population after excluding them. This approach made it possible to calculate the contribution of hybrids to the overlap of morphological traits with their cryptic parental species.

245

246 **3 | RESULTS**

247 **3.1 | Testing for morphological differences between cryptic *Eptesicus* species**

Our results showed significant differences of both morphometric and colour variables along the experimental groups. Morphometric differences occurred for the variables FA, D3 MC, D5 MC, D5 F1, C1-C1 and CM3 but not for the variable D3 F1 (Table 1). For coat colour, we found significant differences between the groups in the variables L* dorsal, a* dorsal, b* dorsal, a* ventral and b* ventral, but not for the variable L* ventral (Figure 2). The information between both morphometric and colour variables was summarized in two main orthogonal components, explaining respectively 59.8% and 83.4% of the total variance of the original morphometric and colour variables (Table S2). The first morphometric component was associated with bats' "Size", whereby generally, the weight of all variables was very high and positive. The second morphometric component essentially summarized the wing "Shape", namely the metacarpals and first phalanges proportion. Additionally, the inversely proportional relationship between the length of the first phalanges and the dentition variables, mainly CM3, had a very high and negative score in this second component (Table S2). Despite an evident overlap, the two-dimensional PCA map showed that *E. serotinus* is

generally larger in both wing and dentition, particularly in the allopatric zone with respect to *E. isabellinus*. In sympatry there was a greater overlap between both species despite maintaining the same pattern (Figure 3).

E. isabellinus both in allopatry and sympatry showed a greater proportion between first phalanges and both metacarpals (e.g. smaller ratio of length of both metacarpals to first phalange), revealing an inversely proportional relationship between the length of the first phalanges and both dentition variables (larger phalanges and smaller C1-C1 and mainly CM3) (Figure 3). In contrast, *E. serotinus* revealed, in both sympatry and allopatry, to have substantially smaller first phalanges relative to metacarpals, as well as to both dentition variables (mainly CM3) (Figure 3).

The first colour component of the PCA was associated with a range of colours from grey to brown, named as "a*b* Grey-Brown scale", while the second component essentially summarized the "L*Brightness" (Table S2). Despite an evident overlap, it was possible to characterize allopatric *E. serotinus* as being darker and greyer by showing a combination of higher black, green and yellow components in both dorsal and ventral colourations (Figure 4). All the remaining groups varied mainly along the brown pallet by having higher values for red and blue. Sympatric *E. serotinus* was in the other extreme of that Grey-Brown colour pallet, being the brownest group (Table S4). Likewise, sympatric *E. serotinus* shared the darkest position with allopatric *E. serotinus*, into brightness scale ("L* brightness"). Allopatric *E. isabellinus* was the brightest group. In sympatry, once again, *E. isabellinus* showed brightest colour patterns. The ventral colour was always brighter than the dorsal one in all experimental groups due to its higher L* values, showing even more subtle colour differences between groups (Figure 2).

287

288 *Sympatry vs Allopatry – influence on morphology*

289 There were no significant differences in the bats' size and shape between allopatric
 290 and sympatric groups within each species (except in metacarpals). However, all
 291 morphological variables differed significantly between allopatric groups. Regarding
 292 morphometric variables (D5 MC, D5 F1 and C1C1), especially for bats' "shape", these
 293 significant differences disappear in sympatry (a detailed description of the
 294 morphometric comparisons is available in Supplemental material).
 295 Regarding the colour variables, all experimental groups differed significantly from
 296 allopatric *E. serotinus* in the a* b* Grey-Brown scale, which were the only individuals in
 297 the grey range of the colour pallet. In terms of brightness, allopatric *E. serotinus* was
 298 only not significantly different from individuals of the same species when in sympatry
 299 (bats were equally dark, though in sympatry they tended to be significantly browner).
 300 In sympatry, both species also differed significantly, however, contrary to the
 301 morphometric variables, this difference was slightly greater than that found between
 302 species in allopatry.

303

304 *Hybrids vs Parental species – impact of hybridization on morphology*

305 Hybrids did not differ significantly from the other groups of allopatry/sympatry in wing
 306 size (except for metacarpals), showing intermediate wing morphometric values
 307 relative to both parental species. Hybrids differed significantly in the dentition
 308 between the two species, even in comparison with both sympatric groups with which
 309 they coexist (e.g. CM3). Nonetheless, hybrids showed consistently intermediate
 310 phenotypes in both dentition and wing size, as well as wing shape (a detailed

description of the morphometric comparisons between hybrids and parental species is available in the Supplemental material).

Hybrids showed the brightest pelage colour (both in their dorsal and ventral coat), although not significantly different from *E. isabellinus* in both groups (sympatry and allopatry) (Figure 3; Table S5). On the other hand, hybrids were significantly browner than allopatric *E. serotinus* and they were also the brownest group together with sympatric *E. serotinus* (Table S5).

3.2 | Species discrimination through classification statistics

Stepwise DFA with and without hybrids

The morphometric stepwise DFA generated one discriminant function mainly defined by D3_MC and CM3 ($\Lambda=0.579$, $\chi^2_{(7)} = 53.773$, $p<0.001$). The percentage of individuals classified correctly in the presence of hybrids was 81.7%. After hybrids removing, discriminant analysis generated also one discriminant function, with FA, D3_MC, D5_MC (marginally significant [$F=3.450$, $p=0.069$]) and CM3 as statistically significant variables ($\Lambda=0.632$, $\chi^2_{(4)}=21.073$, $p<0.001$). The results of Classification Statistics showed that the total percentage of individuals classified correctly increased to 84.0% after hybrids removing.

The colour stepwise DFA generated also only one discriminant function, with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant variables ($\Lambda=0.842$, $\chi^2_{(4)}=10.115$, $p=0.039$). The percentage of individuals classified correctly in the presence of hybrids was 71.4%. After removing the hybrids, the colour discriminant analysis generated also one discriminant function, once again with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant ($\Lambda=0.762$, $\chi^2_{(4)}=14.114$,

334 $p=0.007$). The results of Classification Statistics showed that the total percentage of
 335 individuals classified correctly increased to 78.6% after hybrids removing.

336

337 *Support Vector Machine with and without hybrids*

338 SVM generated one discriminant function based on morphometric PC1 and PC2 as
 339 predictors' variables that summarized all morphometric traits. After simulations, the
 340 results of Classification Statistics showed that the percentage of individuals classified
 341 correctly in the presence of hybrids was 75.0%. Without hybrids, SVM generated also
 342 one discriminant function. The percentage of individuals classified correctly increased
 343 to 76.9% after removing hybrids.

344 Based on colour PC1 and PC2 as predictors' variables, SVM generated also one
 345 discriminant function. After simulations, the results of Classification Statistics showed
 346 that the percentage of individuals classified correctly in the presence of hybrids was
 347 68.3%. After hybrids removing, the colour SVM also generated one discriminant
 348 function. The results of Classification Statistics showed that the total percentage of
 349 individuals classified correctly increased to 76.8% after removing hybrids (detail
 350 description is available in Supplemental Material).

351 Finally, both species showed a statistically significant differential behaviour in relation
 352 to the correct classification rate for both classification methods tested (χ^2_{kW}
 353 (1)=10.678, $p=0.01$, $N=16$) and *E. isabellinus* individuals were significantly classified
 354 correctly than the individuals of *E. serotinus* ($F=15.976$; $p=0.001$) (Table 2).

355

356 *General impact of introgressive hybridization on classification success*

Based on the two tested algorithms and the two sets of traits (morphometry and colour), the overlap between the two parental species was around $25.9 \pm 5.76\%$. The contribution of hybrids to overlap among parental species was significantly higher for colour ($26.0 \pm 1.13\%$) than morphometry ($10.6 \pm 4.24\%$) ($F=24.602$; $p=0.038$). Overall, hybrids contributed on average $18.3 \pm 9.25\%$ to traits overlapping between their parental species (Table 2).

4 | DISCUSSION

Differences in morphology have been commonly used to differentiate taxa undergoing preliminary steps of macroevolution. However, as predicted by the particular challenges posed by the similarity of cryptic species, overlap in all morphological variables was the most evident pattern. Yet, for the two species of Iberian *Eptesicus* the differences in size and shape were strikingly larger when comparing allopatric populations than when comparing populations in sympatry. Still, the high overlap in all morphological traits meant that no single variable could be used as a diagnostic characteristic to distinguish the two species. Even so, the analyses of the external morphological traits (wing and dentition) confirmed that *E. serotinus* is slightly, but significantly, larger and darker than *E. isabellinus*. Although allopatric *E. serotinus* bats showed a greyer coat, the remaining four groups were distributed along the brown pallet, with sympatric groups showing the brownest coat. Molecularly confirmed hybrids showed intermediate morphometric values between both parental species in terms of size and shape, particularly when compared to allopatric populations. Hybrids were significantly browner than allopatric *E. serotinus*, showing the brightest coats of all, significantly brighter than both allopatric and sympatric *E. isabellinus*. Thus, alongside a probable process of adaptation to the local environmental conditions in

the sympatric zone, bidirectional adaptive introgression (even if asymmetrical) can lead to convergence in size and shape, increasing morphological overlap among parental species (Grant and Grant, 2016). Hybrids, distributed along a sympatric zone, show intermediate values in morphometric traits (both in size and shape), while differences between both parental species in morphometry decreased significantly in sympatry. Therefore, it is probable that hybridization and adaptive introgression affect the morphology of the parental species through backcrossing (Boratyński et al., 2011; Gramlich et al., 2018; Nichols et al., 2015; Yang et al., 2018).

External traits are priority targets for natural selection as they directly impact the fitness of individuals and the ecological niche in which they occur (Ochoa-López et al., 2020). According to Grant and Grant (2016), it is possible to make genetic inferences grounded in two morphological aspects, size and shape, due to the narrow connection between introgressed alleles and species morphology. This fact is based on high frequency of heritable variation and polygenic origin of external traits (Grant and Grant, 1994). This relationship is supported by evidence from genes that were identified as regulating the development of vertebrate' size and shape (Abzhanov et al., 2006; Abzhanov et al., 2004; Mallarino et al., 2011). There is considerable amount of evidence that supports the influence of adaptive introgression on morphometry impacting both size and shape (Boratyński et al., 2011; Nichols et al., 2015; vonHoldt et al., 2016; Yang et al., 2018). Adaptive introgression consequences seem plastic enough to be able to promote divergent adaptations in response to the particularities of environmental conditions (Gramlich et al., 2018). For example, adaptive introgression events promoted size reduction in ancient humans, allowing them to adapt to insular

404 environments (Mondal et al., 2016), while on the other hand they enabled carnivores
405 to obtain larger prey by increasing their body size (vonHoldt et al., 2016).
406 Adaptive introgression of bat morphological traits should respond to the
407 circumstances in which they co-occur within the sympatric zone. Adaptive
408 introgression in *Eptesicus* dentition and wing morphology, for example, could impact
409 their trophic space, being connected to their diet, as well as their ecological niches,
410 responding directly to the macro-habitat characteristics of the sympatric zone and to
411 local prey availability. With increasing dentition size, *E. isabellinus* is more able to
412 capture larger prey, while the smaller dentition of *E. serotinus* makes it more efficient
413 in capturing smaller prey (Santana et al., 2011). On the other hand, increased wing size
414 and shape changes (namely decreasing the proportion between first phalanges and
415 metacarpals) may have enabled *E. isabellinus* to become more efficient in exploring
416 more open habitats (Kalcounis and Brigham, 1995) and disperse over longer distances
417 (Muijres, et al., 2011). In contrast, decreased wing length and shape changes (namely
418 increasing the proportion between first phalanges and metacarpals) may have
419 rendered *E. serotinus* more prone to explore close habitats than those used in
420 allopatry (Kalcounis and Brigham, 1995).
421 Mammals are not frequently colourful being mostly colour-blind to the red-green
422 spectrum because they tend to be crepuscular or nocturnal (Bradley and Mundy,
423 2008). Bats are an extreme example of it. Under low-light conditions, dichromatic
424 vision seems to be advantageous over colour vision because the reduced number of
425 colour-sensitive cones in the retina means they focus on more light-sensitive rods, thus
426 improving their visual acuity (Müller and Peichl, 2005). Similar to other nocturnal
427 mammals, bats are commonly shades of black, grey or brown, with only small colour

428 differences between species (Winter et al., 2003). Thus, the differences found in bat
429 colours are substantially smaller than morphometric ones. Still, contrary to the
430 patterns found in morphometry, colour characteristics of hybrids are in the extreme of
431 the brown colour palette. In parallel, they are also consistently the brightest ones. Still,
432 the differences in colour parameters of both parental species seem slightly greater in
433 sympatry.

434 Colour patterns have been linked to communication and physiological processes, such
435 as thermoregulation (Caro, 2005). However, most bats use vocal and olfactory cues
436 rather than visual signals to perceive the environment and for social interactions
437 (Chaverri et al., 2018). On the other hand, brighter colours cannot affect mating
438 recognition without the development of tri- or tetra-chromatic vision (Caro, 2005). Bat
439 colouration is most probably the result of adaptation to a nocturnal niche, likely
440 associated with concealment from predators (Caro, 2005). So, bats colouration should
441 reflect environmental pressures, for example, from the roosts that they occupy.

442 Different colour patterns can be expected in species occupying different types of
443 roosts because roost conditions differ in their visual environment (e.g. luminance and
444 colour spectrum), as well as in their level of exposure to twilight or diurnal predators
445 (Caro, 2005).

446 The two Iberian *Eptesicus* species do not share roosts, despite their colonial behaviour
447 with nursery colonies comprising up to 300 animals (Dietz et al., 2009), and their
448 tendency to share roosts with other species (Martinoli et al., 2020). This suggests that
449 these two bats may compete actively for the best spots when in sympatry. *E. serotinus*
450 colonies are mainly associated with buildings in Central Europe (Dinger, 1991), while in
451 the Mediterranean region, they also roost in crevices of cliffs and at the entrance of

452 caves (Dietz et al., 2009). *E. isabellinus*, instead, seems to prefer crevices (cliffs or
453 bridges) and tree hollows in date palms in North Africa (Kowalski and Rzebik-Kowalska,
454 1991).

455 Resource partitioning and geographic avoidance have been described for several pairs
456 of cryptic bat species across Europe (Nicholls and Racey, 2006, Novella-Fernandez et
457 al., 2020, Novella-Fernandez et al., 2021). Cryptic species can exploit different
458 microhabitats and roosts to avoid competition when sharing the same sympatric area
459 (Novella-Fernandez et al., 2020), and this may be the case for the Iberian *Eptesicus* in
460 sympatry. Therefore, roost-mediated coevolution could be one plausible hypothesis to
461 explain the different colour patterns in the bats. The light environment of nocturnal
462 niches can be dominated by yellow-green wavelengths, for example in more closed
463 foraging spots, which coincides with the spectral sensitivity of bats (Galván et al.,
464 2020). Therefore, the natural pressure of nocturnal light conditions occurring over the
465 various microhabitats that are explored by each species in sympatry may have
466 interacted with diurnal light conditions in roosts to favour the pelage colour
467 differences in *Eptesicus*. Thus, any possible differences promoted by the interactions
468 between the two cryptic bats in sympatry through potential competition for roosts and
469 microhabitats will not only have consequences for their colour and their
470 discrimination, but fundamentally for their interactions with predators and the
471 environment (Wang et al., 2005).

472 The extent of morphological overlap between the two cryptic bats was around 26%.
473 The presence of hybrids contributes substantially to a fifth of the total traits overlap.
474 Even so, classification statistics showed high differentiation rate between the two

parental species in sympatry, particularly for *E. isabellinus*, with higher correct identification rates for morphometric traits, which were more distinct than colour. Discriminant functions showed D3_MC and CM3 are the main variables discriminating between the species. However, only CM3 showed limited overlap between them with values below 7.3 cm found only in *E. isabellinus*, whereas values above 8.4 cm only in *E. serotinus*. Therefore CM3 is the only measure that can be used to confidently distinguish between the two species.

Morphological diversity is a critical facet of evolution and adaptation (Anderson et al., 2009). However, morphology is also extremely important for field identification, particularly for endangered species. Accurate field identification is particularly important for *Eptesicus* species because they are hosts of different lineages of the European bat Lyssavirus type 1 (EBLV-1), the most common rabies related virus found in European bats (Vázquez-Moron et al., 2011, Mingo-Casas et al., 2018). Moreover, using morphological traits for cryptic species identification in sympatry, instead of molecular approaches that are frequently used for *in-situ* identification, could be particularly useful due to the reduced associated costs.

491

492 *Caveats and limitations*

We classified individuals as hybrids following Centeno-Cuadros et al. (2019) and applying the conservative criteria proposed by Burgarella et al. (2009) to the microsatellite genotypes to guarantee there were no misclassifications. On the other hand, this approach does not allow us to exclude the possibility of the presence of other possible hybrids in the other sympatric groups. In addition, the lab methodology used to detect hybrids does not detect the presence of second generation and later

499 hybrids, as well as backcrosses. These potential overlooked hybrids may be falsely
500 inflating the overlap between morphological characteristics of the two sibling bat
501 species. Despite this, we still obtained high values of correct identifications in the
502 classification statistics, which indicates that the proportion of undetected hybrids was
503 low.

504 **5 | CONCLUSIONS**

505 We demonstrated that cryptic Iberian *Eptesicus* species can coexist during secondary
506 contacts under antagonistic evolutionary forces, imposed simultaneously by
507 introgressive hybridization and potential niche-partitioning. This balance may be
508 driven by the partitioning of resources along two niche axes, microhabitats and roosts.
509 The situation may be different in other niche axes, such as trophic resources, prey
510 characteristics and macro-habitats, which are under adaptive pressure from local
511 conditions. Divergence due to niche differentiation and adaptive introgression should
512 impact on different aspects of morphology (Abrams, 1986). The latter seems to have a
513 greater effect on the divergence of bat pelage colour. Instead, adaptive introgression
514 seems to act as a homogenising force over morphometric traits, such as wing and
515 dentition shape and size. Finally, we argue that a balance between adaptive
516 introgression and interspecific competition, beyond mediating species divergence,
517 shapes their interactions with the environment by impacting morphological traits
518 under selection.

519

520

521

522

523

524

525

526 **REFERENCES**

527 Abrams, P.A. (1986). Character displacement and niche shift analyzed using consumer-
528 resource models of competition. *Theoretical population biology* 29, 107-160.

529 Abzhanov, A., Kuo, W.P., Hartmann, C., Grant, B.R., Grant, P.R., and Tabin, C.J. (2006).

530 The calmodulin pathway and evolution of elongated beak morphology in Darwin's
531 finches. *Nature* 442, 563-567.

532 Abzhanov, A., Protas, M., Grant, B.R., Grant, P.R., and Tabin, C.J. (2004). Bmp4 and

533 morphological variation of beaks in Darwin's finches. *Science (New York, NY)* 305,
534 1462-1465.

535 Adams, D.C., and Rohlf, F.J. (2000). Ecological character displacement in

536 *Plethodon*: Biomechanical differences found from a geometric

537 morphometric study. *Proceedings of the National Academy of Sciences* 97, 4106-
538 4111.

539 Aleksic, J.M., Skondric, S., and Lakusic, D. (2018). Comparative phylogeography of

540 capitulate *Campanula* species from the Balkans, with description of a new species,

541 *C. daucooides*. *Plant Systematics and Evolution* 304, 549-575.

542 Alexander, A.M., Su, Y.C., Oliveros, C.H., Olson, K.V., Travers, S.L., and Brown, R.M.

543 (2017). Genomic data reveals potential for hybridization, introgression, and

544 incomplete lineage sorting to confound phylogenetic relationships in an adaptive

545 radiation of narrow-mouth frogs. *Evolution; international journal of organic*

546 *evolution* 71, 475-488.

- 547 Anderson, E., and Hubricht, L. (1938). Hybridization in *Tradescantia*. III. The evidence
548 for introgressive hybridization. *American Journal of Botany* 25, 396-402.
- 549 Anderson, R.P., Peterson, A.T., and Gómez-Laverde, M. (2002). Using niche-based GIS
550 modeling to test geographic predictions of competitive exclusion and competitive
551 release in South American pocket mice. *Oikos* 98, 3-16.
- 552 Anderson, T.M., vonHoldt, B.M., Candille, S.I., Musiani, M., Greco, C., Stahler, D.R.,
553 Smith, D.W., Padhukasahasram, B., Randi, E., Leonard, J.A., et al. (2009). Molecular
554 and evolutionary history of melanism in North American gray wolves. *Science*
555 (New York, NY) 323, 1339-1343.
- 556 Baiz, M.D., Tucker, P.K., and Cortés-Ortiz, L. (2019). Multiple forms of selection shape
557 reproductive isolation in a primate hybrid zone. *Molecular ecology* 28, 1056-1069.
- 558 Boratyński, Z., Alves, P.C., Berto, S., Koskela, E., Mappes, T., and Melo-Ferreira, J.
559 (2011). Introgression of mitochondrial DNA among *Myodes* voles: consequences
560 for energetics? *BMC Evolutionary Biology* 11, 355.
- 561 Bradley, B.J., and Mundy, N.I. (2008). The primate palette: The evolution of primate
562 coloration. *Evolutionary Anthropology Issues News and Reviews* 17, 97-111.
- 563 Brower, A.V.Z. (2013). Introgression of wing pattern alleles and speciation via
564 homoploid hybridization in *Heliconius* butterflies: a review of evidence from the
565 genome. *Proceedings of the Royal Society B-Biological Sciences* 280, 9.
- 566 Burgarella, C., Lorenzo, Z., Jabbour-Zahab, R., Lumaret, R., Guichoux, E., Petit, R.J.,
567 Soto, Á., and Gil, L. (2009). Detection of hybrids in nature: application to oaks
568 (*Quercus suber* and *Q. ilex*). *Heredity* 102, 442-452.
- 569 Cahill, J.A., Stirling, I., Kistler, L., Salamzade, R., Ersmark, E., Fulton, T.L., Stiller, M.,
570 Green, R.E., and Shapiro, B. (2015). Genomic evidence of geographically

- 571 widespread effect of gene flow from polar bears into brown bears. *Molecular*
572 *ecology* 24, 1205-1217.
- 573 Caro, T. (2005). The Adaptive Significance of Coloration in Mammals. *BioScience* 55,
574 125-136.
- 575 Centeno-Cuadros, A., Razgour, O., García-Mударra, J.L., Mingo-Casas, P., Sandonís, V.,
576 Redondo, A., Ibáñez, C., de Paz, O., Martinez-Alós, S., Pérez Suarez, G., et al.
577 (2019). Comparative phylogeography and asymmetric hybridization between
578 cryptic bat species. *Journal of Zoological Systematics and Evolutionary Research*
579 57, 1004-1018.
- 580 Chaverri, G., Ancillotto, L., and Russo, D. (2018). Social communication in bats.
581 *Biological Reviews* 93, 1938-1954.
- 582 Dasmahapatra, K.K., Walters, J.R., Briscoe, A.D., Davey, J.W., Whibley, A., Nadeau, N.J.,
583 Zimin, A.V., Hughes, D.S.T., Ferguson, L.C., Martin, S.H., et al. (2012). Butterfly
584 genome reveals promiscuous exchange of mimicry adaptations among species.
585 *Nature* 487, 94-98.
- 586 de Lafontaine, G., Prunier, J., Gerardi, S., and Bousquet, J. (2015). Tracking the
587 progression of speciation: variable patterns of introgression across the genome
588 provide insights on the species delimitation between progenitor-derivative
589 spruces (*Picea mariana* x *P. rubens*). *Molecular ecology* 24, 5229-5247.
- 590 Dinger G. (1991). Winternachweise von Breitflügelfledermaus (*Eptesicus serotinus*) in
591 Kirchen. *Nyctalus* (N.F.). 7:614-616.
- 592 Dietz C, Von Helversen O, Nill D (2009) Bats of Britain, Europe and Northwest Africa.
593 A&C Black Publishers Ltd. 320-333.

- 594 Djogbénou, L., Chandre, F., Berthomieu, A., Dabiré, R., Koffi, A., Alout, H., and Weill, M.
 595 (2008). Evidence of introgression of the ace-1(R) mutation and of the ace-1
 596 duplication in West African *Anopheles gambiae* s. s. *PloS one* 3, e2172.
- 597 Dunn, B., Paulish, T., Stanbery, A., Piotrowski, J., Koniges, G., Kroll, E., Louis, E.J., Liti,
 598 G., Sherlock, G., and Rosenzweig, F. (2013). Recurrent Rearrangement during
 599 Adaptive Evolution in an Interspecific Yeast Hybrid Suggests a Model for Rapid
 600 Introgression. *Plos Genetics* 9, 16.
- 601 Enciso-Romero, J., Pardo-Diaz, C., Martin, S.H., Arias, C.F., Linares, M., McMillan, W.O.,
 602 Jiggins, C.D., and Salazar, C. (2017). Evolution of novel mimicry rings facilitated by
 603 adaptive introgression in tropical butterflies. *Molecular ecology* 26, 5160-5172.
- 604 Gagnaire, P.A., Albert, V., Jonsson, B., and Bernatchez, L. (2009). Natural selection
 605 influences AFLP intraspecific genetic variability and introgression patterns in
 606 Atlantic eels. *Molecular ecology* 18, 1678-1691.
- 607 Galván, I., Vargas-Mena, J.C., and Rodríguez-Herrera, B. (2020). Tent-roosting may
 608 have driven the evolution of yellow skin coloration in *Stenodermatinae* bats.
 609 *Journal of Zoological Systematics and Evolutionary Research* 58, 519-527.
- 610 Giska, I., Farelo, L., Pimenta, J., Seixas, F.A., Ferreira, M.S., Marques, J.P., Miranda, I.,
 611 Letty, J., Jenny, H., Hackländer, K., et al. (2019). Introgression drives repeated
 612 evolution of winter coat color polymorphism in hares. *Proceedings of the National*
 613 *Academy of Sciences of the United States of America* 116, 24150-24156.
- 614 Gramlich, S., Wagner, N.D., and Horandl, E. (2018). RAD-seq reveals genetic structure
 615 of the F-2-generation of natural willow hybrids (*Salix* L.) and a great potential for
 616 interspecific introgression. *Bmc Plant Biology* 18, 12.

- 617 Grant, P.R., and Grant, B.R. (1994). PHENOTYPIC AND GENETIC EFFECTS OF
 618 HYBRIDIZATION IN DARWIN'S FINCHES. *Evolution; international journal of organic*
 619 *evolution* 48, 297-316.
- 620 Grant, P.R., and Grant, B.R. (2006). Evolution of Character Displacement in Darwin's
 621 Finches. *Science (New York, NY)* 313, 224-226.
- 622 Grant, P.R., and Grant, B.R. (2016). Introgressive hybridization and natural selection in
 623 Darwin's finches. *Biological Journal of the Linnean Society* 117, 812-822.
- 624 Ibáñez, C., García-Mudarra, J.L., Ruedi, M., Stadelmann, B., and Juste, J. (2006). The
 625 Iberian contribution to cryptic diversity in European bats. *Acta Chiropterologica* 8,
 626 277-297.
- 627 Illumination, I.C.o. (2004). A colour appearance model for colour management
 628 systems: CIECAM02. Technical Report No CIE 159: 2004.
- 629 Jones, G (1997). 'Acoustic signals and speciation: the roles of natural and sexual
 630 selection in the evolution of cryptic species', *Advances in the Study of Behavior*,
 631 vol. 26, pp. 317 - 354.
- 632 Jones, M.R., Mills, L.S., Alves, P.C., Callahan, C.M., Alves, J.M., Lafferty, D.J.R., Jiggins,
 633 F.M., Jensen, J.D., Melo-Ferreira, J., and Good, J.M. (2018). Adaptive introgression
 634 underlies polymorphic seasonal camouflage in snowshoe hares. *Science (New*
 635 *York, NY)* 360, 1355-1358.
- 636 Juste, J., Ibáñez, C., Muñoz, J., Trujillo, D., Benda, P., Karataş, A., and Ruedi, M. (2004).
 637 Mitochondrial phylogeography of the long-eared bats (*Plecotus*) in the
 638 Mediterranean Palaearctic and Atlantic Islands. *Molecular phylogenetics and*
 639 *evolution* 31, 1114-1126.

- 640 Kalcounis, M.C., and Brigham, R.M. (1995). Intraspecific variation in wing loading
641 affects habitat use by little brown bats (*Myotis lucifugus*). *Canadian Journal of*
642 *Zoology* 73, 89-95.
- 643 Karatzoglou A, Smola A, Hornik K, Zeileis A (2004). "kernlab – An S4 Package for Kernel
644 Methods in R." *Journal of Statistical Software*, 11(9), 1–20.
645 <http://www.jstatsoft.org/v11/i09/>.
- 646 Kooyers, N.J., James, B., and Blackman, B.K. (2017). Competition drives trait evolution
647 and character displacement between *Mimulus* species along an environmental
648 gradient. *Evolution; international journal of organic evolution* 71, 1205-1221.
- 649 Kowalski, K., and Rzebik-Kowalska, B. (1991). *Mammals of algeria*.
- 650 Latch, E.K., Harveson, L.A., King, J.S., Hobson, M.D., and Rhodes JR. (2006). Assessing
651 Hybridization in Wildlife Populations Using Molecular Markers: A Case Study in
652 Wild Turkeys. *The Journal of Wildlife Management* 70, 485-492.
- 653 Ma, F., Zhao, C., Milne, R., Ji, M., Chen, L., and Liu, J. (2010). Enhanced drought-
654 tolerance in the homoploid hybrid species *Pinus densata*: implication for its
655 habitat divergence from two progenitors. *New Phytologist* 185, 204-216.
- 656 Mallarino, R., Grant, P.R., Grant, B.R., Herrel, A., Kuo, W.P., and Abzhanov, A. (2011).
657 Two developmental modules establish 3D beak-shape variation in Darwin's
658 finches. *Proceedings of the National Academy of Sciences of the United States of*
659 *America* 108, 4057-4062.
- 660 Maroco, J. (2010) *Análise estatística com utilização do SPSS. 3ª edição. Edições Silabo*.
- 661 Marsteller, S., Adams, D.C., Collyer, M.L., and Condon, M. (2009). Six cryptic species on
662 a single species of host plant: morphometric evidence for possible reproductive
663 character displacement. *Ecological Entomology* 34, 66-73.

- 664 Martinoli, A., Mazzamuto, M.V., and Spada, M. (2020). Serotine *Eptesicus serotinus*
 665 (Schreber, 1774). Handbook of the Mammals of Europe, 1-17.
- 666 Mavárez, J., Salazar, C.A., Bermingham, E., Salcedo, C., Jiggins, C.D., and Linares, M.
 667 (2006). Speciation by hybridization in *Heliconius* butterflies. *Nature* 441, 868-871.
- 668 Meier, J.I., Sousa, V.C., Marques, D.A., Selz, O.M., Wagner, C.E., Excoffier, L., and
 669 Seehausen, O. (2017). Demographic modelling with whole-genome data reveals
 670 parallel origin of similar *Pundamilia* cichlid species after hybridization. *Molecular*
 671 *ecology* 26, 123-141.
- 672 Melo-Ferreira, J., Seixas, F.A., Cheng, E., Mills, L.S., and Alves, P.C. (2014). The hidden
 673 history of the snowshoe hare, *Lepus americanus*: extensive mitochondrial DNA
 674 introgression inferred from multilocus genetic variation. *Molecular ecology* 23,
 675 4617-4630.
- 676 Melville, J. (2002). Competition and character displacement in two species of scincid
 677 lizards. *Ecology letters* 5, 386-393.
- 678 Meyer D, Dimitriadou E, Hornik K, Weingessel A, Leisch F (2012). e1071: Misc
 679 Functions of the Department of Statistics, Probability Theory Group (Formerly:
 680 E1071), TU Wien. <https://cran.r-project.org/web/packages/e1071/index.html>.
- 681 Mims, M.C., Hulsey, C.D., Fitzpatrick, B.M., and Streelman, J.T. (2010). Geography
 682 disentangles introgression from ancestral polymorphism in Lake Malawi cichlids.
 683 *Molecular ecology* 19, 940-951.
- 684 Mingo-Casas P, Sandoni's V, Obo'n E, Berciano JM, Vazquez-Moron S, Juste J, et al.
 685 (2018) First cases of European bat lyssavirus type 1 in Iberian serotine bats:
 686 Implications for the molecular epidemiology of bat rabies in Europe. *PLoS Negl*
 687 *Trop Dis* 12(4): e0006290.

- 688 Mondal, M., Casals, F., Xu, T., Dall'Olio, G.M., Pybus, M., Netea, M.G., Comas, D.,
 689 Laayouni, H., Li, Q., Majumder, P.P., et al. (2016). Genomic analysis of
 690 Andamanese provides insights into ancient human migration into Asia and
 691 adaptation. *Nature Genetics* 48, 1066-1070.
- 692 Muijres F.T., Johansson L.C., Winter Y. and Anders H. (2011). Comparative aerodynamic
 693 performance of flapping flight in two bat species using time-resolved wake
 694 visualization. *J. R. Soc. Interface.* 81418–1428.
- 695 Müller, B., and Peichl, L. (2005). Retinal Cone Photoreceptors in Microchiropteran Bats.
 696 *Investigative Ophthalmology & Visual Science* 46, 2259-2259.
- 697 Naisbit, R.E., Jiggins, C.D., and Mallet, J. (2003). Mimicry: developmental genes that
 698 contribute to speciation. *Evolution & Development* 5, 269-280.
- 699 Neubaum, M.A., Douglas, M.R., Douglas, M.E., and O'Shea, T.J. (2007). Molecular
 700 Ecology of the Big Brown Bat (*Eptesicus fuscus*): Genetic and Natural History
 701 Variation in a Hybrid Zone. *Journal of Mammalogy* 88, 1230-1238.
- 702 Nicholls, B., and Racey, P. (2006). Habitat selection as a mechanism of resource
 703 partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus*
 704 *pygmaeus*. *Ecography* 29, 697-708.
- 705 Nichols, P., Genner, M.J., van Oosterhout, C., Smith, A., Parsons, P., Sungani, H.,
 706 Swanstrom, J., and Joyce, D.A. (2015). Secondary contact seeds phenotypic
 707 novelty in cichlid fishes. *Proceedings of the Royal Society B-Biological Sciences*
 708 282, 8.
- 709 Novella-Fernandez, R., Ibañez, C., Juste, J., Clare, E. L., Doncaster, C. P., & Razgour, O.
 710 (2020). Trophic resource partitioning drives fine-scale coexistence in cryptic bat
 711 species. *Ecology and evolution*, 10(24), 14122-14136.

- 712 Novella-Fernandez, R., Juste, J., Ibáñez, C., Rebelo, H., Russo, D., Alberdi, A., Kiefer, A.,
 713 Graham, L., Paul, H., Doncaster, C. P., & Razgour, O. (2021). Broad-scale patterns
 714 of geographic avoidance between species emerge in the absence of fine-scale
 715 mechanisms of coexistence. *Diversity and Distributions*, 27, 1606–1618.
- 716 Ochoa-López, S., Damián, X., Rebollo, R., Fornoni, J., Domínguez, C.A., and Boege, K.
 717 (2020). Ontogenetic changes in the targets of natural selection in three plant
 718 defenses. *New Phytologist* 226, 1480-1491.
- 719 Oliveira, R., Godinho, R., Randi, E., and Alves, P.C. (2008). Hybridization versus
 720 conservation: are domestic cats threatening the genetic integrity of wildcats (*Felis*
 721 *silvestris silvestris*) in Iberian Peninsula? *Philosophical transactions of the Royal*
 722 *Society of London Series B, Biological sciences* 363, 2953-2961.
- 723 Ottenburghs, J., Megens, H.J., Kraus, R.H.S., van Hooft, P., van Wieren, S.E.,
 724 Crooijmans, R., Ydenberg, R.C., Groenen, M.A.M., and Prins, H.H.T. (2017). A
 725 history of hybrids? Genomic patterns of introgression in the True Geese. *Bmc*
 726 *Evolutionary Biology* 17, 14.
- 727 Pauquet, G., Salzburger, W., and Egger, B. (2018). The puzzling phylogeography of the
 728 haplochromine cichlid fish *Astatotilapia burtoni*. *Ecology and Evolution* 8, 5637-
 729 5648.
- 730 Pfennig, D.W., and Murphy, P.J. (2000). Character Displacement in Polyphenic
 731 Tadpoles. *Evolution; international journal of organic evolution* 54, 1738-1749.
- 732 Pfennig, David W., and Pfennig, Karin S. (2010). Character Displacement and the
 733 Origins of Diversity. *The American Naturalist* 176, S26-S44.
- 734 Pfennig, K.S. (2007). Facultative Mate Choice Drives Adaptive Hybridization. *Science*
 735 (New York, NY) 318, 965-967.

- 736 Redgwell, R.D., Szewczak, J.M., Jones, G., and Parsons, S. (2009). Classification of
 737 Echolocation Calls from 14 Species of Bat by Support Vector Machines and
 738 Ensembles of Neural Networks. *Algorithms* 2, 907-924.
- 739 Renault, S., Grassa, C.J., Yeaman, S., Moyers, B.T., Lai, Z., Kane, N.C., Bowers, J.E.,
 740 Burke, J.M., and Rieseberg, L.H. (2013). Genomic islands of divergence are not
 741 affected by geography of speciation in sunflowers. *Nature Communications* 4, 8.
- 742 Sáez, J.A., Galar, M., and Krawczyk, B. (2019). Addressing the Overlapping Data
 743 Problem in Classification Using the One-vs-One Decomposition Strategy. *IEEE*
 744 *Access* 7, 83396-83411.
- 745 Salazar, C., Baxter, S.W., Pardo-Diaz, C., Wu, G., Surridge, A., Linares, M., Bermingham,
 746 E., and Jiggins, C.D. (2010). Genetic Evidence for Hybrid Trait Speciation in
 747 *Heliconius* Butterflies. *PLOS Genetics* 6, e1000930.
- 748 Santos, H., Juste, J., Ibáñez, C., Palmeirim, J.M., Godinho, R., Amorim, F., Alves, P.,
 749 Costa, H., de Paz, O., Pérez-Suarez, G., Martínez-Alos, S., Jones, G. and Rebelo, H.
 750 (2014), Shaping of Bat Cryptic Distribution in Iberia. *Biological Journal of the*
 751 *Linnean Society* 112, 150-162.
- 752 Schluter, D. (2000). Ecological Character Displacement in Adaptive Radiation. *The*
 753 *American Naturalist* 156, S4-S16.
- 754 Schreber J. (1774). *Die Säugthiere in Abbildungen nach der Natur, mit Beschreibungen.*
 755 *Erlangen - Expedition des Schreber'schen säugthier- und des Esper'schen*
 756 *Schmetterlingswerkes.* Ernst Mayr Library of the MCZ, Harvard University, pp 1774
 757 –1855.

- 758 Slager, D.L., Epperly, K.L., Ha, R.R., Rohwer, S., Wood, C., Van Hemert, C., and Klicka, J.
 759 (2020). Cryptic and extensive hybridization between ancient lineages of American
 760 crows. *Molecular ecology* 29, 956-969.
- 761 Song, Y., Endepols, S., Klemann, N., Richter, D., Matuschka, F.-R., Shih, C.-H., Nachman,
 762 Michael W., and Kohn, Michael H. (2011). Adaptive Introgression of Anticoagulant
 763 Rodent Poison Resistance by Hybridization between Old World Mice. *Current*
 764 *Biology* 21, 1296-1301.
- 765 Santana, S.E., Strait, S., and Dumont, E.R. (2011). The better to eat you with: functional
 766 correlates of tooth structure in bats. *Functional Ecology* 25, 839-847.
- 767 Staubach, F., Lorenc, A., Messer, P.W., Tang, K., Petrov, D.A., and Tautz, D. (2012).
 768 Genome patterns of selection and introgression of haplotypes in natural
 769 populations of the house mouse (*Mus musculus*). *PLoS Genet* 8, e1002891.
- 770 Temminck C.J. (1840). *Monographies de Mammologie, ou description de quelques*
 771 *genres de Mammifères, dont les espèces ont été observés dans les différents*
 772 *Musées de l'Europe* 2(302):26–70.
- 773 Tene Fossog, B., Ayala, D., Acevedo, P., Kengne, P., Ngomo Abeso Mebuy, I., Makanga,
 774 B., Magnus, J., Awono-Ambene, P., Njiokou, F., Pombi, M., et al. (2015). Habitat
 775 segregation and ecological character displacement in cryptic African malaria
 776 mosquitoes. *Evol Appl* 8, 326-345.
- 777 Vázquez-Moron, S., Juste, J., Ibáñez, C., Berciano, J.M., and Echevarria, J.E. (2011).
 778 Phylogeny of European bat Lyssavirus 1 in *Eptesicus isabellinus* bats, Spain. *Emerg*
 779 *Infect Dis* 17, 520-523.

- 780 vonHoldt, B.M., Kays, R., Pollinger, J.P., and Wayne, R.K. (2016). Admixture mapping
781 identifies introgressed genomic regions in North American canids. *Molecular*
782 *ecology* 25, 2443-2453.
- 783 Wang, Z.-l., Zhang, D.-Y., and Wang, G. (2005). Does spatial structure facilitate
784 coexistence of identical competitors. *Ecological Modelling* 181, 17-23.
- 785 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Golemund,
786 G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S.,
787 Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., ... Yutani, H. (2019).
788 Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686,
789 <https://doi.org/10.21105/joss.01686>.
- 790 Winter, Y., López, J., and von Helversen, O. (2003). Ultraviolet vision in a bat. *Nature*
791 425, 612-614.
- 792 Worthington-Wilmer, J., & Barratt, E. (1996). A non-lethal method of tissue sampling
793 for genetic studies of chiropterans. *Bat Research News*, 37(1), 1-4.
- 794 Yang, W.Z., While, G.M., Laakkonen, H., Sacchi, R., Zuffi, M.A.L., Scali, S., Salvi, D., and
795 Uller, T. (2018). Genomic evidence for asymmetric introgression by sexual
796 selection in the common wall lizard. *Molecular ecology* 27, 4213-4224.
- 797 Zhang, W., Dasmahapatra, K.K., Mallet, J., Moreira, G.R.P., and Kronforst, M.R. (2016).
798 Genome-wide introgression among distantly related *Heliconius* butterfly species.
799 *Genome Biology* 17, 15.
- 800 Zhang, W., Kunte, K., and Kronforst, M.R. (2013). Genome-Wide Characterization of
801 Adaptation and Speciation in Tiger Swallowtail Butterflies Using De Novo
802 Transcriptome Assemblies. *Genome Biology and Evolution* 5, 1233-1245.
- 803

804 **FIGURES AND TABLES**

805

806



807

808 **Figure 1.** Wing and dentition morphometric measurements taken from *Eptesicus* bat
809 species during field work.

810

811

812

813

814

815

816

817

818

819

820

821

822

823

824

825

826

827

828 **Table 1.** Descriptive statistics of the morphometric traits of *Eptesicus serotinus*, *E.*
 829 *isabellinus* and their hybrids.
 830

	Wing				Dentition	
	FA	D3 MC	D3 F1	D5 MC	D5 F1	C1-C1 CM3
<i>E. isabellinus</i> allopatric (Eisa allo; n=31 individuals)	51.6 49.9 – 55.7	47.1 44.0 – 52.0	17.8 12.2 – 19.8	44.1 41.3 – 48.0	10.9 10.0 – 12.0	6.7 6.3 – 7.2 7.2 6.8 – 7.7
<i>E. isabellinus</i> sympatric (Eisa sym; n=33 individuals)	51.6 48.6 – 54.3	46.1 42.6 – 48.6	18.0 16.5 – 20.5	43.0 40.1 – 48.5	11.3 10.2 – 12.6	6.9 6.3 – 7.4 7.2 6.5 – 8.4
<i>Hybrids</i> (n=8 individuals)	52.6 49.7 – 53.7	46.8 42.7 – 47.7	18.8 16.8 – 19.1	43.4 39.9 – 45.9	12.0 11.0 – 13.3	6.7 6.5 – 6.9 7.4 7.1 – 7.5
<i>E. serotinus</i> sympatric (Eser sym; n=19 individuals)	52.8 49.7 – 55.2	47.5 44.7 – 49.7	17.8 16.8 – 20.4	44.5 40.5 – 47.2	11.7 9.9 – 13.1	6.9 6.6 – 7.5 7.6 7.3 – 8.5
<i>E. serotinus</i> allopatric (Eser allo; n=35 individuals)	52.6 48.8 – 56.1	49.0 41.4 – 51.6	18.0 13.2 – 19.5	46.5 41.6 – 49.6	11.3 10.0 – 12.5	6.9 6.6 – 7.5 7.7 7.4 – 8.7
$\chi^2_{KS}(4)$	13.302	38.271	1.698	25.234	12.244	15.300 64.410
<i>p-value</i>	0.010	<0.001	ns	<0.001	0.016	0.004 <0.001

Medians are shown above
range

831
832
833
834
835
836
837
838
839
840
841
842
843
844
845
846
847

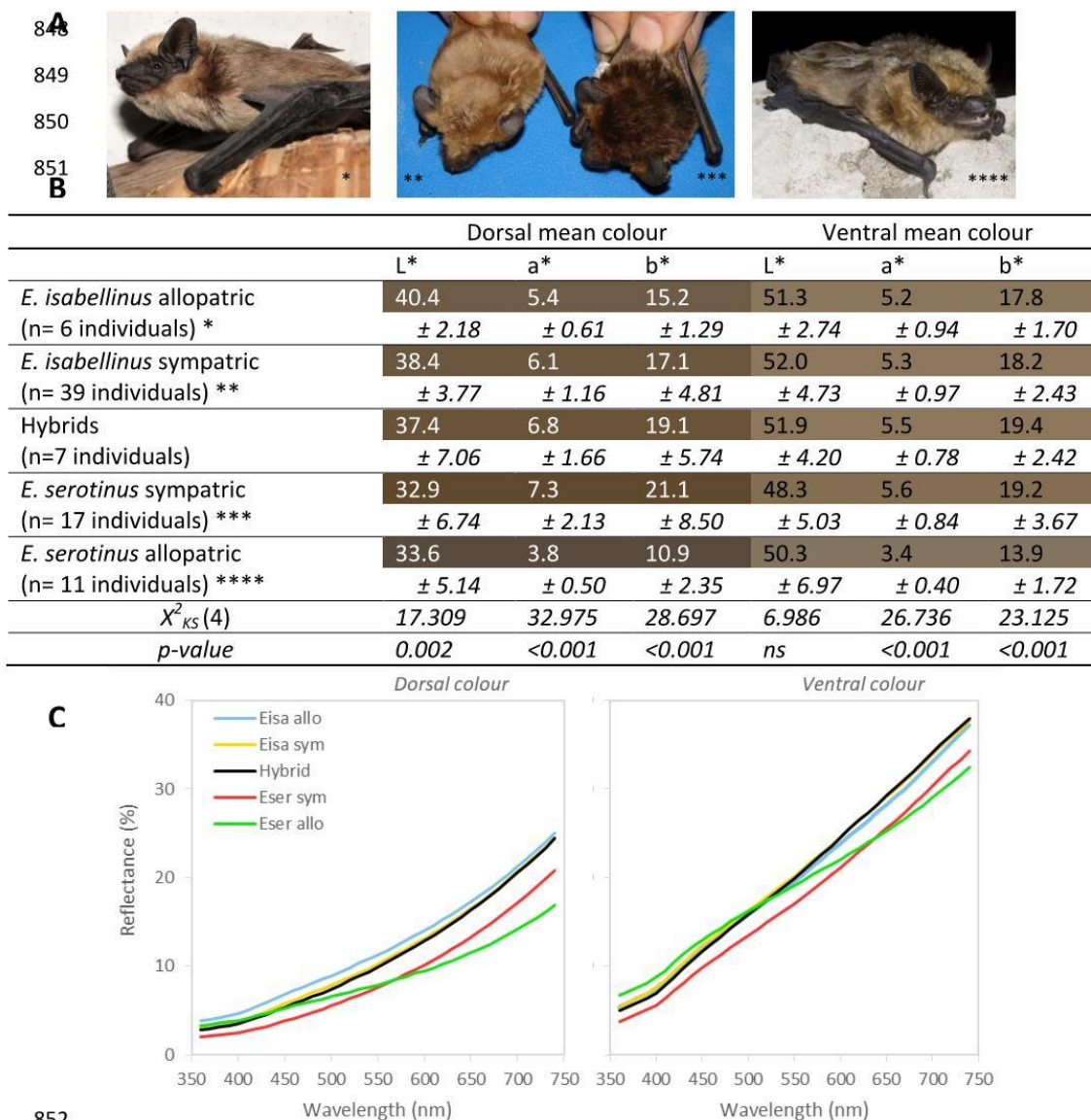
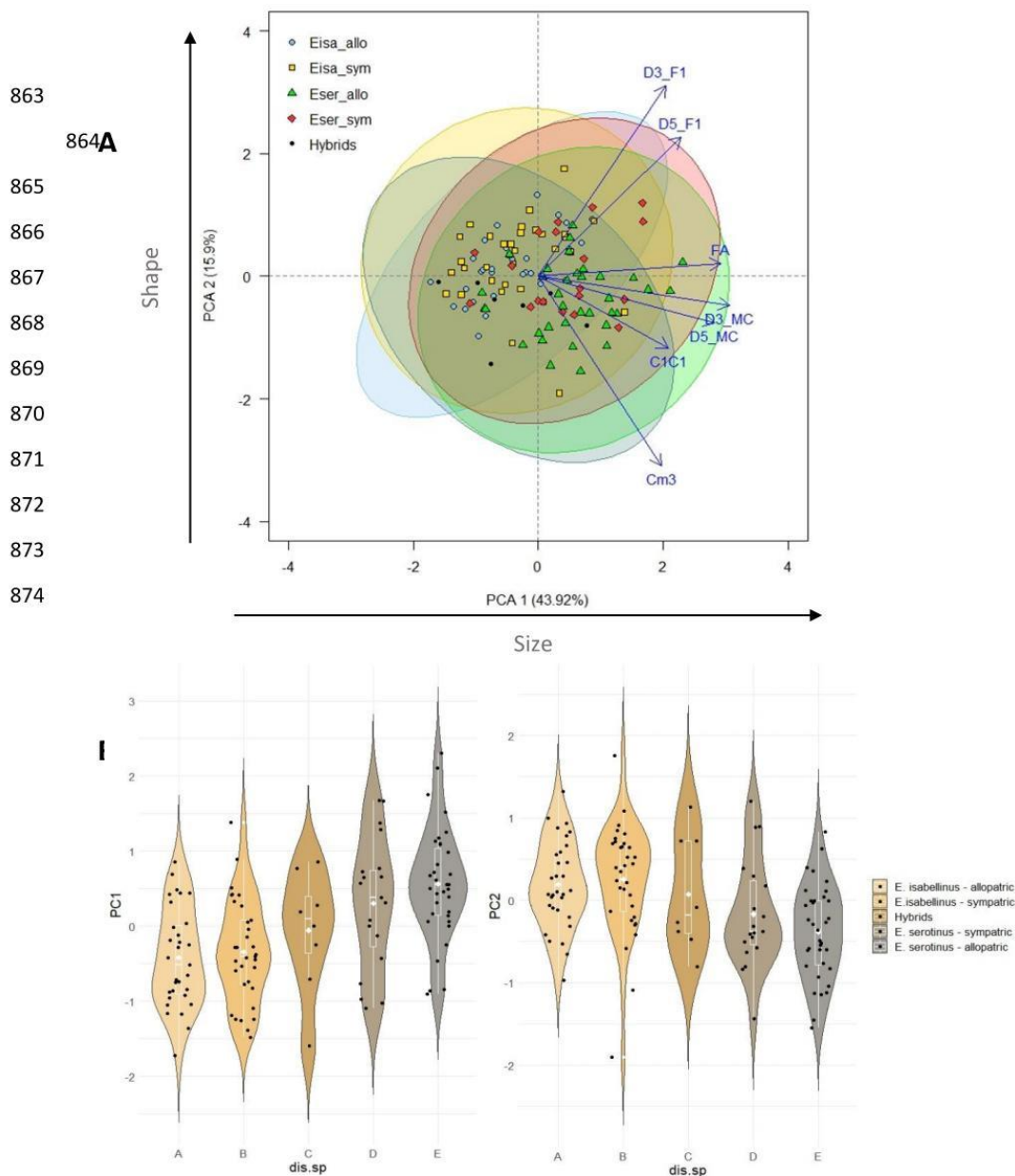


Figure 2. Colour differences between bat groups. (A) Photographic representation of hair colour of representative specimens of both parental species groups (*Eptesicus isabellinus* and *E. serotinus*) as a function of their geographical relationships. (B) Descriptive statistics of dorsal and ventral colour of *E. serotinus*, *E. isabellinus* and their hybrids. Background colour represents the mean colour of the dorsum and belly in the CIELAB colour space of each parental species and in function to their different geographical relationships and their hybrids. (C) Percentage of reflectance measured by colorimeter across the visible wavelength scale. Acronyms are available in Table 1.



875

876

877 **Figure 3.** Positioning of each individual in the two-dimensional space defined by the
 878 main PCA components retained and their position relative to the original
 879 morphometric variables (**A**). The violin plots represent *E. isabellinus* (allopatric and
 880 sympatric), *E. serotinus* (allopatric and sympatric) and Hybrids PCA scores compared to
 881 size (PC1) and shape (PC2) (**B**). Within violin plots white solid lines boxplots include
 882 medians (horizontal white line) and averages (white dot); boxes and vertical white
 883 lines indicate quartiles and ranges (excluding outliers), respectively. Acronyms are
 884 available in Table 1.

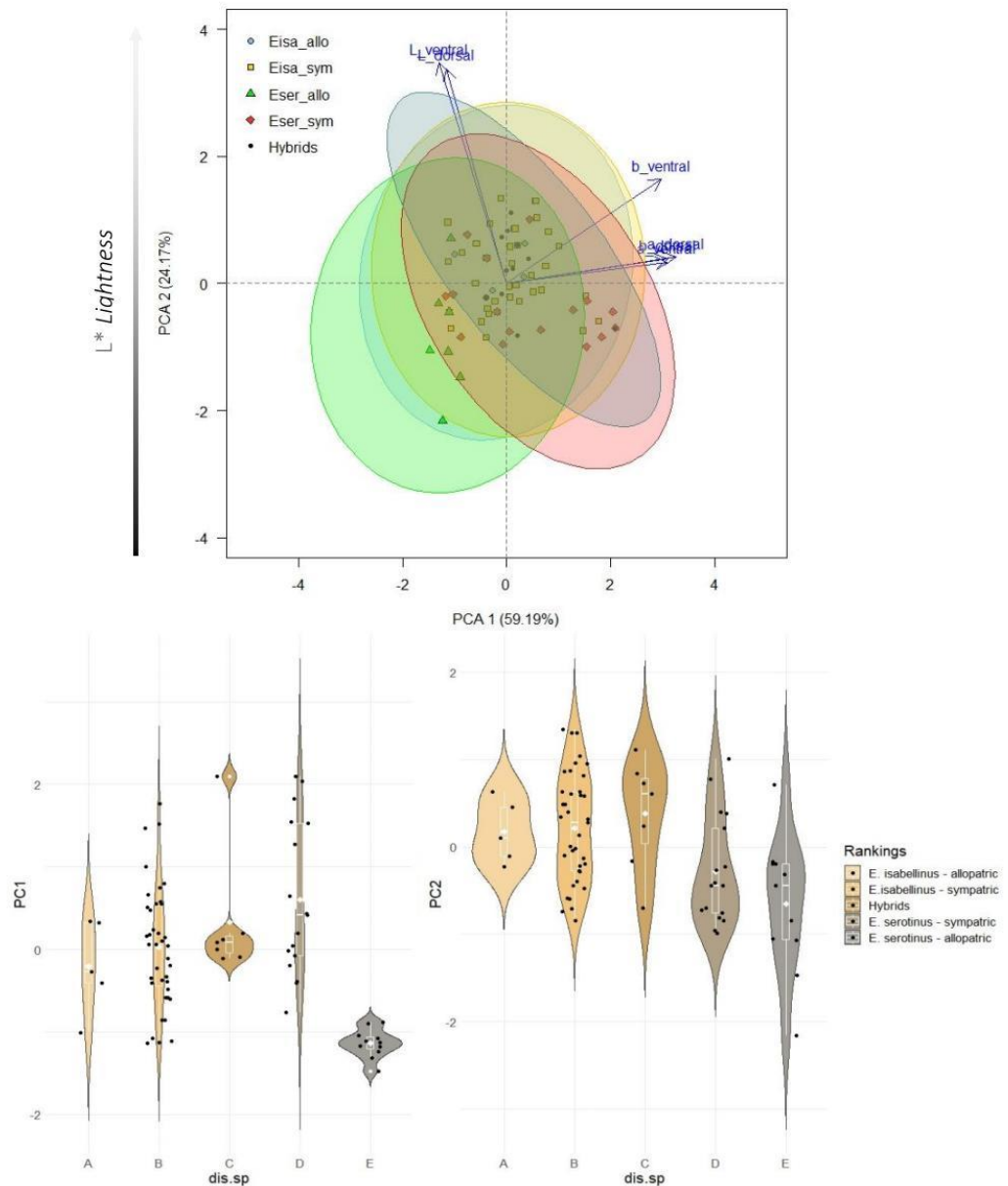
A

Figure 4. Positioning of each individual in the two-dimensional space defined by the PCA main components retained and their position relative to the original dorsal colour variables (A). The violin plots represent *E. isabellinus* (allopatric and sympatric), *E. serotinus* (allopatric and sympatric) and Hybrids PCA scores compared to dorsal a^*b^* Grey-Brown (PC1 Colour) and dorsal L^* lightness (PC2 Colour) (B). Within violin plots white solid lines boxplots include medians (horizontal white line) and averages (white

dot); boxes and vertical white lines indicate quartiles and ranges (excluding outliers), respectively. Acronyms are available in Table 1.

Table 2. Correct species classification rates, species overlap and hybrids contribution to species overlap obtained by two different methods of classification statistics (DFA and SVM) based on morphometric and colour traits of *E. isabellinus* and *E. serotinus* in sympatry.

	DFA	SVM
	Morphometry	
<i>E. isabellinus</i> correct classification rate	84.5%	78.9%
<i>E. serotinus</i> correct classification rate	78.3%	72.3%
<i>E. isabellinus</i> correct classification rate without hybrids presence	96.0%	83.9%
<i>E. serotinus</i> correct classification rate without hybrids presence	66.7%	66.7%
Global correct classification rate	81.7%	75.0%
Global correct classification rate without hybrids presence	84.0%	76.9%
Overlap in sympatry	18.3%	25.0%
Hybrids contribution to species overlap	13.6%	7.6%
	Colour	
<i>E. isabellinus</i> correct classification rate	92.3%	92.3%
<i>E. serotinus</i> correct classification rate	37.5%	29.2%
<i>E. isabellinus</i> correct classification rate without hybrids presence	92.3%	77.1%
<i>E. serotinus</i> correct classification rate without hybrids presence	47.1%	75.0%
Global correct classification rate	71.4%	68.3%
Global correct classification without hybrids presence	78.6%	76.8%
Overlap in sympatry	28.6%	31.7%
Hybrids contribution to species overlap	25.2%	26.8%

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

SUPPLEMENTAL MATERIAL

Counteracting forces of introgressive hybridization and interspecific competition shape
the morphological traits of cryptic Iberian *Eptesicus* bats

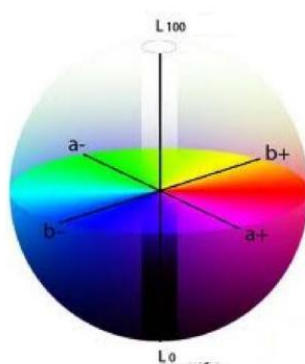


Figure S1. CIELAB colour space expressing colours in three values: L^* for perceptual lightness, and a^* and b^* for the scales of the four colours of human vision: red and green, blue and yellow, respectively.

70 Multiple comparisons of morphometric variables

71 Allopatry vs sympatry

72 Within each species there were no differences in forearm (FA) length between
73 allopatric and sympatric groups, though both groups of both species differed
74 significantly from the others of its sibling. Nevertheless, FA differences between the
75 two species in allopatry was slightly higher than that found in sympatry.

76 Allopatric and sympatric groups differed significantly in the variable D3 MC within each
77 species. The same also occurred between sympatric groups of species, as well as
78 between their allopatric groups. Differences between both species in allopatry was
79 also slightly higher than that found in sympatry. Multiple comparison in D5 MC
80 followed the same pattern. Allopatric and sympatric groups differed significantly
81 within each species. However, there were no significant differences between species in
82 the sympatric area, only between individuals of allopatric regions.

83 For phalange measures, such as D5 F1, all groups differed from allopatric *E. isabellinus*
84 due to its lowest length, except from individuals living in sympatry with *E. serotinus*.
85 Therefore, in allopatry both species differed significantly in the size of the first
86 phalanges, while in sympatry there were no significant differences.

87 There were no differences in the dentition variable CM3 within species between
88 allopatric and sympatric groups. However, both groups of both species differed
89 significantly from the other species. In this case, differences in CM3 between both
90 species in allopatry was essentially similar than that found in sympatry.

91 Finally, the results demonstrated statistically significant differences in C1-C1 variable
92 between allopatric *E. isabellinus* and both groups of *E. serotinus* (sympatric and
93 allopatric). However, in that case, under sympatry there was no significant differences
94 between both species unlike what happens in allopatry.

95 From a multivariate point of view, there were no significant differences in the bats'
96 size between allopatric and sympatric groups within each species. However, both
97 groups of both species differed significantly from the other species' groups.
98 Nevertheless, size differences between both species in allopatry was slightly higher
99 than that found in sympatry. Regarding the shape component (PC2 morphology), there
100 were no significant differences within each species when in the presence or absence of
101 its sibling. No significant differences were found among individuals of the two species

when they were in sympatry, while in allopatry the differences in the bats' shape were clearly significant. For allopatric *E. serotinus* the shape component stood out as substantially different, making it significantly different even from the sympatric *E. serotinus* group.

106

107 **Hybrids vs parental species**

The FA length of hybrids did not differ significantly between groups, with both parental species showing intermediate values. *E. serotinus* had the longer average length of FA (both allopatric and sympatric, in this order) followed by the hybrids and *E. isabellinus* (sympatric and allopatric).

Regarding the metacarpals, hybrids only differed significantly from allopatric *E. serotinus*, having significantly lower D3 MC and D5 MC. Allopatric *E. serotinus* had the longest metacarpals and hybrids showed the lowest values in both finger (D3 and D5). Sympatric groups revealed intermediate values between the respective allopatric groups of each species and the hybrids (Table 1). The exception was sympatric *E. isabellinus* group that shared the lowest values with hybrids in the metacarpals of the fifth finger.

In contrast, hybrids had the longest first phalanges although they did not differ from the rest of the groups. Both sympatric groups had higher values than the respective allopatric groups and intermediate between them and the hybrids (Table 1).

Hybrids showed intermediate values of CM3 between both parental species, with significantly higher values than both *E. isabellinus* groups. *E. serotinus* had the longest CM3 (mainly allopatric *E. serotinus*), followed by the hybrids and *E. isabellinus* (sympatric and allopatric) (Table 1). Regarding C1-C1, hybrids showed the lowest values alongside the allopatric *E. isabellinus*, which was the only group from which hybrids did not significantly differ (Table S1). In the multivariate analysis, hybrids showed intermediated phenotypes in dentition, wing sizes (PC1 morphology) and the metacarpals and first phalanges proportion, as well as between the length of the first phalanges and the dentition (mainly CM3) (PC2 morphology).

131

132

Table S1. Statistical values of multiple comparisons of original morphometric variables according to the post-hoc Fisher's LSD test. Green cells represent significant differences ($P < 0.05$).

Fisher's LSD						
		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
FA						
Eisa_all			0.826	0.451	0.008	0.006
Eisa_sy		0.026		0.535	0.013	0.010
Hybrid	D3	0.524	0.670		0.253	0.317
Eser_sy	M	0.249	0.003	0.219		0.752
Eser_all	C	0.000	0.000	0.005	0.005	
D5 MC						
Eisa_all			0.047	0.513	0.891	0.001
Eisa_sy		0.085		0.771	0.066	0.000
Hybrid	D5	0.011	0.080		0.483	0.029
Eser_sy	F1	0.004	0.132	0.375		0.008
Eser_all		0.036	0.721	0.110	0.220	
CM3						
Eisa_all			0.254	0.000	0.000	0.000
Eisa_sy		0.019		0.002	0.000	0.000
Hybrid	C1	0.572	0.040		0.171	0.059
Eser_sy	-	0.003	0.301	0.009		0.563
Eser_all	C1	0.004	0.593	0.017	0.554	

Multiple comparisons of colour variables

All groups differed significantly from allopatric *E. serotinus* in the a^* b^* Grey-Brown scale (PC1 colour), being the only one in the grey space of the colour pallet. In terms of lightness (PC2 colour), allopatric *E. serotinus* was only not significantly different from individuals of the same species when in sympatry (they were equally dark although in sympatry they tended to be significantly browner). In sympatry both species also differed significantly, however, contrary to the morphometric variables, this difference was slightly higher than that found between species in allopatry. According to colour multivariate analyses, hybrids were browner than *E. serotinus* in allopatry and lighter than it both in sympatry and allopatry (Table S5). For L^* Lightness component (PC2 colour), hybrids demonstrated the lightest colour patterns (both in their dorsal and ventral coat) despite being not significantly different from both *E. isabellinus* groups (sympatric or allopatric) (Figure 3 and Table S5).

Table S2. Statistical values of multiple comparisons of dorsal and ventral original colour variables (L^* , a^* and b^*). Green cells represent significant differences ($P < 0.05$).

Fisher's LSD

		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
L* dorsal						
Eisa_all			0.423	0.318	0.004	0.015
Eisa_sy				0.618	0.000	0.006
Hybrid					0.045	0.120
Eser_sy						0.692
Eser_all						
b* dorsal						
Eisa_all			0.474	0.240	0.043	0.152
Eisa_sy			0.286	0.395	0.018	0.002
Hybrid	a*		0.077	0.194	0.435	0.003
Eser_sy	dorsal		0.010	0.005	0.501	0.000
Eser_all			0.045	0.000	0.000	0.000
b* ventral						
Eisa_all			0.747	0.311	0.298	0.007
Eisa_sy			0.938	0.283	0.196	0.000
Hybrid	a*		0.581	0.486	0.885	0.000
Eser_sy	ventral		0.390	0.170	0.799	0.000

Eser_all	0.000	0.000	0.000	0.000
----------	-------	-------	-------	-------

Table S3. Principal components extracted from the PCA analysis, with the respective eigenvalues, % variance explained, Cronbach's α and weight of each variable.

Morphometric variables	Morphometry		Colour	
	PC1 (Size)	PC2 (Shape)	PC1 (a*b* Grey-Brown)	PC2 (L* lightness)
FA	0.973	-0.071	-	-
D3 MC	1.020	-0.159	-	-
D3 F1	0.679	1.035	-	-
D5 MC	0.939	-0.253	-	-
D5 F1	0.759	0.757	-	-
C1-C1	0.693	-0.390	-	-
CM3	0.656	-1.030	-	-
L* dorsal	-	-	-0.387	1.125
a* dorsal	-	-	1.084	0.139
b* dorsal	-	-	1.032	0.128
L* ventral	-	-	-0.436	1.157
a* ventral	-	-	1.028	0.114
b* ventral	-	-	0.989	0.546
<i>Eigenvalue</i>	3.315	1.245	3.552	1.450
Variance explained	43.92%	15.90%	59.19%	24.17%
Cronbach's α	0.815	0.230	0.862	0.373

Table S4. Statistical values of multiple comparisons of means orders of morphometric PCA variables. Green cells represent significant differences ($P < 0.05$).

Tukey's LSD

		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
		PC1 Size				
Eisa_all			0.992	0.715	0.009	0.000
Eisa_sy				0.860	0.024	0.000
Hybrid	PC2	0.987	0.940		0.781	0.214
Eser_sy	Shape	0.267	0.124	0.889		0.732
Eser_all		0.002	0.000	0.328	0.727	

Table S5. Statistical values of multiple comparisons of means orders of dorsal and ventral PCA colour variables. Green cells represent significant differences ($P < 0.05$).

Fisher's LSD

		Eisa_all	Eisa_sy	Hybrid	Eser_sy	Eser_all
		PC1 a*b* Grey-Brown				
Eisa_all			0.505	0.214	0.033	0.021
Eisa_sy				0.315	0.008	0.000
Hybrid	PC2 L*	0.578	0.532		0.409	0.000
Eser_sy	Lightness	0.164	0.008	0.023		0.000
Eser_all		0.018	0.000	0.001	0.133	

208 Detail description of classification analyses

209

210 Species discrimination through classification statistics

211 1) Stepwise DFA with and without hybrids

212 The morphometric stepwise DFA generated one discriminant function, retaining all
 213 variables as statistically significant (D3_F1 only marginally [$F=3.643$, $p=0.058$]). A single
 214 discriminant function was defined mainly by D3_MC and CM3. This function
 215 discriminated the two species ($\Lambda=0.579$, $\chi^2_{(7)} = 53.773$, $p<0.001$). The results of
 216 Classification Statistics showed that 49 out of 58 *E. isabellinus* individuals (84.5%) and
 217 36 out of 46 *E. serotinus* individuals (78.3%) were classified correctly. The percentage
 218 of individuals classified correctly by stepwise DFA to morphometric variables in the
 219 presence of hybrids was 81.7%.

220 The morphometric stepwise discriminant analysis after hybrids removing generated
 221 also one discriminant function, with FA, D3_MC, D5_MC (marginally significant
 222 [$F=3.450$, $p=0.069$]) and CM3 as statistically significant variables. A single discriminant
 223 function was defined mainly by D3_MC and CM3. This function discriminated the two
 224 species ($\Lambda=0.632$, $\chi^2_{(4)}=21.073$, $p<0.001$). The results of Classification Statistics showed
 225 that 30 out of 32 *E. isabellinus* individuals (96.0%) and 12 out of 18 *E. serotinus*
 226 individuals (66.7%) were classified correctly. The total percentage of individuals
 227 classified correctly by stepwise DFA of morphometric variables increased to 84.0%
 228 after hybrids removing.

229

230 The colour stepwise DFA generated also only one discriminant function, with
 231 L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral as statistically significant variables. A
 232 single discriminant function was defined mainly by dorsal colour scales (a*_dorsal,
 233 L*_dorsal and b*_dorsal - in this decreasing order of influence). This function
 234 discriminated the two species ($\Lambda=0.842$, $\chi^2_{(4)}=10.115$, $p=0.039$). The results of
 235 Classification Statistics showed that 36 out of 39 *E. isabellinus* individuals (92.3%), but
 236 only 9 out of 24 *E. serotinus* individuals (37.5%) were classified correctly. The
 237 percentage of individuals classified correctly by stepwise DFA to colour variables in the
 238 presence of hybrids was 71.4%.

239 After removing hybrids the colour stepwise discriminant analysis generated also one
 240 discriminant function, once again with L*_dorsal, a*_dorsal, b*_dorsal and L*_ventral
 241 as statistically significant variables. A single discriminant function was defined mainly
 242 by variable L*_dorsal. This function discriminated the two species ($\Lambda=0.762$,
 243 $\chi^2_{(4)}=14.114$, $p=0.007$). The results of Classification Statistics showed that 36 out of 39
 244 *E. isabellinus* individuals (92.3%), but only 8 out of 17 *E. serotinus* individuals (47.1%)
 245 were classified correctly. The total percentage of individuals classified correctly by
 246 stepwise DFA of colour variables increased to 78.6% after hybrids removing.

247

248 2) Support Vector Machine with and without hybrids

249 SVM generated one discriminant function based on morphometric PC1 and PC2 as
 250 predictors' variables that summarized all morphometric traits. Once composed of only
 251 two variables, a single classification function was defined similarly by PC1 and PC2 in
 252 the same direction. After simulations, the results of Classification Statistics showed
 253 that 45 of 57 individuals of *E. isabellinus* (78.9%) and 34 of 47 individuals from *E.*
 254 *serotinus* (72.3%) were classified correctly (Figure S2). The percentage of individuals
 255 classified correctly by SVM of morphometric variables in the presence of hybrids was
 256 75.0%.

257 Without hybrids, SVM generated one discriminant function based on morphometric
 258 PC1 and PC2 as predictors' variables that summarized all morphometric traits. Once
 259 composed of only two variables, a single classification function was defined especially
 260 by PC1. After simulations, the results of Classification Statistics showed that 26 of 31
 261 individuals of *E. isabellinus* (83.9%) and 14 of 21 individuals from *E. serotinus* (66.7%)
 262 were classified correctly (Figure S2). The percentage of individuals classified correctly
 263 by SVM to summarized morphometric variables increased to 76.9% after removing
 264 hybrids.

265

266 SVM generated also one discriminant function based on colour PC1 and PC2 as
 267 predictors' variables that summarized all colour variables. Composed by only two
 268 variables, a single classification function was defined mainly by PC1. After simulations,
 269 the results of Classification Statistics showed that 36 of 39 individuals of *E. isabellinus*
 270 (92.3%) and only 7 of 24 individuals from *E. serotinus* (29.2%) were classified correctly

(Figure S2). The percentage of individuals classified correctly by SVM of colour variables in the presence of hybrids was 68.3%.

Without hybrids, the colour SVM generated one discriminant function based on PC1 and PC2 as predictors' variables that summarized all colour variables. Once composed by only two variables, a single classification function is defined similarly by PC1 and PC2 in opposite directions. The results of Classification Statistics showed that 37 of 48 individuals of *E. isabellinus* (77.1%) and only 2 of 8 individuals from *E. serotinus* (25.0%) were classified correctly (Figure S2). The percentage of individuals classified correctly by SVM of summarized colour variables increased to 76.8% after removing hybrids.

280

281 Discriminant and classification functions

282 1) Stepwise DFA with hybrids

283 Morphometry

284 Discriminant function (eigenvalue=0.726):

$$285 \text{ Species} = 0.183 (\text{FA}) + 0.692 (\text{D3_MC}) - 0.468 (\text{D3_F1}) - 0.259 (\text{D5_MC}) - 0.359} \\ 286 (\text{D5_F1}) + 0.271 (\text{C1_C1}) + 0.837 (\text{CM3}).$$

287

288 Classification functions:

$$289 \text{ E. isabellinus} = 16.760 (\text{FA}) + 6.148 (\text{D3_MC}) - 4.801 (\text{D3_F1}) - 3.999 (\text{D5_MC}) - \\ 290 6.861 (\text{D5_F1}) + 31.608 (\text{C1_C1}) + 25.371 (\text{CM3}) + 600.300$$

$$291 \text{ E. serotinus} = 16.948 (\text{FA}) + 6.790 (\text{D3_MC}) - 5.576 (\text{D3_F1}) - 4.214 (\text{D5_MC}) - \\ 292 6.077 (\text{D5_F1}) + 30.035 (\text{C1_C1}) + 29.193 (\text{CM3}) + 643.292$$

293 Colour

294 Discriminant function (eigenvalue=0.187):

$$295 \text{ Species} = 0.686 (\text{L*_dorsal}) - 0.825 (\text{a*_dorsal}) + 0.571 (\text{b*_dorsal}) + 0.111} \\ 296 (\text{L*_ventral}).$$

297 Classification functions:

$$298 \text{ E. isabellinus} = 2.094 (\text{L*_dorsal}) + 13.092 (\text{a*_dorsal}) - 0.840 (\text{b*_dorsal}) + \\ 299 2.243 (\text{L*_ventral}) - 131.706$$

$$300 \text{ E. serotinus} = 1.979 (\text{L*_dorsal}) + 13.568 (\text{a*_dorsal}) - 0.922 (\text{b*_dorsal}) + \\ 301 2.223 (\text{L*_ventral}) - 128.605$$

302

303 2) *Support Vector Machine with hybrids*

304 Morphometry

305 SVM function:

306 Species = - 4.59 (PC1_morphometry) – 4.08 (PC2_morphometry) + 0.02.

307 Colour

308 SVM function:

309 Species = - 4.39 (PC1_colour) – 0.28 (PC2_colour) - 0.42.

310

311 3) *Stepwise DFA without hybrids*

312 Morphometry

313 Discriminant function (eigenvalue=0.581):

314 Species = 0.026 (FA) + 0.501 (D3_MC) – 0.148 (D5_MC) + 0.815 (CM3).

315 Classification functions:

316 *E. isabellinus* = 21.383 (FA) + 6.178 (D3_MC) – 1.729 (D5_MC) + 34.384 (CM3) –
317 780.827

318 *E. serotinus* = 21.412 (FA) + 6.696 (D3_MC) – 1.850 (D5_MC) + 38.063 (CM3) –
319 829.241

320 Colour

321 Discriminant function (eigenvalue=0.312):

322 Species = 0.830 (L*_dorsal) – 0.395 (a*_dorsal) + 0.395 (b*_dorsal) + 0.182
323 (L*_ventral).

324 Classification functions:

325 *E. isabellinus* = 2.258 (L*_dorsal) + 12.308 (a*_dorsal) – 0.786 (b*_dorsal) +
326 2.193 (L*_ventral) – 131.525

327 *E. serotinus* = 2.054 (L*_dorsal) + 12.619 (a*_dorsal) – 0.851 (b*_dorsal) +
328 2.148 (L*_ventral) – 123.650

329

330 4) *Support Vector Machine without hybrids*

331 Morphometry

332 SVM function:

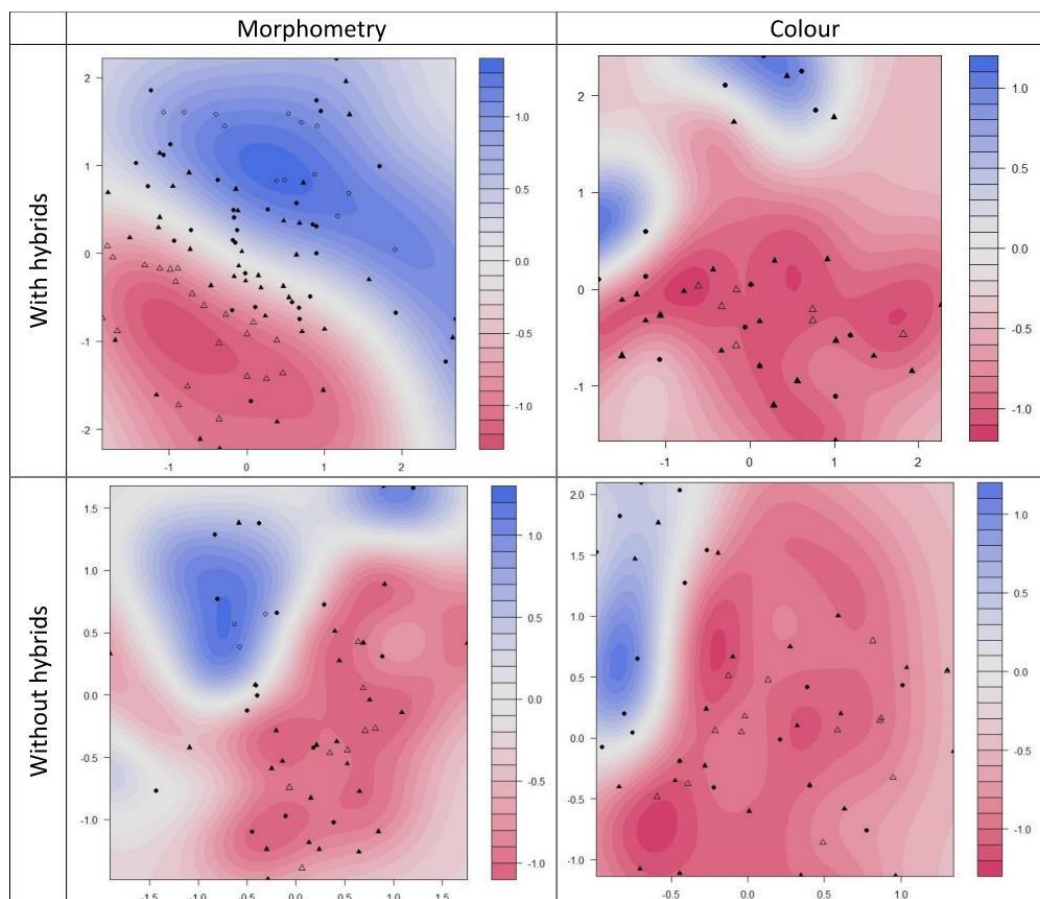
333 Species = -57.49 (PC1_morphometry) – + 25.91 (PC2_morphometry) – 2.97.

334 Colour

335 SVM function:

336 Species = -4.44 (PC1_colour) + 3.29 (PC2_colour) - 0.51.

337



338

339

340 **Figure S2.** Support Vector Machine classification plots based on morphometric (on left)
 341 and colour traits (on right) for both parental species in sympatry, including hybrids on
 342 top and excluding them on the bottom. Density of probability of correct classification
 343 rate was based on Kernel statistics. Red spots regard *E. isabellinus* and the blue ones *E.*
 344 *serotinus*.

345

346

347

348

349

350

351

Editorial Board
Communications Biology,
10. November 2021

Dear Editors,

We are pleased to submit the manuscript entitled “**Counteracting forces of introgressive hybridization and interspecific competition shape the morphological traits of cryptic Iberian *Eptesicus* bats**” for consideration for publication as an Article in *Communications Biology*. We believe that our paper merits consideration for publication in *Communications Biology* and will have broad appeal in the fields of evolutionary biology, functional ecology, ecophysiology and zoology. In this paper, we demonstrate the effect of two counteracting evolutionary forces, such as introgressive hybridization and competition, whose balance shapes the path of evolution, namely through divergent impacts on morphologic traits under selection.

The evolutionary direction of the functional traits of species remains under discussion, when they co-exist under introgressive hybridization and potential competition. On one hand, closely-related species can share introgressed alleles that are responsible for well-adapted traits to particular habitats or conditions in the sympatric area. As a consequence adaptive introgression can promote an approximation of morphological traits in the two species. On the other hand, each species is expected to pose a trophic pressure on the other in sympatry, leading to a specialization of the resources explored and promoting a traits displacement. Cryptic species are particularly valuable to test the effect of antagonistic evolutionary processes on morphological trait displacement, mainly when associated with sympatric or parapatric distributions, due to their phylogenetic proximity and partial niche overlap, as well as morphological similarity and high potential for introgressive hybridization.

We have analyzed the variation in wing and dentition morphometric characters and coat colours in two parental bat species (Iberian *Eptesicus* bats), both in sympatric and allopatric colonies, and in their first generation hybrids. We have found a greater overlap in dentition or wing traits in sympatry with the hybrids showing intermediate morphometry. This pattern indicates that morphometry is possibly affected by adaptive introgression that could result in a better adaptation of both species to a specific diet and macro ecological conditions in the sympatric area. On the contrary, sympatric bats show traits displacement in their coat colour, possibly as a response to environmental factor such as the characteristics of the roosts they compete for.

These results suggest new avenues for fostering the progress of the knowledge on the balance between adaptive introgression and competition and adjust its course in evolutionary biology. Specifically, the need to further explore the genomic bases of the morphological characteristics that are being impacted differently by the different evolutionary forces, as well as in-depth study of the ecological effect of its phenotypic expression. We argue that a balance between adaptive introgression and niche partitioning shapes species interactions with the

environment, including preys and predators, through affecting morphological traits under selection.

All authors agree with the conclusions and show no conflict of interests. The manuscript is not being considered for publication anywhere else. In order to comply with the assumptions of the Double-blind peer review guidelines I describe below the authors' affiliations and acknowledgments section of the work.

Thank you for your consideration of this manuscript.

Yours sincerely,

Pedro Horta

Pedro Horta^{1,2,3,9*} & Helena Raposeira^{1,2,3,9} & Adrián Baños⁴ & Carlos Ibáñez^{5,6} & Orly Razgour⁷ & Hugo Rebelo^{1,8,9} & Javier Juste^{5,6}

¹CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal

²Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal

³OII – Observatório Inovação Investigação, Seia, Portugal

⁴University Pablo de Olavide, Sevilla, Spain

⁵Departamento de Ecología Evolutiva, Estación Biológica de Doñana (CSIC), Sevilla, Spain, Avda. Américo Vespucio 26, 41092 Sevilla, Spain

⁶CIBER de Epidemiología y Salud Pública, CIBERESP, Madrid, Spain

⁷Biosciences, University of Exeter, Exeter, UK (O.Razgour@exeter.ac.uk)

⁸CIBIO/InBio, Centro de Investigação em Biodiversidade e Recursos Genéticos da Universidade do Porto, Instituto Superior de Agronomia, Universidade de Lisboa, Portugal

⁹BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal

*Corresponding author: pedro.horta@cibio.up.pt

ACKNOWLEDGMENTS

PH and HRa were funded by the Portuguese Foundation for Science and Technology (FCT) with a PhD grant (SFRH/BD/117979/2016 and SFRH/BD/124367/2016, respectively). HRe was also funded by FCT (DL57/2016/EEC2018/07). OR was funded through a Natural Environment Research Council Independent Research Fellowship (NE/M018660/1). This research was supported under the scope of the FCT project PTDC/BIA-ECO/31731/2017.

Appendix B

Other papers arising from the PhD research

During my PhD I was invited to collaborate in other scientific projects with researchers from several institutions. Six of these projects were not directly included in my thesis, but are outlined in this appendix because the respective publications partially resulted from the work developed in my PhD. As a result of these collaborations I was co-author of one article, two data papers, one occurrence dataset and two chapters in the book *Bat calls of Britain and Europe*. All of these publications are already published or accepted for publication. They arose from by-catches of several bats species during mist-netting sessions aimed for *Eptesicus serotinus/isabellinus*. In the first data paper, we used this information to analyse the performance of barcoding methodologies to catalogue bats' biodiversity. Through this techniques it was possible to prove the presence of *Myotis alcathoe* in Portugal for the first time. In the second publication, under the scope of the InBIO Barcoding Initiative Database I was co-author of a database of Portuguese bats' barcodes. In the third publication we provided detailed information on pest species predation by bats in Mediterranean ecosystems relevant for conservation biocontrol. Both book chapters are incorporated into a reference work on the echolocation characteristics of European bats in which I have reviewed and synthesized all relevant information about both target species of my PhD, namely *E. serotinus* and *E. isabellinus*. Finally, we published a data paper about the current and historical records of terrestrial, volant and marine mammal in Portugal. All of these publications are available below:

1. Hidden in our pockets: building of a DNA barcode library unveils the first record of *Myotis alcathoe* for Portugal - Biodiversity Data Journal 8: e54479. DOI: <https://doi.org/10.3897/BDJ.8.e54479>
2. The InBIO Barcoding Initiative Database: Portuguese Bats (Chiroptera) - Occurrence dataset accessed via GBIF.org. DOI: <https://doi.org/10.15468/a4r5x9>
3. Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators – Ecological Applications. DOI: 10.1002/eap.2457
4. MAMMALS IN PORTUGAL: data set of terrestrial, volant and marine mammal occurrences in Portugal – Ecology. DOI: <https://doi.org/10.6084/m9.figshare.14938437>
5. Bat calls of Britain and Europe: *Eptesicus serotinus*. - Pelagic Publishing.
6. Bat calls of Britain and Europe: *Eptesicus isabellinus*. - Pelagic Publishing.

Hidden in our pockets: building of a DNA barcode library unveils the first record of *Myotis alcathoe* for Portugal

Rebelo, H., Ferreira, S., Amorim, F., **Horta, P.**, Raposeira, H., Santos, H., Beja, P., and Vanessa A. M. (2020). Hidden in our pockets: building of a DNA barcode library unveils the first record of *Myotis alcathoe* for Portugal. Biodiversity Data Journal 8, e54479. DOI: <https://doi.org/10.3897/BDJ.8.e54479>



Biodiversity Data Journal 8: e54479
doi: [10.3897/BDJ.8.e54479](https://doi.org/10.3897/BDJ.8.e54479)



Data Paper

Hidden in our pockets: building of a DNA barcode library unveils the first record of *Myotis alcathoe* for Portugal

Hugo Rebelo^{‡,§}, Sónia Ferreira[‡], Francisco Amorim[‡], Pedro Horta^{‡,||}, Helena Raposeira^{‡,||},
Helena Santos[‡], Pedro Beja^{‡,§}, Vanessa A. Mata[‡]

[‡] CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal
[§] CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Instituto Superior de Agronomia, Lisboa, Portugal
^{||} Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal

Corresponding author: Vanessa A. Mata (vanessamata@hotmail.com)

Academic editor: Ricardo Moratelli

Received: 19 May 2020 | Accepted: 29 Jun 2020 | Published: 28 Jul 2020

Citation: Rebelo H, Ferreira S, Amorim F, Horta P, Raposeira H, Santos H, Beja P, Mata VA (2020) Hidden in our pockets: building of a DNA barcode library unveils the first record of *Myotis alcathoe* for Portugal. Biodiversity Data Journal 8: e54479. <https://doi.org/10.3897/BDJ.8.e54479>

Abstract

Background

The advent and boom of DNA barcoding technologies have provided a powerful tool for the fields of ecology and systematics. Here, we present the InBIO Barcoding Initiative Database: Portuguese Bats (Chiroptera) dataset containing DNA sequences of 63 specimens representing the 25 bat species currently known for continental Portugal. For that, we sequenced tissues samples obtained in a vast array of projects spanning the last two decades.

New information

We added four new Barcoding Index Numbers (BINs) to existing Chiroptera barcodes on BOLD, two belonging to *Myotis escaleraei*, one to *Plecotus auritus* and the other to

The InBIO Barcoding Initiative Database Portuguese Bats (Chiroptera)

Rebelo, H., Ferreira, S., Amorim, F., **Horta, P.**, Raposeira, H., Santos, H., Beja, P., Sousa, P., and Mata V. (2020): The InBIO Barcoding Initiative Database: Portuguese Bats (Chiroptera). v1.2. CIBIO (Research Center in Biodiversity and Genetic Resources) Portugal. Dataset/Occurrence. DOI: <https://doi.org/10.15468/a4r5x9>

06/11/2020

The InBIO Barcoding Initiative Database: Portuguese Bats (Chiroptera)

OCCURRENCE DATASET | REGISTERED JULY 29, 2020

The InBIO Barcoding Initiative Database: Portuguese Bats (Chiroptera)

Published by [CIBIO \(Research Center in Biodiversity and Genetic Resources\)](#), Portugal

✉ Hugo Rebelo • Sónia Ferreira • Francisco Amorim • Pedro Horta • Helena Raposeira • Helena Santos •
Pedro Beja • Pedro Sousa • Vanessa Mata

63 OCCURRENCES 1 CITATION

[DATASET](#) [PROJECT](#) [METRICS](#) [ACTIVITY](#) [↓ DOWNLOAD](#) [↔ HOME PAGE](#)

The dataset contains 63 records of Chiroptera species collected in continental Portugal. All specimens were identified to species level, for a total of 26 species belonging to three different families. Bat samples were collected under the scope of several projects spanning from 2005 to 2018. All bats were captured during mist-netting sessions or using harp-traps at roost exits. A non-lethal 3mm wing punch was collected from several individuals and stored in 96% ethanol from where DNA was extract...

[More](#)**Project ID:** InBIO Barcoding Initiative**Metadata last modified:** August 4, 2020**Hosted by:** Instituto Superior de Agronomia / Universidade de Lisboa**License:** CC BY 4.0
[” How to cite](#) [DOI](#) 10.15468/a4r5x9

63

Occurrences



100%

With taxon match



100%

With coordinates



100%

With year

63 GEOREFERENCED RECORDS


<https://www.gbif.org/dataset/a4ffebe0-6711-4687-8c74-0a4da3fd84f9#description>

1/7

Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators

Mata, V. A., da Silva, L. P., Veríssimo, J., **Horta, P.**, Raposeira, H., McCracken, G. F., Rebelo, H., and Beja, P. (2021). Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators. *Ecological Applications* 00(00), e02457. DOI: <https://doi.org/10.1002/eap.2457>



Ecological Applications, 0(0), 2021, e02457

© 2021 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America
This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators

VANESSA A. MATA ,^{1,2,6} LUIS P. DA SILVA ,^{1,2} JOANA VERÍSSIMO,^{1,2,3} PEDRO HORTA,^{1,2,3} HELENA RAPOSEIRA,^{1,2,3} GARY F. MCCracken,⁴ HUGO REBELO ,^{1,2,5} AND PEDRO BEJA ,^{1,2,5}

¹CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão 4485-661 Portugal

²BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão 4485-661 Portugal

³Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto 4099-002 Portugal

⁴Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610 USA

⁵CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa, Lisboa 1349-017 Portugal

Citation: Mata, V. A., L. P. da Silva, J. Veríssimo, P. Horta, H. Raposeira, G. F. McCracken, H. Rebelo, and P. Beja. 2021. Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators. *Ecological Applications* 00(0):e02457. 10.1002/eap.2457

Abstract. In multifunctional landscapes, diverse communities of flying vertebrate predators provide vital services of insect pest control. In such landscapes, conservation biocontrol should benefit service-providing species to enhance the flow, stability and resilience of pest control services supporting the production of food and fiber. However, this would require identifying key service providers, which may be challenging when multiple predators interact with multiple pests. Here we provide a framework to identify the functional role of individual species to pest control in multifunctional landscapes. First, we used DNA metabarcoding to provide detailed data on pest species predation by diverse predator communities. Then, these data were fed into an extensive network analysis, in which information relevant for conservation biocontrol is gained from parameters describing network structure (e.g., modularity) and species roles in such network (e.g., centrality, specialization). We applied our framework to a Mediterranean landscape, where 19 bat species were found to feed on 132 insect pest species. Metabarcoding data revealed potentially important bats that consumed insect pest species in high frequency and/or diversity. Network analysis showed a modular structure, indicating sets of bat species that are required to regulate specific sets of insect pests. A few generalist bats had particularly important roles, either at network or module levels. Extinction simulations highlighted six bats, including species of conservation concern, which were sufficient to ensure that over three-quarters of the pest species had at least one bat predator. Combining DNA metabarcoding and ecological network analysis provides a valuable framework to identify individual species within diverse predator communities that might have a disproportionate contribution to pest control services in multifunctional landscapes. These species can be regarded as candidate targets for conservation biocontrol, although additional information is needed to evaluate their actual effectiveness in pest regulation.

Key words: bats; community; ecosystem services; food webs; pest control; predator-prey interactions.

INTRODUCTION

Landscapes providing multiple products and services (i.e., multifunctional) are key to combine food security and biodiversity conservation worldwide, as they integrate human activities with the preservation of ecosystem structure and function (Kremen and Merenlender 2018, Manning et al. 2018). In such landscapes, biodiversity contributes to food and fiber production, and to reduce its negative environmental externalities, by providing critical services such as pollination and pest control (Mace et al. 2012, Maas et al. 2016, Kaiser-

Bunbury et al. 2017, Heath and Long 2019). The management of multifunctional landscapes should therefore target at benefiting service-providing organisms to enhance the flow, stability and resilience of ecosystem services supporting production (Doré et al. 2011, Bommarco et al. 2013, Titttonell 2014). An important example is conservation biocontrol, which aims at increasing populations of natural enemies to reduce crop and forestry losses by pests (Shields et al. 2019).

Designing conservation biocontrol strategies is particularly challenging in multifunctional landscapes, because multiple land uses coexist across space and over time (e.g., crop rotation), with each land use associated with multiple pests, and each pest preyed by multiple predators (Bianchi et al. 2006, Chaplin-Kramer et al. 2011).

Manuscript received 21 October 2020; revised 22 April 2021; accepted 20 May 2021. Corresponding Editor: Adam T. Ford.

⁶E-mail: vanessamata@cibio.up.pt

MAMMALS IN PORTUGAL: a data set of terrestrial, volant and marine mammal occurrences in Portugal

Grilo, C., Afonso, B.C., Afonso, F., Alexandre, M., Aliácar, S., Almeida, A., (...) **Horta, P.**, *et. al.*,
MAMMALS IN PORTUGAL: a data set of terrestrial, volant and marine mammal occurrences in
Portugal. Ecology. 1. DOI: <https://doi.org/10.6084/m9.figshare.14938437>

MAMMALS IN PORTUGAL: a data set of terrestrial, volant and marine mammal occurrences in Portugal

CLARA GRILO,^{1,2,85} BEATRIZ C. AFONSO,^{3,4} FILIPE AFONSO,⁴⁸ MARTA ALEXANDRE,¹ SARA ALIÁCAR,⁵ ANA ALMEIDA,⁶ IVAN PREGO ALONSO, FRANCISCO ÁLVARES,⁷ PAULO ALVES,⁸ PAULO CÉLIO ALVES,^{7,9} PEDRO ALVES,^{10,11} ANABELA AMADO, VITOR AMENDOEIRA, FRANCISCO AMORIM,^{7,13} GUILHERME DA SILVA APARÍCIO,¹ RICARDO ARAÚJO,¹⁴ FERNANDO ASCENSÃO,³ MARGARIDA AUGUSTO,^{15,16} VICTOR BANDEIRA,¹⁷ A. MÁRCIA BARBOSA,¹⁸ SORAIA BARBOSA,^{7,19} SÉRGIO BARBOSA,¹⁶ SILVIA BARREIRO,²⁰ PAULO BARROS,^{21,22} TÂNIA BARROS,¹⁷ FILOMENA BARROS,²³ MAFALDA BASTO,³ JOANA BERNARDINO,⁷ SARA BICHO, LUIS EDUARDO BIEDMA,²⁴ MARTA BORGES,¹² LUIS BRAZ,^{21,22} JOSÉ CARLOS BRITO,⁷ TIAGO BRITO, JOÃO ALEXANDRE CABRAL,^{21, 22} JAVIER CALZADA,²⁴ CLAUDIA CAMARINHA,³ MAFALDA CARAPUÇO,²⁵ PAULO CARDOSO,¹⁵ MÁRIO CARMO,²⁶ CARLOS CARRAPATO,²⁷ MAÍLIS DA SILVA CARRILHO,¹ DIOGO FILIPE TCS CARVALHO,^{21,22} FILIPE CARVALHO,^{7,30} JOÃO CARVALHO,¹⁷ DIANA CASTRO,⁷ GUILHERME CASTRO,¹⁷ JOANA CASTRO,³¹ LUIS ROMA CASTRO,²⁷ FILIPE XAVIER CATRY,²⁹ ANA M. CERVEIRA,^{1,17} ANDRÉ CID,³¹ RAFAEL CLARKE, CONCEIÇÃO CONDE,²⁷ JOSÉ CONDE, JORGE COSTA, MAFALDA COSTA,³² PEDRO COSTA,³³ CRISTINA COSTA,²⁷ ANDRÉ PEDRO DO COUTO,⁵ JOÃO CRAVEIRO,³⁴ MARTA DIAS,³ SOFIA DIAS, BEATRIZ DUARTE,⁶ VIRGINIA DURO,²² CLÁUDIA ENCARNÇÃO,^{35,36} SOFIA EUFRÁZIO,³⁷ ANTÓNIO FAEL,^{15,83} JOÃO SALVADOR FALÉ,²³ SANDRA FARIA,²² CARLOS FERNANDES,^{3,38} MARGARIDA FERNANDES,²⁷ GONÇALO FERRÃO DA COSTA,^{15,17} CLARA FERREIRA,^{7,39} DIOGO F. FERREIRA,^{7, 40,41} EDUARDO FERREIRA,¹⁷ JOAQUIM PEDRO FERREIRA,¹⁷ JOÃO FERREIRA, DIANA FERREIRA,⁶ CARLOS FONSECA,^{17,42} INÊS FONTES,⁴ RICARDO FRAGOSO,²⁷ CLAUDIA FRANCO, TAMIRA FREITAS,⁴³ SOFIA I. GABRIEL,^{1,17} RORY GIBB,⁴⁰ PATRICIA GIL,⁷ CARLA PATRICIA JORGE GOMES,^{21,22} PEDRO HORTA,^{7,9,13,44} PEDRO GOMES,¹⁷ VERÓNICA GOMES,⁷ FILIPA GRILO,³ AMÉRICO GUEDES,⁴⁵ FILIPA GUILHERME,⁷ IVÁN GUTIÉRREZ,⁴⁵ HENRY HARPER,³¹ JOSÉ M. HERRERA,²⁰ DÁRIO HIPÓLITO,^{17,46} SAMUEL INFANTE,⁸ JOSÉ JESUS,⁴³ KATE E. JONES,⁴⁰ MARINA I LABORDE,^{31,47} LUÍS LAMAS DE OLIVEIRA,²² INÊS LEITÃO,⁴⁸ RITA LEMOS,¹⁰ CÁTIA LIMA,¹⁷ PALOMA LINCK,¹⁷ HUGO LOPES,²³ SUSANA LOPES,⁷ ADRIÀ LÓPEZ-BAUCELLS,⁴⁹ ARMANDO LOUREIRO,²⁷ FILIPA LOUREIRO,³ RUI LOURENÇO,⁵⁰ SOFIA

Abstract: Mammals are threatened worldwide, with ca. 26% of all species being included in the IUCN threatened categories. This overall pattern is primarily associated to habitat loss or degradation, and human persecution for terrestrial mammals, and pollution, open net fishing, climate change and prey depletion for marine mammals. Mammals play a key role in maintaining ecosystems functionality and resilience, and therefore information on their distribution is crucial to delineate and support conservation actions. Here we present MAMMALS IN PORTUGAL a publicly available data set compiling unpublished geo-referenced occurrence records of 92 terrestrial and marine mammals in mainland Portugal and archipelagos of Azores and Madeira that includes 107,853 data entries between 1873 and 2021 (72% of the data occurring between 2000 and 2021). The methods used to collect the data were: live observation/captures (42%), sign surveys (38%), camera trapping (16%), bioacoustics surveys (4%) with radio-tracking and inquiries representing less than 1% of the records. The data set includes 13 types of records: 1) burrows | soil mounds | tunnel, 2) capture, 3) colony, 4) dead animal | hair | skulls | jaws, 5) genetic confirmation, 6) inquiries, 7) observation of live animal, 8), observation in shelters, 9) photo trapping | video, 10), predator diet | pellets | pine cones/nuts, 11) scat | track | ditch, 12) telemetry and 13) vocalization | echolocation. The spatial uncertainty of most records ranges between 0 and 100 m (76%). Rodentia (n= 34,754) has the highest number of records followed by Carnivora (n= 18,594), Chiroptera (n= 18,858), Lagomorpha (n= 17,679), Cetartiodactyla (n= 11,568) and Eulipotyphla (n= 6,400). The data set includes records of species classified by the IUCN as Endangered [*Oryctolagus cuniculus* (n=12, 407), *Monachus monachus* (n= 1512), *Lynx pardinus* (n=197), *Balaenoptera borealis* (n=4) and *Eubalaena glacialis* (n=1)]. We believe that this data set may stimulate the beginning of a series of European mammals data sets which would certainly contribute to ecology and conservation-related research, and therefore assisting on the development of more accurate and tailored conservation management strategies for

each species throughout their European range. Please cite this data paper when the data are used in publications.

Key words: 1873-2021, Carnivora, Cetartiodactyla, Chiroptera, Eulipotyphla, Europe, Iberian Peninsula, Lagomorpha, Rodentia, Species distribution

Open Research: The complete data set is available as Supporting Information at: [*to be completed at proof stage*]. Associated data is also available at <https://doi.org/10.6084/m9.figshare.14938437>

Corresponding Editor: William K. Michener.

⁸⁵ E-mail: [clarabentesgrilo@gmail.com]

Bat calls of Britain and Europe: A Guide to Species Identification – Serotine *Eptesicus serotinus* (Schreber, 1774)

Horta, P., Raposeira, H. Rebelo., Russ, J., Korsten, E., and De Sjipte, M. (2021). Bat calls of Britain and Europe: A Guide to Species Identification – Serotine *Eptesicus serotinus* (Schreber, 1774). Pelagic Publishing. 304-312.

8.25 Serotine *Eptesicus serotinus* (Scheber, 1774)

Pedro Horta, Helena Raposeira, Hugo Rebelo, Jon Russ, Erik Korsten
and Marc Van De Sijpe



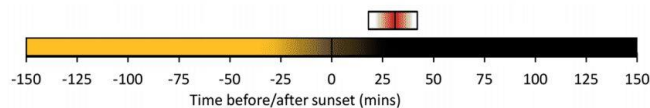
© René Janssen

DISTRIBUTION

The serotine is mainly distributed along the Eurosiberian biogeographical region (Santos *et al.* 2014). It has a broad range covering most of Europe up to a latitude of 55°N, including the south of England, the southernmost areas of Sweden and the Baltic region. Despite some indications about the species spreading northwards, albeit with a fragmented distribution, it is apparently absent from Ireland, Norway, Finland and north of the Baltic region (Dietz *et al.* 2009). It is widely distributed in Mediterranean Europe (Santos *et al.* 2014), though with no records in the Atlantic islands (Dietz *et al.* 2009).



EMERGENCE



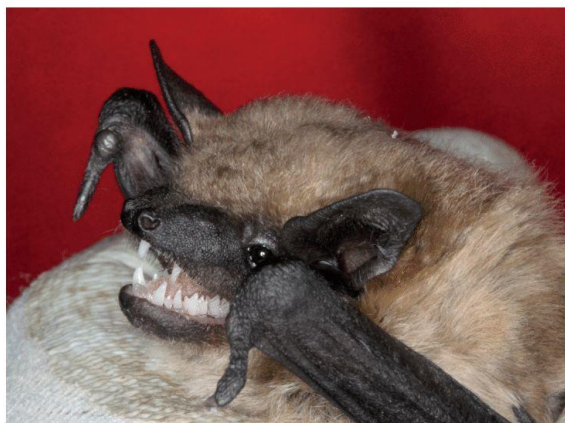
Bat calls of Britain and Europe: A Guide to Species Identification – Meridional serotine *Eptesicus isabellinus* (Temminck, 1840)

Raposeira, H. Rebelo., and **Horta, P.** (2021). Bat calls of Britain and Europe: A Guide to Species Identification – Meridional serotine *Eptesicus isabellinus* (Temminck, 1840). Pelagic Publishing. 313-318.

8.26 Meridional serotine

Eptesicus isabellinus (Temminck, 1840)

Helena Raposeira, Hugo Rebelo and Pedro Horta



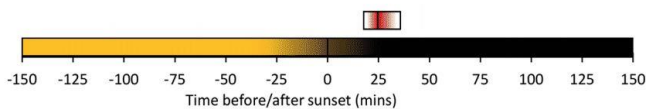
© Martyn Cooke

DISTRIBUTION

The meridional serotine occurs over the Mediterranean biogeographical region of the Iberian peninsula and north Africa (Ibáñez *et al.* 2006). The species is limited to the south by the Sahara Desert, with the Atlas Mountains being the southern limit of its distribution (Dietz *et al.* 2009). It is present to the west in the Canary Islands (Trujillo 1991), occurring from Morocco, Algeria, Tunisia to Libya, the eastern extreme of their distribution (Ibáñez *et al.* 2006). In the north, the meridional serotine is found only in the centre and south of the Iberian peninsula, the only European region where it is present (Santos *et al.* 2014).



EMERGENCE



Appendix C

Papers retrieved from the systematic review

Table C1 - List of articles retrieved from the systematic review and used in various meta-analyses that were incorporated into chapter 2, chapter 3 and chapter 4 of this thesis.

ID	Authors	Year	Title	Journal
1	Abi-Rached, L.; Jobin, M. J.; Kulkarni, S.; McWhinnie, A.; Dalva, K.; Gragert, L.; Babrzadeh, F.; Gharizadeh, B.; Luo, M.; Plummer, F. A.; Kimani, J.; Carrington, M.; Middleton, D.; Rajalingam, R.; Beksac, M.; Marsh, S. G. E.; Maiers, M.; Guethlein, L. A.; Tavoularis, S.; Little, A. M.; Green, R. E.; Norman, P. J.; Parham, P.	2011	The Shaping of Modern Human Immune Systems by Multiregional Admixture with Archaic Humans	Science
2	Acosta, M. C.; Premoli, A. C.	2018	Understanding the extensive hybridization in South American Nothofagus through karyotype analysis	Botanical Journal of the Linnean Society
3	Aeschbacher, S.; Selby, J. P.; Willis, J. H.; Coop, G.	2017	Population-genomic inference of the strength and timing of selection against gene flow	Proceedings of the National Academy of Sciences of the United States of America
4	Akkuratov, E. E.; Gelfand, M. S.; Khrameeva, E. E.	2018	Neanderthal and Denisovan ancestry in Papuans: A functional study	Journal of Bioinformatics and Computational Biology
5	Aleksic, J. M.; Skondric, S.; Lakusic, D.	2018	Comparative phylogeography of capitulate Campanula species from the Balkans, with description of a new species, C-daucoides	Plant Systematics and Evolution
6	Alexander, A. M.; Su, Y. C.; Oliveros, C. H.; Olson, K. V.; Travers, S. L.; Brown, R. M.	2017	Genomic data reveals potential for hybridization, introgression, and incomplete lineage sorting to confound phylogenetic relationships in an adaptive radiation of narrow-mouth frogs	Evolution
7	Antelope, C. X.; Marnetto, D.; Casey, F.; Huerta-	2017	Leveraging Multiple Populations across Time Helps Define Accurate	Human Biology

	Sanchez, E.		Models of Human Evolution: A Reanalysis of the Lactase Persistence Adaptation	
8	Arcella, T.; Hood, G. R.; Powell, T. H. Q.; Sim, S. B.; Yee, W. L.; Schwarz, D.; Egan, S. P.; Goughnour, R. B.; Smith, J. J.; Feder, J. L.	2015	Hybridization and the spread of the apple maggot fly, <i>Rhagoletis pomonella</i> (Diptera: Tephritidae), in the northwestern United States	Evolutionary Applications
9	Arnold, M. L.; Ballerini, E. S.; Brothers, A. N.; Hamlin, J. A. P.; Ishibashi, C. D. A.; Zuellig, M. P.	2012	The genomics of natural selection and adaptation: Christmas past, present and future(?)	Plant Ecology & Diversity
10	Baduel, P.; Hunter, B.; Yeola, S.; Bomblies, K.	2018	Genetic basis and evolution of rapid cycling in railway populations of tetraploid <i>Arabidopsis arenosa</i>	Plos Genetics
11	Bagley, J. C.; Alda, F.; Breitman, M. F.; Bermingham, E.; van den Berghe, E. P.; Johnson, J. B.	2015	Assessing Species Boundaries Using Multilocus Species Delimitation in a Morphologically Conserved Group of Neotropical Freshwater Fishes, the <i>Poecilia sphenops</i> Species Complex (Poeciliidae)	Plos One
12	Ballerini, E. S.; Brothers, A. N.; Tang, S. X.; Knapp, S. J.; Bouck, A.; Taylor, S. J.; Arnold, M. L.; Martin, N. H.	2012	QTL mapping reveals the genetic architecture of loci affecting pre- and post-zygotic isolating barriers in Louisiana Iris	Bmc Plant Biology
13	Baldassarre, D.; White, T.; Karubian, J.; Webster M	2014	Genomic and morphological analysis of a semipermeable avian hybrid zone suggests asymmetrical introgression of a sexual signal	Evolution
14	Bay, R. A.; Ruegg, K.	2017	Genomic islands of divergence or opportunities for introgression?	Proceedings of the Royal Society B-Biological Sciences
15	Beckman, E. J.; Benham, P. M.; Cheviron, Z. A.; Witt, C. C.	2018	Detecting introgression despite phylogenetic uncertainty: The case of the South American siskins	Molecular Ecology
16	Beresford, J.; Elias, M.; Pluckrose, L.; Sundstrom, L.; Butlin, R. K.; Pamilo, P.; Kulmuni, J.	2017	Widespread hybridization within mound-building wood ants in Southern Finland results in cytonuclear mismatches and potential for sex-specific hybrid breakdown	Molecular Ecology

17	Bisson, L. F.	2012	Geographic Origin and Diversity of Wine Strains of <i>Saccharomyces</i>	American Journal of Enology and Viticulture
18	Black, W. C.; Lanzaro, G. C.	2001	Distribution of genetic variation among chromosomal forms of <i>Anopheles gambiae</i> s.s.: introgressive hybridization, adaptive inversions, or recent reproductive isolation?	Insect Molecular Biology
19	Blancher, A.; Aarnink, A.; Tanaka, K.; Ota, M.; Inoko, H.; Yamanaka, H.; Nakagawa, H.; Apoil, P. A.; Shiina, T.	2012	Study of cynomolgus monkey (<i>Macaca fascicularis</i>) Mhc DRB gene polymorphism in four populations	Immunogenetics
20	Bog, M.; Bassler, C.; Oberprieler, C.	2017	Lost in the hybridisation vortex: high-elevation <i>Senecio hercynicus</i> (Compositae, Senecioneae) is genetically swamped by its congener <i>S. ovatus</i> in the Bavarian Forest National Park (SE Germany)	Evolutionary Ecology
21	Bonnet, T.; Leblois, R.; Rousset, F.; Crochet, P. A.	2017	A reassessment of explanations for discordant introgressions of mitochondrial and nuclear genomes	Evolution
22	Boratynski, Z.; Melo-Ferreira, J.; Alves, P. C.; Berto, S.; Koskela, E.; Pentikainen, O. T.; Tarroso, P.; Ylilauri, M.; Mappes, T.	2014	Molecular and ecological signs of mitochondrial adaptation: consequences for introgression?	Heredity
23	Bouck, A.; Peeler, R.; Arnold, M. L.; Wessler, S. R.	2005	Genetic mapping of species boundaries in Louisiana irises using IRRE retrotransposon display markers	Genetics
24	Brand, C. L.; Kingan, S. B.; Wu, L. J.; Garrigan, D.	2013	A Selective Sweep across Species Boundaries in <i>Drosophila</i>	Molecular Biology and Evolution
25	Brandvain, Y.; Amanda M. Kenney, Lex Flagel, Graham Coop, Andrea L. Sweigart	2014	Speciation and Introgression between <i>Mimulus nasutus</i> and <i>Mimulus guttatus</i>	Plos one
26	Brennan, A. C.; Harris, S. A.; Hiscock, S. J.	2013	The population genetics of sporophytic self-incompatibility in three hybridizing <i>Senecio</i> (Asteraceae) species with contrasting population histories	Evolution

27	Brower, A. V. Z.	2018	Alternative facts: a reconsideration of putatively natural interspecific hybrid specimens in the genus <i>Heliconius</i> (Lepidoptera: Nymphalidae)	Zootaxa
28	Cahill JA, Stirling I, Kistler L, Salamzade R, Ersmark E, Fulton TL, Stiller M, Green RE, Shapiro B	2015	Genomic evidence of geographically widespread effect of gene flow from polar bears into brown bears.	Molecular Ecology
29	Candia, M; Routman, E.	2007	Cytonuclear discordance across a leopard frog contact zone	Molecular Phylogenetics and Evolution
30	Caputo, B.; Pichler, V.; Mancini, E.; Pombi, M.; Vicente, J. L.; Dinis, J.; Steen, K.; Petrarca, V.; Rodrigues, A.; Pinto, J.; Della Torre, A.; Weetman, D.	2016	The last bastion? X chromosome genotyping of <i>Anopheles gambiae</i> species pair males from a hybrid zone reveals complex recombination within the major candidate 'genomic island of speciation'	Molecular Ecology
31	Caseys, C.; Glauser, G.; Stolting, K. N.; Christe, C.; Albrechtsen, B. R.; Lexer, C.	2012	Effects of interspecific recombination on functional traits in trees revealed by metabolomics and genotyping-by-sequencing	Plant Ecology & Diversity
32	Castric, V.; Bechsgaard, J.; Schierup, M. H.; Vekemans, X.	2008	Repeated Adaptive Introgression at a Gene under Multiallelic Balancing Selection	Plos Genetics
33	Cavender-Bares, J.; Gonzalez-Rodriguez, A.; Eaton, D. A. R.; Hipp, A. A. L.; Beulke, A.; Manos, P. S.	2015	Phylogeny and biogeography of the American live oaks (<i>Quercus</i> subsection <i>Virentes</i>): a genomic and population genetics approach	Molecular Ecology
34	Ceballos, S. G.; Roesti, M.; Matschiner, M.; Fernandez, D. A.; Damerau, M.; Hanel, R.; Salzburger, W.	2019	Phylogenomics of an extra-Antarctic notothenioid radiation reveals a previously unrecognized lineage and diffuse species boundaries	Bmc Evolutionary Biology
35	Chen, Y. M.; Hou, Y. S.; Guo, Z. X.; Wang, W. Q.; Zhong, C. R.; Zhou, R. C.; Shi, S. H.	2015	Applications of Multiple Nuclear Genes to the Molecular Phylogeny, Population Genetics and Hybrid Identification in the Mangrove Genus <i>Rhizophora</i>	Plos One

36	Chhatre, V. E.; Evans, L. M.; DiFazio, S. P.; Keller, S. R.	2018	Adaptive introgression and maintenance of a trispecies hybrid complex in range-edge populations of <i>Populus</i>	Molecular Ecology
37	Choi, K. S.; Townson, H.	2012	Evidence for X-linked introgression between molecular forms of <i>Anopheles gambiae</i> from Angola	Medical and Veterinary Entomology
38	Clarkson, C. S.; Weetman, D.; Essandoh, J.; Yawson, A. E.; Maslen, G.; Manske, M.; Field, S. G.; Webster, M.; Antao, T.; MacInnis, B.; Kwiatkowski, D.; Donnelly, M. J.	2014	Adaptive introgression between <i>Anopheles</i> sibling species eliminates a major genomic island but not reproductive isolation	Nature Communications
39	Collins, E.; Sullivan, A. R.; Gailing, O.	2015	Limited effective gene flow between two interfertile red oak species	Trees-Structure and Function
40	Corcoran, P.; Anderson, J. L.; Jacobson, D. J.; Sun, Y.; Ni, P. X.; Lascoux, M.; Johannesson, H.	2016	Introgression maintains the genetic integrity of the mating-type determining chromosome of the fungus <i>Neurospora tetrasperma</i>	Genome Research
41	Cullingham, C. I.; Cooke, J. E. K.; Coltman, D. W.	2013	Effects of introgression on the genetic population structure of two ecologically and economically important conifer species: lodgepole pine (<i>Pinus contorta</i> var. <i>latifolia</i>) and jack pine (<i>Pinus banksiana</i>)	Genome
42	Dannemann, M.; Andres, A. M.; Kelso, J.	2016	Introgression of Neandertal- and Denisovan-like Haplotypes Contributes to Adaptive Variation in Human Toll-like Receptors	American Journal of Human Genetics
43	Dasmahapatra, K. K.; Walters, J. R.; Briscoe, A. D.; Davey, J. W.; Whibley, A.; Nadeau, N. J.; Zimin, A. V.; Hughes, D. S. T.; Ferguson, L. C.; Martin, S. H.; Salazar, C.; Lewis, J. J.; Adler, S.; Ahn, S. J.; Baker, D. A.; Baxter, S. W.; Chamberlain, N. L.; Chauhan, R.; Counterman, B. A.; Dalmay, T.; Gilbert, L. E.; Gordon, K.; Heckel, D. G.; Hines, H. M.; Hoff, K. J.; Holland, P. W. H.; Jacquin-Joly, E.;	2012	Butterfly genome reveals promiscuous exchange of mimicry adaptations among species	Nature

	Jiggins, F. M.; Jones, R. T.; Kapan, D. D.; Kersey, P.; Lamas, G.; Lawson, D.; Mapleson, D.; Maroja, L. S.; Martin, A.; Moxon, S.; Palmer, W. J.; Papa, R.; Papanicolaou, A.; Pauchet, Y.; Ray, D. A.; Rosser, N.; Salzberg, S. L.; Supple, M. A.; Surridge, A.; Tenger-Trolander, A.; Vogel, H.; Wilkinson, P. A.; Wilson, D.; Yorke, J. A.; Yuan, F. R.; Balmuth, A. L.; Eland, C.; Gharbi, K.; Thomson, M.; Gibbs, R. A.; Han, Y.; Jayaseelan, J. C.; Kovar, C.; Mathew, T.; Muzny, D. M.; Onger, F.; Pu, L. L.; Qu, J. X.; Thornton, R. L.; Worley, K. C.; Wu, Y. Q.; Linares, M.; Blaxter, M. L.; French-Constant, R. H.; Joron, M.; Kronforst, M. R.; Mullen, S. P.; Reed, R. D.; Scherer, S. E.; Richards, S.; Mallet, J.; McMillan, W. O.; Jiggins, C. D.; Heliconius Genome Consortium			
44	Deschamps, M.; Laval, G.; Fagny, M.; Itan, Y.; Abel, L.; Casanova, J. L.; Patin, E.; Quintana-Murci, L.	2016	Genomic Signatures of Selective Pressures and Introgression from Archaic Hominins at Human Innate Immunity Genes	American Journal of Human Genetics
45	Djogbenou, L., Chandre, F., Berthomieu, A., Dabiré, R., Koffi, A., Alout, A.; Weill, M.	2008	Evidence of introgression of the ace-1(R) mutation and of the ace-1 duplication in West African Anopheles gambiae s.s	PloS One
46	Doniger, S. W.; Kim, H. S.; Swain, D.; Corcuera, D.; Williams, M.; Yang, S. P.; Fay, J. C.	2008	A Catalog of Neutral and Deleterious Polymorphism in Yeast	Plos Genetics
47	Duchoslav, M.; Safarova, L.; Jandova, M.	2013	Role of adaptive and non-adaptive mechanisms forming complex	Annals of Botany

			patterns of genome size variation in six cytotypes of polyploid <i>Allium oleraceum</i> (Amaryllidaceae) on a continental scale	
48	El Mujtar, V. A.; Gallo, L. A.; Lang, T.; Garnier-Gere, P.	2014	Development of genomic resources for <i>Nothofagus</i> species using next-generation sequencing data	Molecular Ecology Resources
49	Enard, D.; Petrov, D. A.	2018	Evidence that RNA Viruses Drove Adaptive Introgression between Neanderthals and Modern Humans	Cell
50	Enciso-Romero, J.; Pardo-Diaz, C.; Martin, S. H.; Arias, C. F.; Linares, M.; McMillan, W. O.; Jiggins, C. D.; Salazar, C.	2017	Evolution of novel mimicry rings facilitated by adaptive introgression in tropical butterflies	Molecular Ecology
51	Evans, P. D.; Mekel-Bobrov, N.; Vallender, E. J.; Hudson, R. R.; Lahn, B. T.	2006	Evidence that the adaptive allele of the brain size gene <i>microcephalin</i> introgressed into <i>Homo sapiens</i> from an archaic <i>Homo</i> lineage	Proceedings of the National Academy of Sciences of the United States of America
52	Fan, S. H.; Grossnickle, S. C.; Sutton, B. C. S.	1997	Relationships between gas exchange adaptation of Sitka x interior spruce genotypes and ribosomal DNA markers	Tree Physiology
53	Feder, J. L.; Xie, X. F.; Rull, J.; Velez, S.; Forbes, A.; Leung, B.; Dambroski, H.; Filchak, K. E.; Aluja, M.	2005	Mayr, Dobzhansky, and Bush and the complexities of sympatric speciation in <i>Rhagoletis</i>	Proceedings of the National Academy of Sciences of the United States of America
54	Filialt, D. L.; Ballerini, E. S.; Mandakova, T.; Akoz, G.; Derieg, N. J.; Schmutz, J.; Jenkins, J.; Grimwood, J.; Shu, S. Q.; Hayes, R. D.; Hellsten, U.; Barry, K.; Yan, J. Y.; Mihaltcheva, S.; Karafiatova, M.; Nizhynska, V.; Kramer, E. M.; Lysak, M. A.; Hodges, S. A.; Nordborg, M.	2018	The <i>Aquilegia</i> genome provides insight into adaptive radiation and reveals an extraordinarily polymorphic chromosome with a unique history	Elife

55	Fraisse, C.; Belkhir, K.; Welch, J. J.; Bierne, N.	2016	Local interspecies introgression is the main cause of extreme levels of intraspecific differentiation in mussels	Molecular Ecology
56	Fraisse, C.; Roux, C.; Welch, J. J.; Bierne, N.	2014	Gene-Flow in a Mosaic Hybrid Zone: Is Local Introgression Adaptive?	Genetics
57	Friar, E. A.; Prince, L. M.; Cruse-Sanders, J. M.; McGlaughlin, M. E.; Butterworth, C. A.; Baldwin, B. G.	2008	Hybrid origin and genomic mosaicism of <i>Dubautia scabra</i> (Hawaiian Silversword Alliance; Asteraceae, Madiinae)	Systematic Botany
58	Gagnaire, P. A.; Albert, V.; Jonsson, B.; Bernatchez, L.	2009	Natural selection influences AFLP intraspecific genetic variability and introgression patterns in Atlantic eels	Molecular Ecology
59	Gagnaire, P. A.; Pavey, S. A.; Normandeau, E.; Bernatchez, L.	2013	The genomic architecture of reproductive isolation during speciation-with-gene-flow in Lake whitefish species pairs assessed by RAD-sequencing	Evolution
60	Gante, H. F.; Matschiner, M.; Malmstrom, M.; Jakobsen, K. S.; Jentoft, S.; Salzburger, W.	2016	Genomics of speciation and introgression in Princess cichlid fishes from Lake Tanganyika	Molecular Ecology
61	Garrigan D, Kingan SB, Geneva AJ, Andolfatto P, Clark AG, Thornton KR, et al	2012	Genome sequencing reveals complex speciation in the <i>Drosophila simulans</i> clade.	Genome Research
62	Gaudeul, M.; Siljak-Yakovlev, S.; Jang, T. S.; Rouhan, G.	2018	Reconstructing Species Relationships within the Recently Diversified Genus <i>Odontites</i> Ludw. (Orobanchaceae): Evidence for Extensive Reticulate Evolution	International Journal of Plant Sciences
63	Giannoulis, T.; Plageras, D.; Stamatis, C.; Chatzivagias, E.; Tsipourlianos, A.; Birtsas, P.; Billinis, C.; Suchentrunk, F.; Mamuris, Z.	2019	Islands and hybrid zones: combining the knowledge from "Natural Laboratories" to explain phylogeographic patterns of the European brown hare	Bmc Evolutionary Biology
64	Gittelman, R. M.; Schraiber, J. G.; Vernot, B.; Mikacenic, C.; Wurfel, M. M.; Akey, J. M.	2016	Archaic Hominin Admixture Facilitated Adaptation to Out-of-Africa Environments	Current Biology
65	Gramlich, S.; Wagner, N. D.; Horandl, E.	2018	RAD-seq reveals genetic structure of the F-2-generation of natural willow hybrids (<i>Salix</i> L.) and a great potential for interspecific	Bmc Plant Biology

			introgression	
66	Grant, P; GRANT BR	2016	Introgressive hybridization and natural selection in Darwin's finches	Biological Journal of the Linnean Society
67	Grant, P; GRANT BR	2002	Unpredictable Evolution in a 30-Year Study of Darwin's Finches	Science
68	Green, R.; Krause, J.; Briggs, A.; Maricic, T.; Stenzel, U.; Kircher, M.; Patterson, N.; Li, H.; Zhai, W.; Fritz, M.; Hansen, N.; Durand, E.; Malaspina, A.; Jensen, J.; Marques-Bonet, T.; et al.	2010	A Draft Sequence of the Neandertal Genome	Science
69	Hackinger, S.; Kraaijenbrink, T.; Xue, Y. L.; Mezzavilla, M.; Asan,.; van Driem, G.; Jobling, M. A.; de Knijff, P.; Tyler-Smith, C.; Ayub, Q.	2016	Wide distribution and altitude correlation of an archaic high-altitude-adaptive EPAS1 haplotype in the Himalayas	Human Genetics
70	Hardy J, Pittman A, Myers A, Gwinn-Hardy K, Fung HC, de Silva R, Hutton M, Duckworth J	2005	Evidence suggesting that Homo neanderthalensis contributed the H2 MAPT haplotype to Homo sapiens.	Biochemical Society Transactions
71	Hawkins, M. T. R.; Leonard, J. A.; Helgen, K. M.; McDonough, M. M.; Rockwood, L. L.; Maldonado, J. E.	2016	Evolutionary history of endemic Sulawesi squirrels constructed from UCEs and mitogenomes sequenced from museum specimens	Bmc Evolutionary Biology
72	Hejase, H. A.; Liu, K. J.	2016	Mapping the genomic architecture of adaptive traits with interspecific introgressive origin: a coalescent-based approach	Bmc Genomics
73	Herrig, D. K.; Modrick, A. J.; Brud, E.; Llopart, A.	2014	Introgression in the <i>Drosophila subobscura</i> – <i>D. madeirensis</i> sister species: Evidence of gene flow in nuclear genes despite mitochondrial differentiation	Evolution
74	Hsieh, P.; Woerner, A. E.; Wall, J. D.; Lachance, J.; Tishkoff, S. A.; Gutenkunst, R. N.; Hammer, M. F.	2016	Model-based analyses of whole-genome data reveal a complex evolutionary history involving archaic introgression in Central African Pygmies	Genome Research
75	Huerta-Sánchez, E., Jin, X., Asan, Bianba, Z.,	2014	Altitude adaptation in Tibetans caused by introgression of	Nature

	Peter, B. M., Vinckenbosch, N., ... Nielsen, R		Denisovan-like DNA	
76	Irwin, D. E.; Mila, B.; Toews, D. P. L.; Brelsford, A.; Kenyon, H. L.; Porter, A. N.; Grossen, C.; Delmore, K. E.; Alcaide, M.; Irwin, J. H.	2018	A comparison of genomic islands of differentiation across three young avian species pairs	Molecular Ecology
77	Jeong, C., Alkorta-Aranburu, G., Basnyat, B., Neupane, M., Witonsky, D. B., Pritchard, J. K., ... Di Rienzo, A.	2014	Admixture facilitates genetic adaptations to high altitude in Tibet	Nature Communications
78	Jones, M. R., Mills, L. S., Alves, P. C., Callahan, C. M., Alves, J. M., Lafferty, D. J. R., ... Good, J. M.	2018	Adaptive introgression underlies polymorphic seasonal camouflage in snowshoe hares	Science
79	Khrameeva, E. E., K. Bozek, L. He, Z. Yan, X. Jiang, Y. Wei, K. Tang, M. S. Gelfand, K. Prufer, J. Kelso, et al.,	2014	Neanderthal ancestry drives evolution of lipid catabolism in contemporary Europeans	Nature communications
80	Kim, S. C.; Rieseberg, L. H.	1999	Genetic architecture of species differences in annual sunflowers: Implications for adaptive trait introgression	Genetics
81	Lamichhaney S, Han F, Berglund J, Wang C, Almén MS, Webster MT, Grant BR, Grant PR, Andersson L	2016	A beak size locus in Darwin's finches facilitated character displacement during a drought.	Science
82	Leducq, J. B., M. Henault, G. Charron, L. Nielly-Thibault, Y. Terrat et al.	2017	Mitochondrial Recombination and Introgression during Speciation by Hybridization	Molecular Biology and Evolution
83	Lee, Y.; Marsden, C.; Norris, L.; Collier, T.; Main, B.; Fofana, A.; Cornel, A. and G. Lanzaro	2013	Spatiotemporal dynamics of gene flow and hybrid fitness between the M and S forms of the malaria mosquito, <i>Anopheles gambiae</i>	Proceedings of the National Academy of Sciences of the United States of America
84	Leroy, T.; Roux, C.; Villate, L.; Bodenes, C.; Romiguier, J.; Paiva, J. A. P.; Dossat, C.; Aury, J.	2017	Extensive recent secondary contacts between four European white oak species	New Phytologist

	M.; Plomion, C.; Kremer, A.			
85	Lesur, I.; Alexandre, H.; Boury, C.; Chancerel, E.; Plomion, C.; Kremer, A.	2018	Development of Target Sequence Capture and Estimation of Genomic Relatedness in a Mixed Oak Stand	Frontiers in Plant Science
86	Lexer, C.; Heinze, B.; Alia, R.; Rieseberg, L. H.	2004	Hybrid zones as a tool for identifying adaptive genetic variation in outbreeding forest trees: lessons from wild annual sunflowers (<i>Helianthus</i> spp.)	Forest Ecology and Management
87	Lexer, C.; Joseph, J. A.; van Loo, M.; Barbara, T.; Heinze, B.; Bartha, D.; Castiglione, S.; Fay, M. F.; Buerkle, C. A.	2010	Genomic Admixture Analysis in European <i>Populus</i> spp. Reveals Unexpected Patterns of Reproductive Isolation and Mating	Genetics
88	Liu KJ, Steinberg E, Yozzo A, Song Y, Kohn MH, Nakhleh L.	2015	Interspecific introgressive origin of genomic diversity in the house mouse	Proceedings of the National Academy of Sciences of the United States of America
89	Llopart, A., Herrig, D., Brud, E., ; Stecklein, Z. (2014).	2014	Sequential adaptive introgression of the mitochondrial genome in <i>Drosophila yakuba</i> and <i>Drosophila santomea</i>	Molecular Ecology
90	Lohse, K.; Clarke, M.; Ritchie, M. G.; Etges, W. J.	2015	Genome-wide tests for introgression between cactophilic <i>Drosophila</i> implicate a role of inversions during speciation	Evolution
91	Maguilla, E.; Escudero, M.; Hipp, A. L.; Luceno, M.	2017	Allopatric speciation despite historical gene flow: Divergence and hybridization in <i>Carex furva</i> and <i>C. lucennoiberica</i> (Cyperaceae) inferred from plastid and nuclear RAD-seq data	Molecular Ecology
92	Martin, N. H.; Bouck, A. C.; Arnold, M. L.	2006	Detecting adaptive trait introgression between <i>Iris fulva</i> and <i>I. brevicaulis</i> in highly selective field conditions	Genetics
93	Mavárez J.; Salazar CA.; Bermingham E.; Salcedo C.; Jiggins CD.; Linares M.	2006	Speciation by hybridization in <i>Heliconius</i> butterflies.	Nature
94	Maxwell, C. S.; Mattox, K.; Turissini, D. A.	2019	Gene exchange between two divergent species of the fungal human	Evolution

	Teixeira, M. M.; Barker, B. M.; Matute, D. R.		pathogen, <i>Coccidioides</i>	
95	Melo-Ferreira, J.; Seixas, F. A.; Cheng, E.; Mills, L. S.; Alves, P. C.	2014	The hidden history of the snowshoe hare, <i>Lepus americanus</i> : extensive mitochondrial DNA introgression inferred from multilocus genetic variation	Molecular Ecology
96	Melo-Ferreira, J.; Vilela, J.; Fonseca, M. M.; da Fonseca, R. R.; Boursot, P.; Alves, P. C.	2014	The Elusive Nature of Adaptive Mitochondrial DNA Evolution of an Arctic Lineage Prone to Frequent Introgression	Genome Biology and Evolution
97	Mendez, F. L.; Watkins, J. C.; Hammer, M. F.	2013	Neandertal Origin of Genetic Variation at the Cluster of OAS Immunity Genes	Molecular Biology and Evolution
98	Mendez, F. L.; Watkins, J. C.; Hammer, M. F.	2012	A Haplotype at STAT2 Introgressed from Neanderthals and Serves as a Candidate of Positive Selection in Papua New Guinea	American Journal of Human Genetics
99	Mendez, F. L.; Watkins, J. C.; Hammer, M. F.	2012	Global Genetic Variation at OAS1 Provides Evidence of Archaic Admixture in Melanesian Populations	Molecular Biology and Evolution
100	Minder, A. M.; Widmer, A.	2008	A population genomic analysis of species boundaries: neutral processes, adaptive divergence and introgression between two hybridizing plant species	Molecular Ecology
101	Morales, H. E.; Pavlova, A.; Amos, N.; Major, R.; Kilian, A.; Greening, C.; Sunnucks, P.	2018	Concordant divergence of mitogenomes and a mitonuclear gene cluster in bird lineages inhabiting different climates	Nature Ecology & Evolution
102	Morales, H. E.; Sunnucks, P.; Joseph, L.; Pavlova, A.	2017	Perpendicular axes of differentiation generated by mitochondrial introgression	Molecular Ecology
103	Nadachowska-Brzyska K, Zielinski P, Radwan J, Babik W	2012	Interspecific hybridization increases MHC class II diversity in two sister species of newts	Molecular Ecology
104	Ng, N. S. R.; Wilton, P. R.; Prawiradilaga, D. M.; Tay, Y. C.; Indrawan, M.; Garg, K. M.; Rheindt, F. E.	2017	The effects of Pleistocene climate change on biotic differentiation in a montane songbird Glade from Wallacea	Molecular Phylogenetics and Evolution
105	Niang, A.; Epopa, P. S.; Sawadogo, S. P.; Maiga,	2015	Does extreme asymmetric dominance promote hybridization between	Parasites & Vectors

	H.; Konate, L.; Faye, O.; Dabire, R. K.; Tripet, F.; Diabate, A.		Anopheles coluzzii and Anopheles gambiae s.s. in seasonal malaria mosquito communities of West Africa?	
106	Nichols, P.; Genner, M. J.; van Oosterhout, C.; Smith, A.; Parsons, P.; Sungani, H.; Swanstrom, J.; Joyce, D. A.	2015	Secondary contact seeds phenotypic novelty in cichlid fishes	Proceedings of the Royal Society B-Biological Sciences
107	Norris, E. T.; Wang, L.; Conley, A. B.; Rishishwar, L.; Marino-Ramirez, L.; Valderrama-Aguirre, A.; Jordan, I. K.	2018	Genetic ancestry, admixture and health determinants in Latin America	Bmc Genomics
108	Norris, L. C.; Main, B. J.; Lee, Y.; Collier, T. C.; Fofana, A.; Cornel, A. J.; Lanzaro, G. C.	2015	Adaptive introgression in an African malaria mosquito coincident with the increased usage of insecticide-treated bed nets	Proceedings of the National Academy of Sciences of the United States of America
109	Nurnberger, B.; Lohse, K.; Fijarczyk, A.; Szymura, J. M.; Blaxter, M. L.	2016	Para-allopatry in hybridizing fire-bellied toads (Bombina bombina and B. variegata): Inference from transcriptome-wide coalescence analyses	Evolution
110	Oney-Birol, S.; Fitz-Gibbon, S.; Chen, J. M.; Gugger, P. F.; Sork, V. L.	2018	Assessment of shared alleles in drought-associated candidate genes among southern California white oak species (Quercus sect. Quercus)	Bmc Genetics
111	Osborne, O. G.; Chapman, M. A.; Nevado, B.; Filatov, D. A.	2016	Maintenance of Species Boundaries Despite Ongoing Gene Flow in Ragworts	Genome Biology and Evolution
112	Ottenburghs, J.; Megens, H. J.; Kraus, R. H. S.; van Hooft, P.; van Wieren, S. E.; Crooijmans, Rpm; Ydenberg, R. C.; Groenen, M. A. M.; Prins, H. H. T.	2017	A history of hybrids? Genomic patterns of introgression in the True Geese	Bmc Evolutionary Biology
113	Pardo-Diaz, C., Salazar, C., Baxter, S. W., Merot,	2012	Adaptive Introgression across Species Boundaries	Plos Genetics

	C., Figueiredo-Ready, W., Joron, M., ... Jiggins, C. D.		in <i>Heliconius</i> Butterflies	
114	Paun, O.; Turner, B.; Trucchi, E.; Munzinger, J.; Chase, M. W.; Samuel, R.	2016	Processes Driving the Adaptive Radiation of a Tropical Tree (<i>Diospyros</i> , Ebenaceae) in New Caledonia, a Biodiversity Hotspot	Systematic Biology
115	Payseur BA, Krenz JG, Nachman MW	2004	Differential patterns of introgression across the X chromosome in a hybrid zone between two species of house mice	Evolution
116	Peris, D., A. Arias, S. Orlic, C. Belloch, L. Perez-Traves et al	2015	Mitochondrial introgression suggests extensive ancestral hybridization events among <i>Saccharomyces</i> species	Molecular Phylogenetics and Evolution
117	Poelstra, J. W.; Richards, E. J.; Martin, C. H.	2018	Speciation in sympatry with ongoing secondary gene flow and a potential olfactory trigger in a radiation of Cameroon cichlids	Molecular Ecology
118	Racimo, F.; Gokhman, D.; Fumagalli, M.; Ko, A.; Hansen, T.; Moltke, I.; Albrechtsen, A.; Carmel, L.; Huerta-Sanchez, E.; Nielsen, R.	2015	Archaic Adaptive Introgression in TBX15/WARS2	Molecular Biology and Evolution
119	Racimo, F.; Marnetto, D.; Huerta-Sanchez, E.	2017	Signatures of Archaic Adaptive Introgression in Present-Day Human Populations	Molecular Biology and Evolution
120	Reidenbach, K. R.; Neafsey, D. E.; Costantini, C.; Sagnon, N.; Simard, F.; Ragland, G. J.; Egan, S. P.; Feder, J. L.; Muskavitch, M. A. T.; Besansky, N. J.	2012	Patterns of Genomic Differentiation between Ecologically Differentiated M and S Forms of <i>Anopheles gambiae</i> in West and Central Africa	Genome Biology and Evolution
121	Rieseberg LH, Kim SC, Randell RA et al.	2007	Hybridization and the colonization of novel habitats by annual sunflowers	Genetica
122	Ritz, K. R.; Noor, M. A. F.	2016	Mistaken Identity: Another Bias in the Use of Relative Genetic Divergence Measures for Detecting Interspecies Introgression	Plos One
123	Roux, C.; Fraisse, C.; Castaic, V.; Vekemans, X.; Pogson, G. H.; Bierne, N.	2014	Can we continue to neglect genomic variation in introgression rates when inferring the history of speciation? A case study in a <i>Mytilus</i>	Journal of Evolutionary Biology

			hybrid zone	
124	Sachdeva, H.; Barton, N. H.	2018	Introgression of a Block of Genome Under Infinitesimal Selection	Genetics
125	Sackton TB, Montenegro H, Hartl DL, Lemos B.	2011	Interspecific Y chromosome introgressions disrupt testis-specific gene expression and male reproductive phenotypes in <i>Drosophila</i>	Proceedings of the National Academy of Sciences of the United States of America
126	Salazar C, Baxter SW, Pardo-Diaz C, Wu G, Surridge A, Mauricio Linares, Eldredge Bermingham, Chris D. Jiggins	2010	Genetic Evidence for Hybrid Trait Speciation in <i>Heliconius</i> Butterflies	Plos Genetics
127	Sankararaman, S. Mallick, M. Dannemann, K. Prüfer, J. Kelso, S. Pääbo, N. Patterson, D. Reich	2014	The genomic landscape of Neanderthal ancestry in present-day humans	Nature
128	Scascitelli, M.; Whitney, K. D.; Randell, R. A.; King, M.; Buerkle, C. A.; Rieseberg, L. H.	2010	Genome scan of hybridizing sunflowers from Texas (<i>Helianthus annuus</i> and <i>H. debilis</i>) reveals asymmetric patterns of introgression and small islands of genomic differentiation	Molecular ecology
129	Schlebusch, C. M.; Skoglund, P.; Sjodin, P.; Gattepaille, L. M.; Hernandez, D.; Jay, F.; Li, S.; De Jongh, M.; Singleton, A.; Blum, M. G. B.; Soodyall, H.; Jakobsson, M.	2012	Genomic Variation in Seven Khoe-San Groups Reveals Adaptation and Complex African History	Science
130	Schrider, D. R.; Ayroles, J.; Matute, D. R.; Kern, A. D.	2018	Supervised machine learning reveals introgressed loci in the genomes of <i>Drosophila simulans</i> and <i>D. sechellia</i>	Plos Genetics
131	Schweizer, M.; Warmuth, V.; Kakhki, N. A.; Aliabadian, M.; Forschler, M.; Shiriha, H.; Suh, A.; Burri, R.	2019	Parallel plumage colour evolution and introgressive hybridization in wheatears	Journal of Evolutionary Biology
132	Song Y, Endepols S, Klemann N, Richter D, Matuschka FR, Shih CH, Nachman MW, Kohn	2011	Adaptive introgression of anticoagulant rodent poison resistance by hybridization between old world mice.	Current Biology

	MH.			
133	Staubach, F., Lorenc, A., Messer, P. W., Tang, K., Petrov, D. A., ; Tautz, D.	2012	Genome patterns of selection and introgression of haplotypes in natural populations of the house mouse (<i>Mus musculus</i>).	PLoS Genetics
134	Storchova, R., S. Gregorova, D. Buckiova, V. Kyselova, P. Divina, and J. Forejt.	2004	Genetic analysis of X-linked hybrid sterility in the house mouse	Mamm. Genome
135	Streicher, J; Devitt, T,; Goldberg, C; Malone, J; Blackmon, H; FUJITA, M	2014	Diversification and asymmetrical gene flow across time and space: lineage sorting and hybridization in polytypic barking frogs	Molecular Ecology
136	Stryjewski, K. F., ; Sorenson, M. D.	2017	Mosaic genome evolution in a recent and rapid avian radiation	Nature Ecology & Evolution
137	Suarez-Gonzalez, A.; Hefer, C. A.; Christe, C.; Corea, O.; Lexer, C.; Cronk, Q. C. B.; Douglas, C. J.	2016	Genomic and functional approaches reveal a case of adaptive introgression from <i>Populus balsamifera</i> (balsam poplar) in <i>P. trichocarpa</i> (black cottonwood)	Molecular Ecology
138	Suarez-Gonzalez, A.; Hefer, C. A.; Lexer, C.; Douglas, C. J.; Cronk, Q. C. B.	2018	Introgression from <i>Populus balsamifera</i> underlies adaptively significant variation and range boundaries in <i>P. trichocarpa</i>	New Phytologist
139	Takahashi H, Takata K	2000	Multiple lineages of the mitochondrial DNA introgression from <i>Pungitius pungitius</i> (L.) to <i>Pungitius tymensis</i> (Nikolsky).	Canadian Journal of Fisheries and Aquatic Sciences
140	Takahashi, H.; Toyoda, A.; Yamazaki, T.; Narita, S.; Mashiko, T.; Yamazaki, Y.	2017	Asymmetric hybridization and introgression between sibling species of the pufferfish <i>Takifugu</i> that have undergone explosive speciation	Marine Biology
141	Trigo, T. C.; Schneider, A.; de Oliveira, T. G.; Lehugeur, L. M.; Silveira, L.; Freitas, T. R. O.; Eizirik, E.	2013	Molecular Data Reveal Complex Hybridization and a Cryptic Species of Neotropical Wild Cat	Current Biology
142	Trigo, T. C.; Tirelli, F. P.; de Freitas, T. R. O.; Eizirik, E.	2014	Comparative Assessment of Genetic and Morphological Variation at an Extensive Hybrid Zone between Two Wild Cats in Southern Brazil	Plos One
143	Trucco, F.; Tatum, T.; Rayburn, A. L.; Tranel, P. J.	2005	Fertility, segregation at a herbicide-resistance locus, and genome	Molecular Ecology

			structure in BC1 hybrids from two important weedy <i>Amaranthus</i> species	
144	Vega, Y.; Marques, I.; Castro, S.; Loureiro, J.	2013	Outcomes of Extensive Hybridization and Introgression in <i>Epidendrum</i> (Orchidaceae): Can We Rely on Species Boundaries?	Plos One
145	vonHoldt, B. M.; Kays, R.; Pollinger, J. P.; Wayne, R. K.	2016	Admixture mapping identifies introgressed genomic regions in North American canids	Molecular Ecology
146	Wallbank, R. W. R.; Baxter, S. W.; Pardo-Diaz, C.; Hanly, J. J.; Martin, S. H.; Mallet, J.; Dasmahapatra, K. K.; Salazar, C.; Joron, M.; Nadeau, N.; McMillan, W. O.; Jiggins, C. D.	2016	Evolutionary Novelty in a Butterfly Wing Pattern through Enhancer Shuffling	Plos Biology
147	Wang, H. Y.; Hsieh, C. H.; Huang, C. G.; Kong, S. W.; Chang, H. C.; Lee, H. H.; Wang, W. K.; Chen, S. L.; Tzeng, H. Y.; Wu, W. J.	2013	Genetic and physiological data suggest demographic and adaptive responses in complex interactions between populations of figs (<i>Ficus pumila</i>) and their pollinating wasps (<i>Wiebesia pumilae</i>)	Molecular Ecology
148	Wang, X.; Lu, J.; Yue, W.; Li, L.; Zou, J. B.; Li, X. W.; He, X. D.; Duan, B. B.; Liu, J. Q.	2016	Determining the extent and direction of introgression between three spruce species based on molecular markers from three genomes with different rates of gene flow	Plant Systematics and Evolution
149	Ward, C. M.; Baxter, S. W.	2018	Assessing Genomic Admixture between Cryptic <i>Plutella</i> Moth Species following Secondary Contact	Genome Biology and Evolution
150	Weetman, D.; Steen, K.; Rippon, E. J.; Mawejje, H. D.; Donnelly, M. J.; Wilding, C. S.	2014	Contemporary gene flow between wild <i>An. gambiae</i> s.s. and <i>An. arabiensis</i>	Parasites & Vectors
151	Whitney KD, Randell RA, Rieseberg LH	2006	Adaptive introgression of herbivore resistance traits in the weedy sunflower <i>Helianthus annuus</i>	The American Naturalist
152	Whitney, K. D., Broman, K. W., Kane, N. C., Hovick, S. M., Randell, R. A., ; Rieseberg, L. H.	2015	QTL mapping identifies candidate alleles involved in adaptive introgression and range expansion in a wild sunflower	Molecular Ecology
153	Whitney, K. D., Randell, R. A., ; Rieseberg, L. H.	2010	Adaptive introgression of abiotic tolerance traits in the sunflower	New Phytologist

			<i>Helianthus annuus</i>	
154	Willis, S. C.; Macrander, J.; Farias, I. P.; Orti, G.	2012	Simultaneous delimitation of species and quantification of interspecific hybridization in Amazonian peacock cichlids (genus cichla) using multi-locus data	Bmc Evolutionary Biology
155	Wolters, J. F.; Charron, G.; Gaspary, A.; Landry, C. R.; Fiumera, A. C.; Fiumera, H. L.	2018	Mitochondrial Recombination Reveals Mito-Mito Epistasis in Yeast	Genetics
156	Wu, M.; Kostyun, J. L.; Hahn, M. W.; Moyle, L. C.	2018	Dissecting the basis of novel trait evolution in a radiation with widespread phylogenetic discordance	Molecular Ecology
157	Xu, D.; Pavlidis, P.; Taskent, R. O.; Alachiotis, N.; Flanagan, C.; DeGiorgio, M.; Blekhman, R.; Ruhl, S.; Gokcumen, O.	2017	Archaic Hominin Introgression in Africa Contributes to Functional Salivary MUC7 Genetic Variation	Molecular Biology and Evolution
158	Xu, T.; Sun, J.; Watanabe, H. K.; Chen, C.; Nakamura, M.; Ji, R. B.; Feng, D.; Lv, J.; Wang, S.; Bao, Z. M.; Qian, P. Y.; Qiu, J. W.	2018	Population genetic structure of the deep-sea mussel Bathymodiolus platifrons (Bivalvia: Mytilidae) in the Northwest Pacific	Evolutionary Applications
159	Yang, W. Z.; While, G. M.; Laakkonen, H.; Sacchi, R.; Zuffi, M. A. L.; Scali, S.; Salvi, D.; Uller, T.	2018	Genomic evidence for asymmetric introgression by sexual selection in the common wall lizard	Molecular Ecology
160	Zeng, Y. F.; Zhang, J. G.; Duan, A. G.; Abuduhamiti, B.	2016	Genetic structure of Populus hybrid zone along the Irtysh River provides insight into plastid-nuclear incompatibility	Scientific Reports
161	Zhang, W.; Dasmahapatra, K. K.; Mallet, J.; Moreira, G. R. P.; Kronforst, M. R.	2016	Genome-wide introgression among distantly related Heliconius butterfly species	Genome Biology
162	Zhang, W.; Kunte, K.; Kronforst, M. R.	2013	Genome-Wide Characterization of Adaptation and Speciation in Tiger Swallowtail Butterflies Using De Novo Transcriptome Assemblies	Genome Biology and Evolution
163	Zhou, Y.; Duvaux, L.; Ren, G.; Zhang, L.; Savolainen, O.; Liu, J.	2017	Importance of incomplete lineage sorting and introgression in the origin of shared genetic variation between two closely related pines with overlapping distributions	Heredity

164	Zielinski, P.; Nadachowska-Brzyska, K.; Wielstra, B.; Szkotak, R.; Covaciu-Marcov, S. D.; Cogalniceanu, D.; Babik, W.	2013	No evidence for nuclear introgression despite complete mtDNA replacement in the Carpathian newt (<i>Lissotriton montandoni</i>)	Molecular Ecology
165	Mao, X. G.; Tsagkogeorga, G.; Bailey, S. E.; Rossiter, S. J.	2017	Genomics of introgression in the Chinese horseshoe bat (<i>Rhinolophus sinicus</i>) revealed by transcriptome sequencing	Biological Journal of the Linnean Society
166	Jacobsen, F.; Omland KE	2012	Extensive introgressive hybridization within the northern oriole group (Genus <i>Icterus</i>) revealed by three-species isolation with migration analysis	Ecology and Evolution
167	Carling MD; Brumfield RT	2008	Haldane's rule in an avian system: using cline theory and divergence population genetics to test for differential introgression of mitochondrial, autosomal, and sex-linked loci across the <i>Passerina</i> bunting hybrid zone.	Evolution
168	Walsh, J.; Kovach, A. I.; Olsen, B. J.; Shriver, W. G.; Lovette, I. J.	2018	Bidirectional adaptive introgression between two ecologically divergent sparrow species	Evolution
169	Walsh, J.; Shriver, W. G.; Olsen, B. J.; Kovach, A. I.	2016	Differential introgression and the maintenance of species boundaries in an advanced generation avian hybrid zone	Bmc Evolutionary Biology
170	Wadsworth, C. B.; Li, X.; Dopman, E. B.	2015	A recombination suppressor contributes to ecological speciation in <i>OSTRINIA</i> moths	Heredity
171	Wade, M. J.; Goodnight, C. J.	2006	Cyto-nuclear epistasis: Two-locus random genetic drift in hermaphroditic and dioecious species	Evolution
172	Main, B. J.; Lee, Y.; Collier, T. C.; Norris, L. C.; Brisco, K.; Fofana, A.; Cornel, A. J.; Lanzaro, G. C.	2015	Complex genome evolution in <i>Anopheles coluzzii</i> associated with increased insecticide usage in Mali	Molecular Ecology
173	Anderson TM, Vonholdt BM, Candille SI et al.	2009	Molecular and evolutionary history of melanism in North American gray wolves	Science
174	Nolte, A. W.; Gompert, Z.; Buerkle, C. A.	2009	Variable patterns of introgression in two sculpin hybrid zones suggest	Molecular Ecology

			that genomic isolation differs among populations	
175	Hamilton, J. A.; Lexer, C.; Aitken, S. N.	2013	Genomic and phenotypic architecture of a spruce hybrid zone (<i>Picea sitchensis</i> P. <i>glauca</i>)	Molecular Ecology
176	Hamlin, J. A. P.; Arnold, M. L.	2014	Determining population structure and hybridization for two iris species	Ecology and Evolution
177	Tang, S., R. A. Okashah, S. J. Knapp, M. L. Arnold, and N. H. Martin.	2010	Transmission ratio distortion results in asymmetric introgression in Louisiana Iris	BMC Plant Biology
178	Cruzan, M. B. and M. L. Arnold	1994	Assortative mating and natural-selection in an iris hybrid zone	Evolution
179	Bouck AC, Wessler SR, Arnold ML	2007	QTL analysis of floral traits in Louisiana Iris hybrids	Evolution
180	McAshan SK, Vergin KL, Giovannoni SJ, Thaler DS	1999	Interspecies recombination between Enterococci: genetic and phenotypic diversity of vancomycin-resistant transconjugants.	MICROBIAL DRUG RESISTANCE
181	Palmer, K.; Kos, V.; and M.S. Gilmore	2007	Horizontal Gene Transfer and the Genomics of Enterococcal Antibiotic Resistance	Curr Opin Microbiol
182	de Lafontaine, G.; Bousquet, J.	2017	Asymmetry matters: A genomic assessment of directional biases in gene flow between hybridizing spruces	Ecology and Evolution
183	de Lafontaine, G.; Prunier, J.; Gerardi, S.; Bousquet, J.	2015	Tracking the progression of speciation: variable patterns of introgression across the genome provide insights on the species delimitation between progenitor-derivative spruces (<i>Picea mariana</i> x <i>P. rubens</i>)	Molecular Ecology
184	Naisbit, R. E.; Jiggins, C. D.; Mallet, J.	2003	Mimicry: developmental genes that contribute to speciation	Evolution & Development
185	Ravinet, M.; Yoshida, K.; Shigenobu, S.; Toyoda, A.; Fujiyama, A.; Kitano, J.	2018	The genomic landscape at a late stage of stickleback speciation: High genomic divergence interspersed by small localized regions of introgression	Plos Genetics
186	Sams, A. J.; Dumaine, A.; Nedelec, Y.; Yotova, V.; Alfieri, C.; Tanner, J. E.; Messer, P. W.; Barreiro, L. B.	2016	Adaptively introgressed Neandertal haplotype at the OAS locus functionally impacts innate immune responses in humans	Genome Biology

187	Souissi, A.; Bonhomme, F.; Machado, M.; Bahri-Sfar, L.; Gagnaire, P. A.	2018	Genomic and geographic footprints of differential introgression between two divergent fish species (<i>Solea</i> spp.)	Heredity
188	Setoguchi, H.; Watanabe, I.	2000	Intersectional gene flow between insular endemics of <i>Ilex</i> (Aquifoliaceae) on the Bonin Islands and the Ryukyu Islands	American Journal of Botany
189	de Meaux, J.; Pop, A.; Mitchell-Olds, T.	2006	Cis-regulatory evolution of chalcone-synthase expression in the genus <i>Arabidopsis</i>	Genetics
190	De La Torre, A. R.; Roberts, D. R.; Aitken, S. N.	2014	Genome-wide admixture and ecological niche modelling reveal the maintenance of species boundaries despite long history of interspecific gene flow	Molecular Ecology
191	De La Torre, A. R.; Wang, T. L.; Jaquish, B.; Aitken, S. N.	2014	Adaptation and exogenous selection in a <i>Picea glauca</i> x <i>Picea engelmannii</i> hybrid zone: implications for forest management under climate change	New Phytologist
192	Stift M, Luttikhuis PC, Visser EJW, Van Tienderen PH.	2008	Different flooding responses in <i>Rorippa amphibia</i> and <i>Rorippa sylvestris</i> , and their modes of expression in F1 hybrids	New Phytologist
193	Ma F, Zhao C, Milne R, Ji M, Chen L, Liu J	2010	Enhanced drought-tolerance in the homoploid hybrid species <i>Pinus densata</i> : implications for its habitat divergence from two progenitors.	New Phytologist
194	Goulson D.	2009	Evaluating the role of ecological isolation in maintaining the species boundary between <i>Silene dioica</i> and <i>S. latifolia</i>	Plant Ecology
195	Kingston, S. E.; Parchman, T. L.; Gompert, Z.; Buerkle, C. A.; Braun, M. J.	2017	Heterogeneity and concordance in locus-specific differentiation and introgression between species of towhees	Journal of Evolutionary Biology
196	Fontaine MC, Pease JB, Steele A, Waterhouse RM	2015	Extensive introgression in a malaria vector species complex revealed by phylogenomics	Science
197	Martin, S.H., K. K. Dasmahapatra, N. J. Nadeau, C. Salazar, J. R. Walters, F. Simpson, M. Blaxter, A. Manica, J. Mallet, C. D. Jiggins	2013	Genome-wide evidence for speciation with gene flow in <i>Heliconius</i> butterflies	Genome Research

198	White, MA; C. Ané, C. N. Dewey, B. R. Larget, B. A. Payseur,	2009	Fine-scale phylogenetic discordance across the house mouse genome.	PLoS Genetics
199	Meyer, M. Kircher, M. T. Gansauge, H. Li, F. Racimo, S. Mallick, J. G. Schraiber, F. Jay, K. Prüfer, C. de Filippo, P. H. Sudmant, C. Alkan, Q. Fu, R. Do, N. Rohland, A. Tandon, M. Siebauer, R. E. Green, K. Bryc, A. W. Briggs, U. Stenzel, J. Dabney, J. Shendure, J. Kitzman, M. F. Hammer, M. V. Shunkov, A. P. Derevianko, N. Patterson, A. M. Andrés, E. E. Eichler, M. Slatkin, D. Reich, J. Kelso, S. Pääbo, A	2012	A high-coverage genome sequence from an archaic Denisovan individual.	Science
200	Horn, R. L.; Marques, A. J. D.; Manseau, M.; Golding, B.; Klutsch, C. F. C.; Abraham, K.; Wilson, P. J.	2018	Parallel evolution of site-specific changes in divergent caribou lineages	Ecology and Evolution
201	Mao, Y. F.; Economo, E. P.; Satoh, N.	2018	The Roles of Introgression and Climate Change in the Rise to Dominance of Acropora Corals	Current Biology
202	Mao, X. G.; Zhu, G. J.; Zhang, L. B.; Zhang, S. Y.; Rossiter, S. J.	2014	Differential introgression among loci across a hybrid zone of the intermediate horseshoe bat (<i>Rhinolophus affinis</i>)	Bmc Evolutionary Biology
203	Hulsey, C. D.; Keck, B. P.; Alamillo, H.; O'Meara, B. C.	2013	Mitochondrial genome primers for Lake Malawi cichlids	Molecular Ecology Resources
204	Vijverberg, K.; Mes, T. H. M.; Bachmann, K.	1999	Chloroplast DNA evidence for the evolution of <i>Microseris</i> (Asteraceae) in Australia and New Zealand after long-distance dispersal from Western North America	American Journal of Botany
205	Vicente, J. L.; Clarkson, C. S.; Caputo, B.; Gomes, B.; Pombi, M.; Sousa, C. A.; Antao, T.; Dinis, J.	2017	Massive introgression drives species radiation at the range limit of <i>Anopheles gambiae</i>	Scientific Reports

	Botta, G.; Mancini, E.; Petrarca, V.; Mead, D.; Drury, E.; Stalker, J.; Miles, A.; Kwiatkowski, D. P.; Donnelly, M. J.; Rodrigues, A.; della Torre, A.; Weetman, D.; Pinto, J.			
206	While, G.M., Sozos Michaelides Robert J. P. Heathcote Hannah E. A. MacGregor Natalia Zajac Joscha Beninde Pau Carazo Guillem Pérez i de Lanuza Roberto Sacchi Marco A.L. Zuffi Terézia Horváthová Belén Fresnillo Ulrich Schulte Michael Veith Axel Hochkirch Tobias Uller	2015	Sexual selection drives asymmetric introgression in wall lizards	Ecology Letters
207	Stein and Uy	2006	Unidirectional introgression of a sexually selected trait across an avian hybrid zone: a role for female choice?	Evolution
208	Vallin, N., Rice, A.M., Bailey, R.I., Husby, A. ; Qvarnstrom, A	2012	Positive feedback between ecological and reproductive character displacement in a young avian hybrid zone.	Evolution
209	Pfennig K.S.	2007	Facultative mate choice drives adaptive hybridization	Science
210	Parsons, T.J., Olson, S.L. ; Braun, M.J	1993	Unidirectional spread of secondary plumage traits across an avian hybrid zone	Science
211	Pearson, S.F.	2000	Behavioral symmetries in a moving hybrid zone	Behavioral Ecology
212	McDonald, D.B., Clay, R.P., Brumfield, R.T. ; Braun, M.J	2001	Sexual selection on plumage and behaviour in an avian hybrid zone: experimental tests of male-male interactions.	Evolution
213	Gompert, Z.; Lucas, L. K.; Nice, C. C.; Buerkle, C. A.	2013	GENOME DIVERGENCE AND THE GENETIC ARCHITECTURE OF BARRIERS TO GENE FLOW BETWEEN LYCAEIDES IDAS AND L-MELISSA	Evolution
214	Sætre, G. -P., T. Moum, S. Bures, M. Kral, M. Adamjan, and J. Moreno	1997	A sexually selected character displacement in flycatchers reinforces premating isolation	Nature

215	Nadeau, N. J., A. Whibley, R. T. Jones, J. Davey, C. K. Dasmahapatra, S. W. Baxter, M. Joron, R. H. French-Constant, M. Blaxter, J. Mallet, et al.	2012	Evidence for genomic islands of divergence among hybridizing <i>Heliconius</i> butterflies obtained by large-scale targeted sequencing.	Philosophical Transactions of the Royal Society B: Biological Sciences
216	Vernot, B.; Tucci, S.; Kelso, J.; Schraiber, J. G.; Wolf, A. B.; Gittelman, R. M.; Dannemann, M.; Grote, S.; McCoy, R. C.; Norton, H.; Scheinfeldt, L. B.; Merriwether, D. A.; Koki, G.; Friedlaender, J. S.; Wakefield, J.; Paabo, S.; Akey, J. M.	2016	Excavating Neandertal and Denisovan DNA from the genomes of Melanesian individuals	Science
217	Vernot, B.; Akey, J. M.	2014	Resurrecting Surviving Neandertal Lineages from Modern Human Genomes	Science
218	Vargas, O. M.; Ortiz, E. M.; Simpson, B. B.	2017	Conflicting phylogenomic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: <i>Diplostephium</i>)	New Phytologist
219	Valencia, L. M.; Martins, A.; Ortiz, E. M.; Di Fiore, A.	2018	A RAD-sequencing approach to genome-wide marker discovery, genotyping, and phylogenetic inference in a diverse radiation of primates	Plos One
220	Vaillant, J. J.; Bock, D. G.; Haffner, G. D.; Cristescu, M. E.	2013	Speciation patterns and processes in the zooplankton of the ancient lakes of Sulawesi Island, Indonesia	Ecology and Evolution
221	Bogdanowicz, W., Piksa, K., Tereba A.	2012	Hybridization Hotspots at Bat Swarming Sites	Plos one
222	Afonso, E.; Goyadin, AC; Giraudoux, P.; G. Farny	2017	Investigating Hybridization between the Two Sibling Bat Species <i>Myotis myotis</i> and <i>M. blythii</i> from Guano in a Natural Mixed Maternity Colony	Plos one
223	Kavanaugh, L. A.; Fraser, J. A.; Dietrich, F. S.	2006	Recent evolution of the human pathogen <i>Cryptococcus neoformans</i> by intervarietal transfer of a 14-gene fragment	Molecular Biology and Evolution

224	Koralewski, T. E.; Mateos, M.; Krutovsky, K. V.	2016	Conflicting genomic signals affect phylogenetic inference in four species of North American pines	Aob Plants
225	Turner, B.; Paun, O.; Munzinger, J.; Chase, M. W.; Samuel, R.	2016	Sequencing of whole plastid genomes and nuclear ribosomal DNA of Diospyros species (Ebenaceae) endemic to New Caledonia: many species, little divergence	Annals of Botany
226	Deitz, K. C.; Athrey, G. A.; Jawara, M.; Overgaard, H. J.; Matias, A.; Slotman, M. A.	2016	Genome-Wide Divergence in the West-African Malaria Vector Anopheles melas	G3-Genes Genomes Genetics
227	Turissini, D. A.; Matute, D. R.	2017	Fine scale mapping of genomic introgressions within the Drosophila yakuba clade	Plos Genetics
228	Dibattista, J. D.; Saenz-Agudelo, P.; Piatek, M. J.; Wang, X.; Aranda, M.; Berumen, M. L.	2017	Using a butterflyfish genome as a general tool for RAD-Seq studies in specialized reef fish	Molecular Ecology Resources
229	DiBattista, J. D.; Whitney, J.; Craig, M. T.; Hobbs, J. P. A.; Rocha, L. A.; Feldheim, K. A.; Berumen, M. L.; Bowen, B. W.	2016	Surgeons and suture zones: Hybridization among four surgeonfish species in the Indo-Pacific with variable evolutionary outcomes	Molecular Phylogenetics and Evolution
230	Doiron, S.; Bernatchez, L.; Blier, P. U.	2002	A comparative mitogenomic analysis of the potential adaptive value of arctic charr mtDNA introgression in brook charr populations (Salvelinus fontinalis Mitchill)	Molecular Biology and Evolution
231	Dunn, B.; Paulish, T.; Stanbery, A.; Piotrowski, J.; Koniges, G.; Kroll, E.; Louis, E. J.; Liti, G.; Sherlock, G.; Rosenzweig, F.	2013	Recurrent Rearrangement during Adaptive Evolution in an Interspecific Yeast Hybrid Suggests a Model for Rapid Introgression	Plos Genetics
232	Thielsch, A.; Knell, A.; Mohammadyari, A.; Petrusek, A.; Schwenk, K.	2017	Divergent clades or cryptic species? Mito-nuclear discordance in a Daphnia species complex	Bmc Evolutionary Biology
233	Miller, D. J.; van Oppen, M. J. H.	2003	A 'fair go' for coral hybridization	Molecular Ecology
234	Taylor, S. J.; Arnold, M.; Martin, N. H.	2009	The genetic architecture of reproductive isolation in Louisiana irises: hybrid fitness in nature	Evolution

235	Taylor, S. A.; Curry, R. L.; White, T. A.; Ferretti, V.; Lovette, I.	2014	Spatiotemporally consistent genomic signatures of reproductive isolation in a moving hybrid zone	Evolution
236	Emms, S. K., S. A. Hodges, and M. L. Arnold.	1996	Pollen-tube competition, siring success, and consistent asymmetric hybridization in Louisiana irises.	Evolution
237	Fijarczyk, A.; Dudek, K.; Babik, W.	2016	Selective Landscapes in newt Immune Genes Inferred from Patterns of Nucleotide Variation	Genome Biology and Evolution
238	Fijarczyk, A.; Dudek, K.; Niedzicka, M.; Babik, W.	2018	Balancing selection and introgression of newt immune-response genes	Proceedings of the Royal Society B-Biological Sciences
239	Kim, B. Y.; Huber, C. D.; Lohmueller, K. E.	2018	Deleterious variation shapes the genomic landscape of introgression	Plos Genetics
240	Sung, C. J.; Bell, K. L.; Nice, C. C.; Martin, N. H.	2018	Integrating Bayesian genomic cline analyses and association mapping of morphological and ecological traits to dissect reproductive isolation and introgression in a Louisiana Iris hybrid zone	Molecular Ecology
241	Sun, Y.; Corcoran, P.; Menkis, A.; Whittle, C. A.; Andersson, S. G. E.; Johannesson, H.	2012	Large-Scale Introgression Shapes the Evolution of the Mating-Type Chromosomes of the Filamentous Ascomycete Neurospora tetrasperma	Plos Genetics
242	Sullivan, A. R.; Owusu, S. A.; Weber, J. A.; Hipp, A. L.; Gailing, O.	2016	Hybridization and divergence in multi-species oak (Quercus) communities	Botanical Journal of the Linnean Society
243	Rezende, V. B.; Congrains, C.; Lima, A. L. A.; Campanini, E. B.; Nakamura, A. M.; de Oliveira, J. L.; Chahad-Ehlers, S.; Sobrinho, I.; de Brito, R. A.	2016	Head Transcriptomes of Two Closely Related Species of Fruit Flies of the Anastrepha fraterculus Group Reveals Divergent Genes in Species with Extensive Gene Flow	G3-Genes Genomes Genetics
244	James, K. E.; Schneider, H.; Ansell, S. W.; Evers, M.; Robba, L.; Uszynski, G.; Pedersen, N.; Newton, A. E.; Russell, S. J.; Vogel, J. C.; Kilian, A.	2008	Diversity Arrays Technology (DART) for Pan-Genomic Evolutionary Studies of Non-Model Organisms	Plos One

245	Kulmuni, J.; Pamilo, P.	2014	Introgression in hybrid ants is favored in females but selected against in males	Proceedings of the National Academy of Sciences of the United States of America
246	Massey, S. E.	2017	Strong Amerindian Mitonuclear Discordance in Puerto Rican Genomes Suggests Amerindian Mitochondrial Benefit	Annals of Human Genetics
247	Owusu, S. A.; Sullivan, A. R.; Weber, J. A.; Hipp, A. L.; Gailing, O.	2015	Taxonomic Relationships and Gene Flow in Four North American Quercus Species (Quercus section Lobatae)	Systematic Botany
248	Schwarzer, J.; Herder, F.; Misof, B.; Hadiaty, R. K.; Schlieven, U. K.	2008	Gene flow at the margin of Lake Matano's adaptive sailfin silverside radiation: Telmatherinidae of River Petea in Sulawesi	Hydrobiologia
249	Ropiquet, A.; Hassanin, A.	2006	Hybrid origin of the Pliocene ancestor of wild goats	Molecular Phylogenetics and Evolution
250	Runemark, A.; Trier, C. N.; Eroukmanoff, F.; Hermansen, J. S.; Matschiner, M.; Ravinet, M.; Elgvin, T. O.; Saetre, G. P.	2018	Variation and constraints in hybrid genome formation	Nature Ecology & Evolution
251	Suarez-Gonzalez, A.; Hefer, C. A.; Lexer, C.; Cronk, Q. C. B.; Douglas, C. J.	2018	Scale and direction of adaptive introgression between black cottonwood (Populus trichocarpa) and balsam poplar (P.balsamifera)	Molecular Ecology
252	Stuckas, H.; Stoof, K.; Quesada, H.; Tiedemann, R.	2009	Evolutionary implications of discordant clines across the Baltic Mytilus hybrid zone (Mytilus edulis and Mytilus trossulus)	Heredity
253	Stryjewski, K. F.; Sorenson, M. D.	2017	Mosaic genome evolution in a recent and rapid avian radiation	Nature Ecology & Evolution
254	Song, S. V.; Downes, S.; Parker, T.; Oakeshott, J. G.; Robin, C.	2015	High nucleotide diversity and limited linkage disequilibrium in Helicoverpa armigera facilitates the detection of a selective sweep	Heredity
255	Song, B. H.; Clauss, M. J.; Pepper, A.; Mitchell-Olds, T.	2006	Geographic patterns of microsatellite variation in Boechera stricta, a close relative of Arabidopsis	Molecular Ecology

256	Rieseberg LH, Raymond O, Rosenthal DM et al.	2003	Major Ecological Transitions in Wild Sunflowers Facilitated by Hybridization	Science
257	Sobel, J. M.; Streisfeld, M. A.	2015	Strong premating reproductive isolation drives incipient speciation in <i>Mimulus aurantiacus</i>	Evolution
258	Semenov, G. A.; Koblik, E. A.; Red'kin, Y. A.; Badyaev, A. V.	2018	Extensive phenotypic diversification coexists with little genetic divergence and a lack of population structure in the White Wagtail subspecies complex (<i>Motacilla alba</i>)	Journal of Evolutionary Biology
259	Brumfield, R.T., Jernigan, R.W., McDonald, D.B. ; Braun, M.J	2001	Evolutionary implications of divergent clines in an avian (<i>Manacus</i> : Aves) hybrid zone	Evolution
260	Krosby, M. ; Rohwer, S.	2009	A 2000 km genetic wake yields evidence for northern glacial refugia and hybrid zone movement in a pair of songbirds	Proceedings of the Royal Society
261	Lewontin R.; Birch L.	1966	Hybridization as a Source of Variation for Adaptation to New Environments	Evolution
262	Spratt B.G.; Zhang QY; Jones DM; Hutchison A; Brannigan JÁ; Dowson CG	1989	Recruitment of a penicillin-binding protein gene from <i>Neisseria flavescens</i> during the emergence of penicillin resistance in <i>Neisseria meningitidis</i> .	PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA
263	Kronforst, M. R.; Hansen, M. E. B.; Crawford, N. G.; Gallant, J. R.; Zhang, W.; Kulathinal, R. J.; Kapan, D. D.; Mullen, S. P.	2013	Hybridization Reveals the Evolving Genomic Architecture of Speciation	Cell Reports
264	Schumer, M.; Cui, R. F.; Powell, D. L.; Rosenthal, G. G.; Andolfatto, P.	2016	Ancient hybridization and genomic stabilization in a swordtail fish	Molecular Ecology
265	Schumer, M.; Cui, R. F.; Boussau, B.; Walter, R.; Rosenthal, G.; Andolfatto, P.	2013	An evaluation of the hybrid speciation hypothesis for <i>Xiphophorus clemenciae</i> based on whole genome sequences	Evolution

266	Schories, S.; Lampert, K. P.; Lamatsch, D. K.; de Leon, F. J. G.; Scharl, M.	2007	Analysis of a possible independent origin of triploid <i>P. formosa</i> outside of the Rio Purificacion river system	Frontiers in Zoology
267	Kunte, K., C. Shea, M. L. Aardema, J. M. Scriber, T. E. Juenger, L. E. Gilbert, and M. R. Kronforst.	2011	Sex chromosome Mosaicism and Hybrid Speciation among Tiger Swallowtail Butterflies.	PLoS Genetics
268	Janousek V, Munclinger P, Wang L, Teeter KC, Tucker PK	2015	Functional organization of the genome may shape the species boundary in the house mouse.	Molecular Biology and Evolution
269	Foighil, D. O.; Hilbish, T. J.; Showman, R. M.	1996	Mitochondrial gene variation in <i>Mercenaria</i> clam sibling species reveals a relict secondary contact zone in the western Gulf of Mexico	Marine Biology
270	Nosil, P.; Parchman, T. L.; Feder, J. L.; Gompert, Z.	2012	Do highly divergent loci reside in genomic regions affecting reproductive isolation? A test using next-generation sequence data in <i>Timema</i> stick insects	Bmc Evolutionary Biology
271	Figueiró, H.; Li G., Trindade, F. J.; Assis, J.; Pais, F.; Fernandes, G.; Santos, S. H. D.; Hughes G.M.; Komissarov, A.; Antunes, A.; Trinca, C.S.; Rodrigues, M. R. Linderoth, T.; Bi, K.; Silveira, L.; Azevedo, F. C. C.; Kantek, D.; Ramalho, E.; Brassaloti, R. A.; Villela, P. M. S.; Nunes, A. L. V.; Teixeira, R. H. F.; Morato, R. G.; Loska, D.; Patricia Saragüeta, P.; Gabaldón, T.; Teeling, E. C.; O'Brien, S. J.; Nielsen, R. Coutinho L. Oliveira, G.; Murphy, W.J.; Eizirik E.	2017	Genome-wide signatures of complex introgression and adaptive evolution in the big cats	Evolutionary Biology

272	Li, G.; Brian W. Davis, ^{1,2,4} Eduardo Eizirik, ³ and William J. Murphy	2016	Phylogenomic evidence for ancient hybridization in the genomes of living cats (Felidae)	Genome Research
273	Combosch D.; Steven V. Vollmer	2015	Trans-Pacific RAD-Seq population genomics confirms introgressive hybridization in Eastern Pacific Pocillopora corals	Molecular Phylogenetics and Evolution
274	Sawamura, K.; Maehara, K.; Keira, Y.; Ishikawa, H. O.; Sasamura, T.; Yamakawa, T.; Matsuno, K.	2014	A Test of Double Interspecific Introgression of Nucleoporin Genes in <i>Drosophila</i>	G3-Genes Genomes Genetics
275	Fouet, C.; Kamdem, C.; Gamez, S.; White, B. J.	2017	Genomic insights into adaptive divergence and speciation among malaria vectors of the <i>Anopheles nili</i> group	Evolutionary Applications
276	Sarver, B. A. J.; Demboski, J. R.; Good, J. M.; Forshee, N.; Hunter, S. S.; Sullivan, J.	2017	Comparative Phylogenomic Assessment of Mitochondrial Introgression among Several Species of Chipmunks (<i>Tamias</i>)	Genome Biology and Evolution
277	Garcia-Elfring, A.; Barrett, R. D. H.; Combs, M.; Davies, T. J.; Munshi-South, J.; Millien, V.	2017	Admixture on the northern front: population genomics of range expansion in the white-footed mouse (<i>Peromyscus leucopus</i>) and secondary contact with the deer mouse (<i>Peromyscus maniculatus</i>)	Heredity
278	Ghenu, A. H.; Blanckaert, A.; Butlin, R. K.; Kulmuni, J.; Bank, C.	2018	Conflict between heterozygote advantage and hybrid incompatibility in haplodiploids (and sex chromosomes)	Molecular Ecology
279	Palma-Silva, C.; Wendt, T.; Pinheiro, F.; Barbara, T.; Fay, M. F.; Cozzolino, S.; Lexer, C.	2011	Sympatric bromeliad species (<i>Pitcairnia</i> spp.) facilitate tests of mechanisms involved in species cohesion and reproductive isolation in Neotropical inselbergs	Molecular Ecology
280	Palma-Silva, C.; Ferro, M.; Bacci, M.; Turchetto-Zolet, A. C.	2016	De novo assembly and characterization of leaf and floral transcriptomes of the hybridizing bromeliad species (<i>Pitcairnia</i> spp.) adapted to Neotropical Inselbergs	Molecular Ecology Resources
281	Salazar, C.; Jiggins, C. D.; Taylor, J. E.; Kronforst, M. R.; Linares, M.	2008	Gene flow and the genealogical history of <i>Heliconius heurippa</i>	Bmc Evolutionary Biology
282	Guichoux, E.; Garnier-Gere, P.; Lagache, L.; Lang, T.; Boury, C.; Petit, R. J.	2013	Outlier loci highlight the direction of introgression in oaks	Molecular Ecology

283	Pujolar, J. M.; Jacobsen, M. W.; Als, T. D.; Frydenberg, J.; Munch, K.; Jonsson, B.; Jian, J. B.; Cheng, L.; Maes, G. E.; Bernatchez, L.; Hansen, M. M.	2014	Genome-wide single-generation signatures of local selection in the panmictic European eel	Molecular Ecology
284	Hume, J. B.; Recknagel, H.; Bean, C. W.; Adams, C. E.; Mable, B. K.	2018	RADseq and mate choice assays reveal unidirectional gene flow among three lamprey ecotypes despite weak assortative mating: Insights into the formation and stability of multiple ecotypes in sympatry	Molecular Ecology
285	Lind-Riehl, J. F.; Gailing, O.	2017	Adaptive Variation and Introgression of a CONSTANS-Like Gene in North American Red Oaks	Forests
286	Rosenzweig, B. K.; Pease, J. B.; Besansky, N. J.; Hahn, M. W.	2016	Powerful methods for detecting introgressed regions from population genomic data	Molecular Ecology
287	McCluskey, B. M.; Postlethwait, J. H.	2015	Phylogeny of Zebrafish, a "Model Species," within Danio, a "Model Genus"	Molecular Biology and Evolution
288	Richards, E. J.; Martin, C. H.	2017	Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic adaptive radiation of trophic specialist pupfishes	Plos Genetics
289	Richards, E. J.; Poelstra, J. W.; Martin, C. H.	2018	Don't throw out the sympatric speciation with the crater lake water: fine-scale investigation of introgression provides equivocal support for causal role of secondary gene flow in one of the clearest examples of sympatric speciation	Evolution Letters
290	Ryan, S. F.; Deines, J. M.; Scriber, J. M.; Pfrender, M. E.; Jones, S. E.; Emrich, S. J.; Hellmann, J. J.	2018	Climate-mediated hybrid zone movement revealed with genomics, museum collection, and simulation modeling	Proceedings of the National Academy of Sciences of the United States of America

291	Rogers, S. M.; Campbell, D.; Baird, S. J. E.; Danzmann, R. G.; Bernatchez, L.	2001	Combining the analyses of introgressive hybridisation and linkage mapping to investigate the genetic architecture of population divergence in the lake whitefish (<i>Coregonus clupeaformis</i> , Mitchill)	Genetica
292	Renaut, S.; Grassa, C. J.; Yeaman, S.; Moyers, B. T.; Lai, Z.; Kane, N. C.; Bowers, J. E.; Burke, J. M.; Rieseberg, L. H.	2013	Genomic islands of divergence are not affected by geography of speciation in sunflowers	Nature Communications
293	Hallstrom, B. M.; Schneider, A.; Zoller, S.; Janke, A.	2011	A Genomic Approach to Examine the Complex Evolution of Laurasiatherian Mammals	Plos One
294	Reid, N.; Demboski, J. R.; Sullivan, J.	2012	Phylogeny Estimation of the Radiation of Western North American Chipmunks (<i>Tamias</i>) in the Face of Introgression Using Reproductive Protein Genes	Systematic Biology
295	Ray, N.; Excoffier, L.	2009	Inferring Past Demography Using Spatially Explicit Population Genetic Models	Human Biology
296	Eswaran, V	2002	A diffusion wave out of Africa: The mechanism of the modern human revolution?	Current Anthropol
297	Hanemaaijer, M. J.; Collier, T. C.; Chang, A.; Shott, C. C.; Houston, P. D.; Schmidt, H.; Main, B. J.; Cornel, A. J.; Lee, Y.; Lanzaro, G. C.	2018	The fate of genes that cross species boundaries after a major hybridization event in a natural mosquito population	Molecular Ecology
298	Peters JL, Sonsthagen SA, Lavretsky P, et al.	2014	Interspecific hybridization contributes to high genetic diversity and apparent effective population size in an endemic population of mottled ducks (<i>Anas fulvigula maculosa</i>)	Conservation genetics
299	Kulikova IV, Zhuravlev YN, McCracken KG, Haukos D	2004	Asymmetric hybridization and sex -biased gene flow between Eastern Spot -billed Ducks (<i>Anas zonorhyncha</i>) and Mallards (<i>A. platyrhynchos</i>) in the Russian Far East	The Auk
300	Pool, J. E.; Corbett-Detig, R. B.; Sugino, R. P.;	2012	Population Genomics of Sub-Saharan <i>Drosophila melanogaster</i> :	Plos Genetics

	Stevens, K. A.; Cardeno, C. M.; Crepeau, M. W.; Duchon, P.; Emerson, J. J.; Saelao, P.; Begun, D. J.; Langley, C. H.		African Diversity and Non-African Admixture	
301	Maddamsetti, R.; Lenski, R. E.	2018	Analysis of bacterial genomes from an evolution experiment with horizontal gene transfer shows that recombination can sometimes overwhelm selection	Plos Genetics
302	Harris, K.; Nielsen, R.	2016	The Genetic Cost of Neanderthal Introgression	Genetics
303	Hebert, F. O.; Renaut, S.; Bernatchez, L.	2013	Targeted sequence capture and resequencing implies a predominant role of regulatory regions in the divergence of a sympatric lake whitefish species pair (<i>Coregonus clupeaformis</i>)	Molecular Ecology
304	Lin, Y. L.; Pavlidis, P.; Karakoc, E.; Ajay, J.; Gokcumen, O.	2015	The Evolution and Functional Impact of Human Deletion Variants Shared with Archaic Hominin Genomes	Molecular Biology and Evolution
305	Pease, J. B.; Haak, D. C.; Hahn, M. W.; Moyle, L. C.	2016	Phylogenomics Reveals Three Sources of Adaptive Variation during a Rapid Radiation	Plos Biology
306	Hohmann, N.; Koch, M. A.	2017	An Arabidopsis introgression zone studied at high spatio-temporal resolution: interglacial and multiple genetic contact exemplified using whole nuclear and plastid genomes	Bmc Genomics
307	Houldcroft, C. J.; Underdown, S. J.	2016	Neanderthal genomics suggests a pleistocene time frame for the first epidemiologic transition	American Journal of Physical Anthropology
308	Jagoda, E.; Lawson, D. J.; Wall, J. D.; Lambert, D.; Muller, C.; Westaway, M.; Leavesley, M.; Capellini, T. D.; Lahr, M. M.; Gerbault, P.; Thomas, M. G.; Migliano, A. B.; Willerslev, E.; Metspalu, M.; Pagani, L.	2018	Disentangling Immediate Adaptive Introgression from Selection on Standing Introgressed Variation in Humans	Molecular Biology and Evolution
309	Huang, C. L.; Ho, C. W.; Chiang, Y. C.; Shigemoto,	2014	Adaptive divergence with gene flow in incipient speciation of	Plant Journal

	Y.; Hsu, T. W.; Hwang, C. C.; Ge, X. J.; Chen, C.; Wu, T. H.; Chou, C. H.; Huang, H. J.; Gojobori, T.; Osada, N.; Chiang, T. Y.		Miscanthus floridulus/sinensis complex (Poaceae)	
310	Johnson, K. E.; Voight, B. F.	2018	Patterns of shared signatures of recent positive selection across human populations	Nature Ecology & Evolution
311	Ding, Q., Hu, Y., Xu, S., Wang, J. ; Jin, L.	2014	Neanderthal introgression at chromosome 3p21.31 was under positive natural selection in East Asians.	Molecular Biology Evolution
312	Pauquet, G.; Salzburger, W.; Egger, B.	2018	The puzzling phylogeography of the haplochromine cichlid fish Astatotilapia burtoni	Ecology and Evolution
313	Malinsky, M.; Svoldal, H.; Tyers, A. M.; Miska, E. A.; Genner, M. J.; Turner, G. F.; Durbin, R.	2018	Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow	Nature Ecology & Evolution
314	Parchman, T. L.; Gompert, Z.; Braun, M. J.; Brumfield, R. T.; McDonald, D. B.; Uy, J. A. C.; Zhang, G.; Jarvis, E. D.; Schlinger, B. A.; Buerkle, C. A.	2013	The genomic consequences of adaptive divergence and reproductive isolation between species of manakins	Molecular Ecology
315	Nye, J.; Laayouni, H.; Kuhlwilm, M.; Mondal, M.; Marques-Bonet, T.; Bertranpetit, J.	2018	Selection in the Introgressed Regions of the Chimpanzee Genome	Genome Biology and Evolution
316	de Manuel M et al.	2016	Chimpanzee genomic diversity reveals ancient admixture with bonobos	Science
317	Mondal M, Casals F, Xu T, Dall'Olio GM, Pybus M, Netea MG5, Comas D1, Laayouni H1,6, Li Q3, Majumder PP7, Bertranpetit J	2016	Genomic analysis of Andamanese provides insights into ancient human migration into Asia and adaptation	Nature Genet
318	Novo, M.; Bigey, F.; Beyne, E.; Galeote, V.; Gavory, F.; Mallet, S.; Cambon, B.; Legras, J. L.; Wincker, P.; Casaregola, S.; Dequin, S.	2009	Eukaryote-to-eukaryote gene transfer events revealed by the genome sequence of the wine yeast <i>Saccharomyces cerevisiae</i> EC1118	Proceedings of the National Academy of Sciences of the United

				States of America
319	Mancini, E.; Spinaci, M. I.; Gordicho, V.; Caputo, B.; Pombi, M.; Vicente, J. L.; Dinis, J.; Rodrigues, A.; Petrarca, V.; Weetman, D.; Pinto, J.; della Torre, A.	2015	Adaptive Potential of Hybridization among Malaria Vectors: Introgression at the Immune Locus TEP1 between <i>Anopheles coluzzii</i> and <i>A. gambiae</i> in 'Far-West' Africa	Plos One
320	Martin, C. H.; Crawford, J. E.; Turner, B. J.; Simons, L. H.	2016	Diabolical survival in Death Valley: recent pupfish colonization, gene flow and genetic assimilation in the smallest species range on earth	Proceedings of the Royal Society B-Biological Sciences
321	Martin, C. H.; Feinstein, L. C.	2014	Novel trophic niches drive variable progress towards ecological speciation within an adaptive radiation of pupfishes	Molecular Ecology
322	Martinsen, G. D.; Whitham, T. G.; Turek, R. J.; Keim, P.	2001	Hybrid populations selectively filter gene introgression between species	Evolution
323	Matosiuk, M.; Sheremetyeva, I. N.; Sheremetyev, I. S.; Saveljev, A. P.; Borkowska, A.	2014	Evolutionary neutrality of mtDNA introgression: evidence from complete mitogenome analysis in roe deer	Journal of Evolutionary Biology
324	Ng, J.; Glor, R. E.	2011	Genetic differentiation among populations of a Hispaniolan trunk anole that exhibit geographical variation in dewlap colour	Molecular Ecology
325	Neophytou, C.; Aravanopoulos, F. A.; Fink, S.; Dounavi, A.	2010	Detecting interspecific and geographic differentiation patterns in two interfertile oak species (<i>Quercus petraea</i> (Matt.) Liebl. and <i>Q. robur</i> L.) using small sets of microsatellite markers	Forest Ecology and Management
326	Muirhead, C. A.; Presgraves, D. C.	2016	Hybrid Incompatibilities, Local Adaptation, and the Genomic Distribution of Natural Introgression between Species	American Naturalist
327	Mims, M. C.; Hulseay, C. D.; Fitzpatrick, B. M.; Streelman, J. T.	2010	Geography disentangles introgression from ancestral polymorphism in Lake Malawi cichlids	Molecular Ecology
328	Meyer, B. S.; Matschiner, M.; Salzburger, W.	2017	Disentangling Incomplete Lineage Sorting and Introgression to Refine Species-Tree Estimates for Lake Tanganyika Cichlid Fishes	Systematic Biology

329	Meier, J. I.; Sousa, V. C.; Marques, D. A.; Selz, O. M.; Wagner, C. E.; Excoffier, L.; Seehausen, O.	2017	Demographic modelling with whole-genome data reveals parallel origin of similar <i>Pundamilia</i> cichlid species after hybridization	Molecular Ecology
330	Menon, M.; Bagley, J. C.; Friedline, C. J.; Whipple, A. V.; Schoettle, A. W.; Leal-Saenz, A.; Wehenkel, C.; Molina-Freaner, F.; Flores-Renteria, L.; Gonzalez-Elizondo, M. S.; Snieszko, R. A.; Cushman, S. A.; Waring, K. M.; Eckert, A. J.	2018	The role of hybridization during ecological divergence of southwestern white pine (<i>Pinus strobiformis</i>) and limber pine (<i>P. flexilis</i>)	Molecular Ecology
331	Leroy, T., Rougemont, Q., Dupouey, J. L., Bodenes, C., Lalanne, C., Belser, C., Labadie, K., Le Provost, G., Aury, J. M., Kremer, A. and Plomion, C.	2019	Massive postglacial gene flow between European white oaks uncovered genes underlying species barriers	New Phytologist
332	Monnahan, P., Kolar, F., Baduel, P., Sailer, C., Koch, J., Horvath, R., Laenen, B., Schmickl, R., Paajanen, P., Sramkova, G., Bohutinska, M., Arnold, B., Weisman, C. M., Marhold, K., Slotte, T., Bomblies, K. and Yant, L.	2019	Pervasive population genomic consequences of genome duplication in <i>Arabidopsis arenosa</i>	Nature Ecology & Evolution
333	Rifkin, J. L., Castillo, A. S., Liao, I. T. and Rausher, M. D.	2019	Gene flow, divergent selection and resistance to introgression in two species of morning glories (<i>Ipomoea</i>)	Molecular Ecology
334	Tang, Y. T., Li, C. H., Wanghe, K. Y., Feng, C. G., Tong, C., Tian, F. and Zhao, K.	2019	Convergent evolution misled taxonomy in schizothoracine fishes (Cypriniformes: Cyprinidae)	Molecular Phylogenetics and Evolution
335	Aguirre-Liguori, J. A., Gaut, B. S., Jaramillo-Correa, J. P., Tenaillon, M. I., Montes-Hernandez, S., Garcia-Oliva, F., Hearne, S. J. and Eguiarte, L. E.	2019	Divergence with gene flow is driven by local adaptation to temperature and soil phosphorus concentration in teosinte subspecies (<i>Zea mays parviglumis</i> and <i>Zea mays mexicana</i>)	Molecular Ecology
336	Sotola, V. A., Ruppel, D. S., Bonner, T. H., Nice, C. C. and Martin, N. H.	2019	Asymmetric introgression between fishes in the Red River basin of Texas is associated with variation in water quality	Ecology and Evolution

337	Pfeifer, B. and Kapan, D. D.	2019	Estimates of introgression as a function of pairwise distances	Bmc Bioinformatics
338	Brown, A. P., McGowan, K. L., Schwarzkopf, E. J., Greenway, R., Rodriguez, L. A., Tobler, M. and Kelley, J. L.	2019	Local ancestry analysis reveals genomic convergence in extremophile fishes	Philosophical Transactions of the Royal Society B-Biological Sciences
339	Kuhlwilm, M., Han, S., Sousa, V. C., Excoffier, L. and Marques-Bonet, T.	2019	Ancient admixture from an extinct ape lineage into bonobos	Nature Ecology & Evolution
340	Haselhorst, M. S. H., Parchman, T. L. and Buerkle, C. A.	2019	Genetic evidence for species cohesion, substructure and hybrids in spruce	Molecular Ecology
341	Paetzold, C., Wood, K. R., Eaton, D. A. R., Wagner, W. L. and Appelhans, M. S.	2019	Phylogeny of Hawaiian Melicope (Rutaceae): RAD-seq Resolves Species Relationships and Reveals Ancient Introgression	Frontiers in Plant Science
342	Silvert, M., Quintana-Murci, L. and Rotival, M.	2019	Impact and Evolutionary Determinants of Neanderthal Introgression on Transcriptional and Post-Transcriptional Regulation	American Journal of Human Genetics
343	Alhazmi, D., Fudyk, S. K. and Civetta, A.	2019	Testes Proteases Expression and Hybrid Male Sterility Between Subspecies of <i>Drosophila pseudoobscura</i>	G3-Genes Genomes Genetics
344	Baiz, M. D., Tucker, P. K. and Cortes-Ortiz, L.	2019	Multiple forms of selection shape reproductive isolation in a primate hybrid zone	Molecular Ecology
345	Rougeux, C., Gagnaire, P. A. and Bernatchez, L.	2019	Model-based demographic inference of introgression history in European whitefish species pairs'	Journal of Evolutionary Biology
346	Beysard, M., Perrin, N., Jaarola, M., Heckel, G., ; Vogel, P.	2011	Asymmetric and differential gene introgression at a contact zone between two highly divergent lineages of field voles (<i>Microtus agrestis</i>).	Journal of Evolutionary Biology
347	Hsu, C. W., Lo, C. Y. and Lee, C. R.	2019	On the postglacial spread of human commensal <i>Arabidopsis thaliana</i> : journey to the East	New Phytologist
348	Nader, J. L., Mathers, T. C., Ward, B. J., Pachebat, J. A., Swain, M. T., Robinson, G., Chalmers, R. M.,	2019	Evolutionary genomics of anthroponosis in <i>Cryptosporidium</i>	Nature Microbiology

	Hunter, P. R., van Oosterhout, C. and Tyler, K. M.			
349	Quigley, K. M., Bay, L. K. and van Oppen, M. J. H.	2019	The active spread of adaptive variation for reef resilience	Ecology and Evolution
350	Koenig, D., Hagmann, J., Li, R., Bemm, F., Slotte, T., Nueffer, B., Wright, S. I. and Weigel, D.	2019	Long-term balancing selection drives evolution of immunity genes in <i>Capsella</i>	Elife
351	Lehnert, S. J., Bentzen, P., Kess, T., Lien, S., Horne, J. B., Clement, M. and Bradbury, I. R.	2019	Chromosome polymorphisms track trans-Atlantic divergence and secondary contact in Atlantic salmon	Molecular Ecology
352	Ma, Y. Z., Wang, J., Hu, Q. J., Li, J. L., Sun, Y. S., Zhang, L., Abbott, R. J., Liu, J. Q. and Mao, K. S.	2019	Ancient introgression drives adaptation to cooler and drier mountain habitats in a cypress species complex	Communications Biology
353	Boratynski, Z.; Alves, P. C.; Berto, S.; Koskela, E., Mappes, T.; Melo-Ferreira, J.	2011	Introgression of mitochondrial DNA among <i>Myodes</i> voles: consequences for energetics?	BMC. Evol. Biol.
354	Bachtrog, D., K. Thornton, A. Clark, and P. Andolfatto	2006	Extensive introgression of mitochondrial DNA relative to nuclear genes in the <i>Drosophila yakuba</i> species group.	Evolution
355	Slager, D., Kevin L. Epperly, Renee R. Ha, Sievert Rohwer, Chris Wood, Caroline Van Hemert, John Klicka	2018	Cryptic and extensive hybridization between ancient lineages of American crows	bioRxiv
356	Giska, I.; Farelo, L.; Pimenta.; Melo-Ferreira, J.	2019	Introgression drives repeated evolution of winter coat color polymorphism in hares	Proceedings of the National Academy of Sciences of the United States of America
357	Lee, K. M.; Coop, G.	2017	Distinguishing Among Modes of Convergent Adaptation Using Population Genomic Data.	Genetics
358	Seixas F. A.; Boursot P., Melo-Ferreira J.	2018	The genomic impact of historical hybridization with massive mitochondrial DNA introgression.	Genome Biology