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The impact of competition on global-change induced range shifts in birds

Daniel A. Nesbit

Submitted for the degree of Doctor of Philosophy

Department of Biosciences

Durham University

June 2025

To the birds, each and every one of them.

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Author's Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Parts of Chapter 5 have been published as:

Nesbit, D.A., Cowen, M.C., Grether, G.F. and Drury, J.P. (2023), Interspecific territoriality has facilitated recent increases in the breeding habitat overlap of North American passerines. *Ecography*, 2023: e06573. <https://doi.org/10.1111/ecog.06573>

The author contributions were as follows:

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Gregory F. Grether: Data curation (equal); Funding acquisition (equal); Supervision-Supporting, Writing – original draft-Supporting, Writing – review and editing-Supporting.

Jonathan P. Drury: Conceptualization (equal); Data curation (equal); Formal analysis-Supporting, Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Daniel A. Nesbit

June 2025

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Acknowledgements

First and foremost, I must offer my sincerest gratitude to my incredible supervisor, Dr Jonathan Drury, for his continued support, expertise, patience and kindness throughout my master's, PhD and fledgling scientific career. I am also grateful to Professor Stephen Willis and Professor Kirsty Park for their supervision and advice. A special thanks must also go to Professor Phil Stephens and Professor Bob Baxter for their excellent company in Kenya.

I must also thank Leonard Davis, Maya Solly and Ted Poulett for their diligent assistance cleaning, trimming and sorting thousands of audio files. Many thanks to the Durham Advanced Computing team, in particular Dr Karen Bower at Hamilton and Dr Rob Powell at NCC, for their support and endless patience, without which much of my modelling would not have been possible.

Thank you so much to my friends and colleagues in the Conservation Ecology Group at Durham for the happiness and joy they have brought me throughout my PhD. It would have been a far less enjoyable few years without them.

I'd also like to extend my thanks to everyone at BirdLife International, particularly Alex Berryman and Dr Nigel Collar, for an amazing placement and wonderful time in Cambridge.

I must also thank Dr David Leat, my ringing trainer, for taking me under his wing, sharing his wealth of knowledge and passion, but also giving me an excuse to escape the office from time to time.

Finally, an acknowledgements section would be incomplete without thanking my friends and family for their unending love and support, for which I will be eternally grateful.

Abstract

Species do not exist in isolation but among a host of others with which they interact. These interactions can influence species distributions both positively and negatively, at a variety of scales. Understanding how species interactions influence distributions is of particular importance in this current era of rapid anthropogenic change, in which species distributions and assemblages are shifting. Species interactions may influence the ease with which species track their suitable climate niche and colonise new areas, they may facilitate or preclude range expansion. Throughout this thesis, we focus primarily on competitive interactions, more specifically, exploitative competition, interspecific territoriality and hybridisation. We present large-scale, comparative, species-pair analyses across North America and Europe, spanning a large taxonomic breadth of passerines and non-passerines.

We begin by focusing on the predictors of hybridisation, which can have pronounced effects on species coexistence. This is the first time hybridisation has been studied at such a large scale in a species-pair framework, and incorporating phylogenetic relationships. We find strong support for the mistaken identity hypothesis, in that similar, and more closely related species are more likely to hybridise than dissimilar species. We find that as species encounter each other more with greater range and habitat overlap, their likelihood of hybridisation increases. As species ranges change, novel interactions can form, and these interactions can be costly. For instance, hybridisation between natives and non-natives is a widespread conservation problem, and as such, being able to accurately predict interactions between species that don't currently coexist has important conservation ramifications. We compare the predictive performance of two modelling methods when predicting 'unknown' hybridisation events.

Understanding how species interactions have influenced coexistence in the past is vital to understand how they may influence coexistence in the future. We hindcast the effect of competition on historical range dynamics in North America and Europe using two large-scale citizen science datasets (the North American Breeding Bird

Survey and the Pan-European Common Bird Monitoring Scheme). We find that interspecifically territorial pairs increased their fine-scale habitat overlap more than non-territorial pairs in North America. We believe this is the result of interspecific territoriality creating spatial segregation within habitats, which subsequently facilitates resource partitioning, allowing similar species to coexist.

We then examine the impact of species interactions on current species distributions using the predictions from Species Distribution Models. We calculate measures of geographic avoidance across North America and Eurasia. Geographic avoidance quantifies exclusion patterns as the proportion of a pair's predicted range that is realised in overlapping areas compared to the proportion realised in non-overlapping areas. We found that most pairs exhibited some level of avoidance across their ranges. However, we found no evidence for the role of competitive interactions in the observed patterns of avoidance. Finally, we use high-resolution Joint Species Distribution Models across a large spatial extent and attempt to detect the effect of biotic interactions in the residual associations of species pairs. We find that associations between species are overwhelmingly positive and find little evidence that JSDMs can detect species interactions in their residual associations. Instead, we find evidence that unaccounted-for environmental covariates are responsible for observed patterns of association between species. This research greatly expands our knowledge of avian hybridisation and the impact of species interactions on the distributions and coexistence of birds at a variety of geographic scales.

Chapter 1

General Introduction

1.1 Species distributions

Species distributions have been the focus of extensive research for centuries (Darwin, 1859a; Wallace, 1876). The global distribution of species is intrinsically linked to biodiversity; some regions, such as the tropics, harbour exceptional levels of diversity, while others, like the poles, are far more depauperate in flora and fauna (Pianka, 1966; MacArthur, 1969; Gaston, 2000; Hillebrand, 2004). Species distributions have changed throughout time and are currently changing as a result of anthropogenic global changes; many are shrinking while others are shifting or expanding (Chris D. Thomas and Lennon, 1999; Parmesan and Yohe, 2003; Tingley and Beissinger, 2013; Stephens *et al.*, 2016a). Understanding where species can persist and where they may exist in the future is of the utmost importance for the protection of biodiversity. To do so requires extensive knowledge of the determinants of species distributions.

Species fundamental niches encompass the abiotic conditions in which they can exist and reproduce (Hutchinson, 1957; Holt, 2009). However, species do not exist in isolation, but alongside a host of others, some of which they interact with directly or indirectly. These interactions may include herbivory, predation, parasitism, competition, commensalism, facilitation or mutualism, and they can influence species distributions, both positively and negatively, creating a species realised niche (Grinnell, 1917; Hutchinson, 1957; Soberón, 2007; Holt, 2009). That said, abiotic and biotic interactions are not solely responsible for where species exist. Fundamental niches can be constrained by dispersal barriers, such as oceans and mountain ranges, historical events such as glaciation, persecution, or stochasticity, among others (Svenning and Skov, 2004; Toews, 2017; Newton, 2024).

The abiotic and biotic determinants of species distributions act at a variety of scales. At the largest scale, species distributions are constrained largely by broad abiotic conditions, such as temperature and precipitation (Pearson and Dawson, 2003a; Howard *et al.*, 2015; King *et al.*, 2021). At a more local scale, species occupy only particular habitats, the distributions of which are also controlled by climate (Holdridge, 1947; Whittaker, 1975; Woodward and Williams, 1987). At a smaller scale, topography and microclimatic conditions can influence the occurrence of species,

dependent on their size and the scale at which they interact with the environment (Karr and Freemark, 1983; Suggitt *et al.*, 2011; Lembrechts, Nijs and Lenoir, 2019). Biotic interactions impact species distributions locally (Connor and Bowers, 1987; Wisz *et al.*, 2013; Araújo and Rozenfeld, 2014). However, they can scale up to influence distributions at a regional and continental scale (Sexton *et al.*, 2009; Gotelli, Graves and Rahbek, 2010; Blois *et al.*, 2013; Araújo and Rozenfeld, 2014; Gutiérrez, Boria and Anderson, 2014; Mönkkönen *et al.*, 2017; Machado-Stredel, Atauchi, Nuñez-Penichet, Cobos, Osorio-Olvera, Khalighifar, Peterson and R. J. Fletcher, 2024). Abiotic and biotic factors act with varying intensity across species distributions. Biotic interactions are more likely to determine species range limits in climatically ameliorable areas, while abiotic conditions are more responsible for setting range limits in areas of abiotic stress, such as high latitudes or elevations (Darwin, 1859a; Connell, 1961; Gross and Price, 2000; Louthan, Doak and Angert, 2015; McQuillan and Rice, 2015; Paquette and Hargreaves, 2021).

Species distributions are dynamic and rarely in equilibrium (Alexander *et al.*, 2016a; Pecl *et al.*, 2017; Lawlor *et al.*, 2024). Ranges expand and contract, and species disperse across landscapes, tracking suitable niche space or exploiting novel environments. These range changes happen on evolutionary and ecological timescales. For instance, upon the formation of the Isthmus of Panama 3 million years ago, the Great American Biotic Interchange (GABI) occurred and saw the colonisation of South America by North American taxa such as camelids, horses and sabre-toothed cats, while ground sloths, opossums, and phorusrhacids colonised North America from the south (Wallace, 1876; Webb, 2006; Weir, Bermingham and Schluter, 2009). However, species distributions are also rapidly changing as a result of anthropogenic climate change, land-use change, and even artificial food and nest-site provisioning 29/11/2025 12:14:00. Many species are tracking their climatic niche northwards and upslope (Chris D. Thomas and Lennon, 1999; Hitch and Leberg, 2007; Colwell *et al.*, 2008; Zuckenberg, Woods and Porter, 2009a; Stephens *et al.*, 2016a); however, directional niche-tracking can be idiosyncratic and species-specific (VanDerWal *et al.*, 2013). Further, the introduction of species to non-native areas by humans has allowed many to cross previously insurmountable dispersal barriers and colonise novel regions and environments 29/11/2025 12:14:00. As species distributions change, interactions can be lost and novel interactions form

(Huxel, 1999; Briceño *et al.*, 2019; Tsuchida *et al.*, 2019; Brambilla *et al.*, 2020; Pereira, Lourenço and Mota, 2020; Hernández-Brito *et al.*, 2021; Machado-Stredel, Atauchí, Nuñez-Penichet, Cobos, Osorio-Olvera, Khalighifar, Peterson and R. J. Fletcher, 2024).

1.2 Species interactions

Although a variety of biotic interactions influence range dynamics, in this thesis, we explore two main forms of competition and their impact on species distributions: exploitative competition and behavioural interference. We further subdivide behavioural interference into interspecific territoriality and hybridisation, which are the forms of behavioural interference we believe to be some of the most influential on species distributions and coexistence (Grether *et al.*, 2017). I will first describe the various forms of competition and discuss their impact on species distributions. I will then discuss the interactive effects of these forms of competition on distributions as they rarely occur in isolation, and their influence on coexistence is often intrinsically linked (Vallin *et al.*, 2012; Drury *et al.*, 2015; Drury, Cowen and Grether, 2020).

1.2.1 Exploitative competition

Exploitative competition is the indirect depletion of shared and finite resources, such as food, water, or nutrients (Volterra, 1926; Lotka, 1932; Gause, 1934b). Ecological theory posits that species exploiting the same resources in the same way cannot occupy the same niche or coexist without some form of resource partitioning (Gause, 1934b; MacArthur and Levins, 1967; MacArthur, 1972; Den Boer, 1986). Competitive exclusion occurs when competitively superior species outcompete subordinate species, lowering their fitness and causing local extinction. This competitive exclusion is supported by empirical studies, with many ecologically similar species excluding one another from particular habitats or microhabitats (Schoener, 1983). The impacts of competitive exclusion can also propagate from local levels to influence patterns of species cooccurrence at regional and continental levels (Connor and Bowers, 1987).

The effects of competitive exclusion manifest in a number of distributional patterns at a variety of scales, both spatially and temporally (Schoener, 1983; Connor and Bowers, 1987; Pigot and Tobias, 2013a; Pigot *et al.*, 2018). For instance, many tropical birds exhibit patchy distributions and are absent from seemingly suitable habitats that are occupied by closely related replacements (Diamond, 1973; Terborgh and Weske, 1975; Remsen and Graves, 1995; Gutiérrez, Boria and Anderson, 2014; Pimm, Diamond and Bishop, 2023). Many montane species occupy narrower elevational bands in the presence of competitors (Diamond, 1973; Terborgh and Weske, 1975; Cadena and Loiselle, 2007; Jankowski *et al.*, 2013; Freeman, 2015a; Freeman, Strimas-Mackey and Miller, 2022). Within habitats, similar species can segregate based on various niche axes. Species may differ in their foraging height (MacArthur and MacArthur, 1961; Remešová *et al.*, 2020), distance along branches (MacArthur, 1958; Diamond, 1973; Kent and Sherry, 2020), and they may shift their diel rhythms to avoid one another (Kronfeld-Schor and Dayan, 1999; Levy, Dayan and Kronfeld-Schor, 2011). Competitors may shift their habitat choice in the presence of one another, reducing exploitative competition (Reif *et al.*, 2018a; Sottas *et al.*, 2018). Many of these mechanisms to reduce resource competition are mediated by direct interactions between species (Grether *et al.*, 2017).

1.2.2 Behavioural Interference

Behavioural interference is a widespread form of competition in animals and encompasses direct, behaviourally mediated forms of aggressive and reproductive interference between species (Grether *et al.*, 2017). Aggressive forms of interference competition can include physical aggression, chasing and territoriality, but also associated signalling behaviours (Grether *et al.*, 2017). Reproductive interference includes a variety of behaviours such as signal jamming, interspecific mate guarding, courtship, mating and hybridisation (Gröning and Hochkirch, 2008). Competition for nest sites and mates could be considered exploitative, as these are finite resources that are depleted by competitors; however, interactions over these resources are likely to be direct and may be aggressive, and they are therefore more closely allied to behavioural interference (Duckworth *et al.*, 2017a). Behavioural interference can influence species coexistence, range dynamics and eco-evolutionary processes at a variety of scales (Hochkirch, Gröning and Bücken, 2007; Drury *et al.*, 2015; Grether *et al.*, 2017, 2020a; Cowen, Drury and Grether, 2020; Drury, Cowen and Grether, 2020;

Patterson and Drury, 2023). Throughout this thesis we focus primarily on aggressive interference in the form of interspecific territoriality and reproductive interference via hybridisation.

1.2.2.1 Interspecific territoriality

Definitions of territories and territoriality vary throughout the literature. Maher and Lott (1995) defined a territory as “a fixed space from which an individual, or group of mutually tolerant individuals, actively exclude competitors for a specific resource or resources”, and as such, territoriality is the defence of said space. Territoriality ensures access to finite resources (Nice, 1941a; Maher and Lott, 1995) and, as such, is an adaptive response to resource competition both within species and between them (Drury, Cowen and Grether, 2020). Interspecific territoriality is widespread and can involve closely related species, but there are also instances of territoriality between distantly related species (Mac Nally *et al.*, 2012a; Maron *et al.*, 2013; Drury, Cowen and Grether, 2020).

Interspecific territoriality can have pronounced effects on the distribution of species (reviewed in Patterson and Drury, 2023). Territoriality is inherently exclusionary; individuals are excluded from a defended space (Nice, 1941a). However, this exclusion may facilitate coexistence within habitats if it allows resource partitioning between competing species (Sorjonen, 1986). Interspecific territoriality and aggression can create fine-scale, ‘checkerboard’ distributions of species within broad habitat types (Sorjonen, 1986; Robinson and Terborgh, 1995; Jankowski *et al.*, 2012; Freeman, 2016a). Common (*Luscinia megarhynchos*) and Thrush Nightingales (*L. luscinia*) co-occur in Polish deciduous forests, with little habitat differentiation, occupy exclusive territories and respond aggressively to one another (Sorjonen, 1986). Thrush Nightingale song has converged in sympatry towards that of Common Nightingale, suggesting territoriality is adaptive between these two species (Sorjonen, 1986). Territorial aggression can result in shifts in habitat usage when competitors occur in sympatry, and a subordinate species can be confined to suboptimal habitats by a more dominant competitor (Svensson, 1978; Robinson, 1992; Robinson and Terborgh, 1995; Vallin *et al.*, 2012; Rybinski *et al.*, 2016; Maldonado-Coelho *et al.*, 2017; Reif *et al.*, 2018a; Sottas *et al.*, 2018). Territorial exclusion can scale up to

influence geographical range boundaries, particularly parapatric altitudinal boundaries, in which interspecifically territorial species occupy narrower elevational bands where their ranges abut with competitors (Chappell, 1978; Jankowski, Robinson and Levey, 2010; Gifford and Kozak, 2012; Jankowski *et al.*, 2013; Pasch, Bolker and Phelps, 2013a; Freeman, 2015a; Freeman and Montgomery, 2016; Freeman, Class Freeman and Hochachka, 2016; Boyce and Martin, 2019; Freeman, Strimas-Mackey and Miller, 2022). Heterospecific playback experiments have shown that congeners replacing each other along elevational gradients respond aggressively to one another, and that this aggression diminishes away from the contact zone and is often asymmetric (Jankowski, Robinson and Levey, 2010). In Costa Rica, Orange-billed Nightingale-Thrushes (*Catharus aurantiirostris*) exhibit strong aggression towards their upslope replacement: Black-headed Nightingale-Thrushes (*C. mexicanus*), which show reciprocal, though weaker, aggression towards the downslope Orange-billed Nightingale-Thrushes but also upslope Slaty-backed Nightingale-Thrushes (*C. fuscater*), which show no aggression towards Slaty-backed Nightingale-Thrushes (Jankowski, Robinson and Levey, 2010). Similarly, in Papua New Guinea, asymmetric aggression occurs at elevational replacement zones between White-rumped (*Melanodryas bimaculata*) and White-eyed Robins (*Pachycephalopsis poliosoma*), White-eyed Robins and Slaty Robins (*M. cyanus*), and Black (*Rhipidura atra*) and Dimorphic Fantails (*R. brachyrhyncha*) (Freeman, Class Freeman and Hochachka, 2016). These aggression-mediated distributional patterns are not restricted to birds and have been demonstrated in *Eutamias* chipmunks (Chappell, 1978), *Scotinomys* singing mice and *Plethodon* salamanders (Gifford and Kozak, 2012). However, aggression is not a prerequisite for parapatric elevational distributions, and differing habitat preferences can also be responsible (Able and Noon, 1976; Cadena and Loiselle, 2007; Bastianelli *et al.*, 2017; Boyce and Martin, 2019; Jones *et al.*, 2020).

1.2.2.2 Hybridisation

Hybridisation is the production of offspring between different species, and although the term hybridisation can also be used to describe mating between subspecies and populations (Short, 1969), in this thesis, we consider only interspecific hybridisation.

It could be argued that hybrid individuals are the most tangible evidence of reproductive interference compared to some of the more ephemeral behaviours, such as interspecific courtship. It can also be the costliest form of reproductive interference in terms of fitness, and as such, has the greatest impact on species distributions and coexistence (Ribeiro and Spielman, 1986; Baker and Boylan, 1999; Tsuchida *et al.*, 2019; Ålund *et al.*, 2024), hence our decision to focus on hybridisation.

Hybridisation is taxonomically widespread (McCarthy, 2006), more common than often thought (Grant and Grant, 1992; McCarthy, 2006; Ottenburghs, 2023) and has even influenced our own evolutionary trajectory (Herrera *et al.*, 2009; Huerta-Sánchez *et al.*, 2014). In essence, hybridisation is the manifestation of incomplete reproductive isolation between species (Mallet, 2005; Price, 2008; Abbott *et al.*, 2013) and contradicts more stringent definitions of the biological species concept (Mayr, 1942; Mallet, 2008).

Hybridisation is often an important step in the speciation process and the transition to sympatry (Coyne and Orr, 1989; Lily W. Liou and Price, 1994; Price, 2008). After diverging in allopatry, species may disperse and come into secondary contact. If divergence has been insufficient and reproductive isolation is incomplete, the incipient species will hybridise (Moore, 1977; Barton and Hewitt, 1989; McEntee, Burleigh and Singhal, 2020). Depending on the degree of divergence achieved before secondary contact and the associated hybrid fitness, the incipient species will either collapse into a hybrid swarm if fitness is high (Behm, Ives and Boughman, 2010) or, if hybrid fitness is low, reinforcement will occur (Lily W. Liou and Price, 1994; Vallin and Qvarnström, 2011a). Reinforcement occurs when selection favours traits that minimise the likelihood of hybridisation, reinforcing pre- or post-zygotic isolating mechanisms and facilitating coexistence in sympatry as a result (Price, 2008). These traits may involve species perceptual mechanisms, morphology, physiology or behaviour (Coyne and Orr, 1989; Vallin and Qvarnström, 2011a). However, hybridisation can persist for millions of years post-divergence and is not restricted to sister species (Toews *et al.*, 2022). Although many hybrids are infertile, many hybrids can introgress and backcross with their parental species (Dowling and Secor, 1997; Shapiro *et al.*, 2004; Borge *et al.*, 2005; Krosby and Rohwer, 2008; Rheindt and

Edwards, 2011) and even their non-parental species, transferring genes between lineages (Toews *et al.*, 2020; Natola, Seneviratne and Irwin, 2022).

Hybridisation itself can result in speciation (Dowling and Secor, 1997; Mallet, 2007; Abbott *et al.*, 2013; Ottenburghs, 2018). Although more common in plants (Dowling and Secor, 1997; Mallet, 2007), hybrid speciation has been recorded in animals (*Drosophila* (Schwarz *et al.*, 2005); butterflies (Mavárez *et al.*, 2006); fish (DeMarais *et al.*, 1992; Nolte *et al.*, 2005) and birds (Ottenburghs, 2018)). To illustrate the rapidity with which this hybrid speciation could occur, consider the example of a male Española Ground-Finch (*Geospiza conirostris*) that arrived on Daphne Major in 1981 and hybridised with a Medium Ground Finch (*G. fortis*) (Lamichhaney *et al.*, 2018). One of their F1 offspring bred with another Medium Ground-Finch, but all subsequent matings were endogamous, and despite being highly inbred, fitness was high (Lamichhaney *et al.*, 2018). As of 2012, there were eight breeding pairs and 23 birds from generations 4-6 (Lamichhaney *et al.*, 2018). While the fate of this lineage is unknown, and it is not considered a true species, its existence highlights the remarkable evolutionary ramifications of hybridisation.

Some species have previously been described which have turned out to be hybrids (Parkes, 1951; vonHoldt *et al.*, 2016). Since their discovery in 1924 until the early 2000s, Imperial Pheasants (*Lophura imperialis*) were considered to be one of the rarest galliforms in the world, with a single pair taken into captivity in 1924, and males caught in 1990 and 2000 (Hennache *et al.*, 2003; Eames and Mahood, 2017). However, Imperial Pheasants are actually hybrids between Silver Pheasants (*L. nycthemera*) and a truly rare galliform, Vietnam Pheasants (*L. edwardsi*) (Hennache *et al.*, 2003), which is now considered possibly extinct in the wild with an extinction probability of 0.97 (BirdLife International, 2024). This case highlights the conservation importance of a greater understanding of hybridisation, associated with the prioritisation and allocation of conservation resources.

Hybridisation influences species distributions and coexistence and can alter the speed with which species can move across landscapes (Pfennig, Kelly and Pierce, 2016). If hybridisation occurs frequently and reduces the fitness of individuals sufficiently, it can lead to sexual exclusion (Kuno, 1992a; Huxel, 1999; Gröning *et al.*,

2007a; Hochkirch, Gröning and Bückner, 2007; Kishi, Nishida and Tsubaki, 2009a; Vallin *et al.*, 2012), which can scale up to influence geographic distributions and has the potential to lead to extinction, particularly if species are already rare (Ribeiro and Spielman, 1986; Rhymer and Simberloff, 1996; Wolf, Takebayashi and Rieseberg, 2001). Narrow and relatively stable tension zones can form where species meet and hybridise if hybrid fitness is lower than that of the parent species (Moore, 1977; Barton and Hewitt, 1985; Rohwer and Wood, 1998; Mettler and Spellman, 2009; Natola *et al.*, 2021; Alexander *et al.*, 2022; Walsh *et al.*, 2023). Stability in these zones is maintained by selection against hybrids alongside continued dispersal and gene flow into the zone by parent species (Barton and Hewitt, 1985), which can prevent species ranges shifting (Moore and Buchanan, 1985; Pizarro, DeRaad and McCormack, 2023). However, some hybrid zones are moving with one species being replaced by the other as the hybrid zone invades their range (Faivre *et al.*, 1999; Pearson, 2000a; Krosby and Rohwer, 2008, 2010; McQuillan and Rice, 2015). Hybrid zone movements are also influenced by climate change (Scott A. Taylor *et al.*, 2014; Dougherty and Carling, 2024).

1.2.3 Interactions between exploitative competition, interspecific territoriality, hybridisation and range dynamics

Exploitative competition, hybridisation and interspecific territoriality often occur in tandem and can be inherently linked. Interspecific aggression is often an adaptive response to both resource and mate competition (Drury *et al.*, 2015; Cowen, Drury and Grether, 2020; Drury, Cowen and Grether, 2020; Grether *et al.*, 2020a). If species compete for the same resources, interspecific territoriality can create spatial segregation, allowing resource partitioning and subsequent coexistence within the same habitats (Sorjonen, 1986; Glenn A Marvin, 1998; Amarasekare, 2002; Ovadia and zu Dohna, 2003). Hybridisation and interspecific territoriality often result in exclusion. Black-capped (*Poecile atricapillus*) and Carolina Chickadees (*P. carolinensis*) are parapatric and hybridise where their ranges meet (Bronson *et al.*, 2005; Reudink *et al.*, 2007; Scott A. Taylor *et al.*, 2014; McQuillan and Rice, 2015). Female Black-capped Chickadees preferentially mate with dominant males, and in heterospecific interactions, these are typically Carolina Chickadees (Bronson *et al.*, 2003). Black-capped, but not Carolina, Chickadees have unoccupied climatically

suitable range beyond the hybrid zone (McQuillan and Rice, 2015). The hybrid zone has also been shifting northwards in the last century, invading the range of Black-capped Chickadees (Bronson *et al.*, 2003). The movement of this hybrid zone, coupled with unoccupied range beyond it, suggests the lower fitness of hybrids (Bronson *et al.*, 2005) and social subordinacy prevents Black-capped Chickadees fulfilling their entire climatic niche (McQuillan and Rice, 2015). A similar pattern emerges in parapatric *Hippolais* warblers in Europe (Engler *et al.*, 2013).

Territoriality can initially increase the likelihood of hybridisation (Rybinski *et al.*, 2016). Collared Flycatchers (*Ficedula albicollis*) colonised the Swedish islands of Gotland and Öland within the last few centuries (Lundberg and Alatalo, 1992). Male Collared Flycatchers are behaviourally dominant towards male Pied Flycatchers (*F. hypoleuca*) and exclude them from higher quality territories in deciduous forest plots, confining them to lower quality coniferous plantations (Vallin *et al.*, 2012; Rybinski *et al.*, 2016). As a result, there are fewer conspecific males in an area, and female Pied Flycatchers are more likely to hybridise with heterospecific Collared Flycatchers, as it is better to mate with the 'wrong' species than not at all (Hubbs, 1955; Vallin *et al.*, 2012; Rybinski *et al.*, 2016; Qvarnström *et al.*, 2023). However, hybrid fitness is low and reinforces spatial segregation between the two species; this spatial segregation, in turn, reduces encounter rates and subsequent hybridisation between the two species (Vallin *et al.*, 2012; Rybinski *et al.*, 2016).

In the northwestern United States, Mountain (*Sialia mexicana*) and Western Bluebirds (*S. currucoides*) undergo consistent cycles of post-fire succession that involve both territoriality and hybridisation. Mountain and Western Bluebirds are secondary cavity nesters and, as such, are unable to excavate their own nest cavities, which means nests are a highly sought-after resource and the subject of intense competition (Duckworth and Badyaev, 2007; Duckworth, 2013; Duckworth *et al.*, 2017a).

Typically, bluebirds rely on forest fires to create suitable habitat and nesting cavities (although they now utilise and compete over nestboxes (Duckworth, 2013)), and as such are adapted to continual recolonisation of successional habitats. However, their colonisation strategies differ. Mountain Bluebirds colonise new habitats first as they are more dispersive than Western Bluebirds. However, Western Bluebirds are aggressive and competitively dominant; when they arrive, they rapidly usurp nest

sites from and replace Mountain Bluebirds (Duckworth and Badyaev, 2007). However, in the early stages of colonisation Western Bluebirds are far outnumbered by Mountain Bluebirds and struggle to find conspecific mates, with hybridisation occurring as a result (Duckworth and Semenov, 2017). Additionally, as nest sites are taken over by male Western Bluebirds, female Mountain Bluebirds may resort to hybridisation in order to secure high-quality nest sites while seeking intraspecific extra-pair copulations (Duckworth and Semenov, 2017). These transient cycles of aggression and hybridisation are regularly repeated as bluebirds track their suitable habitat.

1.2.4 Species interactions and responses to global change

As species ranges change in light of climate change (Chris D. Thomas and Lennon, 1999; Parmesan and Yohe, 2003), land-use change (Regos *et al.*, 2018) and introduction to non-native areas (Dyer *et al.*, 2017), species interactions will modulate species responses to these global changes and will impact the ease with which species will move across the landscape, colonise new areas or persist in their current habitats (Blois *et al.*, 2013; Ockendon *et al.*, 2014; J.-C. Svenning *et al.*, 2014; Alexander, Diez and Levine, 2015; Pfennig, Kelly and Pierce, 2016; Early and Keith, 2019; Legault *et al.*, 2020a). The intensity of existing interactions may change under new conditions, and novel interactions will form as species assemblages shift and reassemble (van Dongen *et al.*, 2013; Alexander, Diez and Levine, 2015; Briceño *et al.*, 2019; Oswald *et al.*, 2019; Hernández-Brito *et al.*, 2021; Ramirez *et al.*, 2024).

Interactions do not act in isolation; species that compete exploitatively often defend territories against one another and may hybridise (Secondi *et al.*, 2003; Vallin *et al.*, 2012; Duckworth *et al.*, 2017a). This trifecta of competitive interactions is currently threatening Northern Spotted Owls (*Strix occidentalis caurina*) in the Pacific Northwest, which are already vulnerable as a result of extensive habitat loss. Barred Owls (*S. varia*) began their westward range expansion in the early 20th Century (Livezey, 2009). It has been suggested that this expansion was the result of climate change, forest management practices and the creation of shelterbelts and riparian corridors across the Great Plains (Kelly, Forsman and Anthony, 2003). The current range of the Barred Owl now totally encompasses that of the Northern Spotted Owl

(Kelly, Forsman and Anthony, 2003; Livezey, 2009). Barred and Spotted Owls compete for many of the same prey, and Barred Owls are dominant and aggressive towards, and even kill, Spotted Owls (Van Lanen *et al.*, 2011; Wiens, Anthony and Forsman, 2014a). The presence of Barred Owls dramatically reduces the fecundity of Spotted Owls; in one study, all Spotted Owls nesting within 1.5km of Barred Owl nests failed to fledge any young (Wiens, Anthony and Forsman, 2014a). The genetic integrity of Spotted Owls is threatened by hybridisation with Barred Owls (Hamer *et al.*, 1994). Hybrids are fertile, and introgression can occur (Hamer *et al.*, 1994). Barred and Spotted Owls highlight the need to view species interactions holistically as they rarely occur in isolation.

While Barred and Spotted Owls highlight the impact of novel species interactions, many species will be responding to global changes alongside species with which they have coexisted for millennia, and competition may impact their ability to respond to these changes. Upslope altitudinal range shifts are a well-documented response to climate change (Colwell *et al.*, 2008; Freeman and Class Freeman, 2014; Freeman *et al.*, 2018), and this process has been described as the 'escalator to extinction' as species will eventually run out of upslope suitable habitat to colonise (Marris, 2007; Sekercioglu *et al.*, 2008; Jankowski, Robinson and Levey, 2010; Freeman and Class Freeman, 2014; Freeman *et al.*, 2018). Many montane species exhibit asymmetric, aggressive, interspecific territoriality and occupy non-overlapping parapatric elevational bands as a result (Jankowski, Robinson and Levey, 2010; Freeman, 2015a; Freeman, Class Freeman and Hochachka, 2016; Boyce and Martin, 2019). If species are bounded at their upper elevational limit by a dominant competitor, they may be unable to track their climate niche and shift upslope. Alternately, subordinate species may have their range usurped by a more dominant competitor shifting upslope. For instance, White-rumped Robins (*Peneothello bimaculatus*), White-eyed Robins (*Pachycephalopsis poliosoma*) and Black Fantails (*Rhiphidura atra*) are all behaviourally dominant over their upper-elevation replacements (Freeman, Class Freeman and Hochachka, 2016). Between 1965 and 2012, their upper range limits on Mt. Karimui, Papua New Guinea, rose by 169m, 123m, and 197 respectively (Freeman, Class Freeman and Hochachka, 2016). Chestnut-backed Jewel-babblers (*Ptilorrhoa castanonota*) and Blue-grey Robins (*Melanodryas cyanus*) are not interspecifically aggressive towards their upslope replacement and have only shifted

their upper elevational limit by 10m and 24m, respectively, in those 47 years (Freeman, Class Freeman and Hochachka, 2016). This pattern alludes to the possibility that interspecific territoriality may facilitate upslope niche-tracking (Freeman, Class Freeman and Hochachka, 2016).

1.3 Thesis aims and outline

In this thesis, I aim to further our understanding of the impact of species interactions on global change-induced range shifts in birds. Although the following thesis focuses solely on birds, the findings and concepts discussed are relevant to many taxa and have broad-scale applicability. This work provides fundamental knowledge on which conservation-informing practices can be developed and highlights the importance of considering species not as singular entities, but as nodes within complex networks of interactions. In this age of rapid anthropogenic change and biodiversity crises, understanding species interactions and their impact on where species can exist, or coexist, is of particular importance. The thesis is made up of three main components and five constituent data chapters. The first component focuses on predicting hybridisation, the second on hindcasting the impacts of competition on historical range changes, and finally, the third focuses on examining the impact of species interactions on projections of species current ranges. Below, I detail the aims of the thesis and outline the structure of the following chapters.

1.3.1 Predicting hybridisation

As previously mentioned, the two forms of behavioural interference we focus on in this thesis are interspecific territoriality and hybridisation. Previous work on interspecific territoriality identified its determinants in North American passerines (Drury, Cowen and Grether, 2020). In Chapter 2, we conduct complementary and expanded analyses focusing on the determinants of hybridisation in North American and European passerines and non-passerines. We conduct comparative, phylogenetic species pair analyses with a variety of species-pair-specific life-history and ecological trait variables to identify those which influence the likelihood of hybridisation.

In Chapter 3, we highlight the importance of being able to predict the likelihood of novel interactions considering anthropogenic global changes. We assess and compare the performance of two predictive modelling approaches, Random Forest (RF) machine learning algorithms and Phylogenetic Generalised Linear Mixed Models (PLMMs), when predicting the likelihood of hybridisation in specific species pairs. We train models on North American species pair data and test them on unseen European species pairs, for which we have already extracted hybridisation classifications from the literature, allowing us to calculate a variety of performance metrics. As a demonstration of the potential value of these predictive modelling frameworks, we predict the likelihood of hybridisation for North American and European species that are projected to co-occur in the future and plot maps of current and future hybrid hotspots.

1.3.2 Hindcasting the impacts of biotic interactions on species distributions

In Chapter 4, we calculate measures of change in species pair fine-scale habitat and large-scale range overlap between 1997 and 2019 using the North American Breeding Bird Survey (NABBS) (Pardieck *et al.*, 2020) and the Pan-European Common Bird Monitoring Scheme (PECBMS) data (Brlík *et al.*, 2021). We include these measures of change in overlap as response variables in PLMMs alongside a variety of predictor variables that correspond to various forms of competition, including interspecific territoriality and hybridisation, to determine if they have influenced historical range dynamics and coexistence.

1.3.3 Examining the impacts of biotic interactions on species distributions

In Chapter 5, we utilise current projections from Species Distribution Models (SDMs) and BirdLife International range maps (BirdLife International and Handbook of the Birds of the World, 2021) to calculate measures of geographic avoidance (Novella-Fernandez *et al.*, 2021) for North American and European pairs. Geographic avoidance measures the extent to which the predicted ranges of a species pair are realised in the presence, versus in the absence, of one another, which may be indicative of competition. We include geographic avoidance as a response variable in PLMMs, once again with predictor variables corresponding to various forms of competition, to disentangle the effect of competition on the observed patterns of large-scale avoidance.

Finally, in Chapter 6, we create Joint Species Distribution Models (JSDMs) using a Hierarchical Modelling of Species Communities (HMSC) framework (Tikhonov *et al.*, 2020). We run JSDMs for 41 European families and extract residual association matrices for each. Residual association matrices contain the pairwise values of association between species after accounting for environmental covariates. We include residual association values as a response variable in PLMMs with predictors associated with behavioural interference and exploitative competition to determine if competition is responsible for the observed patterns of association. We also predict the spatial distribution of four species of *Phylloscopus* warbler across Europe using JSDMs and with identical models that differ only by including a single species. We then compare the spatial predictions of these two models, highlighting the impact of including species interactions in the predictions of species distributions.

Collectively, this thesis furthers our understanding of the role of exploitative competition and behavioural interference on species distributions and provides greater insight into the causes and consequences of avian hybridisation. These insights contribute to a growing body of work attempting to incorporate biotic interactions into predictions of species distributions and provide a basis for positive conservation outcomes.

Chapter 2

Predicting hybridisation

2.1 Introduction

Sexual interactions between species (reproductive interference) are common, widespread, and form a continuum ranging from, but not exclusive to, signal jamming, misdirected courtship, heterospecific mating and hybridisation (Gröning and Hochkirch, 2008). The cost of these interactions varies and is context-, species- and sex- dependent, from relatively uncostly (e.g., males mating with a heterospecific female) to a total loss of fitness, e.g., death without having produced fertile offspring, as a result of heterospecific matings (Gröning and Hochkirch, 2008; Tsuchida *et al.*, 2019). Hybridisation can be costly (Ålund *et al.*, 2024); however, fertile offspring can be produced, and in some contexts, hybridisation can confer direct benefits to one or both parents (Veen *et al.*, 2001), and their offspring may be of higher fitness than conspecific offspring (Pfennig, 2007) or either parent species (i.e., positive heterosis) (Good *et al.*, 2000; Wiley *et al.*, 2007).

Hybridisation is widespread and well-studied in birds (Grant and Grant, 1992; McCarthy, 2006; Ottenburghs, 2023). At its most basic, hybridisation is the manifestation of incomplete reproductive isolation between species (Mallet, 2005). It ranges from being extremely rare (i.e., only a single record of a particular pair combination (e.g., Toews *et al.*, 2022)) to frequent pairings and introgression within extensive hybrid zones (Toews, Brelsford and Irwin, 2011; McEntee, Burleigh and Singhal, 2020; Walsh *et al.*, 2020). Hybridisation has been the focus of a large body of research, including the description of novel hybrid pairings (Toews *et al.*, 2022), the genetic and genomic analyses of hybrids and hybrid zones (Ranasinghe, Seneviratne and Irwin, 2024), to the impact of hybridisation on species conservation (Cubrinovska, Massaro and Hale, 2016) and eco-evolutionary patterns, such as speciation, extinction and range dynamics (Rhymer and Simberloff, 1996; Gröning and Hochkirch, 2008; Abbott *et al.*, 2013; Gómez-Llano *et al.*, 2021; Pfennig, 2021). However, the ecological causes of hybridisation have received less attention (e.g., Grant and Grant, 1997; Randler, 2002, 2005, 2006; Willis, 2013; Willis, Symula and Lovette, 2014; Leighton *et al.*, 2021).

Understanding why species hybridise and which species pairs are likely to hybridise

is particularly important for species that are likely to experience range shifts as a result of ongoing anthropogenic climate change or introduction to non-native areas. Hybridisation with native species and its associated fitness costs may preclude potential colonists from becoming established in suitable habitat and slow range expansion (Pfennig, Kelly and Pierce, 2016). Conversely, natives may be detrimentally impacted through hybridisation with novel heterospecifics (Rhymer and Simberloff, 1996; Wallis, 1999; Allendorf *et al.*, 2001; Haig *et al.*, 2004; Muñoz-Fuentes *et al.*, 2007). For example, the genetic integrity of Pacific Black (*Anas superciliosa*), Hawaiian (*A. wyvilliana*), Yellow-billed (*A. undulata*) and Mottled Ducks (*A. fulvigula*) is threatened by hybridisation with introduced Mallards (*A. platyrhynchos*) (Rhymer and Braun, 1994; Weir and Price, 2011a; Guay *et al.*, 2014; Wells *et al.*, 2019; Stephens *et al.*, 2020). Natural colonisers can also threaten native species, especially those with already perilously low populations, as is the case with Pied Stilts (*Himantopus leucocephalus*), which have colonised New Zealand from Australia and are hybridising with critically endangered Black Stilts (*H. novaeseelandiae*) (Wallis, 1999). Similarly, native 'invaders' can pose a threat to rare species. Barred Owls (*Strix varia*) have expanded their range westwards, competing and hybridising with threatened Northern Spotted Owls (*S. occidentalis caurina*) (Haig *et al.*, 2004; van Lanen *et al.*, 2011; Wiens, Anthony and Forsman, 2014b).

Several hypotheses have been put forward in an attempt to explain why species hybridise with one another. Firstly, Hubbs' principle, often referred to as the desperation hypothesis, posits that hybridisation is more likely when one species is rare, whether that be across their entire range, at their range boundaries, in non-native areas, or as the number of conspecifics diminishes temporally throughout the breeding season (Hubbs, 1955; Brodsky and Weatherhead, 1984; Grant and Grant, 1997; Nuechterlein and Buitron, 1998; Wirtz, 1999; Randler, 2002; McCracken and Wilson, 2011; Willis, Symula and Lovette, 2014). Under this hypothesis, hybridisation occurs because of the disparity in the availability of conspecific mates, and despite hybrids often being of lower fitness than their parents, it is often better to mate with the 'wrong' species than not at all (Wirtz, 1999; Pfennig, 2007; Willis, 2013; Baker 1996). However, Hubbs' principle cannot be solely responsible for hybridisation as it also occurs between species occurring in

similar numbers and densities (Grant and Grant, 1997; Randler, 2006; Qvarnström *et al.*, 2023).

Hybridisation may also result from failures in species and mate recognition mechanisms, where heterospecifics are mistaken for conspecific mates. This mistaken identity is more likely to occur in behaviourally, morphologically and vocally similar species, which, as a result of phylogenetic conservatism, are often closely related (Blomberg, Garland JR. and Ives, 2003; Wiens and Graham, 2005) and their reproductive barriers, perceptual systems, and associated species recognition mechanisms are weaker (Baker and Boylan, 1999; Qvarnström *et al.*, 2006). Within species, there are trait distributions of the 'chosen sex' (often, and hereafter, males (Wirtz, 1999)) that fall within the perceptual trait space of the discriminating sex (often, and hereafter, females (Wirtz, 1999)) that they consider to be potential mates (Rosenthal, 2013). Heterospecific overlaps in these trait distributions and perceptual mate recognition functions can lead to species and, therefore, mate recognition errors (Price, 2008; Rosenthal, 2013; but see Mendelson and Shaw, 2012; Sullivan, 2010). Supernormal stimuli (Tinbergen, 1951) are a special case in which the traits of heterospecifics fall closer to the peak of the preferred trait distribution than conspecific traits (Ryan and Keddy-Hector, 1992; Ryan and Rand, 1993; Pfennig, 1998; Luddem *et al.*, 2004). For instance, consider a hypothetical species in which body size is an important mate selection trait and females preferentially mate with the largest conspecifics. If there is a second species that is larger than the first, differing only in size, females of the smaller species will preferentially mate with the larger heterospecific males. These mate selection traits may include body size (Nagel and Schluter, 1998), brighter plumage (Stein and Uy, 2006), more extravagant ornamentation (Ryan and Wagner, 1987; Jones and Hunter, 1998), more elaborate songs (Ryan and Rand, 1993), or higher quality territories and social dominance (Good *et al.*, 2000; Wiley *et al.*, 2007).

While mistaken identity and Hubbs' principle may lead to hybridisation at a species-pair level, there are species-specific life history traits that can influence the presence and/or extent of their hybridisation (Leighton *et al.*, 2021). Species with long-term social bonds,

for instance, are less likely to hybridise and hybridise with fewer species (Leighton *et al.*, 2021). Species with long-term pair bonds may be choosier during the mate selection process as their chosen mate has the potential to impact their fitness over multiple breeding seasons, or their entire lives in some cases, compared to species that mate with multiple individuals or have only single-season pair bonds (Leighton *et al.*, 2021). Long-distance migrants are also more likely to hybridise than sedentary species (Leighton *et al.*, 2021). Migrants experience a greater temporal pressure compared to residents (Soriano-Redondo *et al.*, 2023). Upon arrival on breeding grounds, migrants have less time to secure a mate, whereas residents have been able to form pair bonds throughout the non-breeding season, and as such, migrants may be less discerning and mistaken identity may result (Leighton *et al.*, 2021).

At an individual level, species with song learning and mate recognition mechanisms associated with imprinting as juveniles may be predisposed to hybridise if exposed to heterospecifics at an early age (Ten Cate and Vos, 1999; Randler, 2005). Birds that imprint upon heterospecifics may select heterospecific mates in the future (Fabricius, 1991; Grant and Grant, 1997; Slagsvold *et al.*, 2002), or those that sing heterospecific songs, as a result of misprinting, may be mistaken for suitable mates by heterospecifics (Grant and Grant, 1997; Randler, 2005). Wildfowl that practice interspecific brood amalgamation ('egg dumping') hybridise more than species that do not, likely a result of these imprinting mechanisms (Randler, 2005).

Species must also co-occur at some point for hybridisation to occur, and as such, both the number of co-occurring heterospecifics and the extent of breeding range overlap increase the likelihood of hybridisation (Willis, Symula and Lovette, 2014). That said, out-of-range vagrants also show a high propensity for hybridisation (Holling, 2016, 2017; Moore and Coulson, 2020; Lees and Gilroy, 2022), and hybridisation can be more common between parapatric species compared to sympatric species (Randler, 2006), both likely a result of Hubbs' principle.

Few studies have addressed the causes of hybridisation in a comparative framework (e.g., Willis, Symula and Lovette, 2014). This study aims to address this knowledge gap

and determine which species pair-specific phenotypic and life history traits are important predictors of hybridisation in pairs of North American and European birds. We attempt to test for Hubbs' principle and/or the mistaken identity hypothesis, while controlling for species-specific traits that may influence hybridisation. To test these hypotheses, we utilise two large datasets of hybridising and potentially, but non-hybridising, North American and European passerine and non-passerine pairs. To our knowledge, this is the first study of this scale that utilises a phylogenetic comparative framework with species pair data to determine the predictors of hybridisation while accounting for relatedness. We aim to use the knowledge gained from this research to allow us to predict how likely specific species, that may or may not currently coexist, are to hybridise, which has important future conservation implications.

2.2 Methods

2.2.1 Creating species lists

2.2.1.1 North American species

A list of species breeding within the contiguous United States was created using the American Birding Association (ABA) checklist codes (Pyle *et al.*, 2021) and the eBird ‘Lower 48’ regional checklist (Sullivan *et al.*, 2009). Our species concepts followed the 2021 eBird taxonomy (Clements *et al.*, 2021). Only ABA-designated Code-1 and Code-2 species (those which regularly occur and breed within the ABA area) were included to exclude rare vagrants and non-breeders. Range maps from Birds of the World were consulted to ensure species bred within the contiguous United States; 64 non-breeders were removed at this stage (Billerman *et al.*, 2022). Non-native species were included if they occurred on the ABA list or the United States Register of Introduced and Invasive Species (US-RIIS) (Simpson, Blake and Dorado, 2021). While inclusion on these lists depends on different criteria, it requires species to be established and breeding, which is decided by expert panels. 22 non-natives were shared by both lists, eight were included only on the ABA list, and one was only on the US-RIIS list. Pelagic seabirds (larids, alcids, procellariiforms) were excluded from the species list (using data from Drury *et al.*, (2021)) due to their pelagic habits and underreporting using traditional, terrestrial survey methods. This left 524 species that breed within the contiguous United States.

2.2.1.2 European species

Our European species list was based on those present in the Pan-European Common Bird Monitoring Scheme (PECBMS) dataset (Brlík *et al.*, 2021). The countries/schemes with available survey data were Austria, Brussels, Catalonia, Denmark, France, Germany, Ireland, Italy, Netherlands, Norway, Poland, Sweden, United Kingdom and Wallonia. Non-native species present in the PECBMS data were included, and Birds of the World accounts (Billerman *et al.*, 2022) and eBird range maps (Sullivan *et al.*, 2009)

were consulted to confirm that their established non-native ranges fell within the study area. Again, pelagic seabirds were removed from the species list using data from Drury *et al.*, (2021). A total of 386 European species remained.

2.2.2 Creating species pairs

2.2.2.1 Hybridising species pairs

Three separate sources were consulted to identify hybridising pairs in our species list. Only naturally occurring hybrids were included. The first source was the Handbook of Avian Hybrids of the World (McCarthy, 2006). The second was the 2021 eBird Taxonomy (Clements *et al.*, 2021), which includes hybrid taxa that are distinct enough to be recognised in the field by birders. Lastly, a literature search was carried out using Web of Science (webofscience.com) utilising species current and historical vernacular and scientific names and Boolean search terms to encompass the terms ‘hybrid’, ‘introgression’, ‘reproductive interference’, ‘mixed species pair’, ‘cross-species mating’ and their associated derivations. Only articles published post-2000 were searched to avoid duplication of effort with McCarthy (2006). Species pairs, therefore, had a maximum of three classifications of hybridisation, one from each source. Only pairs with convincing evidence of natural hybridisation were included in this pair list. McCarthy (2006) classified records as no doubt, some doubt and marked doubt; only records with no doubt were included in our analyses. Similarly, from the literature search, only records corroborated in peer-reviewed literature were included; anecdotal or unconfirmed hybrids were ignored. While we have less certainty of hybrids from the eBird taxonomy, their inclusion is the result of expert review (Justyn, Callaghan and Hill, 2020). There were 310 North American (Figure 1) and 323 European (Figure 2) species pairs with convincing evidence of natural hybridisation from at least one source.

2.2.2.2 Potentially, but non-hybridising pairs

To create a comparison group comprised of species pairs that have not been reported to hybridise, every species on the aforementioned species list was paired with every

other member of its own family with which it co-occurs. Pairs were restricted to the same family because interfamilial hybridisation is exceedingly rare and, to our knowledge, has never been observed in the wild (McCarthy, 2006). As such, monotypic families were not included in analyses. BirdLife International range maps (BirdLife International and Handbook of the Birds of the World, 2021) were used to calculate range overlap alongside the number of North American Breeding Bird Survey (BBS) (Pardieck *et al.*, 2020) routes and stops shared by a pair in any year between 1976 and 2019. If a pair had any overlap in either method and did not hybridise, they were considered to be potentially but non-hybridising ($n = 3337$ pairs in our comparison group). Our total pair list for North America now stood at 3647 pairs, 1321 of which were passerines, while the remaining 2326 were non-passerines. In European analyses range overlap from BirdLife International maps (BirdLife International and Handbook of the Birds of the World, 2021) was also calculated, and whether species pairs shared any Pan-European Common Bird Monitoring Scheme (PECBMS) sites between 1976 and 2019 was determined. 2203 European pairs fulfilled at least one of these criteria, 682 were passerine pairs, and 1521 were non-passerines.

2.2.3 Predictors of hybridisation

2.2.3.1 Morphometric dissimilarity

Nine morphometric traits (beak length: culmen-to-tip, beak length: nares-to-tip, beak width, beak depth, tarsus length, wing length, secondary length, tail length and mass) were extracted from the AVONET dataset for each species (Tobias *et al.*, 2022). These variables were log transformed, centred and scaled, and included in a principal components analysis (PCA) as in Pigot *et al.*, (2020a)(Figure 3). The Euclidean distance between each species pair in the resulting PC space was calculated to provide a measure of morphometric dissimilarity.

2.2.3.2 Colour and pattern dissimilarity

Using methods developed by Miller *et al.*, (2019), we utilised illustrations from Birds of the World (Billerman *et al.*, 2022) to quantify dissimilarity in colour and pattern within pairs. Full body plates of males, not in flight (except swifts, which do not have perched illustrations, but were still included in analyses), of the subspecies that occurs in the contiguous United States or Western Europe were used. If multiple subspecies occur in the study area, a random number generator was used to select one. If the subspecies that occurs within the study area did not have an associated illustration, the most closely related subspecies with an illustration was utilised. Male plates were used as errors in mate recognition are often cited as occurring in the more discriminating sex, which is often the female (Wirtz, 1999). Using the program GIMP the background, legs and any branches were removed from illustrations. The illustrations were then scaled so that they were approximately the same size and then saved as TIF files. While in some species, legs may be an important feature in species and mate recognition (Iverson and Karubian, 2017), for these analyses, they were removed to enable illustrations to be scaled more accurately.

To quantify plumage colour dissimilarity between species pairs in our dataset, we used ImageJ 32bit/FIJI (Schindelin *et al.*, 2012) and macros developed by Miller *et al.* (2019). 1000 random points from across each illustration were sampled and the Red (R) Green (G) Blue (B) colour coordinates were extracted from each point and converted to perceptually uniform CIELAB colour coordinates. For each pair, the 1000 colour coordinates of each species were plotted in CIELAB space, and the average Mahalanobis distance between all the points of a pair was calculated to provide a measure of colour dissimilarity. The average colour of each species is shown in Figure 4.

To quantify plumage pattern similarity between species pairs in our dataset, we split illustrations into their corresponding RGB channels (following Miller *et al.* 2019). Pattern analysis was conducted on the G channel only, as it corresponds more closely to avian luminance channels associated with pattern processing (Stevens and Cuthill, 2006). Granularity-based pattern analysis was carried out using ImageJ/FIJI (Schindelin *et al.*, 2012) with macros from Miller *et al.* (2019). Illustrations were band-pass filtered using the Fast Fourier Transform into 17 granularity bands corresponding to spatial

frequencies ranging from 2 to 512 pixels, increasing by multiples of $\sqrt{2}$. The 'energy' at each scale was quantified as the standard deviation of filtered pixel values and corresponds to the contribution to overall appearance from pattern elements of that size. For example, high energy at a high granularity band (e.g., 2 pixels) corresponds to many small pattern elements, and low energy at that band corresponds to few small pattern elements. Alternately, high energy at a low granularity band (e.g., 512 pixels) corresponds to many large pattern elements, and low energy would be few large elements. Each species, therefore, has 17 values of pattern energy, one for each granularity band. These 17 energy values were incorporated into a PCA, and the Euclidean distance between species within each pair was calculated to provide a measure of pattern dissimilarity (Figure 5). Absolute differences between energy spectra at each bandwidth were summed to provide a second measure of pattern dissimilarity. Absolute differences and Euclidean distances were strongly positively correlated, so only the latter was included in models.

2.2.3.3 Vocalisation dissimilarity

Following sensitivity analyses carried out by Cowen, Drury and Grether (2020), Birds of the World (Billerman *et al.*, 2022) species accounts were consulted to determine species vocal repertoire size. If species had fewer than four courtship/territorial vocalisation types, they were considered to have a small repertoire, and two sound files were downloaded from xeno-canto (xeno-canto.org). Four sound files were downloaded for those with large repertoires (four or more vocalisation types). We endeavoured to download the highest quality sound files recorded in the United States and Europe. However, this was not always possible, in which case recordings were requested from the Macaulay Library at the Cornell Lab of Ornithology (www.macaulaylibrary.org). Only recordings of individual males were used, and given the difficulty in disentangling the vocalisations of individuals of lekking species, e.g. *Tympanuchus* grouse, we removed lekking species from analyses. Further, to compare like for like, non-vocal sounds such as the drumming of woodpeckers, winnowing of snipe and dive displays of hummingbirds were not included in analyses despite their role in species recognition and mate selection, with vocal sounds used instead (Hurly, Scott and Healy, 2001; Miles

et al., 2018). Black (*Ciconia nigra*) and White Storks (*C. ciconia*) were removed from European analyses as the only available sounds for White Storks were non-vocal bill clattering. The hissing exhalations of otherwise mute Cathartid vultures and Muscovy Ducks (*Cairina moschata*) were also removed from analyses.

Sound files were cleaned using noise reduction in Audacity (version 3.7.1, audacityteam.org) (starting values of Noise Reduction (dB) = 12, Sensitivity= 10, Frequency Smoothing = 0, but were altered depending on the specific file) and were trimmed to encompass a single vocalisation (songs in passerines and calls in non-passerines). We defined a single vocalisation as vocal elements separated from one another by less than one second. Once trimmed, sound files were saved as 44100Hz, 16-bit, mono, .wav files. They were then all normalised to standardise their amplitude. Raven Lite (version 2.0.5, Charif, Ponirakis and Krein, 2006) was then used to create selection tables for each sound file that included the start and end time of each element within a vocalisation.

To quantify vocalisation dissimilarity within pairs, we began by using the function *specan* from the R Package warbleR (Araya-Salas and Smith-Vidaurre, 2017) to extract 28 acoustic parameters; six additional parameters were calculated manually. The final 34 acoustic parameters were transformed (see appendix A for a list of acoustic parameters and transformations), centred and scaled, and included in a PCA (Figure 6). Each species had either 2 or 4 sets of associated PC coordinates, one for each sound file. The average Euclidean distance between the vocalisations of each species within a pair was calculated to provide a measure of vocalisation dissimilarity.

2.2.3.4 Patristic distance

To create a quantitative measure of relatedness, we calculated patristic distance using the *cophenetic.phylo* function from the R package ape (Paradis and Schliep, 2019) and a Cornell Lab of Ornithology Open Tree of Life (CLOOTL) tree (McTavish et al., 2025; Miller, Sanchez-Reyes and McTavish, 2025). Patristic distance is the pairwise distance between the species tips of a phylogenetic tree, calculated using branch lengths.

2.2.3.5 Syntopy and Sympatry

Using the R package Auk (Strimas-Mackey *et al.*, 2023), we extracted eBird occurrence data (Cornell Lab of Ornithology, 2022) for each species. We filtered eBird observations to those from complete checklists, 0 to 0.25 miles in length, between 1st January 2011 and 31st December 2020, in the United States and Canada, for North American pairs, and Andorra, Austria, Belgium, Czech Republic, Denmark, Estonia, Finland, France, Germany, Ireland, Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Monaco, Netherlands, Norway, Poland, Portugal, Spain, Sweden, Switzerland, United Kingdom for European analyses. Following Drury, Cowen and Grether (2020), these observations were used to calculate measures of range (sympatry) and breeding habitat (syntopy) overlap. For each species, Birds of the World (Billerman *et al.*, 2022) species accounts were consulted to determine their breeding months (i.e., the months eggs are laid). For some species, breeding month information was not available from Birds of the World, so a literature search was conducted, and if that failed, breeding months were inferred from closely related species with available data. For each pair, eBird observations were filtered to include only those from the overlapping breeding months. For each pair, we extracted the total number of records matching the aforementioned criteria. Then, for each species in a pair, the number of records that were within 39.4km (the length of a North American BBS route) of a record of the other species was calculated. Mean sympatry (i.e., broad-scale range overlap) for each year was then calculated as the number of records of each species within 39.4km, divided by the total number of records of each species, summed and then divided by 2.

$$(Eq. 1) \quad Sympatry_y = \frac{1}{2} \left(\frac{N_{1,2}^y}{N_1^y} + \frac{N_{2,1}^y}{N_2^y} \right)$$

Where N_1^y is the number of records of species 1 in year y , N_2^y is the number of records of species 2 in year y , $N_{1,2}^y$ is the number of eBird records of species 1 within 39.4km of species 2 within year y and $N_{2,1}^y$ is the number of eBird records of species 2 within 39.4km of species 1 within year y . This value was then averaged across the ten-year period to give an overall measure of range overlap:

$$(Eq. 2) \quad \text{Mean sympatry} = \frac{1}{10} \sum_{y=1}^{10} \text{Sympatry}_y$$

Syntopy (i.e., fine-scale range overlap) was calculated in the same way, but instead of records within 39.4km of each other, they were within 0.25 miles (the radius of a point count at a North American BBS stop) of one another ($n_{1,2}^y, n_{2,1}^y$).

$$(Eq. 3) \quad \text{Syntopy}_y = \frac{1}{2} \left(\frac{n_{1,2}^y}{N_1^y} + \frac{n_{2,1}^y}{N_2^y} \right)$$

$$(Eq. 4) \quad \text{Mean Syntopy} = \frac{1}{10} \sum_{y=1}^{10} \text{Syntopy}_y$$

A species pair cannot be syntopic if they are not sympatric. If the breeding months of a species pair do not overlap, or either had no filtered eBird records within the ten-year period, they had no values for sympatry and syntopy and were omitted from analyses. Similarly, in an effort to filter out inaccurate records, there needed to be at least ten records in each year to calculate syntopy. As such, pairs with fewer than ten sympatric records in every year may have had a sympatry value but no value for syntopy and were subsequently removed from analyses. In North America, this left 3339 (2189 passerines, 1150 non-passerines) pairs with spatial data, while in Europe, 1647 (522 passerines, 1125 non-passerines) pairs remained. Of these remaining pairs, the North American dataset contained 290 hybridising pairs, while the European dataset contained 273 hybridising pairs.

2.2.3.6 Life history traits

Data on migratory strategy and social bond length were taken from Tobias *et al.*, (2016) for each species. For migratory strategy, species were classified as sedentary, partially migratory and migratory. For social bond length, species were classified as solitary, having short-term pair/group bonds, and long-term pair/group bonds. Species were classified as being native or non-native when species lists were being created. If either species in a pair were migratory/had long-term pair bonds/were non-native, the pair were assigned the binary classifier “1” for that specific variable, if neither were they were assigned “0”. 2602 North American pairs contained at least one migratory species, 1874 contained at least one species with long-term social bonds and 166 contained at least one non-native. In Europe, 1585 pairs contained at least one migratory species, 1551 contained at least one species with long-term social bonds and 356 contained at least one non-native.

2.2.3.7 eBird count ratios

In an effort to test for Hubbs’ principle and the effect of asymmetries in the number of individuals in an area on the likelihood of hybridisation, we calculated a ratio of the estimated eBird counts within the area of overlap of a species pairs using the eBird Status and Trends count data (Fink *et al.*, 2023) with the ebirdST R package (Strimas-Mackey *et al.*, 2023). We downloaded the eBird mean seasonal count rasters at a 3km resolution for all available species (these data were only available for the year 2022). Estimated mean counts were used in place of estimated relative abundance, as relative abundance is not comparable between species. We then cropped estimated count rasters to North America and Western Europe, respectively, and selected only the resident/breeding layer. For each species pair, we extracted the area of overlap and then cropped the individual species rasters to that area of overlap. We calculated the mean count across the area of overlap for each species and then calculated a ratio of the larger to smaller mean count for each pair with available data. We were able to calculate this metric for 3160 North American pairs but only 253 European pairs.

2.2.4 Analysis

All statistical analyses were carried out in R using the package MCMCglmm (Hadfield, 2010). Phylogenetic linear mixed models (PLMMs) were run with hybridisation as a binary response variable and the aforementioned predictors as dependent variables. Pairs containing species without vocalisation data and those without eBird syntopy and sympatry measures were removed from analyses (n=308), leaving 3339 North American and 1647 European pairs to be used in models. As not all species are present in the eBird Status and Trends dataset, models utilising those data contained only 3039 North American pairs (1023 passerines and 2016 non-passerines) and 243 European pairs (53 passerines and 190 non-passerines). For North America and Europe, models were run using the full dataset for all pairs, passerines alone and non-passerines alone. A second set of models were run, including eBird count ratio as a predictor variable for all pairs, passerines only and non-passerines only with available data. Species identity and a maximum clade credibility CLOOTL phylogeny (Miller, Sanchez-Reyes and McTavish, 2025) specifying nodes representing a pair's most recent common ancestor were included as random effects. Uninformative, inverse-Wishart distribution priors were used (Hadfield, 2014), and four chains for each model were run for two million iterations with a burn-in of 20,000 and a thinning interval of 1000. Model convergence was assessed using Gelman-Rubin diagnostics (Gelman and Rubin, 1992) and visual inspection of trace plots.

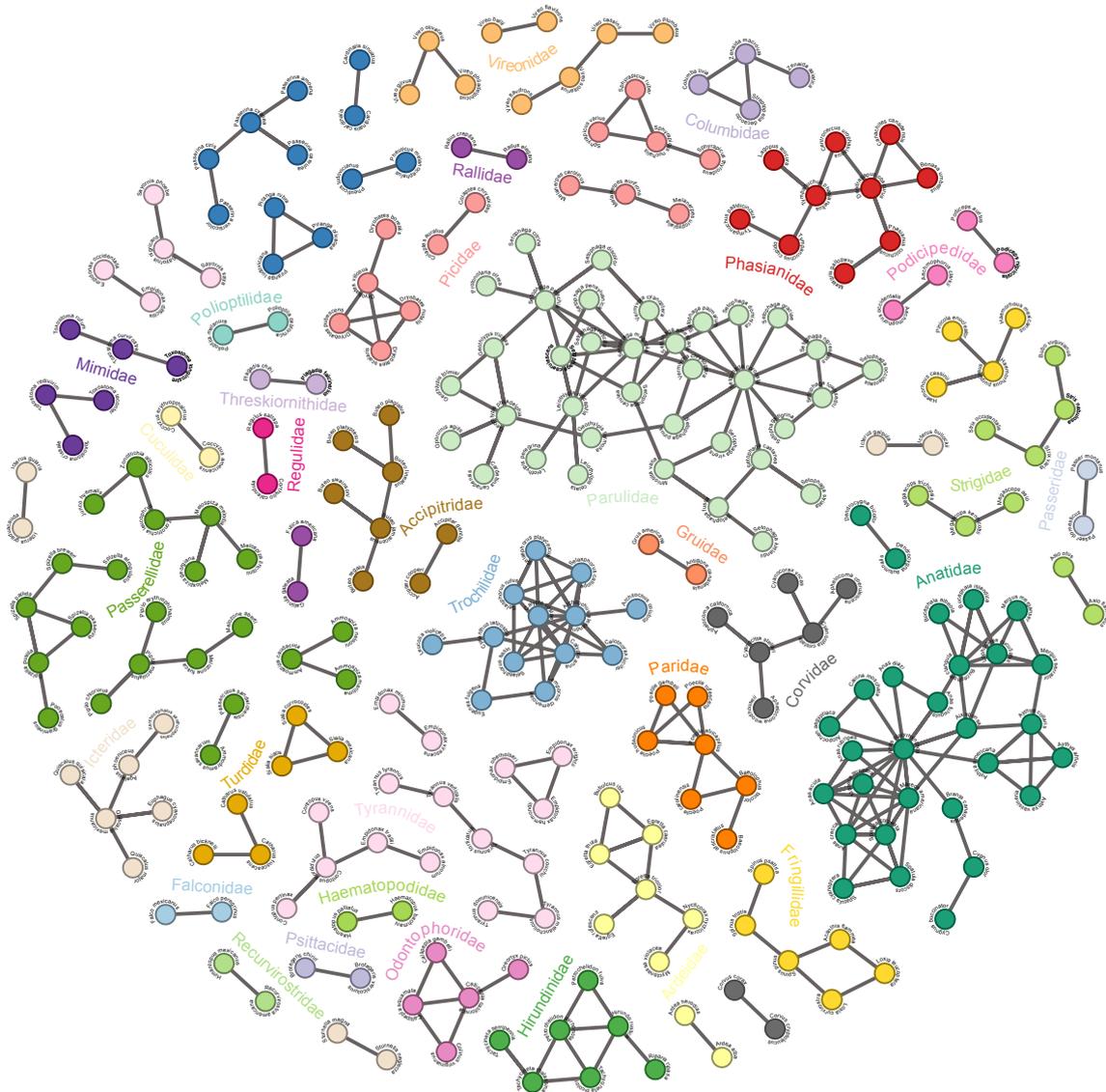


Figure 1. Network of North American hybridisation. Nodes represent species (coloured by family), and lines indicate recorded hybridisation in the wild. Non-hybridising pairs are not included.

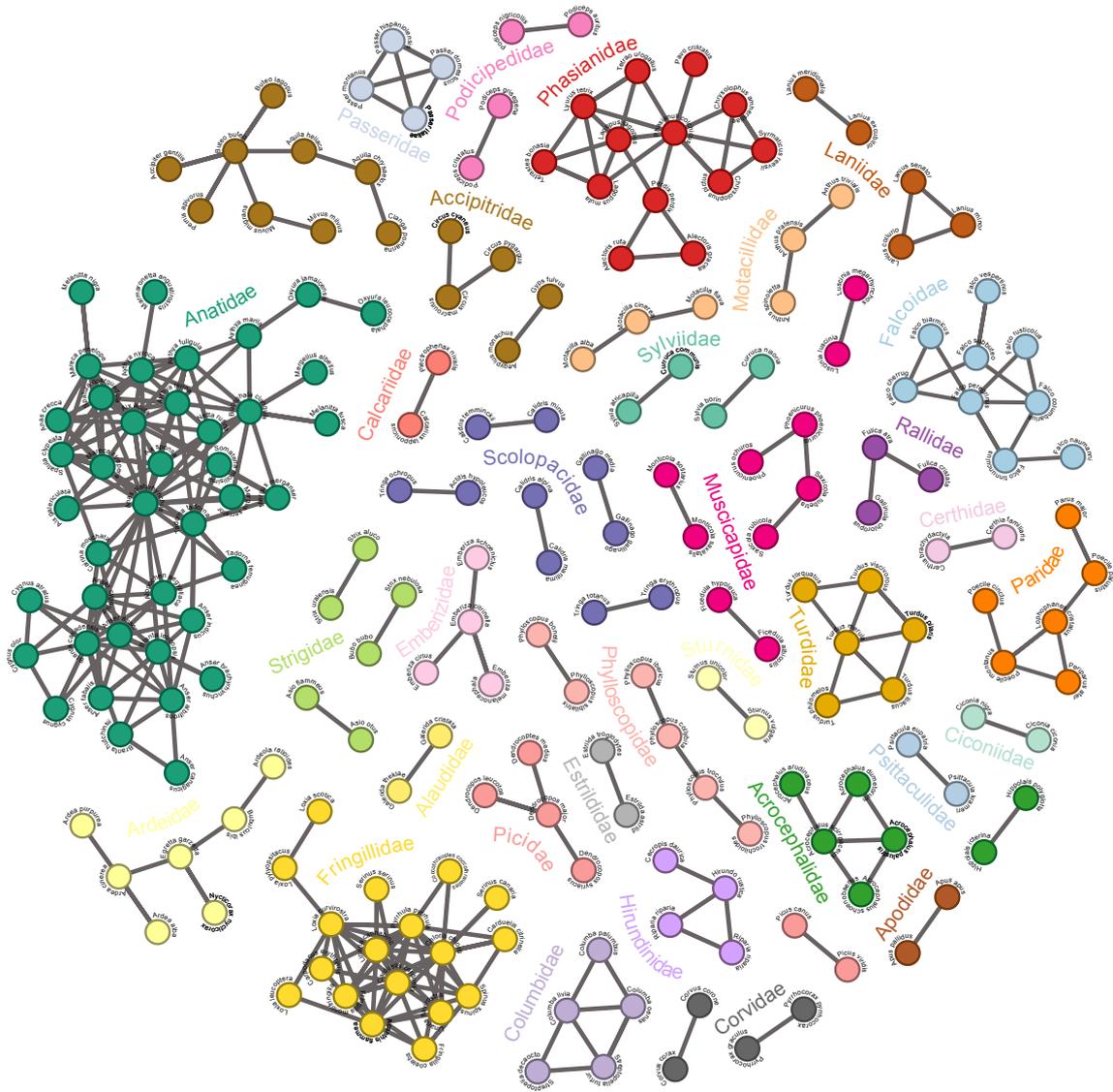
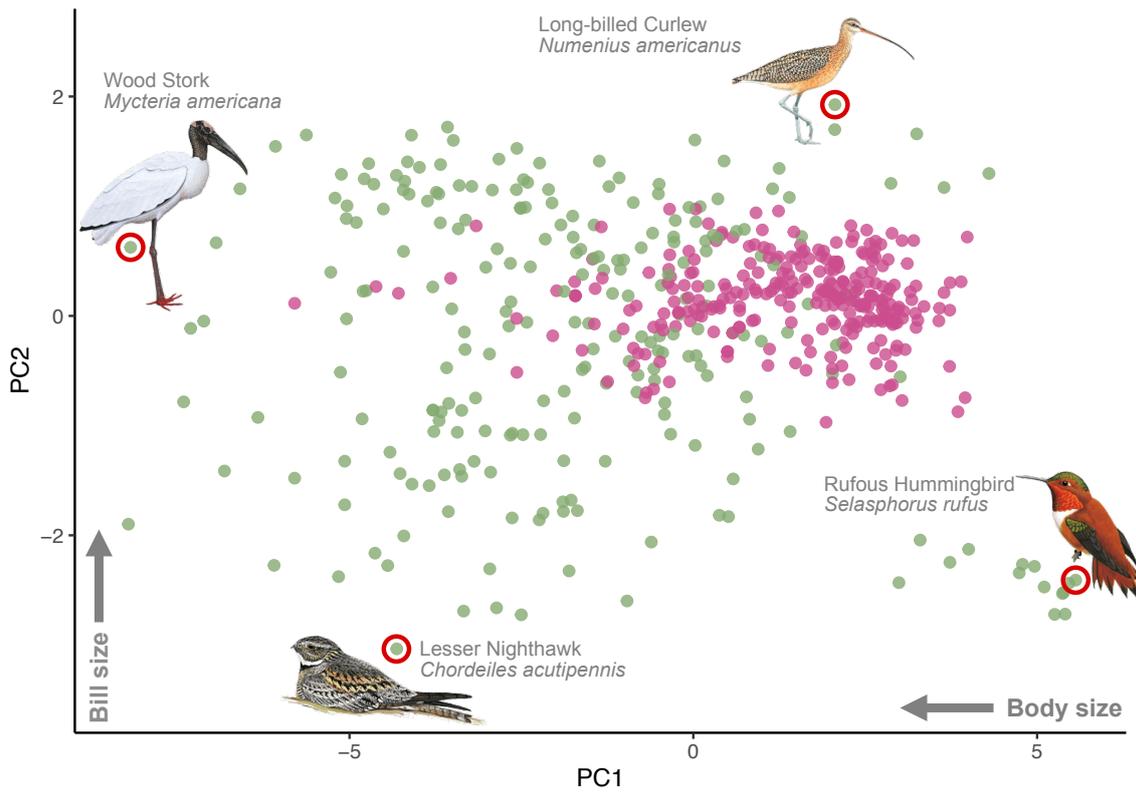


Figure 2. Network of European hybridisation. Nodes represent species (coloured by family), and lines indicate recorded hybridisation in the wild. Non-hybridising pairs are not included.

A) North American morpho-space



B) European morpho-space

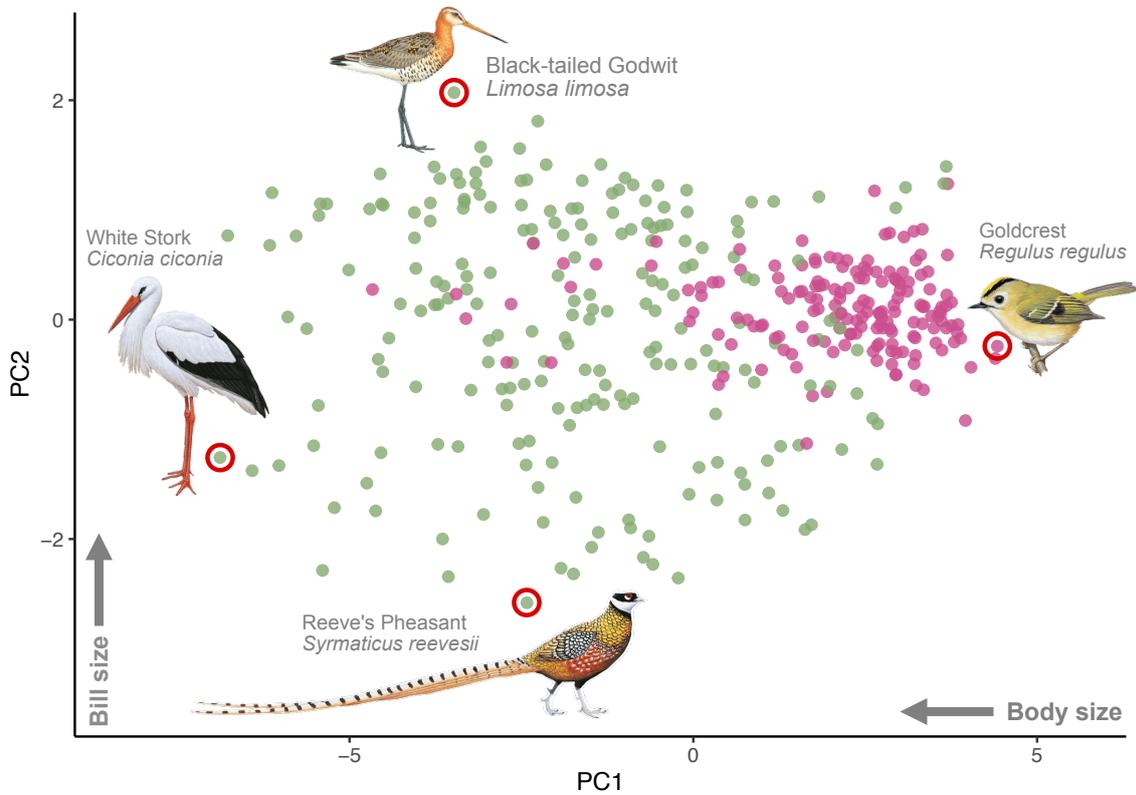
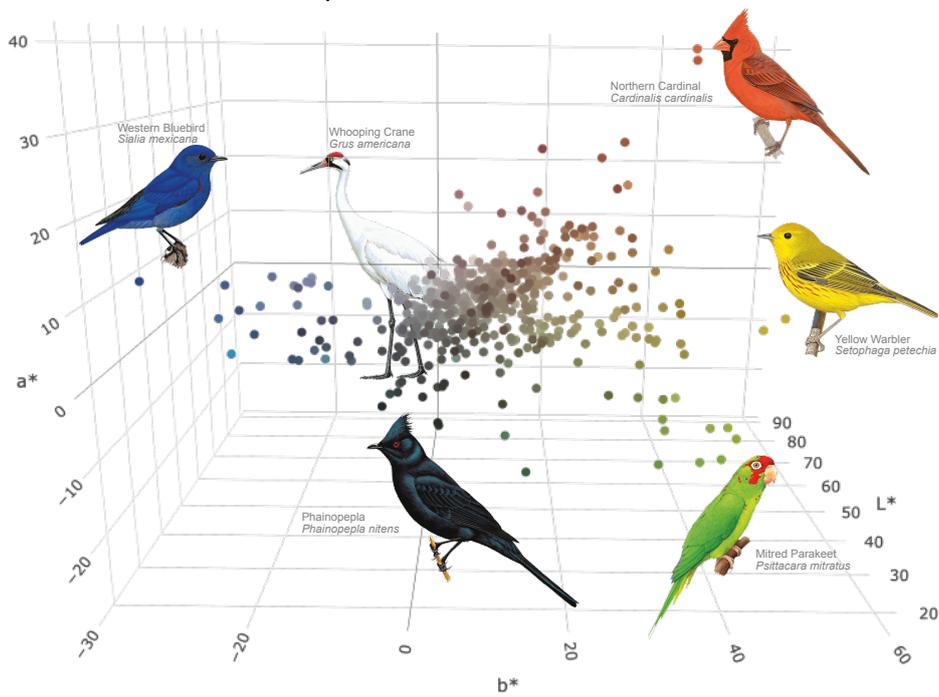


Figure 3. Principal component plots of North American (A) (n=524) and European (B) (n=386) species in morpho-space. Passerines are shown in pink, non-passerines in green. PCA were conducted separately between continents, so plots are not directly comparable.

Illustrations: Cornell Lab of Ornithology | Birds of the World [Francesc Jutglar, Dave Nurney, Antoni Llobet, Antoni Lombarte, Hilary Burn].

A) North American CIELAB colour space



B) European CIELAB colour space

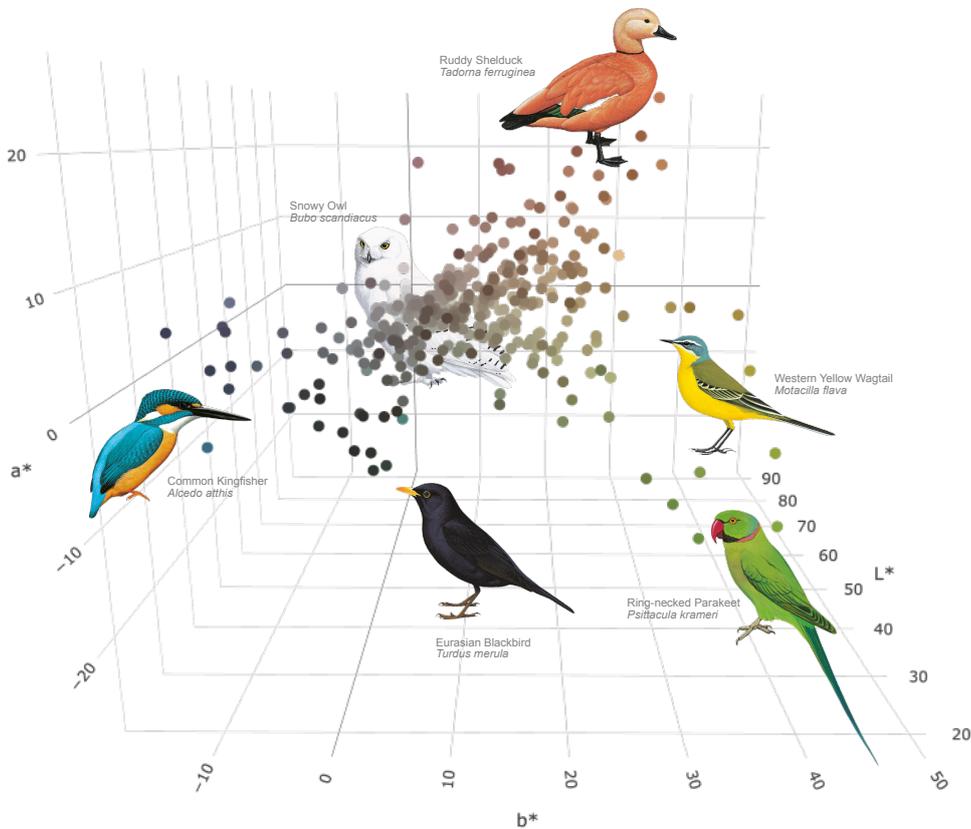
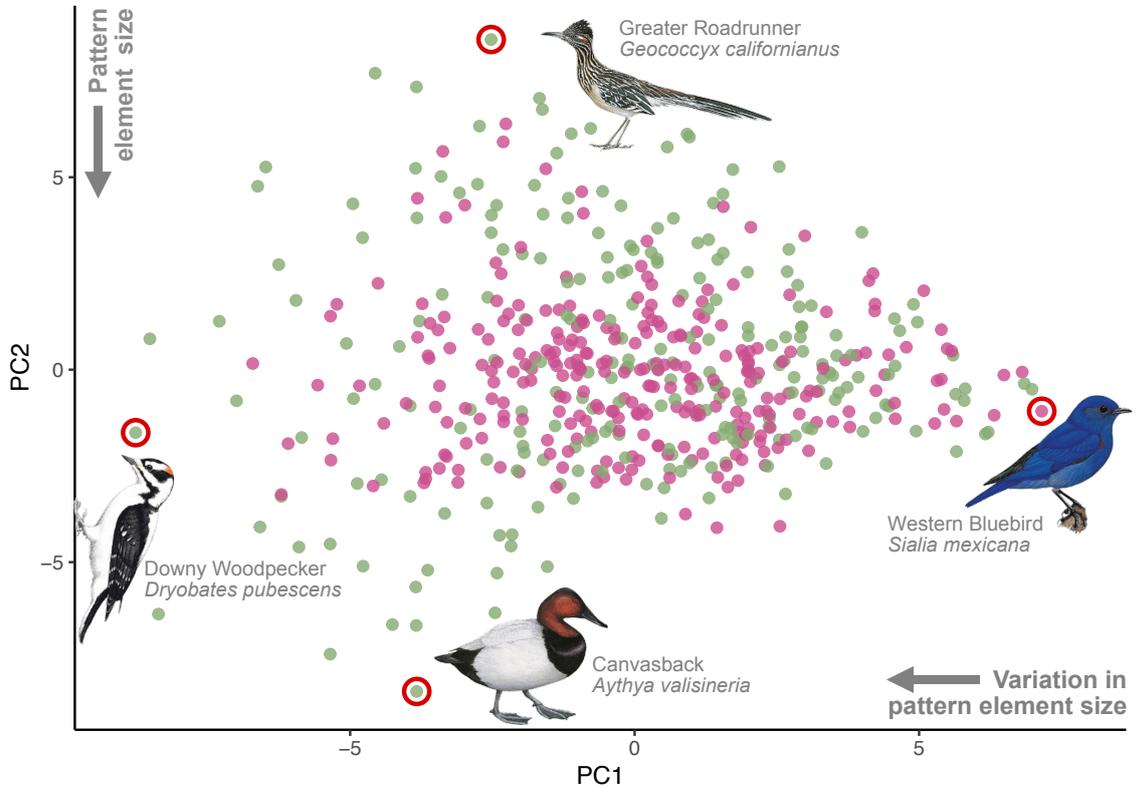


Figure 4. The average colour of North American (A)($n=524$) and European birds (B) ($n=386$) plotted in CIELAB colour space, calculated as the average colour coordinates of 1000 random points on Birds of the World species illustrations. L^* corresponds to lightness, a^* is

the green-red axis and b^* is the blue-yellow axis. Illustrations: Cornell Lab of Ornithology | Birds of the World [Ian Willis, Hilary Burn, Brian Small, Doug Pratt, David Quinn, Àngels Jutglar, Tim Worfolk, Norman Arlott, Francesc Jutglar, Ren Hathway].

A) North American pattern-space



B.) European pattern-space

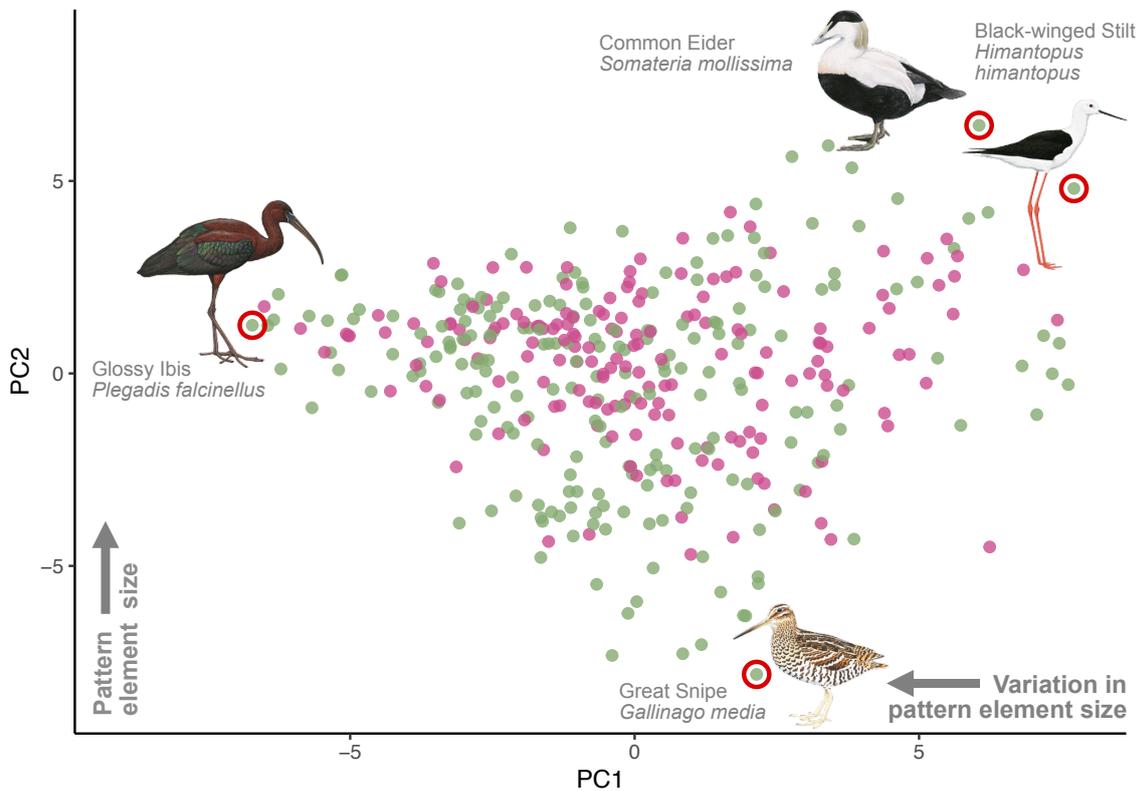
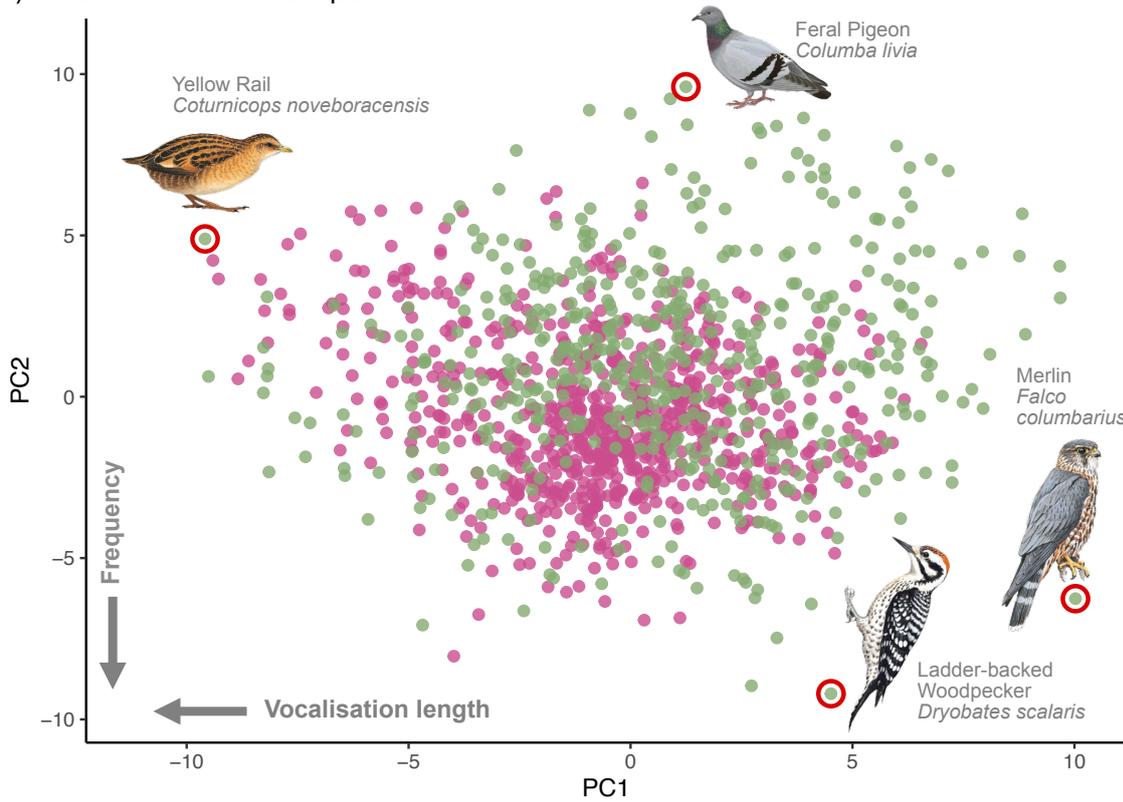


Figure 5. Principal component plots of North American (A) (n=524) and European (B) (n=386) species in pattern-space. Passerines are shown in pink, non-passerines in green. PCA were conducted separately between continents, so plots are not directly comparable. Illustrations: Cornell Lab of Ornithology | Birds of the World [Tim Worfolk, Ian Willis, Àngels Jutglar, Francesc Jutglar].

A) North American vocal-space



B) European vocal-space

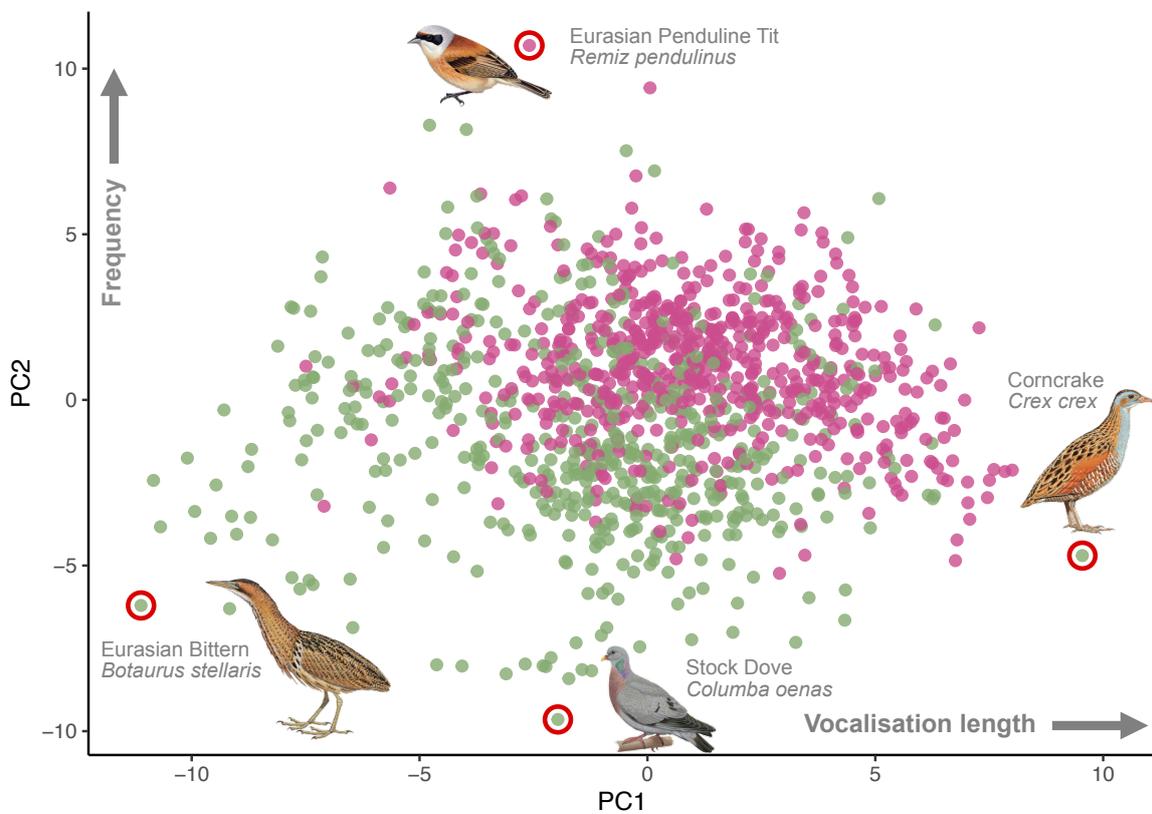


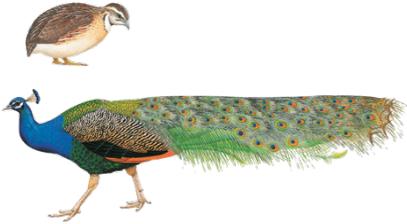
Figure 6. Principal component plots of North American (A) (n=524) and European (B) (n=386) species in vocal-space. Passerines are shown in pink, non-passerines in green. PCA were conducted separately between continents, so plots are not directly comparable. Each species has 2 or 4 vocalisations in vocal-space plots, depending on repertoire size.

Illustrations: Cornell Lab of Ornithology | Birds of the World [Norman Arlott, Martin Elliott, Jan Wilczur, Hilary Burn, Francesc Jutglar].

2.3 Results

Of the 2189 North American passerine pairs included in the full models, only 7% (n=153) hybridise. Non-passerines have a slightly higher incidence of hybridisation at 12% of 1150 pairs (n=137). In European pairs, 21% (n=108) of passerines hybridise and 15% (n=165) of non-passerines hybridise. Species pairs with the maximum and minimum morphometric, colour, pattern and song dissimilarity, and patristic distance are shown in Table 1, and the convex hull volumes for dissimilarity predictors using Euclidean distances are shown in Table 15.

Table 1. The most similar and dissimilar pairs in morphology, colour, pattern, vocalisations and relatedness in North America and Europe. Distance values refer to Euclidean distance for morphometric, pattern, and vocalisation dissimilarity. Colour dissimilarity is Mahalanobis distance and patristic distance is the branch length between two species in a phylogeny. Distance measures were calculated separately for both continents. Not all of these pairs hybridise. Illustrations: Cornell Lab of Ornithology | Birds of the World [Tim Worfolk, Norman Arlott, Francesc Jutglar, David Quinn, Brian Small, Ian Willis, Àngels Jutglar, Hilary Burn, Ian Lewington, Ren Hathway, Jan Wilczur].

Variable	Distance	
	Europe	North America
Morphometric dissimilarity	<p>Most similar</p>  <p><i>Lanius excubitor</i> <i>Lanius meridionalis</i> 0.15</p>	 <p><i>Catharus fuscescens</i> <i>Catharus ustulatus</i> 0.16</p>
	<p>Most dissimilar</p>  <p><i>Coturnix coturnix</i> <i>Pavo cristatus</i> 6.97</p>	 <p><i>Corvus corax</i> <i>Pica nuttalli</i> 6.41</p>
Colour dissimilarity	<p>Most similar</p>  <p><i>Aythya marila</i> <i>Bucephala clangula</i> 0.03</p>	 <p><i>Dryobates pubescens</i> <i>Dryobates villosus</i> 0.07</p>

**Most
dissimilar**



Cygnus cygnus
Melanitta nigra
10.9



Anas rubripes
Cygnus buccinator
7.91

**Most
similar**



Loxia pytyopsittacus
Loxia scotica
0.38



Aegolius funereus
Athene cunicularia
0.69

**Pattern
dissimilarity**

**Most
dissimilar**



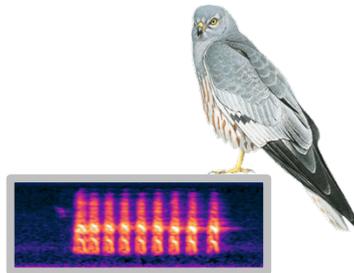
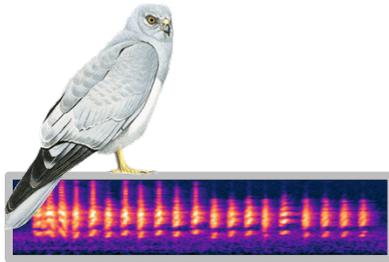
Melanitta nigra
Somateria mollissima
13.5



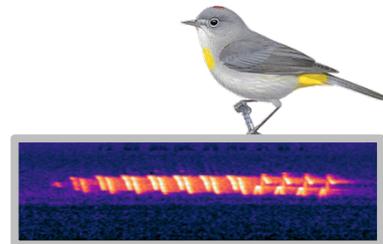
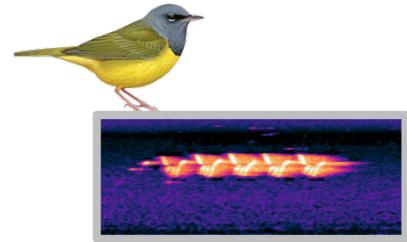
Aythya valisineria
Spatula cyanoptera
14.0

Vocalisation
dissimilarity

Most
similar

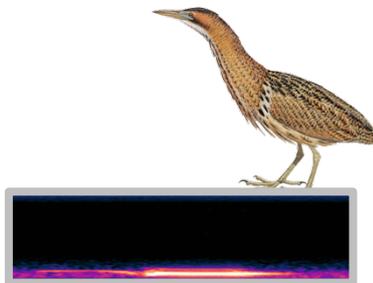
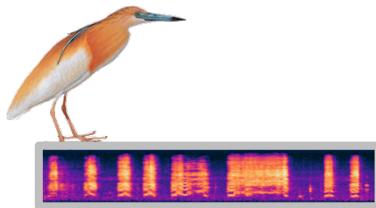


Circus cyaneus
Circus pygargus
2.97

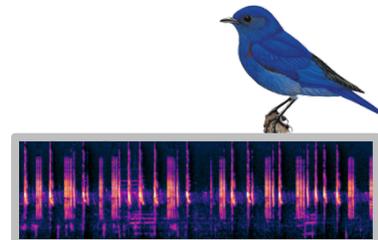
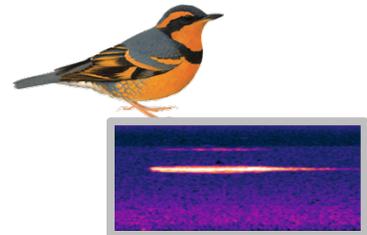


Geothlypis tolmiei
Leiothlypis virginiae
2.23

Most
dissimilar



Ardeola ralloides
Botaurus stellaris
17.1



Ixoreus naevius
Sialia mexicana
13.4

Patristic
distance

Most
similar



Phylloscopus collybita
Phylloscopus ibericus
0.004



Vireo cassinii
Vireo solitarius
0.29

**Most
dissimilar**



Clamator glandarius
Cuculus canorus
88.9



Coccyzus americanus
Geococcyx californianus
104.6

In the full models (without eBird count ratio), morphometric dissimilarity decreased the likelihood of hybridisation across all pairs, passerines and non-passerines in both Europe and North America (Tables 2-7, Figure 7, summarised in Table 8). Similarly, patristic distance decreased the likelihood of hybridisation in all models; more distantly related species are less likely to hybridise (Tables 2-7, Figure 7, summarised in Table 8). Colour and pattern dissimilarity both decreased the likelihood of hybridisation. Colour was a significant negative predictor of hybridisation in all models bar North American passerines and European non-passerines (Table 2, 4, 5 & 6, Figure 7A, 7C, 7D & 7E, summarised in Table 8), while pattern influenced hybridisation in all but European passerines. Species with more disparate vocalisations were less likely to hybridise in models containing all North American pairs and those with North American passerines. Vocalisation dissimilarity did not emerge as a significant predictor in North American non-passerines nor in any European models.

Patristic distance consistently emerged as a significant negative predictor of hybridisation, and genomic divergence reaches a tipping point where hybridisation is just not possible (Figure 9). The maximum value of patristic distance in North American pairs was 104.6 between Yellow-billed Cuckoo (*Coccyzus americanus*) and Greater Roadrunner (*Geococcyx californianus*), in hybridising North American pairs it was 55.5 (Cattle Egret (*Bubulcus ibis*) and Snowy Egret (*Egretta thula*)). In Europe, the maximum value was 88.9 between Great Spotted Cuckoo (*Clamator glandarius*) and Common Cuckoo (*Cuculus canorus*), and the maximum patristic distance for hybridising pairs in Europe was 66.9 in Common Buzzard (*Buteo buteo*) and European Honey Buzzard (*Pernis apivorus*). The minimum North American value was 0.293 (Cassin's Vireo (*Vireo cassinii*) and Blue-headed Vireo (*Vireo solitarius*)), and in Europe it was 0.004 (Common Chiffchaff (*Phylloscopus collybita*) and Iberian Chiffchaff (*Phylloscopus ibericus*))—both of these pairs hybridise.

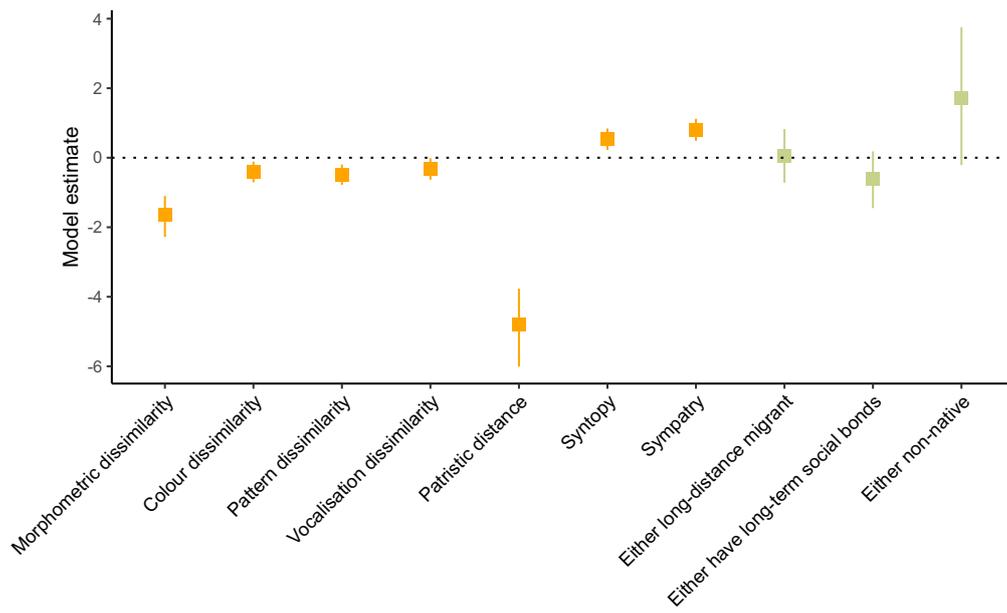
Migratory strategy did not influence hybridisation in any models (Tables 2-7, Figure 7, summarised in Table 8). Social bond length decreased the likelihood of hybridisation in North American passerines, but no other models (Table 2, Figure 7B, summarised in

Table 8). Non-nativeness increased the likelihood of hybridisation in both European and North American non-passerines (Table 4 & 7, Figure 7C & 7F, summarised in Table 8).

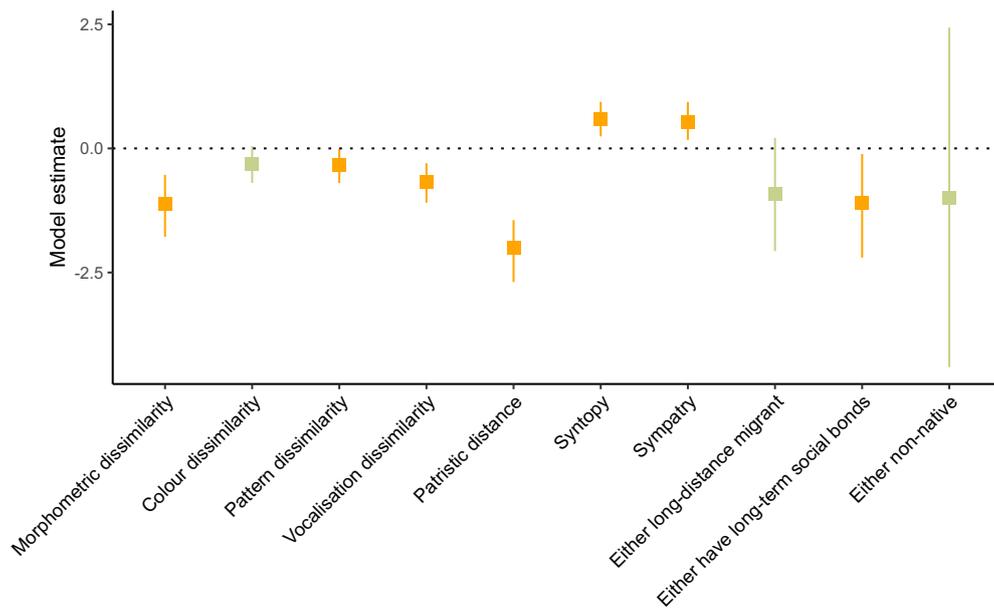
Syntopy increased the likelihood of hybridisation in models including all pairs and passerines but not in non-passerines in both North America and Europe (Table 2, 3, 5 & 6, Figure 7A, 7B, 7D, & 7E, summarised in Table 8). In North American models, sympatry increased the likelihood of hybridisation in those containing all pairs, passerines and non-passerines; this was also the case in Europe, bar passerines (Table 2, 3, 4, 5 & 7, Figure 7A, 7B, 7C, 7D, & 7F, summarised in Table 8).

eBird count ratio was a predictor of hybridisation in only the model containing all North American pairs, the likelihood of hybridisation decreased as the eBird count ratio and the disparity in the estimated number of individuals within the area of overlap increased (Table 8A, Figure 9).

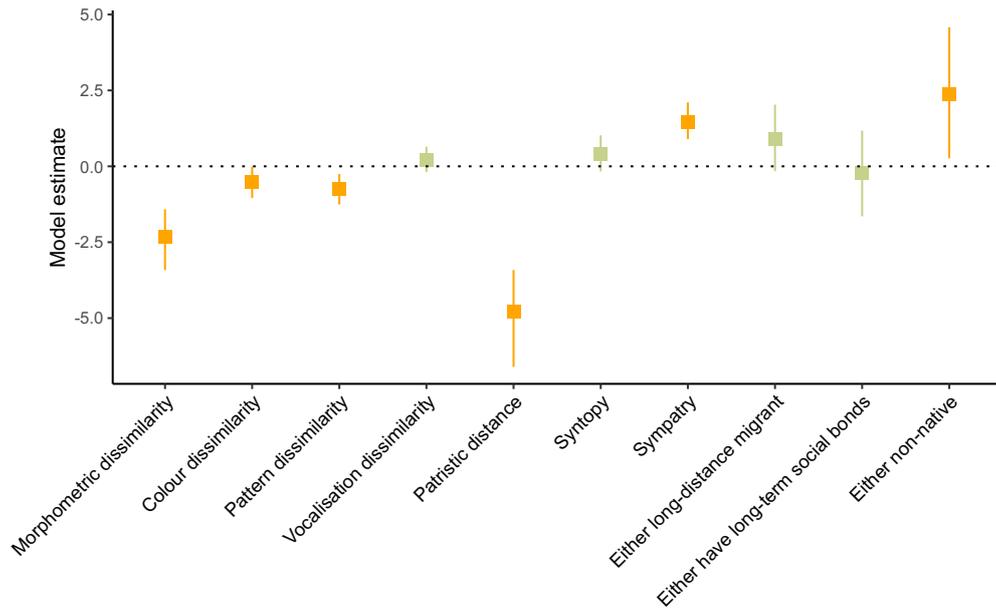
A) North America, all pairs



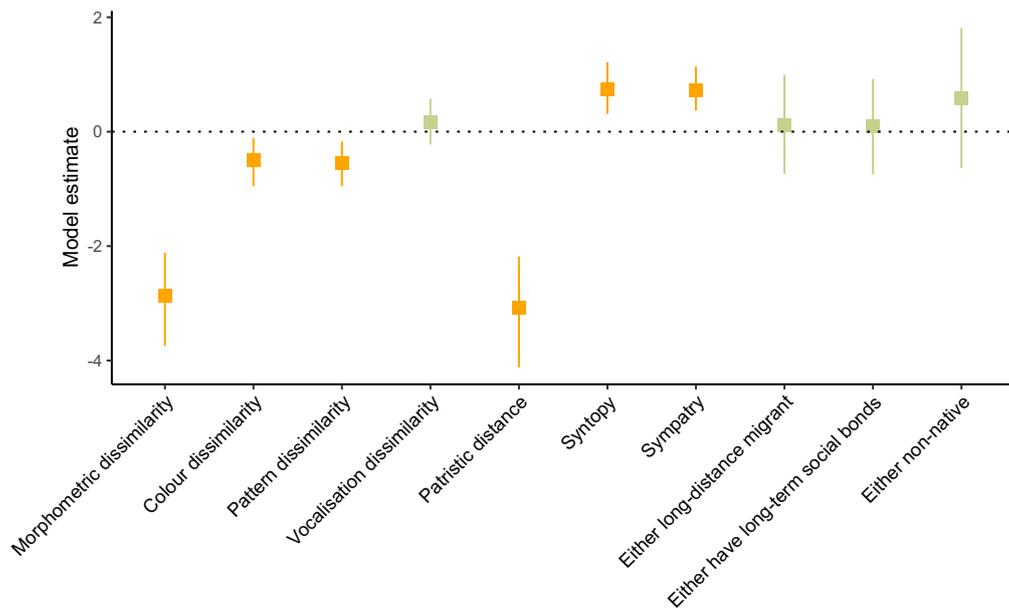
B) North America, passerines



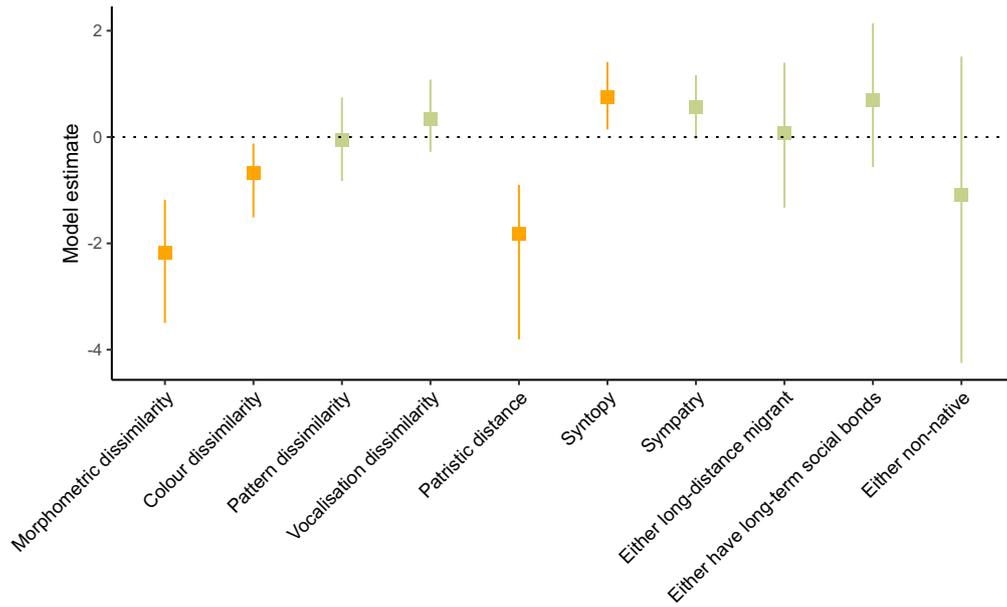
C) North America, non-passerines



D) Europe, all pairs



E) Europe, passerines



F) Europe, non-passerines

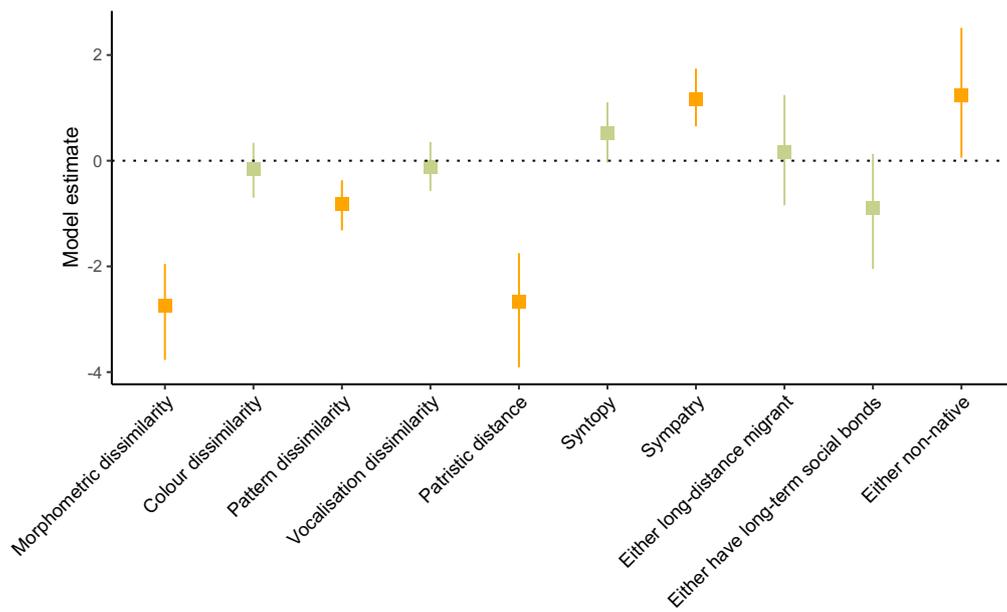


Figure 7: Predictors of hybridisation in North American (A, B, C, n=3339, 2189 and 1150, respectively) and European pairs (D, E, F, n=1647, 522, 1125, respectively). Plotted values are coefficient estimates from phylogenetic generalised linear mixed models with hybridisation as the response variable. Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0.

Table 2. Predictors of hybridisation for North American pairs (both passerines and non-passerines) from phylogenetic generalised linear mixed models (n=3339 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.940 (95% CI = 0.893, 0.969). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
All pairs	Intercept	-0.097	-3.800	3.549	0.989	
	Morphometric dissimilarity	-1.647	-2.278	-1.098	<0.0005	***
	Colour dissimilarity	-0.401	-0.708	-0.113	0.004	**
	Pattern dissimilarity	-0.483	-0.781	-0.197	<0.0005	***
	Vocalisation dissimilarity	-0.320	-0.633	-0.017	0.035	*
	Patristic distance	-4.785	-6.009	-3.768	<0.0005	***
	Syntopy	0.530	0.221	0.841	0.002	**
	Sympatry	0.787	0.489	1.119	<0.0005	***
	Either long-distance migrant	0.048	-0.717	0.825	0.921	
	Either have long-term social bonds	-0.605	-1.448	0.182	0.141	
Either non-native	1.719	-0.212	3.756	0.076		

Table 3. Predictors of hybridisation for North American passerine pairs from phylogenetic linear mixed models (n=2189 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.963 (95% CI = 0.919, 0.986). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Passerines	Intercept	-0.094	-4.201	3.955	0.960	
	Morphometric dissimilarity	-1.116	-1.779	-0.532	<0.0005	***
	Colour dissimilarity	-0.306	-0.696	0.045	0.072	
	Pattern dissimilarity	-0.336	-0.698	-0.010	0.042	*
	Vocalisation dissimilarity	-0.676	-1.093	-0.299	<0.0005	***
	Patristic distance	-2.006	-2.691	-1.446	<0.0005	***
	Syntopy	0.589	0.243	0.938	0.001	**
	Sympatry	0.528	0.174	0.936	0.006	**
	Either long-distance migrant	-0.909	-2.068	0.211	0.100	
	Either have long-term social bonds	-1.094	-2.199	-0.113	0.023	*
Either non-native	-0.988	-4.404	2.434	0.559		

Table 4. Predictors of hybridisation for North American non-passerine pairs from phylogenetic linear mixed models (n=1150 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.890 (95% CI = 0.765, 0.957). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
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Non-passerines	Intercept	-1.726	-5.371	1.871	0.347	
	Morphometric dissimilarity	-2.310	-3.416	-1.416	<0.0005	***
	Colour dissimilarity	-0.502	-1.046	-0.014	0.039	*
	Pattern dissimilarity	-0.732	-1.256	-0.250	0.001	**
	Vocalisation dissimilarity	0.221	-0.188	0.646	0.257	
	Patristic distance	-4.792	-6.606	-3.415	<0.0005	***
	Syntopy	0.414	-0.168	1.021	0.156	
	Sympatry	1.469	0.899	2.104	<0.0005	***
	Either long-distance migrant	0.884	-0.158	2.029	0.101	
	Either have long-term social bonds	-0.208	-1.647	1.175	0.782	
	Either non-native	2.381	0.266	4.574	0.029	*

Table 5. Predictors of hybridisation for European pairs (both passerines and non-passerines) from phylogenetic linear mixed models (n=1647 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.786 (95% CI = 0.023, 0.975). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
All pairs	Intercept	-1.449	-4.787	2.017	0.432	
	Morphometric dissimilarity	-2.872	-3.741	-2.116	<0.0005	***
	Colour dissimilarity	-0.501	-0.952	-0.110	0.010	*
	Pattern dissimilarity	-0.548	-0.954	-0.171	0.008	**
	Vocalisation dissimilarity	0.172	-0.225	0.577	0.391	
	Patristic distance	-3.073	-4.118	-2.183	<0.0005	***
	Syntopy	0.745	0.312	1.212	<0.0005	***
	Sympatry	0.731	0.366	1.137	<0.0005	***
	Either long-distance migrant	0.111	-0.740	0.992	0.776	
	Either have long-term social bonds	0.088	-0.748	0.920	0.825	
	Either non-native	0.577	-0.640	1.814	0.365	

Table 6. Predictors of hybridisation for European passerine pairs from phylogenetic linear mixed models (n=522 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.786 (95% CI = 0.023, 0.975). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Passerines	Intercept	-0.688	-4.759	3.424	0.741	
	Morphometric dissimilarity	-1.973	-3.120	-1.133	<0.0005	***
	Colour dissimilarity	-0.776	-1.568	-0.114	0.028	*
	Pattern dissimilarity	0.093	-0.597	0.807	0.779	
	Vocalisation dissimilarity	0.431	-0.305	1.120	0.212	
	Patristic distance	-1.590	-2.847	-0.856	<0.0005	***
	Syntopy	0.733	0.103	1.445	0.0202	*
	Sympatry	0.479	-0.075	1.165	0.0869	
	Either long-distance migrant	0.034	-1.433	1.487	0.998	
	Either have long-term social bonds	0.916	-0.368	2.233	0.165	
	Either non-native	-1.691	-4.438	1.020	0.225	

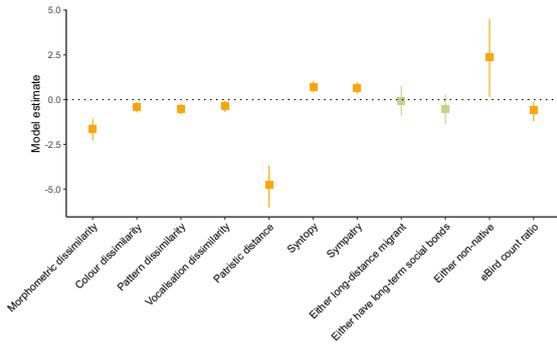
Table 7. Predictors of hybridisation for European non-passerine pairs from phylogenetic linear mixed models (n=1125 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.739 (95% CI = 0.499, 0.897). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Non-passerines	Intercept	-1.949	-5.005	1.452	0.253	
	Morphometric dissimilarity	-2.739	-3.770	-1.954	<0.0005	***
	Colour dissimilarity	-0.160	-0.699	0.340	0.529	
	Pattern dissimilarity	-0.810	-1.317	-0.370	<0.0005	***
	Vocalisation dissimilarity	-0.115	-0.571	0.353	0.582	
	Patristic distance	-2.664	-3.910	-1.749	<0.0005	***
	Syntopy	0.515	-0.033	1.105	0.0697	
	Sympatry	1.164	0.650	1.741	<0.0005	***
	Either long-distance migrant	0.171	-0.844	1.243	0.756	
	Either have long-term social bonds	-0.902	-2.049	0.129	0.082	
	Either non-native	1.234	0.058	2.514	0.048	*

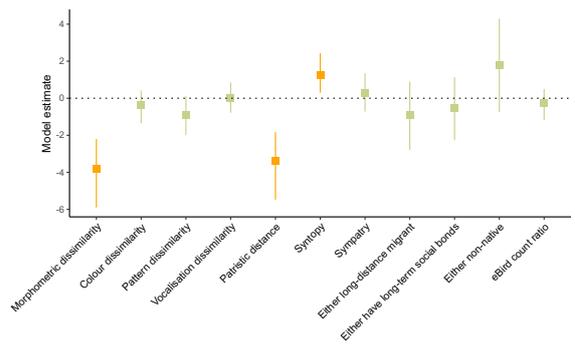
Table 8. Summary of trends from phylogenetic generalised linear mixed models with hybridisation as a response variable for North American and European pairs. Orange/green cells represent statistically significant results (pMCMC <0.05), and the colour and number of arrows indicates significance level. Dark orange/green (3 arrows) pMCMC <0.0005, mid-orange/green (2 arrows) pMCMC <0.001, light orange/green (1 arrow) pMCMC <0.05. Arrows indicate direction of effect, upward arrows (\uparrow) indicate the variable increases the likelihood of hybridisation. Downward arrows (\downarrow) indicate the variable decreases the likelihood of hybridisation.

Variable	North America			Europe		
	All	Passerine	Non-passerine	All	Passerine	Non-passerine
Morphometric dissimilarity	↓↓↓	↓↓↓	↓↓↓	↓↓↓	↓↓↓	↓↓↓
Colour dissimilarity	↓↓		↓	↓	↓	
Pattern dissimilarity	↓↓↓	↓	↓↓	↓		↓↓↓
Vocalisation dissimilarity	↓	↓↓↓				
Patristic distance	↓↓↓	↓↓↓	↓↓↓	↓↓	↓↓↓	↓↓↓
Syntopy	↑↑	↑↑		↑↑↑	↑	
Sympatry	↑↑↑	↑↑	↑↑↑	↑↑↑		↑↑↑
Either long-distance migrant						
Either have long-term social bonds		↓				
Either non-native			↑			↑

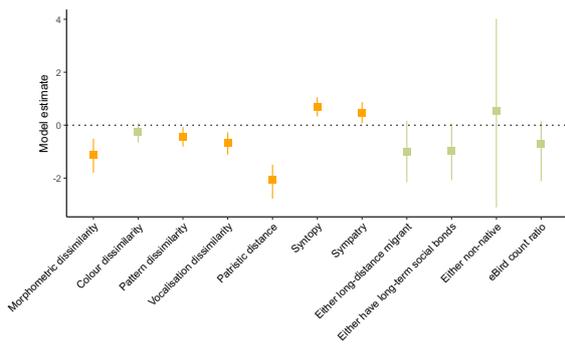
A) North America, all pairs, with eBird count ratios



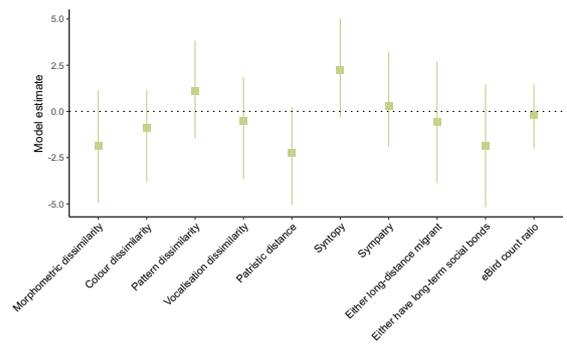
D) Europe, all pairs, with eBird count ratios



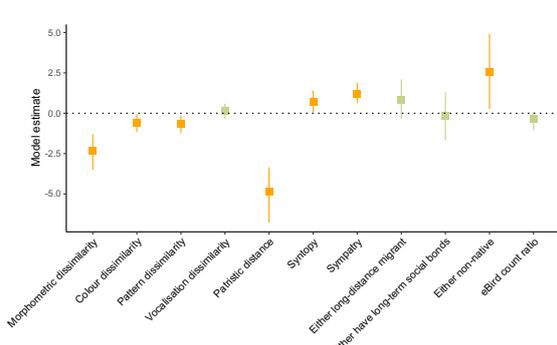
B) North America, passerines, with eBird count ratios



E) Europe, passerines, with eBird count ratios



C) North America, non-passerines, with eBird count ratios



F) Europe, non-passerines, with eBird count ratios

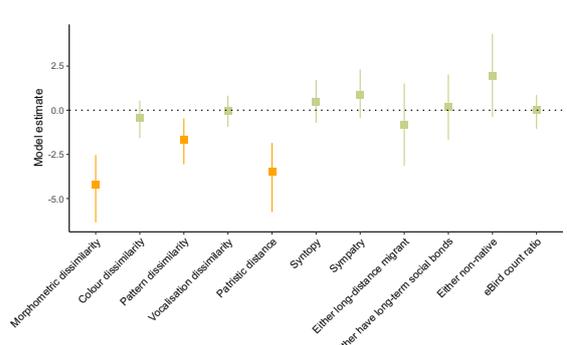


Figure 8: Predictors of Hybridisation in North American (A, B, C, n=3039, 1023 and 2016, respectively) and European pairs (D, E, F, n=243, 53, 190, respectively) subset to those with data for eBird count ratios. In the European passerine model (E) there were no pairs containing non-natives, as such, that variable was removed from models. Plotted values are coefficient estimates from a phylogenetic generalised linear mixed models with hybridisation as the response variable. Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0.

Table 9. Predictors of hybridisation for North American pairs (both passerines and non-passerines), with eBird count ratio data, from phylogenetic linear mixed models (n=3039 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.936 (95% CI = 0.883, 0.969). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
All pairs	Intercept	-0.085	-3.828	3.608	0.957	
	Morphometric dissimilarity	-1.631	-2.291	-1.057	<0.0005	***
	Colour dissimilarity	-0.395	-0.722	-0.106	0.010	*
	Pattern dissimilarity	-0.505	-0.823	-0.211	<0.0005	***
	Vocalisation dissimilarity	-0.364	-0.698	-0.052	0.025	*
	Patristic distance	-4.740	-6.024	-3.696	<0.0005	***
	Syntopy	0.700	0.393	-1.040	<0.0005	***
	Sympatry	0.625	0.314	0.974	<0.0005	***
	Either long-distance migrant	-0.082	-0.888	0.762	0.819	
	Either have long-term social bonds	-0.511	-1.359	0.289	0.201	
	Either non-native	-2.365	0.147	4.511	0.036	*
	eBird count ratio	-0.579	-1.224	-0.117	0.009	**

Table 10. Predictors of hybridisation for North American passerine pairs, with eBird count ratio data, from phylogenetic linear mixed models (n=1023 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.955 (95% CI = 0.900, 0.983). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Passerines	Intercept	-0.149	-4.070	3.856	0.959	
	Morphometric dissimilarity	-1.123	-1.794	-0.513	<0.0005	***
	Colour dissimilarity	-0.266	-0.654	0.076	0.132	
	Pattern dissimilarity	-0.425	-0.805	-0.076	0.015	*
	Vocalisation dissimilarity	-0.659	-1.105	0.269	<0.0005	***
	Patristic distance	-2.055	-2.774	-1.493	<0.0005	***
	Syntopy	0.687	0.334	1.052	<0.0005	***
	Sympatry	0.453	0.072	0.866	0.018	*
	Either long-distance migrant	-0.990	-2.153	0.162	0.105	
	Either have long-term social bonds	-0.972	-2.077	0.059	0.070	
	Either non-native	0.528	-3.105	4.013	0.759	
	eBird count ratio	-0.693	-2.114	0.152	0.133	

Table 11. Predictors of hybridisation for North American non-passerine pairs, with eBird count ratio data, from phylogenetic linear mixed models (n=2016 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.887 (95% CI = 0.729, 0.963). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
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Non-passerines	Intercept	-1.733	-5.255	1.928	0.359	
	Morphometric dissimilarity	-2.296	-3.506	-1.307	<0.0005	***
	Colour dissimilarity	-0.573	-1.171	-0.053	0.032	*
	Pattern dissimilarity	-0.665	-1.230	-0.142	0.008	**
	Vocalisation dissimilarity	0.127	-0.355	0.590	0.575	
	Patristic distance	-4.831	-6.760	-3.356	<0.0005	***
	Syntopy	0.704	0.071	1.398	0.030	*
	Sympatry	1.217	0.615	1.889	<0.0005	***
	Either long-distance migrant	0.836	-0.353	2.087	0.148	
	Either have long-term social bonds	-0.165	-1.665	1.298	0.822	
	Either non-native	2.533	0.265	4.917	0.033	*
	eBird count ratio	-0.352	-1.042	0.090	0.156	

Table 12. Predictors of hybridisation for European pairs (both passerines and non-passerines), with eBird count ratio data, from phylogenetic linear mixed models (n=243 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.796 (95% CI = 0.345, 0.968). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
All pairs	Intercept	-0.797	-4.202	2.802	0.618	
	Morphometric dissimilarity	-3.811	-5.896	-2.199	<0.0005	***
	Colour dissimilarity	-0.393	-1.352	0.424	0.339	
	Pattern dissimilarity	-0.881	-1.988	0.112	0.074	
	Vocalisation dissimilarity	0.028	-0.783	0.855	0.922	
	Patristic distance	-3.400	-5.478	-1.830	<0.0005	***
	Syntopy	1.261	0.299	2.435	0.013	*
	Sympatry	0.300	-0.718	1.344	0.542	
	Either long-distance migrant	-0.909	2.789	0.901	0.316	
	Either have long-term social bonds	0.502	-2.263	1.123	0.537	
	Either non-native	1.767	-0.749	4.284	0.157	
	eBird count ratio	-0.243	-1.186	0.499	0.548	

Table 13. Predictors of hybridisation for European passerine pairs, with eBird count ratio data, from phylogenetic linear mixed models (n=53 species pairs). There were no European passerine pairs containing non-native species and as such the variable was removed from models. The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.208 (95% CI = 0.00002, 0.981). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Passerines	Intercept	-0.707	-4.173	2.957	0.700	
	Morphometric dissimilarity	-1.859	-4.916	1.143	0.220	
	Colour dissimilarity	-0.880	-3.798	1.164	0.422	

Pattern dissimilarity	1.131	-1.456	3.825	0.351
Vocalisation dissimilarity	-0.501	-3.682	1.865	0.682
Patristic distance	-2.254	-5.051	0.230	0.094
Syntopy	2.230	-0.321	5.004	0.087
Sympatry	0.289	-1.888	3.190	0.776
Either long-distance migrant	-0.542	-3.885	2.691	0.756
Either have long-term social bonds	-1.852	-5.188	1.457	0.272
eBird count ratio	-0.206	-1.994	1.459	0.768

Table 14. Predictors of hybridisation for European non-passerine pairs, with eBird count ratio data, from phylogenetic linear mixed models (n=190 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.696 (95% CI = 0.001, 0.967). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Non-passerines	Intercept	-2.297	-5.832	1.757	0.265	
	Morphometric dissimilarity	-4.201	-6.352	-2.536	<0.0005	***
	Colour dissimilarity	-0.421	-1.579	0.544	0.387	
	Pattern dissimilarity	-1.693	-3.065	-0.464	0.009	**
	Vocalisation dissimilarity	-0.010	-0.939	0.821	0.938	
	Patristic distance	-3.476	-5.772	-1.856	<0.0005	***
	Syntopy	0.473	-0.712	1.712	0.434	
	Sympatry	0.857	-0.437	2.313	0.193	
	Either long-distance migrant	-0.830	-3.152	1.512	0.497	
	Either have long-term social bonds	0.172	-1.674	2.026	0.854	
	Either non-native	1.928	-0.386	4.324	0.104	
eBird count ratio	-0.001	-1.056	0.864	0.992		

Table 15. Convex hull volume in PC space for all pairs, passerines and non-passerines in North America and Europe. Convex hull volume is given for metrics that utilise Euclidean distances. PCA were conducted separately between continents, so plots are not directly comparable.

	North America			Europe		
	All pairs	Passerine	Non-passerine	All pairs	Passerine	Non-passerine
Morphometric	130.3	16.2	128.6	87.26	16.3	80.1
Pattern	713.2	297.8	705.9	576.2	250.4	530.6
Vocalisation	2082.9	1018.4	846.0	2123.6	1048.9	1718.2

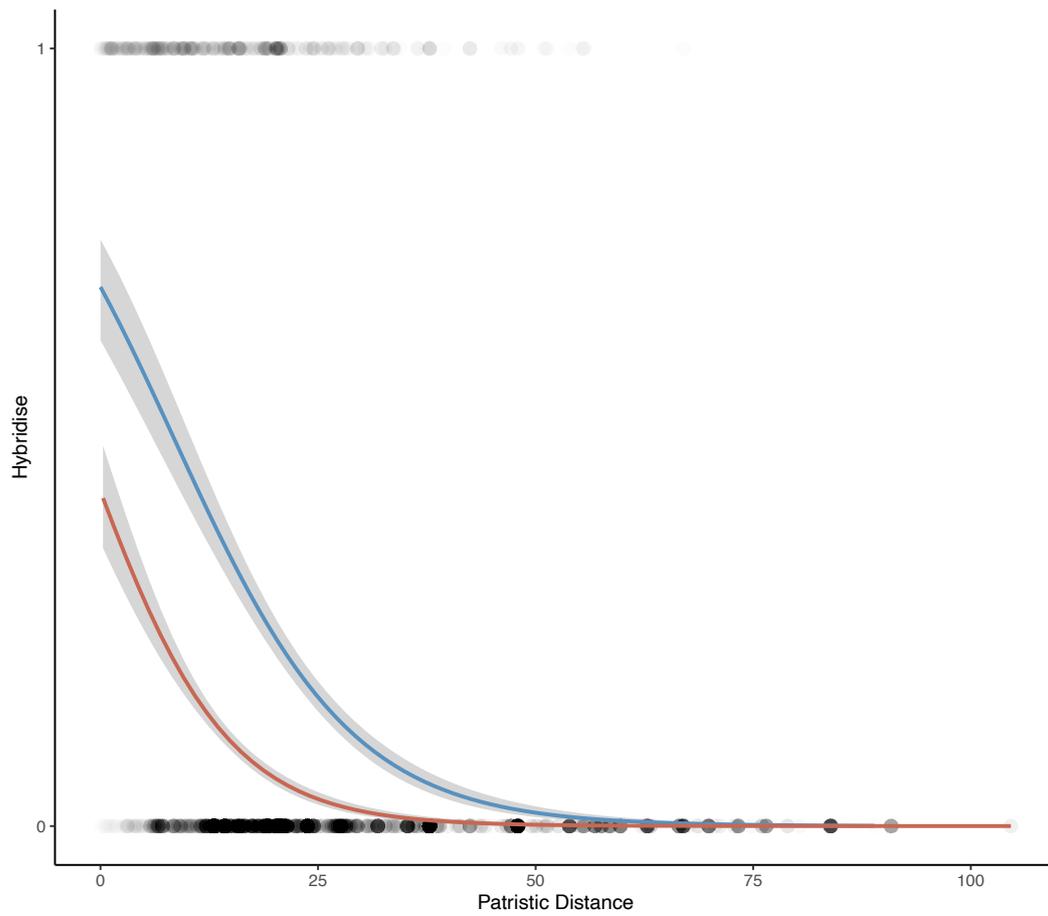


Figure 9. The relationship between patristic distance and hybridisation in European (blue line) (n=2203) and North American pairs (red line) (n=3647).

2.4 Discussion

We find strong evidence to suggest species similarity is an important driver of hybridisation, lending support for the mistaken identity hypothesis (Grant and Grant, 1997; Qvarnström *et al.*, 2006, 2023; Rosenthal, 2013; Willis, Symula and Lovette, 2014; Devarajan, Morelli and Tenan, 2020). We found that the likelihood of hybridisation decreases as species pairs become more dissimilar in several important species and mate recognition traits, including morphology, colour, pattern and vocalisations. Similarly, as species become more distantly related (i.e., patristic distance increases), they are less likely to hybridise (Johnsgard, 1960; Tubaro and Lijtmaer, 2002). As a result of phylogenetic conservatism, distantly related species are more phenotypically, perceptually and behaviourally different (De Kort and Ten Cate, 2001; Wiens and Graham, 2005) and are also likely to have stronger pre- and post-mating reproductive barriers due to greater divergence times (Coyne and Orr, 1989; Price, 2008).

Morphometric dissimilarity had a consistently strong negative effect on the likelihood of hybridisation in both passerines and non-passerines, and on both continents. While errors in mate recognition are less likely in dissimilar species, there must also come a point at which species become so different in shape and size that mating is physically impossible (Karl, Bowen and Avise, 1995). In North American passerines, colour dissimilarity was not a significant predictor of hybridisation, but it reduced the likelihood of hybridisation in non-passerines, whereas vocalisation dissimilarity reduced the likelihood of hybridisation in passerines but not non-passerines. These results may imply a differing role of vocal and visual stimuli in mate selection and species recognition between passerines and non-passerines.

Patristic distance consistently reduced the likelihood of hybridisation in our models. Given pairs are confamilial, this supports the hypothesis that genomic divergence reaches a critical threshold after which hybridisation is not possible, and post-zygotic isolation is complete. For hybridisation to occur, species must not only bypass prezygotic isolating mechanisms in species and mate recognition, but also intrinsic postzygotic isolating mechanisms such as Dobzhansky-Muller incompatibilities

(Dobzhansky, 1936; Muller, 1942). These incompatibilities accumulate during allopatric speciation as species diverge, and genetic substitutions occur. In the parental species, natural selection allows only benign or beneficial substitutions to persist. However, these substitutions can be deleterious when brought together in a hybrid zygote and result in inviability or sterility, reinforcing isolating mechanisms and the speciation process (Dobzhansky, 1936; Muller, 1942). Hybridisation occurs most frequently within genera and often between sister species (Gholamhosseini *et al.*, 2013). Intergeneric hybridisation also occurs, although less frequently. Intergeneric hybridisation has been reported among North American Parulid warblers (Toews *et al.*, 2020), birds of paradise (Thörn *et al.*, 2024), parrots (Hernández-Brito *et al.*, 2021) and *Fulica coots* and *Gallinula moorhens* in both North America and Europe (Rodriguez, Curbelo and Carrasco, 2010; Erickson and Rottenborn, 2020). To our knowledge, there are no records of wild interfamilial hybridisation. Even in captivity, hybridisation between families is exceptionally rare and has only occurred between Domestic Chickens (*Gallus gallus domesticus*) (Phasianidae) and Helmeted Guineafowl (*Numida meleagris*) (Numididae), and Helmeted Guineafowl and Indian Peafowl (*Pavo cristatus*) (Phasianidae) (Hanebrink, Gruver and Van Grouw, 1973). Chickens and guineafowl diverged approximately 47 million years ago, so it is remarkable that hybridisation is possible (Alfieri *et al.*, 2023).

Here we demonstrate that species with greater range (sympatry) and habitat (syntopy) overlap are more likely to hybridise, likely due to increased mating opportunities through greater heterospecific encounter rates (Willis, Symula and Lovette, 2014). However, in 65 Western Palearctic pairs, Randler (2002) found the number of recorded individual hybrids (rather than the likelihood of hybridisation) to be lower in sympatric pairs than those in parapatry (although sympatry was coded as a binary variable, rather than a quantitative measure of overlap as in our analyses). Parapatric pairs may be more likely to hybridise through Hubbs' principle as population densities and abundances are lower at range edges (Worm *et al.*, 2019). Alternatively, hybridisation may be more frequent in parapatry as reproductive isolation is incomplete among parapatric pairs that have recently come into secondary contact (Weir and Price, 2011b). In both North America and Europe, we found that higher syntopy increased the

likelihood of hybridisation in passerines but not in non-passerines, whereas sympatry increased the likelihood of hybridisation in both European and North American non-passerines but did not influence hybridisation in European passerines. The reason for this disparity in the effect of overlap at different spatial scales between passerines and non-passerines is unknown.

Long-term social bonds decreased the likelihood of hybridisation in North American passerines. This may suggest that birds likely to suffer fitness consequences over multiple breeding seasons if paired with a heterospecific may be more cautious during the mate selection process than those which may only suffer those consequences over a single season (Leighton *et al.*, 2021). Perhaps species with long-term bonds can assess mates on multiple occasions and have more opportunities to discover the heterospecific identity of their mate. Therefore, the likelihood of mate choice errors is lower in comparison to those that have no social bonds and mate with multiple individuals only once (Leighton *et al.*, 2021). Why this result only holds for North American passerines, as opposed to non-passerines, all pairs, or European species, is not known.

Migratory strategy was included in models under the assumption that pairs containing migratory species would be more likely to hybridise than residents, as when migrants arrive on breeding grounds, they have less time to assess mates compared to residents that will have started pair bonding earlier in the season (Grist *et al.*, 2017; Leighton *et al.*, 2021). However, unlike the findings of Leighton *et al.*, (2021), we found no evidence in any of our models for the impact of migratory strategy on the likelihood of hybridisation. That said, our two studies do fundamentally differ; we utilise species pair analyses, and we are therefore modelling the likelihood of hybridisation among specific species combinations. We have identified the predictors that cause specific species to hybridise with specific sets of other species, as opposed to what causes individual species to hybridise generally and with how many other species. As such, it is unsurprising that our results and conclusions differ somewhat.

Non-nativeness was included as a predictor in our analyses to understand if non-native species were inherently predisposed to hybridise, which is of particular importance given the context of this research and the potential negative impacts of hybridisation on native species. That said, hybridisation involving non-native species is not always between a native and a non-native. House (*Passer domesticus*) and European Tree Sparrows (*P. montanus*) hybridise in their introduced North American range. Species in their introduced range may be at much lower abundances than native species, which may lead to hybridisation through Hubbs' principle (Blackburn, Lockwood and Cassey, 2009). However, this may not always be the case, as many non-native species become invasive and their abundance and distribution increase rapidly (Linz, Johnson and Thiele, 2017). In those instances, the non-native species may not be the rare pair-member; it may outnumber the native by some considerable margin, especially if the other species is already rare, and hybridisation may result (Wallis, 1999; Muñoz-Fuentes *et al.*, 2007). Alternately, since coming into anthropogenically-mediated secondary contact in the last few centuries, closely related and previously allopatric species may not have had the time to sufficiently diverge in their perceptual species and mate recognition mechanisms and pre- and post-zygotic reproductive barriers (Coyne and Orr, 1989). We found that non-nativeness increased the likelihood of hybridisation in non-passerines only. Exactly why this is the case is unknown. Of the 356 European pairs containing at least one non-native, only 21 are passerines, of which only two hybridise. Of the 166 North American non-native pairs, only 11 pairs are passerines, and only one of those hybridises (House and European Tree Sparrow). In Europe, 82% (294) of non-native pairs are anseriforms, 20% of which hybridise. Wildfowl are renowned for their propensity to hybridise (Johnsgard, 1960; Tubaro and Lijtmaer, 2002), as a result of genetic and behavioural factors, such as interspecific brood amalgamation (Randler, 2005), which we are unable to control for in our models and therefore may be responsible for non-nativeness emerging as a significant predictor of hybridisation in non-passerines.

Contrary to the predictions of Hubbs' principle (Hubbs, 1955), we found that as the disparity in the estimated counts of a species pair within their area of overlap (eBird count ratio) increased, the likelihood of hybridisation decreased. However, this was only

the case for North American models with both passerines and non-passerines. While Hubbs' principle may be responsible for hybridisation in some cases (Hubbs, 1955; Rohwer, 1972; Brodsky and Weatherhead, 1984; Grant and Grant, 1997; Nuechterlein and Buitron, 1998; Wallis, 1999; Wirtz, 1999; McCracken and Wilson, 2011; Duckworth *et al.*, 2017b), it is certainly not always responsible, and hybridisation does occur between species with similar abundances (Grant and Grant, 1997; Randler, 2006; Qvarnström *et al.*, 2023). Furthermore, disparities in abundance may not always result in hybridisation. For example, at an individual level, if the rarer species is a male (i.e., the 'chosen' sex), females of the common species will still be more likely to mate with conspecific males as they are readily available, rather than the rarer heterospecific (Wirtz, 1999). If the rarer species were a female, however, and there is a shortage of conspecific males, hybridisation may be more likely as there would still be a fitness advantage to mating heterospecifically compared to not at all (Baker, 1996; Wirtz, 1999). While a greater abundance disparity may increase hybridisation in some cases through Hubbs' principle (McCracken and Wilson, 2011), there may be a threshold at which encounter rates between the two species become low enough to decrease the likelihood of hybridisation (Qvarnström *et al.*, 2023), which may explain why we find opposing evidence to Hubbs' principle.

It should be noted that Hubbs' principle and mistaken identity are unlikely to be mutually exclusive within species. One hybrid pairing between two species may result from Hubbs' principle, while another pairing of the same species may be due to mistaken identity. In addition, the likelihood of mistaken identity is likely to be more constant between species, inasmuch as species traits are consistently dissimilar from one another (to a certain degree). Hubbs' principle, however, appears to be more context-dependent and variable (Nuechterlein and Buitron, 1998). Species abundance may vary spatially between habitats (Vallin *et al.*, 2012), across species' ranges (Sexton, 2024), temporally throughout the breeding season (Nuechterlein and Buitron, 1998), successionaly (Duckworth and Semenov, 2017), or with varying degrees of anthropogenic pressure (Hubbard *et al.*, 1992). As such, phylogenetic comparative methods may not be the most suitable analyses to test for the impact of Hubbs' principle on the likelihood of hybridisation at a species-pair level.

To conclude, we present the first study of its kind and scale that utilises phylogenetic linear mixed models in a species pair framework to determine the predictors of hybridisation in North American and European birds. We find overwhelming, multifaceted evidence that species similarity and relatedness influence the likelihood of hybridisation. Species pairs that differ more in morphology, colour, pattern, song, and relatedness are less likely to hybridise, all of which lend support for the role of mistaken identity in avian hybridisation. We also found opposing evidence for the effect of Hubbs' principle on hybridisation. These findings further our knowledge of avian hybridisation and facilitate future research on the topic.

2.5 Acknowledgements

I am extremely grateful to Leonard Davis, Maya Solly and Ted Poulett for their assistance preparing vocalisation data. Many thanks to those who have carried out North American Breeding Bird and Pan-European Common Bird Monitoring Scheme surveys (a full list of PECBMS regional coordinators can be found in the appendix), uploaded their observations to eBird, and recordings to xeno-canto and the Macauley Library.

Chapter 3

A comparison of the predictive performance of Random Forests and Phylogenetic Linear Mixed models when predicting hybridisation

3.1 Introduction

Species interactions are often transient and ephemeral. However, they play a key role in a multitude of ecological and evolutionary frameworks and are vital to our understanding of how species will respond to global changes. Comprehensive descriptions of species interactions and behaviours are lacking in the literature, particularly for species outside North America and Europe. Documenting species interactions, such as interspecific territoriality, often requires extensive field observations and experiments (e.g., Robinson and Terborgh, 1995; Jankowski, Robinson and Levey, 2010; Vallin *et al.*, 2012), which are not feasible for every species. As such, there is a need to be able to predict the likelihood of interactions between species. Developing methods to predict species interactions is not only important to fill current knowledge gaps for understudied species, but could also be useful to predict interactions between species that do not currently coexist but may do so in the future through climate-mediated range shifts or introduction to non-native areas. These interactions could be territorial, predatory, parasitic, or reproductive. However, this chapter will focus solely on hybridisation.

In the context of conservation, hybridisation can be problematic, particularly when one or both hybridising species are rare (Rhymer and Simberloff, 1996; Simberloff, 1996). In fact, this rarity may be somewhat responsible for hybridisation in some cases (Hubbs, 1955, but see Chapter 2). Hybridisation can lead to 'erosion' of the genome, genetic swamping and hybrid swarms (Rhymer and Simberloff, 1996; Todesco *et al.*, 2016; Wells *et al.*, 2019), and when species are on the brink of extinction, could prevent recovery and drive them towards extinction (Rhymer and Simberloff, 1996; Wallis, 1999; Wolf, Takebayashi and Rieseberg, 2001; Muñoz-Fuentes *et al.*, 2007). As such, being able to predict hybridisation before it occurs has important conservation ramifications.

Hybridisation has occurred naturally, long before humans began altering the biosphere (Lavretsky *et al.*, 2021). When species come into secondary contact following allopatric speciation and reproductive isolation is incomplete, hybridisation can occur and can either lead to reinforcement of species boundaries or species collapse (Price, 2008;

Fuchs *et al.*, 2013; Ottenburghs *et al.*, 2017). As a result of the near ubiquity of anthropogenic impacts, it is becoming increasingly difficult to determine which hybridisation events we are responsible for, either directly or indirectly, and which have occurred naturally. For example, Pied Stilts (*Himantopus leucocephalus*) colonised New Zealand from Australia during the 19th century and hybridise with Black Stilts (*H. novaeseelandiae*) (Wallis, 1999), which, at first, may seem to be a natural phenomenon. However, the expansion and establishment of Pied Stilts in New Zealand was likely facilitated by widespread deforestation, modification of rivers, and creation of wetland habitats suitable for generalists adapted to the presence of mammalian predators (Pierce, 1984). However, these same factors are responsible for the range contraction of Black Stilts, a predator-naïve specialist of braided river channels (Pierce, 1984). This subsequent decline in Black Stilts may, in turn, increase the likelihood of hybridisation through Hubbs' principle, as conspecific mates become harder to find (Hubbs, 1955). Hybridisation also occurs when species come into contact for the first time due to direct anthropogenic introduction to non-native areas (Simberloff, 1996). Several conservation interventions have attempted to limit the hybridisation of rare natives with non-natives. White-headed Ducks (*Oxyura leucocephala*) are extinct as a breeder in Europe, bar a small population in Spain, where they are threatened by competition and hybridisation, among other threats, with Ruddy Ducks (*O. jamaicensis*) (Muñoz-Fuentes *et al.*, 2007; Robertson *et al.*, 2015). Ruddy Ducks became established in the United Kingdom following introduction from North America in the 1950s and subsequently spread across Europe (Robertson *et al.*, 2015). Eradication efforts in Spain, France, Belgium and the United Kingdom have been largely successful, with numbers of Ruddy Ducks across Europe a fraction of what they were in 2000, and consequently, the incidence of hybridisation has diminished significantly (Muñoz-Fuentes *et al.*, 2007; Robertson *et al.*, 2015). Being able to predict which species are likely to hybridise with one another before it occurs may allow preparations to be put into place before introduction, colonisation or hybridisation and could expedite the conservation process, saving valuable time. Had the threat to White-headed Ducks from hybridisation been predicted, attempts could have been made to prevent the establishment of Ruddy Duck, and culling could have begun earlier. We consider this

research a first step towards this predictive and proactive conservation goal and a useful proof of concept.

A variety of modelling approaches can be used to predict the presence of unsampled species interactions or networks, such as plant-pollinator (Pichler *et al.*, 2020; Peralta *et al.*, 2024), seed-dispersal (Papadogeorgou *et al.*, 2023), parasite-host (Dallas, Park and Drake, 2017), predator-prey (Strydom *et al.*, 2022) and in this case, reproductive interactions. These include generalised linear models (GLMs), latent variable approaches (Ovaskainen *et al.*, 2016; Strydom *et al.*, 2022) and machine learning models such as K-nearest neighbour algorithms, decision trees and random forests, boosted regression trees, deep and convolutional neural networks (Desjardins-Proulx *et al.*, 2017; Pichler *et al.*, 2020). Each has advantages and drawbacks but, in this instance, we chose to utilise and compare the performance of two approaches for predicting hybridising species: We made use of predictions from Phylogenetic Linear Mixed Models (PLMMs), and Random Forest (RFs) machine learning algorithms trained on North American species pairs to predict the likelihood of hybridisation between European pairs, following the approach developed for interaction networks by Strydom *et al.* 2022. RFs and PLMMs were chosen primarily for their flexibility and ability to deal with both categorical and continuous data simultaneously. PLMMs utilise Markov Chain Monte Carlo (MCMC) sampling in a Bayesian framework and account for the phylogenetic relationships within the data (Hadfield, 2010). While RFs do not directly incorporate phylogenies or random effect structures, they often have greater accuracy than other modelling techniques (Cutler *et al.*, 2007; Pichler *et al.*, 2020). The predictive abilities of these models are also likely to provide some insight into the specificity of the variables and traits that influence hybridisation. For example, if models trained on North American pairs can predict European hybridisation well, it suggests there are general principles that transcend continental boundaries and influence hybridisation at a global scale. However, if predictions are poor, it may be more indicative that the variables that cause hybridisation are more localised and context-dependent.

To illustrate the potential uses of this predictive modelling framework, we predict the likelihood of hybridisation for North American and European species pairs that are

projected to coexist in the future and create maps of potential future hybridisation hotspots.

3.2 Methods

3.2.1 Comparing predictive performance

To assess the predictive abilities of RFs and PLMMs, we first collated species lists for both North America and Europe, as detailed in Chapter 2. These lists of species pairs for North America and Europe contained 310 and 323 hybridising pairs, and 3337 and 1880 potentially but non-hybridising pairs, respectively. Using both RFs and PLMMs, we made predictions of European hybridisation using models trained on North American data. The predictor variables used to generate models that formed the basis for prediction (see Chapter 2) included: morphometric dissimilarity, colour dissimilarity, pattern dissimilarity, vocalisation dissimilarity, patristic distance, eBird syntopy and sympatry, migratory strategy and social bond length. We are not able to calculate syntopy nor sympatry for species pairs that currently do not exist, and as such, we ran two separate sets of models (see Table 1): one set including syntopy and sympatry and one set without. For each of those sets, we fit models on passerine pairs only, non-passerine pairs only, and passerine and non-passerine pairs combined. Syntopy and sympatry were included in some models to determine if their inclusion improved model performance. If performance improvements were substantial, efforts could be made to calculate predicted measures of future syntopy and sympatry, perhaps using species distribution models (Bewick *et al.*, 2014). Species pairs lacking syntopy, sympatry, and vocalisation data were removed from analyses that included those predictors (for sample sizes, see Table 2).

Table 1. Predictor variables included in Random Forests (RFs) and Phylogenetic Linear Mixed Models (PLMMs) to predict European hybridisation. Models were run on passerine pairs only, non-passerine pairs only and passerines and non-passerines combined.

Model	Predictor variables
Full model	Morphometric dissimilarity, colour dissimilarity, pattern dissimilarity, vocalisation dissimilarity, patristic distance, migratory strategy, social bond length, syntopy and sympatry.
No Synt, No Symp	All of the above, minus syntopy and sympatry.

To make PLMM predictions, we utilised the same modelling methodology from Chapter 2. These models were run on North American pairs with 4 chains for 2 million iterations each, with a burn-in of 20000 and a thinning interval of 1000 using the R package MCMCglmm (Hadfield, 2010). We then used the predict() function and the North American-trained PLMMs to predict European hybridisation using the corresponding European data.

RF predictions were made using the tidymodels package (Kuhn and Wickham, 2020). North American data were split into training and testing groups (80% training, 20% testing) using randomised stratified sampling to keep the proportion of hybridising and non-hybridising pairs in each group representative of the whole dataset (<10% hybridising and >90% non-hybridising). Testing and training groups did not contain the same pairs in each of the three model sets. The hyperparameters mtry (the number of predictors randomly sampled at each split in each decision tree) and ntrees (the number of decision trees) were tuned to find the optimal model configuration, optimal hyperparameters varied between model groups (TABLE 3). Six possible values for mtry (2-7) and six for ntrees (500, 1000, 5000, 10000, 50000, 100000) were tested in 36 combinations. For each combination of hyperparameters, the model is trained and evaluated repeatedly using 3-fold cross-validation, with training being carried out on two folds and testing on the third. ROC AUC measures how well the model separates hybrids from non-hybrids. The optimal model is that which uses the hyperparameters that give the highest ROC AUC value across cross-validation folds. The optimal model is then tested on the original test set from the initial split to provide an estimate of model performance on unseen data. The optimal model was then used to predict European hybridisation for each group. A hybridisation probability value was calculated for each species pair, and if it was greater than 0.5 (i.e., a pair were more likely to hybridise than not), they were considered to have been predicted to hybridise.

For both PLMM and RF predictions, confusion matrices and the corresponding number of false positives, false negatives, true positives and true negatives were used to

calculate measures of accuracy, precision, sensitivity, specificity and an F1 score that could be compared between methods and model groups. Accuracy corresponds to the overall correctness of the model (Equation 1). Precision is the proportion of predicted hybrid pairs that do actually hybridise (Equation 2). Sensitivity is the ability of the model to correctly predict hybrids when they do hybridise, i.e., how many of the actual hybrid pairs were correctly identified as such (Equation 3). Specificity is the model's ability to correctly predict non-hybrids that do not actually hybridise (Equation 4) and finally, the F1 score is the balance between how many pairs predicted to hybridise actually do so (precision) and how many of the actually hybridising pairs were predicted to do so (sensitivity) (Equation 5), which is of particular importance for imbalanced data (Sasaki, 2007; Wardhani *et al.*, 2019; Kamalov, Thabtah and Leung, 2023). If F1 is high, the model is accurately identifying hybridising pairs and not missing many hybrids. If precision is high but sensitivity is low, the F1 score will be lower, suggesting the model is cautious, under-detecting hybridising pairs. F1 will also be low if precision is low and sensitivity is high, suggesting the model overpredicts hybridisation. Accuracy is an arithmetic mean, whereas the F1 score is a harmonic mean. Accuracy provides the overall correctness of the model and treats each class equally, and as such, is less informative when the data is imbalanced. For example, hypothetically, if 95% of pairs did not hybridise, and the model predicts none of them hybridise, it would be 95% accurate but a misleading representation of the data. Therefore, improving precision and sensitivity, and subsequently the F1 score, should be prioritised.

$$(Eq. 1) \quad Accuracy = \frac{TP + TN}{\# \text{ pairs}}$$

$$(Eq. 2) \quad Precision = \frac{TP}{(TP + FP)}$$

$$(Eq. 3) \quad Sensitivity = \frac{TP}{(TP + FN)}$$

$$(Eq. 4) \quad Specificity = \frac{TN}{TN + FP}$$

$$(Eq. 5) \quad F1 = 2 * \frac{Precision \times Sensitivity}{Precision + Sensitivity}$$

3.2.2 Hotspots of Hybridisation

3.2.2.1 Geographic overlap

Lists of European and North American species pairs were created by pairing every species on the North American and European species lists with every other member of their family. Some of these pairs were not included in the comparisons between RFs and PLMMs, described above, as they do not currently coexist, although they may do in the future. Non-native species were removed from these analyses prior to this stage, as the species distribution models used were modelled on their native range only. Non-natives were removed from their non-native continent only. For instance, House sparrow (*Passer domesticus*) remained in the European group, and Canada Goose (*Branta canadensis*) remained in the North American group, but not *vice versa*. Pair lists were created separately for each continent, as our species trait data dissimilarity matrices required for prediction were continent-specific.

Species distribution models were created by (Gillie, 2024) and discussed in more detail in Chapter 5. Species pairs were limited to those with available SDMs for both members (n=4969). Rasters of current geographical overlap for pairs were created using rasterised BirdLife International range polygons (BirdLife International and Handbook of the Birds of the World, 2021) at a 0.5° resolution on a Behrman equal-area projection. Future distributions were modelled by Gillie (2024) using an ensemble of Generalised Linear Models (GLMs), General Additive Models (GAMs), Generalised Boosted Regression Trees (BRTs) and Random Forests (RFs). We used projections for Shared Socioeconomic Pathway 3-7.0 (SSP370). SSP370 is a ‘middle of the road’ scenario associated with a resurgence of nationalism, regional conflicts and growing inequalities, a radioactive forcing of 7.0W/m² and average temperature increase of 4.1 °C by 2100 (O’Neill *et al.*, 2016; Riahi *et al.*, 2017). Future predictions were clipped by suitable habitat area and species-specific dispersal buffers accounting for generation length and natal dispersal distance, which itself is calculated as a function

of range size, body mass and Hand-Wing Index (HWI) (see Gillie (2024)). We extracted rasters of the predicted area of future overlap for each pair.

3.2.2.2 Predicting hybridisation

For each species pair, we extracted data on predictors of hybridisation: Morphometric, colour, pattern and vocalisation dissimilarity; patristic distance and whether either pair member was a long-distance migrant and if either had long-term social bonds. As described above, RF algorithms were optimised and used to predict the likelihood of hybridisation for 4969 pairs. Random forests are computationally less intensive than PLMMs and outperformed them in accuracy, precision and specificity. Although PLMMs outperform RFs in relation to F1 score, due to time constraints, we were unable to make predictions using both methods.

3.2.2.3 Mapping hybrid hotspots

We plotted maps of summed areas of current overlap of hybridising pairs with known classifications (n=420 (Figure 1A), and summed areas of predicted future overlap for pairs known to hybridise (Figure 1B). We also plotted future maps for pairs predicted to hybridise (n=322)(Figure 1C), and a combined set of pairs that are either known to hybridise or are predicted to hybridise by RFs (n=499) (Figure 1D). It should be noted that the same species can be in multiple pairs. The cell values in Figure 1 correspond to the number of hybridising pairs, or the number of potential hybrid combinations.

3.3 Results

In all models (full models, no syntopy no sympatry models and passerines only, non-passerines only and combined pairs), accuracy, precision and specificity were all higher when predictions were made using RFs (Table 3 & 4). However, sensitivity and F1 score were always higher when predictions used PLMMs (Table 3 & 4). Out of a possible 30 combinations of performance metric, species group and predictor variables included, RFs performed better in 18, while PLMMs were superior in 12 (Table 3 & 4).

In the full models, using combined pairs, RF algorithms trained on North American data predicted European hybridisation with 86.0% accuracy while PLMMs had an accuracy of 61.1% (Table 3). Precision was also higher using RFs for this group, of pairs predicted to hybridise, 88.9% of them do hybridise, whereas only 25.7% of pairs predicted to hybridise using PLMMs hybridise. Specificity was extremely high with RFs– 99.6% of non-hybridising pairs were correctly predicted as such, but only 54.5% of non-hybridising pairs were correctly identified using PLMMs. On the other hand, sensitivity was far higher using PLMMs. 94.5% of actually hybridising pairs were predicted to do so compared to only 17.6% using RFs. Finally, the F1 score (the balance between precision and sensitivity) was higher when predicted using PLMMs compared to RFs (44.6% and 29.4%, respectively), but relatively low for both methods.

Including syntopy and sympatry in models made only slight differences to predictive performance. In many instances, including syntopy and sympatry, improved performance, more so in RFs than PLMMs. The greatest improvement was seen in the precision of RFs predicting hybridisation in non-passerines, including syntopy and sympatry improved precision by 12.9%. However, accuracy was 4.3% higher in PLMMs predicting non-passerines when syntopy and sympatry were omitted, highlighting the absence of a clear trend.

Similarly, restricting analyses to passerines and non-passerines did not substantially change the predictions using RFs or PLMMs for full or no syntopy, no sympatry models (Table 3). For example, accuracy in the full model using RFs was 86.0% for combined pairs, 80.8% for passerines only and 88.8% for non-passerines only.

Agreement between the two prediction types on hybrid classification was fairly low in most cases (Table 5). The maximum level of agreement between RFs and PLMMs was 72.4% in passerines without syntopy, sympatry. The lowest agreement was in the combined group with syntopy and sympatry at 49.7%. Agreement levels were higher when models were run on passerines and non-passerines separately.

Table 2. The number of pairs used for model training (North America) and the number of pairs for which hybridisation was predicted (Europe).

		Combined	Passerines	Non-passerines
North America	Full Model	3339	2189	1150
	No synt, No symp	3558	2326	1232
Europe	Full Model	1647	522	1125
	No synt, No symp	2176	682	1494

Table 3. Hybridisation prediction metrics for Random Forest (RF) and Phylogenetic Generalised Linear Mixed Model (PLMM) predictions of European pairs using models trained on North American pairs for passerine and non-passerine pairs combined, passerine pairs only and non-passerine pairs only. Predictor variables for full models include morphometric dissimilarity, colour dissimilarity, pattern dissimilarity, vocalisation dissimilarity, patristic distance, migratory strategy, social bond length, syntopy and sympatry. No synt, no symp models: as the full models but without syntopy and sympatry.

	Full Model	No synt, No symp	Full Model	No synt, No symp	Full Model	No synt, No symp
	Combined		Passerine		Non-passerine	
Random forest machine learning						
Opt. mtry	2	2	7	6	2	6
Opt. ntrees	500	50000	500	1000	1000	1000
Total pairs	1647	2176	522	682	1125	1494
Actual hyb.	273	316	108	114	165	202
Actual non-hyb.	1374	1860	414	568	960	1292
Pred hyb.	54	52	22	23	53	69
Pred non-hyb.	1593	2124	500	659	1072	1425
True -ve	1368	1848	407	558	953	1274
True +ve	48	40	15	13	46	51
False -ve	225	276	93	101	119	151
False +ve	6	12	7	10	7	18
Accuracy	0.860	0.868	0.808	0.837	0.888	0.887
Precision	0.889	0.769	0.682	0.565	0.868	0.739
Sensitivity	0.176	0.127	0.139	0.114	0.279	0.252
Specificity	0.996	0.994	0.983	0.982	0.993	0.986
F1 score	0.294	0.217	0.231	0.190	0.422	0.376
Phylogenetic generalised linear mixed models						
Total pairs	1647	2176	522	682	1125	1494
Actual hyb.	273	316	108	114	165	202
Actual non-hyb.	1374	1860	414	568	960	1292
Pred hyb.	883	1134	178	205	477	531
Pred non-hyb.	764	1042	344	477	648	963
True -ve	749	1016	302	430	639	941
True +ve	258	290	66	67	156	180
False -ve	15	26	42	47	9	22
False +ve	625	844	112	138	321	351
Accuracy	0.611	0.600	0.705	0.729	0.707	0.750
Precision	0.292	0.256	0.371	0.327	0.327	0.339
Sensitivity	0.945	0.918	0.611	0.588	0.945	0.891
Specificity	0.545	0.546	0.729	0.757	0.666	0.728
F1 score	0.446	0.400	0.462	0.420	0.486	0.491

Table 4: The best performing model for each metric and group. Purple: Random Forest Machine Learning (RFML). Green: Phylogenetic Generalised Linear Mixed Models (PLMM).

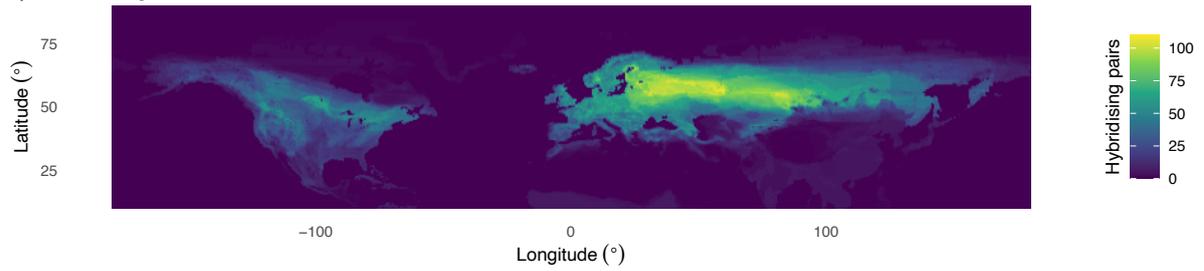
	Full Model	No synt, No symp	Full Model	No synt, No symp	Full Model	No synt, No symp
	Combined		Passerine		Non-passerine	
Accuracy	RFML	RFML	RFML	RFML	RFML	RFML
Precision	RFML	RFML	RFML	RFML	RFML	RFML
Sensitivity	PLMM	PLMM	PLMM	PLMM	PLMM	PLMM
Specificity	RFML	RFML	RFML	RFML	RFML	RFML
F1 Score	PLMM	PLMM	PLMM	PLMM	PLMM	PLMM

Table 5. Proportion of hybridisation classifications in agreement between RFML and PLMM.

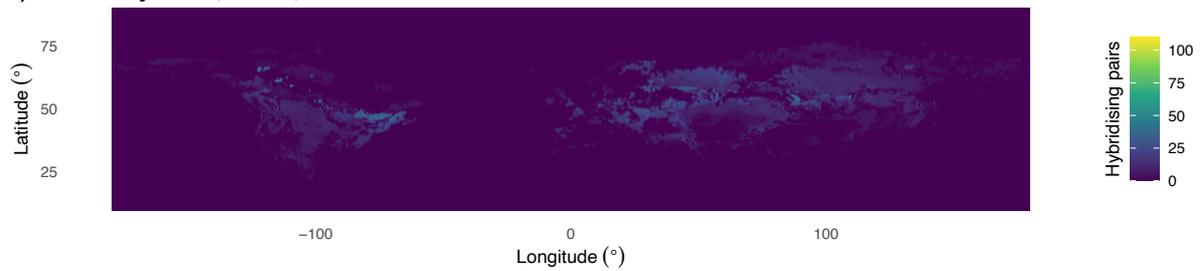
	Combined	Passerines	Non-passerines
Full Model	0.497	0.701	0.623
No synt, No symp	0.503	0.724	0.691

The greatest current assemblages of hybridising pairs are in Eastern Europe and Central Asia, with the maximum number of hybridising pairs in a cell being 110 (Figure 1A). In known hybridising pairs and predicted hybridising pairs, the spatial overlap of hybridising pairs decreases drastically by 2070 (Figure 1 & 3). This reduction in overlap appears to be due to extensive future range contractions (Figure 2). However, future range predictions are clipped by habitat suitability (see Gillie 2024 for details), so species will naturally occupy fewer cells than the range polygon-derived current estimates. From previous analyses (Chapter 2), we had hybrid classifications available for 4206 pairs, and as such, we were able to estimate predictive performance for these pairs. Accuracy was 95.2%, sensitivity 58.7%, specificity 99.6%, precision 94.2%, and the F1 score was 72.3%.

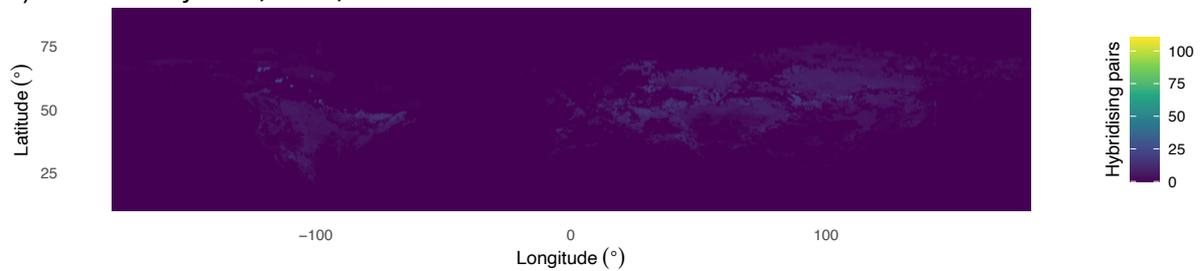
A) Actual hybrids, current



B) Actual hybrids, 2070, SSP370



C) Predicted hybrids, 2070, SSP370



D) Predicted and actual hybrids combined, 2070, SSP370

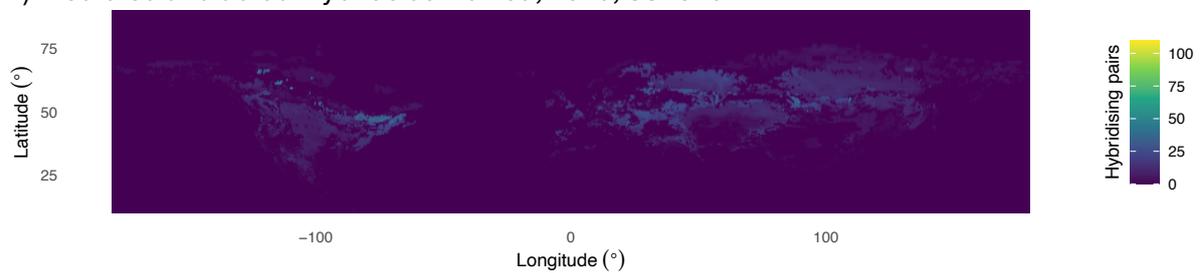


Figure 1. Spatial overlap of hybridising pairs, cell values correspond to the number of hybridising pairs that co-occur in said cell. Species can appear multiple times in different pair combinations. Maps only show sympatric areas for pairs. Hybrid predictions are made using random forest machine learning algorithms.

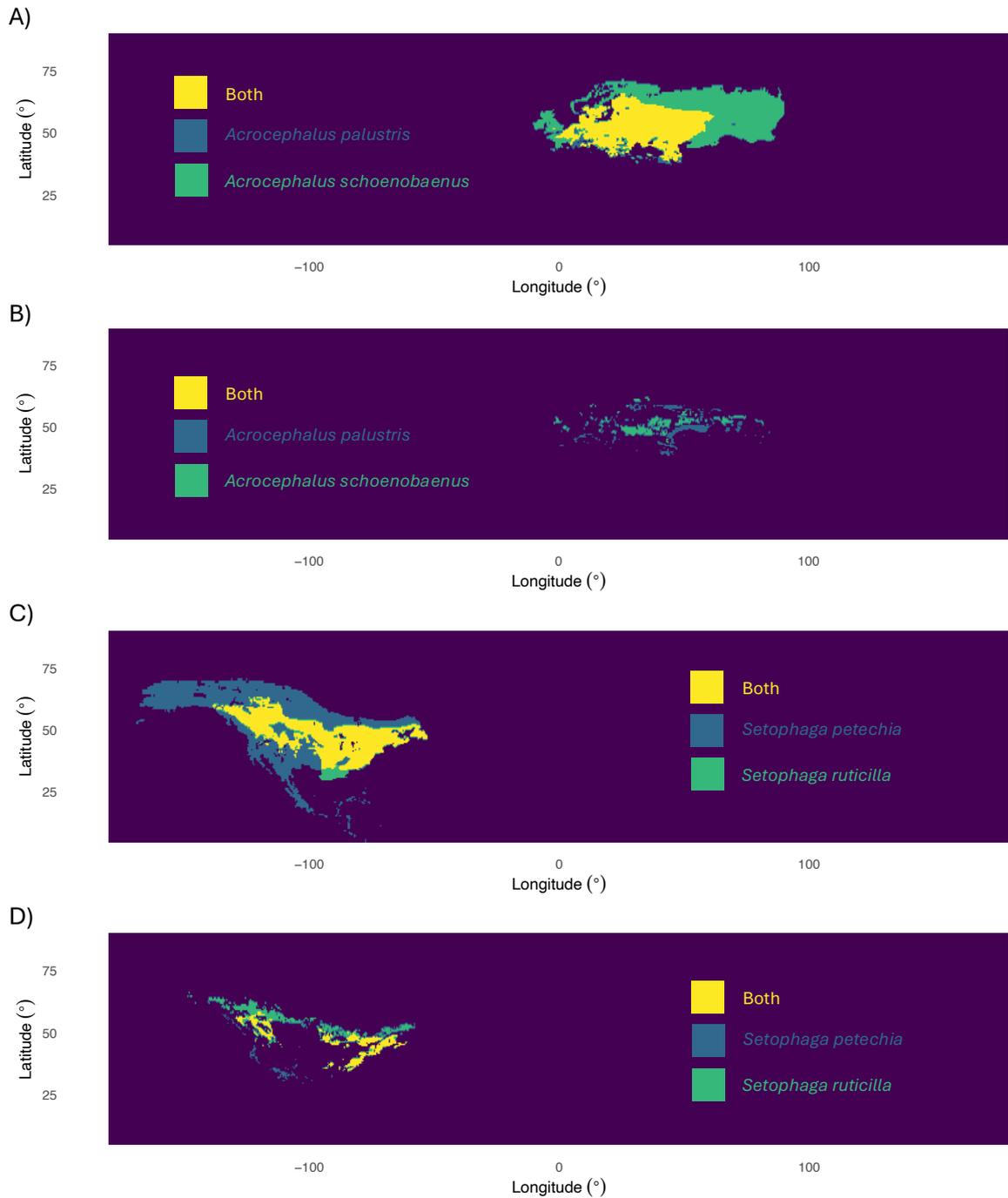
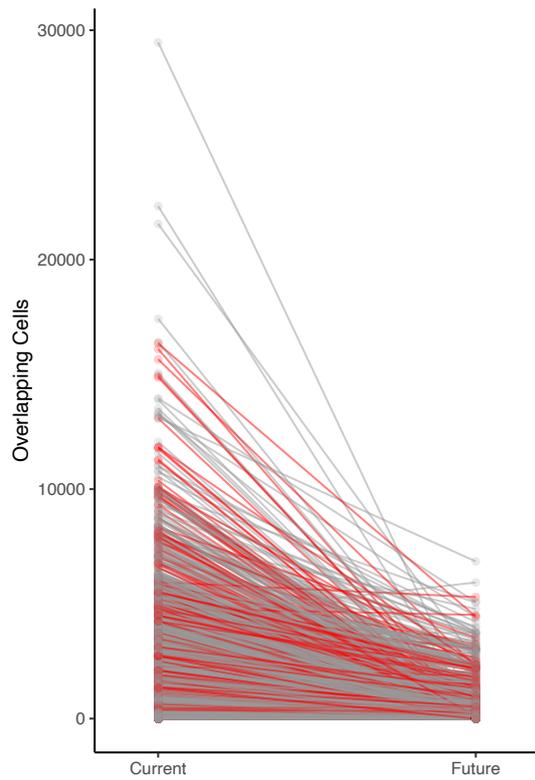


Figure 2. The current (A, C) and future distributions of two hybridising pairs; Marsh Warbler (*Acrocephalus palustris*) (blue) and Sedge Warbler (*A. schoenobaenus*) (green) and their overlap (yellow). Marsh and Sedge Warbler currently cooccur in 3182 cells but are projected to share zero by 2070 under a SSP370 pathway. Yellow Warbler and American Redstart currently occupy 3456 cells together, which is projected to decrease to 818 by 2070.

A) Known hybrid classifications



B) Predicted hybrid classifications

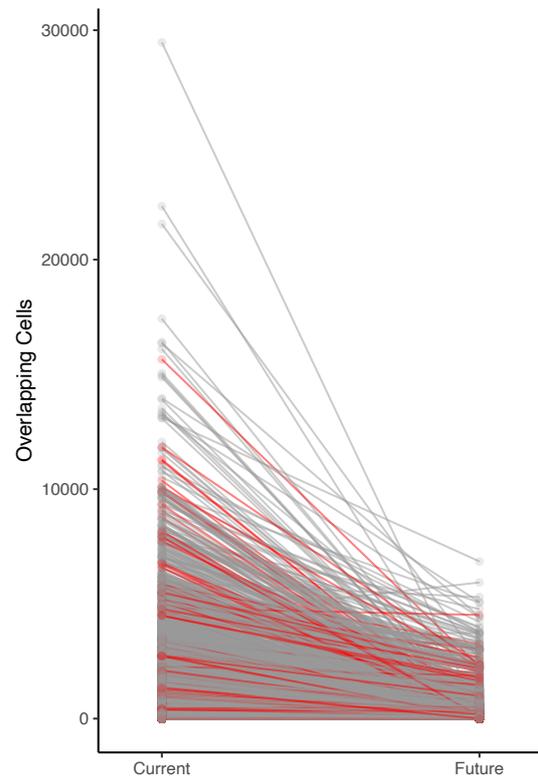


Figure 3. The number of overlapping 0.5° cells for pairs in their current distribution and in 2070 under an SSP370 projection. Red lines indicate hybridising pairs. Those with known hybridisation classifications (A) ($n=3929$, $n_{Hyb}= 420$) and those with predicted hybrid classifications (B) ($n=4969$, $n_{Hyb}= 322$).

3.4 Discussion

We have demonstrated it is possible to predict unknown hybridisation events with relatively high accuracy, precision and specificity using models trained on a variety of ecological and life history traits from a different species assemblage. Sensitivity and F1 scores, however, are relatively low (Sidumo, Sonono and Takaidza, 2022). While all the pairs in our European data set currently coexist, this need not be the case; we have shown it is possible to make predictions of hybridisation without detailed spatial data. The omission of spatial overlap metrics made little difference to the predictive performance of models. The ability to predict the likelihood of hybridisation for species that do not currently coexist could prove useful for predicting hybridisation between native species and potential colonists or natives and non-natives that are likely to be introduced.

Predictive power may be improved if models are trained on a combined group of North American and European pairs, which appears to be the case for the random forests we used to predict hybridisation for our global hybrid hotspot analysis—accuracy, precision, sensitivity, specificity, and F1 score were all higher than those from both RFs and PLMM in the comparative analysis.

Both RFs and PLMMs tend to overestimate the number of hybridising pairs in our data. It is possible that some of these pairs do, or will, hybridise, and it has yet to be documented. While this may be the case for one or two pairs, given the level of ornithological research in the Northern Hemisphere, it seems unlikely to be responsible for most misclassifications. In the RF model for all pairs, without syntopy and sympatry, the greatest probability of hybridisation was 0.80, between Common Crossbill (*Loxia curvirostra*) and Scottish Crossbill (*L. scotica*), two very similar species. Common and Scottish Crossbills are so similar that they were previously considered conspecific, so it is unsurprising that models predict they would hybridise. However, current evidence supports their heterospecific status (Summers, Dawson and Phillips, 2007), and no hybridisation has been reported (Knox, 1990). Similarly, once conspecific, Marmora's

(*Currucua sarda*) and Balearic Warbler (*C. balearica*) are predicted to hybridise with relatively high certainty (0.72), yet are not known to hybridise and have recently been split as separate species (Nespoli *et al.*, 2021). On the other hand, the probability of Lapland (*Calcarius lapponicus*) and Snow Bunting (*Plectrophenax nivalis*) not hybridising was 0.95 and yet hybrids have been reported since 2011 (Macdonald *et al.*, 2012).

Our two model types seem to be fairly evenly matched in predictive power, while RFs consistently perform better in some metrics (overall accuracy, precision and specificity), PLMMs consistently give a better F1 score and sensitivity. It could be argued that the F1 score is more important than overall accuracy, as it considers how many of the predicted hybridising pairs actually hybridise and how many of the actually hybridising pairs were predicted to do so. Which, in an imbalanced dataset as ours, with far more non-hybridising than hybridising pairs, is of particular importance (Sasaki, 2007; Wardhani *et al.*, 2019; Sidumo, Sonono and Takaidza, 2022; Kamalov, Thabtah and Leung, 2023). While RFs are designed for prediction (Cutler *et al.*, 2007), PLMMs are primarily designed for inference (Hadfield, 2010).

Our overall predictions could be improved by utilising an ensemble approach with a variety of other modelling techniques such as K-mean nearest neighbours, boosted regression trees and deep neural networks (Sidumo, Sonono and Takaidza, 2022). We have shown that the predictions from our two modelling methods tend to agree with each other on just over half of the species pairs in all but one scenario. As such, there is definite room for improvement and incorporating additional models into an ensemble could facilitate improved predictions through a majority vote.

As a proof of concept, we applied RF algorithms and predicted hybridisation for a range of North American and European pairs, some of which do not currently coexist. We utilised SDMs to predict where these potentially hybridising species may coexist in the future. The SDMs we utilised predict substantial range contractions for most species, which in turn reduces the area of overlap of hybridising pairs. Given we found evidence that increased range and habitat overlap increases the likelihood of hybridisation

(Chapter 2), this predicted reduction in range overlap suggests hybridisation will dramatically decline under future warming. Notwithstanding massive range reductions, this decrease in hybridisation could be somewhat positive from a conservation viewpoint, given hybridisation can threaten the genetic integrity of rare species (Rhymer and Simberloff, 1996; Wolf, Takebayashi and Rieseberg, 2001). However, hybridisation could also introduce genetic diversity for which natural selection can act on and allow species to adapt to warming temperatures (Chunco, 2014; Brauer *et al.*, 2023). On the other hand, hybridisation can be more likely in parapatry (Randler, 2006), and as species ranges fragment, the extent of range edges may increase, which could increase the occurrence of hybridisation among parapatric species.

An alternate explanation for the predicted dramatic reduction in hybridisation could be inaccuracies in our SDM predictions. However, the SDMs we utilised all had excellent AUC values (See Gillie 2024). Range fragmentation has also been forecast in other future projections (Duan *et al.*, 2016; Harishchandra *et al.*, 2022; Curd *et al.*, 2023). Furthermore, it should be reiterated that the current species range maps are based on range polygons and therefore encompass unsuitable habitat within those polygons, while future projections are clipped by suitable habitat overlap, which may be responsible for some of the predicted fragmentation and reduction in hybridisation.

This research is a first step in demonstrating our ability to predict hybridisation. It is hoped our ability to do so will improve with advances in modelling techniques and data availability. Although time-consuming, it would be feasible to create a quasi-global hybridisation dataset on which to train models and most of the predictor variables used in these models originate from global datasets (see Chapter 2). The greatest hurdle to this endeavour is the availability of hybridisation data, and while this does exist outside of Europe and North America, there is certainly a research bias towards these regions (McCarthy, 2006). Additionally, the availability of high-quality vocalisation data for most species and the time it would take to clean and process, would be a limiting factor. That said, with the rise of artificial intelligence and machine learning, this processing hurdle may become more surmountable in the future. This pipeline could also be applied to

predict a variety of other species interactions with important conservation implications, such as territoriality, parasitism, seed-dispersal and plant-pollinator interactions.

Chapter 4

Hindcasting the effects of competition on range dynamics

4.1 Introduction

Species ranges are changing as a result of climate change, land-use change, and introduction to non-native areas (C D Thomas and Lennon, 1999; La Sorte and Boecklen, 2005b; Hitch and Leberg, 2007; Zuckerberg, Woods and Porter, 2009b; Brommer, Lehikoinen and Valkama, 2012; Elmhagen *et al.*, 2015; Dyer *et al.*, 2017; Regos *et al.*, 2018). Such movement across landscapes is expected to be impacted (either positively or negatively) by interactions between currently coexisting taxa (J. C. Svenning *et al.*, 2014). Similarly, shifts into new areas may give rise to novel species interactions, which may in turn determine the likelihood that a range-shifting lineage successfully becomes established (HilleRisLambers *et al.*, 2013a; J. C. Svenning *et al.*, 2014; Sirén and Morelli, 2020). The impact of such species interactions on range dynamics has been investigated extensively for interactions between trophic levels (e.g. predator-prey or plant-pollinator interactions; Wisz *et al.*, 2013; Svenning *et al.*, 2014) and within trophic levels (e.g. exploitative competition or facilitation; Connor and Bowers, 1987; Heikkinen *et al.*, 2007; Wisz *et al.*, 2013; Svenning *et al.*, 2014; Novella-Fernandez *et al.*, 2021). Yet, in addition to competition for resources, many animals engage in behavioural interference, a widespread phenomenon that encompasses interspecific interactions such as interference competition (e.g. interspecific territoriality) and reproductive interference (e.g. hybridisation) (Connor and Bowers, 1987; Gross and Price, 2000; Gotelli, Graves and Rahbek, 2010; Krosby and Rohwer, 2010; Vallin *et al.*, 2012; McQuillan and Rice, 2015; Grether *et al.*, 2017).

An emerging body of research suggests that behavioural interference between species can influence the outcome of range shifts (Pearson and Rohwer, 2000; Duckworth and Badyaev, 2007; Krosby and Rohwer, 2010; Mac Nally *et al.*, 2012b). The hypothesised impacts of such interference largely depend on the fitness costs and benefits of engaging in territorial or reproductive interactions with heterospecifics. On the one hand, when behavioural interference incurs net fitness costs for one or more interacting species, these costs diminish population growth and lead to an increased risk of local extinction (i.e., sexual or competitive exclusion; (Kuno, 1992b; Lily W Liou and Price, 1994; Amarasekare, 2002; Hochkirch, Gröning and Bückner, 2007; Gröning and

Hochkirch, 2008; Pfennig and Pfennig, 2012; Kishi and Nakazawa, 2013; Legault *et al.*, 2020b). On the other hand, if behavioural interference instead diminishes interspecific resource competition by reducing spatial overlap, such interference may enable ecologically similar species pairs to coexist (Case and Gilpin, 1974; Zhang and Hanski, 1998; Mikami and Kawata, 2004; Grether *et al.*, 2013; Kishi and Nakazawa, 2013; Ruokolainen and Hanski, 2016; Gómez-Llano *et al.*, 2021; Grether and Okamoto, 2022). Interspecific territoriality, for instance, can stabilise coexistence between species that exhibit high levels of resource competition (Grether and Okamoto, 2022). In the absence of interspecific territoriality, the more efficient exploiter of resources should outcompete and exclude the less efficient exploiter of resources from the region of overlap. Interspecific territoriality can also arise as an adaptive response to reproductive interference (Payne, 1980; Drury *et al.*, 2015; Grether *et al.*, 2020b), which, given that such interference should lead to reproductive exclusion (Ribeiro and Spielman, 1986; Kuno, 1992b), may also indicate a role for interspecific territoriality in stabilising coexistence in species pairs that engage in reproductive interference.

Empirical research confirms that behavioural interference can lead to competitive or reproductive exclusion at a variety of scales (Connor and Bowers, 1987; Robinson and Terborgh, 1995; Gross and Price, 2000; Duckworth and Badyaev, 2007; Jankowski, Robinson and Levey, 2010; Vallin *et al.*, 2012; Grether *et al.*, 2013, 2017; Pasch, Bolker and Phelps, 2013b; Rybinski *et al.*, 2016; Freeman, Tobias and Schluter, 2019; Freeman, Strimas-mackey and Miller, 2022) At local scales, behavioural interference can lead to the exclusion of species from particular habitat patches so that species pairs coexist in sympatry (i.e., range overlap) but not syntopy (i.e., local, habitat-scale overlap) (Robinson and Terborgh, 1995; Vallin *et al.*, 2012; Rybinski *et al.*, 2016; Reif *et al.*, 2018b). For instance, Collared Flycatchers (*Ficedula albicollis*) that have colonised the Swedish island of Öland in the last century are competitively dominant over Pied Flycatchers (*Ficedula hypoleuca*) and confine them to lower quality coniferous woodlots through both interspecific territoriality and reproductive interference via costly hybridisation (Vallin and Qvarnström, 2011b; Vallin *et al.*, 2012; Rybinski *et al.*, 2016). At larger scales, more extensive exclusion occurs at geographical range boundaries when behavioural interference precludes coexistence in sympatry (Gross

and Price, 2000; Duckworth and Badyaev, 2007; Jankowski, Robinson and Levey, 2010; Krosby and Rohwer, 2010; McQuillan and Rice, 2015; Freeman and Montgomery, 2016; Freeman, Class Freeman and Hochachka, 2016; Legault *et al.*, 2020b). For instance, several studies of montane species pairs occupying abutting altitudinal ranges suggest that interspecific territoriality, rather than abiotic factors and differing habitat requirements, is the key factor preventing range overlap at elevational boundaries (Jankowski, Robinson and Levey, 2010; Freeman and Montgomery, 2016; Freeman, Class Freeman and Hochachka, 2016; Boyce and Martin, 2019; Freeman, Tobias and Schluter, 2019; Freeman, Strimas-mackey and Miller, 2022). Behavioural interference has also been implicated as the primary factor limiting species ranges along latitudinal and habitat gradients (Gross and Price, 2000; Duckworth and Badyaev, 2007; Krosby and (, 2010; McQuillan and Rice, 2015; Martin and Bonier, 2018).

Though theoretical models demonstrate that behavioural interference could stabilise species coexistence, there is relatively little empirical work investigating this possibility; nevertheless, studies in a few taxa directly support this idea (salamanders: Marvin, (1998), and gerbils: Ovadia and Zu Dohna (2003); Ziv and Kotler (2003)). Moreover, several studies demonstrate stable coexistence between interspecifically territorial and ecologically similar species (Rohwer, 1973; Jankowski *et al.*, 2012; Drury *et al.*, 2015, 2019; Reif *et al.*, 2015; Freeman, 2016b), which is consistent with the hypothesis that interspecific territoriality can enable resource partitioning through spatial segregation, thereby enabling coexistence. Further compelling evidence that behavioural interference can lead to stable coexistence comes from examples of convergent character displacement acting on territorial signals (Cody, 1969; Tobias and Seddon, 2009; Reif *et al.*, 2015; Souriau *et al.*, 2018; Kirschel, Seddon and Tobias, 2019; Miller *et al.*, 2019). Eastern (*Sturnella magna*) and Western Meadowlarks (*Sturnella neglecta*), for example, have converged in plumage patterning and colouration where they co-occur and defend non-overlapping interspecific territories (Rohwer, 1973).

Consistent with theoretical work showing that interspecific territoriality can stabilise coexistence between ecologically similar species (through trade-offs between interference and exploitative competition ability; Grether and Okamoto, 2022), recent

comparative analyses on North American passerines have shown that interspecific territoriality is positively associated with resource use and fine-scale habitat overlap (Cowen, Drury and Grether, 2020; Drury, Cowen and Grether, 2020). Here, we test additional predictions that follow from the hypothesis that interspecific territoriality can stabilise coexistence. First, in taxa with shifting or expanding ranges, the extent of range overlap (sympatry) should increase more over time between interspecifically territorial species compared to non-interspecifically territorial species, because interspecific territoriality reduces exploitative resource competition between species and thus the likelihood of competitive exclusion at range boundaries. Second, regardless of whether species ranges are changing, the magnitude of fine-scale habitat overlap (syntopy) within the areas of range overlap should increase more (or decrease less) over time between interspecifically territorial species compared to non-interspecifically territorial species. The second prediction not only applies to taxa with expanding ranges, but it assumes that dispersal is a regular occurrence and that some suitable habitats within the species' ranges remain unoccupied.

For hybridising species, frequency-dependent interactions can generate Allee effects that might prevent one species from expanding into another species' range (Kishi, Nishida and Tsubaki, 2009b; Kyogoku and Nishida, 2012; Kishi and Nakazawa, 2013; Bargielowski and Lounibos, 2016; Noriyuki and Osawa, 2016; Whitton, Sears and Maddison, 2017). In areas where the species' ranges do overlap, however, selection against interspecific mating could cause fine-scale habitat partitioning (Gröning *et al.*, 2007b; Gómez-Llano *et al.*, 2021), which in turn could reduce interspecific exploitative competition for resources and facilitate further increases in range overlap. Thus, it is difficult to predict whether hybridisation would be positively or negatively associated with temporal changes in sympatry, but it seems robust to predict that hybridisation should not be associated with temporal increases in syntopy

To test the above predictions in North American passerines, we combined data on interspecific territoriality and hybridisation (Drury, Cowen and Grether, 2020) with data on recent range dynamics (1997-2019) (Sauer, Link and Hines, 2020). Analyses were also carried out on European passerines. However, some of the predictor variables

utilised in North American models were unavailable, and as such, analogous variables were used in their place.

4.2 Methods

4.2.1 Syntopy and sympatry

4.2.1.1 North America

We calculated several indices of temporal change in interspecific spatial overlap for 1602 species pairs using data from the North American Breeding Bird Survey (BBS) (Pardieck *et al.*, 2020). The BBS has been running since 1966 and is conducted by trained observers carrying out roadside 3-minute point counts at 50 stops along each 39.4 km route. As of 2019, 5756 routes had been surveyed (Figure 1), although not all routes had been surveyed annually (Pardieck *et al.*, 2020). Because data for each individual stop (i.e., the ‘50-stop’ dataset) are only available consistently for surveys conducted after 1996, and because the number of routes surveyed each year (i.e., the ‘10-stop’ dataset, where the data from every 10 stops are grouped together) plateaued around 1995 (Figure 2), for the sake of comparability, we focused our analyses on the years from 1997 to 2019. Our analyses cover the trends and dynamics of species ranges within the BBS area; however, the ranges of some species extend beyond these limits.

From the 50-stop BBS data, we calculated a BBS-derived index of syntopy, or cooccurrence in the same breeding habitat within the zone of sympatry (Rivas, 1964), as the number of stops shared by both species divided by the number of stops with only one species present (Equation 1) (Figure 5)

$$(Eq. 1) \quad \frac{1}{Y} \sum_{i=1}^Y \frac{1}{R_{1,2,i}} \sum_{k=1}^{R_{1,2,i}} \left(\frac{S_{1,2,k}}{S_{1,k} + S_{2,k} - S_{1,2,k}} \right)$$

Where $S_{1,2,k}$ refers to the number of stops where species 1 and 2 co-occur in year i on route k . $S_{1,k}$ and $S_{2,k}$ refer to stops where species 1 and species 2 were recorded on route k , respectively. $R_{1,2,i}$ refers to routes on which both species 1 and species 2 were recorded in year i . Y is the total number of years, in this instance, 4 for each time period. This approach assumes that birds detected at the same BBS stop occupy the same

breeding habitat (i.e., are syntopic); they could, however, still occupy non-overlapping territories (Losin *et al.*, 2016; Drury, Cowen and Grether, 2020). We calculated one syntopy value for each route and averaged the values across all routes on which both species were present in each year. Then, we calculated the temporal change in syntopy (Δ syntopy) for each species pair by subtracting the mean annual syntopy value between 1997 and 2000 from the mean annual syntopy between 2016 and 2019.

Using the 10-stop BBS data, we calculated an index of sympatry (range overlap) as the number of routes with both species divided by the number of routes with the species that occurred on the fewest routes (similar to the Szymkiewicz–Simpson index used on range maps, (Pigot, Tobias and Jetz, 2016) in each year (Equation 2):

$$(Eq. 1) \quad \begin{cases} \frac{1}{Y} \sum_{i=1}^Y \frac{R_{1,2_i}}{R_{1_i}}, \text{ if } R_{1_i} < R_{2_i} \\ \frac{1}{Y} \sum_{i=1}^Y \frac{R_{1,2_i}}{R_{2_i}}, \text{ if } R_{2_i} < R_{1_i} \end{cases}$$

Where all terms are as above. We calculated the temporal change in sympatry (Δ sympatry) by subtracting the mean of 1997–2000 sympatry values from the mean of 2016–2019 values. All BBS routes with at least one member of each pair present that were surveyed in a given year were included in the syntopy and sympatry calculations.

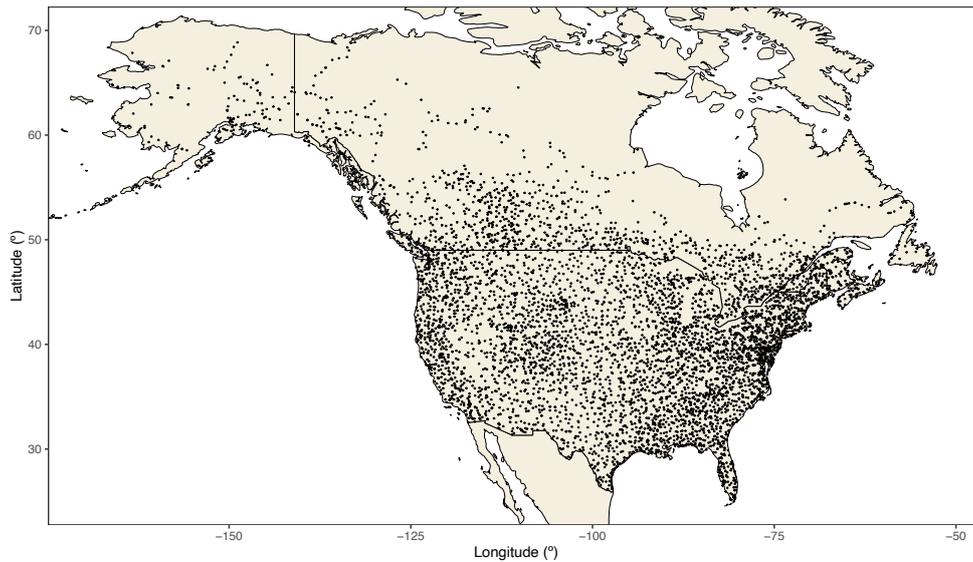


Figure 1. Location of all North American Breeding Bird Survey routes between 1966 and 2019 (n=5756), not every route is surveyed annually.

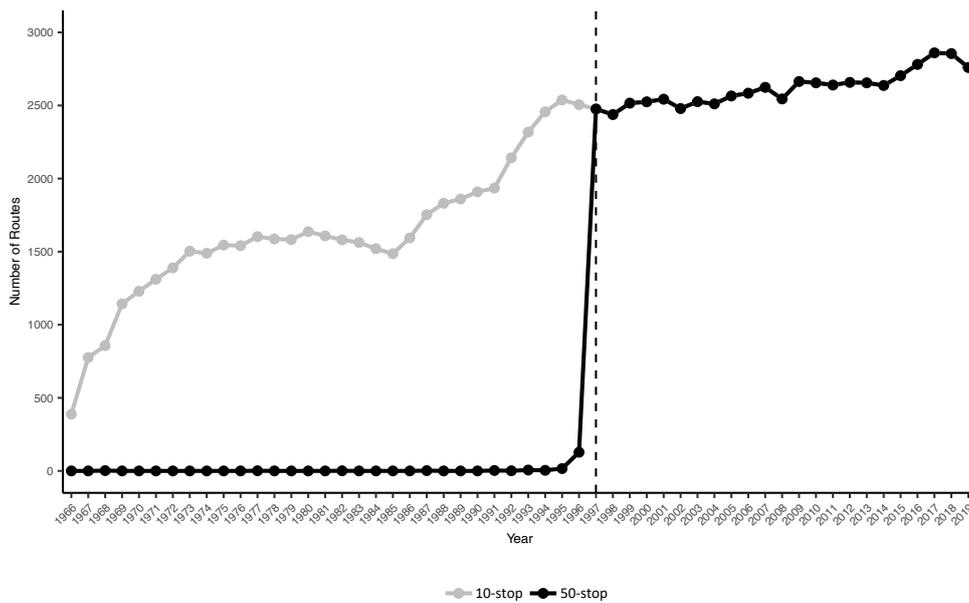


Figure 2. The number of North American BBS Routes with available data in each year. 10-stop data was used to calculate sympatry (grey). 50-stop data was used to calculate syntopy (black). Vertical dashed line denotes the first year (1997) in which both datasets contain all the same routes.

4.2.1.2 Europe

Unlike the North American BBS data, the Pan-European Common Bird Monitoring Scheme (PECBMS) (Brlík *et al.*, 2021) data are not hierarchically structured, as in stops within routes, but instead are collected at single survey sites. The PECBMS collates data from national survey schemes, but given that the data are collected under different schemes in different countries, survey protocols, spatial resolution, scheme duration, and species recorded differ (Figures 3 & 4). For our spatial analyses, we required presence/absence data for species at a high resolution with accurate site coordinates. Data from Spain, Switzerland, Finland and the Czech Republic did not meet these criteria and were omitted from analyses. For instance, the coordinates of Spanish survey sites refer to the centroid of a 10km grid cell, therefore, two sites within 10km of one another could have identical coordinates. While in the Czech Republic, site coordinates refer to the nearest municipality (A. Gamero 2023, pers. comm). In Switzerland, surveyors only record 'common breeders' and as such, we have no way of knowing if species were absent from sites or just not recorded. The following schemes remained: Austria, Brussels, Catalonia, Denmark, France, Germany, Ireland, Italy, Netherlands, Norway, Poland, Sweden, UK and Wallonia. Unfortunately, seven schemes had not begun before the historical period used in North American analyses (1997-2000) (Figure 4). But, given that syntopy and sympatry are proportional metrics, and for the sake of comparability, we utilised the same survey periods in both North America and Europe (1997-2000 and 2016-2019). Like the North American BBS, PECBMS surveys are carried out during the breeding season.

European sympatry was calculated in the same way as North American sympatry, but the number of routes shared was replaced by the number of sites both species were present at within 40km of each other (40km is slightly longer than a NABBS route [39.4km]). Similarly, when calculating syntopy, the number of shared stops was replaced by the number of shared sites within 1km of one another (although the point count radii at NABBS stops are only 400m, few survey sites in Europe are that close

together). Temporal changes in syntopy and sympatry were calculated in the same way for both continents.

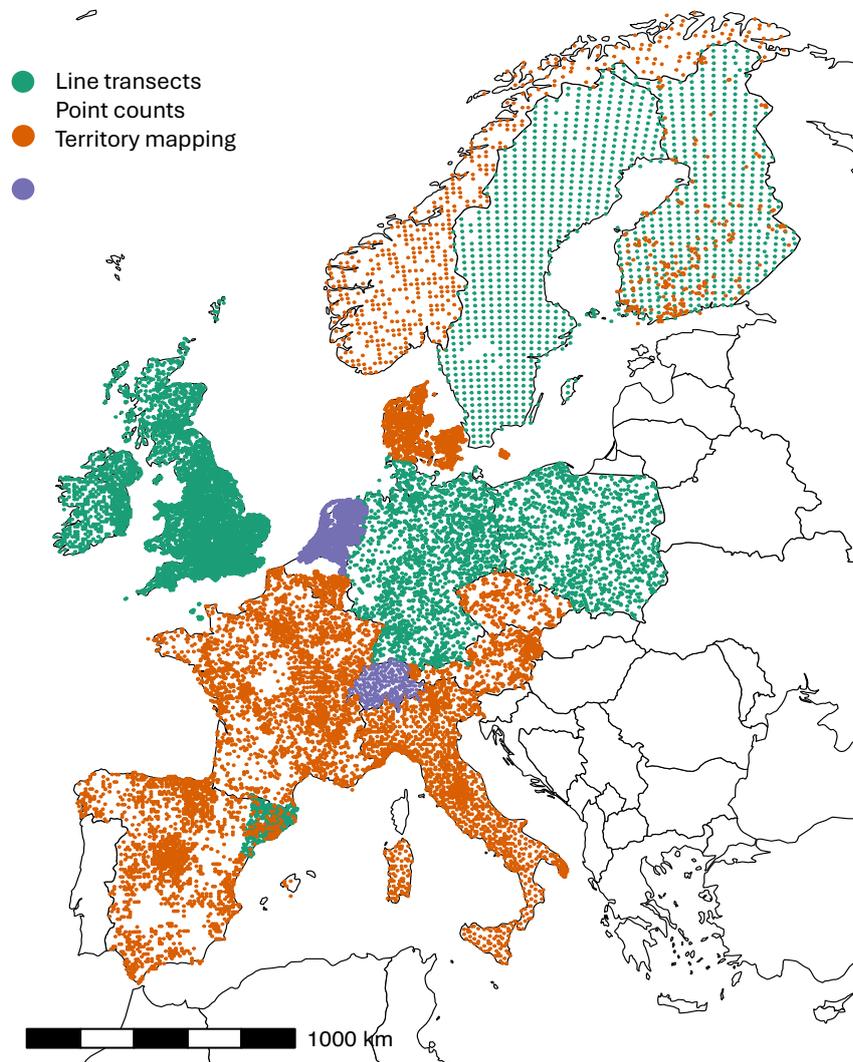


Figure 3. Distribution of Pan-European Common Bird Monitoring (PECBMS) sites and their survey methodology. Line transects (green), point counts (orange) and territory mapping (purple). Spain, Switzerland, Finland and Czech Republic were removed from analyses.

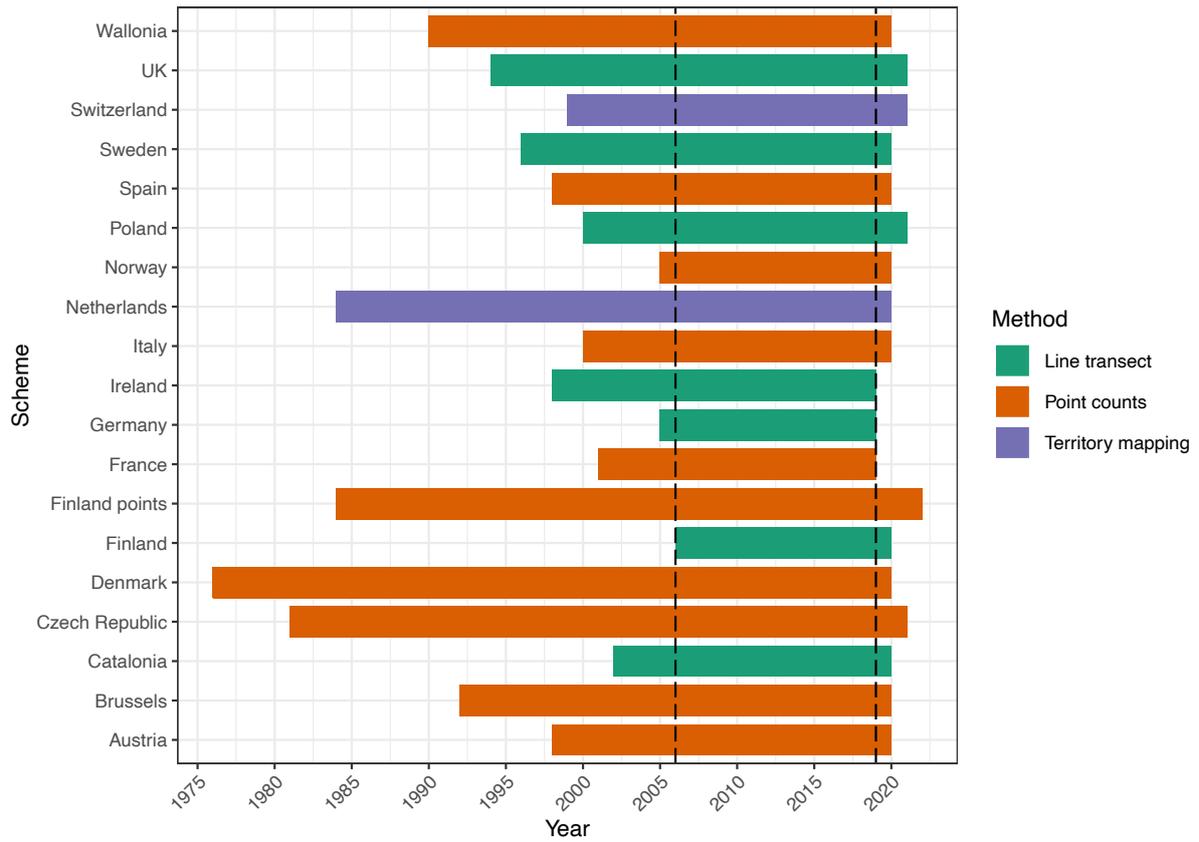


Figure 4. Duration of available survey schemes. Bar colour denotes survey method. Line transects (green), point counts (orange) and territory mapping (purple). Vertical dotted lines denote the time-period with data available for all schemes (2006-2019). Spain, Switzerland, Finland and Czech Republic were removed from analyses.

4.2.2 Interspecific behavioural interference

4.2.2.1 North America

We used a database of interspecific territorial behaviour in North American passerines compiled by Drury, Cowen and Grether (2020). Briefly, species pairs in this database were considered to be interspecifically territorial if there were multiple reported territorial interactions between them in the literature. The database also includes a list of species pairs that were considered not to be interspecifically territorial based on census data from regions and time periods where observations of interspecific territorial behaviour were made (Losin *et al.*, 2016; Drury, Cowen and Grether, 2020). Hybridisation classifications were also taken from Drury, Cowen and Grether (2020) and did not include captive hybridisation or unsubstantiated reports of hybridisation. In total, we included 1602 out of 1618 pairs identified by Drury, Cowen and Grether (2020), as 16 pairs were not found on any of the same routes in both time periods. Of the 1602 pairs used in analyses, 74 pairs were interspecifically territorial, 1528 were not, 68 pairs hybridised, whereas 1534 did not, and 27 pairs were both interspecifically territorial and hybridising.

4.2.2.2 Europe

Data on interspecific territoriality were unavailable for European species, and due to time constraints, we were unable to collect these data ourselves. However, we were able to predict European interspecific territoriality using random forest machine learning algorithms (see Chapter 3) trained on 682 North American pairs using the R package *tidymodels* (Kuhn and Wickham, 2020). The following variables were used to predict interspecific territoriality and were based on those used to predict territoriality by Drury, Cowen and Grether (2020): Hybridisation, morphometric dissimilarity, colour dissimilarity, pattern dissimilarity, song dissimilarity, syntopy, sympatry, and if both species were secondary cavity nesters (for more details on the derivation of these metrics see Chapter 2). To verify whether this approach produces reasonable predictions, we conducted a cross-validation analysis on known interspecifically

territorial pairs from North America. North American data were split into training and testing groups (80% training, 20% testing) using randomised stratified sampling. The proportion of interspecifically territorial and non-territorial pairs in the training and testing groups was as close to representative of the whole dataset as possible (All data: territorial=0.086, non-territorial=0.913. Training: T=0.091, NT=0.908. Testing: T=0.066, NT=0.934). The hyperparameters *mtry* (the number of predictors randomly sampled at each split in each decision tree) and *ntrees* (the number of decision trees) were tuned to find the optimal model configuration. Six possible values for *mtry* (2-7) and six for *ntrees* (500, 1000, 5000, 10000, 50000, 100000) were tested in 36 combinations. For each combination of hyperparameters, the model was trained and evaluated repeatedly using 3-fold cross-validation. The training data was split into 3 folds, models were trained on two folds and validated on the third. This was repeated thrice (once for each fold), and the performance metrics were averaged across folds. We identified the optimal model parameters for prediction as those which yielded the highest ROC AUC value (which measures how well the model separates territorial pairs from non-territorial pairs) across cross-validation folds. The optimal model was then tested on the original test data from the initial split to provide an estimate of model performance on unseen data. The optimal model (*mtry*=2, *ntrees*=50,000) was then used to predict European territoriality. The probability of territoriality was calculated for each pair, and if it was greater than 0.5 (i.e., a pair were more likely to be interspecifically territorial than not), they were considered to be territorial. Of the 522 European passerine pairs, 24 were predicted to be interspecifically territorial (Table 1), some of which do defend interspecific territories against one another (e.g., Melodious (*Hippolais polyglotta*) and Icterine Warblers (*H. icterina*) (Secondi, Faivre and Kreutzer, 1999); Thrush (*Luscinia luscinia*) and Common Nightingale (*L. luscinia*) (Sorjonen, 1986)).

Table 1. European species pairs predicted to be interspecifically territorial (n=24) using random forest algorithms (mtry=2, ntrees=50000) trained on North American pairs. A lack of documented territoriality is not indicative of an absence of territoriality.

Species pair	Documented territoriality
<i>Acrocephalus paludicola</i> & <i>Acrocephalus schoenobaenus</i>	
<i>Acrocephalus palustris</i> & <i>Acrocephalus scirpaceus</i>	Catchpole (1978)
<i>Certhia brachydactyla</i> & <i>Certhia familiaris</i>	Aggression but overlapping territories (Clouet and Gerard, 2020)
<i>Cyanistes caeruleus</i> & <i>Parus major</i>	
<i>Cyanistes caeruleus</i> & <i>Periparus ater</i>	
<i>Estrilda astrild</i> & <i>Estrilda troglodytes</i>	
<i>Ficedula albicollis</i> & <i>Ficedula hypoleuca</i>	Alatalo, Gustafsson and Lundberg (1997)
<i>Ficedula hypoleuca</i> & <i>Phoenicurus phoenicurus</i>	
<i>Fringilla coelebs</i> & <i>Fringilla montifringilla</i>	Overlapping territories (Mikkonen, 1985)
<i>Hippolais icterina</i> & <i>Hippolais polyglotta</i>	(Secondi, Faivre and Kreutzer, 1999)
<i>Lophophanes cristatus</i> & <i>Periparus ater</i>	
<i>Lophophanes cristatus</i> & <i>Poecile montanus</i>	
<i>Lophophanes cristatus</i> & <i>Poecile palustris</i>	
<i>Loxia curvirostra</i> & <i>Loxia pytyopsittacus</i>	
<i>Luscinia luscinia</i> & <i>Luscinia megarhynchos</i>	Sorjonen (1986)
<i>Passer domesticus</i> & <i>Passer hispaniolensis</i>	
<i>Passer domesticus</i> & <i>Passer italiae</i>	
<i>Passer hispaniolensis</i> & <i>Passer italiae</i>	
<i>Periparus ater</i> & <i>Poecile palustris</i>	
<i>Phylloscopus bonelli</i> & <i>Phylloscopus sibilatrix</i>	Aggression, but overlapping territories (Luepold, Carlotti and Pasinelli, 2024)
<i>Phylloscopus collybita</i> & <i>Phylloscopus ibericus</i>	
<i>Phylloscopus collybita</i> & <i>Phylloscopus trochilus</i>	Sæther (1983)
<i>Phylloscopus ibericus</i> & <i>Phylloscopus trochilus</i>	
<i>Sturnus unicolor</i> & <i>Sturnus vulgaris</i>	Motis Berta (1994)

Hybridisation data used for European hindcasting and to train random forests on North American pairs to predict interspecific territoriality differed slightly from those derived from Drury, Cowen and Grether (2020) and used in North American Hindcasting analyses. Drury, Cowen and Grether (2020) consulted McCarthy (2006) and a literature review of publications released after 2000 to find records of hybridisation. We also utilised these sources, but additionally included hybrids listed in the eBird taxonomy (Sullivan *et al.*, 2009) (Chapter 2). Hybrid classifications between the two datasets agreed in 95% of cases.

4.2.3 Indices of niche overlap

4.2.3.1 North America

Foraging guild classifications, the square root of body mass, and the square root of bill length difference were also taken from Drury, Cowen and Grether (2020) and included as fixed effects as measures of niche overlap. Foraging guild components were classified according to De Graaf, Tilghman and Anderson (1985) and included the main dietary component, foraging technique, and foraging substrate. The proportion of overlap across foraging axes for each pair was calculated as a measure of foraging niche overlap. Species pairs that overlap in foraging guild are likely to occupy similar niches and therefore compete with one another (De Graaf, Tilghman and Anderson, 1985), which may in turn influence coexistence (Gause, 1934b). Similarly, species with similar body masses and bill lengths are also more likely to occupy similar niches and compete for resources (Pigot *et al.*, 2020b). Whether both members of a pair were secondary cavity nesters was also included as a fixed effect, as these species may compete for nest sites as well as food resources (Brawn and Balda, 1988). Whether species in a pair share the same habitat density was included as a fixed effect as another indicator of potential niche overlap and coexistence. Habitat classifications were based on scores from Drury, Cowen and Grether (2020) and refer to the preferred habitat of each species. Categories 1 to 3 equate to open, semi-dense and dense habitats, respectively. To test whether the type of breeding territory a species defends impacts changes in range overlap (Freeman, Tobias and Schluter, 2019), we included an

index indicating whether both members of a pair defended the same intraspecific territory type (using a categorical index ranging from 1 [not territorial] to 5 [defending a ‘multipurpose’ territory in which both foraging and nesting occurs]; Drury, Cowen and Grether (2020)). Patristic distance, the time separating members of a pair on the phylogeny, was included in models to control for the time available for evolutionary divergence between taxa (Tobias *et al.*, 2014).

4.2.3.2 Europe

North American analyses were carried out before the publication of AVONET (Tobias *et al.*, 2022); hence, the use of body mass and bill length difference as a proxy for resource competition. However, with the subsequent availability of these comprehensive trait data, we decided to calculate a combined measure of morphometric dissimilarity for nine traits derived from AVONET data (Tobias *et al.*, 2022). This morphometric dissimilarity is the Euclidean distance between species in principal component space that includes beak length: culmen-to-tip, beak length: nares-to-tip, beak width, beak depth, tarsus length, wing length, secondary length, tail length and mass (see Chapter 2). The proportion of overlap across foraging axes for Europe was derived slightly differently as well. For each species, primary lifestyle (e.g. generalist, insessorial, aerial) and trophic niche (e.g. invertivore, vertivore, granivore) were extracted from AVONET (Tobias *et al.*, 2022), and if a species pair occupied the same lifestyle and niche, they were coded as ‘1’ in a binary variable. Preferred habitat classifications were also taken from AVONET (Tobias *et al.*, 2022), and if species occupied the same habitat type, they were coded as ‘1’. Intraspecific territoriality was the same as in North American models, as was patristic distance.

4.2.4 Range expansion and contraction

4.2.4.1 North America

Given that changes in range size could affect our index of changes in sympatry, we aimed to control for these changes so as to not conflate changes in overlap that result

from temporal variability in overall range size with changes that can be attributed to behavioural interference per se. We therefore included indices of range expansion and range contraction across a species' whole range within the BBS area. Specifically, if a species was present at a route between 1997 and 2000 but not present between 2016 and 2019, it was considered to have been extirpated from the route. Conversely, if a species was absent between 1997 and 2000 but present between 2016 and 2019, it was considered to have colonised the route. Both routes had to have been sampled in both time periods. For each species, the change in range size was derived as the number of routes colonised between 1997-2000 and between 2016-2019 minus the number of routes at which the species was extirpated. If this value was positive, a species was considered to have undergone range expansion, whereas if it was negative, it was considered to have experienced range contraction. Species pairs were then classified according to whether both species had undergone range expansion and range contraction. Out of 1602 pairs, both members of 607 pairs underwent range contraction, while both members of 242 pairs experienced range expansions (Table 2).

4.2.4.2 Europe

Measures of range contraction and expansion for Europe were calculated as above, but used colonisation of and extirpation from, PECBMS sites instead of North American BBS routes. Of the 418 European pairs, 55 pairs had members that both underwent range contraction, 142 pairs contained species that both experienced range expansion between 1997-2000 and 2016-2019. Only 1 pair contained species that neither contracted nor expanded (Table 2).

Table 2. The number of pairs in which the constituent species expanded, contracted, or had no net change in the number of BBS routes (North America) and PECBMS sites (Europe) between 1997 and 2019. Only routes/sites surveyed in both time periods are included.

		Number of pairs		
		Species 1		
		Range expansion	Range contraction	No change
North America	Range expansion	242	408	14
	Range contraction	271	607	21
	No change	16	21	2
Europe	Range expansion	142	99	7
	Range contraction	95	55	12
	No change	6	1	1

4.2.5 Statistical analysis

All analyses were conducted using R (www.r-project.org). To test the hypotheses that behavioural interference influenced recent changes in sympatry or syntopy, we fit phylogenetic linear mixed models (PLMMs) using an MCMC approach in the R package MCMCglmm (Hadfield, 2010). Relatively non-informative priors that correspond to an inverse-Wishart distribution were used for random effects. Flat priors were used for fixed effects (Hadfield, 2014). In addition to the fixed effects described above, the initial (i.e., 1997–2000) values of mean sympatry and syntopy were included as covariates to control for initial levels of overlap (Vickers and Altman, 2001; Barnett, van der Pols and Dobson, 2005). Random effects included species identity and a maximum clade credibility phylogeny (Jetz *et al.*, 2012), specifying the nodes representing the most recent common ancestor of a pair (see further details in Losin *et al.*, 2016; Drury, Cowen and Grether, 2020). A Cornell Lab of Ornithology Open Tree of Life (CLOOTL) phylogeny (Miller, Sanchez-Reyes and McTavish, 2025, 2025) was used for European analyses. Continuous response and predictor variables were scaled in each model. Every model was run for two million iterations with a burn-in of 20,000 and a thinning interval of 1000. We repeated each model fit four times and verified model convergence using Gelman–Rubin diagnostics (Gelman and Rubin, 1992) and visual inspection of trace plots.

For North American passerines, models with interaction terms between interspecific territoriality and hybridisation (i.e., where species pairs that engage in both forms of behavioural interference are coded as ‘1’ in the interaction term) and between interspecific territoriality and non-hybridisation (i.e., where species pairs that defend interspecific territories but do not hybridise are coded as ‘1’ in the interaction term) were also fitted, as these combinations of behavioural interference may have differing impacts on coexistence (Grether *et al.*, 2017; Cowen, Drury and Grether, 2020). If syntopy is a proxy for the similarity in habitat use between species, those pairs that are highly syntopic and therefore have similar requirements will respond more to changes in habitat availability than those with dissimilar requirements. To control for potential

changes in habitat availability (e.g., due to land-use change), we ran additional models in which both sympatry and syntopy datasets were subset to contain only pairs that shared the same habitat type (n=871). Then, the habitat type of either species was included as a fixed effect to determine if changes in habitat have contributed to changes in sympatry and syntopy.

Table 3. Predictor variables used in hindcasting phylogenetic generalised linear mixed models for North American and European data.

North American predictor variables	European predictor variables
Interspecific territoriality	Interspecific territoriality (imputed)
Hybridisation	Hybridisation
Same intraspecific territory type	Same intraspecific territory type
Patristic distance	Patristic distance
Shared foraging axes	Same lifestyle and trophic niche
Both secondary cavity nesters	Both secondary cavity nesters
Same habitat density	Same habitat type
Mass difference	Morphometric dissimilarity
Bill length difference	
Both expand	Both expand
Both contract	Both contract
Syntopy/sympatry 1997-2000	Syntopy/sympatry 1997-2000

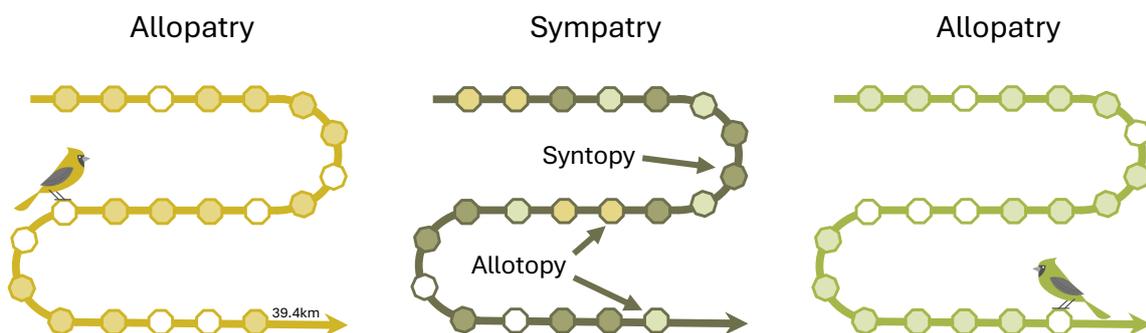
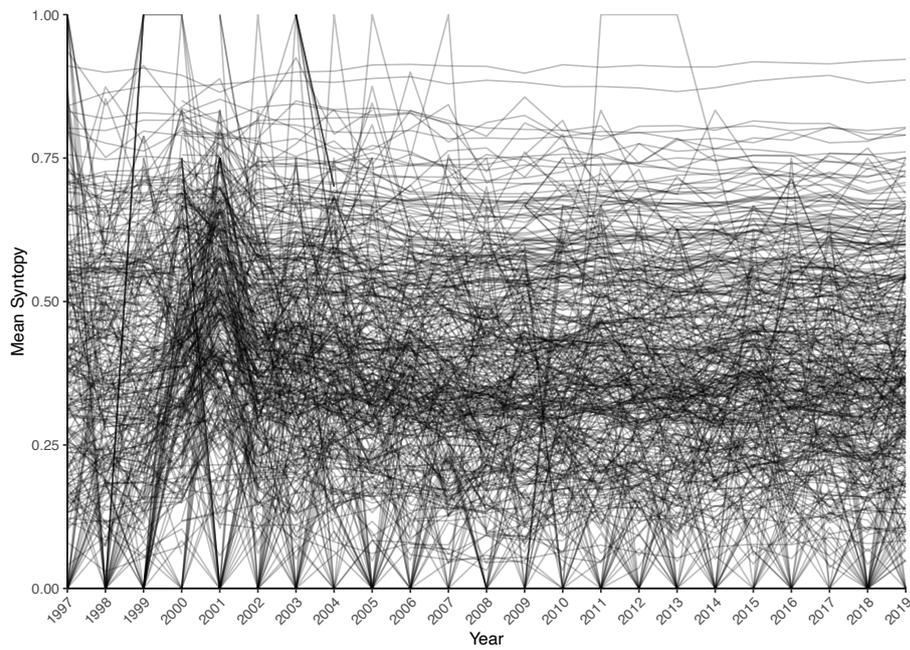


Figure 5. Schematic diagram of North American Breeding Bird Survey (NABBS) routes in Sympatry (dark green) and Allopatry (yellow and light green). Octagons represent syntopic (dark green) and allotopic (yellow, light green) NABBS stops at each route. Filled Octagons indicate species presence. Routes are 39.4km long with 50 stops along them.

A) Syntopy



B) Sympatry

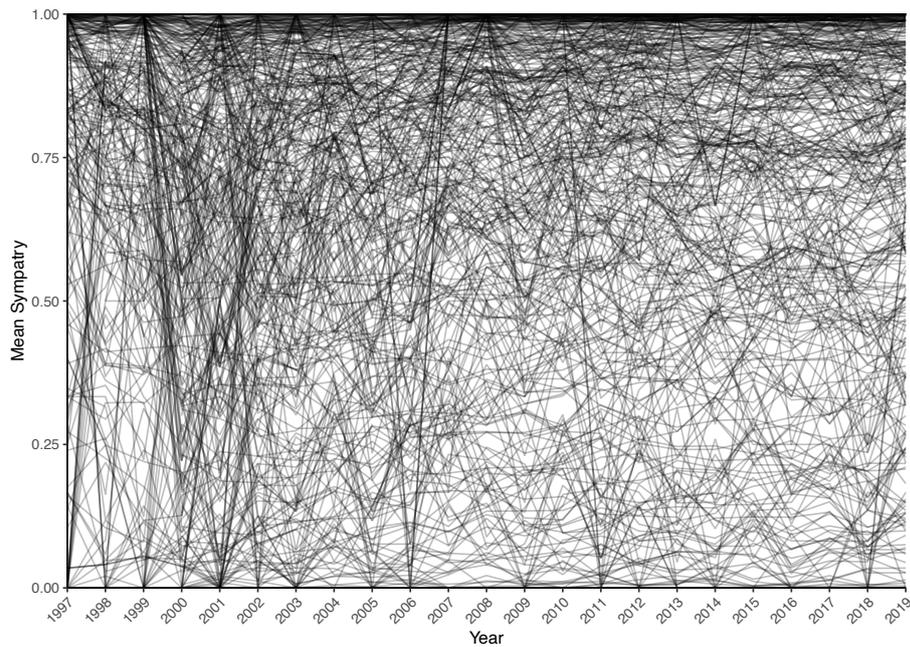


Figure 6. Mean syntopy (A) and mean sympatry (B) between 1997 and 2019 for European pairs ($n=418$). Each line corresponds to a pair. For rarer species, found at fewer sites, or years with fewer sites surveyed, it is possible that all the sites they occur at are within 40km of the other member of their species pair, hence the high frequency of sympatry equalling one.

4.3 Results

4.3.1 Syntopy

We found that interspecific territorial behaviour predicted changes in syntopy of North American passerines between 1997 and 2019 (Table 4, Figure 7A). Consistent with the hypothesis that forms of behavioural interference that cause spatial partitioning within habitats should facilitate coexistence, interspecifically territorial species pairs showed larger increases in syntopy than non-interspecifically territorial pairs (Table 4, Figure 7A). Specifically, interspecifically territorial pairs experienced an average 17% greater increase in syntopy than non-interspecifically territorial pairs (range across MCMC chains=15–19%). We also found that pairs occupying the same habitat types increased in syntopy more than those occupying different habitats (Table 4, Figure 7A). Further analyses restricted to species found in the same habitat still recovered an effect of interspecific territoriality (Appendix B), suggesting that our findings are robust to the potential confounding effects of changes in habitat suitability over this time period. We also found that pairs that defend different classes of intraspecific territories exhibit larger increases in syntopy than pairs that defend the same class of territory (Table 4, Figure 7A). When we restricted analyses to species pairs that defend the same type of territory and included terms for the type of intraspecific territoriality, thereby accounting for a potential confounding effect of intraspecific territory, we still recovered a strong effect of interspecific territoriality on Δ syntopy (Appendix B). We found no effect of hybridisation on Δ syntopy (Table 4, Figure 7A), nor did we find any evidence that the interaction between interspecific territoriality and hybridisation influenced syntopy.

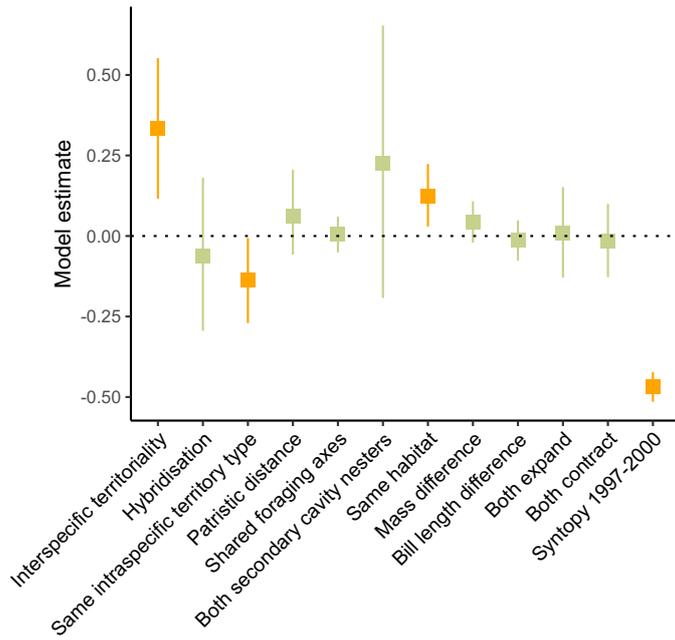
We found no effect of behavioural interference on changes in syntopy in European pairs (Table 6, Figure 8A). Morphometric dissimilarity emerged as a marginal predictor of Δ syntopy (p MCMC < 0.05 in 2 out of 4 chains, mean = 0.05025) (Table 6, Figure 8A). Species pairs that are more different morphologically became less syntopic between 1997 and 2019 than morphologically similar pairs.

4.3.2 Sympatry

After controlling for range expansions and contractions, we found no evidence for an effect of behavioural interference on changes in sympatry (Table 5, Figure 7B). Both mass difference and bill length difference were associated with Δ sympatry. As mass difference increased, Δ sympatry decreased. Contrastingly, as bill length difference increased, Δ sympatry increased. As with syntopy analyses, we found no effect of either hybridisation or an interaction between interspecific territoriality and hybridisation on Δ sympatry (Table 5, Figure 7B).

Similarly, in Europe, we found no evidence for the effect of territoriality or hybridisation on changes in sympatry (Table 7, Figure 8B). However, we did find pairs in which both species are secondary cavity nesters increased in sympatry more so than non-secondary cavity nesters between 1997 and 2019 (Table 7, Figure 8B).

A)



B)

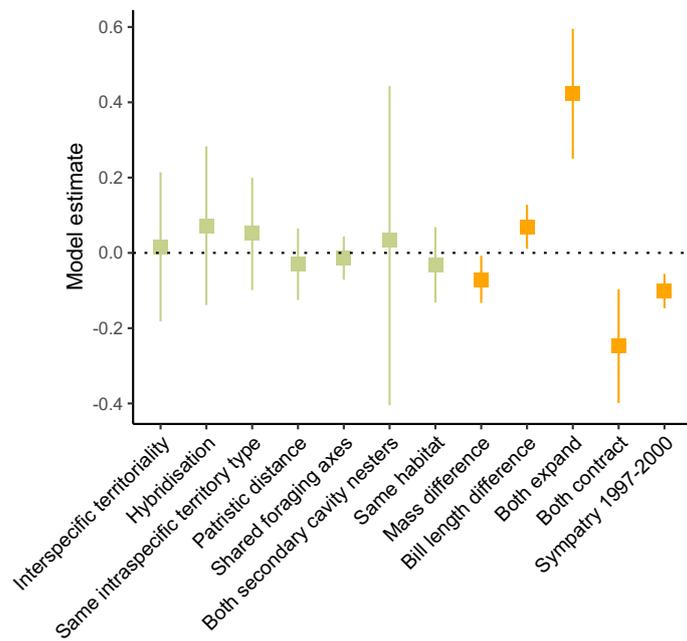


Figure 7: Predictors of Δ syntopy (A) and Δ sympatry (B) in North American pairs. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed models with Δ syntopy and Δ sympatry as the response variables. Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0.

Table 4. Predictors of the change in syntopy between 1997–2000 and 2016–2019 (Δ syntopy) for North American pairs from phylogenetic linear mixed models (n = 1602 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.101 (95% CI = 0.002, 0.343). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
	Intercept	0.046	-0.319	0.415	0.773	
Δ syntopy	Interspecific territoriality	0.335	0.116	0.552	0.001	**
North	Hybridisation	-0.061	-0.294	0.181	0.613	
America	Same intraspecific territory type	-0.138	-0.270	-0.007	0.045	*
	Patristic distance	0.061	-0.058	0.205	0.251	
	Shared foraging axes	0.005	-0.051	0.060	0.848	
	Both secondary cavity nesters	0.226	-0.192	0.654	0.275	*
	Same habitat	0.125	0.029	0.224	0.012	
	Mass difference	0.043	-0.020	0.108	0.183	
	Bill length difference	-0.014	-0.077	0.048	0.658	
	Both undergone range expansion	0.010	-0.129	0.152	0.891	
	Both undergone range contraction	-0.014	-0.127	0.100	0.817	
	Syntopy 1997–2000	-0.468	-0.515	-0.422	<0.0005	***

Table 5. Predictors of the change in sympatry between 1997–2000 and 2016–2019 (Δ sympatry) for North American pairs from phylogenetic linear mixed models (n = 1602 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.024 (95% CI = 0.0005, 0.162). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
	Intercept	0.016	-0.265	0.287	0.885	
Δ sympatry	Interspecific territoriality	0.017	-0.182	0.214	0.857	
North	Hybridisation	0.071	-0.138	0.283	0.509	
America	Same intraspecific territory type	0.052	-0.099	0.200	0.494	
	Patristic distance	-0.030	-0.125	0.065	0.437	
	Shared foraging axes	-0.013	-0.071	0.044	0.660	
	Both secondary cavity nesters	0.034	-0.404	0.443	0.891	
	Same habitat	-0.033	-0.132	0.068	0.519	
	Mass difference	-0.071	-0.133	-0.008	0.029	*
	Bill length difference	0.069	0.011	0.128	0.022	*
	Both undergone range expansion	0.425	0.250	0.595	<0.0005	***
	Both undergone range contraction	-0.247	-0.399	-0.097	0.001	**
	Sympatry 1997–2000	-0.102	-0.147	-0.056	<0.0005	***

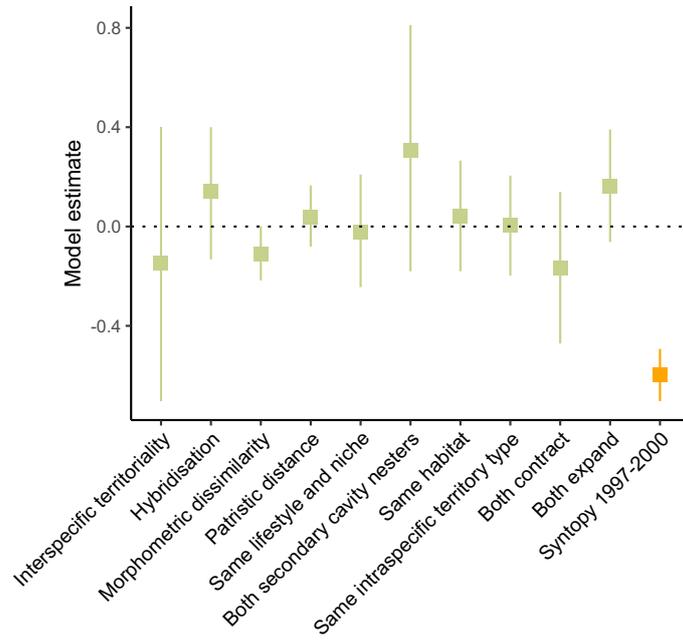
Table 6. Predictors of the change in syntopy between 1997–2000 and 2016–2019 (Δ syntopy) for European pairs from phylogenetic linear mixed models (n = 418 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 although values for morphometric dissimilarity differ slightly across chains (1= 0.049, 2=0.042, 3=0.057, 4=0.055). The mean phylogenetic signal (λ) for this model was 0.066 (95% CI = 0.0002, 0.342). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Δ syntopy Europe	Intercept	-0.068	-1.141	1.129	0.797	
	Interspecific territoriality	-0.149	-0.704	0.401	0.586	
	Hybridisation	0.141	-0.132	0.400	0.316	
	Same intraspecific territory type	0.004	-0.198	0.205	0.996	
	Patristic distance	0.038	-0.081	0.166	0.527	
	Same lifestyle and trophic niche	-0.022	-0.244	0.209	0.841	
	Both secondary cavity nesters	0.308	-0.180	0.811	0.214	
	Same habitat type	0.042	-0.180	0.266	0.698	
	Morphometric dissimilarity	-0.109	-0.217	0.000	0.049	*
	Both expand	0.164	-0.062	0.391	0.276	
	Both contract	-0.167	-0.471	0.139	0.155	
	Syntopy 1997-2000		-0.596	-0.703	-0.493	<0.0005

Table 7. Predictors of the change in sympatry between 1997–2000 and 2016–2019 (Δ sympatry) for European pairs from phylogenetic linear mixed models (n = 418 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.0323 (95% CI=0.0002, 0.201). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
Δ sympatry Europe	Intercept	0.035	-0.687	0.884	0.862	
	Interspecific territoriality	-0.301	-0.855	0.249	0.292	
	Hybridisation	-0.018	-0.292	0.248	0.870	
	Same intraspecific territory type	0.028	-0.174	0.233	0.773	
	Patristic distance	0.057	-0.062	0.176	0.357	
	Same lifestyle and trophic niche	-0.032	-0.252	0.190	0.785	
	Both secondary cavity nesters	0.558	0.088	1.053	0.027	*
	Same habitat type	-0.103	-0.319	0.114	0.348	
	Morphometric dissimilarity	0.033	-0.074	0.143	0.554	
	Both expand	-0.074	-0.379	0.232	0.666	
	Both contract	0.041	-0.184	0.273	0.769	
	Sympatry 1997-2000		-0.415	-0.519	-0.312	<0.0005

A)



B)

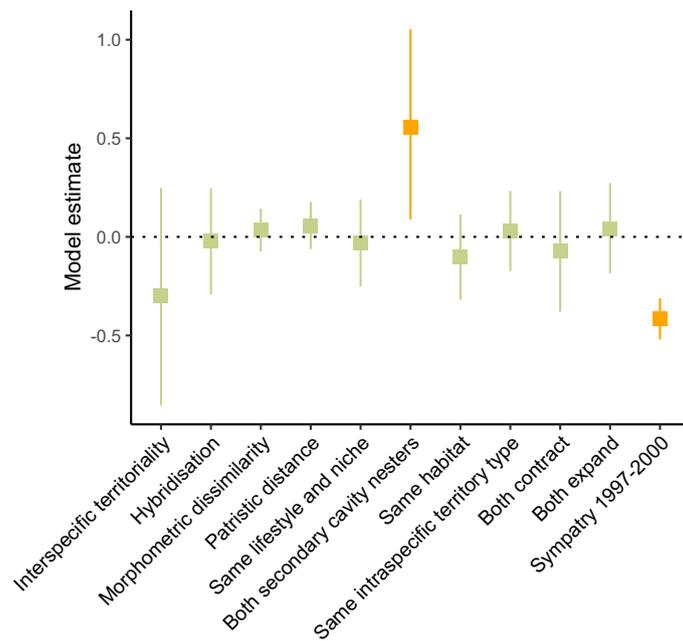


Figure 8: Predictors of Δ syntopy (A) and Δ sympatry (B) between 1997-2000 and 2016-2019 in European pairs. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed models with Δ syntopy and Δ sympatry as the response variables. Points correspond to the median and error bars represent the 95% credibility interval from

four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0.

4.4 Discussion

We found support for the hypothesis that interspecific territoriality has accelerated fine-scale habitat overlap in North American passerines. To our knowledge, ours is the first study examining temporal changes in syntopy on a continental scale, showing a clear effect even over a short time period (22 years). The finding that interspecific territoriality facilitates fine-scale habitat overlap echoes several recent investigations demonstrating that behavioural interference affects spatiotemporal dynamics of assemblages (Pearson, 2000b; Pearson and Rohwer, 2000; Duckworth and Badyaev, 2007; Krosby and Rohwer, 2010; Vallin *et al.*, 2012; McQuillan and Rice, 2015; Rybinski *et al.*, 2016). However, while several studies of individual species pairs have shown that behavioural interference can impede coexistence in birds, our analysis of 1602 pairs shows that interspecific territoriality appears to have an overall positive effect on coexistence in North American passerines. However, for our 418 European passerine pairs, we found no support for the impact of territoriality on changes in fine-scale habitat overlap. This could be a genuine biological pattern or could be the result of inaccuracies in the imputation of European interspecific territoriality by random forest models trained on North American pairs.

Other factors, in addition to behavioural interference, may have impacted the patterns of range dynamics that we documented. For instance, in North American pairs, we found evidence that habitat type affected changes in syntopy, in line with previous studies finding that bird population dynamics in North America are not uniform across different habitat types (La Sorte and Boecklen, 2005a; Rosenberg *et al.*, 2019). Similarly, we found that defending the same intraspecific territory type was negatively associated with Δ syntopy. Given that the vast majority of North American passerines defend multipurpose territories, a non-zero value for this variable largely (in 97.5% of pairs) represents cases where both species defend multipurpose territories, which may suggest that strong intraspecific territory defence on average slows down spatial

movement (an important avenue for future research). Nevertheless, even after accounting for these factors, we found an effect of interspecific territoriality on recent shifts in fine-scale habitat overlap.

The presence or magnitude of interspecific territoriality may vary across space and time (e.g. across different habitat types, Reed (1982)), but the sparse nature of data on observations of territorial aggression in birds means that information on this variation is currently unavailable. As such, we were unable to relate variation in interspecific territoriality to variation in range dynamics for each species pair. Gathering data on geographic variation in behavioural interference would require fieldwork on a much larger geographic scale than is typically attempted in avian empirical studies. However, platforms such as eBird (Sullivan *et al.*, 2009) offer the potential to enlist large numbers of birders in the effort to classify local breeding populations in this way, and potentially open the door to deeper investigations of the relationship between behavioural interference and range overlap on different scales.

Models of sympatry dynamics did not support a role for behavioural interference driving shifts in range-wide overlap. This finding supports the notion that simple indices of range overlap may fail to capture the potential for species interactions adequately (Drury, Cowen and Grether, 2020). At a continental level, processes tend to be expressed on an evolutionary timescale rather than the ecological timescale of habitat-scale processes (Connor and Bowers, 1987), and as such, the relatively brief time span of this study may have failed to detect these processes. Nevertheless, we found evidence that traits related to resource competition are associated with changes in range-wide overlap; in North America, mass and bill similarity did predict changes in sympatry, though in opposing directions (mass similarity corresponded to increases in range overlap and bill length similarity corresponded to decreases in range overlap). The relationship between mass and range overlap could be related to higher dispersal ability in larger birds (Pigot and Tobias, 2015) and/or habitat filtering (Polo and Carrascal, 1999a). The contrasting relationship between bill length and range overlap, on the other hand, could indicate a role for competitive exclusion (Pigot and Tobias, 2013a). Yet, why these effects would only act at a range-wide scale and not a local habitat scale is not

clear. Further work could shed more light on whether these patterns hold at larger timescales or across other functional traits.

The marginal negative effect of morphometric dissimilarity on changes in syntopy in European pairs is somewhat surprising. At a habitat-scale, we expected species that differ more morphologically to be able to coexist more so than morphologically similar species that are more likely to compete with one another (Gause, 1934b; Schoener, 1974; Abrams, 1983). However, particular environments may favour certain morphologies, resulting in the co-occurrence of morphologically similar species. Species with similar beak morphologies and diets can be more syntopic (Remeš and Harmáčková, 2023, 2025), although this increased syntopy is associated with divergence in foraging strata (Remeš and Harmáčková, 2023).

In Europe, we found species pairs in which both members are secondary cavity nesters increased in sympatry more so than non-cavity nesters or those able to excavate their own cavities. With nest cavities being a highly sought-after resource (Brawn and Balda, 1988), it would be expected that species competing for them may exhibit competitive exclusion (Duckworth *et al.*, 2017b). Why we find the opposite, and at a range-scale rather than habitat scale, is not known. Perhaps an increase in nest box provisioning (Davies *et al.*, 2009) has allowed species competing for nest boxes to expand their ranges and coexist more (Davies *et al.*, 2009; Duckworth, 2013; Lima and Garcia, 2016).

We found no evidence in models of syntopy or sympatry dynamics that either hybridisation or the joint action of hybridisation and interspecific territoriality impacted range dynamics. In contrast, recent analyses on sister-taxa suggest that behavioural interference, including hybridisation, influences the attainment of secondary sympatry (Cowen, Drury and Grether, 2020). The discrepancy between our findings and those of Cowen, Drury and Grether (2020) is likely a result of the vastly different timescales of our analyses. Indeed, most studies investigating the influence of species interactions on range dynamics concern changes that have taken place over millions of years (Gross and Price, 2000; Jankowski, Robinson and Levey, 2010; Jankowski *et al.*, 2012; Pigot and Tobias, 2013a; Freeman, Class Freeman and Hochachka, 2016; Boyce and Martin,

2019). Nevertheless, others have focused on the influence of species interactions on contemporary range dynamics (Pearson, 2000b; Pearson and Rohwer, 2000; Poling and Hayslette, 2006; Duckworth and Badyaev, 2007; Mac Nally *et al.*, 2012b; Vallin *et al.*, 2012; van Dongen *et al.*, 2013; Wiens, Anthony and Forsman, 2014c; Rybinski *et al.*, 2016; Friedemann *et al.*, 2017). Another consideration that may explain discrepancies between our study and other studies relates to starting levels of interspecific range overlap. Theoretical models posit that range dynamics in the face of behavioural interference are likely to be positively frequency-dependent, and therefore, systems with interference are often prone to competitive and/or sexual exclusion when at least one species occurs at a low frequency (Kuno, 1992b). The species pairs studied here, however, were already sympatric at the onset of the study period, and therefore, interspecific territoriality between these lineages is likely to be evolutionarily stable (Drury *et al.* 2020, Cowen *et al.* 2020).

Determining how processes that unfold on ecological timescales scale up to generate macroevolutionary dynamics is an open challenge in the field (Weber *et al.*, 2017; Harmon *et al.*, 2019; Hembry and Weber, 2020). Further research harnessing the power of long-term census data like those from the North American BBS promises to play an important role in achieving this micro-to-macro link. Our analyses contribute to a growing body of work demonstrating how behavioural interference impacts fundamental ecological and evolutionary processes. Further understanding of these impacts will improve our ability to predict the consequences of species interactions that form in novel assemblages as a result of ongoing, human-induced global change.

Chapter 5

Geographic Avoidance

5.1 Introduction

Species distributions are affected by abiotic factors, such as climate and topography (Grinnell, 1917; Woodward and Williams, 1987), biotic factors (e.g., species interactions such as predation, parasitism, mutualism and competition (Wiszniewski *et al.*, 2013; Louthan, Doak and Angert, 2015)), alongside dispersal ability (Pigot and Tobias, 2015), productivity (Heuck *et al.*, 2013) and some degree of stochasticity. However, the relative influence of each of these factors on distributions at various spatial scales is uncertain. Abiotic interactions and the effects of environmental filtering appear to be more important at larger scales, while biotic interactions exert more influence at local scales (Araújo and Rozenfeld, 2014; Howard *et al.*, 2015, 2020). Nevertheless, biotic interactions can scale up to affect broad-scale species distributions (Connor and Bowers, 1987; Araújo and Luoto, 2007; Heikkinen *et al.*, 2007; Sexton *et al.*, 2009; Gotelli, Graves and Rahbek, 2010; Pigot and Tobias, 2013b; Wiszniewski *et al.*, 2013; Araújo and Rozenfeld, 2014; Belmaker *et al.*, 2015; Mönkkönen *et al.*, 2017; Machado-Stredel, Atauchi, Nuñez-Penichet, Cobos, Osorio-Olvera, Khalighifar, Peterson and R. J. Fletcher, 2024).

This chapter focuses primarily on the effects of competition on large-scale range limits. As part of this, we differentiate between two types of competition: exploitative competition and behavioural interference. Exploitative competition is indirect, acting through the depletion of shared resources (Maurer, 1984). Species with similar foraging niches are likely to exhibit exploitative competition (Alatalo *et al.*, 1987). Without some form of resource partitioning, direct competitors are unable to coexist and competitive exclusion results (Gause, 1934a). This competitive exclusion occurs at a habitat scale, with one species being excluded from a particular habitat (Reif *et al.*, 2018a; Sottas *et al.*, 2018; Ulrich *et al.*, 2018), which can then scale up to influence large-scale range limits (MacArthur and Levins, 1964; Diamond, 1973; Terborgh and Weske, 1975; Bull, 1991). Species distributions are not static (Chris D. Thomas and Lennon, 1999; Parmesan and Yohe, 2003), and competition for resources can influence range dynamics and the ease with which species move across landscapes (HilleRisLambers *et al.*, 2013b; Alexander *et al.*, 2016b; Lawlor *et al.*, 2024).

While exploitative competition results in exclusion, mechanisms exist in which it can ultimately lead to coexistence, primarily as a result of character displacement (Brown and Wilson, 1956). Ecological character displacement occurs between species experiencing exploitative competition. Selection favours divergence in phenotypic traits associated with resource acquisition, which can then facilitate coexistence as species niches diverge and competition between them lessens (Brown and Wilson, 1956; Grether *et al.*, 2009).

Exploitative competition is not the sole way in which species compete. Behavioural interference—direct and costly species interactions that encompass interference competition (e.g., interspecific aggression and territoriality) and reproductive interference (e.g. interspecific courtship, signal blocking and hybridisation) can also influence species distributions and range dynamics (see Chapter 4)(Grether *et al.*, 2017; Patterson and Drury, 2023). Territoriality is intrinsically linked to exclusion; by definition, territoriality is the exclusion of individuals from a defended area (Nice, 1941b). Species may occupy checkerboard distributions at a local-scale as a result of interspecific territoriality (Robinson and Terborgh, 1995). Increasing in scale, interspecific territoriality can lead to habitat-scale exclusion in which subordinate species are confined to certain habitat types in the presence of a competitor. On the Islands of Gotland and Öland, dominant Collared Flycatchers (*Ficedula albicollis*) exclude subordinate Pied Flycatchers (*F. hypoleuca*) from high-quality deciduous forest patches, confining them to relatively poorer coniferous woodland (Vallin and Qvarnström, 2011b; Vallin *et al.*, 2012; Rybinski *et al.*, 2016). Exclusion in the *Ficedula* flycatchers is the result of aggression, interspecific territoriality and hybridisation (Vallin and Qvarnström, 2011b; Vallin *et al.*, 2012; Rybinski *et al.*, 2016). Behaviourally mediated exclusion can scale up beyond local habitats and lead to large-scale range exclusion and the formation of parapatric range boundaries (reviewed in Patterson and Drury, 2023). This interference-mediated parapatry can occur at altitudinal boundaries (Jankowski, Robinson and Levey, 2010; Freeman, 2016b; Freeman and Montgomery, 2016; Freeman, Class Freeman and Hochachka, 2016; Boyce and Martin, 2019; Freeman, Tobias and Schluter, 2019; Freeman, Strimas-mackey and Miller, 2022) , as is

the case in some Costa Rican *Catharus* thrushes (Jankowski, Robinson and Levey, 2010) and Papuan robins (Freeman, 2016b; Freeman, Class Freeman and Hochachka, 2016). Interspecific territoriality also limits non-elevational range boundaries and creates abutting distributions (Gross and Price, 2000; McQuillan and Rice, 2015).

Rather than precluding coexistence, in some instances, interspecific territoriality may facilitate coexistence, creating spatial segregation and subsequent resource partitioning that allows similar species to coexist within the same habitat (Glenn A. Marvin, 1998; Ovadia and Zu Dohna, 2003; Ziv and Kotler, 2003; Nesbit *et al.*, 2023)(see Chapter 4). Several instances of interspecifically territorial and ecologically similar species exhibiting stable coexistence support this hypothesis (Rohwer, 1973; Jankowski *et al.*, 2012; Drury *et al.*, 2015, 2019; Reif *et al.*, 2015; Freeman, 2016b).

Hybridisation and interspecific territoriality are intrinsically linked (Drury, Cowen and Grether, 2020) , and reproductive interference often occurs in conjunction with interspecific territoriality to influence coexistence (Vallin *et al.*, 2012; Duckworth and Semenov, 2017). On Öland, male Pied Flycatchers struggle to establish territories in the presence of dominant Collared Flycatchers. As such, the density of male Pied Flycatchers decreases, increasing the likelihood of female Pied Flycatchers hybridising with Collared Flycatchers, in turn accelerating exclusion through the reduced fitness of hybrid offspring (Vallin *et al.*, 2012). Of all forms of reproductive interference, hybridisation may be the most pertinent in determining range limits and dynamics due to the greater fitness costs often associated with hybrid offspring and its less ephemeral nature (Gröning and Hochkirch, 2008). When hybridisation is frequent at parapatric boundaries, hybrid zones can form (Barton and Hewitt, 1985; Bull, 1991a; Good *et al.*, 2000; Howard *et al.*, 2004; Vallin *et al.*, 2012; McEntee, Burleigh and Singhal, 2020), and multiple hybrid zones can occur in suture zones, where biogeography facilitates secondary contact between multiple species groups (Swenson and Howard, 2004; Swenson, 2006). If hybrid fitness is low, hybrid zones can be exceptionally narrow (sometimes only a few kilometres (Moore, 1977)) and stable, preventing the range expansion of one species into the other (Mettler and Spellman, 2009; Natola, Seneviratne and Irwin, 2022). However, if hybridisation is asymmetric and one species

is competitively dominant, the hybrid zone can shift, and the subordinate species' range may be usurped through reproductive exclusion (Ribeiro and Spielman, 1986; Krosby and Rohwer, 2010; McQuillan and Rice, 2015).

If competition is responsible for determining a species' range boundaries, in the absence of natural barriers and obvious environmental gradients (Bull, 1991), a species should be absent from climatically suitable habitat where a competitor is present, but occupy that climatic niche where the competitor is absent (Diamond, 1973; Terborgh and Weske, 1975; Freeman, Tobias and Schluter, 2019; Freeman, Strimas-Mackey and Miller, 2022). In other words, competition should cause a species to occupy a smaller amount of its fundamental niche than would be occupied in the absence of competition (Hutchinson, 1957). This concept is the basis of geographic avoidance, a metric developed by Novella-Fernandez *et al.* (2021), which utilises the outputs from species distribution models (SDMs) to determine the extent to which the predicted ranges of a species pair are realised in the presence, versus in the absence, of one another. First tested on ten species of cryptic Palearctic bats with varying degrees of ecological similarity, geographic avoidance was greatest in those species with the highest ecological similarity and lack of partitioning mechanisms (Novella-Fernandez *et al.*, 2021). This avoidance, greater than null expectations (based on the ranges of virtual species), suggests a role for competition in the structuring of ecological communities and range boundaries more so than would be expected by chance (Novella-Fernandez *et al.*, 2021).

In the current era of rapid anthropogenic climate change, it is vital that we further our understanding of species distributions and the impact of species interactions upon them. It is important to understand if, and which, species will be prevented from tracking their climate niche by competitors or excluded from suitable areas by competitors tracking their own niche (Blois *et al.*, 2013; J.-C. Svenning *et al.*, 2014; Alexander, Diez and Levine, 2015; Early and Keith, 2019; Legault *et al.*, 2020a). As such, here we calculate geographic avoidance between thousands of North American and European pairs of birds. We also examine the effects of various forms of competition on this avoidance. We aim to discover whether exploitative competition and/or behavioural

interference influence geographic avoidance at large spatial scales. We also calculate measures of avoidance for individual members of each pair, from which we create a measure of avoidance symmetry. We then test to see if competition influences the degree of avoidance symmetry within pairs.

5.2 Methods

5.2.1 Geographic avoidance

To identify the influence of species interactions on large-scale species distributions, we used the geographic avoidance metric developed by Novella-Fernandez et al. (2021). Geographic avoidance makes use of predictions of species fundamental niches (climatically suitable areas), and species realised ranges from species distribution models (SDMs [see below]) and range maps, respectively, to determine the extent to which species pairs realise their fundamental niche in areas of sympatry versus areas of allopatry.

Geographic avoidance is calculated as:

$$(Eq. 1) \quad GA_{ij} = 1 - \frac{RO_{ij}(PR_i + PR_j - 2(PO_{ij}))}{PO_{ij}(RR_i + RR_j - 2(RO_{ij}))}$$

Where PR_i and PR_j are the predicted ranges of species i and j , respectively. PO_{ij} is the predicted overlap between species i and j . While RR_i and RR_j are the realised ranges of species i and j , respectively, and RO_{ij} is the realised overlap between them. The unit for each of these metrics is the number of 0.5° grid cells on a Behrman equal-area projection with which a species' range (realised or predicted) overlaps by at least 10%, as an arbitrary threshold. An overlap threshold is utilised as the polygons used to create SDMs are likely imprecise along the borders, so to assume cells with little overlap with polygons are occupied could be unrealistic. Also, mean values for climate are typically used in large cells, so if a species only occurs at the periphery of a cell, it is less likely to be utilising the climatic environments typical of that cell.

If $GA_{ij} < 0$, a higher proportion of a species pair's combined predicted range is realised in overlapping (sympatric) areas than in non-overlapping (allopatric) areas. If $GA_{ij} > 0$, a lower proportion of the pair's combined predicted range is realised in sympatric areas, which would be expected if the presence of a competitor resulted in less of the

climatically suitable range (of one or both species) being occupied. If $GA_{ij} = 0$, an equal proportion of a pair's combined predicted range is realised in sympatry and allopatry (see exemplar in Figure 1).

GA_{ij} is a symmetric measure of avoidance between species in a pair, but it is not particularly informative regarding differences between the responses of individual species within a pair. As such, we developed asymmetric measures of avoidance, GA_i and GA_j , that account for the individual responses of species i and species j , respectively, to the presence of one another. GA_i and GA_j are calculated as follows:

$$(Eq. 2) \quad GA_i = \frac{RO_{ij}}{PO_{ij}} \times \frac{PR_i - PO_{ij}}{RR_i - RO_{ij}}$$

$$(Eq. 3) \quad GA_j = \frac{RO_{ij}}{PO_{ij}} \times \frac{PR_j - PO_{ij}}{RR_j - RO_{ij}}$$

Where PR_i , PR_j , PO_{ij} , RR_i , RR_j and RO_{ij} are as above. Using these asymmetric geographic avoidance measures, we then calculated a measure of symmetry (GA_{sym}) for each individual species in a species pair to determine how the species within a pair differ in their level of geographic avoidance, where:

$$(Eq. 4) \quad p = \left(\frac{\min(GA_i, GA_j)}{\max(GA_i, GA_j)} \right) + 0.0001$$

$$(Eq. 5) \quad GA_{sym} = \log\left(\frac{p}{1-p}\right)$$

0.0001 is added to p to prevent it from equalling 0 or 1, which would prevent GA_{sym} from being calculated. Pairs with lower GA_{sym} values have more asymmetric levels of avoidance. For instance, species i may be unable to fulfil most of its suitable climate niche due to the presence of species j , whereas species j may be able to occupy the

entirety of its climatic niche despite the presence of species *i*. Higher values of GA_{sym} mean more symmetric species-specific avoidance values, in that species are more equal in their responses to the presence of one another (see exemplar in Figure 1).

We filtered our dataset in several ways, as follows. Species pairs with no predicted (PO_{ij}) or realised overlap (RO_{ij}) were removed from analyses as they gave GA_{ij} values of NA and 1, respectively. Further, Novella-Fernandez et al. (2021) identified that due to GA_{ij} being based on ratios, species with proportionally very small range overlaps (less than 0.5% of the realised range of either species) can provide unreliable, inflated estimates of GA_{ij} . This 0.5% threshold was specific to the 10 pairs of bats analysed by Novella-Fernandez et al. (2021). Visual inspection of scatterplots of the proportion of the range of species *i* or species *j* encompassed by RO_{ij} against GA_{ij} suggested that adopting a 1% overlap threshold would remove most outliers. Consequently, such low-overlap species pairs were removed from subsequent analyses. When calculating asymmetric measures of GA_i and GA_j , we inspected scatterplots of the proportion of the range of species *i* or species *j* encompassed by RO_{ij} against GA_i and GA_j , respectively. We found species with a high proportion, or all, of their realised range within the area of realised overlap had exceptionally high values of GA_i and GA_j . As a result, pairs with species whose ranges were more than 90% within the area of realised overlap were also removed.

5.2.2 Species predicted ranges

The SDMs used to extract predicted ranges (PR_i , PR_j) and predicted overlap (PO_{ij}) were created by Gillie (2024). The species we could include in our analyses for North America and Eurasia were limited to those with available SDMs. These were species classified as occupying the Nearctic, Palearctic or Holarctic by the IUCN. There were SDMs available for 445 North American species and 324 European species from our species lists in Chapter 2. Non-native species were excluded from analyses as their non-native ranges were not included in the original SDM creation. Further, a few species were removed from analyses due to recent taxonomic splits and SDM data being unavailable for both taxa, these included *Anas platyrhynchos* and *A. diazi*, *Aphelocoma californica* and *A. woodhousii*, *Icterus galbula* and *I. bullockii*, and *Loxia curvirostra* and *L. sinesciuris*.

SDMs were created using rasterised breeding and resident range polygons from BirdLife International (BirdLife International and Handbook of the Birds of the World, 2021). Rasters had a resolution of 0.5° and a Behrman equal-area projection. Five WorldClim bioclimatic variables, for 1970-2000, were used to create SDMs, including BIO1; annual mean temperature, BIO4; temperature seasonality, BIO13; precipitation of the wettest period, BIO14; precipitation of the driest period and BIO15; precipitation seasonality (Fick and Hijmans, 2017). These variables are the most parsimonious combination of bioclimatic variables that correspond most closely to the determinants of species distributions (Titley *et al.*, 2021). Species distributions were modelled using presence-absence data in an ensemble approach with generalised linear models (GLMs), general additive models (GAMs), generalised boosted regression models (BRTs) and random forest models (RFs) (Elith *et al.*, 2006; Bagchi *et al.*, 2013; Titley *et al.*, 2021). The probability of occurrence for each cell was converted to presence-absence using species-specific thresholds that maximised the sum of sensitivity and specificity (Liu *et al.*, 2005; Titley *et al.*, 2021). Species distributions were clipped by suitable habitat based on IUCN habitat preferences, with habitat data from Jung *et al.*, (2020). The current predicted ranges (PR_i , PR_j) of many species appeared to predict distant and extensive unoccupied areas of suitable range in alternate continents. For example, some North American species were predicted to have suitable climate space in Eurasia, and vice versa (Figure 4), and while the climate may be highly suitable in those areas, it seems unlikely that they do not occupy the opposite continent as a result of competition but more likely limited dispersal and oceanic barriers. To avoid issues of overinflated measures of GA_{ij} as a result of unoccupied suitable areas on alternate continents, global rasters were clipped by two different bounding boxes for both North America and Eurasia. The first cropped rasters longitudinally only, at -18°W, so maps were divided into the Americas and the rest of the world (hereafter long clip). The second included an additional latitudinal clip to limit predictions to the areas of interest in the Northern Hemisphere (North America and Eurasia). For North America, this crop was at 6°N and for Eurasia, 30°N (hereafter lat/long clip). Analyses were carried out on data from both clips separately to determine what, if any, effect the restriction of predicted ranges has on the results and conclusions drawn.

5.2.3 Species realised ranges

The same BirdLife shapefiles of species breeding ranges used to train the SDMs were also used to extract species' current realised range (RR_i , RR_j) and realised overlap (RO_{ij}). As before, shapefiles were rasterised and projected into the Behrman equal-area coordinate reference system. A single raster was created for each species, containing the predicted range (PR_i/PR_j) derived from SDMs and the realised range (RR_i/RR_j) from the rasterised range polygon. Although 24 species in our dataset occur in both North America and Europe, their distributions on each continent were considered separately. Species were paired with every other member of their family, and combined rasters were created for predicted ranges and realised ranges, with the values of predicted overlap (PO_{ij}) and realised overlap (RO_{ij}) being extracted from their respective rasters. Clipping did not affect all pairs, however, for many (1956 in North America and 1402 in Eurasia) it resulted in smaller, more constrained ranges and as such any conclusions drawn regarding geographic avoidance refer only to species ranges within the clipping areas rather than their global range.

5.2.4 Predictors of Geographic Avoidance

We collated data on several ecological and life history traits of species to test if they were related to geographic avoidance and avoidance symmetry. The first of these variables was interspecific territoriality, which was included as territoriality can lead to species coexistence and exclusion, at large scales (Patterson and Drury, 2023). Unfortunately, due to limited data availability, we were only able to run models including interspecific territoriality for a subset of North American passerine pairs ($n=356$) for which territoriality data already existed (Drury, Cowen and Grether, 2020). Hybridisation was included as a predictor of GA_{ij} to account for the potential effects of reproductive interference and sexual exclusion on large-scale range patterns (Patterson and Drury, 2023). Hybridisation data were collected from McCarthy (2006), the eBird taxonomy (Sullivan et al. 2009) and a literature search, as described in Chapter 2. We also included Morphometric dissimilarity as a potential predictor of GA_{ij} , calculated as the

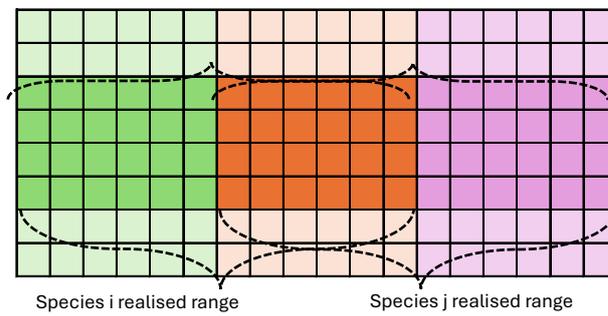
Euclidean distance between species pairs in a principal component space for nine morphometric traits derived from AVONET (Tobias *et al.*, 2022)(see Chapter 2). This was included as a proxy for niche and diet similarity, accounting for exploitative competition. Patristic distance was calculated using the cophenetic function in the R package ape (Paradis and Schliep, 2019) and represents a measure of relatedness and time since species divergence, it also acts somewhat as a latent variable, accounting for phylogenetically-conserved traits not measured by the other predictor variables. Lastly, data on nesting strategy, whether species are secondary-cavity nesters, were extracted from Birds of the World (Billerman *et al.*, 2022). If both species are secondary cavity nesters and therefore unable to excavate their own nest cavities, nest sites are likely to be a highly sought-after resource and the subject of intense competition and therefore may influence large-scale range dynamics (Brawn and Balda, 1988; Heikkinen *et al.*, 2007).

5.2.5 Phylogenetic Generalised Linear Mixed Models

To disentangle the influence of exploitative competition or behavioural interference on geographic avoidance and avoidance symmetry in Eurasia and North America, we ran Phylogenetic Linear Mixed Models (PLMMs) with GA_{ij} and GA_{sym} as response variables using the R package MCMCglmm (Hadfield, 2010). We included interspecific territoriality, hybridisation, morphometric dissimilarity, patristic distance and whether both members of a pair are secondary cavity nesters as predictor variables. For each PLMM, four chains were each run for 2 million iterations, with a burn-in of 20,000, a thinning interval of 1000 and a non-informative inverse-Wishart distribution prior. PLMMs included species identity and nodes specifying the most recent common ancestor as random effects and incorporated a maximum clade credibility Cornell Lab of Ornithology Open Tree of Life (CLOOTL) phylogeny (McTavish *et al.*, 2025; Miller, Sanchez-Reyes and McTavish, 2025). Model convergence was assessed using Gelman-Rubin diagnostics (Gelman and Rubin 2009) and visual inspection of trace plots.

A)

Species i predicted range Species j predicted range

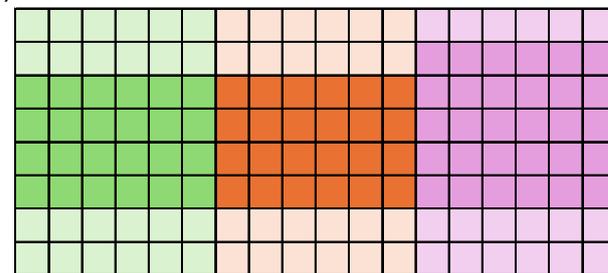


PO _{ij}	48
RO _{ij}	24
PR _i	96
RR _i	48
PR _j	96
RR _j	48

Species i realised range Species j realised range

GA _{ij}	GA _i	GA _j	GA _{sym}
0.00	1.00	1.00	9.21

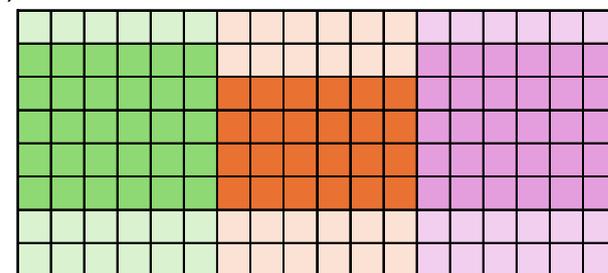
B)



PO _{ij}	48
RO _{ij}	26
PR _i	96
RR _i	48
PR _j	96
RR _j	54

GA _{ij}	GA _i	GA _j	GA _{sym}
0.11	1	0.8	1.39

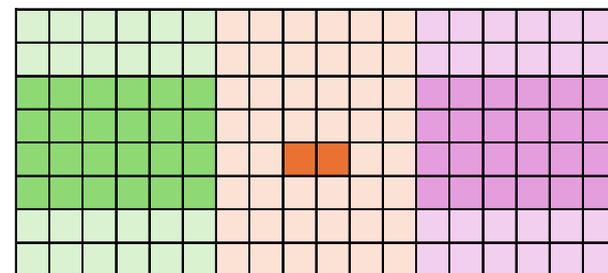
C)



PO _{ij}	48
RO _{ij}	24
PR _i	96
RR _i	54
PR _j	96
RR _j	54

GA _{ij}	GA _i	GA _j	GA _{sym}
0.20	0.80	0.80	8.99

D)



PO _{ij}	48
RO _{ij}	2
PR _i	96
RR _i	26
PR _j	96
RR _j	26

GA _{ij}	GA _i	GA _j	GA _{sym}
0.92	0.08	0.08	6.73

E)

PO _{ij}	48
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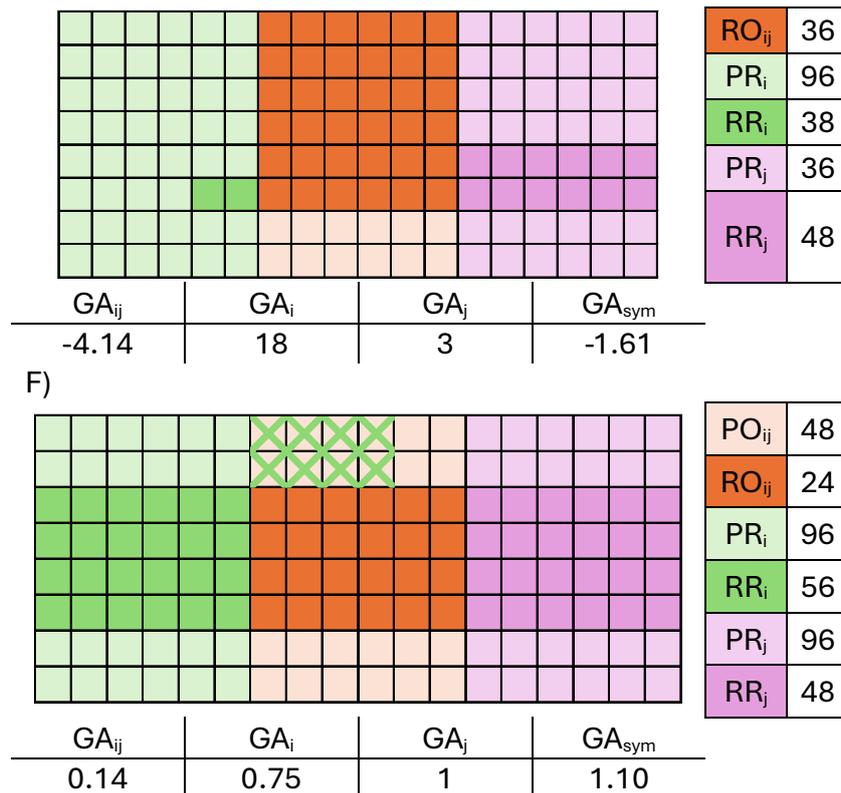


Figure 1. Schematic diagram of the predicted (PR_i= light green, PR_j= light pink) and realised (RR_i=dark green, RR_j= dark pink) ranges of two exemplar species (i=green, j=pink) and their predicted (PO_{ij}= light orange) and realised (RO_{ij}= dark orange) overlap, with relevant geographic avoidance and avoidance symmetry metrics displayed below each diagram. A) symmetric, no avoidance, both species occupy the same proportion of their range inside and outside the area of predicted overlap. B) minor asymmetric avoidance, species j occupies more of its predicted range outside the area of predicted overlap. C) Symmetric minor avoidance, both species occupy more of their range outside the area of predicted overlap. D) High symmetric avoidance, both species realise more of their predicted range outside the area of predicted overlap. E) Asymmetric low geographic avoidance (non-avoidance), both species realise more of their predicted range within the area of predicted overlap, but a greater proportion of species i range is in the area of overlap than outside it. F) Species are also able to occupy areas of predicted overlap alone (green hatching).

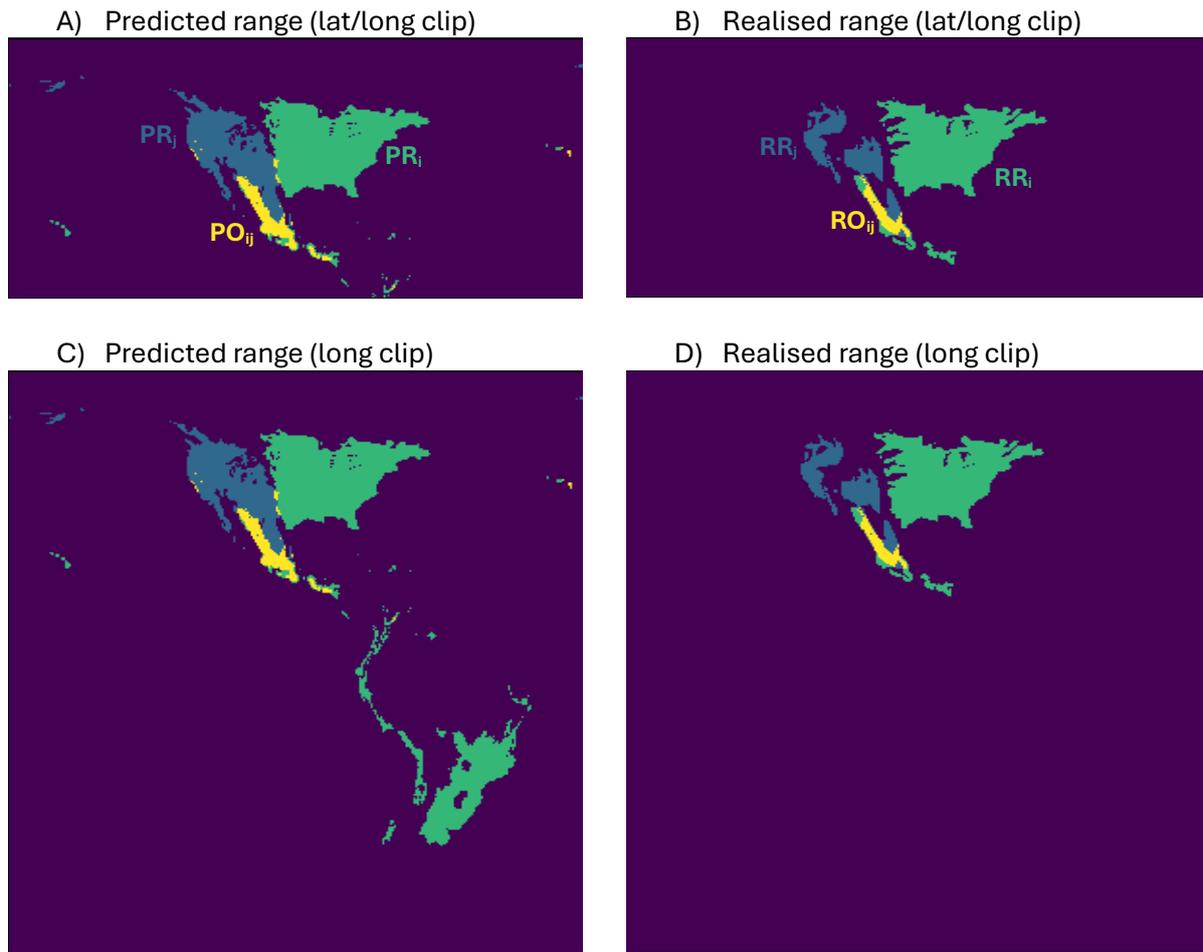


Figure 2: Predicted (A, C) and realised ranges (B,D) of Western Bluebird (*Sialia mexicana*) (Blue, species j) and Eastern Bluebird (*S. sialis*) (Green, species i), and their overlap (yellow), clipped latitudinally and longitudinally (A,B) and by longitude only (C,D). Values to the right are derived from the lat/long clip (A,B) and refer to the number of cells and the derived measures of avoidance.

Species i	PR _i	3483	
	RR _i	3080	
Species j	PR _j	2151	
	RR _j	1126	
Neither	PO _{ij}	414	
	RO _{ij}	214	
Overlap			
GA _{ij}	GA _i	GA _j	GA _{sym}
0.34	0.55	0.98	0.25

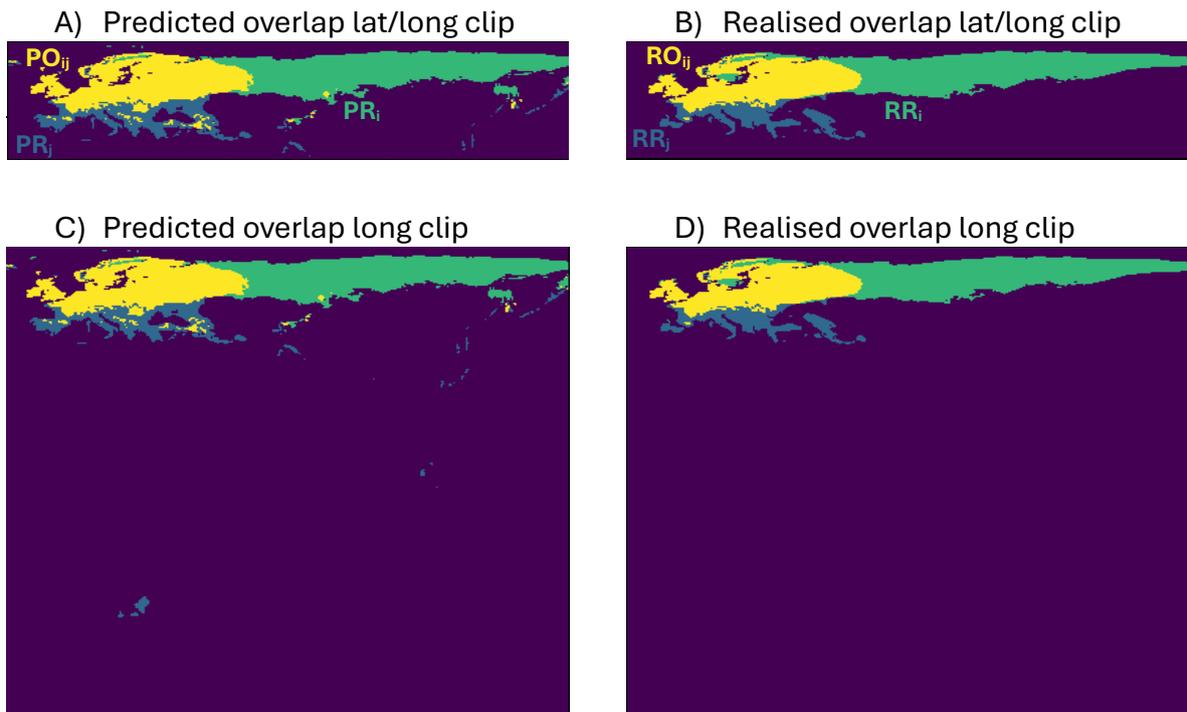


Figure 3: Predicted (A, C) and realised ranges (B,D) of Common Chiffchaff (*Phylloscopus collybita*) (Blue, species j) and Willow Warbler (*P. trochilus*) (Green, species i), and their overlap (yellow), clipped latitudinally and longitudinally (A,B) and by longitude only (C,D). Note the suitable range predicted in South Africa for the Chiffchaff. Values to the right are derived from the lat/long clip (A,B) and refer to the number of cells and the derived measures of avoidance.

Species i	PR_i	8743	
	RR_i	8053	
Species j	PR_j	5456	
	RR_j	8053	
Neither	PO_{ij}	3664	
	RO_{ij}	3115	
Overlap			
GA_{ij}	GA_i	GA_j	GA_{sym}
0.06	0.87	1.16	1.10

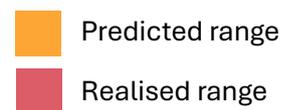
A) Eastern Bluebird (*Sialia sialis*) predicted and realised global range



B) Common Chiffchaff (*Phylloscopus collybita*) predicted and realised global range



Figure 4: Global raster of the predicted (orange) and realised range (pink) of (A) Eastern Bluebird (*Sialia sialis*) and (B) Common Chiffchaff (*Phylloscopus collybita*). Note the extent of predicted suitable range within Eurasia and South America for the Eastern Bluebird and in North America and South Africa for the Common Chiffchaff.



5.3 Results

On average, Eurasian pairs had greater predicted and realised range overlap than North American pairs (Figure 5). We found many species pairs in North America ($n=1049$, 53% (lat/long clip)) and Eurasia ($n=469$, 44%) exhibited some form of geographic avoidance ($GA_{ij} > 0$) (Figure 6A). Average GA_{ij} was slightly higher in Eurasia for both longitudinally clipped and latitudinally and longitudinally clipped datasets (median = 0.424 and 0.450, respectively) than in North America (median = 0.334 and 0.379) (Figures 6A & 7A). In North America, Cassin's Vireo (*Vireo cassinii*) and Plumbeous Vireo (*Vireo plumbeus*) had the greatest levels of avoidance (lat/long clip $GA_{ij}=0.98$). Kentucky Warbler (*Geothlypis formosa*) and Yellow-throated Warbler (*Setophaga dominica*) had the lowest levels of avoidance (lat/long clip $GA_{ij}=-0.81$) in North America. While in Eurasia, Eurasian Spoonbill (*Platalea leucorodia*) and Glossy Ibis (*Plegadis falcinellus*) had the lowest avoidance (lat/long clip $GA_{ij}=-0.68$), and Rock Partridge (*Alectoris graeca*) and Red-legged Partridge (*Alectoris rufa*) had the highest avoidance (lat/long clip $GA_{ij}=0.97$).

All pairs exhibited some level of asymmetry in their avoidance (Figure 6B & 7B). The greatest level of asymmetry in North America was between White-tailed Kite (*Elanus leucurus*) and White-tailed Hawk (*Geranoaetus albicaudatus*) (lat/long clip $GA_{asym}=-8.16$, $GA_i = 0.00$, $GA_j = 0.35$), while the most symmetric pair were Wood Duck (*Aix sponsa*) and Northern Pintail (*Anas acuta*) (lat/long clip $GA_{asym}=8.72$, $GA_i = 0.6452$, $GA_j = 0.6453$). For Eurasia, the greatest asymmetry was between Bonelli's Eagle (*Aquila fasciata*) and Black-winged Kite (*Elanus caeruleus*) (lat/long clip $GA_{asym}=-8.82$, $GA_i=0.00$, $GA_j = 0.67$) while Little Stint (*Calidris minuta*) and Jack Snipe (*Lymnocyptes minimus*) were the most symmetric in their avoidance (lat/long clip $GA_{asym}=6.75$, $GA_i=0.364$, $GA_j = 0.363$). There was little difference in average GA_{sym} between Eurasia and North America (lat/long clip median = 0.843 and 1.08, respectively) (Figures 6B & 7B).

GA_{ij} and GA_{sym} appear to be fairly uncorrelated, although in the long clip North American and Eurasian data show opposite trends (Figure 8A). In North America, as GA_{ij} increases so too GA_{sym} does, whereas the Eurasian data have a negative correlation. In the

lat/long clip as GA_{ij} increases there is a slight decrease in GA_{sym} and North American and European pairs respond similarly (Figure 8B).

We found no support for the effect of hybridisation, morphometric dissimilarity, patristic distance or secondary cavity-nesting on the level of Geographic Avoidance in North America or Eurasia, nor in datasets clipped latitudinally and longitudinally or only longitudinally (Figure 8A, 8B, 9A & 9B, Tables 1, 2, 4 & 5). The same was true for the data subset to North American passerines with available data on interspecific territoriality, interspecific territoriality did not predict GA_{ij} either (Figure 9C & 10C, Tables 3 & 6).

By contrast, in North American pairs, hybridisation emerged as a significant negative predictor of GA_{sym} . Pairs that hybridise were more likely to have more asymmetric measures of GA_i and GA_j than pairs that do not hybridise (Figure 9D & 10D, Table 7 & 10). The same was true for the North American passerine subset that included interspecific territoriality (which remained insignificant), but only for the long clip (Figure 9F, Table 9). In Eurasia, hybridisation did not influence asymmetry, instead, morphometric dissimilarity was a positive predictor of GA_{sym} (Figure 10E, Table 8). As species pairs become more morphologically different, they become more symmetric in their avoidance responses. These results were consistent between models run on lat/long clip data and long clip data (Figure 10E, Table 11).

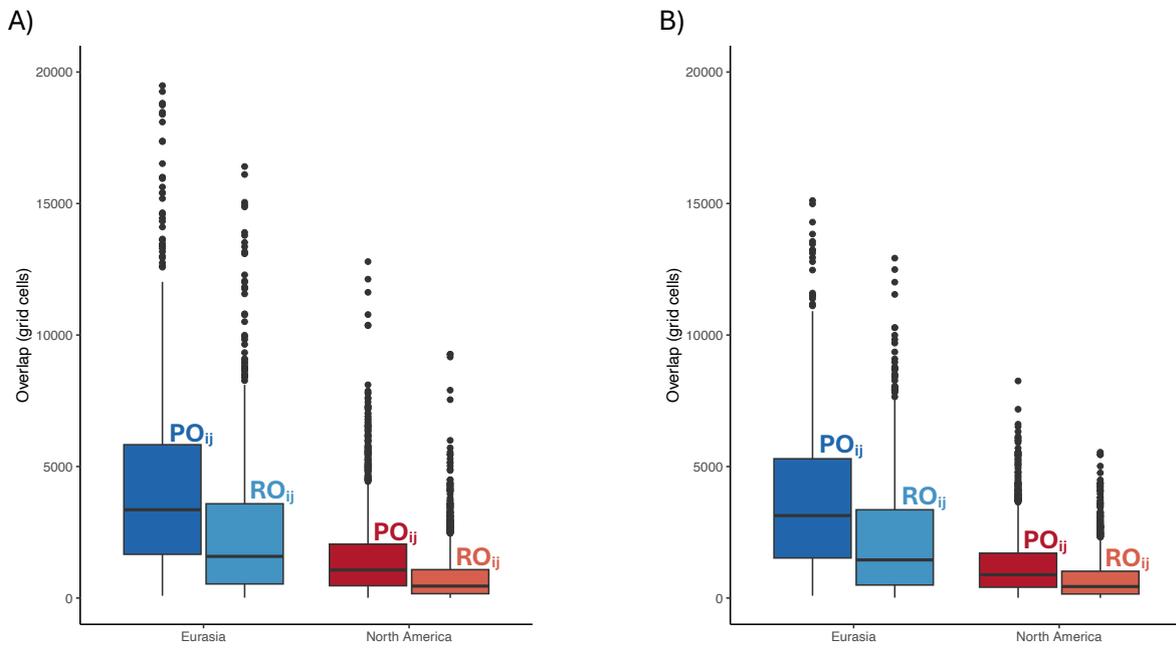


Figure 5: Average number of predicted (PO_{ij} , darker shade) and realised (RO_{ij} , lighter shade) overlapping grid cells for species i and species j in Eurasia (blue) and North America (red). Boxes represent median and interquartile range, while whiskers indicate maximum and minimum values excluding outliers. A) Data from long clip. B) Data from lat/long clip.

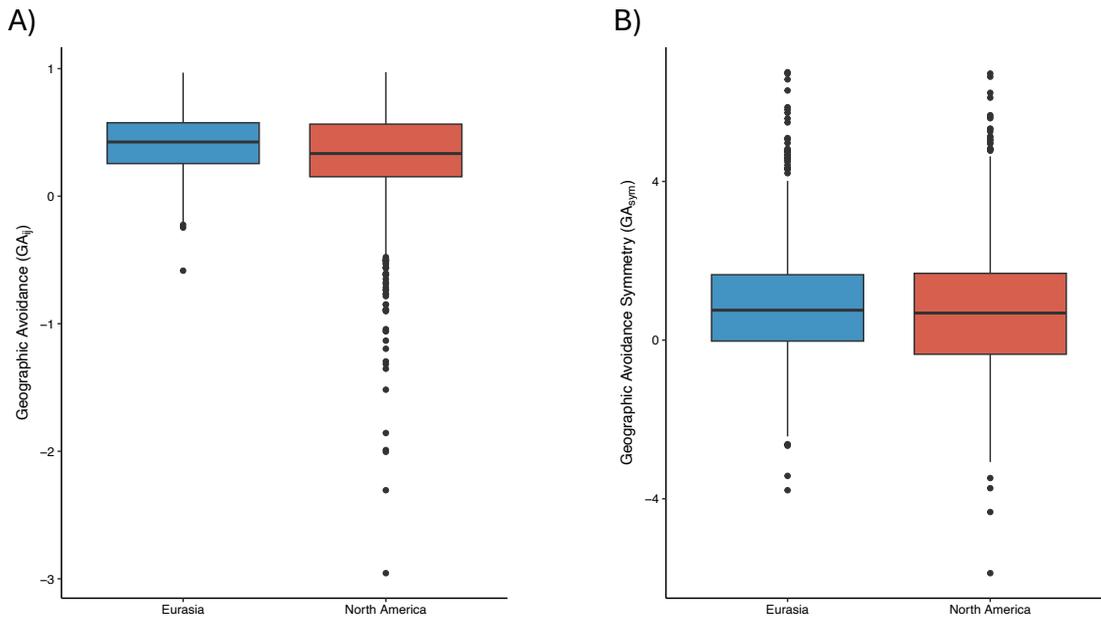


Figure 6. Geographic Avoidance (GA_{ij}) (A) and GA_{ij} symmetry (GA_{sym}) for Eurasia (blue) and North America (red). Boxes represent median and interquartile range, while whiskers indicate maximum and minimum values excluding outliers. Data from long clip.

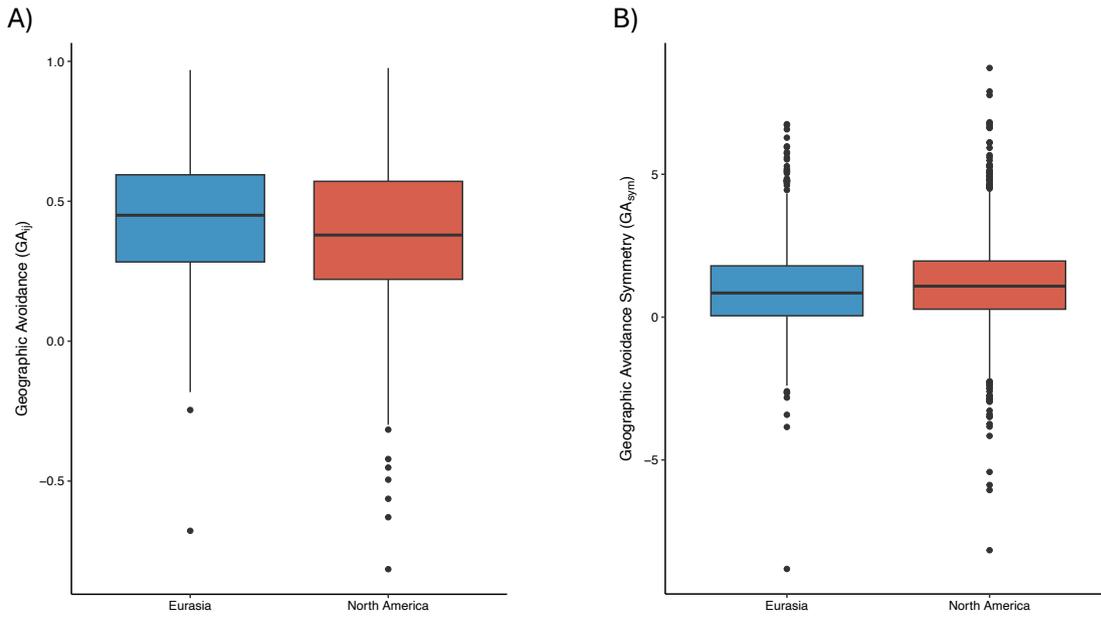


Figure 7. Geographic Avoidance (GA_{ij}) (A) and GA_{ij} symmetry (GA_{sym}) for Eurasia (blue) and North America (red). Boxes represent median and interquartile range, while whiskers indicate maximum and minimum values excluding outliers. Data from lat/long clip.

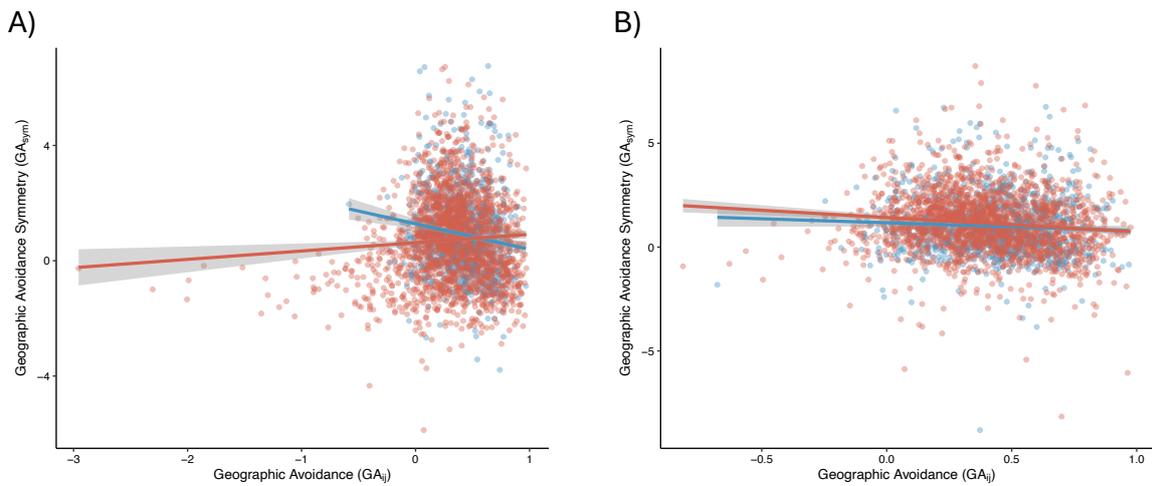
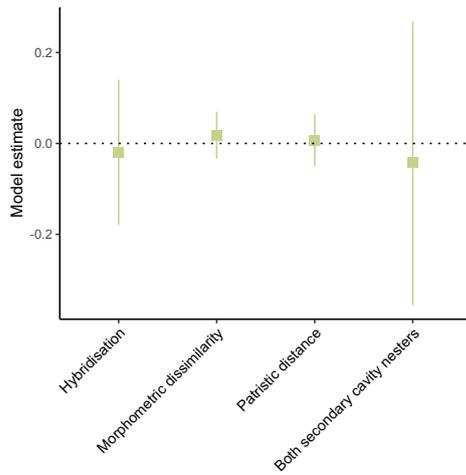
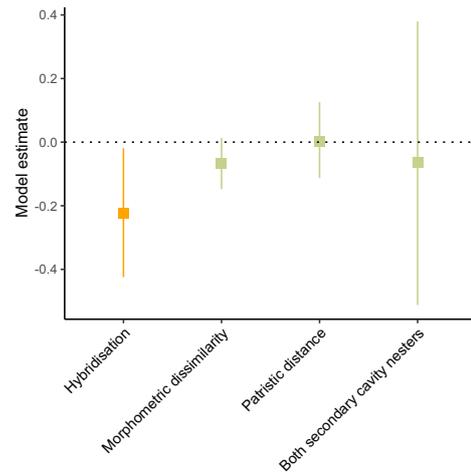


Figure 8. Geographic avoidance (GA_{ij}) and avoidance symmetry (GA_{sym}) for Europe (blue) and North America (red). A) data from long clip. B) data from lat/long clip.

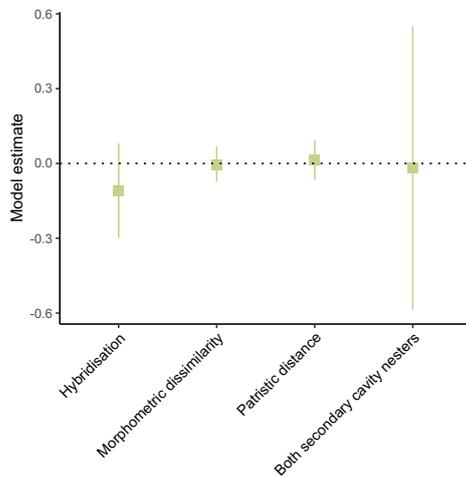
A) GA_{ij} North America long clip



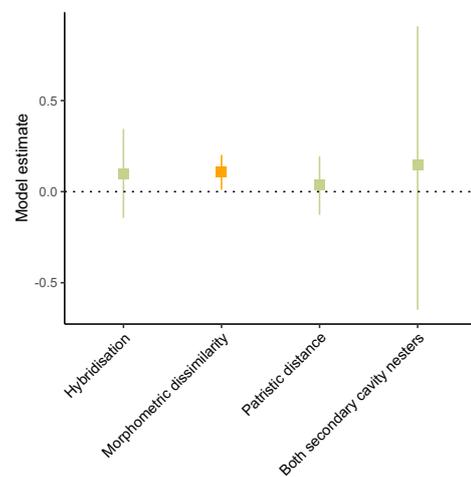
D) GA_{sym} North America long clip



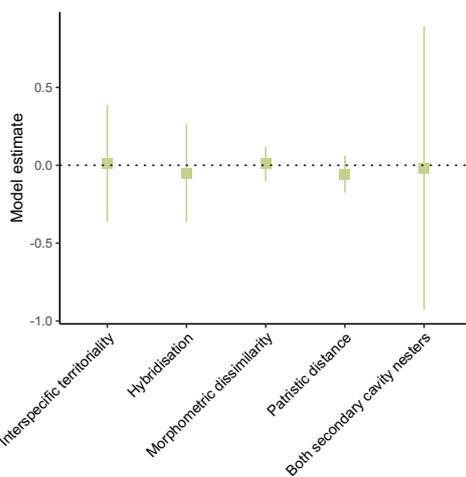
B) GA_{ij} Eurasia long clip



E) GA_{sym} Eurasia long clip



C) GA_{ij} North America IT long clip



F) GA_{sym} North America IT long clip

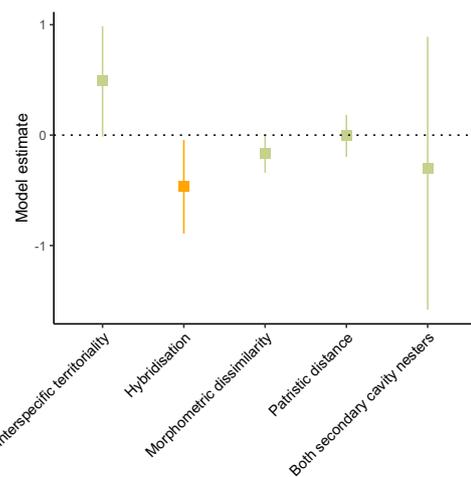
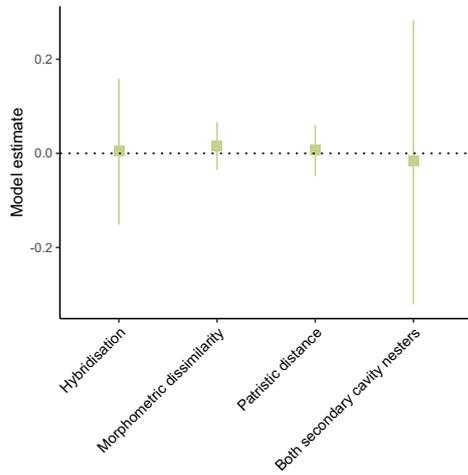


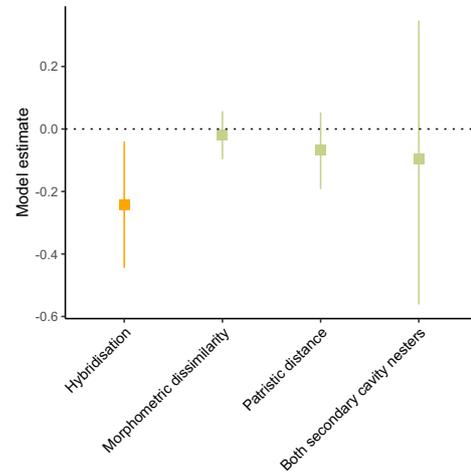
Figure 9: Predictors of the Geographic Avoidance (GA_{ij}) (A,C,E) and GA_{ij} symmetry (GA_{sym}) (B,D,F) in North America (A,B,E,F) and Eurasia (C,D) using data from longitudinal clips. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed model with GA_{ij} and GA_{sym} as the response variables. Points correspond to the median and error bars

represent the 95% credibility interval from four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0. E and F are a subset of North American passerines with available data on interspecific territoriality.

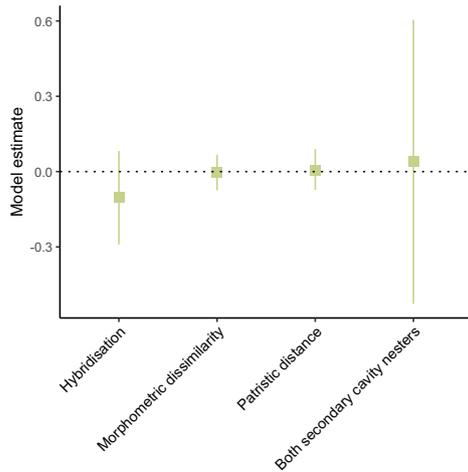
A) GA_{ij} North America lat/long clip



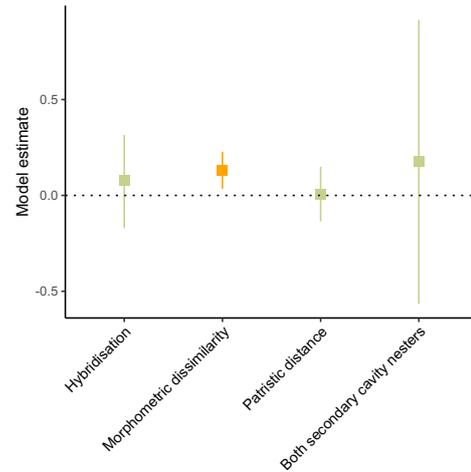
F) GA_{sym} North America lat/long clip



B) GA_{ij} Eurasia lat/long clip



E) GA_{sym} Eurasia lat/long clip



C) GA_{ij} North America w. territoriality lat/long clip

F) GA_{sym} North America w. territoriality IT lat/long clip

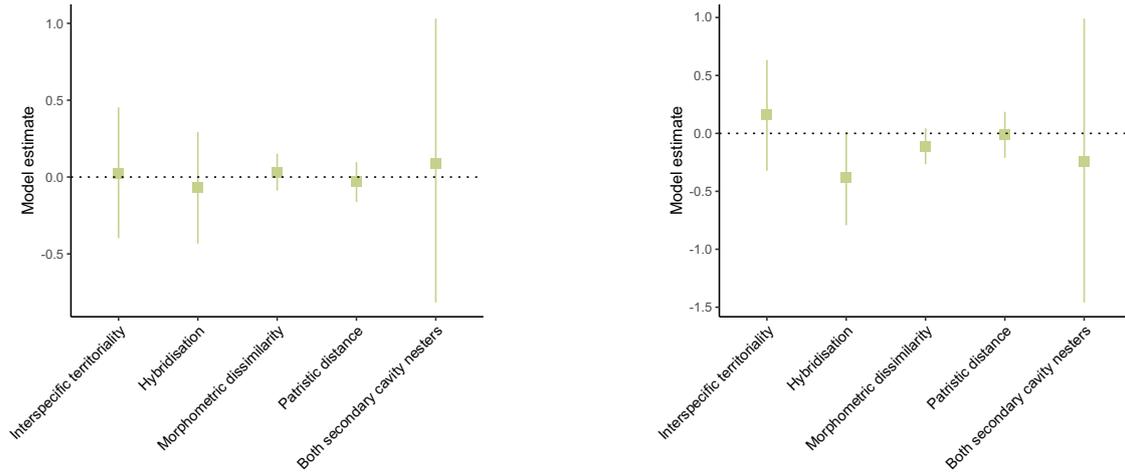


Figure 10: Predictors of the Geographic Avoidance (GA_{ij}) (A,C,E) and GA_{ij} symmetry (GA_{sym}) (B,D,F) in North America (A,B,E,F) and Eurasia (C,D) using data from lat/long clips. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed model with GA_{ij} and GA_{asym} as the response variables. Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0. E and F are a subset of North American passerines with available data on interspecific territoriality.

Table 1. Predictors of Geographic Avoidance (GA_{ij}) for North America (n = 1938 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.0009) (95% CI = 0.0001, 0.003). Mean DIC = 3825.65. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1 (results are similar across all chains). Data from longitudinal clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
	Intercept	0.341	0.270	0.429	<0.0005 ***
North America GA_{ij} long clip	Hybridisation	-0.021	-0.180	0.140	0.782
	Morphometric dissimilarity	0.018	-0.034	0.070	0.472
	Patristic distance	0.007	-0.050	0.063	0.819
	Both secondary cavity nesters	-0.043	-0.356	0.268	0.775

Table 2. Predictors of Geographic Avoidance (GA_{ij}) for Eurasia (n = 1055 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.0010) (95% CI = 0.00010, 0.0043). Mean DIC = 2009.13. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from longitudinal clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
	Intercept	0.421	0.329	0.509	<0.0005 ***
Eurasia GA_{ij} long clip	Hybridisation	-0.109	-0.299	0.081	0.238
	Morphometric dissimilarity	-0.004	-0.075	0.069	0.910
	Patristic distance	0.012	-0.066	0.093	0.773
	Both secondary cavity nesters	-0.018	-0.587	0.550	0.931

Table 3. Predictors of Geographic Avoidance (GA_{ij}) for a subset of North American passerines with available interspecific territoriality data. (n = 354 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.0049) (95% CI = 0.00013, 0.030). Mean DIC = 883.96. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from longitudinal clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
North America territory subset GA_{ij} long clip	Intercept	0.178	-0.082	0.439	0.119
	Interspecific territoriality	0.010	-0.364	0.387	0.949
	Hybridisation	-0.051	-0.365	0.268	0.763
	Morphometric dissimilarity	0.009	-0.101	0.118	0.876
	Patristic distance	-0.056	-0.175	0.061	0.347
	Both secondary cavity nesters	-0.021	-0.927	0.893	0.935

Table 4. Predictors of Geographic Avoidance (GA_{ij}) for North America (n = 1972 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.0008) (95% CI = 0.00009, 0.003). Mean DIC= 3760.92. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1 (results are similar across all chains). Data from lat/long clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
	Intercept	0.399	0.333	0.475	<0.0005 ***
North America GA_{ij} lat/long clip	Hybridisation	0.004	-0.152	0.158	0.967
	Morphometric dissimilarity	0.015	-0.035	0.066	0.541
	Patristic distance	0.007	-0.048	0.06	0.807
	Both secondary cavity nesters	-0.016	-0.321	0.282	0.9

Table 5. Predictors of Geographic Avoidance (GA_{ij}) for Eurasia (n = 1056 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.0011) (95% CI = 0.00010, 0.0046). Mean DIC = 2008.15. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from lat/long clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
	Intercept	0.443	0.352	0.53	<0.0005 ***
Eurasia GA_{ij} lat/long clip	Hybridisation	-0.101	-0.29	0.082	0.257
	Morphometric dissimilarity	-0.003	-0.074	0.067	0.918
	Patristic distance	0.007	-0.073	0.09	0.863
	Both secondary cavity nesters	0.04	-0.527	0.605	0.905

Table 6. Predictors of Geographic Avoidance (GA_{ij}) for a subset of North American passerines with available interspecific territoriality data. (n = 356 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.0039) (95% CI = 0.00013, 0.025). Mean DIC = 688.17. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from lat/long clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
	Intercept	0.269	0.063	0.487	0.020 *
North America Passerine subset GA_{ij} lat/long clip	Interspecific territoriality	0.022	-0.398	0.453	0.894
	Hybridisation	-0.065	-0.433	0.294	0.720
	Morphometric dissimilarity	0.032	-0.088	0.152	0.607
	Patristic distance	-0.032	-0.161	0.097	0.636
	Both secondary cavity nesters	0.091	-0.817	1.031	0.836

Table 7. Predictors of GA_{ij} symmetry (GA_{sym}) for North America (n = 1938 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.066) (95% CI = 0.0006, 0.191). Mean DIC= 6712.98. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1 (results are similar across all chains). Data from longitudinal clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
North America GA_{sym} long clip	Intercept	0.665	0.179	1.122	0.016 *
	Hybridisation	-0.225	-0.424	-0.019	0.028 *
	Morphometric dissimilarity	-0.067	-0.148	0.013	0.097
	Patristic distance	0.002	-0.113	0.126	0.956
	Both secondary cavity nesters	-0.065	-0.512	0.379	0.775

Table 8. Predictors of GA_{ij} symmetry (GA_{sym}) for Eurasia (n = 1055 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.068) (95% CI = 0.0014, 0.18701). Mean DIC = 3461.76. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from longitudinal clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
Eurasia GA_{sym} long clip	Intercept	0.878	0.361	1.314	0.005 ***
	Hybridisation	0.099	-0.143	0.345	0.405
	Morphometric dissimilarity	0.106	0.011	0.202	0.035 *
	Patristic distance	0.038	-0.128	0.194	0.649
	Both secondary cavity nesters	0.145	-0.649	0.908	0.742

Table 9. Predictors of GA_{ij} symmetry (GA_{sym}) for a subset of North American passerines with available interspecific territoriality data. (n = 354 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.026) (95% CI = 0.00014, 0.22312). Mean DIC = 1159.38. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from longitudinal clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC
North America territory subset GA_{sym} long clip	Intercept	0.795	0.086	1.395	0.042 *
	Interspecific territoriality	0.492	-0.014	0.987	0.066
	Hybridisation	-0.467	-0.891	-0.045	0.028 *
	Morphometric dissimilarity	-0.165	-0.341	0.006	0.063
	Patristic distance	-0.006	-0.197	0.183	0.936
Both secondary cavity nesters	-0.302	-1.581	0.891	0.591	

Table 10. Predictors of GA_{ij} symmetry (GA_{sym}) for North America (n = 1972 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.102) (95% CI = 0.018, 0.216). Mean DIC= 6904.28. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1 (results are similar across all chains). Data from lat/long clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC	
North America GA_{asym} lat/long clip	Intercept	1.08	0.631	1.562	<0.0005	***
	Hybridisation	-0.242	-0.444	-0.04	0.016	*
	Morphometric dissimilarity	-0.018	-0.097	0.057	0.637	
	Patristic distance	-0.066	-0.192	0.053	0.282	
	Both secondary cavity nesters	-0.095	-0.561	0.347	0.669	

Table 11. Predictors of GA_{ij} symmetry (GA_{sym}) for Eurasia (n = 1056 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.023) (95% CI = 0.002, 0.104). Mean DIC = 3612.05. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from lat/long clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC	
Eurasia GA_{asym} lat/long clip	Intercept	0.946	0.567	1.204	<0.0005	***
	Hybridisation	0.079	-0.17	0.316	0.527	
	Morphometric dissimilarity	0.133	0.035	0.228	0.006	**
	Patristic distance	0.004	-0.135	0.149	0.97	
	Both secondary cavity nesters	0.177	-0.565	0.916	0.652	

Table 12. Predictors of GA_{ij} symmetry (GA_{sym}) for a subset of North American passerines with available interspecific territoriality data. (n = 356 species pairs). The median coefficient estimates from the posterior distribution across all chains, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from chain 1 (results are similar across all chains). The mean phylogenetic signal (λ) for this model was (0.116) (95% CI = 0.00024, 0.452). Mean DIC = 1145.10. Significance codes: < 0.05*, < 0.01**, < 0.001***. All pMCMC values are from chain 1. Data from lat/long clip.

Model	Fixed effects	Median	2.5%	97.5%	pMCMC	
North America territory subset GA_{asym} lat/long clip	Intercept	1.255	-0.012	2.299	0.061	
	Interspecific territoriality	0.16	-0.322	0.633	0.529	
	Hybridisation	-0.383	-0.792	0.012	0.056	
	Morphometric dissimilarity	-0.109	-0.267	0.043	0.154	
	Patristic distance	-0.011	-0.211	0.186	0.903	
	Both secondary cavity nesters	-0.243	-1.46	0.991	0.687	

5.4 Discussion

We found widespread geographic avoidance among both North American and Eurasian birds, which may suggest that biotic interactions play a role in the formation of species distributions at large spatial scales (Connor and Bowers, 1987; Pigot and Tobias, 2013a; Araújo and Rozenfeld, 2014). We also found that this avoidance was not symmetric within species pairs. No pairs had perfectly equal levels of avoidance towards one another; all pairs had some level of asymmetry in their geographic avoidance responses, although some were more imbalanced than others. Species interactions are rarely symmetric, and dominant and subordinate roles are often occupied by the same species during repeated interactions, forming dominance hierarchies (Martin, Freshwater and Ghalambor, 2017; Miller *et al.*, 2017; Leighton *et al.*, 2023, 2024). The consistency in the outcome of aggressive interactions between subordinate and dominant species may allow large-scale species-specific distributional avoidance patterns to develop through the exclusion of the subordinate species.

Both predicted range overlap and realised range overlap were, on average, greater in Eurasia than in North America. One possible explanation for this is the differing biogeography of the two continents, North America is divided by the Rockies and the Great Plains, which act as stark biogeographic barriers to distributions (Rising, 1983). Although Eurasia contains the Alps, Pyrenees and the Urals, these mountain ranges may be a more surmountable barrier to range expansion and secondary contact in birds (Bruderer and Jenni, 1990; Aebischer, Nyffeler and Arlettaz, 2010; Tarasov, 2024), which may allow the distributions of Eurasian pairs to overlap more so than North American pairs.

We were unable to disentangle the determinants of these observed patterns of geographic avoidance. Neither exploitative competition, modelled with morphometric dissimilarity as a proxy, nor behavioural interference, in the form of interspecific territoriality, hybridisation and competition for nest sites, appears to be responsible for the avoidance we observed. This may suggest our models have failed to account for some element of competition responsible for these patterns, or perhaps, there are few

generalisable patterns in the specific causes of geographic avoidance, and our values of avoidance do not differ from null expectations. Novella-Fernandez et al. (2021) made use of virtual species to assess the significance of their results and to determine if competition among pairs was responsible for the observed patterns. 15-30 virtual species were created that had the same number of occurrence points and the same range size for each of the real bat species, although their distributions differed. For each pair, predicted and realised ranges and overlap were modelled, and GA_{ij} were calculated in the same way as the real species. Real values of GA_{ij} were considered significantly higher than null expectations if they were greater than 95% of the null values. Observed values of GA_{ij} below 95% of the virtual values suggest that GA_{ij} between species is no different to what would be expected by chance. Virtual ranges and measures of GA_{ij} were also calculated for 115 non-competing pairs, and if values of GA_{ij} for potentially competing pairs were greater than 95% of the values of non-competing pairs, they were considered significantly higher and the avoidance the result of competition. Instead of using virtual species to determine the impact of competitive interactions, we used PLMMs with proxies for competition as predictor variables. Although we found no evidence that competition influenced levels of geographic avoidance, Novella-Fernandez et al. (2021) found only limited evidence that this was the case. Only two of the ten pairs of bats in Novella-Fernandez et al. (2021) had GA_{ij} greater than null expectations; of the pairs, these two had the highest levels of ecological similarity and the least habitat and trophic partitioning (although this was not quantified).

However, we did find that hybridisation led to more asymmetric avoidance in North American pairs, highlighting a potential role for sexual exclusion in the patterns of avoidance observed (Hochkirch, Gröning and Bücken, 2007; Gröning and Hochkirch, 2008). Sexual exclusion has been described in several hybridising birds and can lead to the movement of hybrid zones and the range contraction of the subordinate species. For example, in the moving hybrid zone of Townsend's Warblers (*Setophaga townsendi*) and Hermit Warblers (*S. occidentalis*), character transition curves suggest Townsend's Warblers are introgressing into Hermit Warbler populations asymmetrically and replacing them (Rohwer and Wood, 1998). This replacement is the result of behavioural dominance and aggression by Townsend's Warbler (Pearson, 2000b; Pearson and

Rohwer, 2000; Krosby and Rohwer, 2010). This hybrid zone has shifted 2000km southward since secondary contact (Krosby and Rohwer, 2008). We find evidence for this asymmetry in our data with Townsend's and Hermit Warbler exhibiting geographic avoidance ($GA_{ij} = 0.40$, $GA_{\text{Townsend's}} = 0.62$, $GA_{\text{Hermit}} = 0.49$, $GA_{\text{sym}} = 1.40$ lat/long clip) but in the opposite direction than expected. Townsend's Warbler exhibits more avoidance to Hermit Warbler than vice versa. Additionally, the hybrid zone of Carolina Chickadees (*Poecile carolinensis*) and Black-capped Chickadees (*P. atricapillus*) is moving northward 10km per decade. Carolina Chickadees are replacing Black-capped as a result of their competitive dominance and subsequent preference for dominant heterospecific mates in female Black-capped Chickadees (Bronson *et al.*, 2003; Reudink *et al.*, 2007; Scott A. Taylor *et al.*, 2014; McQuillan and Rice, 2015). Hybridisation and interspecific territoriality are intrinsically linked, with hybridising species being more likely to be territorial in response to interspecific mate competition (Drury, Cowen and Grether, 2020).

Greater morphometric dissimilarity resulting in more symmetric avoidance within Eurasia suggests resource competition has played a role in these distributions. Species that have diverged morphologically are less likely to compete for the same resources, as morphology is highly correlated with ecological niches and resource acquisition (Pigot *et al.*, 2020b). Morphologically dissimilar pairs still experience avoidance, but they experience it more equally than morphologically similar pairs, whereas similar pairs are likely to experience more intense competition (MacArthur and Levins, 1967), and the dominant species may exclude the subordinate species from potentially suitable niche space (Jankowski, Robinson and Levey, 2010; Freeman, 2015b, 2016b; Freeman and Montgomery, 2016; Boyce and Martin, 2019; Freeman, Strimas-mackey and Miller, 2022; Freeman, Miller and Strimas-Mackey, 2024). Why only hybridisation affects avoidance asymmetry in North America and only morphometric dissimilarity affects it in Eurasia is not known.

Dispersal limitations and stochasticity are important caveats to consider when discussing species distributions; the absence of a species from climatically suitable areas may not be a result of competition. Areas may be climatically suitable for a

species, but they have just been unable to reach them yet, perhaps due to limited dispersal abilities (an aversion to crossing water in some birds, for example Kerlinger, (1985)) or poor mobility and small size (Sheard *et al.*, 2020). Species may not occupy suitable habitats due to current or historical anthropogenic persecution (Newton, 2024) or simply for no discernible reason other than the effects of stochasticity. If species do not occupy much of their predicted range within the area of predicted overlap, it could give the impression that the species is unable to occupy its suitable range due to the presence of a competitor rather than any of the reasons mentioned above. Perhaps some areas of predicted range overlap are closer to species' range edges, giving a false impression of avoidance. One of the biological assumptions of SDMs is that the distributions of species used to create them are assumed to be at equilibrium, yet this is very rarely the case (Araújo, Pearson and Rahbek, 2005).

The accuracy of the SDMs used to calculate measures of predicted ranges and predicted overlap must also be called into question. Many species have huge predicted ranges, many thousands of kilometres away from their realised ranges. Niche incumbency and the presence of potential competitors may prevent species from colonising Eurasia and North America, and vice versa, as the North Atlantic is not an insurmountable dispersal barrier, nor is the Bering Strait, and there is semi-regular avifaunal interchange between the two continents through vagrancy (Lees and Gilroy, 2022). For most species, however, the ocean is likely too great a barrier to overcome for colonisation to occur. Hence, we analysed the two continents separately. That said, our results are very similar between both long clipped and lat/long clipped rasters, suggesting this clipping may not have been sufficient to combat the effect of overinflated predicted ranges. Equally, while our thresholding protocol removed many extreme values, perhaps we should have been more liberal in the removal of outliers. It can be difficult to evaluate if extreme values are a result of actual geographic avoidance, a lack thereof, or rather an artefact of the data structure and SDMs.

The SDMs we utilised were relatively low-resolution, with grid cells corresponding to 0.5°. The coarseness of these cells could mask any effect of species interactions on distributions and lend support for the idea that the impacts of species interactions do

not scale up to coarser resolutions (Pearson and Dawson, 2003a). Further, by analysing only presence or absence within grid cells, the signature of interactions may be lost. For instance, competition between a species pair may reduce the abundance of the subordinate species but not result in total extirpation from a cell, giving the impression of a lack of competition when viewed as a binary presence or absence (Howard *et al.*, 2014; Zurell, Pollock and Thuiller, 2018; König *et al.*, 2021; Poggiato *et al.*, 2021).

A conceptual limitation of all SDMs attempting to infer patterns related to biotic interactions is that they effectively model a species-environment relationship based on a species' realised, rather than fundamental, range. Therefore, the predicted distribution of species has been influenced by historical or ongoing species interactions on their realised range, which could mask marked competitive effects. If species realised ranges are constrained as a result of competitive interactions, they will occupy a narrower breadth of climate conditions, and as such, SDMs would underestimate their predicted ranges. However, few, if any, of our species had identical predicted and realised ranges, suggesting there are still some factors preventing them from occupying the entirety of their potentially suitable climate space, whether that be dispersal limitations, habitat filtering, stochasticity or species interactions. One possibility that could potentially ameliorate the underestimation of fundamental niche space could be to alter thresholds that were used to convert occurrence probability to presence-absence in SDMs. The SDMs we used utilised species-specific thresholds that maximised the sum of sensitivity and specificity, which optimises model fit to the realised niche. More relaxed thresholds that prioritise sensitivity over specificity may offer a broader estimate of the fundamental niche.

Understanding the influence of species interactions on large-scale distributions is an important area of study as species assemblages shift and reassemble in light of climate change and introduction to non-native areas. We present evidence of extensive geographic avoidance in two large assemblages of birds, but were unable to discern the factors responsible for the observed patterns. However, we found evidence to suggest that asymmetries in avoidance are the result of reproductive interference in North America and exploitative competition in Eurasia. We have also demonstrated that

calculations of geographic avoidance can be upscaled into high-throughput workflows in novel taxa and areas.

Chapter 6

Joint Species Distribution Modelling

6.1 Introduction

In this era of rapid anthropogenic change, species distributions are undergoing a period of relative dynamism (Parmesan, 2006; Elith, Kearney and Phillips, 2010; Chen *et al.*, 2011; HilleRisLambers *et al.*, 2013a; Elmhagen *et al.*, 2015; Freeman *et al.*, 2018; Avidad, Clavero and Viana, 2025). Predicting where species will occur and persist in the future has important conservation and management implications (Araújo *et al.*, 2004; Thomas *et al.*, 2004; Bagchi *et al.*, 2013). Understanding the determinants of species current distributions is vital to accurately predict how species ranges will change in the future or have changed in the past (Davis *et al.*, 1998). Climate and habitat play a substantial role in setting species range limits however, biotic interactions also impact species distributions (Pearson and Dawson, 2003a; Araújo and Luoto, 2007; Meier *et al.*, 2010; González-Salazar, Stephens and Marquet, 2013).

Biotic interactions encompass a whole suite of behaviours, ranging from predation, parasitism, mutualism, facilitation, to competition (HilleRisLambers *et al.*, 2013b). Competition itself can be divided into indirect (exploitative competition (Gause, 1934b; Jensen, 1987)) and direct competition (behavioural interference (Maurer, 1984; Grether *et al.*, 2017)). Historically, the impact of exploitative competition on species distributions received more attention (Gause, 1934b; MacArthur, 1972; Diamond, 1973). However, a rapidly growing body of work now supports the impact of behavioural interference on species distributions and coexistence (Losin *et al.*, 2016; Grether *et al.*, 2017; Cowen, Drury and Grether, 2020; Drury, Cowen and Grether, 2020; Nesbit *et al.*, 2023).

Different abiotic and biotic factors influence species distributions to varying extents at differing spatial resolutions (Connor and Bowers, 1987; Gotelli, Graves and Rahbek, 2010; Araújo and Rozenfeld, 2014; Belmaker *et al.*, 2015; King *et al.*, 2021; Elo *et al.*, 2023). Climate influences species distributions at large spatial scales (Holdridge, 1947; MacArthur, 1972; Pearson and Dawson, 2003a), habitat filtering occurs at a more local level (Barnagaud *et al.*, 2014), and microclimate conditions can influence distributions at an even finer scale (Lembrechts, Nijs and Lenoir, 2019). Biotic interactions influence

species distributions both within and between habitats (Araújo and Luoto, 2007; Wisz *et al.*, 2013) and can scale up to influence assemblage composition at a regional or continental scale (Webb, 2006; Araújo and Luoto, 2007; Gotelli, Graves and Rahbek, 2010; Araújo and Rozenfeld, 2014; Belmaker *et al.*, 2015; Mönkkönen *et al.*, 2017; Machado-Stredel, Atauchi, Nuñez-Penichet, Cobos, Osorio-Olvera, Khalighifar, Peterson and R. J. Fletcher Jr, 2024). Understanding the scale at which interactions play a role in structuring species communities is of importance when predicting future distributions and assemblages (HilleRisLambers *et al.*, 2013b).

Species distribution models (SDMs) utilise current species distributions and the associated bioclimatic conditions in those areas to model a species-climate relationship. These bioclimatic envelope models can be used to predict species distributions elsewhere or in other periods in time (Austin, 2002; Pearson and Dawson, 2003b; Guisan and Thuiller, 2005; Hijmans and Graham, 2006). However, a limitation of SDMs is that they are based on the climatic niche a species currently occupies—their realised niche, as opposed to their fundamental niche—the range of climatic conditions they could occupy (Hutchinson, 1957; Soberón, 2007; Holt, 2009). Species may not realise the entirety of their fundamental niche for a variety of reasons: a lack of suitable habitat, dispersal limitations, biotic interactions or stochasticity (Svenning and Skov, 2004). SDMs also assume species ranges are at equilibrium, which is not the case; species distributions are often in flux (Parmesan and Yohe, 2003; Araújo, Pearson and Rahbek, 2005; Chen *et al.*, 2011; Lindström *et al.*, 2013). Dispersal ability and habitat suitability can be accounted for in SDMs with *post-hoc* clipping of predictions (Barbet-Massin, Thuiller and Jiguet, 2012; Titley *et al.*, 2021; Stewart *et al.*, 2022). However, biotic interactions have proven more difficult to efficiently incorporate into SDMs, but are a key component of assembly processes (Davis *et al.*, 1998; Araújo and Luoto, 2007; Dormann *et al.*, 2018). As such, the integration of species interactions into SDMs is of high priority.

In an extension of traditional SDMs, other species—their presence, abundance or density—can be included in SDMs as a predictor variable alongside environmental covariates (Leathwick, 2002; Araújo and Luoto, 2007; Heikkinen *et al.*, 2007, 2007;

Meier *et al.*, 2010; Fern *et al.*, 2019; Snell Taylor, Umbanhowar and Hurlbert, 2020). Incorporating the presence of even one other species can enhance the predictive power of SDMs (Araújo and Luoto, 2007; Heikkinen *et al.*, 2007; Meier *et al.*, 2010; Pellissier *et al.*, 2010; Fern *et al.*, 2019; Han *et al.*, 2023). For instance, cactus Wrens (*Campylorhynchus brunneicapillus*) often destroy the nests of Verdins (*Auriparus flaviceps*), and by including Cactus Wren density in SDMs alongside environmental covariates, predictions of Verdin distribution were improved (Fern *et al.*, 2019). However, these SDM extensions model only unidirectional relationships and do not account for the reciprocal effects of interactions, lacking the complexity of true assemblages (Kissling *et al.*, 2012).

Joint Species Distribution Models (JSDMs) model species responses to the environment and one another, simultaneously (Pollock *et al.*, 2014; Harris, 2015; Warton *et al.*, 2015; Ovaskainen *et al.*, 2016, 2017; Dormann *et al.*, 2018; Caradima, Schuwirth and Reichert, 2019). One form of JSDM is the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen and Abrego, 2020; Tikhonov *et al.*, 2020). HMSC is a multivariate hierarchical generalised linear mixed model fitted with Bayesian inference that aims to capture residual co-occurrences associated with species interactions (Ovaskainen and Abrego, 2020). These residual associations are the non-random co-occurrence patterns that remain between species after accounting for environmental variation. Positive associations may be the result of mutualism, facilitation or parasitism, which lead to aggregated distributions. In birds, heterospecific attraction or flocking behaviour may be particularly likely to create positive associations (Mönkkönen, Helle and Soppela, 1990; Thomson, Forsman and Mönkkönen, 2003; Heikkinen *et al.*, 2007; Sebastián-González *et al.*, 2010; Kivelä *et al.*, 2014). Negative associations, on the other hand, may be the result of predation, exploitative competition or behavioural interference. That said, residual associations capture not only the effect of biotic interactions but can include species responses to missing environmental covariates unaccounted for in the model (Ovaskainen, Hottola and Siitonen, 2010; Kissling *et al.*, 2012; Pollock *et al.*, 2014; Warton *et al.*, 2015; Poggiato *et al.*, 2021; Vallé *et al.*, 2024). This important caveat limits the inferences that can currently be made using JSDMs, and results should be interpreted in light of potential

missing covariates (Ovaskainen, Hottola and Siitonen, 2010; Kissling *et al.*, 2012; Pollock *et al.*, 2014; Warton *et al.*, 2015; Tikhonov *et al.*, 2017; König *et al.*, 2021; Poggiato *et al.*, 2021; Vallé *et al.*, 2024).

Initially, the motivation for this work was to assess the relative impact of behavioural interference and exploitative competition on shaping species distributions. However, it soon became apparent that JSDMs were not entirely suited to this goal, given their inability to distinguish residual associations caused by biotic interactions and those caused by missing environmental covariates. As such, we sought to determine if JSDMs could detect any trace of competition in residual associations. We exhaustively examined the residual associations of JSDMs for 41 European bird families for a relationship with various forms of competition. We did this by extracting pair-wise residual association values from each family JSDM and including them as response variables in Phylogenetic Linear Mixed Models (PLMMs) with predictor variables associated with behavioural interference and exploitative competition. We also created JSDMs and Single Species Distribution Models (SSDMs, not to be confused with Stacked Species Distribution Models) using the HSMC framework for a subset of species to quantify the differences between predictions of the two model types.

6.2 Methods

6.2.1 Species data

Breeding bird survey data from 19 countries/schemes across Western Europe (some countries have multiple monitoring schemes) were requested from the Pan-European Common Bird Monitoring Scheme (PECBMS), which collates breeding bird survey data from across Europe (Brlík *et al.*, 2021). We utilised data from the following schemes: Austria, Brussels, Catalonia, Czech Republic, Denmark, Finland, Finland Points, France, Germany, Ireland, Italy, Netherlands, Norway, Poland, Portugal, Spain, Sweden, Switzerland, UK and Wallonia. Portugal did not respond to the request, and data from Spain, Finland, the Czech Republic and Switzerland had to be removed from analyses due to the low spatial accuracy of their site coordinates. For example, the site coordinates in Spain refer to the centroid of a 10km square, and there may be multiple sites within the same square. Similarly, in the Czech Republic, site coordinates refer to the nearest municipality (Gamero, 2023, pers. comms) and are therefore unsuitable for the high-resolution modelling of species ranges. The Swiss methodology records only ‘common breeding species’ and, as such, we had no way of knowing if species were absent from a site or just unrecorded. As in Chapter 2, we removed pelagic seabirds from analyses. For the schemes with available data, we converted site coordinates to a 1km resolution raster and any sites within the same cell were combined (Figure 1). Due to computational limitations, it was necessary to reduce the number of sites included at such a large spatial extent and as such, we randomly thinned the number of sites from ~9000 to 4500 (Figure 1). However, slightly fewer than 4500 survey cells (4367) were included in models as rasters were clipped by country polygons, and some cells on the edges were lost. We used species presence-absence data from 2015 only, as current land use/land cover (LULC) data were available for 2015, and contemporary climate data corresponded to 1981-2010. Although these years don’t match perfectly, species distributions tend to lag behind climate (Brommer, Lehikoinen and Valkama, 2012; Essl *et al.*, 2024).

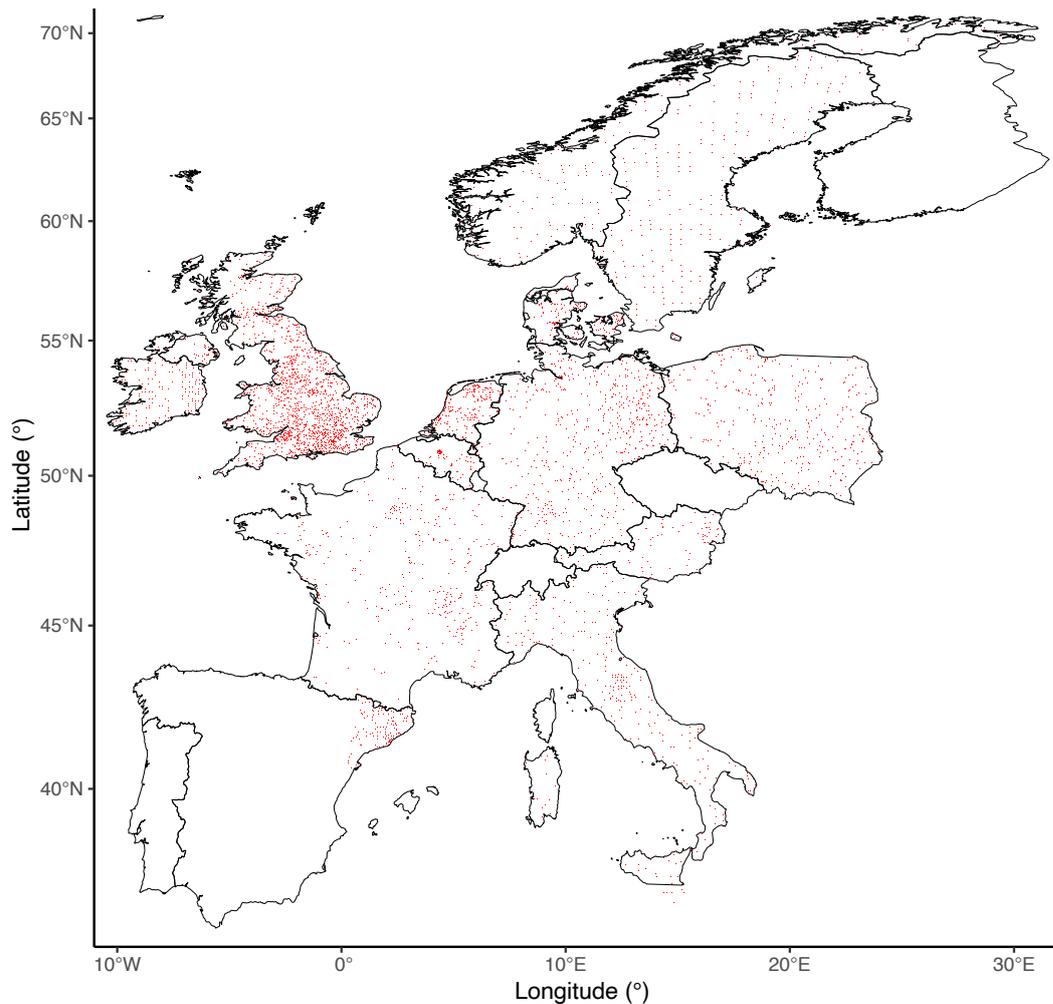


Figure 1. Map of thinned Pan-European Common Bird Monitoring Scheme (PECBMS) sites in 2015 used in models (n=4367). Red 1km cells indicate a survey site is present within said cell. Sites were randomly thinned to allow models to run. Portuguese data was unavailable and Spanish (bar Catalanian), Finnish and Czech data could not be included in models due to spatial coordinates of sites being too coarse for our high-resolution analyses. Swiss data could not be included as not all species were recorded in surveys.

6.2.2 Bioclimate data

We utilised bioclimate data provided by CHELSA (Karger *et al.*, 2017), which is at a 30 arc sec (~1km) resolution, matching our species data. To avoid model overfitting and reduce model complexity and runtime, we included eight bioclimatic variables that capture annual typical conditions, variability, and extremes (Table 1). These eight bioclimatic variables are all pertinent to species distributions and have been used to model distributions accurately under climate change (Stephens *et al.*, 2016b; Titley *et al.*, 2021). CHELSA data were available as climate averages for 1981-2010, 2011-2040,

2041-2070 and 2071-2100. We used 1981-2010 as the contemporary period. For Land-use/Land Cover (LULC) data, we made use of the Chen *et al.* (2022) global land projection data. These simulation products are subdivided into seven land types (e.g. forest, grassland, urban) and then further subdivided into 20 plant functional types (e.g. broadleaf deciduous tree- temperate, needleleaf evergreen tree- temperate)(Figure 2). We made use of 20 plant functional type data (hereafter LULC20) to maximise biological realism and specificity. LULC data were available in 5-year intervals from 2015 to 2100, also at a 1km resolution. We used 2015 as the contemporary period.

Table 1. Descriptions of the eight CHELSA bioclimatic variables used in Joint (JSDMs) and Single Species Distribution Models (SSDMs).

Bioclimatic variable	Description
Bio1 - Mean annual temperature	Mean annual daily mean air temperatures averaged over 1 year.
Bio4 - Temperature seasonality	Standard deviation of the monthly mean temperatures.
Bio5 - Temperature of warmest month	The highest temperature of any monthly daily mean maximum temperature.
Bio6 - Temperature of coldest month	The lowest temperature of any monthly daily mean maximum temperature.
Bio12 - Mean annual precipitation	Accumulated precipitation over 1 year.
Bio13 - Precipitation of wettest month	Total precipitation of the wettest month.
Bio14 - Precipitation of driest month	Total precipitation of the driest month.
Bio15 - Precipitation seasonality	Standard deviation of the monthly mean precipitation.

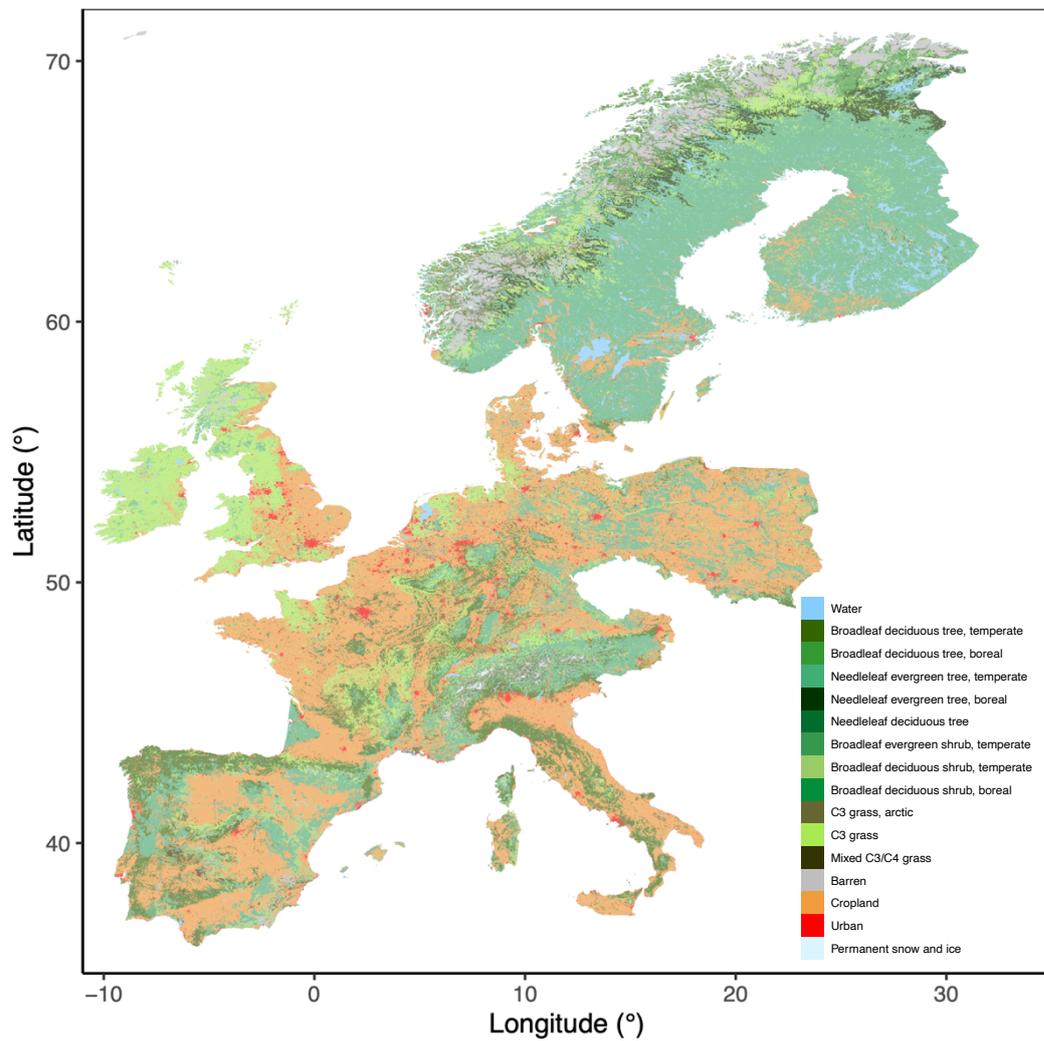


Figure 2. Map of Chen *et al.* (2022) land use/land cover (LULC) 20 plant functional types (PFTs) across Europe for 2015. Not all 20 PFTs occur in Europe.

6.2.3 Hierarchical modelling of species communities

We created JSDMs using the Hierarchical modelling of species communities (HMSC) framework, using the R packages *Hmsc* (Tikhonov *et al.*, 2020) and the *Hmsc-HPC* (Rahman *et al.*, 2024) extension, which augments the traditional HMSC framework to leverage High Performance Computing (HPC) architecture and Graphical Processing Units (GPUs) to reduce model runtime by up to 1000 times (Rahman *et al.*, 2024). By using HMSC-HPC, we were able to maintain our analyses at a high, 1km resolution, expand analyses from the UK to Western Europe and increase the number of species included in models. For instance, a small test model of 3 species and 100 sites, which took ~15 hours per chain on a HPC using the traditional HSMC framework and CPUs, ran in only 43 minutes per chain using HMSC-HPC and GPUs.

Matrices of presence-absence data were created with rows corresponding to the 4367 survey cells and columns corresponding to individual species. Given that some countries were omitted from analyses and sites were thinned, predictions may have differed had all sites been included. While the entire climatic envelope of some species may not be represented in the sites we used, there is still a reasonable latitudinal and longitudinal spread of sites that encompass a large range of bioclimatic conditions. Species only recorded in the omitted countries were removed from analyses; however, a minority of species that occur primarily in those countries but also occur elsewhere may have had a large portion of their spatial records removed from predictions, which may have influenced model outcomes. It was not computationally feasible, nor particularly biologically relevant, to include all 339 European species in a single JSDM. We therefore created JSDMs for individual families, as these species are more likely to compete and influence the distributions of one another (Darwin, 1859b; Violle *et al.*, 2011). However, by restricting models to families, it was necessary to remove species belonging to monotypic families ($n=27$) from analyses. Forty-one families, containing a total of 312 species, remained.

A matrix containing environmental data was also created. Again, rows referred to survey cells, and each column corresponded to one of the 8 bioclimatic variables or LULC. To

capture potential non-linear relationships between climate and species occurrence, bioclimatic variables were included in models as second-degree polynomial terms, with both linear and squared components, allowing for unimodal responses where species may be more likely to occur under intermediate bioclimatic conditions (Ovaskainen and Abrego, 2020). Survey cell coordinates were included as a random effect to account for spatial autocorrelation (Ovaskainen and Abrego, 2020; Tikhonov *et al.*, 2020). Given that our species data were binary presence-absence, our models used a probit link function.

Posterior samples were extracted using a whole block-Gibbs sampler, and four model chains were run for 200,000 iterations each. 1000 samples were retrieved from each, with a thinning interval of 100 and a burn-in of 100,000. In R, model convergence was assessed using Gelman-Rubin diagnostics (Gelman and Rubin, 1992) and visual inspection of trace plots. All models suitably converged within 1000 samples. Model fit and explanatory power were evaluated using the `evaluateModelFit` function, which calculated Root Mean Square Error (RMSE), Area Under the ROC Curve (AUC) and Tjur's R^2 for each species. RMSE quantifies average prediction error, i.e., how well predicted occurrence probabilities match observed values. AUC quantifies how well the model discriminates presence and absence, while Tjur's R^2 is the difference between the mean predicted probability of presences and the mean predicted probability of absences. Variance partitioning plots were created. Posterior means and quantiles of parameter estimates were extracted.

Residual association matrices were extracted for each family (Figure 3). These residual associations aim to capture species-species associations in occurrence after accounting for environmental covariates (Tikhonov *et al.*, 2017, 2020), with values close to 1 implying a strong positive association—species co-occur more often than expected (after accounting for environmental covariates and random effects). While values close to -1 imply strong negative associations (i.e., species co-occur less often than expected). Negative associations could be the result of exploitative competition (Gause, 1934b) or behavioural interference (Grether *et al.*, 2017), while positive associations may arise from facilitation (Heikkinen *et al.*, 2007) or heterospecific attraction (Sebastián-González *et al.*, 2010). Each posterior mean has an associated support

value, which corresponds to the proportion of MCMC iterations in which the sign of the posterior is positive or negative. High support values (close to 1) indicate strong evidence that the correlation is consistently positive or negative across the MCMC iterations. Low values (~ 0.5) suggest the sign fluctuates between positive and negative in different MCMC iterations, implying low confidence in the posterior mean.

6.2.4 Residual associations and species interactions

In an attempt to disentangle the potential biological factors responsible for the observed associations between species, we extracted the posterior mean for all pairs with a support level exceeding 0.9 (i.e., 90% of MCMC samples were the same sign as the posterior mean). We pooled these values from across families as values across fits are comparable, and then logit transformed these values before using them as a response variable in PLMMs. We incorporated covariates corresponding to various forms of competition, including morphometric dissimilarity (see Chapter 2) and whether pairs shared lifestyle and foraging niches to account for exploitative resource competition. We included hybridisation to account for possible effects of reproductive interference or exclusion. Unfortunately, we did not have available data on interspecific territoriality for European species, however, we were able to predict the likelihood of interspecific territoriality in European passerine pairs using random forest algorithms trained on North American data (see Chapter 4). We included these predicted classifications as a predictor variable to account for the impact of interference competition on species co-occurrences. Finally, we included whether species shared the same habitat type as a binary variable to control for possible shared responses or unaccounted latent habitat associations that may be responsible for observed patterns in residual associations if competition is not. Habitat types were extracted from AVONET (Tobias *et al.*, 2022) and include classifications such as forest, woodland, grassland, wetland, etc. Each species had a single habitat classification, although in reality, they may occupy multiple habitat types. The inclusion of this variable may seem superfluous when LULC data is included in JSDMs, however, its inclusion may detect the effect of positive associations arising as a result of occurrence in the same habitats

that are unaccounted for by JSDMs. We also ran PLMMs using the same predictor variables as above, but with a binary response variable corresponding to whether or not the residual associations between species pairs had a significant level of support (>0.9). We ran these additional analyses as models restricted to pairs with strong residual associations had a relatively narrow margin of variance to explain, whereas models with support >0.9 as a response variable allow us to determine what explains the observed strong associations, as there is greater variance to model.

6.2.5 Spatial predictions

Predicting where species occur, or will occur in the future, with greater accuracy is the primary reason for incorporating biotic interactions into species distribution models (Araújo and Luoto, 2007). We wanted to quantify differences in the predictions of JSDMs and SSDMs. HMSC can be used to generate maps of predicted distributions for species while accounting for the presence of other modelled species. To create these spatial predictions, it was necessary to create environmental matrices for all the grid cells in Europe for current and future data. Models trained on the randomly thinned survey cells did not include three LULC categories that were present in the full European dataset (snow and ice, broadleaf deciduous shrub (boreal) and needleleaf deciduous trees), and as such, these had to be removed from predictions. All three are relatively rare habitat types across Europe, and as such, their omission had little impact. Due to computational limitations and circumstances beyond our control, we were only able to create spatial predictions for four species of *Phylloscopus* warblers: Common Chiffchaff (*P. collybita*), Willow Warbler (*P. trochilus*), Wood Warbler (*P. sibilatrix*) and Western Bonelli's Warbler (*P. bonelli*). These species are closely related, ecologically similar and are known to compete and hybridise with one another (Sæther, 1983; Dietzen *et al.*, 2007; Luepold, Carlotti and Pasinelli, 2024); as such, they represent an interesting case study. To determine the effect of incorporating species interactions into SDMs, we ran identical HMSC models, as above, but included only single species and then predicted species distributions across Europe using these models. We compared model fit for SSDMs and JSDMs for each species using RSME, AUC and Tjur's R^2 . To

quantify and visualise the differences between predictions made with species interactions and those without, we created raster layers of the difference between JSDM and SSDM predictions for each species by subtracting the SSDM probability of occurrence from the JSDM probability of occurrence. We did the same for predicted binary presence-absence data (considered present if occurrence probability was >0.5), plotting cells in which species were predicted to occur by both SSDMs and JSDMs, by neither, or where a species was predicted to be present by SSDMs only or JSDMs only. To create summary statistics for each species, we calculated the mean probability difference (mean pJSDM – mean pSSDM), RSME (square root of the mean difference squared), the Pearson correlation coefficient between the two SDMs, and a Jaccard similarity metric on the binary presence-absence predictions of the two SDMs, quantifying the proportion of cells agreed upon.

6.3 Results

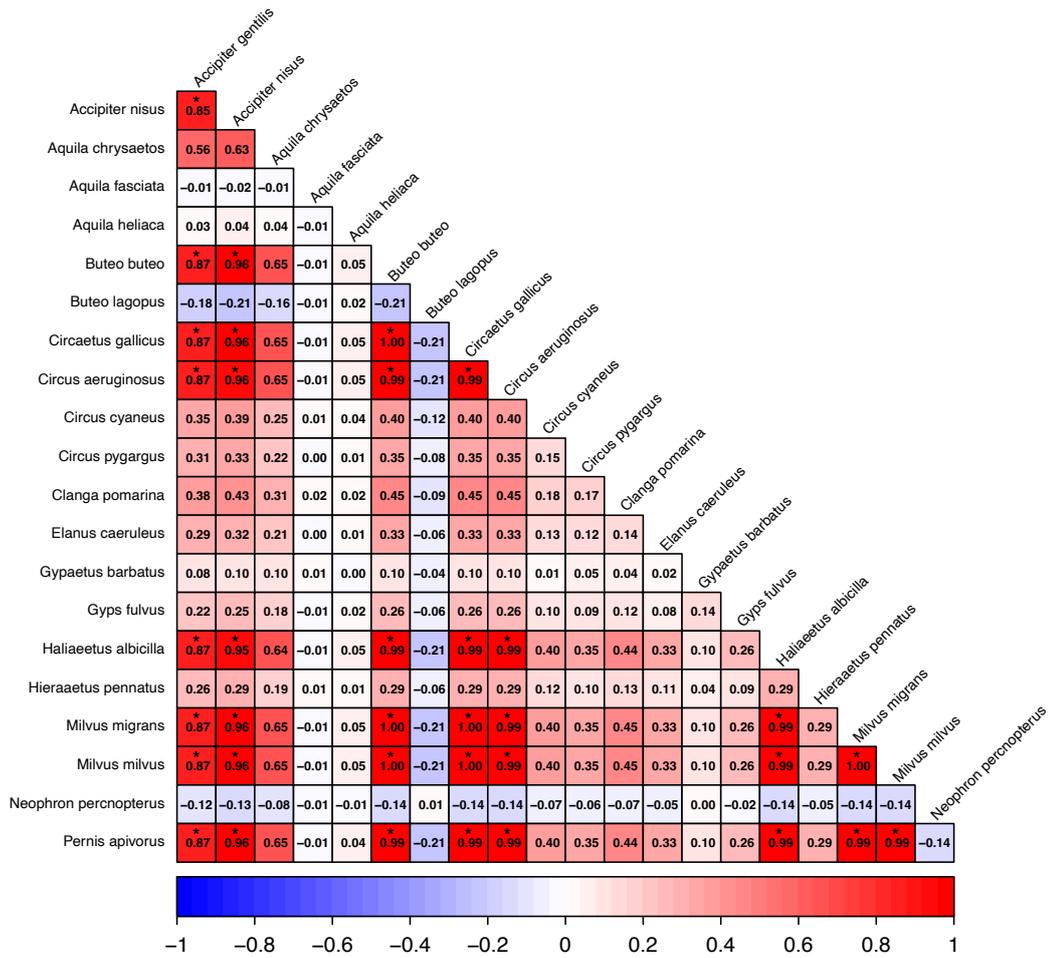
6.3.1 Residual associations

After creating HSMC JSDMs for 41 polytypic families, we generated pair-wise estimates of residual association for 1945 species pairs, of which 708 pairs had a support level greater than 0.9. 75% of residual association values were positive (Figure 3), suggesting most species occur together more often than chance after accounting for environmental covariates. There were no negative associations with support greater than 0.9 (Figure 3); hence, the use of a logit transformation in PLMMs with the posterior means of residual associations as a response variable.

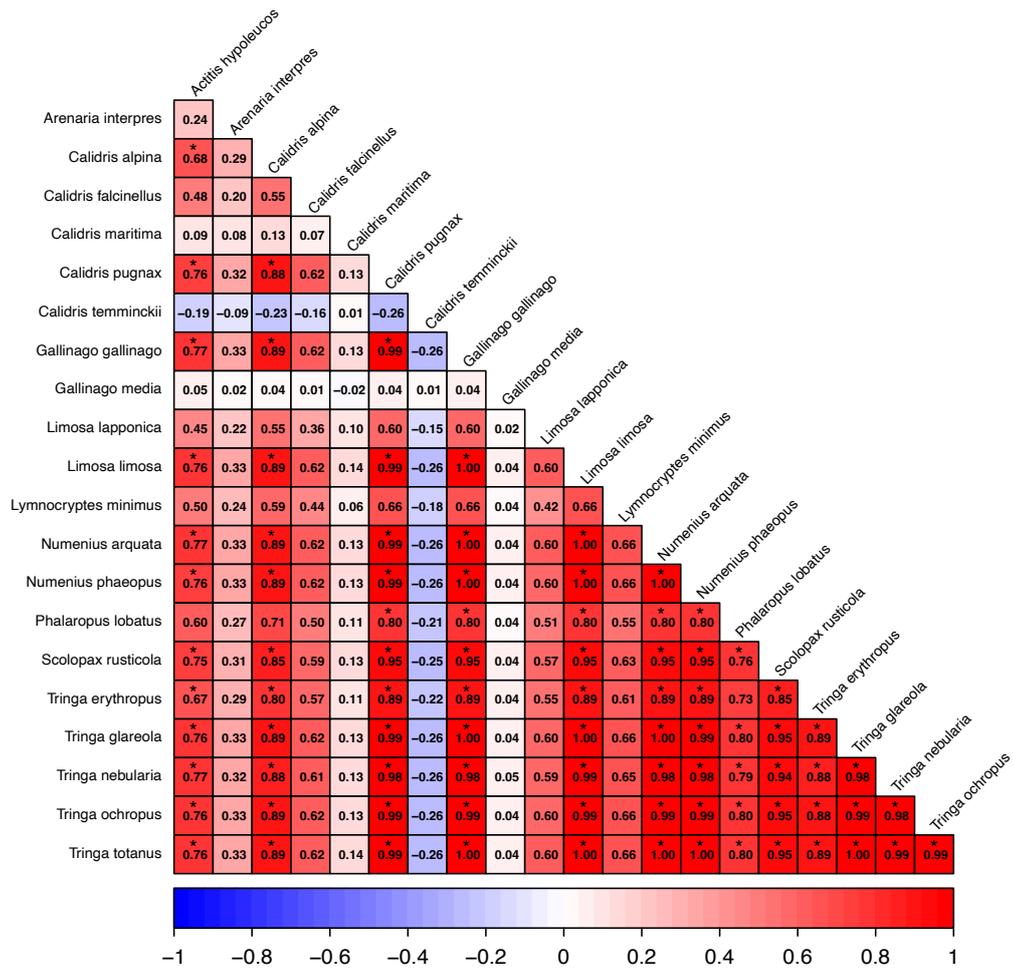
We found that sharing the same habitat type increased the residual association between species. This pattern emerged in PLMMs that included all pairs (Figure 4, Table 3) and those with only (Figure 5, Table 4) passerines with interspecific territoriality classifications.

We also found evidence that hybridising species pairs are more likely to have support for the posterior mean >0.9 than non-hybridising pairs. However, this was only the case for the model including all pairs (Figure 5, Table 4). The model containing passerine pairs with interspecific territoriality classifications also found sharing the same habitat to increase the likelihood of support surpassing the 0.9 threshold (Figure 6, Table 5).

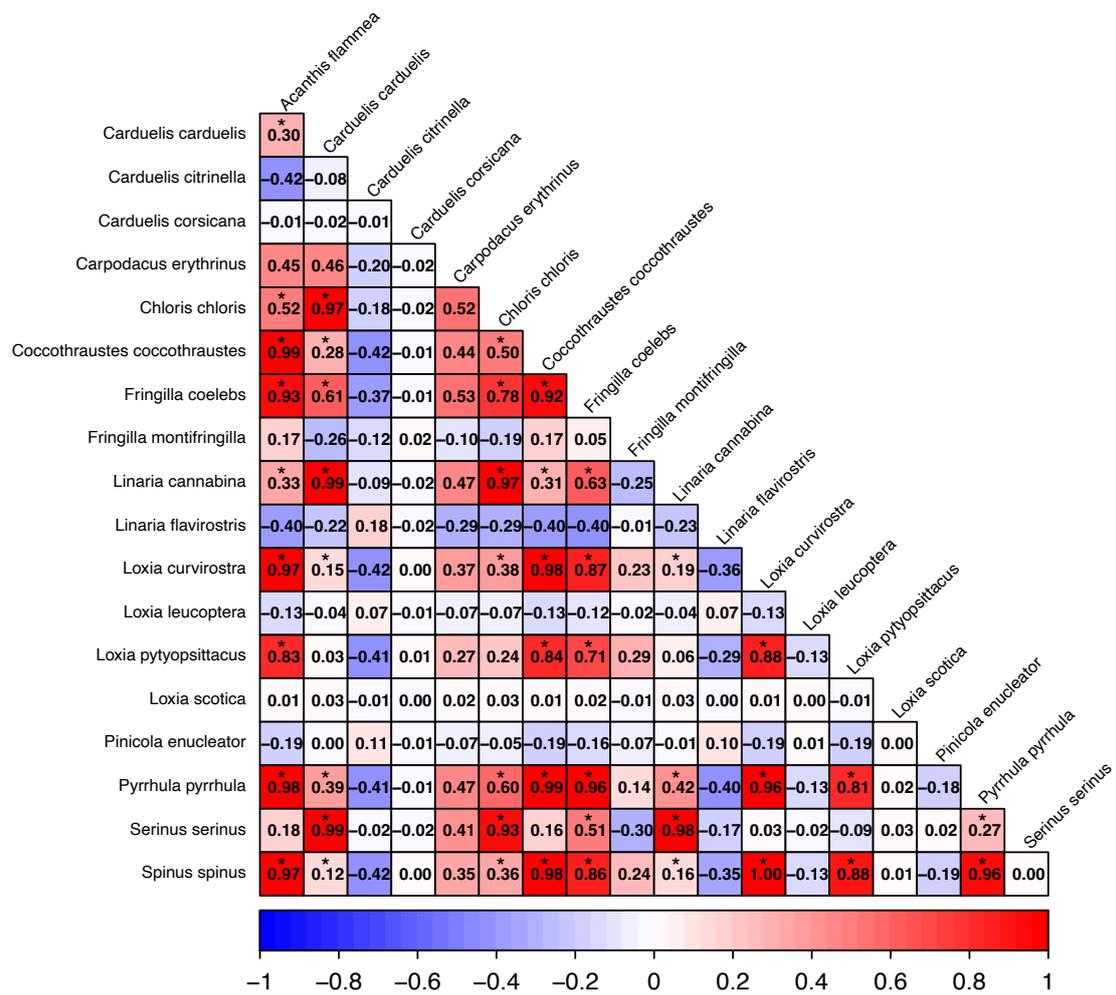
Accipitridae



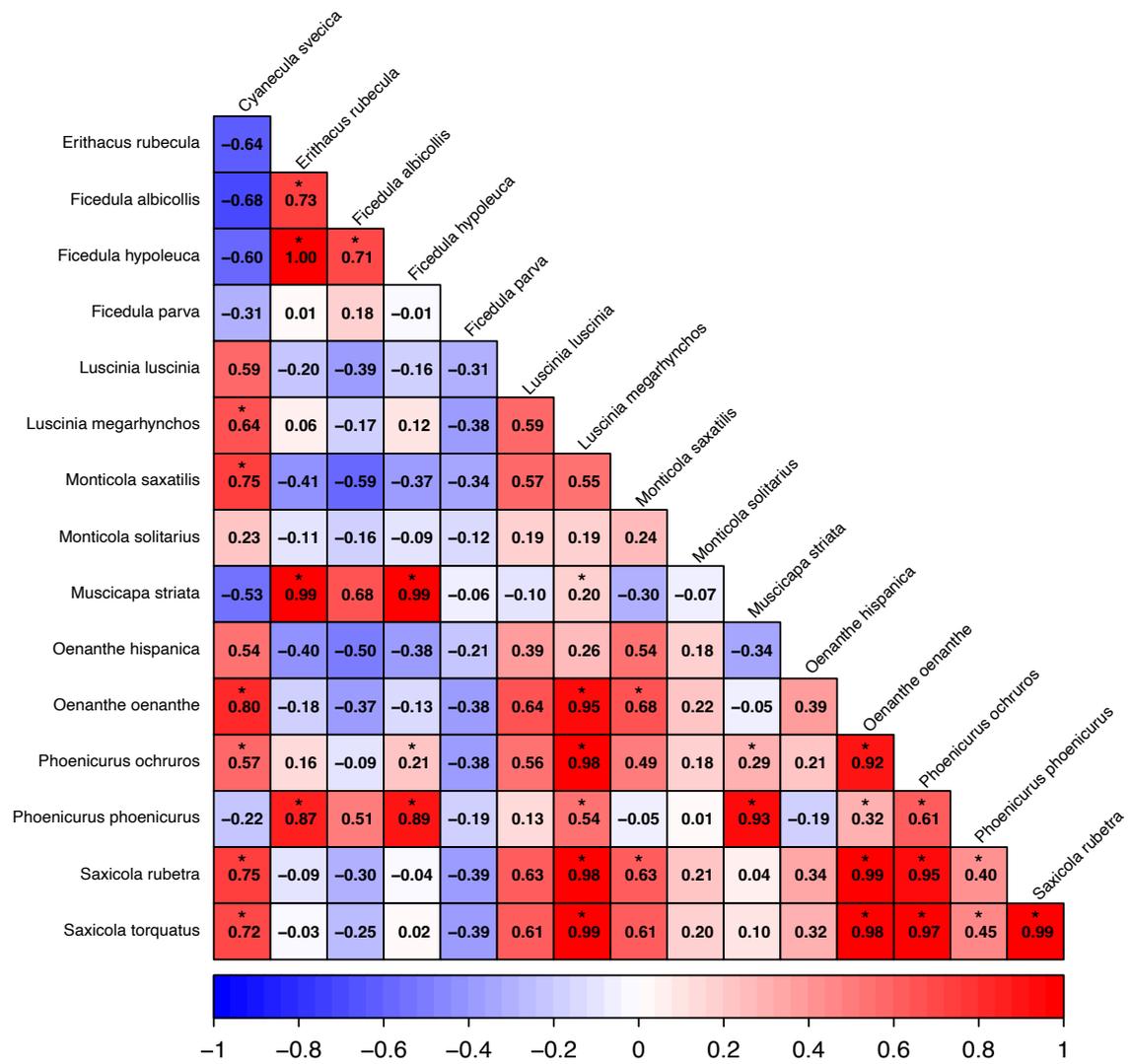
Scolopacidae



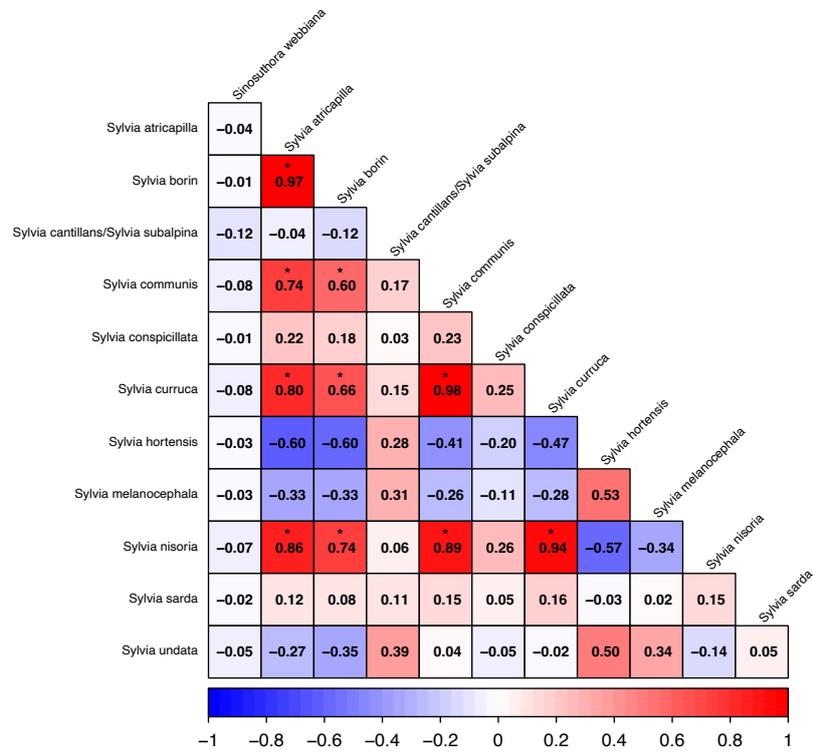
Fringillidae



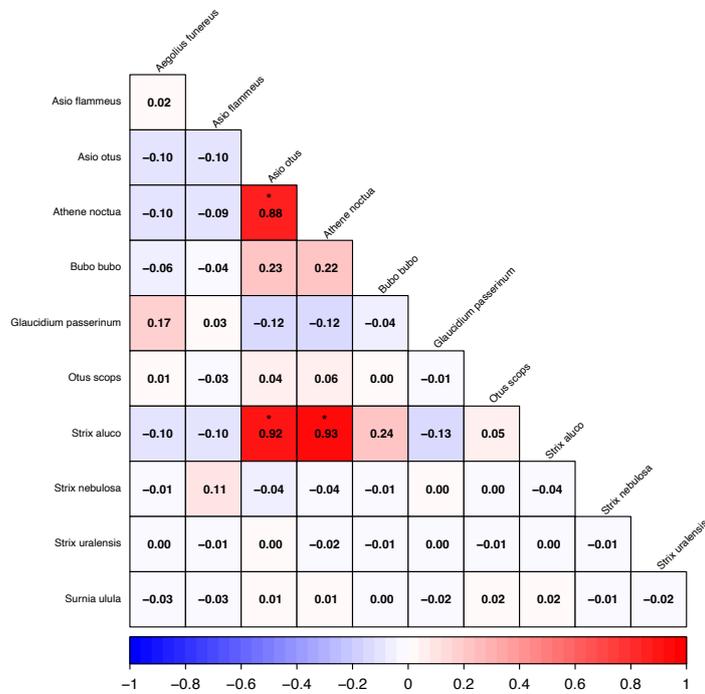
Muscicapidae



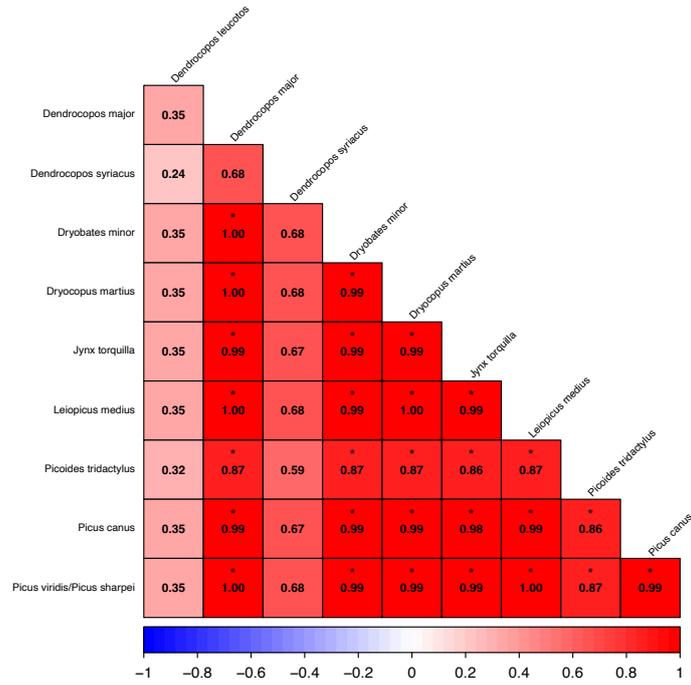
Sylviidae



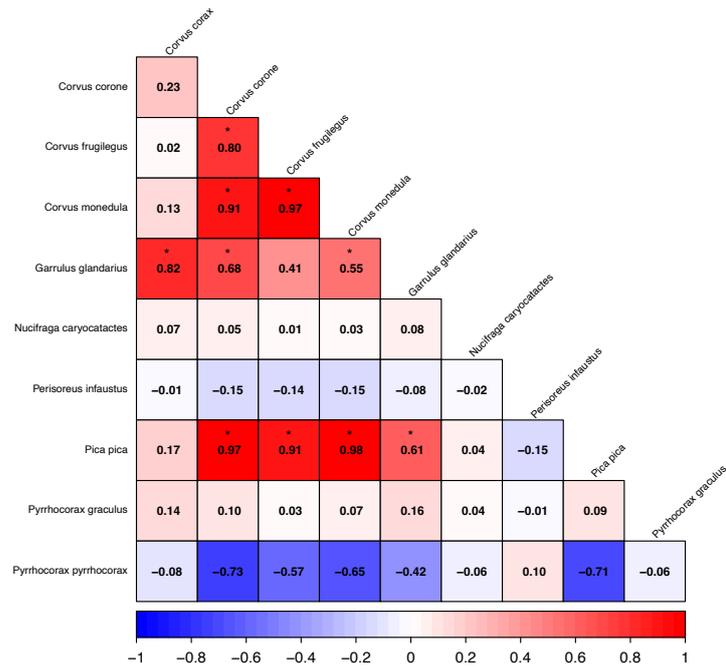
Strigidae



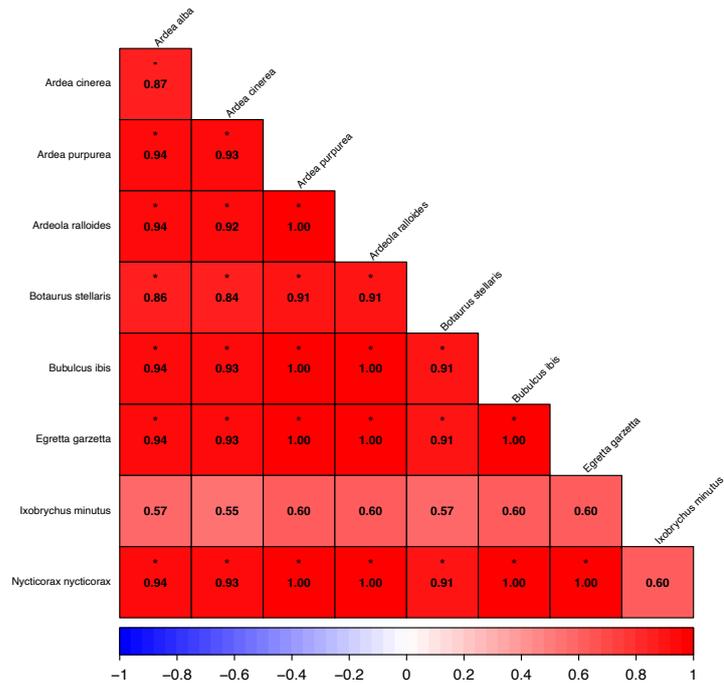
Picidae



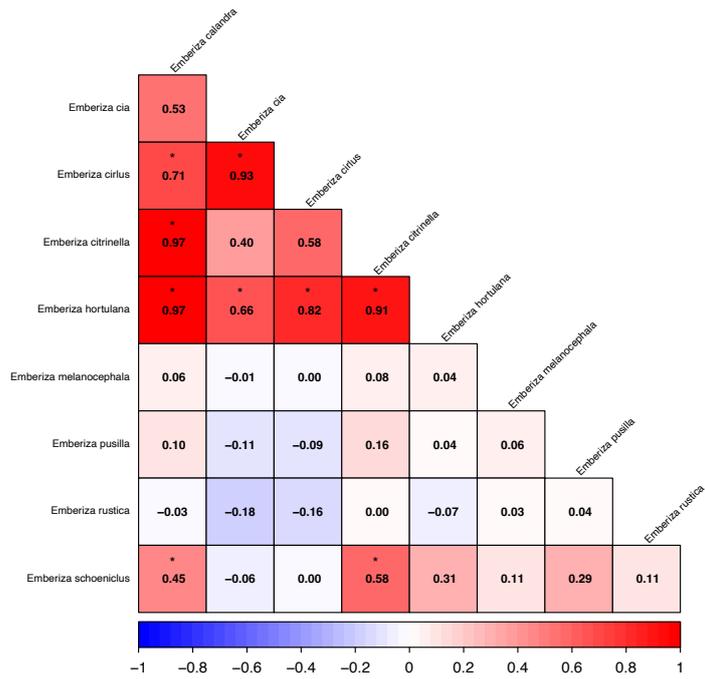
Corvidae



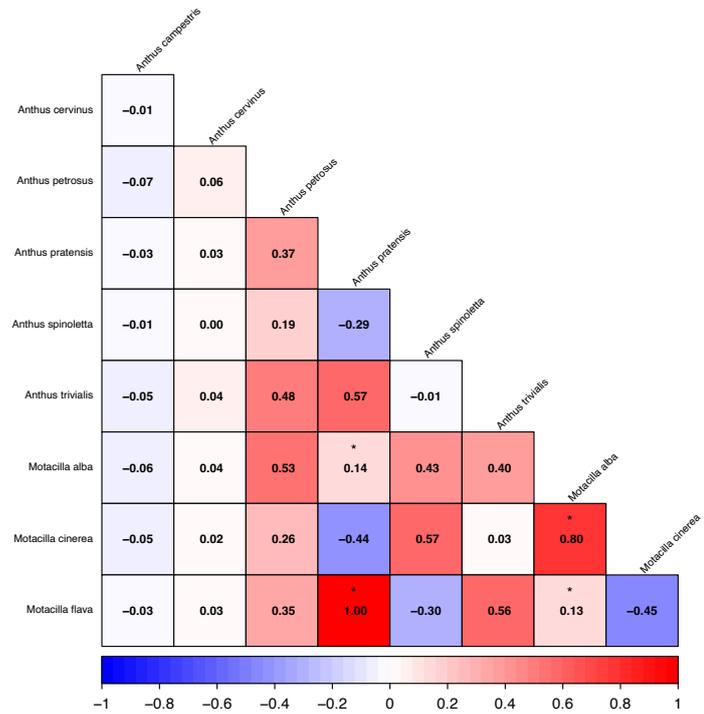
Ardeidae



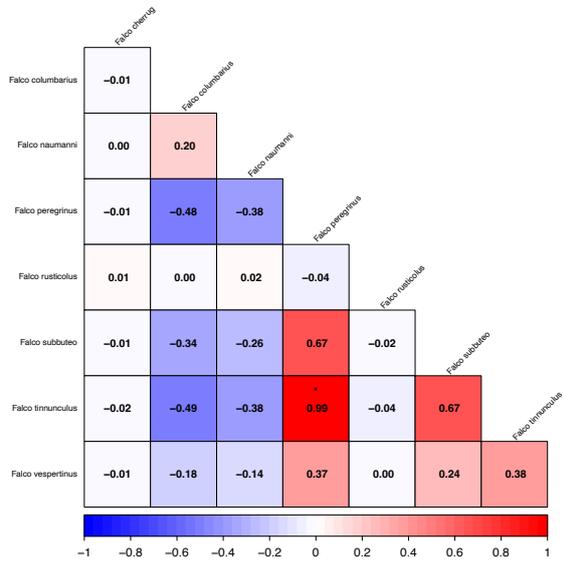
Emberizidae



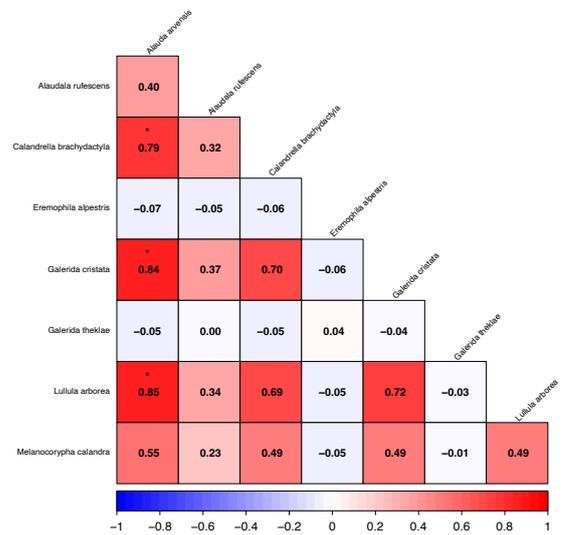
Motacillidae



Falconidae

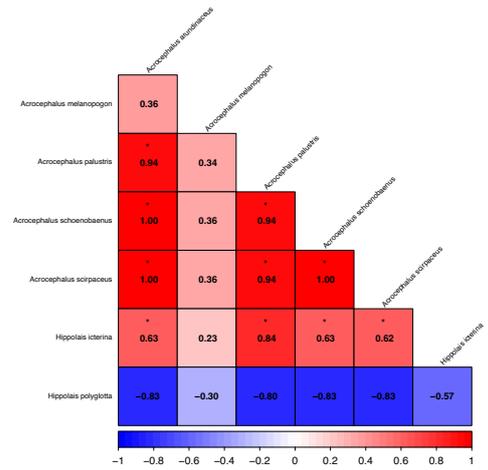
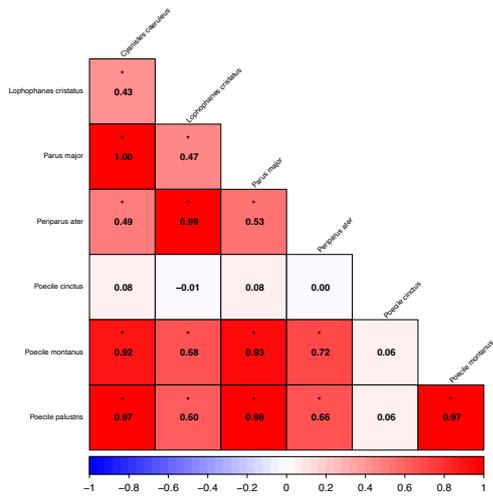


Alaudidae

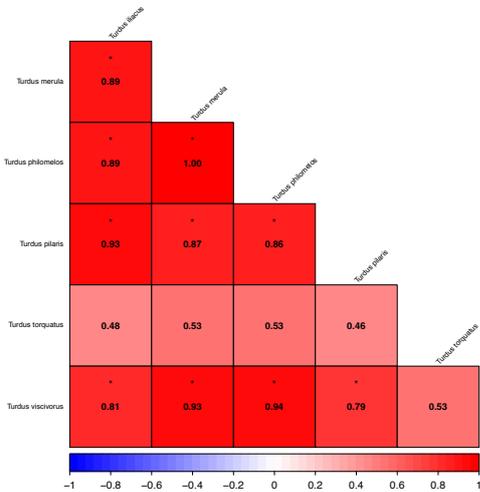


Paridae

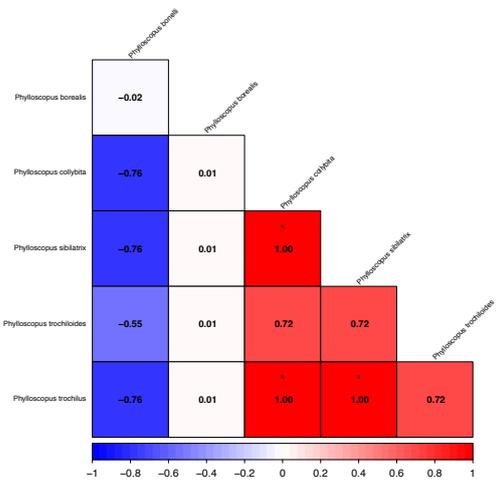
Acrocephalidae



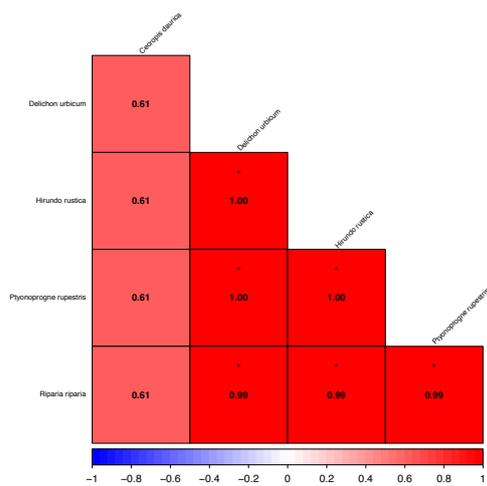
Turdidae



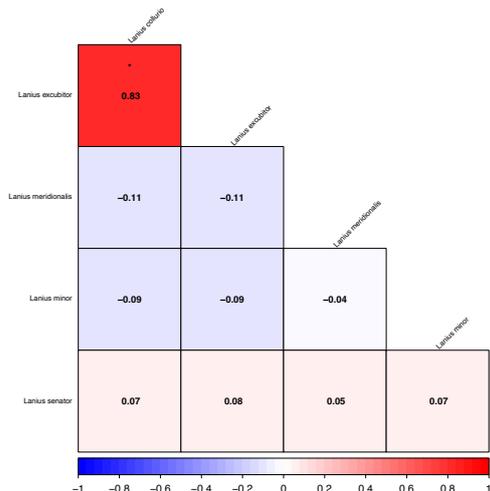
Phylloscopidae



Hirundinidae



Laniidae



Apodidae

Threskiornithidae

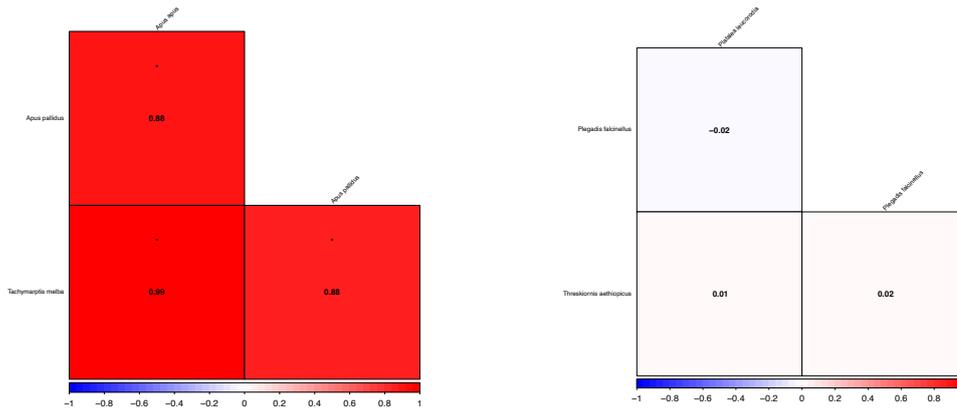


Figure 3. Residual association matrices for a variety of European families. Matrices not shown here can be found in Appendix D. Red indicates positive associations between species and blue indicates negative associations, after accounting for modelled environmental covariates. Asterices indicate a posterior mean support level greater than 0.9, in that more than 90% of the MCMC iteration estimates had the same sign as the posterior mean.

Table 2. Predictors of residual associations, from HMSC JSDBMs, among European species pairs (n=698 pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.108 (95% CI = 0.001, 0.321). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
	Intercept	2.784	1.578	3.749	0.001	**
All pairs	Hybridisation	0.154	-0.134	0.447	0.288	
	Morphometric dissimilarity	0.007	-0.139	0.149	0.907	
	Patristic distance	-0.032	-0.276	0.196	0.824	
	Same lifestyle & niche	0.082	-0.182	0.338	0.505	
	Same habitat type	0.679	0.417	0.945	<0.0005	***

Table 3. Predictors of residual associations, from HMSC JSDBMs, among European passerine pairs with predicted interspecific territoriality classifications available (n=168 pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.726 (95% CI = 0.024, 0.930). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
	Intercept	0.370	-3.466	3.748	0.883	
Passerines with interspecific territoriality predictions	Interspecific territoriality	0.063	-1.048	1.182	0.917	
	Hybridisation	0.338	-0.271	0.970	0.292	
	Morphometric dissimilarity	-0.010	-0.296	0.281	0.966	
	Patristic distance	0.013	-0.404	0.421	0.995	
	Same lifestyle & niche	0.404	-0.256	1.045	0.240	
	Same habitat type	2.162	1.638	2.700	<0.0005	***

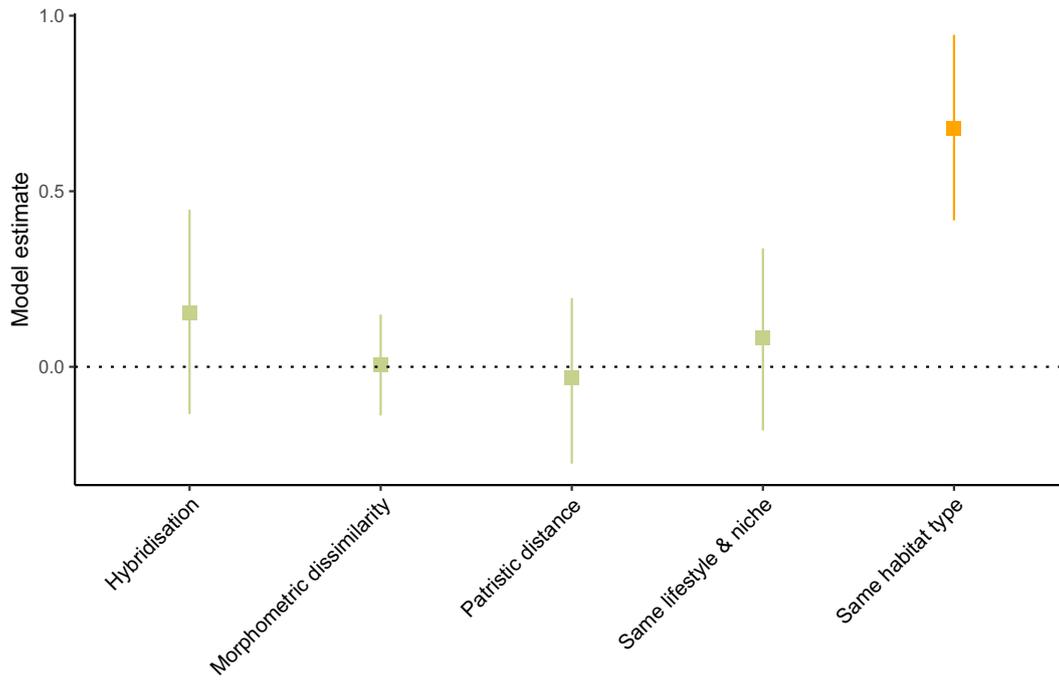
Table 4. Predictors of support for posterior means of residual associations, from HMSC JSDBMs, among European species pairs (n=1811 pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.398 (95% CI = 0.164, 0.631). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
	Intercept	-0.587	-4.434	3.306	0.804	
All pairs	Hybridisation	2.592	0.395	4.857	0.030	*
	Morphometric dissimilarity	-0.123	-1.236	0.914	0.781	
	Patristic distance	-0.963	-3.108	1.066	0.325	
	Same lifestyle & niche	-1.601	-3.544	0.079	0.062	
	Same habitat type	-1.069	-0.575	2.906	0.184	

Table 5. Predictors of support for posterior means of residual associations, from HMSC JSDBMs, among European passerine pairs with predicted interspecific territoriality classifications available (n=418 pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bold rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.476 (95% CI = 0.00005, 0.929). Significance codes: < 0.05*, < 0.01**, < 0.001***

Model	Variables	Median	2.5%	97.5%	pMCMC	
	Intercept	-0.7728	-4.061	3.519	0.715	
Passerines	Interspecific territoriality	0.6041	-2.190	3.457	0.650	
with	Hybridisation	1.6451	-0.168	3.670	0.092	
interspecific	Morphometric dissimilarity	-0.7543	-1.798	0.137	0.088	
territoriality	Patristic distance	-0.1103	-1.354	1.111	0.855	
predictions	Same lifestyle & niche	-0.5161	-2.319	1.086	0.533	
	Same habitat type	1.660	0.135	3.438	0.026	*

A)



B)

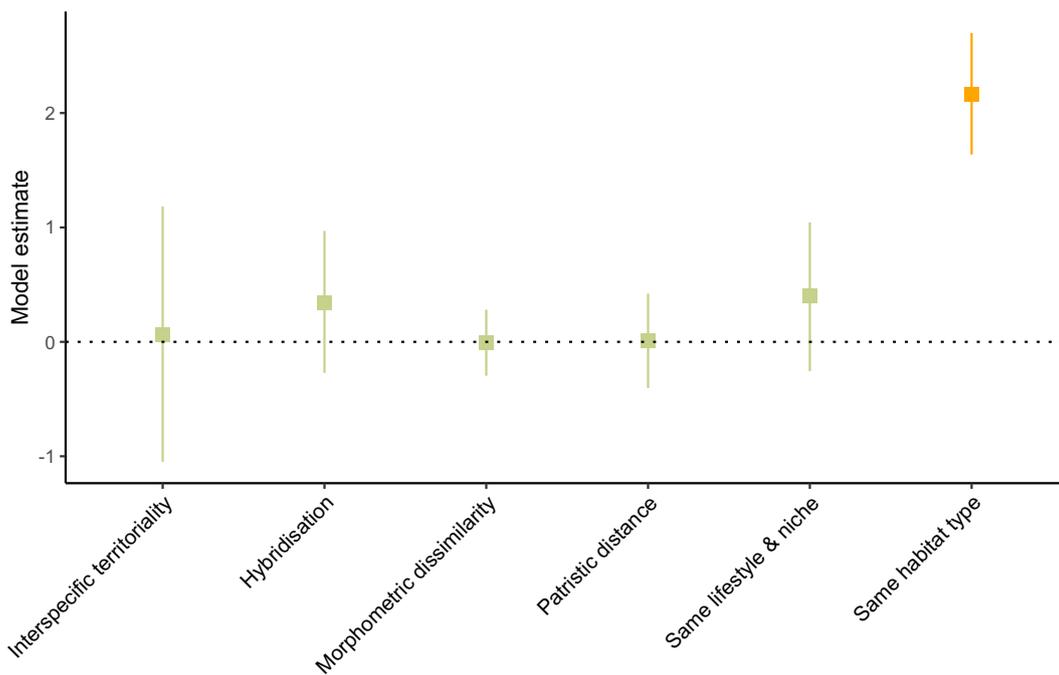
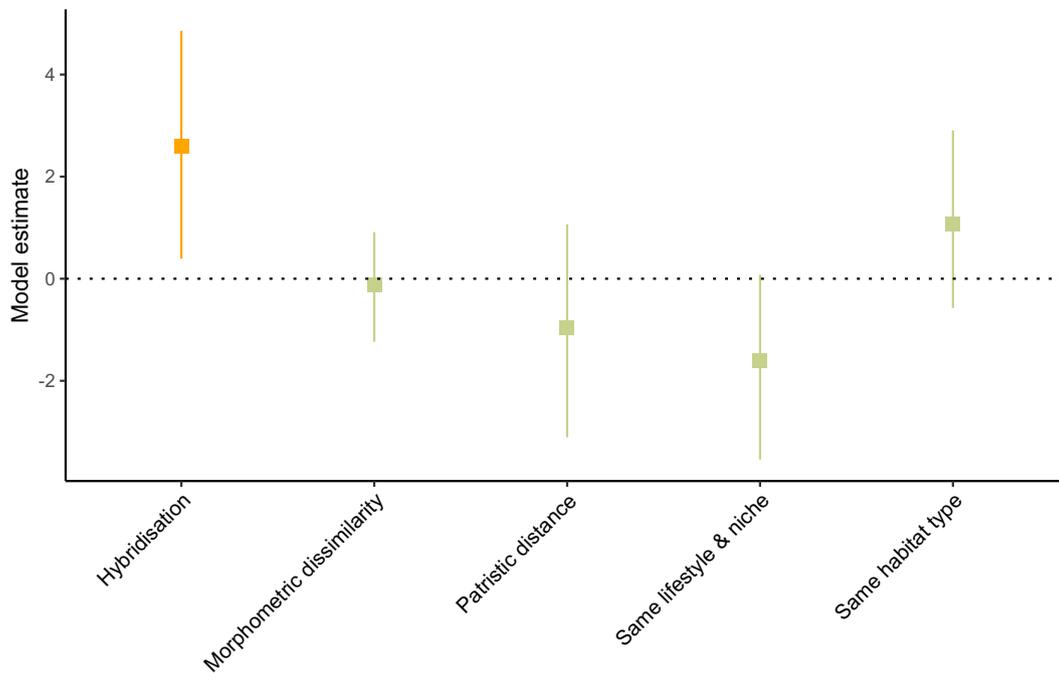


Figure 4: Predictors of residual associations in European pairs (A) (n=698) and European passerines with available predicted interspecific territoriality classifications (B) (n=168). Plotted values are coefficient estimates from phylogenetic generalised linear mixed models. Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Orange points indicate fixed effects with estimates with 95% credibility intervals that do not include 0.

A)



B)

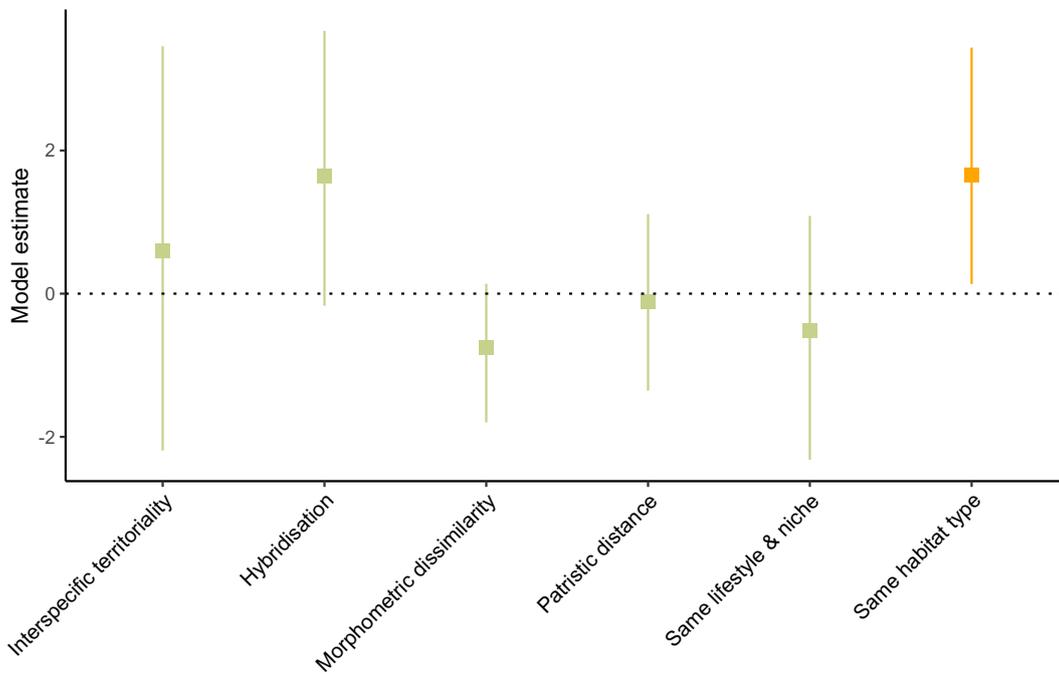


Figure 5: Predictors of support for the posterior means of residual associations in European pairs being greater than 0.9 (A) (n=698) and European passerines with available predicted interspecific territoriality classifications (B) (n=168). Plotted values are coefficient estimates from phylogenetic generalised linear mixed models. Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Orange

points indicate fixed effects with estimates with 95% credibility intervals that do not include 0.

6.3.2 Spatial predictions and quantifying the differences between JSDMs and SSDMs

In our comparison of JSDMs and SSDMs for four *Phylloscopus* warblers, we found little difference in model fit (Table 6). RSME, AUC and Tjur's R^2 were very similar for all species between the two model types. RSME was low for all species (<0.4), and AUC was consistently high (>0.8), suggesting good model fit. However, Tjur's R^2 was slightly low (0.269-0.444), indicating both JSDMs and SSDMs struggle to separate presences from absences.

Overall, spatial predictions differed little between SSDMs and JSDMs (Figure 6, Table 7). Mean differences in occurrence probability were tiny (-0.00159-0.01043). *P. collybita* and *P. trochilus* had negative mean differences, suggesting overall, SSDMs predicted higher occurrence probabilities than JSDMs. The opposite is true for *P. bonelli* and *P. sibilatrix*, which both have positive mean differences, although these differences are minute. RSME was low for all four species (0.005-0.016). Correlation between SSDMs and JSDMs was exceptionally high (>0.99) in all but *P. sibilatrix* (0.024). However, this difference between JSDM and SSDM predictions appears not to have translated into differences in binary presence-absence, as Jaccard similarity was also exceptionally high for *P. sibilatrix* (0.991). *P. sibilatrix* has areas in the Iberian Peninsula, Poland and Germany where the probability of occurrence is higher when projected by SSDMs, without the presence of other species, whereas in the rest of Europe, they are more likely to occur when modelled in the presence of the three other species (Figure 6). Occurrence probability is higher for *P. bonelli* when predicted by JSDMs in higher altitude areas of central Spain and the Alps. When predicted by SSDMs, *P. bonelli* occurrence is higher, without the presence of other species, on Corsica and in Northern Spain (Figure 6). *P. collybita* predicted occurrence was greater under SSDMs than JSDMs in the UK, northern Iberia and Finland; occurrence was lower in France, the

Mediterranean coast and the Baltic (Figure 6). Finally, *P. trochilus* occurrence probability was higher in Scotland and the Norwegian coast when predicted by JSDBMs, but higher when predicted by SSDMs on the southern coast of England and the Italian Alps (Figure 6).

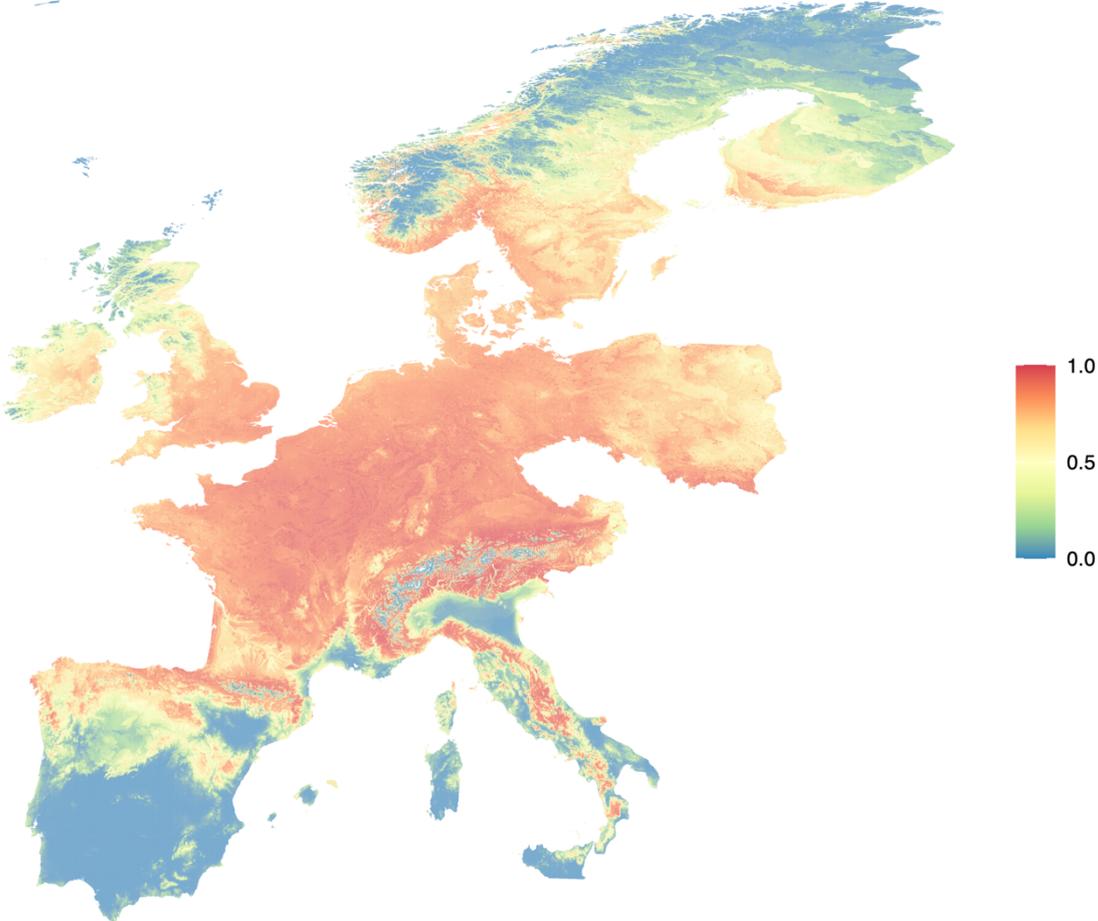
Table 6. Model fit estimates for four species of *Phylloscopus* warbler from a HSMC Joint Species Distribution Model (JSDBM) and an identical HSMC Single Species Distribution Model (SSDM) but run on individual species. Estimates include Root Square Mean Error (RSME), Area Under the ROC Curve (AUC) and Tjur's R²

Species	RSME	AUC	Tjur's R ²
JSDBM			
<i>P. collybita</i>	0.332	0.938	0.389
<i>P. trochilus</i>	0.338	0.935	0.444
<i>P. sibilatrix</i>	0.219	0.957	0.412
<i>P. bonelli</i>	0.156	0.976	0.405
SSDM			
<i>P. collybita</i>	0.390	0.812	0.269
<i>P. trochilus</i>	0.404	0.838	0.323
<i>P. sibilatrix</i>	0.235	0.943	0.359
<i>P. bonelli</i>	0.155	0.977	0.411

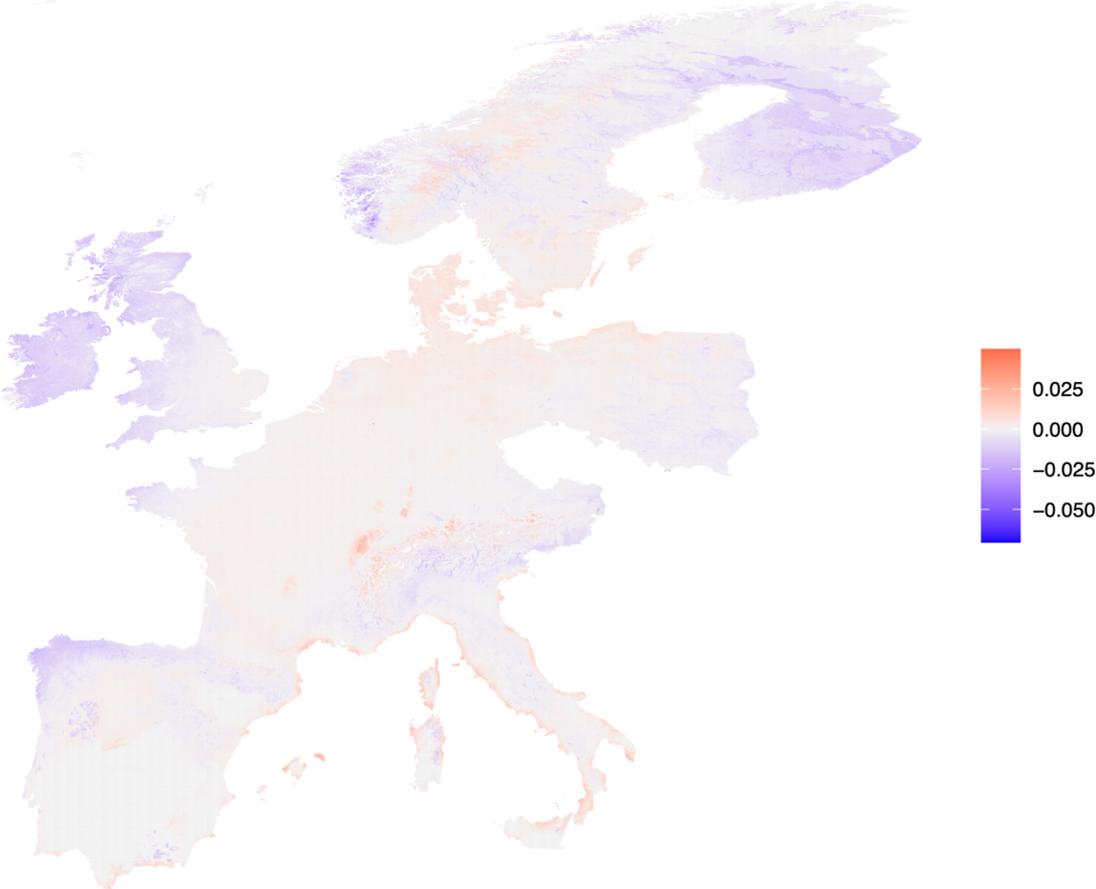
Table 7. Metrics comparing spatial predictions across western Europe for four species of *Phylloscopus* warbler from Joint Species Distribution Models (JSDBMs) and Single Species Distribution Models (SSDMs). Mean difference, Root Square Mean Error (RSME) and correlation utilise probability of occurrence while Jaccard similarity index uses binary predictions of occurrence (i.e. present if probability of occurrence >0.5).

Species	Mean difference	RSME	Correlation	Jaccard similarity
<i>P. collybita</i>	-0.00159	0.007	0.999	0.991
<i>P. trochilus</i>	-0.00024	0.005	0.999	0.992
<i>P. sibilatrix</i>	0.01043	0.016	0.024	0.991
<i>P. bonelli</i>	0.00009	0.010	0.998	0.909

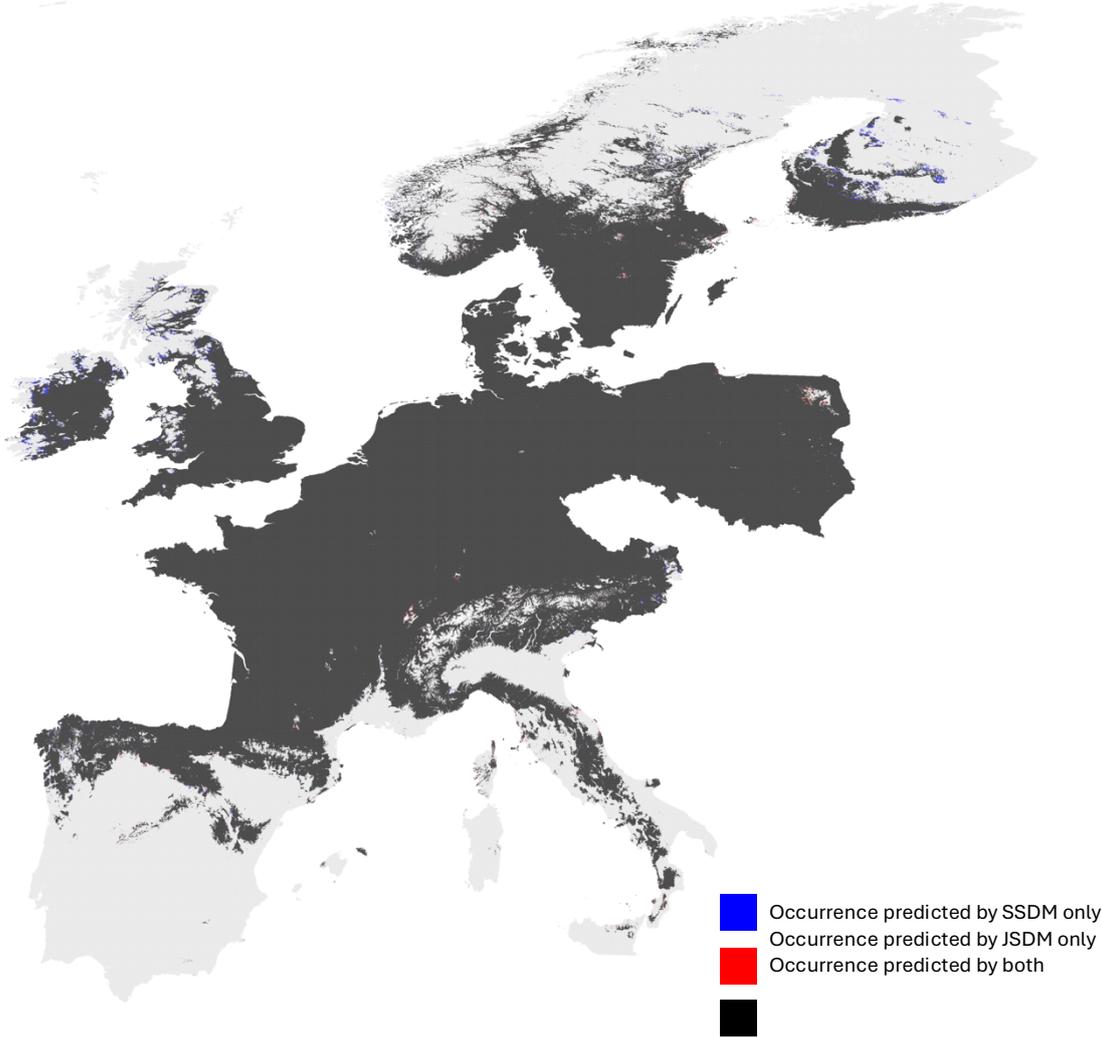
Phylloscopus collybita JSDM



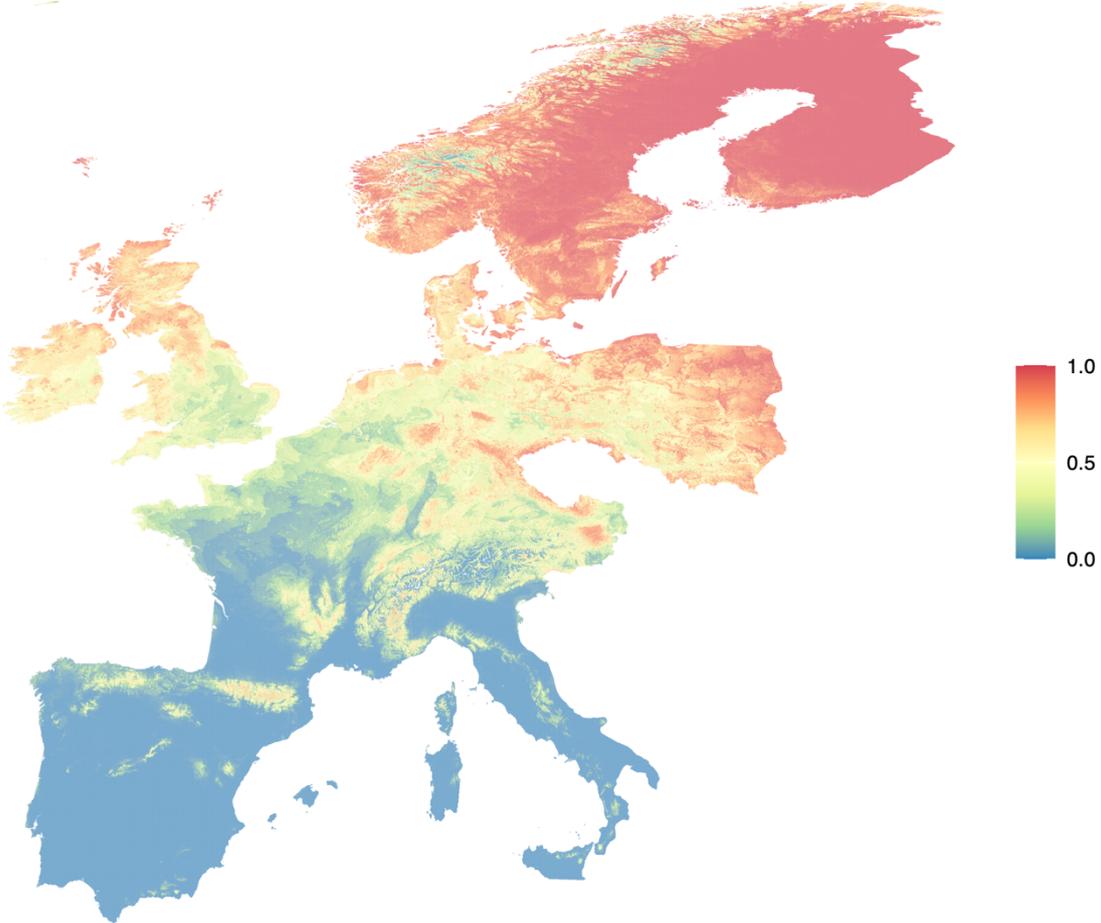
Phylloscopus collybita JSDM occurrence probability minus SSDM occurrence probability



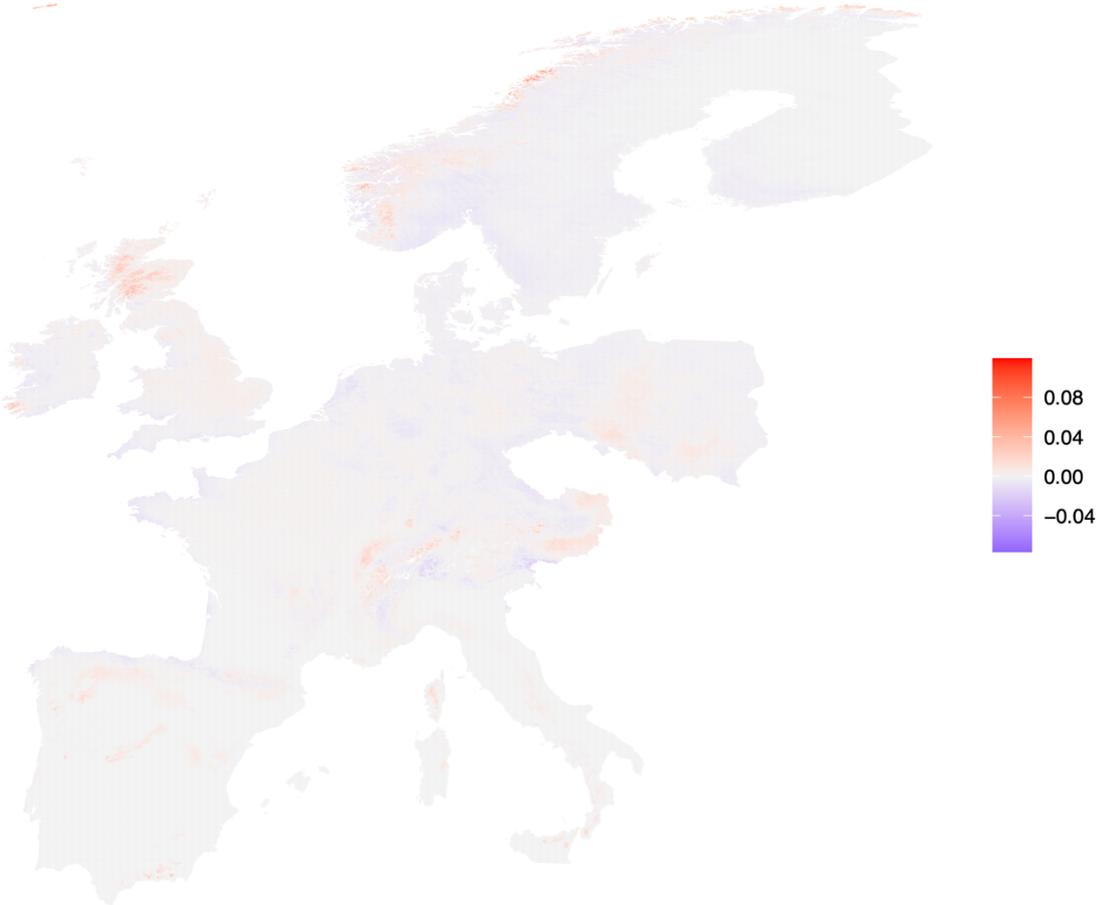
Phylloscopus collybita predicted presence-absence difference



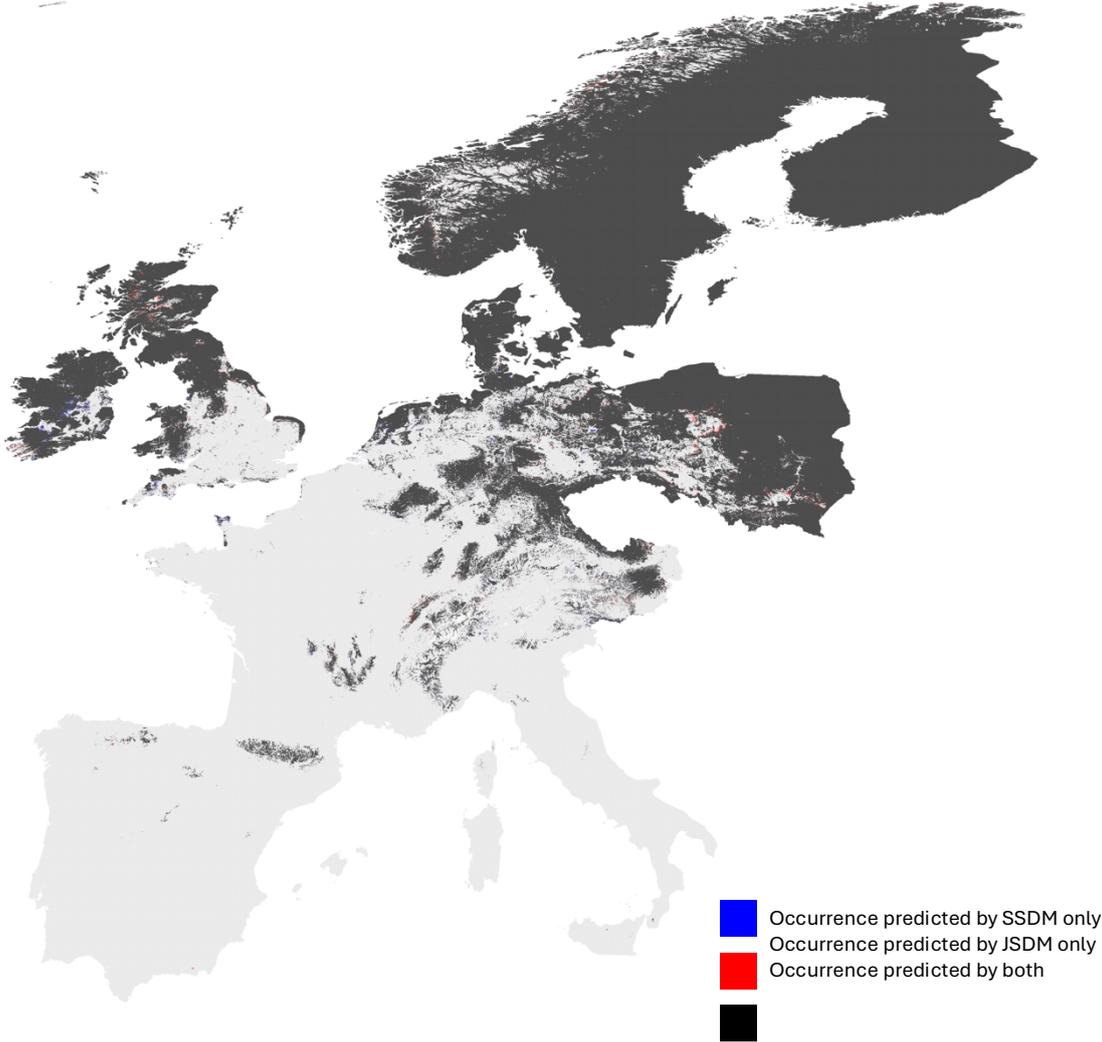
Phylloscopus trochilus JSDM



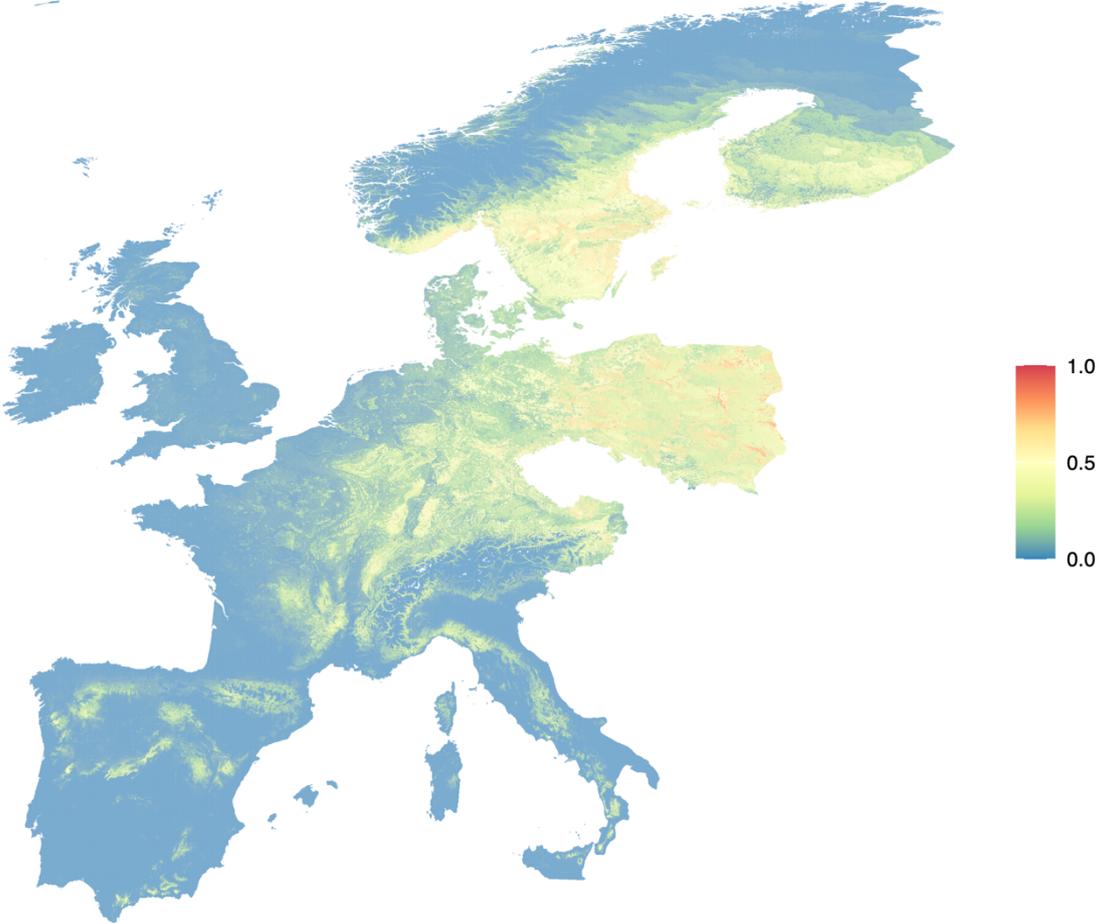
Phylloscopus trochilus JSDM occurrence probability minus SSDM occurrence probability



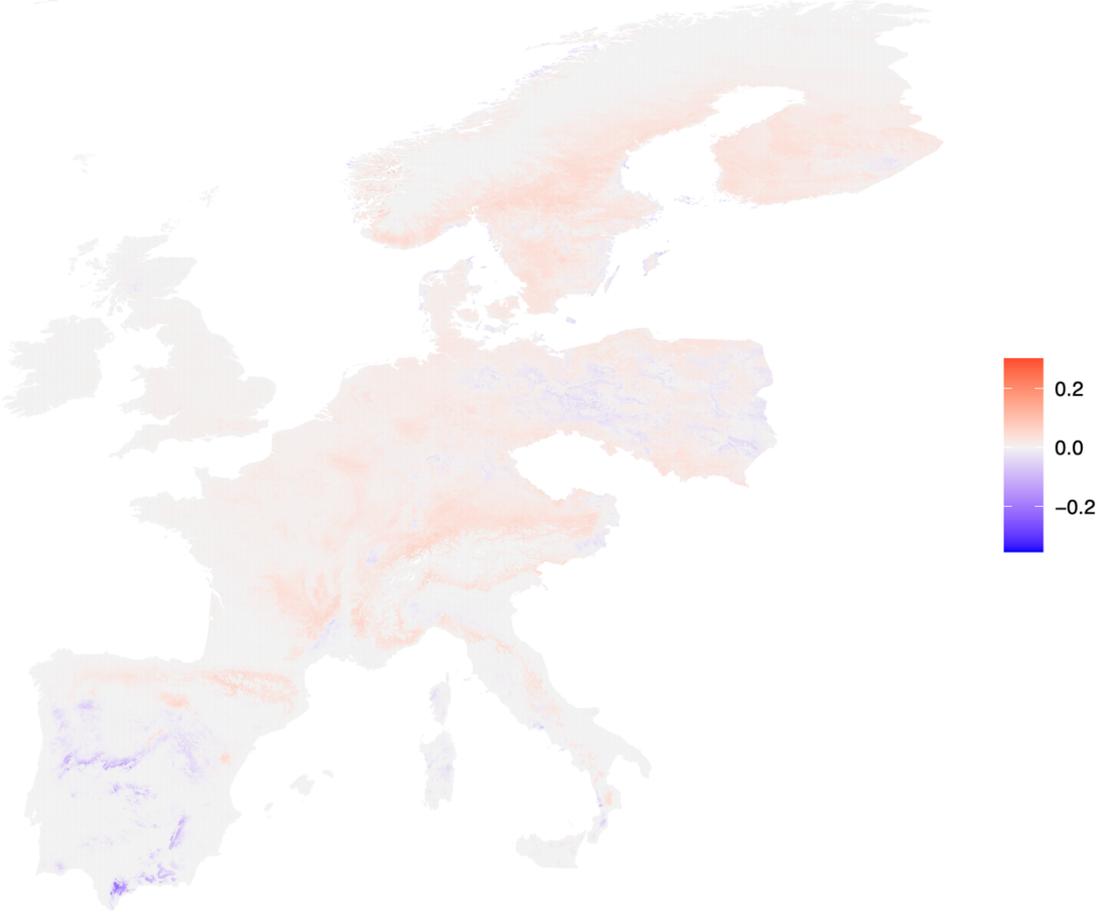
Phylloscopus trochilus predicted presence-absence difference



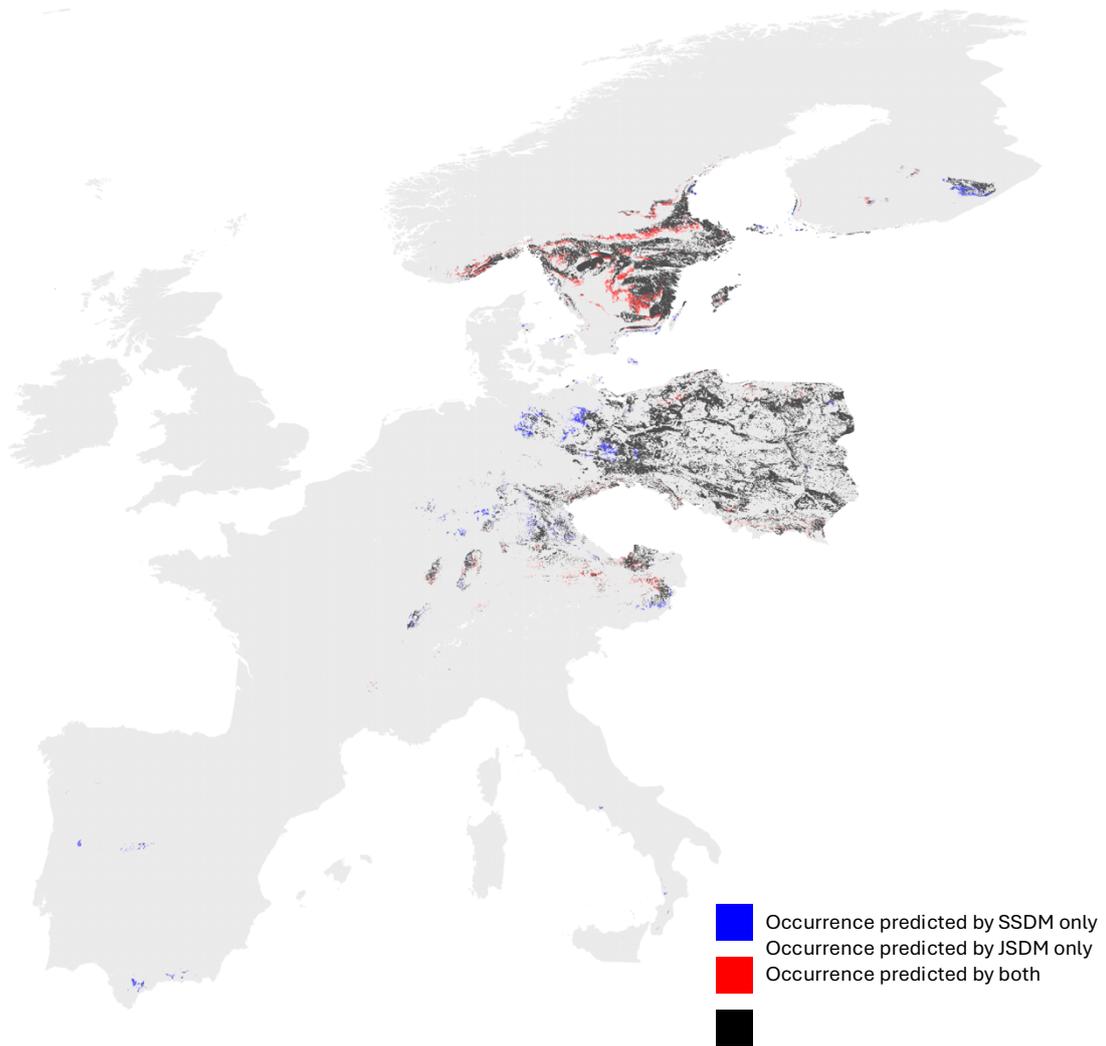
Phylloscopus sibilatrix JSDM



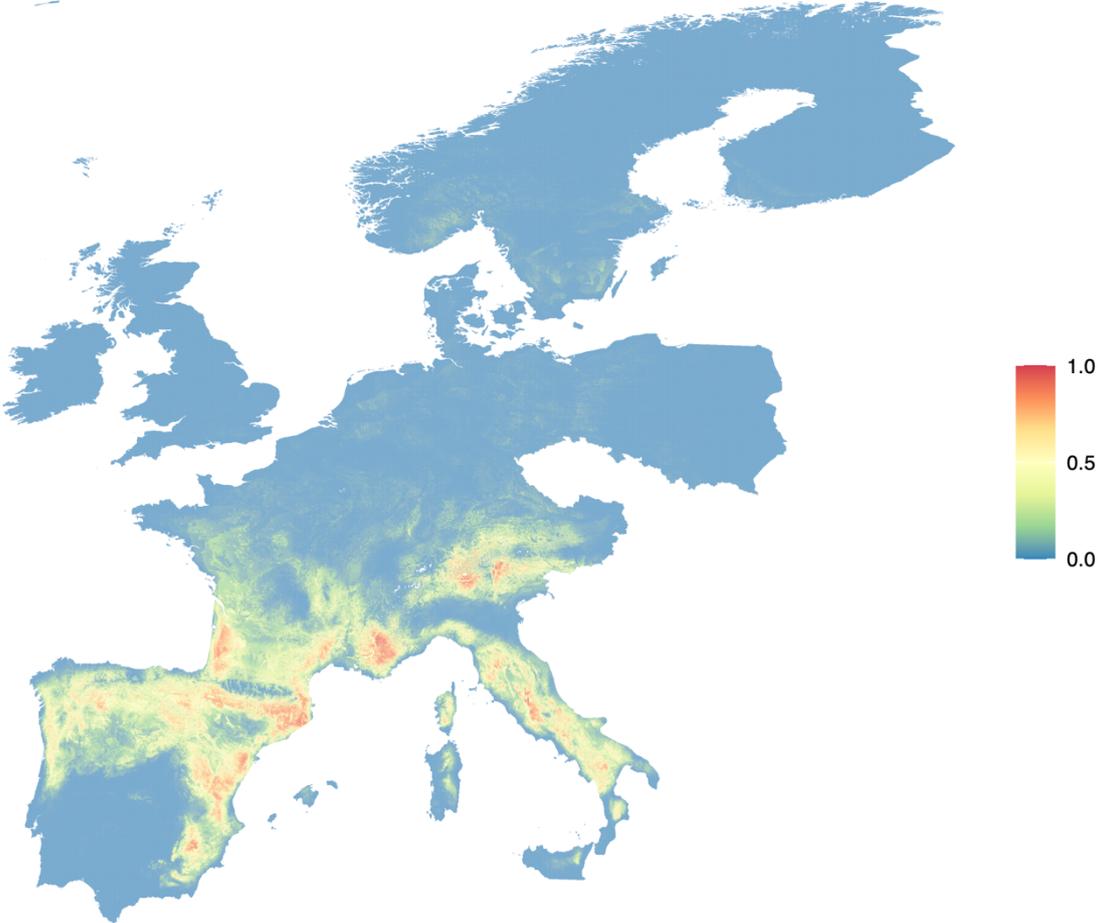
Phylloscopus sibilatrix JSDM occurrence probability minus SSDM occurrence probability



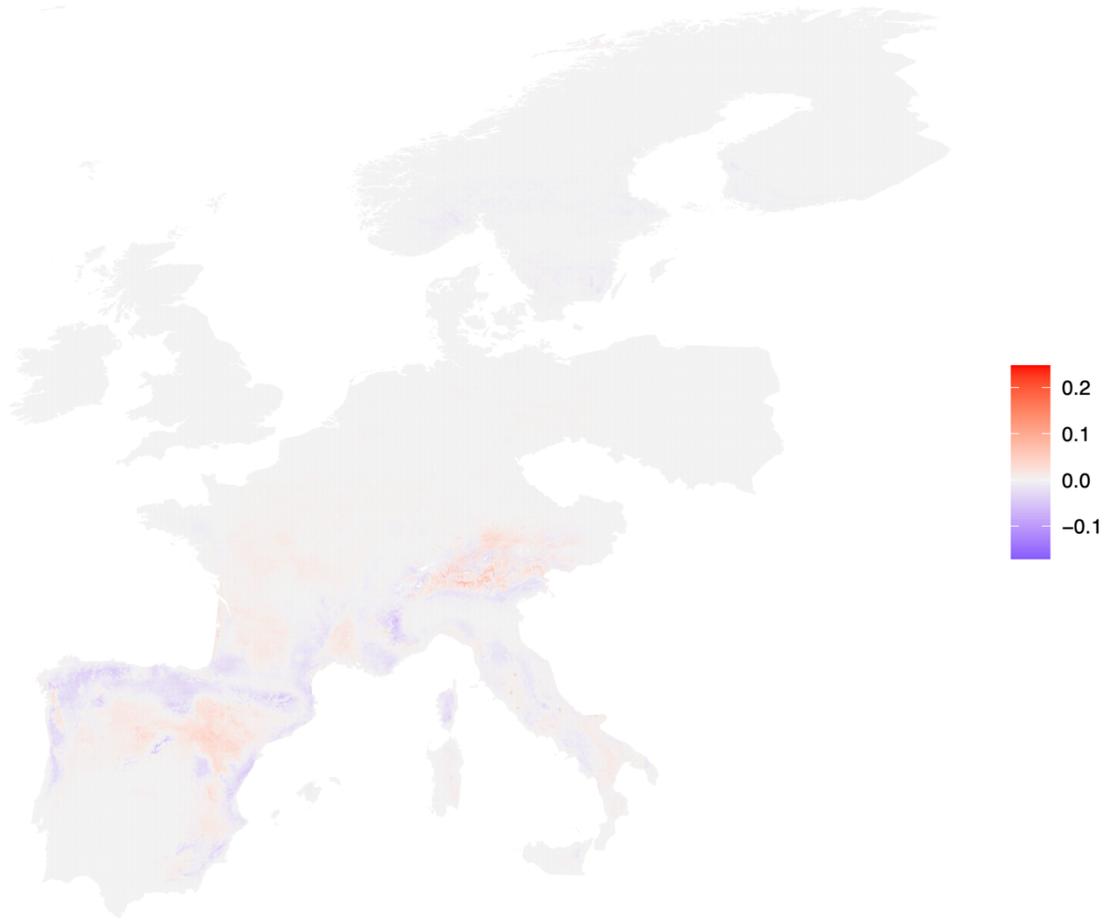
Phylloscopus sibilatrix predicted presence-absence difference



Phylloscopus bonelli JSDM



Phylloscopus bonelli JSDM occurrence probability minus SSDM occurrence probability



Phylloscopus bonelli predicted presence-absence difference

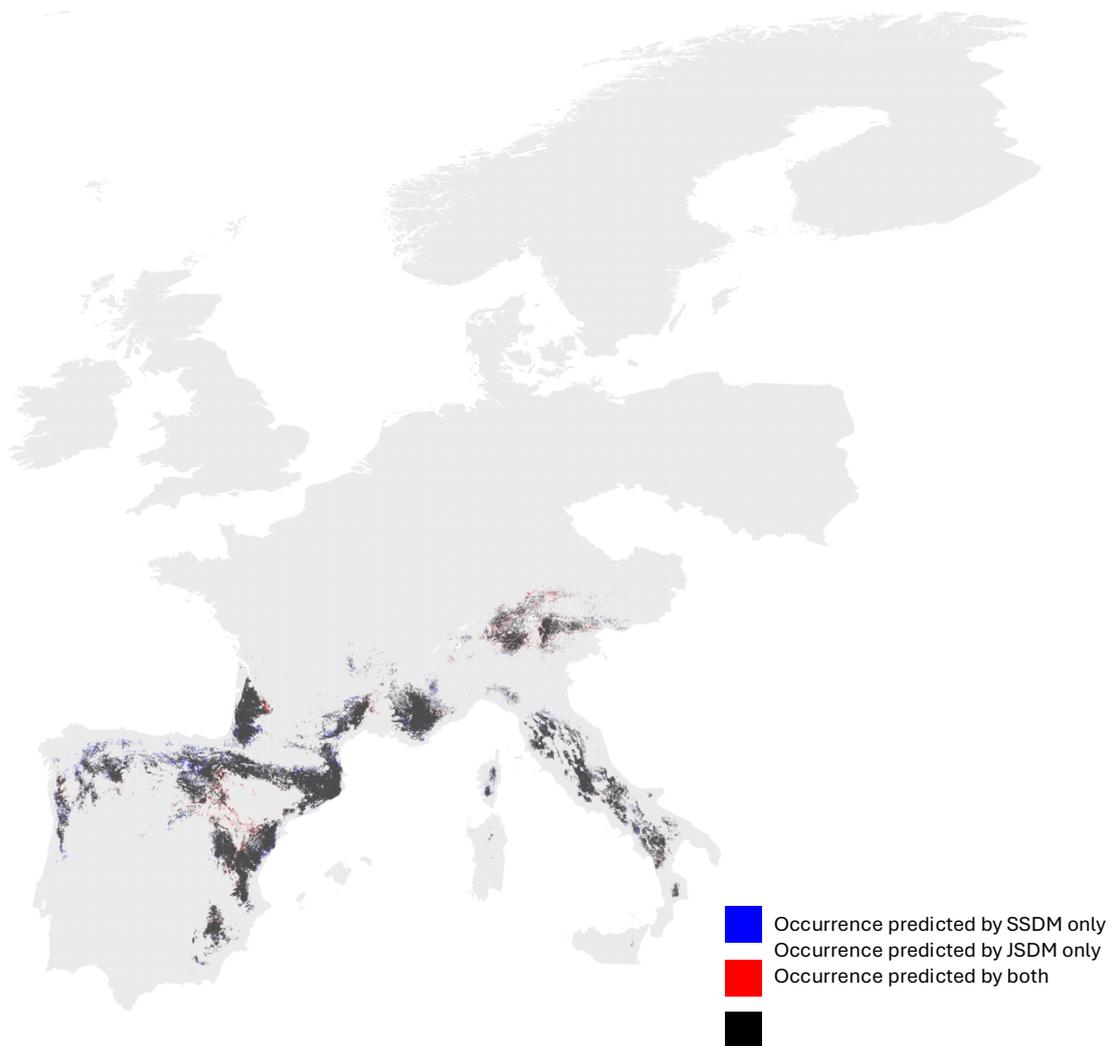


Figure 6. Predicted distributions for four *Phylloscopus* warblers. JSDM predictions of occurrence probability; the difference between JSDM and SSDM predictions (Red cells indicate predicted occurrence probability is higher when predicted by JSDMs and Blue indicates predicted occurrence probability is higher when predicted by SSDMs) and binary differences between JSDM and SSDM predictions. Cell considered occupied if occurrence probability >0.5 . Blue cells are predicted to be occupied by SSDMs only, Red by JSDM only and black by both.

6.4 Discussion

Given the overwhelmingly positive patterns of residual associations between species and the significant positive effect of sharing the same habitat type in our PLMMs, it appears that the observed residual associations are more likely the result of shared responses to unaccounted for environmental variables than true species interactions (Pollock *et al.*, 2014; Tikhonov *et al.*, 2020; Vallé *et al.*, 2024). This echoes the findings of Vallé *et al.* (2024), their HMSC JSDMs, on 40 common French birds found twice as many significant positive associations than significant negative associations. In their linear regressions, species residual associations were significantly influenced by species traits related to ecological niche, but in a manner suggesting similar environmental responses as opposed to ecological competition (Pollock *et al.*, 2014; Tikhonov *et al.*, 2020; König *et al.*, 2021; Wilkinson *et al.*, 2021; Elo *et al.*, 2022; Vallé *et al.*, 2024).

Our species data were at a 1km resolution, which may still be too coarse to capture biotic interactions, particularly negative ones (Araújo and Rozenfeld, 2014; Zurell, Pollock and Thuiller, 2018). For instance, Vallé *et al.* (2024) found negative species associations to be more prevalent in models run at a 200m resolution than those run at a 2km resolution. The availability of such high-resolution bird survey data is lacking across Europe, and it is currently unlikely that climate data could be accurately downscaled much further than 1km. Finer resolution species data exists in North America; the North American Breeding Bird Survey (NABBS) data is nested, with 50 point count stops along a 39.4km transect; the survey radius at each point count is 400m. Nesbit *et al.* (2023) found direct species interactions (interspecific territoriality) to influence distributions at this scale (see Chapter 2). It may be of interest to use this higher resolution species data in JSDMs to see if biotic interactions materialise in residual associations more at this finer scale.

We did, however, find evidence that hybridising species pairs were more likely to have a significant level of support for their posterior mean than non-hybridising pairs. Given that all the posterior means with support >0.9 were positive, it suggests that hybridising pairs are more likely to have positive residual associations. Species must co-occur at

some point for hybridisation to occur, so perhaps hybridising pairs co-occur more than non-hybridising pairs (Willis, Symula and Lovette, 2014).

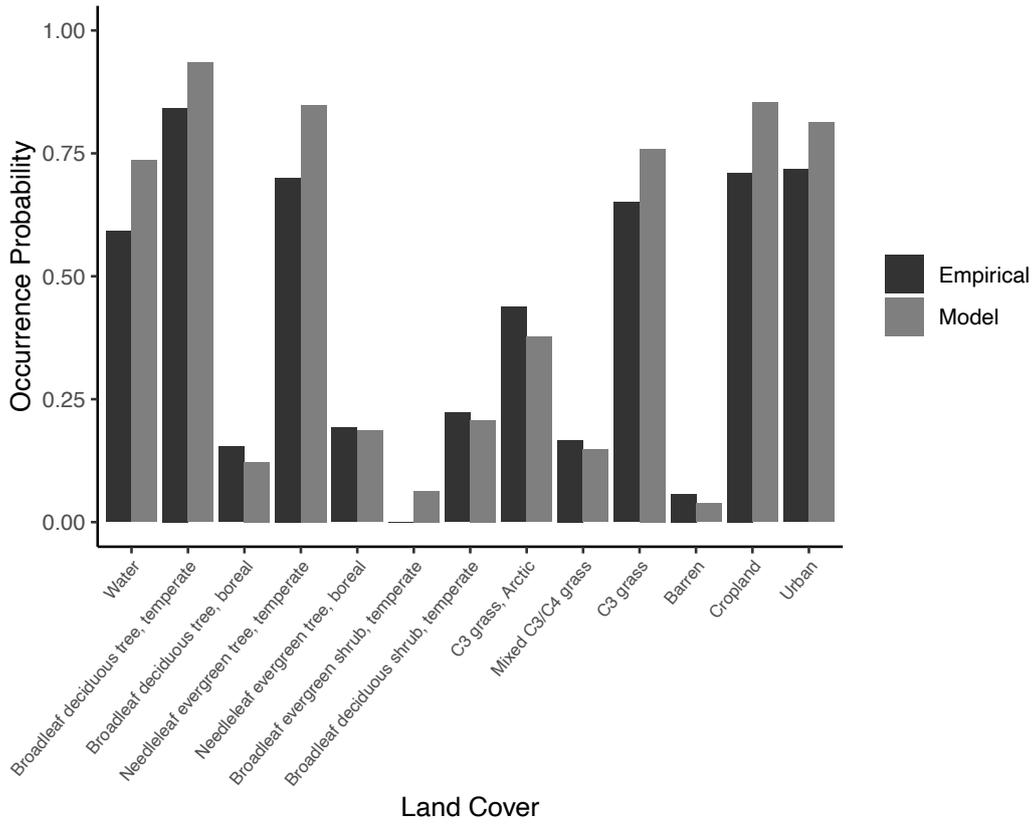
It could be argued that the predictor variables we included in our PLMMs are all indicative of negative species interactions. While that may be the case, we had assumed there would be a more even mix of positive and negative residual associations, that negative associations would be more indicative of competition, and we would be able to determine which type of competition was more important in structuring these associations. That said, if species associations are universally positive, perhaps they are somewhat less positive in pairs that do experience competition. An alternative approach would be to attempt to incorporate variables that are more indicative of affiliative interactions between species, such as a binary variable based on whether species have been recorded in mixed-species foraging flocks, for example.

HMSC JSDMs are correlative models with model covariates unlikely to be able to detect all factors aside from biotic interactions. As such, the interpretation of residual associations as indicative of species interactions should be avoided. However, by comparing models differing only in the inclusion of heterospecifics, we have demonstrated that the inclusion of species interactions in SDMs appears to have little impact on predicted distributions at a continental scale. Perhaps the influence of species interactions on coexistence would have been more apparent had we used count data in our models. For instance, negative interactions may not lead to total exclusion from a site but rather a reduction in abundance (Howard *et al.*, 2014; Ehrlén and Morris, 2015; Zurell, Pollock and Thuiller, 2018; Blanchet, Cazelles and Gravel, 2020; König *et al.*, 2021; Poggiato *et al.*, 2021; Elo *et al.*, 2022; but see Vallé *et al.*, 2024). The HMSC framework can incorporate temporal dynamics into models; however, due to computational constraints, we were only able to include species data for a single year (2015). The inclusion of temporal data into models can improve predictions, as species are not typically in equilibrium with the environment or heterospecifics, as assumed by traditional SDMs (Araújo, Pearson and Rahbek, 2005; Elith and Leathwick, 2009; Mutshinda, O'Hara and Woiwod, 2009, 2011; Sebastián-González *et al.*, 2010; Wisz *et*

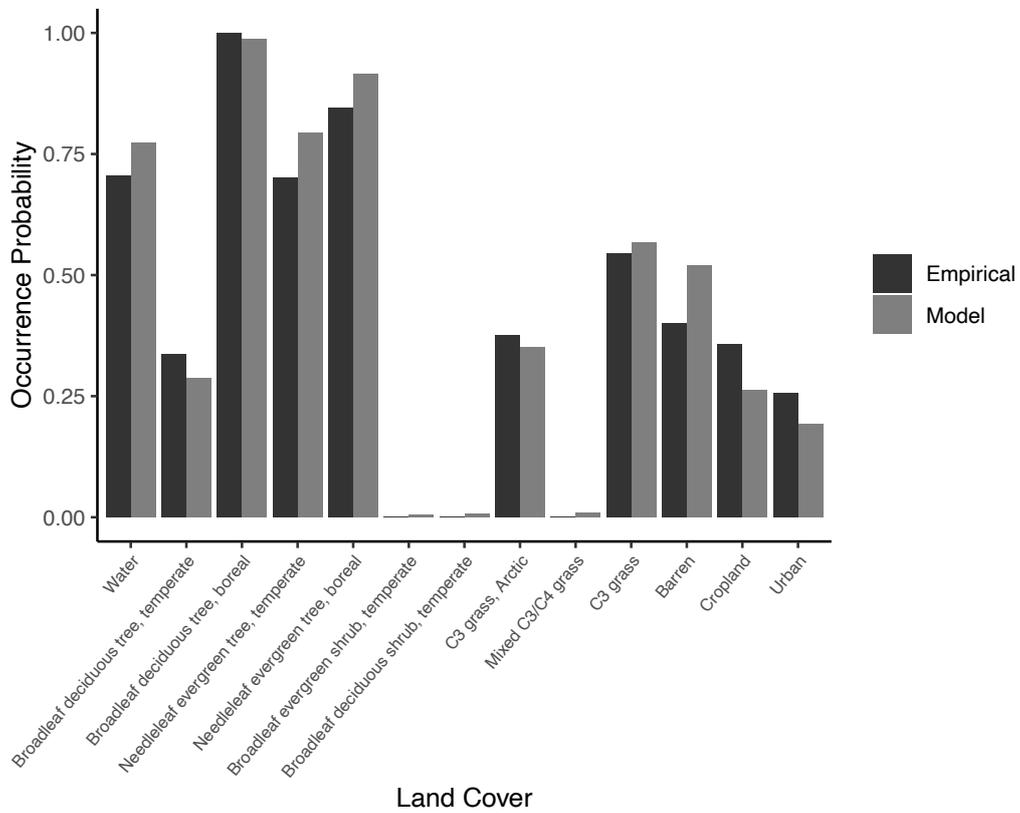
al., 2013; Schliep *et al.*, 2018; Elo *et al.*, 2022). Vallé *et al.* (2024) compared predictions of abundance between models with marginal (environmental covariates only, the equivalent of our SSDMs) and conditional predictions (incorporating the abundance of other species, similar to our JSDBMs) and found that the inclusion of other species abundance improved the predictive performance (R^2) of models (Vallé *et al.*, 2024). Had we modelled species abundance rather than presence-absence, we may have found a more discernible difference between the predictions of JSDBMs and SSDMs.

Given that HSMC residual associations are not solely the result of biotic interactions and can encompass shared responses to missing environmental covariates, it is necessary to include LULC data in models and given habitat filtering is a well-known assembly process, it would be remiss to exclude it from predictions of species distributions (Howard *et al.*, 2015, 2020). However, the LULC data (Chen, Li and Liu, 2022) we used in our models may have influenced model predictions slightly erroneously. This becomes apparent when looking at spatial predictions of occurrence probability, where the occurrence probability for some species in large lakes is not zero (Figure 6). An inspection of the observed and predicted occurrence probabilities for the four *Phylloscopus* warblers across different LULC types highlights this issue (Figure 7), with the observed occurrence probability of *P.collybita* in water being 0.60 and the predicted probability of occurrence 0.74 when in reality it should be zero. This is likely an artefact of survey sites being near waterbodies or the coast, and the water being the main component of the land cover in the cell; there is also no PFT category for marsh or fen vegetation. There are alternate high-resolution LULC datasets available, such as the UKCEH (Morton *et al.*, 2024) or CORINE (Büttner, 2014) land cover data. The reason for using the Chen, Li and Liu (2022) LULC initially was the availability of future LULC predictions. However, we subsequently did not use these future predictions as they appeared somewhat unrealistic and time constraints prevented us from fully exploring future predictions. In further analyses, the higher-resolution (100m) CORINE LULC (Büttner, 2014) data would likely be used.

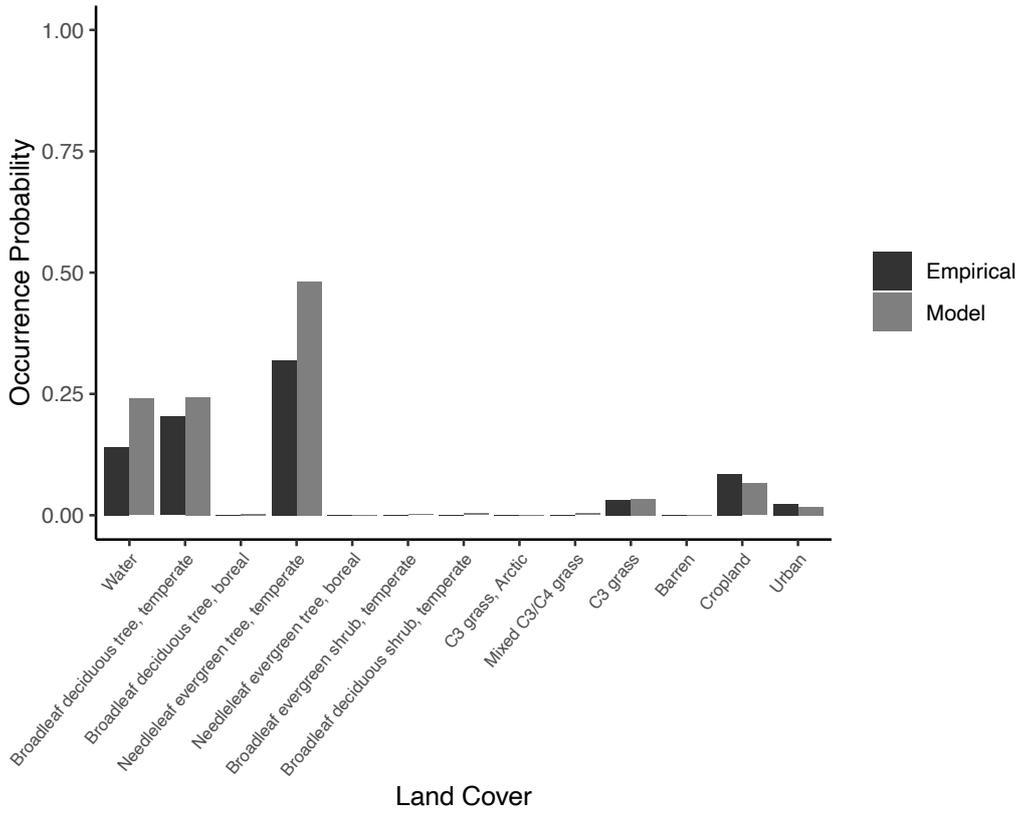
Phylloscopus collybita



Phylloscopus trochilus



Phylloscopus sibilatrix



Phylloscopus bonelli

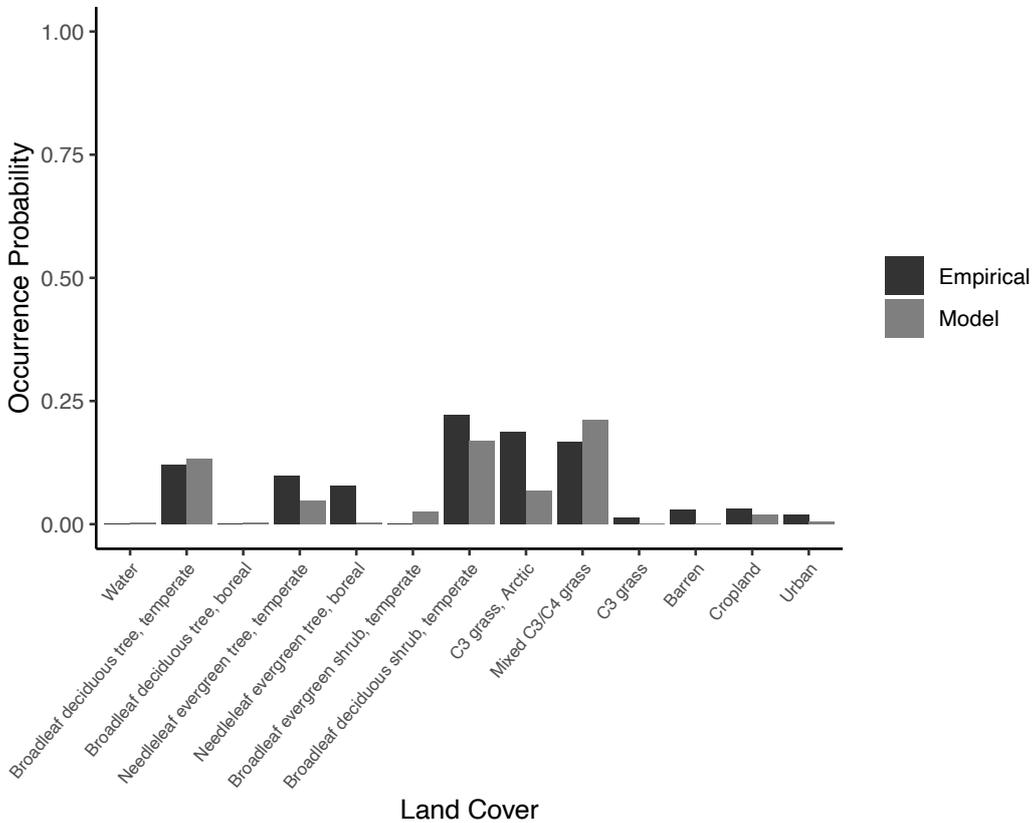


Figure 7. Observed (dark grey bars) and predicted (light grey bars) occurrence probabilities for four *Phylloscopus* warblers across various land use/land cover (LULC) types in Europe. Empirical observations are extracted from 4367 Pan-European Common Bird Monitoring Scheme (PECBMS) survey cells.

One of the more notable conceptual flaws in species distribution modelling is that the species-environment relationships used to make predictions are modelled on a species' current (realised) range, which is inherently a product of biotic interactions and other assembly processes (Poggiato *et al.*, 2021). This becomes particularly problematic when trying to model the impact of said interactions on distributions. HMSC JSDMs appear to do little to account for this. However, the use of count data in place of binary presence-absence data alongside data from multiple years in Joint Dynamic Species Distribution Models (JDSDMs) could overcome this conceptual limitation (Thorson *et al.*, 2016; Elo *et al.*, 2022) as competition is more likely to lead to reduced abundance rather than total exclusion and temporal variation in abundance could be indicative of competition when one species is rare while another is commoner, or positive interactions when both species are concurrently common (Warton *et al.*, 2015; Blanchet, Cazelles and Gravel, 2020; Elo *et al.*, 2023).

This research presents large-scale, high-resolution JSDMs for a large assemblage of European birds. We found little evidence for the impact of species interactions on observed patterns of residual associations nor spatial predictions at a near-continental scale. There were far more positive associations between species than negative; in fact, no negative associations surpassed the support threshold. We also found that species pairs sharing the same habitat type have significantly more positive associations than pairs differing in preferred habitat type, providing further evidence for residual associations primarily encompassing unaccounted environmental covariates. We highlight conceptual limitations with modelling species interactions using joint species distribution models and recommend the incorporation of spatio-temporal abundance into models to overcome these limitations, when computing capabilities allow. Without these modifications, the value of JSDMs and their ability to effectively incorporate biotic interactions into their predictions has to be questioned.

Chapter 7

General Discussion

7.1 Overview

This thesis furthers our understanding of avian species interactions and their impact on species distributions. We present large-scale, comparative, species-pair analyses across North America and Europe, spanning a large taxonomic breadth of passerines and non-passerines. Chapters 2 and 3 focus primarily on hybridisation. This is the first time hybridisation has been studied at such a large scale in a species-pair framework, incorporating phylogenetic relationships. Understanding why hybridisation occurs is of great importance, particularly from a conservation perspective, as hybridisation can threaten the genetic integrity of rare species (Rhymer and Simberloff, 1996; Simberloff, 1996; Muñoz-Fuentes *et al.*, 2007) and can complicate endangered species legislation and policy (vonHoldt *et al.*, 2016). When predicting the determinants of hybridisation, we found strong support for the mistaken identity hypothesis in both North America and Europe, with similar species more likely to hybridise. As expected, hybridisation is also limited by relatedness, with species divergence reaching a threshold beyond which hybridisation does not occur (Orr and Turelli, 2001). We also highlight the role of fine-scale habitat and large-scale range overlap on the likelihood of hybridisation, with the likelihood increasing as habitat and range overlap increase, suggesting heterospecific encounter rates partly influence hybridisation events. We also find evidence to oppose Hubbs' principle with the likelihood of hybridisation decreasing as the disparity in the estimated counts of species within a pair increases, once again suggesting a role for heterospecific encounter rates. As a result of this work, we now have a much greater understanding of the causes of hybridisation across North America and Europe for both passerines and non-passerines. This knowledge base allows us to predict hybridisation in novel species pairs, as described in Chapter 3, which has significant conservation implications.

As species ranges shift due to anthropogenic climate and land use change, and introduction to non-native areas, novel interactions will form (Alexander, Diez and Levine, 2015). Predicting whether these newly interacting species are likely to hybridise could be of great value for conservation practitioners. In Chapter 3, we demonstrate that it is possible to predict 'unknown' hybridisation classifications using models trained

on pairs with known classifications, and discuss the conservation implications of this. We find Random Forest (RF) machine learning algorithms and predictions from Phylogenetic Linear Mixed Models (PLMMs) consistently outperform one another in differing performance metrics. To highlight possible uses of these predictive frameworks, we predict the likelihood of hybridisation for thousands of species pairs, some of which do not currently coexist. We then create maps of range overlap for hybridising pairs, both currently and in the future, plotting potential hotspots of hybridisation. This work is a first step and proof of concept in predicting hybridisation between novel species pairs, and it is hoped that with advances in modelling techniques and data availability, improvements will be made in predictive power. With said improvements, these predictions have the potential to inform conservationists and could act as an early warning system for hybridisation between colonists, introduced species, and natives as species distributions change.

Understanding how species interactions have influenced coexistence in the past is vital to understand how they may influence coexistence in the future. In Chapter 4, we hindcast the effect of competition on historical range dynamics in North America and Europe between 1997 and 2019. We utilise two large-scale citizen science spatial datasets: the North American Breeding Bird Survey (NABBS) and the Pan-European Common Bird Monitoring Scheme (PECBMS). In North America, we find that interspecifically territorial pairs increased their fine-scale habitat overlap between 1997 and 2019 more so than non-territorial pairs. We believe this is the result of interspecific territoriality creating spatial segregation within habitats, which subsequently facilitates resource partitioning, allowing similar species to coexist. In Europe, we find that pairs in which both species are secondary cavity nesters increased their large-scale range overlap more so than non-secondary cavity nesters over the 22-year study period, potentially a result of increased nest-box provisioning (Duckworth, 2013; Lima and Garcia, 2016).

In Chapters 5 and 6, we examine the impact of species interactions on current species distributions using the predictions from Species Distribution Models (SDMs) at differing resolutions (1km and 0.5°). In Chapter 5, we calculate measures of geographic

avoidance (Novella-Fernandez *et al.*, 2021) across North America and Eurasia using the current range predictions from SDMs (Gillie, 2024) and BirdLife International range maps (BirdLife International and Handbook of the Birds of the World, 2021). Geographic avoidance quantifies exclusion patterns as the proportion of a pair's predicted range that is realised in overlapping areas compared to the proportion realised in non-overlapping areas. We found that most pairs exhibited some level of avoidance across their ranges. However, PLMMs with geographic avoidance as a response variable found no evidence for the role of competitive interactions in the observed patterns of avoidance. Geographic avoidance is a pairwise measure of avoidance, so we developed additional metrics that extract avoidance for the individual species within a pair, from which we calculated a measure of avoidance symmetry to quantify to what extent species differed in their levels of avoidance towards one another. Using PLMMs with avoidance symmetry as a response variable, we found that, in North American pairs, hybridisation was indicative of increased asymmetry, suggesting a potential role for sexual exclusion in geographic patterns of avoidance (Hochkirch, Gröning and Bücken, 2007; Gröning and Hochkirch, 2008). In Europe, morphometrically dissimilar pairs had more symmetric levels of avoidance. Morphology is highly correlated with ecological niches and resource acquisition (Pigot *et al.*, 2020a), and these patterns of avoidance are likely the result of exploitative competition. Morphologically dissimilar pairs still experience avoidance, but they experience it more equally than morphologically similar pairs. This work also presents, for the first time, a high-throughput framework for the modelling of geographic avoidance in birds.

Finally, in Chapter 6, we use high-resolution Joint Species Distribution Models (JSDMs) across a large spatial extent and attempt to detect the effect of biotic interactions in the residual associations of species pairs from 41 European families. We find that associations between species are overwhelmingly positive, and we find no evidence that JSDMs can detect species interactions in their residual associations. Instead, we find further evidence that unaccounted-for environmental covariates are responsible for observed patterns of association between species. We compare the predictions of JSDMs and Single Species Distribution Models (SSDMs) for four species of *Phylloscopus* warbler and find little to no difference in their model fit or predictive abilities, providing

further evidence that JSDMs do little to account for species interactions in their predictions.

As a whole, this research greatly expands our knowledge of avian hybridisation and the impact of species interactions on the distributions and coexistence of birds at a variety of geographic scales. Below, I synthesise the findings of this thesis, describe commonalities and differences among chapters and continents, identify key themes and comment on the novelty, applications and potential future work that could arise from it.

7.2 Synthesis

The relationship between species interactions and range dynamics is an overarching theme of this thesis, yet each chapter explores those themes in different ways. Our hindcasting analyses in Chapter 4 focus on the effect of interactions over evolutionary, very short time-periods (22 years) at both a fine scale (<400m) and a coarser scale of ~40km. Chapters 5 and 6 analyse species' contemporary ranges. Geographic Avoidance (Chapter 5) is calculated with 0.5° grid cells, the coarsest spatial resolution in this work. While the JSDMs created in Chapter 6 are at a much higher resolution, with 1km grid cells. All of our analyses cover a large spatial extent. We hindcast the impact of species interactions across North America and Western Europe, and geographic avoidance is analysed in North America and Eurasia, whereas JSDMs focus on Western Europe only. While Chapters 4-6 focus on the impact of species interactions on range dynamics and coexistence, our predicting hybridisation (Chapters 2 and 3) analyses explore, among other things, the effect of coexistence on the likelihood of hybridisation. We highlight that as species encounter each other more, through increased syntopy and sympatry, they are more likely to hybridise, and that as species ranges contract and become more fragmented in the future, the likelihood of hybridisation globally may fall.

Across a number of our analyses, morphology emerged as a significant influence on species coexistence, although occasionally in opposing directions. In our hindcasting analyses (Chapter 4), North American PLMMs included mass difference and bill length

difference as proxies for resource competition. However, in our European analyses, we utilised morphometric dissimilarity, which corresponds to the Euclidean distance between pairs in a Principal Component (PC) space derived from nine AVONET (Tobias *et al.*, 2022) morphological traits. In Europe, we found morphometric dissimilarity to be a marginally significant negative predictor of Δ syntopy. In that, European species pairs that are more morphologically different became less syntopic between 1997 and 2019. The counter to that is that similar species became more syntopic, which, given the relationship between morphology and resource acquisition (Pigot *et al.*, 2020a), we would expect the opposite, with competitive exclusion between similar pairs. However, habitat filtering could be responsible for similar species co-occurring more (Polo and Carrascal, 1999b; Remeš and Harmáčková, 2025). At a larger spatial scale, in North America, mass difference reduced Δ sympatry, which again could be the result of habitat filtering (Polo and Carrascal, 1999b). Bill length difference in North American pairs increased Δ sympatry, suggesting that as species bills, their primary resource acquisition tool (Pigot *et al.*, 2020a), become more different, their ranges can overlap more, suggesting a role for resource competition in structuring species communities at this scale. In our geographic avoidance analyses (Chapter 5), which encompass broad-scale distribution patterns, morphometric dissimilarity increased the symmetry with which species' geographic avoidance occurred, but not the level of avoidance itself. Species that can partition resources through differences in morphology may exhibit more stable coexistence (Diamond, 1973; Grant and Grant, 2006; Pimm, Diamond and Bishop, 2023). Why there is a lack of consensus in the effect of morphology at different scales, particularly between North American and European hindcasting analyses, is unknown, although differences in survey data structure may be responsible. NABBS data are nested, with stops being within routes; the survey radius of a stop is 400m, while the length of a route is 39.4km. PECBMS data, on the other hand, are just sites that are considered syntopic if within 1km of one another and sympatric if within 40km of one another. Therefore, the scale of syntopic measures in Europe is more than double that of those in North America, hence the disparity in the effect of morphology on syntopy between the two continents. It should be reiterated, however, that the effect of morphological dissimilarity on European Δ syntopy was only marginally negative; only two of the four PLMM chains had a p MCMC<0.05.

We spent Chapters 2 and 3 predicting hybridisation; however, hybridisation emerged as a significant predictor of geographic avoidance symmetry in Chapter 5, and support for residual association values in Chapter 6. In Chapter 5, we found hybridisation reduced avoidance symmetry, so that hybridising pairs had more asymmetric avoidance responses than non-hybridising pairs. We suggest this is the result of sexual exclusion (Kuno, 1992a; Hochkirch, Gröning and Bücken, 2007). In Chapter 6, we found that hybridising pairs had a greater likelihood of having significant residual associations (support >0.9) than non-hybridising pairs. All significant residual associations were positive, i.e., species co-occur together more often than chance after accounting for modelled environmental covariates, and as such, it could be argued that hybridising species co-occur together more often than non-hybridising species. This positive co-occurrence of hybrids echoes the findings of Chapter 2, in which hybridising pairs are likely to have higher fine-scale and large-scale range overlap than non-hybridising pairs. We found interspecific territoriality to influence species distributions only once, in Chapter 4. Interspecifically territorial pairs increased their fine-scale habitat overlap between 1997 and 2019 more so than non-territorial pairs, possibly a result of spatial segregation and subsequent resource partitioning that facilitates coexistence. Unfortunately, we only had available territoriality classifications for a subset of North American passerines from Drury, Cowen & Grether (2020). As such, all other analyses that utilised territoriality (Chapters 4, 5 and 6) either modelled a subset of passerines with available values or used imputed values, predicted using random forest machine learning algorithms. While many of these predictions seemed sensible, and some predicted pairs do defend territories against one another, ideally, we would have utilised real classifications. We hope these additional data will be extracted from the literature at some point in the future, and we may be able to repeat some analyses, and perhaps interspecific territoriality will emerge as an important component of species coexistence and range dynamics beyond North American Passerines.

In Chapter 4, we found that European pairs that are both secondary cavity nesters increased their range-wide overlap between 1997 and 2019 more so than pairs that

build and excavate their own nests. However, given that nest cavities are a highly sought-after resource and the subject of intense competition (Brawn and Balda, 1988; Duckworth, 2013), we would expect species competing for them to coexist less. We suggest that the increased provisioning of artificial nestboxes could have led to the increased range overlap (Duckworth, 2013; Duckworth *et al.*, 2017a). Although why this manifests in sympatry and not syntopy is unknown. This increased coexistence in European secondary cavity nesters may be related to interspecific territoriality, despite our predicted territoriality classifications not emerging as significant predictors of Δ sympatry. In North American passerines, secondary cavity nesters are more likely to be interspecifically territorial than non-secondary-cavity nesters, which is likely an adaptive response to this competition for resources (Drury, Cowen and Grether, 2020). This may also be the case in Europe, and those that compete for cavities are also territorial, facilitating coexistence, as we found in North American passerines.

Both Chapters 5 and 6 highlight difficulties and limitations in extracting the effects of biotic interactions when using projections of species ranges from species distribution models or current range maps. It could be argued that we found no effect of competition on geographic avoidance due to the coarse spatial scale of the distribution data used (0.5°). However, we also found no effect of interactions on residual associations that were modelled at a much higher resolution (1km); perhaps this is still too coarse to detect the effect of biotic interactions. That said, both the SDMs created in Chapter 5 and the JSDBMs in Chapter 6 model a species-environment relationship based on species current, realised, range, so if biotic interactions were to influence species distributions, they would have already done so, and there would be no residual traces of interactions for models to capture. In JSDBMs, it may be possible to overcome this limitation by using abundance instead of presence-absence data, as the effects of biotic interactions may not be pronounced enough to lead to total exclusion, but may lead to changes in abundance (Howard *et al.*, 2014; Zurell, Pollock and Thuiller, 2018; Blanchet, Cazelles and Gravel, 2020; König *et al.*, 2021). Similarly, Joint Dynamic Species Distribution Models (JDSDBMs) and HMSC JSDBMs can utilise multi-year data to model temporal dynamics resulting from species interactions (Thorson *et al.*, 2016; Elo

et al., 2023). However, these methods are extremely computationally intensive, and as such, we were unable to utilise them in this thesis.

7.3 Concluding Remarks

Throughout this thesis, we provide compelling evidence for the impact of species interactions; exploitative competition, interspecific territoriality and hybridisation on species distributions and coexistence both historically and currently. We were unable to incorporate species interactions into any future predictions of species distributions. However, we have little doubt that interactions will play an integral role in the restructuring of species communities as a result of global changes. Our analyses span a range of resolutions; our syntopy metrics encapsulate interactions within a 400m radius, our JSDMs utilise 1km cells, our sympatry measures are 40km sites, and our geographic avoidance metrics utilise 0.5° grid cells. We also further our knowledge of the determinants of hybridisation and our ability to predict novel species interactions, with our predictive frameworks being potentially applicable to a variety of other interactions. We caution against the use of single-year presence-absence data in HMSC JSDMs and call for the collection of higher-resolution distributional and behavioural data globally. Our analyses are confined to North American and European birds, however, many of the concepts discussed are likely applicable to other continents and taxa.

References

- Abbott, R. et al. (2013) 'Hybridization and speciation', *Journal of Evolutionary Biology*, 26(2), pp. 229–246. Available at: <https://doi.org/10.1111/j.1420-9101.2012.02599.x>.
- Able, K.P. and Noon, B.R. (1976) 'Avian community structure along elevational gradients in the northeastern United States', *Oecologia*, 26(3), pp. 275–294. Available at: <https://doi.org/10.1007/BF00345296>.
- Abrams, P. (1983) 'The Theory of Limiting Similarity', *Annual Review of Ecology, Evolution, and Systematics*, 14(Volume 14,), pp. 359–376. Available at: <https://doi.org/10.1146/annurev.es.14.110183.002043>.
- Aebischer, A., Nyffeler, P. and Arlettaz, R. (2010) 'Wide-range dispersal in juvenile Eagle Owls (*Bubo bubo*) across the European Alps calls for transnational conservation programmes', *Journal of Ornithology*, 151(1), pp. 1–9. Available at: <https://doi.org/10.1007/s10336-009-0414-2>.
- Alatalo, R.V. et al. (1987) 'Exploitation Competition Influences the Use of Foraging Sites by Tits: Experimental Evidence', *Ecology*, 68(2), pp. 284–290. Available at: <https://doi.org/10.2307/1939259>.
- Alatalo, R.V., Gustafsson, L. and Lundberg, A. (1997) 'Male coloration and species recognition in sympatric flycatchers', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 256(1346), pp. 113–118. Available at: <https://doi.org/10.1098/rspb.1994.0057>.
- Alexander, A. et al. (2022) 'Limited movement of an avian hybrid zone in relation to regional variation in magnitude of climate change', *Molecular Ecology*, 31(24), pp. 6634–6648. Available at: <https://doi.org/10.1111/mec.16727>.
- Alexander, J.M. et al. (2016) 'When Climate Reshuffles Competitors: A Call for Experimental Macroecology', *Trends in Ecology & Evolution*, 31(11), pp. 831–841. Available at: <https://doi.org/10.1016/j.tree.2016.08.003>.

- Alexander, J.M. et al. (2016) 'When Climate Reshuffles Competitors: A Call for Experimental Macroecology', *Trends in Ecology and Evolution*, 31(11), pp. 831–841. Available at: <https://doi.org/10.1016/j.tree.2016.08.003>.
- Alexander, J.M., Diez, J.M. and Levine, J.M. (2015) 'Novel competitors shape species' responses to climate change', *Nature*, 525(7570), pp. 515–518. Available at: <https://doi.org/10.1038/nature14952>.
- Alfieri, J.M. et al. (2023) 'Genomic investigation refutes record of most diverged avian hybrid', *Ecology and Evolution*, 13(1), p. e9689. Available at: <https://doi.org/10.1002/ece3.9689>.
- Allendorf, F.W. et al. (2001) 'The problems with hybrids: setting conservation guidelines', *Trends in Ecology & Evolution*, 16(11), pp. 613–622. Available at: [https://doi.org/10.1016/S0169-5347\(01\)02290-X](https://doi.org/10.1016/S0169-5347(01)02290-X).
- Ålund, M. et al. (2024) 'Tracking hybrid viability across life stages in a natural avian contact zone', *Evolution*, 78(2), pp. 267–283. Available at: <https://doi.org/10.1093/evolut/qpad204>.
- Amarasekare, P. (2002) 'Interference competition and species coexistence', *Proceedings of the Royal Society B: Biological Sciences*, 269(1509), pp. 2541–2550. Available at: <https://doi.org/10.1098/rspb.2002.2181>.
- Araújo, M.B. and Luoto, M. (2007) 'The importance of biotic interactions for modelling species distributions under climate change', *Global Ecology and Biogeography*, 16(6), pp. 743–753. Available at: <https://doi.org/10.1111/j.1466-8238.2007.00359.x>.
- Araújo, M.B. and Rozenfeld, A. (2014) 'The geographic scaling of biotic interactions', *Ecography*, 37(5), pp. 406–415. Available at: <https://doi.org/10.1111/j.1600-0587.2013.00643.x>.
- Araújo, M.B. et al. (2004) 'Would climate change drive species out of reserves? An assessment of existing reserve-selection methods', *Global Change Biology*, 10(9), pp. 1618–1626. Available at: <https://doi.org/10.1111/j.1365-2486.2004.00828.x>.

Araújo, M.B., Pearson, R.G. and Rahbek, C. (2005) 'Equilibrium of Species' Distributions with Climate', *Ecography*, 28(5), pp. 693–695.

Araya-Salas, M. and Smith-Vidaurre, G. (2017) 'warbleR: an r package to streamline analysis of animal acoustic signals', *Methods in Ecology and Evolution* [Preprint]. Available at: <https://dx.doi.org/10.1111/2041-210X.12624>.

Austin, M.P. (2002) 'Spatial prediction of species distribution: an interface between ecological theory and statistical modelling', *Ecological Modelling*, 157(2), pp. 101–118. Available at: [https://doi.org/10.1016/S0304-3800\(02\)00205-3](https://doi.org/10.1016/S0304-3800(02)00205-3).

Avidad, P.M., Clavero, M. and Viana, D.S. (2025) 'Climate and Land-Use Change Leading to Niche Expansion and Shifts in Birds', *Journal of Biogeography*, 52(2), pp. 443–453. Available at: <https://doi.org/10.1111/jbi.15045>.

Bagchi, R. et al. (2013) 'Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty', *Global Change Biology*, 19(4), pp. 1236–1248. Available at: <https://doi.org/10.1111/gcb.12123>.

Baker, M.C. (1996) 'Female buntings from hybridizing populations prefer conspecific mates', *The Wilson Bulletin*, 108(4), pp. 771–775.

Baker, M.C. and Boylan, J.T. (1999) 'Singing Behavior, Mating Associations and Reproductive Success in a Population of Hybridizing Lazuli and Indigo Buntings', *The Condor*, 101(3), pp. 493–504. Available at: <https://doi.org/10.2307/1370179>.

Barbet-Massin, M., Thuiller, W. and Jiguet, F. (2012) 'The fate of European breeding birds under climate, land-use and dispersal scenarios', *Global Change Biology*, 18(3), pp. 881–890. Available at: <https://doi.org/10.1111/j.1365-2486.2011.02552.x>.

Bargielowski, I.E. and Lounibos, L.P. (2016) 'Satyrization and satyrization-resistance in competitive displacements of invasive mosquito species', *Insect Science*, 23(2), pp. 162–174. Available at: <https://doi.org/10.1111/1744-7917.12291>.

Barnagaud, J.-Y. et al. (2014) 'Habitat filtering by landscape and local forest composition in native and exotic New Zealand birds', *Ecology*, 95(1), pp. 78–87. Available at: <https://doi.org/10.1890/13-0791.1>.

Barnett, A.G., van der Pols, J.C. and Dobson, A.J. (2005) 'Regression to the mean: what it is and how to deal with it', *International Journal of Epidemiology*, 34(1), pp. 215–220. Available at: <https://doi.org/10.1093/ije/dyh299>.

Barton, N.H. and Hewitt, G.M. (1985) 'Analysis of hybrid zones', *Annual review of ecology and systematics*. Vol. 16, pp. 113–148. Available at: <https://doi.org/10.1146/annurev.es.16.110185.000553>.

Barton, N.H. and Hewitt, G.M. (1989) 'Adaptation, speciation and hybrid zones', *Nature*, 341(6242), pp. 497–503. Available at: <https://doi.org/10.1038/341497a0>.

Bastianelli, G. et al. (2017) 'Species partitioning in a temperate mountain chain: Segregation by habitat vs. interspecific competition', *Ecology and Evolution*, 7(8), pp. 2685–2696. Available at: <https://doi.org/10.1002/ece3.2883>.

Behm, J.E., Ives, A.R. and Boughman, J.W. (2010) 'Breakdown in Postmating Isolation and the Collapse of a Species Pair through Hybridization.', *The American Naturalist*, 175(1), pp. 11–26. Available at: <https://doi.org/10.1086/648559>.

Belmaker, J. et al. (2015) 'Empirical evidence for the scale dependence of biotic interactions', *Global Ecology and Biogeography*, 24(7), pp. 750–761. Available at: <https://doi.org/10.1111/geb.12311>.

Bewick, S. et al. (2014) 'Predicting future coexistence in a North American ant community', *Ecology and Evolution*, 4(10), pp. 1804–1819. Available at: <https://doi.org/10.1002/ece3.1048>.

Billerman, S. et al. (2022) *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology.

BirdLife International (2024) 'Species factsheet: Vietnam pheasant *Lophura edwardsi*'. Available at: <https://datazone.birdlife.org/species/factsheet/vietnam-pheasant-lophura-edwardsi>.

BirdLife International and Handbook of the Birds of the World (2021) 'Bird species distribution maps of the world'. Available at: <https://datazone.birdlife.org/contact-us/request-our-data>.

Blackburn, T.M., Lockwood, J.L. and Cassey, P. (2009) 'The Genetics of Exotic Bird Introductions', in T.M. Blackburn, J.L. Lockwood, and P. Cassey (eds) *Avian Invasions: The Ecology and Evolution of Exotic Birds*. Oxford University Press, p. 0. Available at: <https://doi.org/10.1093/acprof:oso/9780199232543.003.0008>.

Blanchet, F.G., Cazelles, K. and Gravel, D. (2020) 'Co-occurrence is not evidence of ecological interactions', *Ecology Letters*, 23(7), pp. 1050–1063. Available at: <https://doi.org/10.1111/ele.13525>.

Blois, J.L. et al. (2013) 'Climate Change and the Past, Present, and Future of Biotic Interactions', *Science*, 341(6145), pp. 499–504. Available at: <https://doi.org/10.1126/science.1237184>.

Blomberg, S.P., Garland JR., T. and Ives, A.R. (2003) 'Testing for Phylogenetic Signal in Comparative Data: Behavioral Traits Are More Labile', *Evolution*, 57(4), pp. 717–745. Available at: <https://doi.org/10.1111/j.0014-3820.2003.tb00285.x>.

Borge, T. et al. (2005) 'Amount of introgression in flycatcher hybrid zones reflects regional differences in pre and post-zygotic barriers to gene exchange', *Journal of Evolutionary Biology*, 18(6), pp. 1416–1424. Available at: <https://doi.org/10.1111/j.1420-9101.2005.00964.x>.

Boyce, A.J. and Martin, T.E. (2019) 'Interspecific aggression among parapatric and sympatric songbirds on a tropical elevational gradient', *Behavioral Ecology*, 30(2), pp. 541–547. Available at: <https://doi.org/10.1093/beheco/ary194>.

Brambilla, M. et al. (2020) 'Species interactions and climate change: How the disruption of species co-occurrence will impact on an avian forest guild', *Global Change Biology*, 26(3), pp. 1212–1224. Available at: <https://doi.org/10.1111/gcb.14953>.

Brauer, C.J. et al. (2023) 'Natural hybridization reduces vulnerability to climate change', *Nature Climate Change*, 13(3), pp. 282–289. Available at: <https://doi.org/10.1038/s41558-022-01585-1>.

Brawn, J.D. and Balda, R.P. (1988) 'Population biology of cavity nesters in Northern Arizona: Do nest sites limit breeding densities?', *The Condor*, 90(1), pp. 61–71. Available at: <https://doi.org/10.2307/1368434>.

Briceño, C. et al. (2019) 'Interactions between Invasive Monk Parakeets (*Myiopsitta monachus*) and Other Bird Species during Nesting Seasons in Santiago, Chile', *Animals*, 9(11), p. 923. Available at: <https://doi.org/10.3390/ani9110923>.

Brlík, V. et al. (2021) 'Long-term and large-scale multispecies dataset tracking population changes of common European breeding birds', *Scientific Data*, 8(1), p. 21. Available at: <https://doi.org/10.1038/s41597-021-00804-2>.

Brodsky, L.M. and Weatherhead, P.J. (1984) 'Behavioral and Ecological Factors Contributing to American Black Duck-Mallard Hybridization', *The Journal of Wildlife Management*, 48(3), pp. 846–852.

Brommer, J.E., Lehikoinen, A. and Valkama, J. (2012) 'The Breeding Ranges of Central European and Arctic Bird Species Move Poleward', *PLoS ONE*, 7(9), pp. 1–7. Available at: <https://doi.org/10.1371/journal.pone.0043648>.

Bronson, C.L. et al. (2003) 'Mate preference: a possible causal mechanism for a moving hybrid zone', *Animal Behaviour*, 65(3), pp. 489–500. Available at: <https://doi.org/10.1006/anbe.2003.2103>.

Bronson, C.L. et al. (2005) 'Reproductive success across the Black-capped Chickadee (*Poecile atricapillus*) and Carolina Chickadee (*P. carolinensis*) hybrid zone in Ohio', *Auk*, 122(3), pp. 759–772. Available at: [https://doi.org/10.1642/0004-8038\(2005\)122\[0759:RSATBC\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2005)122[0759:RSATBC]2.0.CO;2).

Brown, W.L. and Wilson, E.O. (1956) 'Character Displacement', *Systematic Zoology*, 5(2), pp. 49–64. Available at: <https://doi.org/10.2307/2411924>.

Bruderer, B. and Jenni, L. (1990) 'Migration Across the Alps', in E. Gwinner (ed.) *Bird Migration*. Berlin, Heidelberg: Springer, pp. 60–77. Available at: https://doi.org/10.1007/978-3-642-74542-3_5.

Bull, C.M. (1991) 'Ecology of Parapatric Distributions', *Annual Review of Ecology and Systematics*, 22, pp. 19–36.

Büttner, G. (2014) 'CORINE Land Cover and Land Cover Change Products', in I. Manakos and M. Braun (eds) *Land Use and Land Cover Mapping in Europe: Practices & Trends*. Dordrecht: Springer Netherlands, pp. 55–74. Available at: https://doi.org/10.1007/978-94-007-7969-3_5.

Cadena, C.D. and Loiselle, B.A. (2007) 'Limits to elevational distributions in two species of emberizine finches: Disentangling the role of interspecific competition, autoecology, and geographic variation in the environment', *Ecography*, 30(4), pp. 491–504. Available at: <https://doi.org/10.1111/j.2007.0906-7590.05045.x>.

Caradima, B., Schuwirth, N. and Reichert, P. (2019) 'From individual to joint species distribution models: A comparison of model complexity and predictive performance', *Journal of Biogeography*, 46(10), pp. 2260–2274.

Case, T.J. and Gilpin, M.E. (1974) 'Interference competition and niche theory', *Proceedings of the National Academy of Sciences of the United States of America*, 71(8), pp. 3073–3077. Available at: <https://doi.org/10.1073/pnas.71.8.3073>.

Catchpole, C.K. (1978) 'Interspecific territorialism and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympathy and allopatry', *Animal Behaviour*, 26, pp. 1072–1080. Available at: [https://doi.org/10.1016/0003-3472\(78\)90096-9](https://doi.org/10.1016/0003-3472(78)90096-9).

Chappell, M.A. (1978) 'Behavioral Factors in the Altitudinal Zonation of Chipmunks (*Eutamias*)', *Ecology*, 59(3), pp. 565–579. Available at: <https://doi.org/10.2307/1936586>.

Charif, R.A., Ponirakis, D.W. and Krein, T.P. (2006) 'Raven Lite 1.0 User's Guide'. Cornell Laboratory of Ornithology, Ithaca, NY.

Chen, G., Li, X. and Liu, X. (2022) 'Global land projection based on plant functional types with a 1-km resolution under socio-climatic scenarios', pp. 1–18. Available at: <https://doi.org/10.1038/s41597-022-01208-6>.

Chen, I.-C. et al. (2011) 'Rapid Range Shifts of Species Associated with High Levels of Climate Warming', *Science*, 333(6045), pp. 1024–1026. Available at: <https://doi.org/10.1126/science.1206432>.

Chunco, A.J. (2014) 'Hybridization in a warmer world', *Ecology and Evolution*, 4(10), pp. 2019–2031. Available at: <https://doi.org/10.1002/ece3.1052>.

Clements, J.F. et al. (2021) 'The eBird/Clements checklist of Birds of the World: v2021.' Available at: <https://www.birds.cornell.edu/clementschecklist/introduction/updateindex/august-2021/2021-citation-checklist-download/>.

Clouet, M. and Gerard, J.-F. (2020) 'Interactions between sibling species of treecreepers *Certhia familiaris* and *C. brachydactyla* in the Pyrenees and the mistaken identity hypothesis', *Bird Study*, 67(3), pp. 385–392. Available at: <https://doi.org/10.1080/00063657.2020.1863332>.

Cody, M.L. (1969) 'Convergent Characteristics in Sympatric Species: A Possible Relation to Interspecific Competition and Aggression', *The Condor*, 71(3), pp. 223–239. Available at: <https://doi.org/10.2307/1366300>.

Colwell, R.K. et al. (2008) 'Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics', *Science*, 322, pp. 258–261.

Connell, J.H. (1961) 'The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus Stellatus*', *Ecology*, 42(4), pp. 710–723. Available at: <https://doi.org/10.2307/1933500>.

Connor, E.F. and Bowers, M.A. (1987) 'The spatial consequences of interspecific competition', *Trends in Ecological Biogeography*, 24(3), pp. 213–226.

Cornell Lab of Ornithology (2022) 'eBird Basic Dataset'. Ithaca, New York.

Cowen, M.C., Drury, J.P. and Grether, G.F. (2020) 'Multiple routes to interspecific territoriality in sister species of North American perching birds', *Evolution*, 74(9), pp. 2134–2148. Available at: <https://doi.org/10.1111/evo.14068>.

Coyne, J.A. and Orr, H.A. (1989) 'Patterns of Speciation in *Drosophila*', *Evolution*, 43(2), pp. 362–381. Available at: <https://doi.org/10.1111/j.1558-5646.1989.tb04233.x>.

Curd, A. et al. (2023) 'Applying landscape metrics to species distribution model predictions to characterize internal range structure and associated changes', *Global Change Biology*, 29(3), pp. 631–647. Available at: <https://doi.org/10.1111/gcb.16496>.

Cutler, D.R. et al. (2007) 'Random Forests for Classification in Ecology', *Ecology*, 88(11), pp. 2783–2792. Available at: <https://doi.org/10.1890/07-0539.1>.

Dallas, T., Park, A.W. and Drake, J.M. (2017) 'Predicting cryptic links in host-parasite networks', *PLOS Computational Biology*, 13(5), p. e1005557. Available at: <https://doi.org/10.1371/journal.pcbi.1005557>.

Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Darwin, C. (ed.) (1859) 'Geographical Distribution', in *The Origin of Species: By Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. 6th edn. Cambridge: Cambridge University Press (Cambridge Library Collection - Darwin, Evolution and Genetics), pp. 316–342. Available at: <https://doi.org/10.1017/CBO9780511694295.016>.

Davies, Z.G. et al. (2009) 'A national scale inventory of resource provision for biodiversity within domestic gardens', *Biological Conservation*, 142(4), pp. 761–771. Available at: <https://doi.org/10.1016/j.biocon.2008.12.016>.

Davis, A.J. et al. (1998) 'Making mistakes when predicting shifts in species range in response to global warming', *Nature*, 391(6669), pp. 783–786. Available at: <https://doi.org/10.1038/35842>.

De Graaf, R.M., Tilghman, N.G. and Anderson, S.H. (1985) 'Foraging guilds of North American birds', *Environmental Management*, 9(6), pp. 493–536. Available at: <https://doi.org/10.1007/BF01867324>.

De Kort, S.R. and Ten Cate, C. (2001) 'Response to interspecific vocalizations is affected by degree of phylogenetic relatedness in *Streptopelia* doves', *Animal Behaviour*, 61(1), pp. 239–247. Available at: <https://doi.org/10.1006/anbe.2000.1552>.

DeMarais, B.D. et al. (1992) 'Origin of *Gila seminuda* (Teleostei: Cyprinidae) through introgressive hybridization: implications for evolution and conservation.', *Proceedings of the National Academy of Sciences*, 89(7), pp. 2747–2751. Available at: <https://doi.org/10.1073/pnas.89.7.2747>.

Den Boer, P.J. (1986) 'The present status of the competitive exclusion principle', *Trends in Ecology & Evolution*, 1(1), pp. 25–28. Available at: [https://doi.org/10.1016/0169-5347\(86\)90064-9](https://doi.org/10.1016/0169-5347(86)90064-9).

Desjardins-Proulx, P. et al. (2017) 'Ecological interactions and the Netflix problem', *PeerJ*, 5, p. e3644. Available at: <https://doi.org/10.7717/peerj.3644>.

Devarajan, K., Morelli, T.L. and Tenan, S. (2020) 'Multi-species occupancy models: review, roadmap, and recommendations', *Ecography*, 43(11), pp. 1612–1624. Available at: <https://doi.org/10.1111/ecog.04957>.

Diamond, J.M. (1973) 'Distributional Ecology of New Guinea Birds', *Science*, 179(4075), pp. 759–769. Available at: <https://doi.org/10.1126/science.179.4075.759>.

Dietzen, C. et al. (2007) 'Genetically confirmed interbreeding between western Bonelli's warbler (*Phylloscopus bonelli*) and wood warbler (*P. sibilatrix*)', *Journal of Ornithology*, 148(1), pp. 85–90. Available at: <https://doi.org/10.1007/s10336-006-0105-1>.

Dobzhansky, Th. (1936) 'Studies on Hybrid Sterility. II. Localization of Sterility Factors in *Drosophila Pseudoobscura* Hybrids', *Genetics*, 21(2), pp. 113–135. Available at: <https://doi.org/10.1093/genetics/21.2.113>.

Dormann, C.F. et al. (2018) 'Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions', *Global Ecology and Biogeography*, 27(9), pp. 1004–1016. Available at: <https://doi.org/10.1111/geb.12759>.

Dougherty, P.J. and Carling, M.D. (2024) 'Go west, young bunting: recent climate change drives rapid movement of a Great Plains hybrid zone', *Evolution*. Edited by N. Therkildsen, 78(11), pp. 1774–1789. Available at: <https://doi.org/10.1093/evolut/qpae118>.

Dowling, T.E. and Secor, C.L. (1997) 'The Role of Hybridization and Introgression in the Diversification of Animals', *Annual Review of Ecology and Systematics*, 28(1), pp. 593–619. Available at: <https://doi.org/10.1146/annurev.ecolsys.28.1.593>.

Drury, J.P. et al. (2015) 'Reproductive interference explains persistence of aggression between species', *Proceedings of the Royal Society B: Biological Sciences*, 282(1804), p. 20142256. Available at: <https://doi.org/10.1098/rspb.2014.2256>.

Drury, J.P. et al. (2019) 'A general explanation for the persistence of reproductive interference', *American Naturalist*, 194(2), pp. 268–275. Available at: <https://doi.org/10.1086/704102>.

Drury, J.P. et al. (2021) 'Tempo and mode of morphological evolution are decoupled from latitude in birds', *PLOS Biology*, 19(8), p. e3001270. Available at: <https://doi.org/10.1371/journal.pbio.3001270>.

Drury, J.P., Cowen, M.C. and Grether, G.F. (2020) 'Competition and hybridization drive interspecific territoriality in birds', *Proceedings of the National Academy of Sciences*, p. 201921380. Available at: <https://doi.org/10.1073/pnas.1921380117>.

Duan, R.-Y. et al. (2016) 'The potential effects of climate change on amphibian distribution, range fragmentation and turnover in China', *PeerJ*, 4, p. e2185. Available at: <https://doi.org/10.7717/peerj.2185>.

Duckworth, R.A. (2013) 'Human-induced changes in the dynamics of species coexistence: an example with two sister species', in D. Gil and H. Brumm (eds) *Avian Urban Ecology*. Oxford University Press, p. 0. Available at: <https://doi.org/10.1093/acprof:osobl/9780199661572.003.0014>.

Duckworth, R.A. and Badyaev, A.V. (2007) 'Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird', *Proceedings of the National Academy of Sciences*, 104(38), pp. 15017–15022. Available at: <https://doi.org/10.1073/pnas.0706174104>.

Duckworth, R.A. and Semenov, G.A. (2017) 'Hybridization Associated with Cycles of Ecological Succession in a Passerine Bird', *The American Naturalist*, 190(4), pp. E94–E105. Available at: <https://doi.org/10.1086/693160>.

Duckworth, R.A. et al. (2017) 'Switch to a Novel Breeding Resource Influences Coexistence of Two Passerine Birds', *Frontiers in Ecology and Evolution*, 5. Available at: <https://doi.org/10.3389/fevo.2017.00072>.

Duckworth, R.A. et al. (2017) 'Switch to a novel breeding resource influences coexistence of two passerine birds', *Frontiers in Ecology and Evolution*, 5(JUL). Available at: <https://doi.org/10.3389/fevo.2017.00072>.

Dyer, E.E. et al. (2017) 'The Global Distribution and Drivers of Alien Bird Species Richness', *PLoS Biology*, 15(1), pp. 1–25. Available at: <https://doi.org/10.1371/journal.pbio.2000942>.

Eames, J.C. and Mahood, S.P. (2017) 'Is Edwards's Pheasant *Lophura edwardsi* extinct in the wild?', *Forktail*, 33, pp. 27–33. Available at: <https://doi.org/10.1017/S0030605317000813>.

Early, R. and Keith, S.A. (2019) 'Geographically variable biotic interactions and implications for species ranges', *Global Ecology and Biogeography*, 28(1), pp. 42–53. Available at: <https://doi.org/10.1111/geb.12861>.

Ehrlén, J. and Morris, W.F. (2015) 'Predicting changes in the distribution and abundance of species under environmental change', *Ecology Letters*, 18(3), pp. 303–314. Available at: <https://doi.org/10.1111/ele.12410>.

Elith, J. and Leathwick, J.R. (2009) 'Species Distribution Models: Ecological Explanation and Prediction Across Space and Time', *Annual Review of Ecology, Evolution, and Systematics*, 40(Volume 40, 2009), pp. 677–697. Available at: <https://doi.org/10.1146/annurev.ecolsys.110308.120159>.

Elith, J. et al. (2006) 'Novel methods improve prediction of species' distributions from occurrence data', *Ecography*, 29(2), pp. 129–151. Available at: <https://doi.org/10.1111/j.2006.0906-7590.04596.x>.

Elith, J., Kearney, M. and Phillips, S. (2010) 'The art of modelling range-shifting species', *Methods in Ecology and Evolution*, 1(4), pp. 330–342. Available at: <https://doi.org/10.1111/j.2041-210X.2010.00036.x>.

Elmhagen, B. et al. (2015) 'A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra', *Ambio*, 44(1), pp. 39–50. Available at: <https://doi.org/10.1007/s13280-014-0606-8>.

Elo, M. et al. (2022) 'Do large-scale associations in birds imply biotic interactions or environmental filtering?', *Journal of Biogeography*, 00, pp. 1–14. Available at: <https://doi.org/10.1111/jbi.14520>.

Elo, M. et al. (2023) 'Do large-scale associations in birds imply biotic interactions or environmental filtering?', *Journal of Biogeography*, 50(1), pp. 169–182. Available at: <https://doi.org/10.1111/jbi.14520>.

Engler, J.O. et al. (2013) 'Species distribution models contribute to determine the effect of climate and interspecific interactions in moving hybrid zones', *Journal of Evolutionary Biology*, 26(11), pp. 2487–2496. Available at: <https://doi.org/10.1111/jeb.12244>.

Erickson, R.A. and Rottenborn, S.C. (2020) 'Two photographed American coot × common gallinule hybrids', *Western Birds*, 51(2), pp. 150–156. Available at: <https://doi.org/10.21199/WB51.2.7>.

Essl, F. et al. (2024) 'Potential sources of time lags in calibrating species distribution models', *Journal of Biogeography*, 51(1), pp. 89–102. Available at: <https://doi.org/10.1111/jbi.14726>.

Fabricius, E. (1991) 'Interspecific Mate Choice Following Cross-fostering in a Mixed Colony of Greylag Geese (*Anser anser*) and Canada Geese (*Branta canadensis*). A Study on Development and Persistence of Species Preferences', *Ethology*, 88(4), pp. 287–296. Available at: <https://doi.org/10.1111/j.1439-0310.1991.tb00283.x>.

Faivre, B. et al. (1999) 'Morphological Variation and the Recent Evolution of Wing Length in the Icterine Warbler: A Case of Unidirectional Introgression?', *Journal of Avian Biology*, 30(2), pp. 152–158. Available at: <https://doi.org/10.2307/3677124>.

Fern, R.R. et al. (2019) 'Incorporating biotic relationships improves species distribution models: Modeling the temporal influence of competition in conspecific nesting birds', *Ecological Modelling*, 408, p. 108743. Available at: <https://doi.org/10.1016/j.ecolmodel.2019.108743>.

Fick, S.E. and Hijmans, R.J. (2017) 'WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas', *International Journal of Climatology*, 37(12), pp. 4302–4315. Available at: <https://doi.org/10.1002/joc.5086>.

Fink, D. et al. (2023) 'eBird status and trends, data version: 2022; released: 2023'. Ithaca, New York: Cornell Lab of Ornithology. Available at: <https://doi.org/10.2173/ebirdst.2022>.

Freeman, B.G. (2015) 'Competitive interactions upon secondary contact drive elevational divergence in tropical birds', *American Naturalist*, 186(4), pp. 470–479. Available at: <https://doi.org/10.1086/682703>.

Freeman, B.G. (2015) 'Competitive Interactions upon Secondary Contact Drive Elevational Divergence in Tropical Birds', *The American Naturalist*, 186(4), pp. 470–479. Available at: <https://doi.org/10.1086/682703>.

Freeman, B.G. (2016) 'Strong asymmetric interspecific aggression between two sympatric New Guinean robins', *Ibis*, 158(1), pp. 75–81. Available at: <https://doi.org/10.1111/ibi.12318>.

Freeman, B.G. and Class Freeman, A.M. (2014) 'Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming', *Proceedings of the National Academy of Sciences*, 111(12), pp. 4490–4494. Available at: <https://doi.org/10.1073/pnas.1318190111>.

Freeman, B.G. and Montgomery, G. (2016) 'Interspecific aggression by the Swainson's Thrush (*Catharus ustulatus*) may limit the distribution of the threatened Bicknell's Thrush (*Catharus bicknelli*) in the Adirondack Mountains', *Condor*, 118(1), pp. 169–178. Available at: <https://doi.org/10.1650/CONDOR-15-145.1>.

Freeman, B.G. et al. (2018) 'Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community', *Proceedings of the National Academy of Sciences of the United States of America*, 115(47), pp. 11982–11987. Available at: <https://doi.org/10.1073/pnas.1804224115>.

Freeman, B.G., Class Freeman, A.M. and Hochachka, W.M. (2016) 'Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient', *Ibis*, 158(4), pp. 726–737. Available at: <https://doi.org/10.1111/ibi.12384>.

Freeman, B.G., Miller, E.T. and Strimas-Mackey, M. (2024) 'Interspecific competition shapes bird species' distributions along tropical precipitation gradients', *Ecology Letters*, 27(8), p. e14487. Available at: <https://doi.org/10.1111/ele.14487>.

Freeman, B.G., Strimas-Mackey, M. and Miller, E.T. (2022) 'Interspecific competition limits bird species' ranges in tropical mountains', *Science*, 377(6604), pp. 416–420. Available at: <https://doi.org/10.1126/science.abl7242>.

Freeman, B.G., Strimas-mackey, M. and Miller, E.T. (2022) 'Interspecific competition limits bird species' ranges in tropical mountains', *Science*, 377, pp. 416–420.

Freeman, B.G., Tobias, J.A. and Schluter, D. (2019) 'Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical birds', *Ecography*, 42(11), pp. 1832–1840. Available at: <https://doi.org/10.1111/ecog.04606>.

Friedemann, G. et al. (2017) 'Nest-site characteristics, breeding success and competitive interactions between two recently sympatric apex predators', *Ibis*, 159(4), pp. 812–827. Available at: <https://doi.org/10.1111/ibi.12498>.

Fuchs, J. et al. (2013) 'A multi-locus phylogeny suggests an ancient hybridization event between *Campephilus* and melanerpine woodpeckers (Aves: Picidae)', *Molecular Phylogenetics and Evolution*, 67(3), pp. 578–588. Available at: <https://doi.org/10.1016/j.ympev.2013.02.014>.

Gaston, K.J. (2000) 'Global patterns in biodiversity', *Nature*, 405(6783), pp. 220–227. Available at: <https://doi.org/10.1038/35012228>.

Gause, G.F. (1934) 'Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence', *Science*, 79(2036), pp. 16–17. Available at: <https://doi.org/10.1126/science.79.2036.16.b>.

Gause, G.F. (1934) *The struggle for existence*. Williams and Wilkins.

Gelman, A. and Rubin, D.B. (1992) 'Inference from iterative simulation using multiple sequences', *Statistical Science*, 7(4), pp. 457–511.

Gholamhosseini, A. et al. (2013) 'Hybridization between sister taxa versus non-sister taxa: a case study in birds', *Bird Study*, 60(2), pp. 195–201. Available at: <https://doi.org/10.1080/00063657.2013.770815>.

Gifford, M.E. and Kozak, K.H. (2012) 'Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders', *Ecography*, 35(3), pp. 193–203. Available at: <https://doi.org/10.1111/j.1600-0587.2011.06866.x>.

Gillie, E. (2024) Biodiversity colonisation of the Arctic under climate change: impacts on land, sea and people. Doctoral. Durham University. Available at: <https://etheses.dur.ac.uk/15837/> (Accessed: 15 May 2025).

Gómez-Llano, M. et al. (2021) 'When Ecology Fails: How Reproductive Interactions Promote Species Coexistence', *Trends in Ecology & Evolution*, 36(7), pp. 610–622. Available at: <https://doi.org/10.1016/j.tree.2021.03.003>.

González-Salazar, C., Stephens, C.R. and Marquet, P.A. (2013) 'Comparing the relative contributions of biotic and abiotic factors as mediators of species' distributions', *Ecological Modelling*, 248, pp. 57–70. Available at: <https://doi.org/10.1016/j.ecolmodel.2012.10.007>.

Good, T.P. et al. (2000) 'Bounded Hybrid Superiority in an Avian Hybrid Zone: Effects of Mate, Diet, and Habitat Choice', *Evolution*, 54(5), pp. 1774–1783.

Gotelli, N.J., Graves, G.R. and Rahbek, C. (2010) 'Macroecological signals of species interactions in the Danish avifauna', *Proceedings of the National Academy of Sciences of the United States of America*, 107(11), pp. 5030–5035. Available at: <https://doi.org/10.1073/pnas.0914089107>.

Grant, P.R. and Grant, B.R. (1992) 'Hybridization of Bird Species', *Science*, 256(5054), pp. 193–197. Available at: <https://doi.org/10.1126/science.256.5054.193>.

Grant, P.R. and Grant, B.R. (1997) 'Hybridization, sexual imprinting, and mate choice', *The American Naturalist*, 149(1), pp. 1–28.

Grant, P.R. and Grant, B.R. (2006) 'Evolution of character displacement in Darwin's finches', *Science*, 313(5784), pp. 224–226. Available at: <https://doi.org/10.1126/science.1128374>.

Grether, G.F. and Okamoto, K.W. (2022) 'Eco-evolutionary dynamics of interference competition', *Ecology Letters*, 00, pp. 1–10. Available at: <https://doi.org/10.1111/ele.14091>.

Grether, G.F. et al. (2009) 'The role of interspecific interference competition in character displacement and the evolution of competitor recognition', *Biological Reviews*, 84(4), pp. 617–635. Available at: <https://doi.org/10.1111/j.1469-185X.2009.00089.x>.

Grether, G.F. et al. (2013) 'The evolutionary consequences of interspecific aggression', *Annals of the New York Academy of Sciences*, 1289(1), pp. 48–68. Available at: <https://doi.org/10.1111/nyas.12082>.

Grether, G.F. et al. (2017) 'Causes and Consequences of Behavioral Interference between species', *Trends in Ecology and Evolution*, 32(10), pp. 760–772. Available at: <https://doi.org/10.1016/j.tree.2017.07.004>.

Grether, G.F. et al. (2020) 'Predicting evolutionary responses to interspecific interference in the wild', *Ecology Letters*, 23(2), pp. 221–230. Available at: <https://doi.org/10.1111/ele.13395>.

Grinnell, J. (1917) 'The Niche-Relationships of the California Thrasher', *The Auk*, 34(4), pp. 427–433. Available at: <https://doi.org/10.2307/4072271>.

Grist, H. et al. (2017) 'Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird', *Journal of Animal Ecology*, 86(5), pp. 1010–1021. Available at: <https://doi.org/10.1111/1365-2656.12691>.

Gröning, J. and Hochkirch, A. (2008) 'Reproductive Interference Between Animal Species', *The Quarterly Review of Biology*, 83(3), pp. 257–282. Available at: <https://doi.org/10.1086/590510>.

Gröning, J. et al. (2007) 'Reproductive interference in two ground-hopper species: testing hypotheses of coexistence in the field', *Oikos*, 116(9), pp. 1449–1460. Available at: <https://doi.org/10.1111/j.0030-1299.2007.15850.x>.

Gröning, J. et al. (2007) 'Reproductive interference in two ground-hopper species: testing hypotheses of coexistence in the field', *Oikos*, 116(9), pp. 1449–1460. Available at: <https://doi.org/10.1111/j.2007.0030-1299.15850.x>.

Gross, S.J. and Price, T.D. (2000) 'Determinants of the northern and southern range limits of a warbler', *Journal of Biogeography*, 27(4), pp. 869–878. Available at: <https://doi.org/10.1046/j.1365-2699.2000.00440.x>.

Guay, P.-J. et al. (2014) 'Hybridization between the Mallard and native dabbling ducks: causes, consequences and management.', *Pacific Conservation Biology*, 20(1), pp. 41–47. Available at: <https://doi.org/10.1071/pc140041>.

Guisan, A. and Thuiller, W. (2005) 'Predicting species distribution: offering more than simple habitat models', *Ecology Letters*, 8(9), pp. 993–1009. Available at: <https://doi.org/10.1111/j.1461-0248.2005.00792.x>.

Gutiérrez, E.E., Boria, R.A. and Anderson, R.P. (2014) 'Can biotic interactions cause allopatry? Niche models, competition, and distributions of South American mouse opossums', *Ecography*, 37(8), pp. 741–753. Available at: <https://doi.org/10.1111/ecog.00620>.

Hadfield, J. (2010) 'MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package', *Journal of Statistical Software*, 33(2), pp. 1–22.

Hadfield, J. (2014) MCMCglmm course notes.

Haig, S.M. et al. (2004) 'Genetic Identification of Spotted Owls, Barred Owls, and Their Hybrids: Legal Implications of Hybrid Identity', *Conservation Biology*, 18(5), pp. 1347–1357. Available at: <https://doi.org/10.1111/j.1523-1739.2004.00206.x>.

Hamer, T.E. et al. (1994) 'Hybridization between Barred and Spotted Owls', *The Auk*, 111(2), pp. 487–492. Available at: <https://doi.org/10.2307/4088616>.

Han, L. et al. (2023) 'Preferred prey reduce species realized niche shift and improve range expansion prediction', *Science of The Total Environment*, 859, p. 160370. Available at: <https://doi.org/10.1016/j.scitotenv.2022.160370>.

Hanebrink, E.L., Gruver, C. and Van Grouw, R. (1973) 'Taxonomic Relationship of Hybrid Peafowl-Guineafowl: Preliminary Study of Serum Proteins', *Journal of the Arkansas Academy of Science*, 27, pp. 33–34.

Harishchandra, A. et al. (2022) 'Thermal physiology integrated species distribution model predicts profound habitat fragmentation for estuarine fish with ocean warming', *Scientific Reports*, 12(1), p. 21781. Available at: <https://doi.org/10.1038/s41598-022-25419-4>.

Harmon, L.J. et al. (2019) 'Detecting the macroevolutionary signal of species interactions', *Journal of Evolutionary Biology*, 32(8), pp. 769–782. Available at: <https://doi.org/10.1111/jeb.13477>.

Harris, D.J. (2015) 'Generating realistic assemblages with a joint species distribution model', *Methods in Ecology and Evolution*, 6(4), pp. 465–473. Available at: <https://doi.org/10.1111/2041-210X.12332>.

Heikkinen, R.K. et al. (2007) 'Biotic interactions improve prediction of boreal bird distributions at macro-scales', *Global Ecology and Biogeography*, 16(6), pp. 754–763. Available at: <https://doi.org/10.1111/j.1466-8238.2007.00345.x>.

Hembry, D.H. and Weber, M.G. (2020) 'Ecological interactions and macroevolution: a new field with old roots', *Annual Review of Ecology, Evolution, and Systematics*, 51, pp. 215–243.

Hennache, A. et al. (2003) 'Hybrid origin of the imperial pheasant *Lophura imperialis* (Delacour and Jabouille, 1924) demonstrated by morphology, hybrid experiments, and DNA analyses', *Biological Journal of the Linnean Society*, 80(4), pp. 573–600. Available at: <https://doi.org/10.1111/j.1095-8312.2003.00251.x>.

Hernández-Brito, D. et al. (2021) 'Successful hybridization between non-congeneric parrots in a small introduced population', *Ibis*, 163(3), pp. 1093–1098. Available at: <https://doi.org/10.1111/ibi.12936>.

Herrera, K.J. et al. (2009) 'To what extent did Neanderthals and modern humans interact?', *Biological Reviews*, 84(2), pp. 245–257. Available at: <https://doi.org/10.1111/j.1469-185X.2008.00071.x>.

Heuck, C. et al. (2013) 'The potential distribution of the Red Kite in Germany', *Journal of Ornithology*, 154(4), pp. 911–921. Available at: <https://doi.org/10.1007/s10336-013-0955-2>.

Hijmans, R.J. and Graham, C.H. (2006) 'The ability of climate envelope models to predict the effect of climate change on species distributions', *Global Change Biology*, 12(12), pp. 2272–2281. Available at: <https://doi.org/10.1111/j.1365-2486.2006.01256.x>.

Hillebrand, H. (2004) 'On the Generality of the Latitudinal Diversity Gradient', *The American Naturalist*, 163(2), pp. 318–321. Available at: <https://doi.org/10.1126/science.26.678.918>.

HilleRisLambers, J. et al. (2013) 'How will biotic interactions influence climate change-induced range shifts?', *Annals of the New York Academy of Sciences*, (July), p. n/a-n/a. Available at: <https://doi.org/10.1111/nyas.12182>.

HilleRisLambers, J. et al. (2013) 'How will biotic interactions influence climate change-induced range shifts?', *Annals of the New York Academy of Sciences*, 1297(1), pp. 112–125. Available at: <https://doi.org/10.1111/nyas.12182>.

HilleRisLambers, J. et al. (2013a) 'How will biotic interactions influence climate change-induced range shifts?', *Annals of the New York Academy of Sciences*, (July), p. n/a-n/a. Available at: <https://doi.org/10.1111/nyas.12182>.

HilleRisLambers, J. et al. (2013b) 'How will biotic interactions influence climate change-induced range shifts?', *Annals of the New York Academy of Sciences*, 1297(1), pp. 112–125. Available at: <https://doi.org/10.1111/nyas.12182>.

Hitch, A.T. and Leberg, P.L. (2007) 'Breeding distributions of North American bird species moving north as a result of climate change', *Conservation Biology*, 21(2), pp. 534–539. Available at: <https://doi.org/10.1111/j.1523-1739.2006.00609.x>.

Hochkirch, A., Gröning, J. and Bücker, A. (2007) 'Sympatry with the devil: reproductive interference could hamper species coexistence', *Journal of Animal Ecology*, 76(4), pp. 633–642. Available at: <https://doi.org/10.1111/j.1365-2656.2007.01241.x>.

- Holdridge, L.R. (1947) 'Determination of World Plant Formations From Simple Climatic Data', *Science*, 105(2727), pp. 367–368. Available at: <https://doi.org/10.1126/science.105.2727.367>.
- Holling, M. (2016) 'Rare breeding birds in the UK in 2016', *British Birds* [Preprint].
- Holling, M. (2017) 'Rare breeding birds in the UK in 2017', *British Birds* [Preprint].
- Holt, R.D. (2009) 'Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives', *Proceedings of the National Academy of Sciences*, 106(supplement_2), pp. 19659–19665. Available at: <https://doi.org/10.1073/pnas.0905137106>.
- Howard, C. et al. (2014) 'Improving species distribution models: the value of data on abundance', *Methods in Ecology and Evolution*, 5(6), pp. 506–513. Available at: <https://doi.org/10.1111/2041-210X.12184>.
- Howard, C. et al. (2015) 'The drivers of avian abundance: patterns in the relative importance of climate and land use', *Global Ecology and Biogeography*, 24(11), pp. 1249–1260. Available at: <https://doi.org/10.1111/geb.12377>.
- Howard, C. et al. (2020) 'Disentangling the relative roles of climate and land cover change in driving the long-term population trends of European migratory birds', *Diversity and Distributions*, 26(11), pp. 1442–1455. Available at: <https://doi.org/10.1111/ddi.13144>.
- Hubbard, A.L. et al. (1992) 'Is survival of European wildcats *Felis silvestris* in Britain threatened by interbreeding with domestic cats?', *Biological Conservation*, 61(3), pp. 203–208. Available at: [https://doi.org/10.1016/0006-3207\(92\)91117-B](https://doi.org/10.1016/0006-3207(92)91117-B).
- Hubbs, C.L. (1955) 'Hybridization between Fish Species in Nature', *Systematic Zoology*, 4, pp. 1–20.
- Huerta-Sánchez, E. et al. (2014) 'Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA', *Nature*, 512(7513), pp. 194–197. Available at: <https://doi.org/10.1038/nature13408>.

Hurly, T.A., Scott, R.D. and Healy, S.D. (2001) 'The Function of Displays of Male Rufous Hummingbirds', *The Condor: Ornithological Applications*, 103(3), pp. 647–651. Available at: <https://doi.org/10.1093/condor/103.3.647>.

Hutchinson, G., E. (1957) 'Concluding Remarks', *Cold Springs Harbor Symposia on Quantitative Biology*, 22, pp. 415–427.

Huxel, G.R. (1999) 'Rapid displacement of native species by invasive species: effects of hybridization', *Biological Conservation*, 89(2), pp. 143–152. Available at: [https://doi.org/10.1016/S0006-3207\(98\)00153-0](https://doi.org/10.1016/S0006-3207(98)00153-0).

Iverson, E.N.K. and Karubian, J. (2017) 'The role of bare parts in avian signaling', *The Auk*, 134(3), pp. 587–611. Available at: <https://doi.org/10.1642/AUK-16-136.1>.

Jankowski, J.E. et al. (2012) 'The Role of Competition in Structuring Tropical Bird Communities', *ORNITOLOGIA NEOTROPICAL*, 23, pp. 115–124. Available at: <https://doi.org/10.1016/b978-0-12-294452-9.50019-9>.

Jankowski, J.E. et al. (2013) 'Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals', *Ecography*, 36(1), pp. 1–12. Available at: <https://doi.org/10.1111/j.1600-0587.2012.07785.x>.

Jankowski, J.E., Robinson, S.K. and Levey, D.J. (2010) 'Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds', *Ecology*, 91(7), pp. 1877–1884. Available at: <https://doi.org/10.1890/09-2063.1>.

Jensen, A.L. (1987) 'Simple models for exploitative and interference competition', *Ecological Modelling*, 35(1), pp. 113–121. Available at: [https://doi.org/10.1016/0304-3800\(87\)90093-7](https://doi.org/10.1016/0304-3800(87)90093-7).

Jetz, W. et al. (2012) 'The global diversity of birds in space and time', *Nature*, 491(7424), pp. 444–448. Available at: <https://doi.org/10.1038/nature11631>.

Johnsgard, P.A. (1960) 'Hybridization in the Anatidae and Its Taxonomic Implications', *The Condor*, 62(1), pp. 25–33. Available at: <https://doi.org/10.2307/1365656>.

- Jones, I.L. and Hunter, F.M. (1998) 'Heterospecific mating preferences for a feather ornament in least auklets', *Behavioral Ecology*, 9(2), pp. 187–192. Available at: <https://doi.org/10.1093/beheco/9.2.187>.
- Jones, S.E.I. et al. (2020) 'Weak asymmetric interspecific aggression and divergent habitat preferences at an elevational contact zone between tropical songbirds', *Ibis*, 162(3), pp. 814–826. Available at: <https://doi.org/10.1111/ibi.12793>.
- Jung, M. et al. (2020) 'A global map of terrestrial habitat types', *Scientific Data*, 7(1), p. 256. Available at: <https://doi.org/10.1038/s41597-020-00599-8>.
- Justyn, N.M., Callaghan, C.T. and Hill, G.E. (2020) 'Birds rarely hybridize: A citizen science approach to estimating rates of hybridization in the wild*', *Evolution*, 74(6), pp. 1216–1223. Available at: <https://doi.org/10.1111/evo.13943>.
- Kamalov, F., Thabtah, F. and Leung, H.H. (2023) 'Feature Selection in Imbalanced Data', *Annals of Data Science*, 10(6), pp. 1527–1541. Available at: <https://doi.org/10.1007/s40745-021-00366-5>.
- Karger, D.N. et al. (2017) 'Climatologies at high resolution for the earth's land surface areas', *Scientific Data*, 4(1), p. 170122. Available at: <https://doi.org/10.1038/sdata.2017.122>.
- Karl, S.A., Bowen, B.W. and Avise, J.C. (1995) 'Hybridization Among the Ancient Mariners: Characterization of Marine Turtle Hybrids With Molecular Genetic Assays', *Journal of Heredity*, 86(4), pp. 262–268. Available at: <https://doi.org/10.1093/oxfordjournals.jhered.a111579>.
- Karr, J.R. and Freemark, K.E. (1983) 'Habitat Selection and Environmental Gradients: Dynamics in the "Stable" Tropics', *Ecology*, 64(6), pp. 1481–1494. Available at: <https://doi.org/10.2307/1937503>.
- Kelly, E.G., Forsman, E.D. and Anthony, R.G. (2003) 'Are Barred Owls Displacing Spotted Owls?', *The Condor: Ornithological Applications*, 105(1), pp. 45–53. Available at: <https://doi.org/10.1093/condor/105.1.45>.

Kent, C.M. and Sherry, T.W. (2020) 'Behavioral niche partitioning reexamined: Do behavioral differences predict dietary differences in warblers?', *Ecology*, 101(8), p. e03077. Available at: <https://doi.org/10.1002/ecy.3077>.

Kerlinger, P. (1985) 'Water-Crossing Behavior of Raptors during Migration', *The Wilson Bulletin*, 97(1), pp. 109–113.

King, T.W. et al. (2021) 'The influence of spatial and temporal scale on the relative importance of biotic vs. abiotic factors for species distributions', *Diversity and Distributions*, 27(2), pp. 327–343. Available at: <https://doi.org/10.1111/ddi.13182>.

Kirschel, A.N.G., Seddon, N. and Tobias, J.A. (2019) 'Range-wide spatial mapping reveals convergent character displacement of bird song', *Proceedings of the Royal Society B: Biological Sciences*, 286(1902), pp. 17–19. Available at: <https://doi.org/10.1098/rspb.2019.0443>.

Kishi, S. and Nakazawa, T. (2013) 'Analysis of species coexistence co-mediated by resource competition and reproductive interference', *Population Ecology*, 55(2), pp. 305–313. Available at: <https://doi.org/10.1007/s10144-013-0369-2>.

Kishi, S., Nishida, T. and Tsubaki, Y. (2009) 'Reproductive interference determines persistence and exclusion in species interactions', *Journal of Animal Ecology*, 78(5), pp. 1043–1049. Available at: <https://doi.org/10.1111/j.1365-2656.2009.01560.x>.

Kissling, W.D. et al. (2012) 'Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents', *Journal of Biogeography*, 39(12), pp. 2163–2178. Available at: <https://doi.org/10.1111/j.1365-2699.2011.02663.x>.

Kivelä, S.M. et al. (2014) 'The past and the present in decision-making: the use of conspecific and heterospecific cues in nest site selection', *Ecology*, 95(12), pp. 3428–3439.

Knox, A.G. (1990) 'The sympatric breeding of Common and Scottish Crossbills *Loxia curvirostra* and *L. scotica* and the evolution of crossbills', *Ibis*, 132(3), pp. 454–466. Available at: <https://doi.org/10.1111/j.1474-919X.1990.tb01063.x>.

König, C. et al. (2021) 'Scale dependency of joint species distribution models challenges interpretation of biotic interactions', *Journal of Biogeography*, 48(7), pp. 1541–1551. Available at: <https://doi.org/10.1111/jbi.14106>.

Kronfeld-Schor, N. and Dayan, T. (1999) 'The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species', *Oecologia*, 121(1), pp. 123–128. Available at: <https://doi.org/10.1007/s004420050913>.

Krosby, M. and Rohwer, S. (2008) '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 B: Biological Sciences*, 276(1657), pp. 615–621. Available at: <https://doi.org/10.1098/rspb.2008.1310>.

Krosby, M. and Rohwer, S. (2010) 'Ongoing movement of the hermit warbler X Townsend's Warbler Hybrid Zone', *PLoS ONE*, 5(11), p. e14164. Available at: <https://doi.org/10.1371/journal.pone.0014164>.

Kuhn, M. and Wickham, H. (2020) 'Tidymodels: a collection of packages for modeling and machine learning using tidyverse principles.' Available at: <https://www.tidymodels.org>.

Kuno, E. (1992) 'Competitive exclusion through reproductive interference', *Researches on Population Ecology*, 34(2), pp. 275–284.

Kuno, E. (1992) 'Competitive exclusion through reproductive interference', *Researches on Population Ecology*, 34(2), pp. 275–284. Available at: <https://doi.org/10.1007/BF02514797>.

Kyogoku, D. and Nishida, T. (2012) 'The presence of heterospecific males causes an Allee effect', *Population Ecology*, 54(3), pp. 391–395. Available at: <https://doi.org/10.1007/s10144-012-0313-x>.

La Sorte, F.A. and Boecklen, W.J. (2005a) 'Changes in the diversity structure of avian assemblages in North America', *Global Ecology and Biogeography*, 14(4), pp. 367–378. Available at: <https://doi.org/10.1111/j.1466-822X.2005.00160.x>.

La Sorte, F.A. and Boecklen, W.J. (2005b) 'Temporal turnover of common species in avian assemblages in North America', *Journal of Biogeography*, 32(7), pp. 1151–1160. Available at: <https://doi.org/10.1111/j.1365-2699.2005.01271.x>.

Lamichhane, S. et al. (2018) 'Rapid hybrid speciation in Darwin's finches', *Science*, 359(6372), pp. 224–228. Available at: <https://doi.org/10.1126/science.aao4593>.

Lavretsky, P. et al. (2021) 'Phylogenomics reveals ancient and contemporary gene flow contributing to the evolutionary history of sea ducks (Tribe Mergini)', *Molecular Phylogenetics and Evolution*, 161(October 2020), p. 107164. Available at: <https://doi.org/10.1016/j.ympev.2021.107164>.

Lawlor, J.A. et al. (2024) 'Mechanisms, detection and impacts of species redistributions under climate change', *Nature Reviews Earth & Environment*, 5(5), pp. 351–368. Available at: <https://doi.org/10.1038/s43017-024-00527-z>.

Leathwick, J.R. (2002) 'Intra-generic competition among *Nothofagus* in New Zealand's primary indigenous forests', *Biodiversity & Conservation*, 11(12), pp. 2177–2187. Available at: <https://doi.org/10.1023/A:1021394628607>.

Lees, A. and Gilroy, J. (2022) *Vagrancy in Birds*. Bloomsbury Publishing.

Legault, G. et al. (2020) 'Interspecific competition slows range expansion and shapes range boundaries', *Proceedings of the National Academy of Sciences*, 117(43), pp. 26854–26860.

Leighton, G.M. et al. (2021) 'Sociality and migration predict hybridization across birds', *Proceedings of the Royal Society B: Biological Sciences*, 288, p. 20201946. Available at: <https://doi.org/10.1098/rspb.2020.1946>.

Leighton, G.M. et al. (2023) 'Both morphological and behavioral traits predict interspecific social dominance in birds', *Journal of Ornithology*, 164(1), pp. 163–169. Available at: <https://doi.org/10.1007/s10336-022-02022-y>.

Leighton, G.M. et al. (2024) 'Unfamiliarity generates costly aggression in interspecific avian dominance hierarchies', *Nature Communications*, 15(1), p. 335. Available at: <https://doi.org/10.1038/s41467-023-44613-0>.

Lembrechts, J.J., Nijs, I. and Lenoir, J. (2019) 'Incorporating microclimate into species distribution models', *Ecography*, 42(7), pp. 1267–1279. Available at: <https://doi.org/10.1111/ecog.03947>.

Levy, O., Dayan, T. and Kronfeld-Schor, N. (2011) 'Interspecific Competition and Torpor in Golden Spiny Mice: Two Sides of the Energy-Acquisition Coin', *Integrative and Comparative Biology*, 51(3), pp. 441–448. Available at: <https://doi.org/10.1093/icb/icr071>.

Lima, C.C. and Garcia, C.M. (2016) 'Pre- and post-experimental manipulation assessments confirm the increase in number of birds due to the addition of nest boxes', *PeerJ*, 4, p. e1806. Available at: <https://doi.org/10.7717/peerj.1806>.

Lindström, Å. et al. (2013) 'Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change', *Ecography*, 36(3), pp. 313–322. Available at: <https://doi.org/10.1111/j.1600-0587.2012.07799.x>.

Linz, G., Johnson, R. and Thiele, J. (2017) 'European Starlings', in *Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States*. CRC Press.

Liou, L.W. and Price, T.D. (1994) 'Speciation by reinforcement of premating isolation', *Evolution*, 48(5), pp. 1451–1459.

Liou, L.W. and Price, T.D. (1994) 'Speciation by reinforcement of premating isolation', *Evolution*, 48(5), pp. 1451–1459. Available at: <https://doi.org/10.1111/j.1558-5646.1994.tb02187.x>.

Liu, C. et al. (2005) 'Selecting thresholds of occurrence in the prediction of species distributions', *Ecography*, 28(3), pp. 385–393. Available at: <https://doi.org/10.1111/j.0906-7590.2005.03957.x>.

- Livezey, K.B. (2009) 'Range Expansion of Barred Owls, Part I: Chronology and Distribution', *The American Midland Naturalist*, 161(1), pp. 49–56.
- Losin, N. et al. (2016) 'The ecological and evolutionary stability of interspecific territoriality', *Ecology Letters*, 19(3), pp. 260–267. Available at: <https://doi.org/10.1111/ele.12561>.
- Lotka, A.J. (1932) 'The growth of mixed populations: Two species competing for a common food supply', *Journal of the Washington Academy of Sciences*, 22(16/17), pp. 461–469.
- Louthan, A.M., Doak, D.F. and Angert, A.L. (2015) 'Where and When do Species Interactions Set Range Limits?', *Trends in Ecology and Evolution*, 30(12), pp. 780–792. Available at: <https://doi.org/10.1016/j.tree.2015.09.011>.
- Ludde, S.T. et al. (2004) 'Some males are choosier than others: Species recognition in blue waxbills', *Behaviour*, 141, pp. 1021–1039.
- Luepold, S.B., Carlotti, S. and Pasinelli, G. (2024) 'A test of the mechanistic process behind the convergent agonistic character displacement hypothesis', *Behavioral Ecology*, 35(6), p. arae072. Available at: <https://doi.org/10.1093/beheco/arae072>.
- Lundberg, A. and Alatalo, R.V. (1992) *The pied flycatcher*. London: T. and A.D. Poyser.
- Mac Nally, R. et al. (2012) 'Despotic, high-impact species and the subcontinental scale control of avian assemblage structure', *Ecology*, 93(3), pp. 668–678. Available at: <https://doi.org/10.1890/10-2340.1>.
- MacArthur, R. and Levins, R. (1964) 'Competition, habitat selection, and character displacement in a patchy environment', *Proceedings of the National Academy of Sciences*, 51(6), pp. 1207–1210. Available at: <https://doi.org/10.1073/pnas.51.6.1207>.
- MacArthur, R. and Levins, R. (1967) 'The Limiting Similarity, Convergence, and Divergence of Coexisting Species', *The American Naturalist*, 101(921), pp. 377–385.

- MacArthur, R.H. (1958) 'Population Ecology of Some Warblers of Northeastern Coniferous Forests', *Ecology*, 39(4), pp. 599–619. Available at: <https://doi.org/10.2307/1931600>.
- MacArthur, R.H. (1969) 'Patterns of communities in the tropics', *Biological Journal of the Linnean Society*, 1(1–2), pp. 19–30. Available at: <https://doi.org/10.1111/j.1095-8312.1969.tb01809.x>.
- MacArthur, R.H. (1972) *Geographical ecology: Patterns in the distribution of species*. New York : Harper & Row. Available at: <http://archive.org/details/geographicaecol0000maca> (Accessed: 3 December 2024).
- MacArthur, R.H. and MacArthur, J.W. (1961) 'On Bird Species Diversity', *Ecology*, 42(3), pp. 594–598. Available at: <https://doi.org/10.2307/1932254>.
- Macdonald, C.A. et al. (2012) 'First Report of a Snow Bunting × Lapland Longspur Hybrid', *Arctic*, 65(3), pp. 344–348.
- Machado-Stredel, F. et al. (2024) 'The roles of abiotic and biotic factors in driving range shifts: An invasive Pomacea snail facilitates *Rostrhamus sociabilis* (Snail Kite) northward range expansion', *Ornithology*, 141(3), p. ukae022. Available at: <https://doi.org/10.1093/ornithology/ukae022>.
- Maher, C.R. and Lott, D.F. (1995) 'Definitions of territoriality used in the study of variation in vertebrate spacing systems', *Animal Behaviour*, 49(6), pp. 1581–1597. Available at: [https://doi.org/10.1016/0003-3472\(95\)90080-2](https://doi.org/10.1016/0003-3472(95)90080-2).
- Maldonado-Coelho, M. et al. (2017) 'The invasive species rules: competitive exclusion in forest avian mixed-species flocks in a fragmented landscape Marcos', *Revista Brasileira de Ornitologia*, 25(1), pp. 54–59.
- Mallet, J. (2005) 'Hybridization as an invasion of the genome', *Trends in Ecology & Evolution*, 20(5), pp. 229–237. Available at: <https://doi.org/10.1016/j.tree.2005.02.010>.
- Mallet, J. (2007) 'Hybrid speciation', *Nature*, 446(7133), pp. 279–283. Available at: <https://doi.org/10.1038/nature05706>.

Mallet, J. (2008) 'Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1506), pp. 2971–2986. Available at: <https://doi.org/10.1098/rstb.2008.0081>.

Maron, M. et al. (2013) 'Avifaunal disarray due to a single despotic species', *Diversity and Distributions*, 19(12), pp. 1468–1479. Available at: <https://doi.org/10.1111/ddi.12128>.

Marris, E. (2007) 'The escalator effect', *Nature Climate Change*, 1(712), pp. 94–96. Available at: <https://doi.org/10.1038/climate.2007.70>.

Martin, P.R. and Bonier, F. (2018) 'Species interactions limit the occurrence of urban-adapted birds in cities', *Proceedings of the National Academy of Sciences of the United States of America*, 115(49), pp. E11495–E11504. Available at: <https://doi.org/10.1073/pnas.1809317115>.

Martin, P.R., Freshwater, C. and Ghalambor, C.K. (2017) 'The outcomes of most aggressive interactions among closely related bird species are asymmetric', *PeerJ*, 5, p. e2847. Available at: <https://doi.org/10.7717/peerj.2847>.

Marvin, G.A. (1998) 'Interspecific aggression and spatial relationships in the salamanders *Plethodon kentucki* and *Plethodon glutinosus*: evidence of interspecific interference competition', *Canadian Journal of Zoology*, 76(1), pp. 94–103. Available at: <https://doi.org/10.1139/z97-158>.

Marvin, G.A. (1998) 'Interspecific aggression and spatial relationships in the salamanders *Plethodon kentucki* and *Plethodon glutinosus*: evidence of interspecific interference competition', *Canadian Journal of Zoology*, 76(1), pp. 94–103. Available at: <https://doi.org/10.1139/cjz-76-1-94>.

Maurer, B.A. (1984) 'Interference and Exploitation in Bird Communities', *The Wilson Bulletin*, 96(3), pp. 380–395.

Mavárez, J. et al. (2006) 'Speciation by hybridization in Heliconius butterflies', *Nature*, 441(7095), pp. 868–871. Available at: <https://doi.org/10.1038/nature04738>.

Mayr, E. (1942) *Systematics and the origin of species: from the viewpoint of a zoologist*. New York: Columbia University Press. Available at: <http://archive.org/details/systematicsorigi0000erne> (Accessed: 25 May 2025).

McCarthy, E.M. (2006) *Handbook of Avian Hybrids of the World*. Oxford, UK: Oxford University Press. Available at: [https://doi.org/10.1676/0043-5643\(2008\)120\[233:hoahot\]2.0.co;2](https://doi.org/10.1676/0043-5643(2008)120[233:hoahot]2.0.co;2).

McCracken, K.G. and Wilson, R.E. (2011) 'Gene Flow and Hybridization between Numerically Imbalanced Populations of Two Duck Species in the Falkland Islands', *PLOS ONE*, 6(8), p. e23173. Available at: <https://doi.org/10.1371/journal.pone.0023173>.

McEntee, J.P., Burleigh, J.G. and Singhal, S. (2020) 'Dispersal Predicts Hybrid Zone Widths across Animal Diversity: Implications for Species Borders under Incomplete Reproductive Isolation', *The American Naturalist*, 196(1), pp. 9–28. Available at: <https://doi.org/10.1086/709109>.

McQuillan, M.A. and Rice, A.M. (2015) 'Differential effects of climate and species interactions on range limits at a hybrid zone: Potential direct and indirect impacts of climate change', *Ecology and Evolution*, 5(21), pp. 5120–5137. Available at: <https://doi.org/10.1002/ece3.1774>.

McTavish, E.J. et al. (2025) 'A complete and dynamic tree of birds', *Proceedings of the National Academy of Sciences*, 122(18), p. e2409658122. Available at: <https://doi.org/10.1073/pnas.2409658122>.

Meier, E.S. et al. (2010) 'Biotic and abiotic variables show little redundancy in explaining tree species distributions', *Ecography*, 33(6), pp. 1038–1048. Available at: <https://doi.org/10.1111/j.1600-0587.2010.06229.x>.

Mendelson, T.C. and Shaw, K.L. (2012) 'The (mis)concept of species recognition', *Trends in Ecology & Evolution*, 27(8), pp. 421–427. Available at: <https://doi.org/10.1016/j.tree.2012.04.001>.

Mettler, R.D. and Spellman, G.M. (2009) 'A hybrid zone revisited: Molecular and morphological analysis of the maintenance, movement, and evolution of a Great Plains avian (Cardinalidae: *Pheucticus*) hybrid zone', *Molecular Ecology*, 18(15), pp. 3256–3267. Available at: <https://doi.org/10.1111/j.1365-294X.2009.04217.x>.

Mikami, O.K. and Kawata, M. (2004) 'Does interspecific territoriality reflect the intensity of ecological interactions? a theoretical model for interspecific territoriality', *Evolutionary Ecology Research*, 6(5), pp. 765–775.

Mikkonen, A.V. (1985) 'Establishment of breeding territory by the chaffinch, *Fringilla coelebs*, and the brambling, *F. montifringilla*, in northern Finland', *Annales Zoologici Fennici*, 22(2), pp. 137–156.

Miles, M.C. et al. (2018) 'Macroevolutionary patterning of woodpecker drums reveals how sexual selection elaborates signals under constraint', *Proceedings of the Royal Society B: Biological Sciences*, 285(1873), p. 20172628. Available at: <https://doi.org/10.1098/rspb.2017.2628>.

Miller, E.T. et al. (2017) 'Fighting over food unites the birds of North America in a continental dominance hierarchy', *Behavioral Ecology*, 28(6), pp. 1454–1463. Available at: <https://doi.org/10.1093/beheco/arx108>.

Miller, E.T. et al. (2019) 'Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers', *Nature Communications*, 10(1), p. 1602. Available at: <https://doi.org/10.1038/s41467-019-09721-w>.

Miller, E.T., Sanchez-Reyes, L. and McTavish, E.J. (2025) 'cloodl: R package for accessing a dynamic avian phylogeny'. Available at: <https://github.com/McTavishLab/AvesData>.

Mönkkönen, M. et al. (2017) 'Linking species interactions with phylogenetic and functional distance in European bird assemblages at broad spatial scales', *Global*

Ecology and Biogeography, 26(8), pp. 952–962. Available at:
<https://doi.org/10.1111/geb.12605>.

Mönkkönen, M., Helle, P. and Soppela, K. (1990) 'Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities?', *Oecologia*, 85(2), pp. 218–225. Available at: <https://doi.org/10.1007/BF00319404>.

Moore, S. and Coulson, J.O. (2020) 'Intergeneric Hybridization of a Vagrant Common Black Hawk and a Red-Shouldered Hawk', *Journal of Raptor Research*, 54(1), pp. 74–80. Available at: <https://doi.org/10.3356/0892-1016-54.1.74>.

Moore, W.S. (1977) 'An Evaluation of Narrow Hybrid Zones in Vertebrates', *The Quarterly Review of Biology*, 52(3), pp. 263–277. Available at: <https://doi.org/10.1086/409995>.

Moore, W.S. and Buchanan, D.B. (1985) 'Stability of the Northern Flicker Hybrid Zone in Historical Times: Implications for Adaptive Speciation Theory', *Evolution*, 39(1), pp. 135–151. Available at: <https://doi.org/10.2307/2408523>.

Morton, R.D. et al. (2024) 'Land cover map 2023 (25m rasterised land parcels, GB)'. NERC EDS Environmental Information Data Centre. Available at:
<https://doi.org/10.5285/ab10ea4a-1788-4d25-a6df-f1aff829dfff>.

Motis Berta, A. (1994) Territorialitat interspecífica de '*Sturnus vulgaris*' L. i '*Sturnus unicolor*' Temm., dues aloespècies en contacte secundari: hàbitat de cria, conducta agonística i cants territorials, Tesis Doctorals - Departament - Biologia Animal. Universitat de Barcelona. Available at:
<https://diposit.ub.edu/dspace/handle/2445/35912> (Accessed: 24 April 2025).

Muller, H.J. (1942) 'Isolating mechanisms, evolution, and temperature', in *Biological symposia*, pp. 71–125.

Muñoz-Fuentes, V. et al. (2007) 'Hybridization between white-headed ducks and introduced ruddy ducks in Spain', *Molecular Ecology*, 16(3), pp. 629–638. Available at: <https://doi.org/10.1111/j.1365-294X.2006.03170.x>.

Mutshinda, C.M., O'Hara, R.B. and Woiwod, I.P. (2009) 'What drives community dynamics?', *Proceedings of the Royal Society B: Biological Sciences*, 276(1669), pp. 2923–2929. Available at: <https://doi.org/10.1098/rspb.2009.0523>.

Mutshinda, C.M., O'Hara, R.B. and Woiwod, I.P. (2011) 'A multispecies perspective on ecological impacts of climatic forcing', *Journal of Animal Ecology*, 80(1), pp. 101–107. Available at: <https://doi.org/10.1111/j.1365-2656.2010.01743.x>.

Natola, L. et al. (2021) 'Introgression between *Sphyrapicus nuchalis* and *S. varius* sapsuckers in a hybrid zone in west-central Alberta', *Journal of Avian Biology*, 52(8). Available at: <https://doi.org/10.1111/jav.02717>.

Natola, L., Seneviratne, S.S. and Irwin, D. (2022) 'Population genomics of an emergent tri-species hybrid zone', *Molecular Ecology*, 31(20), pp. 5356–5367. Available at: <https://doi.org/10.1111/mec.16650>.

Nesbit, D.A. et al. (2023) 'Interspecific territoriality has facilitated recent increases in the breeding habitat overlap of North American passerines', *Ecography*, 2023(6), p. e06573. Available at: <https://doi.org/10.1111/ecog.06573>.

Nespoli, D. et al. (2021) 'Disentangling the taxonomic status and phylogeographic structure of Marmora's (*Curruca sarda*) and Balearic Warbler (*Curruca balearica*): a genetic multi-marker approach', *Journal of Ornithology*, 162(3), pp. 909–918. Available at: <https://doi.org/10.1007/s10336-021-01885-x>.

Newton, I. (2024) 'Effects of human persecution on European raptors', *Journal of Raptor Research*, 13(3), p. 1.

Nice, M.M. (1941) 'The Role of Territory in Bird Life', *American Midland Naturalist*, 26(3), p. 441. Available at: <https://doi.org/10.2307/2420732>.

Nice, M.M. (1941) 'The Role of Territory in Bird Life', *American Midland Naturalist*, 26(3), pp. 441–487. Available at: <https://doi.org/10.2307/2420732>.

Nolte, A.W. et al. (2005) 'An invasive lineage of sculpins, *Cottus* sp. (Pisces, Teleostei) in the Rhine with new habitat adaptations has originated from hybridization between old

phylogeographic groups', *Proceedings of the Royal Society B: Biological Sciences*, 272(1579), pp. 2379–2387. Available at: <https://doi.org/10.1098/rspb.2005.3231>.

Noriyuki, S. and Osawa, N. (2016) 'Reproductive interference and niche partitioning in aphidophagous insects', *Psyche*, 2016, p. 4751280. Available at: <https://doi.org/10.1155/2016/4751280>.

Novella-Fernandez, R. et al. (2021) 'Broad-scale patterns of geographic avoidance between species emerge in the absence of fine-scale mechanisms of coexistence', *Diversity and Distributions*, 27(9), pp. 1606–1618. Available at: <https://doi.org/10.1111/ddi.13375>.

Nuechterlein, G.L. and Buitron, D. (1998) 'Interspecific mate choice by late-courting male western grebes', *Behavioral Ecology*, 9(3), pp. 313–321. Available at: <https://doi.org/10.1093/beheco/9.3.313>.

O'Neill, B.C. et al. (2016) 'The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6', *Geoscientific Model Development*, 9(9), pp. 3461–3482. Available at: <https://doi.org/10.5194/gmd-9-3461-2016>.

Ockendon, N. et al. (2014) 'Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects', *Global Change Biology*, 20(7), pp. 2221–2229. Available at: <https://doi.org/10.1111/gcb.12559>.

Orr, H.A. and Turelli, M. (2001) 'The Evolution of Postzygotic Isolation: Accumulating Dobzhansky-Muller Incompatibilities', *Evolution*, 55(6), pp. 1085–1094. Available at: <https://doi.org/10.1111/j.0014-3820.2001.tb00628.x>.

Oswald, J.A. et al. (2019) 'Evolutionary dynamics of hybridization and introgression following the recent colonization of Glossy Ibis (*Aves: Plegadis falcinellus*) into the New World', *Molecular Ecology*, 28(7), pp. 1675–1691. Available at: <https://doi.org/10.1111/mec.15008>.

Ottenburghs, J. (2018) 'Exploring the hybrid speciation continuum in birds', *Ecology and Evolution*, 8(24), pp. 13027–13034. Available at: <https://doi.org/10.1002/ece3.4558>.

Ottenburghs, J. (2023) 'How common is hybridization in birds?', *Journal of Ornithology*, 164(4), pp. 913–920. Available at: <https://doi.org/10.1007/s10336-023-02080-w>.

Ottenburghs, J. et al. (2017) 'A history of hybrids? Genomic patterns of introgression in the True Geese', *BMC Evolutionary Biology*, 17(1), p. 201. Available at: <https://doi.org/10.1186/s12862-017-1048-2>.

Ovadia, O. and zu Dohna, H. (2003) 'The effect of intra- and interspecific aggression on patch residence time in Negev Desert gerbils: a competing risk analysis', *Behavioral Ecology*, 14(4), pp. 583–591. Available at: <https://doi.org/10.1093/beheco/arg031>.

Ovaskainen, O. and Abrego, N. (2020) *Joint species distribution modelling*. Cambridge, England: Cambridge University Press (Ecology, biodiversity and conservation).

Ovaskainen, O. et al. (2016) 'Using latent variable models to identify large networks of species-to-species associations at different spatial scales', *Methods in Ecology and Evolution*, 7(5), pp. 549–555. Available at: <https://doi.org/10.1111/2041-210X.12501>.

Ovaskainen, O. et al. (2017) 'How to make more out of community data? A conceptual framework and its implementation as models and software', *Ecology Letters*, 20(5), pp. 561–576. Available at: <https://doi.org/10.1111/ele.12757>.

Ovaskainen, O., Hottola, J. and Siitonen, J. (2010) 'Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions', *Ecology*, 91(9), pp. 2514–2521. Available at: <https://doi.org/10.1890/10-0173.1>.

Papadogeorgou, G. et al. (2023) 'Covariate-Informed Latent Interaction Models: Addressing Geographic & Taxonomic Bias in Predicting Bird–Plant Interactions', *Journal of the American Statistical Association*, 118(544), pp. 2250–2261. Available at: <https://doi.org/10.1080/01621459.2023.2208390>.

Paquette, A. and Hargreaves, A.L. (2021) 'Biotic interactions are more often important at species' warm versus cool range edges', *Ecology Letters*, 24(11), pp. 2427–2438. Available at: <https://doi.org/10.1111/ele.13864>.

Paradis, E. and Schliep, K. (2019) 'ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R', *Bioinformatics (Oxford, England)*, 35, pp. 526–528. Available at: <https://doi.org/10.1093/bioinformatics/bty633>.

Pardieck, K.L. et al. (2020) 'North American Breeding Bird Survey Dataset 1966 - 2019: U.S. Geological Survey data release'. Available at: <https://doi.org/10.5066/P9J6QUF6>.

Parkes, K.C. (1951) 'The Genetics of the Golden-winged X Blue-winged Warbler Complex', *Wilson Bulletin*, 63.

Parmesan, C. (2006) 'Ecological and evolutionary responses to recent climate change', *Annual Review of Ecology, Evolution, and Systematics*, 37, pp. 637–669. Available at: <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>.

Parmesan, C. and Yohe, G. (2003) 'A globally coherent fingerprint of climate change impacts across natural systems', *Nature*, 421(6918), pp. 37–42. Available at: <https://doi.org/10.1038/nature01286>.

Pasch, B., Bolker, B.M. and Phelps, S.M. (2013) 'Interspecific Dominance Via Vocal Interactions Mediates Altitudinal Zonation in Neotropical Singing Mice.', *The American Naturalist*, 182(5), pp. E161–E173. Available at: <https://doi.org/10.1086/673263>.

Pasch, B., Bolker, B.M. and Phelps, S.M. (2013) 'Interspecific dominance via vocal interactions mediates altitudinal zonation in neotropical singing mice', *American Naturalist*, 182(5), pp. E161–E173. Available at: <https://doi.org/10.1086/673263>.

Patterson, C.W. and Drury, J.P. (2023) 'Interspecific behavioural interference and range dynamics: current insights and future directions', *Biological Reviews*, 98(6), pp. 2012–2027. Available at: <https://doi.org/10.1111/brv.12993>.

Payne, R.B. (1980) 'Behavior and songs of hybrid parasitic finches', 97(1), pp. 118–134.

Pearson, R.G. and Dawson, T.P. (2003) 'Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?', *Global Ecology and Biogeography*, 12(5), pp. 361–371. Available at: <https://doi.org/10.1046/j.1466-822X.2003.00042.x>.

Pearson, R.G. and Dawson, T.P. (2003a) 'Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?', *Global Ecology and Biogeography*, 12(5), pp. 361–371. Available at: <https://doi.org/10.1046/j.1466-822X.2003.00042.x>.

Pearson, R.G. and Dawson, T.P. (2003b) 'Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful?', *Global Ecology and Biogeography*, 12(5), pp. 361–371. Available at: <https://doi.org/10.1046/j.1466-822X.2003.00042.x>.

Pearson, S.F. (2000) 'Behavioral asymmetries in a moving hybrid zone', *Behavioral Ecology*, 11(1), pp. 84–92. Available at: <https://doi.org/10.1093/beheco/11.1.84>.

Pearson, S.F. and Rohwer, S. (2000) 'Asymmetries in male aggression across an avian hybrid zone', *Behavioral Ecology*, 11(1), pp. 93–101. Available at: <https://doi.org/10.1093/beheco/11.1.93>.

Pecl, G.T. et al. (2017) 'Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being', *Science*, 355(6332), p. eaai9214. Available at: <https://doi.org/10.1126/science.aai9214>.

Pellissier, L. et al. (2010) 'Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants', *Ecography*, 33(6), pp. 1004–1014. Available at: <https://doi.org/10.1111/j.1600-0587.2010.06386.x>.

Peralta, G. et al. (2024) 'Predicting plant–pollinator interactions: concepts, methods, and challenges', *Trends in Ecology & Evolution*, 39(5), pp. 494–505. Available at: <https://doi.org/10.1016/j.tree.2023.12.005>.

Pereira, P.F., Lourenço, R. and Mota, P.G. (2020) 'Two songbird species show subordinate responses to simulated territorial intrusions of an exotic competitor', *Acta Ethologica*, 23(3), pp. 143–154. Available at: <https://doi.org/10.1007/s10211-020-00347-6>.

Pfennig, D. and Pfennig, K. (2012) *Evolution's wedge: Competition and the origins of diversity*. University of California Press.

Pfennig, K.S. (1998) 'The evolution of mate choice and the potential for conflict between species and mate-quality recognition', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1407), pp. 1743–1748. Available at: <https://doi.org/10.1098/rspb.1998.0497>.

Pfennig, K.S. (2007) 'Facultative Mate Choice Drives Adaptive Hybridization', *Science*, 318(5852), pp. 965–967. Available at: <https://doi.org/10.1126/science.1146035>.

Pfennig, K.S. (2021) 'Biased Hybridization and Its Impact on Adaptive Introgression', *Trends in Ecology and Evolution*, 36(6), pp. 488–497. Available at: <https://doi.org/10.1016/j.tree.2021.02.010>.

Pfennig, K.S., Kelly, A.L. and Pierce, A.A. (2016) 'Hybridization as a facilitator of species range expansion', *Proceedings of the Royal Society B: Biological Sciences*, 283, p. 20161329. Available at: <https://doi.org/10.1098/rspb.2016.1329>.

Pianka, E.R. (1966) 'Latitudinal Gradients in Species Diversity: A Review of Concepts', *The American Naturalist*, 100(910), pp. 33–46.

Pichler, M. et al. (2020) 'Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks', *Methods in Ecology and Evolution*, 11(2), pp. 281–293. Available at: <https://doi.org/10.1111/2041-210X.13329>.

Pierce, R.J. (1984) 'The changed distribution of stilts in New Zealand', *Notornis*, 31, pp. 7–18.

Pigot, A.L. and Tobias, J.A. (2013) 'Species interactions constrain geographic range expansion over evolutionary time', *Ecology Letters*. Edited by C. Webb, 16(3), pp. 330–338. Available at: <https://doi.org/10.1111/ele.12043>.

Pigot, A.L. and Tobias, J.A. (2013a) 'Species interactions constrain geographic range expansion over evolutionary time', *Ecology Letters*, 16(3), pp. 330–338. Available at: <https://doi.org/10.1111/ele.12043>.

Pigot, A.L. and Tobias, J.A. (2013b) 'Species interactions constrain geographic range expansion over evolutionary time', *Ecology Letters*. Edited by C. Webb, 16(3), pp. 330–338. Available at: <https://doi.org/10.1111/ele.12043>.

Pigot, A.L. and Tobias, J.A. (2015) 'Dispersal and the transition to sympatry in vertebrates', *Proceedings of the Royal Society B: Biological Sciences*, 282, p. 20141929. Available at: <https://doi.org/10.1098/rspb.2014.1929>.

Pigot, A.L. et al. (2018) 'The macroecological dynamics of species coexistence in birds', *Nature Ecology and Evolution*, 2(7), pp. 1112–1119. Available at: <https://doi.org/10.1038/s41559-018-0572-9>.

Pigot, A.L. et al. (2020) 'Macroevolutionary convergence connects morphological form to ecological function in birds', *Nature Ecology & Evolution*, 4(2), pp. 230–239. Available at: <https://doi.org/10.1038/s41559-019-1070-4>.

Pigot, A.L. et al. (2020) 'Macroevolutionary convergence connects morphological form to ecological function in birds', *Nature Ecology and Evolution*, 4(2), pp. 230–239. Available at: <https://doi.org/10.1038/s41559-019-1070-4>.

Pigot, A.L., Tobias, J.A. and Jetz, W. (2016) 'Energetic Constraints on Species Coexistence in Birds', *PLOS Biology*, 14(3), p. e1002407. Available at: <https://doi.org/10.1371/journal.pbio.1002407>.

Pimm, S.L., Diamond, J. and Bishop, K.D. (2023) 'Species coexistence by wide constant size spacing', *Proceedings of the National Academy of Sciences*, 120(9), p. e2217904120. Available at: <https://doi.org/10.1073/pnas.2217904120>.

Pizarro, A.K., DeRaad, D.A. and McCormack, J.E. (2023) 'Temporal stability of the hybrid zone between *Calocitta magpie-jays* revealed through comparison of museum specimens and iNaturalist photos', *Ecology and Evolution*, 13(3), p. e9863. Available at: <https://doi.org/10.1002/ece3.9863>.

Poggiato, G. et al. (2021) 'On the Interpretations of Joint Modeling in Community Ecology', *Trends in Ecology and Evolution*, 36(5), pp. 391–401. Available at: <https://doi.org/10.1016/j.tree.2021.01.002>.

Poling, T.D. and Hayslette, S.E. (2006) 'Dietary overlap and foraging competition between mourning doves and Eurasian collared-doves', *Journal of Wildlife Management*, 70(4), pp. 998–1004. Available at: [https://doi.org/10.2193/0022-541x\(2006\)70\[998:doafcb\]2.0.co;2](https://doi.org/10.2193/0022-541x(2006)70[998:doafcb]2.0.co;2).

Pollock, L.J. et al. (2014) 'Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM)', *Methods in Ecology and Evolution*, 5(5), pp. 397–406. Available at: <https://doi.org/10.1111/2041-210X.12180>.

Polo, V. and Carrascal, L.M. (1999) 'Shaping the Body Mass Distribution of Passeriformes: Habitat Use and Body Mass are Evolutionarily and Ecologically Related', *Journal of Animal Ecology*, 68(2), pp. 324–337.

Polo, V. and Carrascal, L.M. (1999) 'Shaping the body mass distribution of Passeriformes: Habitat use and body mass are evolutionarily and ecologically related', *Journal of Animal Ecology*, 68(2), pp. 324–337. Available at: <https://doi.org/10.1046/j.1365-2656.1999.00282.x>.

Price, T. (2008) *Speciation in birds*. Greenwood Village, Colo. : Roberts and Co. Available at: <http://archive.org/details/speciationinbird0000pric> (Accessed: 2 May 2025).

Pyle, P. et al. (2021) '32nd Report of the ABA Checklist Committee 2021', *North American Birds*, 72(2), pp. 10–17.

Qvarnström, A. et al. (2006) 'Song similarity predicts hybridization in flycatchers', *Journal of Evolutionary Biology*, 19(4), pp. 1202–1209. Available at: <https://doi.org/10.1111/j.1420-9101.2006.01140.x>.

Qvarnström, A. et al. (2023) 'Assortative Mating in an Ecological Context: Effects of Mate Choice Errors and Relative Species Abundance on the Frequency and Asymmetry of Hybridization', *The American Naturalist*, 201(1), pp. 125–137. Available at: <https://doi.org/10.1086/722156>.

Rahman, A.U. et al. (2024) 'Accelerating joint species distribution modelling with Hmsc-HPC by GPU porting', *PLOS Computational Biology*, 20(9), p. e1011914. Available at: <https://doi.org/10.1371/journal.pcbi.1011914>.

Ramirez, B.R. et al. (2024) 'Convergent niche shifts of endangered parrots (genus *Amazona*) during successful establishment in urban southern California', *Diversity and Distributions*, 30(4), p. e13817. Available at: <https://doi.org/10.1111/ddi.13817>.

Randler, C. (2002) 'Avian hybridization, mixed pairing and female choice', *Animal Behaviour*, 63(1), pp. 103–119. Available at: <https://doi.org/10.1006/anbe.2001.1884>.

Randler, C. (2005) 'Do Forced Extrapair Copulations and Interspecific Brood Amalgamation Facilitate Natural Hybridisation in Wildfowl?', *Behaviour*, 142(4), pp. 477–488.

Randler, C. (2006) 'Behavioural and ecological correlates of natural hybridization in birds', *Ibis*, 148(3), pp. 459–467. Available at: <https://doi.org/10.1111/j.1474-919X.2006.00548.x>.

Reed, T.M. (1982) 'Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: Playback and removal experiments', *Animal Behaviour*, 30(1), pp. 171–181. Available at: [https://doi.org/10.1016/S0003-3472\(82\)80252-2](https://doi.org/10.1016/S0003-3472(82)80252-2).

Regos, A. et al. (2018) 'Hindcasting the impacts of land-use changes on bird communities with species distribution models of Bird Atlas data', *Ecological Applications*, 28(7), pp. 1867–1883. Available at: <https://doi.org/10.1002/eap.1784>.

Reif, J. et al. (2015) 'Interspecific territoriality in two songbird species: Potential role of song convergence in male aggressive interactions', *Animal Behaviour*, 104, pp. 131–136. Available at: <https://doi.org/10.1016/j.anbehav.2015.03.016>.

Reif, J. et al. (2018) 'Competition-driven niche segregation on a landscape scale: Evidence for escaping from syntopy towards allotopy in two coexisting sibling passerine species', *Journal of Animal Ecology*, 87(3), p. 774. Available at: <https://doi.org/10.1111/1365-2656.12808>.

Reif, J. et al. (2018) 'Competition-driven niche segregation on a landscape scale: Evidence for escaping from syntopy towards allotopy in two coexisting sibling passerine species', *Journal of Animal Ecology*, 87(3), pp. 774–789. Available at: <https://doi.org/10.1111/1365-2656.12808>.

Remeš, V. and Harmáčková, L. (2023) 'Resource use divergence facilitates the evolution of secondary syntopy in a continental radiation of songbirds (Meliphagoidea): insights from unbiased co-occurrence analyses', *Ecography*, 2023(2), p. e06268. Available at: <https://doi.org/10.1111/ecog.06268>.

Remeš, V. and Harmáčková, L. (2025) 'Completing the Speciation Cycle: Ecological Niches and Traits Predict Local Species Coexistence in Birds Across the Globe', *Global Ecology and Biogeography*, 34(2), p. e70002. Available at: <https://doi.org/10.1111/geb.70002>.

Remešová, E. et al. (2020) 'Foraging behaviour of songbirds in woodlands and forests in eastern Australia: resource partitioning and guild structure', *Emu - Austral Ornithology*, 120(1), pp. 22–32. Available at: <https://doi.org/10.1080/01584197.2019.1644183>.

Remsen, J.V. and Graves, W.S. (1995) 'Distribution patterns and zoogeography of Atlapetes brush-finches (Emberizinae) of the Andes', 112(1), pp. 210–224.

Reudink, M.W. et al. (2007) 'Structure and Dynamics of the Hybrid Zone between Black-Capped Chickadee (*Poecile atricapillus*) and Carolina Chickadee (*P. carolinensis*) in Southeastern Pennsylvania', *The Auk*, 124(2), pp. 463–478.

Rheindt, F.E. and Edwards, S.V. (2011) 'Genetic Introgression: An Integral but Neglected Component of Speciation in Birds', *The Auk*, 128(4), pp. 620–632. Available at: <https://doi.org/10.1525/auk.2011.128.4.620>.

Rhymer, J.M. and Braun, M.J. (1994) 'Mitochondrial Analysis of Gene Flow between New Zealand Mallards (*Anas platyrhynchos*) and Grey Ducks (*A. superciliosa*)', *The Auk*, 111(4), pp. 970–978. Available at: <https://doi.org/10.2307/4088829>.

Rhymer, J.M. and Simberloff, D. (1996) 'Extinction by hybridisation and introgression', *Annual Review of Ecology and Systematics*, 27(1), pp. 83–109. Available at: <https://doi.org/10.1146/annurev.ecolsys.27.1.83>.

Riahi, K. et al. (2017) 'The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview', *Global Environmental Change*, 42, pp. 153–168. Available at: <https://doi.org/10.1016/j.gloenvcha.2016.05.009>.

Ribeiro, J.M.C. and Spielman, A. (1986) 'The Satyr Effect: A Model Predicting Parapatry and Species Extinction', *The American Naturalist*, 128(4), pp. 513–528.

Rising, J.D. (1983) 'The Great Plains Hybrid Zones', in R.F. Johnston (ed.) *Current Ornithology*. New York, NY: Springer US, pp. 131–157. Available at: https://doi.org/10.1007/978-1-4615-6781-3_5.

Rivas, L.R. (1964) 'A reinterpretation of the concepts "sympatric" and "allopatric" with proposal of the additional terms "syntopic" and "allotopic"', *Systematic Zoology*, 13(1), pp. 42–43.

Robertson, P.A. et al. (2015) 'Towards the European eradication of the North American ruddy duck', *Biological Invasions*, 17(1), pp. 9–12. Available at: <https://doi.org/10.1007/s10530-014-0704-3>.

Robinson, D. (1992) 'Habitat use and foraging behaviour of the scarlet robin and the flame robin at a site of breeding-season sympatry', *Wildlife Research*, 19(4), p. 377. Available at: <https://doi.org/10.1071/WR9920377>.

Robinson, S.K. and Terborgh, J. (1995) 'Interspecific Aggression and Habitat Selection by Amazonian Birds', *Journal of Animal Ecology*, 64(1), pp. 1–11. Available at: <https://doi.org/10.2307/5822>.

Rodriguez, B., Curbelo, J. and Carrasco, N. (2010) 'Hybrid Eurasian Coot *Fulica atra* x Common Moorhen *Gallinula chloropus* on Tenerife, Canary Islands', *Bulletin of the African Bird Club*, 17(2), pp. 207–209. Available at: <https://doi.org/10.5962/p.309914>.

Rohwer, S. and Wood, C. (1998) 'Three Hybrid Zones between Hermit and Townsend's Warblers in Washington and Oregon', *The Auk*, 115(2), pp. 284–310. Available at: <https://doi.org/10.2307/4089188>.

Rohwer, S.A. (1972) 'A Multivariate Assessment of Interbreeding Between the Meadowlarks, *Sturnella*', *Systematic Zoology*, 21(3), pp. 313–338. Available at: <https://doi.org/10.2307/2412170>.

Rohwer, S.A. (1973) 'Significance of Sympatry to Behavior and Evolution of Great Plains Meadowlarks', *Evolution*, 27(1), pp. 44–57.

Rosenberg, K.V. et al. (2019) 'Decline of the North American avifauna', *Science*, 366(6461), pp. 120–124. Available at: <https://doi.org/10.1126/science.aaw1313>.

Rosenthal, G.G. (2013) 'Individual mating decisions and hybridization', *Journal of Evolutionary Biology*, 26(2), pp. 252–255. Available at: <https://doi.org/10.1111/jeb.12004>.

Ruokolainen, L. and Hanski, I. (2016) 'Stable coexistence of ecologically identical species: Conspecific aggregation via reproductive interference', *Journal of Animal Ecology*, 85(3), pp. 638–647. Available at: <https://doi.org/10.1111/1365-2656.12490>.

Ryan, M.J. and Keddy-Hector, A. (1992) 'Directional Patterns of Female Mate Choice and the Role of Sensory Biases', *The American Naturalist*, 139, pp. S4–S35.

Ryan, M.J. and Rand, A.S. (1993) 'Species Recognition and Sexual Selection as a Unitary Problem in Animal Communication', *Evolution*, 47(2), pp. 647–657. Available at: <https://doi.org/10.1111/j.1558-5646.1993.tb02118.x>.

Ryan, M.J. and Wagner, W.E. (1987) 'Asymmetries in Mating Preferences between Species: Female Swordtails Prefer Heterospecific Males', *Science*, 236(4801), pp. 595–597.

Rybinski, J. et al. (2016) 'Competition-driven build-up of habitat isolation and selection favoring modified dispersal patterns in a young avian hybrid zone', *Evolution*, 70(10), pp. 2226–2238. Available at: <https://doi.org/10.1111/evo.13019>.

Sæther, B.-E. (1983) 'Mechanism of Interspecific Spacing out in a Territorial System of the Chiffchaff *Phylloscopus collybita* and the Willow Warbler *P. trochilus*', *Ornis Scandinavica* (Scandinavian Journal of Ornithology), 14(2), pp. 154–160. Available at: <https://doi.org/10.2307/3676020>.

Sasaki, Y. (2007) 'The truth of the F-measure', *Teach Tutor Mater* [Preprint].

Sauer, J.R., Link, W.A. and Hines, J.E. (2020) 'The North American Breeding Bird Survey, analysis results 1966 - 2019: U.S. Geological Survey data release'. Available at: <https://doi.org/10.5066/P96A7675>.

Schindelin, J. et al. (2012) 'Fiji: an open-source platform for biological-image analysis', *Nature Methods*, 9(7), pp. 676–682. Available at: <https://doi.org/10.1038/nmeth.2019>.

Schliep, E.M. et al. (2018) 'Joint species distribution modelling for spatio-temporal occurrence and ordinal abundance data', *Global Ecology and Biogeography*, 27(1), pp. 142–155. Available at: <https://doi.org/10.1111/geb.12666>.

Schoener, T.W. (1974) 'Resource Partitioning in Ecological Communities', *Science*, 185(4145), pp. 27–39. Available at: <https://doi.org/10.1126/science.185.4145.27>.

Schoener, T.W. (1983) 'Field Experiments on Interspecific Competition', *The American Naturalist*, 122(2), pp. 240–285.

Schwarz, D. et al. (2005) 'Host shift to an invasive plant triggers rapid animal hybrid speciation', *Nature*, 436(7050), pp. 546–549. Available at: <https://doi.org/10.1038/nature03800>.

Sebastián-González, E. et al. (2010) 'Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence', *Proceedings of the Royal Society B: Biological Sciences*, 277(1696), pp. 2983–2990. Available at: <https://doi.org/10.1098/rspb.2010.0244>.

Secondi, J. et al. (2003) 'Species-specific song convergence in a moving hybrid zone between two passerines', *Biological Journal of the Linnean Society*, 80(3), pp. 507–517. Available at: <https://doi.org/10.1046/j.1095-8312.2003.00248.x>.

Secondi, J., Faivre, B. and Kreuzer, M. (1999) 'Maintenance of male reaction to the congeneric song in the Hippolais warbler hybrid zone', *Behavioural Processes*, 46(2), pp. 151–158. Available at: [https://doi.org/10.1016/S0376-6357\(99\)00029-7](https://doi.org/10.1016/S0376-6357(99)00029-7).

Sekercioglu, C.H. et al. (2008) 'Climate Change, Elevational Range Shifts, and Bird Extinctions', *Conservation Biology*, 22(1), pp. 140–150. Available at: <https://doi.org/10.1111/j.1523-1739.2007.00852.x>.

Sexton, J.P. (2024) 'Abundance across geographical species ranges and the rare edge hypothesis', *Proceedings of the Royal Society B: Biological Sciences*, 291(2036), p. 20241874. Available at: <https://doi.org/10.1098/rspb.2024.1874>.

Sexton, J.P. et al. (2009) 'Evolution and Ecology of Species Range Limits', *Annual Review of Ecology, Evolution, and Systematics*, 40(1), pp. 415–436. Available at: <https://doi.org/10.1146/annurev.ecolsys.110308.120317>.

Shapiro, L.H. et al. (2004) 'Reciprocal Introgression between Golden-Winged Warblers (*Vermivora chrysoptera*) and Blue-Winged Warblers (*V. pinus*) in Eastern North America', *The Auk*, 121(4), pp. 1019–1030. Available at: <https://doi.org/10.2307/4090472>.

Sheard, C. et al. (2020) 'Ecological drivers of global gradients in avian dispersal inferred from wing morphology', *Nature Communications*, 11(1), p. 2463. Available at: <https://doi.org/10.1038/s41467-020-16313-6>.

Short, L.L. (1969) 'Taxonomic Aspects of Avian Hybridization', *The Auk*, 86(1), pp. 84–105. Available at: <https://doi.org/10.2307/4083543>.

Sidumo, B., Sonono, E. and Takaidza, I. (2022) 'An approach to multi-class imbalanced problem in ecology using machine learning', *Ecological Informatics*, 71, p. 101822. Available at: <https://doi.org/10.1016/j.ecoinf.2022.101822>.

Simberloff, D. (1996) 'Hybridization between native and introduced wildlife species: importance for conservation', *Wildlife Biology*, 2(3), pp. 143–150. Available at: <https://doi.org/10.2981/wlb.1996.012>.

Simpson, T.A., Blake, L.R. and Dorado, D. (2021) 'United States Register of Introduced and Invasive Species: U.S. Geological Survey data release'. Available at: <https://doi.org/10.5066/P95XL09Q>.

Sirén, A.P.K. and Morelli, T.L. (2020) 'Interactive range-limit theory (iRLT): An extension for predicting range shifts', *Journal of Animal Ecology*, 89(4), pp. 940–954.

Slagsvold, T. et al. (2002) 'Mate choice and imprinting in birds studied by cross-fostering in the wild', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1499), pp. 1449–1455. Available at: <https://doi.org/10.1098/rspb.2002.2045>.

Snell Taylor, S., Umbanhowar, J. and Hurlbert, A.H. (2020) 'The relative importance of biotic and abiotic determinants of temporal occupancy for avian species in North America', *Global Ecology and Biogeography*, 29(4), pp. 736–747. Available at: <https://doi.org/10.1111/geb.13064>.

Soberón, J. (2007) 'Grinnellian and Eltonian niches and geographic distributions of species', *Ecology Letters*, 10(12), pp. 1115–1123. Available at: <https://doi.org/10.1111/j.1461-0248.2007.01107.x>.

Soriano-Redondo, A. et al. (2023) 'Fitness, behavioral, and energetic trade-offs of different migratory strategies in a partially migratory species', *Ecology*, 104(10), p. e4151. Available at: <https://doi.org/10.1002/ecy.4151>.

Sorjonen, J. (1986) 'Mixed Singing and Interspecific Territoriality - Consequences of Secondary Contact of Two Ecologically and Morphologically Similar Nightingale Species

in Europe', *Ornis Scandinavica* (Scandinavian Journal of Ornithology), 17(1), pp. 53–67. Available at: <https://doi.org/10.2307/3676753>.

Sottas, C. et al. (2018) 'Interspecific competition promotes habitat and morphological divergence in a secondary contact zone between two hybridizing songbirds', *Journal of Evolutionary Biology*, 31(6), pp. 914–923. Available at: <https://doi.org/10.1111/jeb.13275>.

Souriau, A. et al. (2018) 'Can mixed singing facilitate coexistence of closely related nightingale species?', *Behavioral Ecology*, 29(4), pp. 925–932. Available at: <https://doi.org/10.1093/beheco/ary053>.

Stein, A.C. and Uy, J.A.C. (2006) 'Unidirectional Introgression of a Sexually Selected Trait Across an Avian Hybrid Zone: A Role for Female Choice?', *Evolution*, 60(7), pp. 1476–1485. Available at: <https://doi.org/10.1111/j.0014-3820.2006.tb01226.x>.

Stephens, K. et al. (2020) 'Occurrence and extent of hybridisation between the invasive Mallard Duck and native Yellow-billed Duck in South Africa', *Biological Invasions*, 22(2), pp. 693–707. Available at: <https://doi.org/10.1007/s10530-019-02122-6>.

Stephens, P.A. et al. (2016) 'Consistent response of bird populations to climate change on two continents', *Science*, 352(6281), pp. 84–87. Available at: <https://doi.org/10.1126/science.aac4858>.

Stevens, M. and Cuthill, I.C. (2006) 'Disruptive coloration, crypsis and edge detection in early visual processing', *Proceedings of the Royal Society B: Biological Sciences*, 273(1598), pp. 2141–2147. Available at: <https://doi.org/10.1098/rspb.2006.3556>.

Stewart, P.S. et al. (2022) 'Global impacts of climate change on avian functional diversity', *Ecology Letters*, 25(3), pp. 673–685. Available at: <https://doi.org/10.1111/ele.13830>.

Strimas-Mackey, M. et al. (2023) *ebirdst: Access and analyze eBird status and trends data products. manual*. Available at: <https://ebird.github.io/ebirdst/>.

Strydom, T. et al. (2022) 'Food web reconstruction through phylogenetic transfer of low-rank network representation', *Methods in Ecology and Evolution*, 13(12), pp. 2838–2849. Available at: <https://doi.org/10.1111/2041-210X.13835>.

Suggitt, A.J. et al. (2011) 'Habitat microclimates drive fine-scale variation in extreme temperatures', *Oikos*, 120(1), pp. 1–8. Available at: <https://doi.org/10.1111/j.1600-0706.2010.18270.x>.

Sullivan, B.K. (2010) 'Mate Recognition, Species Boundaries and the Fallacy of "Species Recognition"', *The Open Zoology Journal*, 2(1), pp. 86–90. Available at: <https://doi.org/10.2174/1874336600902010086>.

Sullivan, B.L. et al. (2009) 'eBird: A citizen-based bird observation network in the biological sciences', *Biological Conservation*, 142(10), pp. 2282–2292. Available at: <https://doi.org/10.1016/j.biocon.2009.05.006>.

Summers, R.W., Dawson, R.J.G. and Phillips, R.E. (2007) 'Assortative mating and patterns of inheritance indicate that the three crossbill taxa in Scotland are species', *Journal of Avian Biology*, 38(2), pp. 153–162. Available at: <https://doi.org/10.1111/j.2007.0908-8857.03798.x>.

Svenning, J.-C. and Skov, F. (2004) 'Limited filling of the potential range in European tree species', *Ecology Letters*, 7(7), pp. 565–573. Available at: <https://doi.org/10.1111/j.1461-0248.2004.00614.x>.

Svenning, J.-C. et al. (2014) 'The influence of interspecific interactions on species range expansion rates', *Ecography*, 37(12), pp. 1198–1209. Available at: <https://doi.org/10.1111/j.1600-0587.2013.00574.x>.

Svenning, J.C. et al. (2014) 'The influence of interspecific interactions on species range expansion rates', *Ecography*, 37(12), pp. 1198–1209. Available at: <https://doi.org/10.1111/j.1600-0587.2013.00574.x>.

Svensson, S.E. (1978) 'Territorial Exclusion of *Acrocephalus schoenobaenus* by *A. scirpaceus* in Reedbeds', *Oikos*, 30(3), pp. 467–474. Available at: <https://doi.org/10.2307/3543342>.

Tarasov, V.V. (2024) 'Changes in the Fauna and Distribution of Birds of the Forest-Steppe Trans-Urals in the Late 20th to Early 21st Centuries Under the Influence of Natural and Anthropogenic Factors', *Russian Journal of Ecology*, 55(6), pp. 599–613. Available at: <https://doi.org/10.1134/S1067413624603610>.

Taylor, S.A. et al. (2014) 'Climate-Mediated Movement of an Avian Hybrid Zone', *Current Biology*, 24(6), pp. 671–676. Available at: <https://doi.org/10.1016/j.cub.2014.01.069>.

Taylor, Scott A. et al. (2014) 'Climate-Mediated Movement of an Avian Hybrid Zone', *Current Biology*, 24(6), pp. 671–676. Available at: <https://doi.org/10.1016/j.cub.2014.01.069>.

Ten Cate, C. and Vos, D.R. (1999) 'Sexual Imprinting and Evolutionary Processes in Birds: A Reassessment', in *Advances in the Study of Behavior*. Elsevier, pp. 1–31. Available at: [https://doi.org/10.1016/S0065-3454\(08\)60214-4](https://doi.org/10.1016/S0065-3454(08)60214-4).

Terborgh, J. and Weske, J.S. (1975) 'The role of competition in the distribution of Andean birds', *Ecology*, 56(3), pp. 562–576.

Thomas, C.D. and Lennon, J.J. (1999) 'Birds extend their range northward', *Nature*, 399(May), p. 213.

Thomas, C.D. and Lennon, J.J. (1999) 'Birds extend their ranges northwards', *Nature*, 399(6733), pp. 213–213. Available at: <https://doi.org/10.1038/20335>.

Thomas, C.D. et al. (2004) 'Extinction risk from climate change', *Nature*, 427(6970), pp. 145–148. Available at: <https://doi.org/10.1038/nature02121>.

Thomson, R.L., Forsman, J.T. and Mönkkönen, M. (2003) 'Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis', *Oecologia*, 134(3), pp. 431–438. Available at: <https://doi.org/10.1007/s00442-002-1140-0>.

Thörn, F. et al. (2024) 'Contemporary intergeneric hybridization and backcrossing among birds-of-paradise', *Evolution Letters*, 8(5), pp. 680–694. Available at: <https://doi.org/10.1093/evlett/qrae023>.

Thorson, J.T. et al. (2016) 'Joint dynamic species distribution models: a tool for community ordination and spatio-temporal monitoring', *Global Ecology and Biogeography*, 25(9), pp. 1144–1158. Available at: <https://doi.org/10.1111/geb.12464>.

Tikhonov, G. et al. (2017) 'Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context', *Methods in Ecology and Evolution*, 8(4), pp. 443–452. Available at: <https://doi.org/10.1111/2041-210X.12723>.

Tikhonov, G. et al. (2020) 'Joint species distribution modelling with the r-package Hmsc', *Methods in Ecology and Evolution*, 11(3), pp. 442–447. Available at: <https://doi.org/10.1111/2041-210X.13345>.

Tinbergen, N. (1951) *The study of instinct*. Clarendon Press/Oxford University Press.

Tingley, M.W. and Beissinger, S.R. (2013) 'Cryptic loss of montane avian richness and high community turnover over 100 years', *Ecology*, 94(3), pp. 598–609. Available at: <https://doi.org/10.1890/12-0928.1>.

Titley, M.A. et al. (2021) 'Global inequities and political borders challenge nature conservation under climate change', *Proceedings of the National Academy of Sciences*, 118(7), p. e2011204118. Available at: <https://doi.org/10.1073/pnas.2011204118>.

Tobias, J.A. and Seddon, N. (2009) 'Signal design and perception in hypocoenemid antbirds: Evidence for convergent evolution via social selection', *Evolution*, 63(12), pp. 3168–3189. Available at: <https://doi.org/10.1111/j.1558-5646.2009.00795.x>.

Tobias, J.A. et al. (2014) 'Species coexistence and the dynamics of phenotypic evolution in adaptive radiation', *Nature*, 506(7488), pp. 359–363. Available at: <https://doi.org/10.1038/nature12874>.

Tobias, J.A. et al. (2016) 'Territoriality, social bonds, and the evolution of communal signaling in birds', *Frontiers in Ecology and Evolution*, 4(JUN). Available at: <https://doi.org/10.3389/fevo.2016.00074>.

Tobias, J.A. et al. (2022) 'AVONET: morphological, ecological and geographical data for all birds', *Ecology Letters*, 25(3), pp. 581–597. Available at: <https://doi.org/10.1111/ele.13898>.

Todesco, M. et al. (2016) 'Hybridization and extinction', *Evolutionary Applications*, 9(7), pp. 892–908. Available at: <https://doi.org/10.1111/eva.12367>.

Toews, D.P.L. (2017) 'Habitat suitability and the constraints of migration in New World warblers', *Journal of Avian Biology*, 48(12), pp. 1614–1623. Available at: <https://doi.org/10.1111/jav.01157>.

Toews, D.P.L. et al. (2020) 'Genomic identification of intergeneric hybrids in New World wood-warblers (Aves: Parulidae)', *Biological Journal of the Linnean Society*, 131(1), pp. 183–191. Available at: <https://doi.org/10.1093/biolinnean/blaa085>.

Toews, D.P.L. et al. (2022) 'Genetic confirmation of a hybrid between two highly divergent cardinalid species: A rose-breasted grosbeak (*Pheucticus ludovicianus*) and a scarlet tanager (*Piranga olivacea*)', *Ecology and Evolution*, 12(8), p. e9152. Available at: <https://doi.org/10.1002/ece3.9152>.

Tsuchida, K. et al. (2019) 'Reproductive Interference in an Introduced Bumblebee: Polyandry may Mitigate Negative Reproductive Impact', *Insects*, 10(2), p. 59. Available at: <https://doi.org/10.3390/insects10020059>.

Tubaro, P.L. and Lijtmaer, D.A. (2002) 'Hybridization patterns and the evolution of reproductive isolation in ducks', *Biological Journal of the Linnean Society*, 77(2), pp. 193–200. Available at: <https://doi.org/10.1046/j.1095-8312.2002.00096.x>.

Ulrich, W. et al. (2018) 'Environmentally and behaviourally mediated co-occurrence of functional traits in bird communities of tropical forest fragments', *Oikos*, 127(2), pp. 274–284. Available at: <https://doi.org/10.1111/oik.04561>.

Vallé, C. et al. (2024) 'Species associations in joint species distribution models: from missing variables to conditional predictions', *Journal of Biogeography*, 51(2), pp. 311–324. Available at: <https://doi.org/10.1111/jbi.14752>.

Vallin, N. and Qvarnström, A. (2011) 'Learning the hard way: Imprinting can enhance enforced shifts in habitat choice', *International Journal of Ecology*, 2011, p. 287532. Available at: <https://doi.org/10.1155/2011/287532>.

Vallin, N. and Qvarnström, A. (2011) 'Learning the Hard Way: Imprinting Can Enhance Enforced Shifts in Habitat Choice', *International Journal of Ecology*, 2011(1), p. 287532. Available at: <https://doi.org/10.1155/2011/287532>.

Vallin, N. et al. (2012) 'Combined effects of interspecific competition and hybridization impede local coexistence of *Ficedula* flycatchers', *Evolutionary Ecology*, 26(4), pp. 927–942. Available at: <https://doi.org/10.1007/s10682-011-9536-0>.

van Dongen, W.F.D. et al. (2013) 'Behavioural and genetic interactions between an endangered and a recently-arrived hummingbird', *Biological Invasions*, 15(5), pp. 1155–1168. Available at: <https://doi.org/10.1007/s10530-012-0358-y>.

van Lanen, N.J. et al. (2011) 'Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls', *Biological Conservation*, 144, pp. 2194–2201. Available at: <https://doi.org/10.1016/j.biocon.2011.05.011>.

Van Lanen, N.J. et al. (2011) 'Who hits and hoots at whom? Potential for interference competition between barred and northern spotted owls', *Biological Conservation*, 144(9), pp. 2194–2201. Available at: <https://doi.org/10.1016/j.biocon.2011.05.011>.

VanDerWal, J. et al. (2013) 'Focus on poleward shifts in species' distribution underestimates the fingerprint of climate change', *Nature Climate Change*, 3(3), pp. 239–243. Available at: <https://doi.org/10.1038/nclimate1688>.

Veen, T. et al. (2001) 'Hybridization and adaptive mate choice in flycatchers', *Nature*, 411(6833), pp. 45–50. Available at: <https://doi.org/10.1038/35075000>.

Vickers, A.J. and Altman, D.G. (2001) 'Analysing controlled trials with baseline and follow up measurements', *BMJ*, 323(7321), pp. 1123–1124. Available at: <https://doi.org/10.1136/bmj.323.7321.1123>.

Violle, C. et al. (2011) 'Phylogenetic limiting similarity and competitive exclusion', *Ecology Letters*, 14(8), pp. 782–787. Available at: <https://doi.org/10.1111/j.1461-0248.2011.01644.x>.

Volterra, V. (1926) 'Fluctuations in the Abundance of a Species considered Mathematically', *Nature*, 118(2972), pp. 558–560. Available at: <https://doi.org/10.1038/118558a0>.

vonHoldt, B.M. et al. (2016) 'Whole-genome sequence analysis shows that two endemic species of North American wolf are admixtures of the coyote and gray wolf', *Science Advances*, 2(7), p. e1501714. Available at: <https://doi.org/10.1126/sciadv.1501714>.

Wallace, A.R. (1876) *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*. Cambridge: Cambridge University Press (Cambridge Library Collection - Zoology). Available at: <https://doi.org/10.1017/CBO9781139097116>.

Wallis, G. (1999) Genetic status of New Zealand black stilt (*Himantopus novaezelandiae*) and impact of hybridisation. 239. Wellington: Department of Conservation.

Walsh, J. et al. (2023) 'A complex genomic architecture underlies reproductive isolation in a North American oriole hybrid zone', *Communications Biology*, 6(1), pp. 1–11. Available at: <https://doi.org/10.1038/s42003-023-04532-8>.

Wardhani, N.W.S. et al. (2019) 'Cross-validation Metrics for Evaluating Classification Performance on Imbalanced Data', in 2019 International Conference on Computer, Control, Informatics and its Applications (IC3INA). 2019 International Conference on Computer, Control, Informatics and its Applications (IC3INA), pp. 14–18. Available at: <https://doi.org/10.1109/IC3INA48034.2019.8949568>.

Warton, D.I. et al. (2015) 'So Many Variables: Joint Modeling in Community Ecology', *Trends in Ecology and Evolution*, 30(12), pp. 766–779. Available at: <https://doi.org/10.1016/j.tree.2015.09.007>.

Webb, S.D. (2006) 'The Great American Biotic Interchange: Patterns and Processes', *Annals of the Missouri Botanical Garden*, 93(2), pp. 245–257.

Weber, M.G. et al. (2017) 'Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution', *Trends in Ecology and Evolution*, 32(4), pp. 291–304. Available at: <https://doi.org/10.1016/j.tree.2017.01.003>.

Weir, J.T. and Price, T.D. (2011a) 'Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient', *American Naturalist*, 177(4), pp. 462–469. Available at: <https://doi.org/10.1086/658910>.

Weir, J.T. and Price, T.D. (2011b) 'Limits to Speciation Inferred from Times to Secondary Sympatry and Ages of Hybridizing Species along a Latitudinal Gradient.', *The American Naturalist*, 177(4), pp. 462–469. Available at: <https://doi.org/10.1086/658910>.

Weir, J.T., Bermingham, E. and Schluter, D. (2009) 'The Great American Biotic Interchange in birds', *Proceedings of the National Academy of Sciences of the United States of America*, 106(51), pp. 21737–21742. Available at: <https://doi.org/10.1073/pnas.0903811106>.

Wells, C.P. et al. (2019) 'Persistence of an endangered native duck, feral mallards, and multiple hybrid swarms across the main Hawaiian Islands', *Molecular Ecology*, 28(24), pp. 5203–5216. Available at: <https://doi.org/10.1111/mec.15286>.

Whittaker, R.H. (1975) *Communities and ecosystems*. 2nd edn. New York: Macmillan.

Whitton, J., Sears, C.J. and Maddison, W.P. (2017) 'Co-occurrence of related asexual, but not sexual, lineages suggests that reproductive interference limits coexistence', *Proceedings of the Royal Society B: Biological Sciences*, 284, p. 20171579. Available at: <https://doi.org/10.1098/rspb.2017.1579>.

Wiens, J.D., Anthony, R.G. and Forsman, E.D. (2014) 'Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon', *Wildlife Monographs*, 185, pp. 1–50. Available at: <https://doi.org/10.1002/wmon.1009>.

Wiens, J.D., Anthony, R.G. and Forsman, E.D. (2014) 'Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon', *Wildlife Monographs*, 185(1), pp. 1–50. Available at: <https://doi.org/10.1002/wmon.1009>.

Wiens, J.J. and Graham, C.H. (2005) 'Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology', *Annual Review of Ecology, Evolution, and Systematics*, 36, pp. 519–539.

Wiley, C. et al. (2007) 'Direct benefits and costs for hybridizing *Ficedula* flycatchers', *Journal of Evolutionary Biology*, 20(3), pp. 854–864. Available at: <https://doi.org/10.1111/j.1420-9101.2007.01316.x>.

Wilkinson, D.P. et al. (2021) 'Defining and evaluating predictions of joint species distribution models', *Methods in Ecology and Evolution*, 12(3), pp. 394–404. Available at: <https://doi.org/10.1111/2041-210X.13518>.

Willis, P.M. (2013) 'Why do animals hybridize?', *Acta Ethologica*, 16(3), pp. 127–134. Available at: <https://doi.org/10.1007/s10211-013-0144-6>.

Willis, P.M., Symula, R.E. and Lovette, I.J. (2014) 'Ecology, song similarity and phylogeny predict natural hybridization in an avian family', *Evolutionary Ecology*, 28(2), pp. 299–322. Available at: <https://doi.org/10.1007/s10682-013-9677-4>.

Wirtz, P. (1999) 'Mother species–father species: unidirectional hybridization in animals with female choice', *Animal Behaviour*, 58(1), pp. 1–12. Available at: <https://doi.org/10.1006/anbe.1999.1144>.

Wisz, M.S. et al. (2013) 'The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling',

Biological Reviews, 88(1), pp. 15–30. Available at: <https://doi.org/10.1111/j.1469-185X.2012.00235.x>.

Wolf, D.E., Takebayashi, N. and Rieseberg, L.H. (2001) 'Predicting the Risk of Extinction through Hybridization', *Conservation Biology*, 15(4), pp. 1039–1053. Available at: <https://doi.org/10.1046/j.1523-1739.2001.0150041039.x>.

Woodward, F.I. and Williams, B.G. (1987) 'Climate and plant distribution at global and local scales', *Vegetatio*, 69(1), pp. 189–197. Available at: <https://doi.org/10.1007/BF00038700>.

Worm, A.J. et al. (2019) 'Characterizing patterns of introgressive hybridization between two species of *Tyrannus* following concurrent range expansion', *Ibis*, 161(4), pp. 770–780. Available at: <https://doi.org/10.1111/ibi.12674>.

Zhang, D.-Y. and Hanski, I. (1998) 'Sexual Reproduction and Stable Coexistence of Identical Competitors', *Journal of Theoretical Biology*, 193(3), pp. 465–473. Available at: <https://doi.org/10.1006/jtbi.1998.0712>.

Ziv, Y. and Kotler, B.P. (2003) 'Giving-up densities of foraging gerbils: The effect of interspecific competition on patch use', *Evolutionary Ecology*, 17(4), pp. 333–347. Available at: <https://doi.org/10.1023/A:1027385100393>.

Zuckerberg, B., Woods, A.M. and Porter, W.F. (2009) 'Poleward shifts in breeding bird distributions in New York State', *Global Change Biology*, 15(8), pp. 1866–1883. Available at: <https://doi.org/10.1111/j.1365-2486.2009.01878.x>.

Zurell, D., Pollock, L.J. and Thuiller, W. (2018) 'Do joint species distribution models reliably detect interspecific interactions from co-occurrence data in homogenous environments?', *Ecography*, 41(11), pp. 1812–1819. Available at: <https://doi.org/10.1111/ecog.03315>.

APPENDIX

Appendix A: Chapter 2

Acoustic parameters used in a principal component analysis in order to calculate vocalisation dissimilarity, and their transformations.

Acoustic Parameters	Name	Transformation
Duration	duration	$\log(x + 0.001)$
Mean frequency	meanfreq	Untransformed
Standard deviation of frequency	sd	$\log(x + 0.001)$
Median frequency	freq.median	Untransformed
First quartile frequency	freq.Q25	Untransformed
Third quartile frequency	freq.Q75	sqrt
Frequency interquartile range	freq.IQR	sqrt
Median time (time at which the signal is divided in twotime intervals of equal energy)	time.median	$\log(x + 0.001)$
First quartile time	time.Q25	$\log(x + 0.001)$
Third quartile time	time.Q75	$\log(x + 0.001)$
Time interquartile range	time.IQR	$\log(x + 0.001)$
Spectral skewness	skew	$\log(x + 0.001)$
Spectral kurtosis (peakedness)	kurt	$\log(x + 0.001)$
Spectral entropy (energy distribution of the frequency spectrum)	sp.ent	Untransformed
Time entropy (energy distribution on the time envelope)	time.ent	Untransformed
Product of time and spectral entropy	entropy	Untransformed
Spectral flatness	sfm	$\log(x + 0.001)$
Mean peak frequency	meanpeakf	Untransformed
Average dominant frequency	meandom	Untransformed
Maximum of dominant frequency	maxdom	Untransformed
Minimum dominant frequency	mindom	Untransformed
Range of dominant frequency measured across the acoustic signal	dfrange	Untransformed
Modulation index	modindx	$\log(x + 0.001)$
Dominant frequency measurement at the start of the signal	startdom	sqrt
Dominant frequency measurement at the end of the signal	enddom	sqrt
Slope of the change in dominant frequency through time	dfslope	Untransformed
Number of notes	note.count	$\log(x + 0.001)$
Note rate	note.rate	$\log(x + 0.001)$
Length of longest note	longest.note	$\log(x + 0.001)$

Percentage of the song consisting of notes	note.perc	Untransformed
Average note length	ave.note.length	$\log(x + 0.001)$
Total note duration	total.note.dur	$\log(x + 0.001)$
Average pause length	ave.pause.length	$\log(x + 0.001)$
Length of longest pause	longest.pause	$\log(x + 0.001)$

Recording credits for audio files of European species downloaded from Xeno canto (XC) and the Macaulay Library (ML).

Species	File	Recordist	Species	File	Recordist
<i>Acanthis flammea</i>	XC216985	Janne Bruun	<i>Gulosus aristotelis</i>	XC914590	Aku Kalliomäki
<i>Acanthis flammea</i>	XC687649	Niels Van Doninck	<i>Gypaetus barbatus</i>	XC144936	Fernand Deroussen
<i>Acanthis flammea</i>	XC710795	Lars Edenius	<i>Gypaetus barbatus</i>	XC569323	Stanislas Wroza
<i>Acanthis flammea</i>	XC712649	Lars Edenius	<i>Gyps fulvus</i>	XC423956	Stanislas Wroza
<i>Accipiter gentilis</i>	XC756188	brickejickel	<i>Gyps fulvus</i>	XC542056	Pere Josa
<i>Accipiter gentilis</i>	XC817762	Lars Edenius	<i>Gyps fulvus</i>	XC653855	Eduardo Realinho
<i>Accipiter nisus</i>	XC665236	Eetu Paljakka	<i>Gyps fulvus</i>	XC915617	Sven Normant
<i>Accipiter nisus</i>	XC744165	Romuald Mikusek	<i>Haematopus ostralegus</i>	XC831730	W. Agster
<i>Acrocephalus arundinaceus</i>	XC811727	Ulf Elman	<i>Haematopus ostralegus</i>	XC942096	Arjun Dutta
<i>Acrocephalus arundinaceus</i>	XC813097	Lukas Thiess	<i>Haliaeetus albicilla</i>	XC619160	Stein Ø. Nilsen
<i>Acrocephalus arundinaceus</i>	XC813205	Peter Boesman	<i>Haliaeetus albicilla</i>	XC745843	Lars Edenius
<i>Acrocephalus arundinaceus</i>	XC815947	Guy Kirwan	<i>Hieraaetus pennatus</i>	XC430828	Joost van Bruggen
<i>Acrocephalus dumetorum</i>	XC811764	Dag Österlund	<i>Hieraaetus pennatus</i>	XC668479	Eduardo Realinho
<i>Acrocephalus dumetorum</i>	XC813038	Marcus Fransson	<i>Himantopus himantopus</i>	XC828544	BirdingAlbufera
<i>Acrocephalus dumetorum</i>	XC814045	Anders Westman	<i>Himantopus himantopus</i>	XC905801	Albert Lastukhin
<i>Acrocephalus dumetorum</i>	XC842258	Ulf Elman	<i>Hippolais icterina</i>	XC659733	Bodo Sonnenburg
<i>Acrocephalus melanopogon</i>	XC793095	Stanislas Wroza	<i>Hippolais icterina</i>	XC750858	Ulf Elman
<i>Acrocephalus melanopogon</i>	XC872907	Thierry Thomas	<i>Hippolais icterina</i>	XC800661	Stanislas Wroza
<i>Acrocephalus melanopogon</i>	XC879400	Manuel Oudard	<i>Hippolais icterina</i>	XC815416	Thomas Bergman
<i>Acrocephalus melanopogon</i>	XC891244	Bernard Bousquet	<i>Hippolais polyglotta</i>	XC560575	Jorge Leitão
<i>Acrocephalus paludicola</i>	XC480838	Dries Van de Loock	<i>Hippolais polyglotta</i>	XC560590	Jorge Leitão
<i>Acrocephalus paludicola</i>	XC561499	Jarek Matusiak	<i>Hippolais polyglotta</i>	XC909833	Jacobo Ramil Millarengo
<i>Acrocephalus paludicola</i>	XC688954	Romuald Mikusek	<i>Hippolais polyglotta</i>	XC910101	Olivier Swift, Hélène Cartaud
<i>Acrocephalus paludicola</i>	XC692253	Romuald Mikusek	<i>Hirundo rustica</i>	XC823733	Francesco Sottile
<i>Acrocephalus palustris</i>	XC862700	Mats Rellmar	<i>Hirundo rustica</i>	XC877300	João Tomás
<i>Acrocephalus palustris</i>	XC871930	Mauro Fioretto	<i>Hirundo rustica</i>	XC903563	Stanislas Wroza
<i>Acrocephalus palustris</i>	XC883779	Johan Roeland	<i>Hirundo rustica</i>	XC910186	Uku Paal
<i>Acrocephalus palustris</i>	XC892416	Alain Malengreau	<i>Iduna opaca</i>	XC414658	Stanislas Wroza
<i>Acrocephalus schoenobaenus</i>	XC870841	Alain Malengreau	<i>Iduna opaca</i>	XC414663	Stanislas Wroza
<i>Acrocephalus schoenobaenus</i>	XC871701	Alain Malengreau	<i>Iduna opaca</i>	XC467771	Thijs Fijen
<i>Acrocephalus schoenobaenus</i>	XC884922	Olivier Swift	<i>Iduna opaca</i>	XC798474	Azens
<i>Acrocephalus schoenobaenus</i>	XC895063	Martin Billard	<i>Ixobrychus minutus</i>	XC656126	Lorenzo Maffezzoli
<i>Acrocephalus scirpaceus</i>	XC862813	Olivier Swift	<i>Ixobrychus minutus</i>	XC836679	Esperanza Poveda
<i>Acrocephalus scirpaceus</i>	XC863306	Chèvremont Fabian	<i>Jynx torquilla</i>	XC769997	Michel Veldt
<i>Acrocephalus scirpaceus</i>	XC897725	Lee Alder	<i>Jynx torquilla</i>	XC902613	Ulf Elman
<i>Acrocephalus scirpaceus</i>	XC901326	Susanne Kuijpers	<i>Lagopus lagopus</i>	XC591861	Simon Elliott
<i>Actitis hypoleucos</i>	XC815419	Thomas Bergman	<i>Lagopus lagopus</i>	XC652923	Thomas Bergman
<i>Actitis hypoleucos</i>	XC824403	Romuald Mikusek	<i>Lagopus lagopus</i>	XC798642	Uku Paal
<i>Actitis hypoleucos</i>	XC834283	Paolo Zucca	<i>Lagopus lagopus</i>	XC900335	Uku Paal
<i>Actitis hypoleucos</i>	XC861917	Peter Stronach	<i>Lagopus muta</i>	XC26647	Patrik Åberg
<i>Aegithalos caudatus</i>	XC645359	Regina Eidner	<i>Lagopus muta</i>	XC340677	Tero Linjama
<i>Aegithalos caudatus</i>	XC707059	Shamgar Brook	<i>Lagopus muta</i>	XC420429	Stein Ø. Nilsen
<i>Aegolius funereus</i>	XC708202	Thomas Bergman	<i>Lagopus muta</i>	XC835510	Petter Westberg
<i>Aegolius funereus</i>	XC837555	Romuald Mikusek	<i>Lanius collurio</i>	XC560390	Stanislas Wroza
<i>Aegypius monachus</i>	XC144935	Fernand Deroussen	<i>Lanius collurio</i>	XC700280	Dominique Guillerme
<i>Aegypius monachus</i>	XC915625	Sven Normant	<i>Lanius collurio</i>	XC731753	Marc Anderson
<i>Aix galericulata</i>	XC389998	Jarek Matusiak	<i>Lanius collurio</i>	XC803339	Lars Edenius
<i>Aix galericulata</i>	XC389999	Jarek Matusiak	<i>Lanius excubitor</i>	XC649962	Johan Södercrantz
<i>Aix sponsa</i>	XC509715	Sunny Tseng	<i>Lanius excubitor</i>	XC712619	Lars Edenius
<i>Aix sponsa</i>	XC63109	Jonathon Jongsma	<i>Lanius excubitor</i>	XC838997	Leander Khil
<i>Alauda arvensis</i>	XC890349	Olivier Swift	<i>Lanius excubitor</i>	XC855983	Mats Rellmar
<i>Alauda arvensis</i>	XC893507	Krzysztof Deoniziak	<i>Lanius meridionalis</i>	XC150493	Paulo Alves
<i>Alauda arvensis</i>	XC895628	Agris Celmins	<i>Lanius meridionalis</i>	XC727014	Magnus Wadstein
<i>Alauda arvensis</i>	XC896982	Martin Billard	<i>Lanius meridionalis</i>	XC767941	Stanislas Wroza
<i>Alauda rufescens</i>	XC730308	Stanislas Wroza	<i>Lanius meridionalis</i>	XC795282	Étienne Leroy
<i>Alauda rufescens</i>	XC730310	Stanislas Wroza	<i>Lanius minor</i>	XC295984	Marco Dragonetti
<i>Alauda rufescens</i>	XC730383	Stanislas Wroza	<i>Lanius minor</i>	XC342809	Lars Buckx
<i>Alauda rufescens</i>	XC756693	SonoNatura	<i>Lanius minor</i>	XC813442	Peter Boesman
<i>Alcedo atthis</i>	XC845635	Johannes Dag Mayer	<i>Lanius minor</i>	XC904703	David Darrell-Lambert
<i>Alcedo atthis</i>	XC936832	Johannes Dag Mayer	<i>Lanius senator</i>	XC561941	François Grimal
<i>Alectoris barbara</i>	ML71168	Arnoud B. van den Berg	<i>Lanius senator</i>	XC722557	SonoNatura
<i>Alectoris barbara</i>	XC134392	Fernand Deroussen	<i>Lanius senator</i>	XC754423	Stein Ø. Nilsen
<i>Alectoris barbara</i>	XC347457	Tero Linjama	<i>Lanius senator</i>	XC797821	Xavier Riera
<i>Alectoris barbara</i>	XC901725	Andrew Harrop	<i>Leiothrix lutea</i>	ML14175	William V. Ward
<i>Alectoris graeca</i>	XC182904	Manuel Schweizer	<i>Leiothrix lutea</i>	ML44556814	1
<i>Alectoris graeca</i>	XC247001	Jerome Fischer	<i>Leiothrix lutea</i>	ML58019494	1
<i>Alectoris graeca</i>	XC416855	Jerome Fischer	<i>Leiothrix lutea</i>	ML60022459	1
<i>Alectoris graeca</i>	XC730580	Stanislas Wroza	<i>Limosa lapponica</i>	XC654136	Lars Edenius
<i>Alectoris rufa</i>	XC265614	david m	<i>Limosa lapponica</i>	XC807724	Thomas Bergman
<i>Alectoris rufa</i>	XC334156	Jordi Calvet	<i>Limosa lapponica</i>	XC913545	Thomas Bergman
<i>Alectoris rufa</i>	XC372530	Stanislas Wroza	<i>Limosa lapponica</i>	XC915090	Thomas Bergman
<i>Alectoris rufa</i>	XC794515	Stuart Fisher	<i>Limosa limosa</i>	XC722732	Lars Edenius
<i>Alopochen aegyptiaca</i>	XC546108	Albert Noorlander	<i>Limosa limosa</i>	XC740254	Uku Paal
<i>Alopochen aegyptiaca</i>	XC620525	Francesco Sottile	<i>Limosa limosa</i>	XC740270	Uku Paal
<i>Amandava amandava</i>	XC545983	Peter Ericsson	<i>Limosa limosa</i>	XC818972	Azens
<i>Amandava amandava</i>	XC552807	Bram Piot	<i>Linaria cannabina</i>	XC802274	Thomas Bergman
<i>Amandava amandava</i>	XC824847	He Wenjin	<i>Linaria cannabina</i>	XC876858	João Tomás
<i>Amandava amandava</i>	XC840610	Bram Piot	<i>Linaria cannabina</i>	XC899180	Paul Kelly
<i>Anas acuta</i>	XC712335	Jack Berteau	<i>Linaria cannabina</i>	XC906691	Olivier Swift
<i>Anas acuta</i>	XC721976	Lars Edenius	<i>Linaria flavirostris</i>	XC364664	Elias A. Ryberg
<i>Anas crecca</i>	XC668192	Ireneusz Oleksik	<i>Linaria flavirostris</i>	XC470797	Dries Van de Loock
<i>Anas crecca</i>	XC732343	Marc Anderson	<i>Linaria flavirostris</i>	XC638923	Lars Edenius
<i>Anas platyrhynchos</i>	XC755991	Romuald Mikusek	<i>Linaria flavirostris</i>	XC638934	Lars Edenius
<i>Anas platyrhynchos</i>	XC774431	Irish Wildlife Sounds	<i>Locustella fluviatilis</i>	XC861724	András Schmidt
<i>Anser albifrons</i>	XC644998	Joost van Bruggen	<i>Locustella fluviatilis</i>	XC908882	Erik Söderman
<i>Anser albifrons</i>	XC698271	András Schmidt	<i>Locustella luscinioides</i>	XC740299	Uku Paal
<i>Anser albifrons</i>	XC712047	Joost van Bruggen	<i>Locustella luscinioides</i>	XC813023	Lukas Thiess
<i>Anser albifrons</i>	XC878146	Lars Mogensen	<i>Locustella naevia</i>	XC900840	Martin Billard
<i>Anser anser</i>	XC792700	Lars Edenius	<i>Locustella naevia</i>	XC900843	Martin Billard

<i>Anser anser</i>	XC803358	Lars Edenius	<i>Lophophanes cristatus</i>	XC780340	Lars Edenius
<i>Anser anser</i>	XC896889	Lars Edenius	<i>Lophophanes cristatus</i>	XC790414	Lars Edenius
<i>Anser anser</i>	XC914627	Lennart Jeppsson	<i>Lophophanes cristatus</i>	XC804854	Uku Paal
<i>Anser brachyrhynchus</i>	XC521246	Ireneusz Oleksik	<i>Lophophanes cristatus</i>	XC896344	Jacobo Ramil Millarengo
<i>Anser brachyrhynchus</i>	XC601551	Will Scott	<i>Loxia curvirostra</i>	XC831945	Lars Edenius
<i>Anser canagicus</i>	XC185372	Andrew Spencer	<i>Loxia curvirostra</i>	XC837909	Lars Edenius
<i>Anser canagicus</i>	XC486631	Jens Kirkeby	<i>Loxia curvirostra</i>	XC864185	Andr�as Schmidt
<i>Anser cygnoides</i>	XC635985	Simon Kies�	<i>Loxia curvirostra</i>	XC901928	Lars Edenius
<i>Anser cygnoides</i>	XC765912	Stanislas Wroza	<i>Loxia leucoptera</i>	XC338457	Piotr Szczypinski
<i>Anser fabalis</i>	XC109681	Jelmer Poelstra	<i>Loxia leucoptera</i>	XC484760	Teet Sirotkin
<i>Anser fabalis</i>	XC676859	Thomas Bergman	<i>Loxia leucoptera</i>	XC602666	Christopher McPherson
<i>Anser indicus</i>	XC526948	James Lidster	<i>Loxia leucoptera</i>	XC89151	Patrik �berg
<i>Anser indicus</i>	XC635939	David Darrell-Lambert	<i>Loxia pytyopsittacus</i>	XC403068	Hans Matheve
<i>Anthus berthelotii</i>	XC134391	Fernand Deroussen	<i>Loxia pytyopsittacus</i>	XC829642	Lars Edenius
<i>Anthus berthelotii</i>	XC374980	Peter Boesman	<i>Loxia pytyopsittacus</i>	XC893254	Lars Edenius
<i>Anthus berthelotii</i>	XC764548	Stein �. Nilsen	<i>Loxia pytyopsittacus</i>	XC900834	Johan Forssell
<i>Anthus berthelotii</i>	XC782278	Rub�n Barone	<i>Loxia scotica</i>	XC544934	Peter Stronach
<i>Anthus campestris</i>	XC801392	Manceau Lionel	<i>Loxia scotica</i>	XC715938	Andrew Harrop
<i>Anthus campestris</i>	XC813237	Peter Boesman	<i>Loxia scotica</i>	XC892394	Peter Stronach
<i>Anthus campestris</i>	XC839904	Corentin Riviere	<i>Loxia scotica</i>	XC906960	Peter Stronach
<i>Anthus campestris</i>	XC897500	Tero Linjama	<i>Lullula arborea</i>	XC712592	Joost van Bruggen
<i>Anthus cervinus</i>	XC139099	Fernand Deroussen	<i>Lullula arborea</i>	XC722492	Lars Edenius
<i>Anthus cervinus</i>	XC345769	Tero Linjama	<i>Lullula arborea</i>	XC723523	Olivier Swift, Sylvain REYT
<i>Anthus cervinus</i>	XC382130	Jens Kirkeby	<i>Lullula arborea</i>	XC852698	Rob van Bemmelen
<i>Anthus cervinus</i>	XC424100	Terje Kolaas	<i>Luscinia luscinia</i>	XC654939	maxander
<i>Anthus petrosus</i>	XC146046	Julien Rochefort	<i>Luscinia luscinia</i>	XC727140	Lennart Jeppsson
<i>Anthus petrosus</i>	XC263958	Terje Kolaas	<i>Luscinia luscinia</i>	XC803654	Johannes Sander
<i>Anthus petrosus</i>	XC610047	Lars Edenius	<i>Luscinia luscinia</i>	XC903880	Jocce Ekstrom
<i>Anthus petrosus</i>	XC667502	Irish Wildlife Sounds	<i>Luscinia megarhynchos</i>	XC803656	Johannes Sander
<i>Anthus pratensis</i>	XC779776	Erik Normark	<i>Luscinia megarhynchos</i>	XC901015	Grzegorz Lorek
<i>Anthus pratensis</i>	XC831852	Agris Celmins	<i>Luscinia megarhynchos</i>	XC908425	Leconte Michel
<i>Anthus pratensis</i>	XC831853	Agris Celmins	<i>Luscinia megarhynchos</i>	XC909501	Mats Rellmar
<i>Anthus pratensis</i>	XC857639	Beatrix Saadi-Varchmin	<i>Luscinia svecica</i>	XC707296	Antonio Keira
<i>Anthus spinoletta</i>	XC716570	Xavier Riera	<i>Luscinia svecica</i>	XC731887	SonoNatura
<i>Anthus spinoletta</i>	XC730538	Stanislas Wroza	<i>Luscinia svecica</i>	XC884116	Maarten Stuijter
<i>Anthus spinoletta</i>	XC734861	Magnus Hellstr�m	<i>Luscinia svecica</i>	XC899983	J�rgen Pisch
<i>Anthus spinoletta</i>	XC839878	Romu�ld Mikusek	<i>Lymnocyptes minimus</i>	XC723297	Lars Edenius
<i>Anthus trivialis</i>	XC855476	Jack Berteau	<i>Lymnocyptes minimus</i>	XC799634	Lars Edenius
<i>Anthus trivialis</i>	XC879350	Stein �. Nilsen	<i>Lyrurus tetrix</i>	XC711208	Baltasar Pinheiro
<i>Anthus trivialis</i>	XC895016	Christian Kerihuel	<i>Lyrurus tetrix</i>	XC758859	Lars Edenius
<i>Anthus trivialis</i>	XC897400	Jacobo Ramil Millarengo	<i>Lyrurus tetrix</i>	XC758861	Lars Edenius
<i>Apus apus</i>	XC810578	Susanne Kuijpers	<i>Lyrurus tetrix</i>	XC805524	Lars Edenius
<i>Apus apus</i>	XC817637	Jo�o Tom�s	<i>Mareca penelope</i>	XC767302	Irish Wildlife Sounds
<i>Apus caffer</i>	ML5989	Myles E. W. North	<i>Mareca penelope</i>	XC882155	David Darrell-Lambert
<i>Apus caffer</i>	XC677525	Esperanza Poveda	<i>Mareca strepera</i>	XC679027	Beatrix Saadi-Varchmin
<i>Apus pallidus</i>	XC557421	Jorge Leit�o	<i>Mareca strepera</i>	XC871361	Paul Kelly
<i>Apus pallidus</i>	XC763779	Guillaume Bigayon	<i>Marmaronetta angustirostris</i>	XC780493	Santiago Caballero Carrera
<i>Apus unicolor</i>	XC164524	Antero Lindholm	<i>Marmaronetta angustirostris</i>	XC784480	Santiago Caballero Carrera
<i>Apus unicolor</i>	XC657346	Paulo Alves	<i>Melanitta fusca</i>	XC448663	Patrik �berg
<i>Aquila adalberti</i>	XC148645	Patrik �berg	<i>Melanitta fusca</i>	XC817948	Alan Dalton
<i>Aquila adalberti</i>	XC420390	Jos� Carlos Sires	<i>Melanitta nigra</i>	XC902773	David thorns
<i>Aquila adalberti</i>	XC699619	SonoNatura	<i>Melanitta nigra</i>	XC915469	Thomas Bergman
<i>Aquila adalberti</i>	XC864217	SonoNatura	<i>Melanocorypha calandra</i>	XC510598	Marco Dragonetti
<i>Aquila chrysaetos</i>	XC341722	Tero Linjama	<i>Melanocorypha calandra</i>	XC730261	Stanislas Wroza
<i>Aquila chrysaetos</i>	XC453324	Lars Edenius	<i>Melanocorypha calandra</i>	XC730301	Stanislas Wroza
<i>Aquila chrysaetos</i>	XC753803	Lars Edenius	<i>Melanocorypha calandra</i>	XC880726	Luis Gracia
<i>Aquila chrysaetos</i>	XC820295	Hans Norelius	<i>Mergellus albellus</i>	XC563997	Lars Edenius
<i>Aquila fasciata</i>	ML41189752 1	Fast As Falcon	<i>Mergellus albellus</i>	XC610927	Lars Edenius
<i>Aquila fasciata</i>	XC781530	Peter Boesman	<i>Mergus merganser</i>	XC644424	Lars Edenius
<i>Aquila heliaca</i>	XC582823	Jarek Matusiak	<i>Mergus merganser</i>	XC759927	Simon Elliott
<i>Aquila heliaca</i>	XC731082	brickegickel	<i>Mergus serrator</i>	XC607514	Peter Stronach
<i>Ardea alba</i>	XC615283	Stanislas Wroza	<i>Mergus serrator</i>	XC762330	Simon Elliott
<i>Ardea alba</i>	XC681080	Uku Paal	<i>Merops apiaster</i>	XC824573	Grzegorz Lorek
<i>Ardea alba</i>	XC738072	Marcin Sotowiej	<i>Merops apiaster</i>	XC900856	Jo�o Tom�s
<i>Ardea alba</i>	XC776170	Irish Wildlife Sounds	<i>Microcarbo pygmaeus</i>	XC168146	Andre et Odile Boucher
<i>Ardea cinerea</i>	XC857972	Martin Billard	<i>Microcarbo pygmaeus</i>	XC296075	Marco Dragonetti
<i>Ardea cinerea</i>	XC881881	Esperanza Poveda	<i>Milvus migrans</i>	XC796153	Beatrix Saadi-Varchmin
<i>Ardea cinerea</i>	XC882189	Christian Vemmelund	<i>Milvus migrans</i>	XC899786	Jorge Leit�o
<i>Ardea cinerea</i>	XC897660	Helligs�	<i>Milvus milvus</i>	XC829695	Olivier Swift
<i>Ardea cinerea</i>	ML56828166 1	Paul Kelly	<i>Milvus milvus</i>	XC879195	Olivier Swift
<i>Ardea purpurea</i>	XC485377	Anonymous	<i>Milvus milvus</i>	XC296005	Marco Dragonetti
<i>Ardea purpurea</i>	XC903478	Joost van Bruggen	<i>Monticola saxatilis</i>	XC649771	Jordi Calvet
<i>Ardea purpurea</i>	XC903564	Stanislas Wroza	<i>Monticola saxatilis</i>	XC730219	Stanislas Wroza
<i>Ardeola ralloides</i>	XC577793	Stanislas Wroza	<i>Monticola saxatilis</i>	XC833863	Martin Billard
<i>Ardeola ralloides</i>	XC836622	Cedric Mroczko	<i>Monticola solitarius</i>	XC265241	Michele Vigan�
<i>Arenaria interpres</i>	XC815489	Esperanza Poveda	<i>Monticola solitarius</i>	XC417708	Stanislas Wroza
<i>Arenaria interpres</i>	XC815490	Sonoth�que ADVL	<i>Monticola solitarius</i>	XC811595	Francesco Sottile
<i>Arenaria interpres</i>	XC827973	Sonoth�que ADVL	<i>Monticola solitarius</i>	XC99691	Jordi Calvet
<i>Arenaria interpres</i>	XC895259	Jorge Leit�o	<i>Montifringilla nivalis</i>	XC141184	Fernand Deroussen
<i>Asio flammeus</i>	XC718743	Francisco Sottile	<i>Montifringilla nivalis</i>	XC186477	Michele Peron
<i>Asio flammeus</i>	XC731000	Lars Edenius	<i>Montifringilla nivalis</i>	XC355444	maudoc
<i>Asio otus</i>	XC793292	Lars Edenius	<i>Montifringilla nivalis</i>	XC486810	Audevard Aur�rien
<i>Asio otus</i>	XC793294	Dominique Guillaume	<i>Motacilla alba</i>	XC598489	Tanguy Lo�s
<i>Athene noctua</i>	XC883232	Dominique Guillaume	<i>Motacilla alba</i>	XC656706	Uku Paal
<i>Athene noctua</i>	XC891838	Anthony Roux	<i>Motacilla alba</i>	XC656713	Uku Paal
<i>Athene noctua</i>	XC908597	Andr�as Schmidt	<i>Motacilla alba</i>	XC722531	Jens Kirkeby
<i>Athene noctua</i>	XC915445	Martin Billard	<i>Motacilla alba</i>	XC682324	Jacobo Ramil Millarengo
<i>Aythya ferina</i>	XC769846	Esperanza Poveda	<i>Motacilla cinerea</i>	XC757193	Lars Lachmann
<i>Aythya ferina</i>	XC797060	Dominique Guillaume	<i>Motacilla cinerea</i>	XC797916	brickegickel
<i>Aythya fuligula</i>	XC644316	Alan Dalton	<i>Motacilla cinerea</i>	XC904381	Cedric Mroczko
		Lars Edenius	<i>Motacilla cinerea</i>		

<i>Aythya fuligula</i>	XC644396	Lars Edenius	<i>Motacilla flava</i>	XC745680	Lars Edenius
<i>Aythya marila</i>	ML137835	Gerrit Vyn	<i>Motacilla flava</i>	XC793956	Jacobo Ramil Millarengo
<i>Aythya marila</i>	ML44410428 1	Reid Hildebrandt	<i>Motacilla flava</i>	XC838987	Regina Eidner
<i>Aythya nyroca</i>	XC296088	Marco Dragonetti	<i>Motacilla flava</i>	XC881967	Olivier Swift
<i>Aythya nyroca</i>	XC528021	Jan Daniels-Trautner	<i>Muscicapa striata</i>	XC598245	Niels Van Doninck
<i>Bombycilla garrulus</i>	XC597940	Lars Edenius	<i>Muscicapa striata</i>	XC727741	Paolo Zucca
<i>Bombycilla garrulus</i>	XC861580	Peter Stronach	<i>Muscicapa striata</i>	XC780925	Bas
<i>Botaurus stellaris</i>	XC465220	Gregorio Para	<i>Muscicapa striata</i>	XC877767	Maarten Sluijter
<i>Botaurus stellaris</i>	XC720112	Manuel Grosselet	<i>Myiopsitta monachus</i>	XC622769	jesus carrion
<i>Branta canadensis</i>	XC646159	Lars Edenius	<i>Myiopsitta monachus</i>	XC669961	Manuel Grosselet
<i>Branta canadensis</i>	XC715941	Agris Celmins	<i>Myiopsitta monachus</i>	XC678007	Guilherme Renzo Rocha Brito
<i>Branta canadensis</i>	XC787100	Susanne Kuijpers	<i>Myiopsitta monachus</i>	XC682586	Manuel Grosselet
<i>Branta canadensis</i>	XC909895	Uku Paal	<i>Neophron percnopterus</i>	XC650774	Eduardo Realinho
<i>Branta hutchinsii</i>	ML135491	William W. H. Gunn	<i>Neophron percnopterus</i>	XC654205	Eduardo Realinho
<i>Branta hutchinsii</i>	ML20392886 1	Josep del Hoyo	<i>Netta rufina</i>	XC404318	Pascal Christie
<i>Branta hutchinsii</i>	XC361080	Paul Marvin	<i>Netta rufina</i>	XC407509	Francesco Sottile
<i>Branta hutchinsii</i>	XC838299	Seth Beaudreault (Toolik Field Station)	<i>Netta rufina</i>	XC644652	Audevard Aurélien
<i>Branta leucopsis</i>	XC549292	Lars Edenius	<i>Netta rufina</i>	XC769720	Michel Veldt
<i>Branta leucopsis</i>	XC724651	Uku Paal	<i>Nucifraga caryocatactes</i>	XC736823	Lars Edenius
<i>Branta leucopsis</i>	XC763873	Uku Paal	<i>Nucifraga caryocatactes</i>	XC818171	Lars Edenius
<i>Branta leucopsis</i>	XC903305	Lars Edenius	<i>Nucifraga caryocatactes</i>	XC843797	Richard Brahmstaedt
<i>Bubo bubo</i>	XC836565	Thierry Thomas	<i>Nucifraga caryocatactes</i>	XC906816	Frode Falkenberg
<i>Bubo bubo</i>	XC896167	Bram Vogels	<i>Numenius arquata</i>	XC830500	Lars Edenius
<i>Bubo scandiacus</i>	XC343144	Tero Linjama	<i>Numenius arquata</i>	XC832849	Agris Celmins
<i>Bubo scandiacus</i>	XC343145	Tero Linjama	<i>Numenius phaeopus</i>	XC735243	Lars Edenius
<i>Bubulcus ibis</i>	XC356329	Marco Dragonetti	<i>Numenius phaeopus</i>	XC741684	Lars Edenius
<i>Bubulcus ibis</i>	XC495869	Joost van Bruggen	<i>Numenius phaeopus</i>	XC799611	Niels Van Doninck
<i>Bubulcus ibis</i>	XC766666	Marco Dragonetti	<i>Numenius phaeopus</i>	XC801501	Olivier Swift
<i>Bubulcus ibis</i>	XC831486	Jordi Calvet	<i>Numida meleagris</i>	XC280506	Peter Boesman
<i>Bucanetes githagineus</i>	XC164199	Tero Linjama	<i>Numida meleagris</i>	XC507927	Tim Cockcroft
<i>Bucanetes githagineus</i>	XC855968	Mats Rellmar	<i>Nycticorax nycticorax</i>	XC903475	Stanislas Wroza
<i>Bucephala clangula</i>	XC234677	dmitry yakubovich	<i>Nycticorax nycticorax</i>	XC921344	Sébastien Arriubergé
<i>Bucephala clangula</i>	XC641760	Lars Edenius	<i>Oenanthe hispanica</i>	XC343294	Agostinho Tomás
<i>Burhinus oedicnemus</i>	XC896992	Martin Billard	<i>Oenanthe hispanica</i>	XC416420	Jordi Calvet
<i>Burhinus oedicnemus</i>	XC914574	Thierry Thomas	<i>Oenanthe hispanica</i>	XC730459	Stanislas Wroza
<i>Burhinus oedicnemus</i>	XC923183	Jordi Calvet	<i>Oenanthe hispanica</i>	XC794843	João Tomás
<i>Burhinus oedicnemus</i>	XC934316	Peter Ertl	<i>Oenanthe leucura</i>	XC538884	Xavier Riera
<i>Buteo buteo</i>	XC878780	João Tomás	<i>Oenanthe leucura</i>	XC692725	Santiago Caballero Carrera
<i>Buteo buteo</i>	XC895030	Martin Billard	<i>Oenanthe leucura</i>	XC730407	Stanislas Wroza
<i>Buteo lagopus</i>	XC665960	Lars Edenius	<i>Oenanthe leucura</i>	XC840125	Pere Jose
<i>Buteo lagopus</i>	XC747268	Lars Edenius	<i>Oenanthe oenanthe</i>	XC759707	Ulf Elman
<i>Cairina moschata</i>	ML92424851	Paul Marvin	<i>Oenanthe oenanthe</i>	XC769226	Michel Veldt
<i>Cairina moschata</i>	ML92475411	Paul Marvin	<i>Oenanthe oenanthe</i>	XC769227	Michel Veldt
<i>Calandrella brachydactyla</i>	XC806185	Pere Jose	<i>Oenanthe oenanthe</i>	XC898202	Jochem verweij
<i>Calandrella brachydactyla</i>	XC813260	Peter Boesman	<i>Oriolus oriolus</i>	XC708637	Agris Celmins
<i>Calandrella brachydactyla</i>	XC813265	Peter Boesman	<i>Oriolus oriolus</i>	XC739166	Grzegorz Lorek
<i>Calandrella brachydactyla</i>	XC839296	Corentin Rivière	<i>Oriolus oriolus</i>	XC743901	Romuald Mikusek
<i>Calcarius lapponicus</i>	XC567566	Lars Edenius	<i>Oriolus oriolus</i>	XC809026	Bodo Sonnenburg
<i>Calcarius lapponicus</i>	XC580134	Niels Van Doninck	<i>Otis tarda</i>	XC721833	Lars Lachmann
<i>Calcarius lapponicus</i>	XC639055	Peter Stronach	<i>Otis tarda</i>	XC721834	Lars Lachmann
<i>Calcarius lapponicus</i>	XC688953	Lars Edenius	<i>Otus scops</i>	XC905326	Christian Kerihuel
<i>Calidris alpina</i>	XC739138	Uku Paal	<i>Otus scops</i>	XC910434	Antoine Salmon
<i>Calidris alpina</i>	XC833015	Michaël Bridoux	<i>Oxyura jamaicensis</i>	XC591765	Simon Elliott
<i>Calidris alpina</i>	XC852842	Rob van Bemmelen	<i>Oxyura jamaicensis</i>	XC603727	Peter Ward and Ken Hall
<i>Calidris alpina</i>	XC908418	Lars Edenius	<i>Oxyura leucocephala</i>	XC132436	Fernand Deroussen
<i>Calidris falcinellus</i>	XC654231	Lars Edenius	<i>Oxyura leucocephala</i>	XC462959	Geoffrey Monchaux
<i>Calidris falcinellus</i>	XC911575	Niclas Backstrom	<i>Pandion haliaetus</i>	XC826075	Olli Juhnke
<i>Calidris maritima</i>	XC186400	Stein Ø. Nilsen	<i>Pandion haliaetus</i>	XC924318	Lars Edenius
<i>Calidris maritima</i>	XC321244	Tim de Boer	<i>Panurus biarmicus</i>	XC955702	Jarek Matusiak
<i>Calidris maritima</i>	XC322089	Rob van Bemmelen	<i>Panurus biarmicus</i>	XC955703	Jarek Matusiak
<i>Calidris maritima</i>	XC423507	Johan Råghall	<i>Parus major</i>	XC881427	Michel Veldt
<i>Calidris minuta</i>	XC383563	Terje Kolaas	<i>Parus major</i>	XC899545	Beatrix Saadi-Varchmin
<i>Calidris minuta</i>	XC383564	Terje Kolaas	<i>Parus major</i>	XC899637	Lennart Jeppsson
<i>Calidris pugnax</i>	XC765283	Stanislas Wroza	<i>Parus major</i>	XC902756	Olivier Swift
<i>Calidris pugnax</i>	XC852294	Jordi Calvet	<i>Passer domesticus</i>	XC879927	Paul Kelly
<i>Calidris temminckii</i>	XC765454	Stanislas Wroza	<i>Passer domesticus</i>	XC881740	Olivier Swift
<i>Calidris temminckii</i>	XC809521	Frode Falkenberg	<i>Passer domesticus</i>	XC896493	Martin Billard
<i>Caprimulgus europaeus</i>	XC809979	Olivier Swift	<i>Passer domesticus</i>	XC899351	Jack Berteau
<i>Caprimulgus europaeus</i>	XC957127	Jarek Matusiak	<i>Passer hispaniolensis</i>	XC309787	Cedric Mroczko
<i>Caprimulgus ruficollis</i>	XC724307	Antonio Xeira	<i>Passer hispaniolensis</i>	XC334279	Yoann Blanchon
<i>Caprimulgus ruficollis</i>	XC905834	SonoNatura	<i>Passer hispaniolensis</i>	XC905912	João Tomás
<i>Carduelis carduelis</i>	XC854554	David Pennington	<i>Passer hispaniolensis</i>	XC913059	Stephan Risch
<i>Carduelis carduelis</i>	XC883327	João Tomás	<i>Passer italiae</i>	XC727597	Francesco Sottile
<i>Carduelis carduelis</i>	XC884098	Christian Kerihuel	<i>Passer italiae</i>	XC906612	Frederic Lionel
<i>Carduelis carduelis</i>	XC894563	Jorge Leitão	<i>Passer italiae</i>	XC906614	Frederic Lionel
<i>Carduelis citrinella</i>	XC246416	Jordi Calvet	<i>Passer italiae</i>	XC907069	Mats Rellmar
<i>Carduelis citrinella</i>	XC315443	Jerome Fischer	<i>Passer montanus</i>	XC800953	Daniele Baroni
<i>Carduelis citrinella</i>	XC372554	Jerome Fischer	<i>Passer montanus</i>	XC813881	Susanne Kuijpers
<i>Carduelis citrinella</i>	XC730229	Stanislas Wroza	<i>Passer montanus</i>	XC814643	Uku Paal
<i>Carduelis corsicana</i>	XC349876	Tero Linjama	<i>Passer montanus</i>	XC815513	Susanne Kuijpers
<i>Carduelis corsicana</i>	XC624722	Charlie Bodin	<i>Pavo cristatus</i>	XC812476	Francesco Barberini
<i>Carduelis corsicana</i>	XC662052	Marta Celej	<i>Pavo cristatus</i>	XC902565	Kalle Nibbenhagen
<i>Carduelis corsicana</i>	XC662053	Marta Celej	<i>Perdix perdix</i>	XC651353	Uku Paal
<i>Carpodacus erythrinus</i>	XC743414	Romuald Mikusek	<i>Perdix perdix</i>	XC897003	Martin Billard
<i>Carpodacus erythrinus</i>	XC863138	Mats Rellmar	<i>Periparus ater</i>	XC891510	Frederic Lionel
<i>Carpodacus erythrinus</i>	XC904579	Lars Edenius	<i>Periparus ater</i>	XC902395	Thomas Bergman
<i>Carpodacus erythrinus</i>	XC912797	Hans Matheve	<i>Periparus ater</i>	XC904730	Jorge Leitão
<i>Cecropis daurica</i>	XC485355	Lars Lachmann	<i>Periparus ater</i>	XC910374	Johan Södercrantz
<i>Cecropis daurica</i>	XC723730	Geoff Carey	<i>Perisoreus infaustus</i>	XC611732	Lars Edenius
<i>Cercotrichas galactotes</i>	XC670255	Jonathan Bryant	<i>Perisoreus infaustus</i>	XC652996	Thomas Bergman
<i>Cercotrichas galactotes</i>	XC692573	Santiago Caballero Carrera	<i>Perisoreus infaustus</i>	XC680829	Lars Edenius
<i>Cercotrichas galactotes</i>	XC831603	Esperanza Poveda	<i>Perisoreus infaustus</i>	XC751019	Lars Edenius

<i>Cercotrichas galactotes</i>	XC831605	Esperanza Poveda	<i>Pernis apivorus</i>	XC329631	Kaspars Funts
<i>Certhia brachydactyla</i>	XC899288	David Pennington	<i>Pernis apivorus</i>	XC666557	P. Venema
<i>Certhia brachydactyla</i>	XC901386	Jorge Leitão	<i>Pernis apivorus</i>	XC668502	Sophie Neill
<i>Certhia brachydactyla</i>	XC901387	Jorge Leitão	<i>Pernis apivorus</i>	XC826297	Lars Edenius
<i>Certhia brachydactyla</i>	XC905013	Olivier Swift	<i>Petronia petronia</i>	XC651365	Marta Celej
<i>Certhia familiaris</i>	XC808139	Lars Edenius	<i>Petronia petronia</i>	XC692717	Santiago Caballero Carrera
<i>Certhia familiaris</i>	XC878886	Baltasar Pinheiro	<i>Petronia petronia</i>	XC783481	Jacobo Ramil Millarengo
<i>Certhia familiaris</i>	XC893809	Azens	<i>Petronia petronia</i>	XC783482	Jacobo Ramil Millarengo
<i>Certhia familiaris</i>	XC904077	Corentin Rivière	<i>Phalacrocorax carbo</i>	XC646784	Agris Celmins
<i>Cettia cetti</i>	XC907063	Mats Rellmar	<i>Phalacrocorax carbo</i>	XC737064	Irish Wildlife Sounds
<i>Cettia cetti</i>	XC963920	Jack Berteau	<i>Phalacrocorax carbo</i>	XC776010	Paul Kelly
<i>Cettia cetti</i>	XC964596	Friedrich Richard	<i>Phalacrocorax carbo</i>	XC841971	Jorge Leitão
<i>Cettia cetti</i>	XC965043	Jack Berteau	<i>Phalaropus lobatus</i>	XC342920	Tero Linjama
<i>Charadrius alexandrinus</i>	XC338266	José Carlos Sires	<i>Phalaropus lobatus</i>	XC420149	Stein Ø. Nilsen
<i>Charadrius alexandrinus</i>	XC817932	Sonothèque ADVL	<i>Phalaropus lobatus</i>	XC487653	Stanislas Wroza
<i>Charadrius dubius</i>	XC813186	Lars Edenius	<i>Phalaropus lobatus</i>	XC514049	Timo Janhonen
<i>Charadrius dubius</i>	XC815926	Albert Lastukhin	<i>Phasianus colchicus</i>	XC640749	Tanguy Lois
<i>Charadrius hiaticula</i>	XC653537	Elias A. Ryberg	<i>Phasianus colchicus</i>	XC929867	Bram Piot
<i>Charadrius hiaticula</i>	XC653595	Elias A. Ryberg	<i>Phoenicopterus roseus</i>	XC267542	Andrew Spencer
<i>Charadrius morinellus</i>	XC440167	Stein Ø. Nilsen	<i>Phoenicopterus roseus</i>	XC899996	Paul Coiffard
<i>Charadrius morinellus</i>	XC570939	Lars Edenius	<i>Phoenicurus ochruros</i>	XC832033	Francisco Molinero
<i>Chersophilus duponti</i>	XC216990	Cristian Pérez-Granados	<i>Phoenicurus ochruros</i>	XC844168	Frederic Lionel
<i>Chersophilus duponti</i>	XC235394	Luis Gracia	<i>Phoenicurus ochruros</i>	XC857226	Grzegorz Lorek
<i>Chersophilus duponti</i>	XC315238	Jarmo Pirhonen	<i>Phoenicurus ochruros</i>	XC898801	Nicolas Martinez
<i>Chersophilus duponti</i>	XC536806	Sean Ronayne	<i>Phoenicurus phoenicurus</i>	XC899515	Lars Mogensen
<i>Chloris chloris</i>	XC814746	Martin Billard	<i>Phoenicurus phoenicurus</i>	XC911881	Antonio Xeira
<i>Chloris chloris</i>	XC834605	Esperanza Poveda	<i>Phoenicurus phoenicurus</i>	XC913428	Martin Billard
<i>Chloris chloris</i>	XC879027	João Tomás	<i>Phoenicurus phoenicurus</i>	XC913449	Thomas Bergman
<i>Chloris chloris</i>	XC898912	Nicolas Martinez	<i>Phylloscopus bonelli</i>	XC769307	Michel Veldt
<i>Chrysolophus amherstiae</i>	XC473878	Albert Lastukhin	<i>Phylloscopus bonelli</i>	XC799404	João Tomás
<i>Chrysolophus amherstiae</i>	XC916157	Peter Boesman	<i>Phylloscopus bonelli</i>	XC819672	Jacobo Ramil Millarengo
<i>Chrysolophus pictus</i>	XC375400	David Farrow	<i>Phylloscopus bonelli</i>	XC892813	Frederic Lionel
<i>Chrysolophus pictus</i>	XC908427	Xingyu Li	<i>Phylloscopus borealis</i>	XC401786	Karl-Birger Strann
<i>Ciconia ciconia</i>	XC878180	Мітла Андрій Володимирович	<i>Phylloscopus borealis</i>	XC652032	Lukas Pelikan
<i>Ciconia ciconia</i>	XC878788	João Tomás	<i>Phylloscopus borealis</i>	XC785236	Teet Sirotkin
<i>Ciconia nigra</i>	XC795530	Sven Normant	<i>Phylloscopus borealis</i>	XC896729	Zbigniew Kajzer
<i>Ciconia nigra</i>	XC96963	Edmunds Racinskis	<i>Phylloscopus canariensis</i>	XC626845	Olivier Swift, Ludvine Delamare
<i>Cinclus cinclus</i>	XC687370	Lars Edenius	<i>Phylloscopus canariensis</i>	XC934197	Jose
<i>Cinclus cinclus</i>	XC700209	Stanislas Wroza	<i>Phylloscopus collybita</i>	XC879588	Susanne Kuijpers
<i>Cinclus cinclus</i>	XC700213	Stanislas Wroza	<i>Phylloscopus collybita</i>	XC900042	Thomas Bergman
<i>Cinclus cinclus</i>	XC883370	Teet Sirotkin	<i>Phylloscopus collybita</i>	XC904320	Martin Billard
<i>Circaetus gallicus</i>	XC40049	Doug Knapp	<i>Phylloscopus collybita</i>	XC908343	Olivier Swift, Hélène Cartaud
<i>Circaetus gallicus</i>	XC587198	Eduardo Realinho	<i>Phylloscopus ibericus</i>	XC794962	Jacobo Ramil Millarengo
<i>Circus aeruginosus</i>	XC859056	João Tomás	<i>Phylloscopus ibericus</i>	XC894453	Pere Josa
<i>Circus aeruginosus</i>	XC884134	João Tomás	<i>Phylloscopus ibericus</i>	XC896346	Jacobo Ramil Millarengo
<i>Circus cyaneus</i>	XC341267	Tero Linjama	<i>Phylloscopus ibericus</i>	XC909268	Pere Josa
<i>Circus cyaneus</i>	XC670733	Stanislas Wroza	<i>Phylloscopus sibilatrix</i>	XC729301	Bastian Forkel
<i>Circus macrourus</i>	XC471461	Stanislas Wroza	<i>Phylloscopus sibilatrix</i>	XC769998	Michel Veldt
<i>Circus macrourus</i>	XC643655	Hans Matheve	<i>Phylloscopus sibilatrix</i>	XC840441	Rob van Bemmelén
<i>Circus pygargus</i>	XC433734	José Carlos Sires	<i>Phylloscopus sibilatrix</i>	XC911177	W. Agster
<i>Circus pygargus</i>	XC573274	Jarek Matusiak	<i>Phylloscopus trochiloides</i>	XC802971	Jens Kirkeby
<i>Cisticola juncidis</i>	XC930481	Esperanza Poveda	<i>Phylloscopus trochiloides</i>	XC810536	Romuald Mikusek
<i>Cisticola juncidis</i>	XC962299	Hans Matheve	<i>Phylloscopus trochiloides</i>	XC813612	Peter Boesman
<i>Clamator glandarius</i>	XC708536	Sergi Carreras	<i>Phylloscopus trochiloides</i>	XC913921	Lars Edenius
<i>Clamator glandarius</i>	XC724315	Alexander Schlatmann	<i>Phylloscopus trochilus</i>	XC801762	Lars Edenius
<i>Clamator glandarius</i>	XC877435	João Tomás	<i>Phylloscopus trochilus</i>	XC855110	David Pennington
<i>Clamator glandarius</i>	XC877437	João Tomás	<i>Phylloscopus trochilus</i>	XC905213	Azens
<i>Clanga pomarina</i>	XC329332	Łukasz Bednarz	<i>Phylloscopus trochilus</i>	XC913109	Thomas Bergman
<i>Clanga pomarina</i>	XC563265	Zbigniew Kajzer	<i>Pica pica</i>	XC862133	Olivier Swift, Manuel Grosset
<i>Clangula hyemalis</i>	XC106033	Ryan P. O'Donnell	<i>Pica pica</i>	XC872510	Paul Kelly
<i>Clangula hyemalis</i>	XC203477	Andrew Spencer	<i>Pica pica</i>	XC879895	Susanne Kuijpers
<i>Clangula hyemalis</i>	XC514046	Timo Janhonen	<i>Pica pica</i>	XC897040	Stawomir Karpicki
<i>Clangula hyemalis</i>	XC820344	Johan Willner	<i>Picoides tridactylus</i>	XC715987	Thomas Bergman
<i>Coccothraustes</i>	XC626792	brickegickel	<i>Picoides tridactylus</i>	XC738886	Thomas Bergman
<i>Coccothraustes</i>	XC707043	Lars Edenius	<i>Picus canus</i>	XC878809	András Schmidt
<i>Coccothraustes</i>	XC710720	Török Tamás	<i>Picus canus</i>	XC882147	Lars Edenius
<i>Coccothraustes</i>	XC712663	Alan Dalton	<i>Picus viridis</i>	XC882026	Jean Pierre Sciolla
<i>Colinus virginianus</i>	XC138625	Paul Marvin	<i>Picus viridis</i>	XC927450	Martin Billard
<i>Colinus virginianus</i>	XC567479	Dare Šere	<i>Pinicola enucleator</i>	XC684582	Lars Edenius
<i>Coloeus monedula</i>	XC856321	Thierry Thomas	<i>Pinicola enucleator</i>	XC778268	Lars Edenius
<i>Coloeus monedula</i>	XC904574	Martin Billard	<i>Pinicola enucleator</i>	XC895559	Maarten Sluijter
<i>Columba bollii</i>	XC270048	Peter Boesman	<i>Pinicola enucleator</i>	XC895942	Maarten Sluijter
<i>Columba bollii</i>	XC530191	Mats Rellmar	<i>Platalea leucorodia</i>	XC596491	Tristan Guillobet de Nerville
<i>Columba livia</i>	XC270097	Timo Schnabel	<i>Platalea leucorodia</i>	XC768150	Stanislas Wroza
<i>Columba livia</i>	XC922264	Herman van der Meer	<i>Plectrophenax nivalis</i>	XC350489	Tero Linjama
<i>Columba oenas</i>	XC738668	Simon Elliott	<i>Plectrophenax nivalis</i>	XC379430	Stein Ø. Nilsen
<i>Columba oenas</i>	XC747109	Simon Elliott	<i>Plectrophenax nivalis</i>	XC425901	Terje Kolaas
<i>Columba palumbus</i>	XC915274	Susanne Kuijpers	<i>Plectrophenax nivalis</i>	XC425902	Terje Kolaas
<i>Columba palumbus</i>	XC920599	Lars Edenius	<i>Plegadis falcinellus</i>	XC530553	Jordi Calvet
<i>Coracias garrulus</i>	XC661132	Camille Monnet	<i>Plegadis falcinellus</i>	XC890702	Bernard Bousquet
<i>Coracias garrulus</i>	XC770236	Michel Veldt	<i>Pluvialis apricaria</i>	XC745635	Lars Edenius
<i>Corvus corax</i>	XC791383	Marcin Urbański	<i>Pluvialis apricaria</i>	XC789865	Simon Elliott
<i>Corvus corax</i>	XC800465	Nicolas Martinez	<i>Pluvialis apricaria</i>	XC818974	Azens
<i>Corvus corax</i>	XC880900	Lars Edenius	<i>Pluvialis apricaria</i>	XC831715	W. Agster
<i>Corvus corax</i>	XC880911	Lars Edenius	<i>Podiceps auritus</i>	XC375396	Stein Ø. Nilsen
<i>Corvus corone</i>	XC815510	Susanne Kuijpers	<i>Podiceps auritus</i>	XC715920	Alan Dalton
<i>Corvus corone</i>	XC856556	Martin Billard	<i>Podiceps cristatus</i>	XC130588	maudoc
<i>Corvus corone</i>	XC878485	Anthony Roux	<i>Podiceps cristatus</i>	XC773246	Bernard Bousquet
<i>Corvus corone</i>	XC893406	Pere Josa	<i>Podiceps cristatus</i>	XC790749	Stanislas Wroza

<i>Corvus frugilegus</i>	XC770891	Michel Veldt	<i>Podiceps cristatus</i>	XC801357	Chèvremont Fabian
<i>Corvus frugilegus</i>	XC780915	Jorge Leitão	<i>Podiceps grisegena</i>	XC26934	Patrik Åberg
<i>Corvus frugilegus</i>	XC783382	Stuart Fisher	<i>Podiceps grisegena</i>	XC804818	Uku Paat
<i>Corvus frugilegus</i>	XC883859	Alain Malengreau	<i>Podiceps nigricollis</i>	XC26932	Patrik Åberg
<i>Corvus splendens</i>	XC254340	az dipu	<i>Podiceps nigricollis</i>	XC590654	Simon Elliott
<i>Corvus splendens</i>	XC322403	Thomas Lüthi	<i>Poecile cinctus</i>	XC401785	Karl-Birger Strann
<i>Corvus splendens</i>	XC357593	Oscar Campbell	<i>Poecile cinctus</i>	XC750044	Lars Edenius
<i>Corvus splendens</i>	XC446886	Audevard Aurélien	<i>Poecile cinctus</i>	XC752844	Lars Edenius
<i>Coturnix coturnix</i>	XC915429	Lars Edenius	<i>Poecile cinctus</i>	XC807539	Thomas Bergman
<i>Coturnix coturnix</i>	XC915737	Joost van Bruggen	<i>Poecile montanus</i>	XC818372	Thomas Bergman
<i>Crex crex</i>	XC803640	Frode Falkenberg	<i>Poecile montanus</i>	XC880573	Bodo Sonnenburg
<i>Crex crex</i>	XC918715	Dag Österlund	<i>Poecile montanus</i>	XC896685	Zbigniew Kajzer
<i>Cuculus canorus</i>	XC710111	Alain Malengreau	<i>Poecile montanus</i>	XC896794	Lars Edenius
<i>Cuculus canorus</i>	XC917958	Arjun Dutta	<i>Poecile palustris</i>	XC864410	Bodo Sonnenburg
<i>Curruca balearica</i>	XC410968	Jerome Fischer	<i>Poecile palustris</i>	XC864410	Bodo Sonnenburg
<i>Curruca balearica</i>	XC411039	Jerome Fischer	<i>Poecile palustris</i>	XC893807	Azens
<i>Curruca balearica</i>	XC411067	Jerome Fischer	<i>Poecile palustris</i>	XC913905	Elias A. Ryberg
<i>Curruca balearica</i>	XC411330	Jerome Fischer	<i>Poicephalus senegalus</i>	XC447381	Étienne Leroy
<i>Curruca cantillans</i>	XC807728	Dare Sere	<i>Poicephalus senegalus</i>	XC523303	Joost van Bruggen
<i>Curruca cantillans</i>	XC907144	Peter Carr	<i>Poicephalus senegalus</i>	XC719437	Peter Boesman
<i>Curruca communis</i>	XC898903	Krzysztof Deonizak	<i>Poicephalus senegalus</i>	XC719438	Peter Boesman
<i>Curruca communis</i>	XC898982	Olivier Swift	<i>Porphyrio porphyrio</i>	XC505960	Jordi Calvet
<i>Curruca communis</i>	XC900942	Martin Billard	<i>Porphyrio porphyrio</i>	XC546992	Vincent Palomares
<i>Curruca communis</i>	XC904596	Niels Krabbe	<i>Porphyrio porphyrio</i>	XC702417	Stanislas Wroza
<i>Curruca conspicillata</i>	XC470756	Geoffrey Monchaux	<i>Porphyrio porphyrio</i>	XC799681	Pere Josa
<i>Curruca conspicillata</i>	XC537227	Charlie Bodin	<i>Porzana porzana</i>	XC900764	Mats Olsson
<i>Curruca conspicillata</i>	XC793044	Stanislas Wroza	<i>Porzana porzana</i>	XC917901	Uku Paat
<i>Curruca conspicillata</i>	XC793047	Stanislas Wroza	<i>Prunella collaris</i>	XC569165	Stanislas Wroza
<i>Curruca conspicillata</i>	XC819009	Paul Coiffard	<i>Prunella collaris</i>	XC569172	Stanislas Wroza
<i>Curruca curruca</i>	XC800988	Daniele Baroni	<i>Prunella collaris</i>	XC625477	Marcel Gil Velasco
<i>Curruca curruca</i>	XC809662	Dominique Guilterme	<i>Prunella collaris</i>	XC688398	Stanislas Wroza
<i>Curruca curruca</i>	XC826101	Esperanza Poveda	<i>Prunella modularis</i>	XC581070	Arjun Dutta
<i>Curruca curruca</i>	XC899224	Bodo Sonnenburg	<i>Prunella modularis</i>	XC881318	Martin Billard
<i>Curruca hortensis</i>	XC801094	João Tomás	<i>Prunella modularis</i>	XC902691	Paul Kelly
<i>Curruca hortensis</i>	XC802317	SonoNatura	<i>Prunella modularis</i>	XC912899	Romuald Mikusek
<i>Curruca hortensis</i>	XC845162	Julien Birard	<i>Psittacara mitratus</i>	XC707076	Richard E. Webster
<i>Curruca iberiae</i>	XC722937	Xavier Riera	<i>Psittacara mitratus</i>	XC931278	Jorge Leitão
<i>Curruca iberiae</i>	XC791461	Maxence Fouillade	<i>Psittacula eupatria</i>	XC628895	Stanislas Wroza
<i>Curruca melanocephala</i>	XC792298	SonoNatura	<i>Psittacula eupatria</i>	XC628898	Stanislas Wroza
<i>Curruca melanocephala</i>	XC900159	David Pennington	<i>Psittacula eupatria</i>	XC628899	Stanislas Wroza
<i>Curruca melanocephala</i>	XC917380	Alain Verneau	<i>Psittacula eupatria</i>	XC628900	Stanislas Wroza
<i>Curruca nisoria</i>	XC801193	Bodo Sonnenburg	<i>Psittacula krameri</i>	XC694156	Eduardo Realinho
<i>Curruca nisoria</i>	XC807274	Frank DD4WH	<i>Psittacula krameri</i>	XC933414	Jarek Matusiak
<i>Curruca nisoria</i>	XC816689	Grzegorz Lorek	<i>Psittacula krameri</i>	XC933415	Jarek Matusiak
<i>Curruca nisoria</i>	XC845030	Lukas Thiess	<i>Psittacula krameri</i>	XC933415	Jarek Matusiak
<i>Curruca nisoria</i>	XC905521	Défin Gonzalez	<i>Pterocles alchata</i>	XC142059	Jordi Calvet
<i>Curruca sarda</i>	XC246980	Jerome Fischer	<i>Pterocles alchata</i>	XC924210	Jordi Calvet
<i>Curruca sarda</i>	XC370650	Jerome Fischer	<i>Pterocles orientalis</i>	XC730394	Stanislas Wroza
<i>Curruca sarda</i>	XC471853	Stanislas Wroza	<i>Pterocles orientalis</i>	XC730396	Stanislas Wroza
<i>Curruca sarda</i>	XC666367	Marta Celej	<i>Ptyonoprogne rupestris</i>	XC657489	Camille Monnet
<i>Curruca undata</i>	XC483891	David Bissett	<i>Ptyonoprogne rupestris</i>	XC893409	Pere Josa
<i>Curruca undata</i>	XC530015	Stanislas Wroza	<i>Pyrrhocorax graculus</i>	XC569238	Stanislas Wroza
<i>Curruca undata</i>	XC794772	Jacobo Ramil Millarengo	<i>Pyrrhocorax graculus</i>	XC769199	Frank Lambert
<i>Curruca undata</i>	XC844566	Martin Billard	<i>Pyrrhocorax graculus</i>	XC820207	João Tomás
<i>Cursorius cursor</i>	XC149578	Frank Lambert	<i>Pyrrhocorax graculus</i>	XC898787	Daniele Baroni
<i>Cursorius cursor</i>	XC164193	Tero Linjama	<i>Pyrrhocorax pyrrhocorax</i>	XC288230	Antonio Xeira
<i>Cyanistes caeruleus</i>	XC893737	Guillaume Wetzel	<i>Pyrrhocorax pyrrhocorax</i>	XC584324	Stanislas Wroza
<i>Cyanistes caeruleus</i>	XC894018	Tanguy Lois	<i>Pyrrhocorax pyrrhocorax</i>	XC596499	Simon Elliott
<i>Cyanistes caeruleus</i>	XC898570	Jorge Leitão	<i>Pyrrhocorax pyrrhocorax</i>	XC735115	Irish Wildlife Sounds
<i>Cyanistes caeruleus</i>	XC898938	Paul Kelly	<i>Pyrrhula pyrrhula</i>	XC690409	Lars Edenius
<i>Cyanistes teneriffae</i>	XC367032	Thomas Lüthi	<i>Pyrrhula pyrrhula</i>	XC696696	Lars Edenius
<i>Cyanistes teneriffae</i>	XC458948	Twan Mols	<i>Pyrrhula pyrrhula</i>	XC780464	Lars Edenius
<i>Cyanistes teneriffae</i>	XC530210	Mats Rellmar	<i>Pyrrhula pyrrhula</i>	XC903130	Corentin Rivière
<i>Cyanistes teneriffae</i>	XC796196	Sidnei Dantas	<i>Rallus aquaticus</i>	XC689678	Stanislas Wroza
<i>Cyanopica cooki</i>	XC341189	José Carlos Sires	<i>Rallus aquaticus</i>	XC789677	Mats Olsson
<i>Cyanopica cooki</i>	XC414693	Stanislas Wroza	<i>Rallus aquaticus</i>	XC859387	Pere Josa
<i>Cyanopica cooki</i>	XC747540	Jorge Leitão	<i>Rallus aquaticus</i>	XC879688	João Tomás
<i>Cyanopica cooki</i>	XC747830	Jorge Leitão	<i>Recurvirostra avosetta</i>	XC698221	Olivier Swift, Hélène Cartaud
<i>Cygnus atratus</i>	XC297979	Timo Schnabel	<i>Recurvirostra avosetta</i>	XC883880	Pere Josa
<i>Cygnus atratus</i>	XC674006	Marc Anderson	<i>Regulus ignicapilla</i>	XC893407	Pere Josa
<i>Cygnus cygnus</i>	XC791765	Lars Edenius	<i>Regulus ignicapilla</i>	XC900900	Ireneusz Oleksik
<i>Cygnus cygnus</i>	XC795335	Lars Edenius	<i>Regulus ignicapilla</i>	XC902782	Lars Edenius
<i>Cygnus olor</i>	XC764112	Bodo Sonnenburg	<i>Regulus ignicapilla</i>	XC913156	Romuald Mikusek
<i>Cygnus olor</i>	XC861052	Paul Kelly	<i>Regulus regulus</i>	XC569378	Stanislas Wroza
<i>Cygnus olor</i>	XC864373	Paul Kelly	<i>Regulus regulus</i>	XC570588	Paul Holt
<i>Cygnus olor</i>	XC879427	Olivier Swift	<i>Regulus regulus</i>	XC831497	Mats Rellmar
<i>Delichon urbicum</i>	XC598648	Simon Elliott	<i>Regulus regulus</i>	XC902433	Elias A. Ryberg
<i>Delichon urbicum</i>	XC726339	Jorge Leitão	<i>Remiz pendulinus</i>	XC770244	Michel Veldt
<i>Delichon urbicum</i>	XC792837	João Tomás	<i>Remiz pendulinus</i>	XC828602	Kuzey Cem Kulaçoğlu
<i>Delichon urbicum</i>	XC792855	João Tomás	<i>Remiz pendulinus</i>	XC884995	João Tomás
<i>Dendrocopos leucotos</i>	XC680685	Jerome Fischer	<i>Remiz pendulinus</i>	XC902668	Stephan Risch
<i>Dendrocopos leucotos</i>	XC689011	Romuald Mikusek	<i>Riparia riparia</i>	XC659405	Lars Edenius
<i>Dendrocopos leucotos</i>	XC713501	Lars Edenius	<i>Riparia riparia</i>	XC666843	Domagoj Tomićić
<i>Dendrocopos leucotos</i>	XC719600	Uku Paat	<i>Saxicola dacotiae</i>	XC153273	Herman van Oosten
<i>Dendrocopos major</i>	XC622683	Lars Edenius	<i>Saxicola dacotiae</i>	XC346441	Tero Linjama
<i>Dendrocopos major</i>	XC895779	Lennart Jeppsson	<i>Saxicola rubetra</i>	XC797269	Grzegorz Lorek
<i>Dendrocopos major</i>	XC911171	W. Agster	<i>Saxicola rubetra</i>	XC803189	Lars Edenius
<i>Dendrocopos major</i>	XC926178	Samir Hellal	<i>Saxicola rubetra</i>	XC808861	Lars Edenius
<i>Dendrocopos syriacus</i>	XC480290	Albert Lastukhin	<i>Saxicola rubetra</i>	XC908625	Martin Billard
<i>Dendrocopos syriacus</i>	XC528724	Jarek Matusiak	<i>Saxicola rubicola</i>	XC716408	Christian Kerihuet
<i>Dendrocopos syriacus</i>	XC667315	András Schmidt	<i>Saxicola rubicola</i>	XC789119	João Tomás
<i>Dendrocopos syriacus</i>	XC770414	Michel Veldt	<i>Saxicola rubicola</i>	XC799490	Regina Eidner
<i>Dendrocygna media</i>	XC859063	Maarten Sluijter	<i>Saxicola rubicola</i>	XC909121	Mercier Christophe
<i>Dendrocygna media</i>	XC862406	Martin Billard	<i>Scolopax rusticola</i>	XC397413	Ruud van Beusekom
<i>Dendrocygna media</i>	XC877498	Guilherme Melo	<i>Scolopax rusticola</i>	XC922073	Teet Sirotkin

<i>Dendrocoptes medius</i>	XC913132	Romuald Mikusek	<i>Serinus canaria</i>	XC722081	SonoNatura
<i>Dryobates minor</i>	XC709565	Alan Dalton	<i>Serinus canaria</i>	XC722083	SonoNatura
<i>Dryobates minor</i>	XC712215	Lars Edenius	<i>Serinus canaria</i>	XC722084	SonoNatura
<i>Dryobates minor</i>	XC739164	Uku Paal	<i>Serinus canaria</i>	XC831509	Mats Rellmar
<i>Dryobates minor</i>	XC742967	Pontus Wennesjö	<i>Serinus serinus</i>	XC725616	Uku Paal
<i>Dryocopus martius</i>	XC839151	Lars Edenius	<i>Serinus serinus</i>	XC812475	Romuald Mikusek
<i>Dryocopus martius</i>	XC839284	Lars Edenius	<i>Serinus serinus</i>	XC875263	João Tomás
<i>Dryocopus martius</i>	XC902134	Ulf Elman	<i>Serinus serinus</i>	XC900917	Martin Billard
<i>Dryocopus martius</i>	XC911632	Jelle Scharringa	<i>Sinosuthora webbiana</i>	XC241076	Michael Grunwell
<i>Egretta garzetta</i>	XC774430	Irish Wildlife Sounds	<i>Sinosuthora webbiana</i>	XC464672	Martin Sutherland
<i>Egretta garzetta</i>	XC790717	Stanislas Wroza	<i>Sinosuthora webbiana</i>	XC722418	Common Jeff (麻杰夫)
<i>Egretta garzetta</i>	XC841128	Ray Tsu	<i>Sinosuthora webbiana</i>	XC889840	Geoff Carey
<i>Egretta garzetta</i>	XC856824	Jorge Leitão	<i>Sitta europaea</i>	XC897314	Lennart Jeppsson
<i>Elanus caeruleus</i>	XC351398	José Carlos Sires	<i>Sitta europaea</i>	XC897670	Jacobo Ramil Millarengo
<i>Elanus caeruleus</i>	XC352476	José Carlos Sires	<i>Sitta europaea</i>	XC927958	Ulf Elman
<i>Emberiza calandra</i>	XC835054	Esperanza Poveda	<i>Sitta europaea</i>	XC938013	Francesco Sottile
<i>Emberiza calandra</i>	XC864606	Frederic Lionel	<i>Somateria mollissima</i>	XC383544	Terje Kolaas
<i>Emberiza calandra</i>	XC882055	João Tomás	<i>Somateria mollissima</i>	XC549046	Lars Edenius
<i>Emberiza calandra</i>	XC899277	David Pennington	<i>Spatula clypeata</i>	XC644500	Jarek Matusiak
<i>Emberiza cia</i>	XC467766	Thijs Fijen	<i>Spatula clypeata</i>	XC863292	João Tomás
<i>Emberiza cia</i>	XC722554	SonoNatura	<i>Spatula querquedula</i>	XC544441	Hans Matheve
<i>Emberiza cia</i>	XC724311	brickejickel	<i>Spatula querquedula</i>	XC650914	Lars Edenius
<i>Emberiza cia</i>	XC865950	Azens	<i>Spinus spinus</i>	XC594919	Simon Elliott
<i>Emberiza cirlus</i>	XC799684	Jacobo Ramil Millarengo	<i>Spinus spinus</i>	XC793450	Lars Edenius
<i>Emberiza cirlus</i>	XC831373	Francesco Sottile	<i>Spinus spinus</i>	XC799041	Romuald Mikusek
<i>Emberiza cirlus</i>	XC882008	Azens	<i>Spinus spinus</i>	XC871416	Xavier Riera
<i>Emberiza cirlus</i>	XC892785	Martin Billard	<i>Streptopelia decaocto</i>	XC843476	Joost van Bruggen
<i>Emberiza citrinella</i>	XC819013	Grzegorz Lorek	<i>Streptopelia decaocto</i>	XC881441	Michel Veltdt
<i>Emberiza citrinella</i>	XC826623	Jack Berteau	<i>Streptopelia turtur</i>	XC862628	Olivier Swift
<i>Emberiza citrinella</i>	XC879349	Jarek Matusiak	<i>Streptopelia turtur</i>	XC902789	Olivier Swift
<i>Emberiza citrinella</i>	XC895089	Martin Billard	<i>Strix aluco</i>	XC845803	SonoNatura
<i>Emberiza hortulana</i>	XC795809	Stephan Börnecke	<i>Strix aluco</i>	XC936220	Martin Billard
<i>Emberiza hortulana</i>	XC802483	João Tomás	<i>Strix nebulosa</i>	XC343167	Tero Linjama
<i>Emberiza hortulana</i>	XC902403	Grzegorz Lorek	<i>Strix nebulosa</i>	XC655482	Lars Edenius
<i>Emberiza hortulana</i>	XC903923	Lars Edenius	<i>Strix uralensis</i>	XC705899	Lars Edenius
<i>Emberiza melanocephala</i>	XC729335	Leconte Michel	<i>Strix uralensis</i>	XC750071	Agris Celmins
<i>Emberiza melanocephala</i>	XC741120	Agris Celmins	<i>Strix uralensis</i>	XC797469	Ulf Elman
<i>Emberiza melanocephala</i>	XC801378	Stephan Risch	<i>Strix uralensis</i>	XC884935	Ulf Elman
<i>Emberiza melanocephala</i>	XC813175	Domagoj Tomičić	<i>Sturnus unicolor</i>	XC642973	Marcel Gil Velasco
<i>Emberiza pusilla</i>	XC484445	Fraser Simpson	<i>Sturnus unicolor</i>	XC665188	Jorge Leitão
<i>Emberiza pusilla</i>	XC571116	Ulf Hansson	<i>Sturnus unicolor</i>	XC683425	Jacobo Ramil Millarengo
<i>Emberiza pusilla</i>	XC779437	Erik Normark	<i>Sturnus unicolor</i>	XC752912	David Tattersley
<i>Emberiza pusilla</i>	XC809482	Kasper Wieck	<i>Sturnus vulgaris</i>	XC543800	Thomas Bergman
<i>Emberiza rustica</i>	XC655533	Olavi Hinkkanen	<i>Sturnus vulgaris</i>	XC604977	Simon Elliott
<i>Emberiza rustica</i>	XC815431	Lars Edenius	<i>Sturnus vulgaris</i>	XC652012	Uku Paal
<i>Emberiza rustica</i>	XC900006	Thomas Bergman	<i>Sturnus vulgaris</i>	XC712625	Olivier Swift, Ludivine Delamare
<i>Emberiza rustica</i>	XC904018	Lars Edenius	<i>Surnia ulula</i>	XC793932	Teet Sirotkin
<i>Emberiza schoeniclus</i>	XC790740	Stanislas Wroza	<i>Surnia ulula</i>	XC862737	Stein Ø. Nilsen
<i>Emberiza schoeniclus</i>	XC791229	Marcin Urbański	<i>Sylvia atricapilla</i>	XC858846	Jacobo Ramil Millarengo
<i>Emberiza schoeniclus</i>	XC792702	Stuart Fisher	<i>Sylvia atricapilla</i>	XC880829	Jean Pierre Sciolla
<i>Emberiza schoeniclus</i>	XC796332	Albert Lastukhin	<i>Sylvia atricapilla</i>	XC904739	Thomas Bergman
<i>Eremophila alpestris</i>	XC485435	Stanislas Wroza	<i>Sylvia atricapilla</i>	XC905957	Grzegorz Lorek
<i>Eremophila alpestris</i>	XC571278	Lars Edenius	<i>Sylvia borin</i>	XC836965	Jack Berteau
<i>Erithacus rubecula</i>	XC865221	Jean Pierre Sciolla	<i>Sylvia borin</i>	XC904341	Martin Billard
<i>Erithacus rubecula</i>	XC897347	W. Agster	<i>Sylvia borin</i>	XC906128	Ulf Elman
<i>Erithacus rubecula</i>	XC897396	Jacobo Ramil Millarengo	<i>Sylvia borin</i>	XC906390	Azens
<i>Erithacus rubecula</i>	XC906740	Mats Rellmar	<i>Syrnaticus reevesii</i>	XC360690	Stanislas Wroza
<i>Estrilda astrild</i>	XC640274	Jacobo Ramil Millarengo	<i>Syrnaticus reevesii</i>	XC360691	Stanislas Wroza
<i>Estrilda astrild</i>	XC719273	Nicolas Martinez	<i>Tachybaptus ruficollis</i>	XC634413	Peter Boesman
<i>Estrilda astrild</i>	XC748911	Jacobo Ramil Millarengo	<i>Tachybaptus ruficollis</i>	XC720814	Ulf Elman
<i>Estrilda astrild</i>	XC750258	Jacobo Ramil Millarengo	<i>Tachymarpis melba</i>	XC544109	Jordi Calvet
<i>Estrilda troglodytes</i>	XC164462	Fernand Deroussen	<i>Tachymarpis melba</i>	XC569487	Beatrix Saadi-Varchmin
<i>Estrilda troglodytes</i>	XC719131	Peter Boesman	<i>Tadorna ferruginea</i>	XC683992	Geoff Carey
<i>Estrilda troglodytes</i>	XC719132	Peter Boesman	<i>Tadorna ferruginea</i>	XC778623	Valentin Monnoy
<i>Estrilda troglodytes</i>	XC957262	Julien Birard	<i>Tadorna ferruginea</i>	XC835668	Martin Billard
<i>Euodice malabarica</i>	XC471526	Stanislas Wroza	<i>Tadorna ferruginea</i>	XC872210	Johannes Dag Mayer
<i>Euodice malabarica</i>	XC838993	Piqué Simon	<i>Tadorna tadorna</i>	XC735778	Irish Wildlife Sounds
<i>Falco biarmicus</i>	ML615715308	Shane Sumasgutner	<i>Tadorna tadorna</i>	XC882474	Jean Courtin
<i>Falco biarmicus</i>	ML89506	Justin Schuetz	<i>Tadorna tadorna</i>	XC909997	Uku Paal
<i>Falco biarmicus</i>	XC101188	James and David Bradley	<i>Tadorna tadorna</i>	XC936128	Arjun Dutta
<i>Falco biarmicus</i>	XC398048	Peter Boesman	<i>Tarsiger cyanurus</i>	XC606234	Niels Van Doninck
<i>Falco cherrug</i>	XC412094	Frank Lambert	<i>Tarsiger cyanurus</i>	XC644039	Agris Celmins
<i>Falco cherrug</i>	XC491256	Peter Boesman	<i>Tarsiger cyanurus</i>	XC661672	Lukas Thiess
<i>Falco columbarius</i>	XC731075	Lars Edenius	<i>Tarsiger cyanurus</i>	XC912128	Michel Watelet
<i>Falco columbarius</i>	XC896663	Tero Linjama	<i>Tetrao urogallus</i>	XC473720	Simon Ernst
<i>Falco eleonorae</i>	XC854572	Wim Jacobs	<i>Tetrao urogallus</i>	XC611477	Stanislas Wroza
<i>Falco eleonorae</i>	XC893157	Alain Malengreau	<i>Tetrao urogallus</i>	XC639001	Stanislas Wroza
<i>Falco naumanni</i>	XC383877	maudoc	<i>Tetrao urogallus</i>	XC641981	Stanislas Wroza
<i>Falco naumanni</i>	XC579422	Jordi Calvet	<i>Tetrastes bonasia</i>	XC779196	Lars Edenius
<i>Falco peregrinus</i>	XC748303	Irish Wildlife Sounds	<i>Tetrastes bonasia</i>	XC814145	Cedric Mroczko
<i>Falco peregrinus</i>	XC896686	Sven Normant	<i>Tetrastes bonasia</i>	XC881064	Lars Edenius
<i>Falco rusticolus</i>	XC189210	Andrew Spencer	<i>Tetrastes bonasia</i>	XC904071	Corentin Rivière
<i>Falco rusticolus</i>	XC709104	Lars Edenius	<i>Tetrax tetrax</i>	XC363911	Stanislas Wroza
<i>Falco rusticolus</i>	XC710854	Dag Österlund	<i>Tetrax tetrax</i>	XC722329	SonoNatura
<i>Falco rusticolus</i>	XC713307	Lars Edenius	<i>Thectocercus acuticaudatus</i>	XC189895	Andrew Spencer
<i>Falco subbuteo</i>	XC586296	Hugo Wieleman	<i>Thectocercus acuticaudatus</i>	XC189896	Andrew Spencer
<i>Falco subbuteo</i>	XC796706	Lars Edenius	<i>Thectocercus acuticaudatus</i>	XC635097	Dante Buzzetti
<i>Falco tinnunculus</i>	XC822020	Dominique Guillaume	<i>Thectocercus acuticaudatus</i>	XC879279	Dante Buzzetti

<i>Falco tinnunculus</i>	XC76577	João Tomás	<i>Threskiornis aethiopicus</i>	XC278223	Andrew Spencer
<i>Falco vespertinus</i>	XC770207	Michel Veldt	<i>Threskiornis aethiopicus</i>	XC429511	Frank Lambert
<i>Falco vespertinus</i>	XC813402	Peter Boesman	<i>Threskiornis aethiopicus</i>	XC505935	Lynette Rudman
<i>Ficedula albicollis</i>	XC653221	bricgëjckel	<i>Threskiornis aethiopicus</i>	XC651807	Nature sounds by Simply Birding
<i>Ficedula albicollis</i>	XC653222	bricgëjckel	<i>Tichodroma muraria</i>	XC512330	Thomas Armand
<i>Ficedula albicollis</i>	XC655679	W. Agster	<i>Tichodroma muraria</i>	XC569274	Stanislas Wroza
<i>Ficedula albicollis</i>	XC723932	Ireneusz Oleksik	<i>Tichodroma muraria</i>	XC573620	Sean Ronayne
<i>Ficedula hypoleuca</i>	XC802629	bert de bruin	<i>Tichodroma muraria</i>	XC698260	András Schmidt
<i>Ficedula hypoleuca</i>	XC803215	Mats Rellmar	<i>Tringa erythropus</i>	XC564369	Lars Edenius
<i>Ficedula hypoleuca</i>	XC806550	Alan Dalton	<i>Tringa erythropus</i>	XC915323	Thomas Bergman
<i>Ficedula hypoleuca</i>	XC908488	Jacek Mucha	<i>Tringa glareola</i>	XC903314	Lars Edenius
<i>Ficedula parva</i>	XC736819	Lars Edenius	<i>Tringa glareola</i>	XC906765	Francesco Sottile
<i>Ficedula parva</i>	XC743060	Romuald Mikusek	<i>Tringa nebularia</i>	XC900331	Uku Paal
<i>Ficedula parva</i>	XC804988	Mikael Litsgård	<i>Tringa nebularia</i>	XC917906	Esperanza Poveda
<i>Ficedula parva</i>	XC807830	Lars Edenius	<i>Tringa ochropus</i>	XC803363	Lars Edenius
<i>Fringilla coelebs</i>	XC897397	Jacobo Ramil Millarengo	<i>Tringa ochropus</i>	XC808190	Lars Edenius
<i>Fringilla coelebs</i>	XC908632	Martin Billard	<i>Tringa totanus</i>	XC884810	Olivier Swift
<i>Fringilla coelebs</i>	XC908812	Olivier Swift	<i>Tringa totanus</i>	XC890808	Christian Bøggild
<i>Fringilla coelebs</i>	XC909647	Carlos Pereira	<i>Tringa totanus</i>	XC898939	Paul Kelly
<i>Fringilla montifringilla</i>	XC653538	Agris Celmins	<i>Tringa totanus</i>	XC906104	Thomas Bergman
<i>Fringilla montifringilla</i>	XC675120	Albert Lastukhin	<i>Troglodytes troglodytes</i>	XC916801	Olivier Swift
<i>Fringilla montifringilla</i>	XC731505	Marc Anderson	<i>Troglodytes troglodytes</i>	XC928304	Jorge Leitão
<i>Fringilla montifringilla</i>	XC861643	Nicolas Martinez	<i>Turdus iliacus</i>	XC808871	Lars Edenius
<i>Fulica atra</i>	XC715239	Susanne Kuijpers	<i>Turdus iliacus</i>	XC881694	Eric Roualet
<i>Fulica atra</i>	XC881746	Paul Kelly	<i>Turdus iliacus</i>	XC901039	Kai Rantala
<i>Fulica atra</i>	XC893840	Susanne Kuijpers	<i>Turdus iliacus</i>	XC903924	Lars Edenius
<i>Fulica atra</i>	XC902418	Jack Berteau	<i>Turdus merula</i>	XC815531	Agris Celmins
<i>Fulica cristata</i>	XC306654	Hans Matheve	<i>Turdus merula</i>	XC900559	Lennart Jeppsson
<i>Fulica cristata</i>	XC431996	Joost van Bruggen	<i>Turdus merula</i>	XC906491	Olivier Swift
<i>Fulica cristata</i>	XC860421	Dries Van de Loock	<i>Turdus merula</i>	XC907818	Olivier Swift
<i>Fulica cristata</i>	XC908546	Nelson Conceição	<i>Turdus philomelos</i>	XC831495	Agris Celmins
<i>Galerida cristata</i>	XC832503	Stein Ø. Nilsen	<i>Turdus philomelos</i>	XC879352	Alain Malengreau
<i>Galerida cristata</i>	XC839414	Corentin Rivière	<i>Turdus philomelos</i>	XC897346	W. Agster
<i>Galerida cristata</i>	XC864276	SonoNatura	<i>Turdus philomelos</i>	XC899778	Jorge Leitão
<i>Galerida cristata</i>	XC864607	Frederic Lionel	<i>Turdus pilaris</i>	XC635213	Stanislas Wroza
<i>Galerida theklae</i>	XC463869	Jordi Calvet	<i>Turdus pilaris</i>	XC686589	Niels Van Doninck
<i>Galerida theklae</i>	XC730352	Stanislas Wroza	<i>Turdus pilaris</i>	XC727604	Lars Edenius
<i>Galerida theklae</i>	XC779770	Luis Gracia	<i>Turdus pilaris</i>	XC834617	Grégoire Chauvot
<i>Galerida theklae</i>	XC900368	Christian Kerihuel	<i>Turdus torquatus</i>	XC593279	Simon Elliott
<i>Gallinago gallinago</i>	XC633300	Krzysztof Deoniziak	<i>Turdus torquatus</i>	XC721589	Loan Delpit
<i>Gallinago gallinago</i>	XC729310	Lars Edenius	<i>Turdus torquatus</i>	XC724232	Romuald Mikusek
<i>Gallinago media</i>	XC201361	Stein Ø. Nilsen	<i>Turdus torquatus</i>	XC837014	Petter Westberg
<i>Gallinago media</i>	XC325087	Terje Kolaas	<i>Turdus viscivorus</i>	XC718033	Manuel Grosselet
<i>Gallinula chloropus</i>	XC894656	Lars Mogensen	<i>Turdus viscivorus</i>	XC788562	Jacobo Ramil Millarengo
<i>Gallinula chloropus</i>	XC895059	Martin Billard	<i>Turdus viscivorus</i>	XC807826	Lars Edenius
<i>Gallinula chloropus</i>	XC902620	Lars Mogensen	<i>Turdus viscivorus</i>	XC879652	Christian Vemmelund Helligso
<i>Gallinula chloropus</i>	XC905071	Vandousselaere Patrick	<i>Tyto alba</i>	XC948997	SonoNatura
<i>Garrulus glandarius</i>	XC856324	Thierry Thomas	<i>Tyto alba</i>	XC952015	SonoNatura
<i>Garrulus glandarius</i>	XC881809	Esperanza Poveda	<i>Tyto alba</i>	XC952969	Friedrich Richard
<i>Garrulus glandarius</i>	XC884360	Thomas Bergman	<i>Tyto alba</i>	XC962216	Hans Matheve
<i>Garrulus glandarius</i>	XC902468	Jack Berteau	<i>Upupa epops</i>	XC897074	SonoNatura
<i>Geronticus eremita</i>	XC361510	José Carlos Sires y Eloisa Matheu	<i>Upupa epops</i>	XC917761	Regina Eidner
<i>Geronticus eremita</i>	XC361523	José Carlos Sires y Eloisa Matheu	<i>Vanellus vanellus</i>	XC638538	Thomas Bergman
<i>Glareola pratincola</i>	XC379455	Stanislas Wroza	<i>Vanellus vanellus</i>	XC880717	Olivier Swift
<i>Glareola pratincola</i>	XC758522	Dries Van de Loock	<i>Vanellus vanellus</i>	XC881982	Olivier Swift
<i>Glaucidium passerinum</i>	XC883372	Teet Sirotkin	<i>Vanellus vanellus</i>	XC898816	Thomas Bergman
<i>Glaucidium passerinum</i>	XC902777	David Darrell-Lambert	<i>Zapornia parva</i>	XC732543	Tero Linjama
<i>Grus grus</i>	XC723192	Lars Edenius	<i>Zapornia parva</i>	XC900252	Krzysztof Deoniziak
<i>Grus grus</i>	XC836029	Hannu Varkki	<i>Zapornia pusilla</i>	XC656129	Yannick Jacob
<i>Gulosus aristotelis</i>	XC588002	Simon Elliott	<i>Zapornia pusilla</i>	XC745918	Marcin Sotowiej

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Species	File	Recordist	Species	File	Recordist
<i>Acanthis flammea</i>	XC383642	Terje Kolaas	<i>Himantopus mexicanus</i>	XC778463	Paul Driver
<i>Acanthis flammea</i>	XC589966	Seth Beaudreault, Toolik Field Station	<i>Hirundo rustica</i>	XC129647	Thomas G. Graves
<i>Accipiter cooperii</i>	XC603733	Peter Ward and Ken Hall	<i>Hirundo rustica</i>	XC446455	Ed Pandolfino
<i>Accipiter cooperii</i>	XC609230	Matt Wistrand	<i>Histrionicus histrionicus</i>	XC181783	Andrew Spencer
<i>Accipiter gentilis</i>	XC59174	Taylor Brooks	<i>Histrionicus histrionicus</i>	XC351801	Bruce Lagerquist
<i>Accipiter gentilis</i>	XC818169	Lars Edenius	<i>Hylocichla mustelina</i>	XC692210	Christopher McPherson
<i>Accipiter striatus</i>	XC285549	Paul Driver	<i>Hylocichla mustelina</i>	XC739057	Bobby Wilcox
<i>Accipiter striatus</i>	XC791005	Pedro Rinaldi	<i>Hylocichla mustelina</i>	XC771930	Paul Driver
<i>Acridotheres tristis</i>	XC659209	Sunny Tseng	<i>Hylocichla mustelina</i>	XC818020	Bobby Wilcox
<i>Acridotheres tristis</i>	XC729094	Greg Irving	<i>Icterus gularis</i>	XC318526	Paul Marvin
<i>Acridotheres tristis</i>	XC812211	Geoff Carey	<i>Icterus gularis</i>	XC359069	Paul Marvin
<i>Acridotheres tristis</i>	XC812212	Geoff Carey	<i>Icterus pectoralis</i>	XC224640	Peter Boesman
<i>Actitis macularia</i>	XC183594	Ian Cruickshank	<i>Icterus pectoralis</i>	XC363554	Roland Rumm
<i>Actitis macularia</i>	XC232641	Paul Marvin	<i>Ictinia mississippiensis</i>	XC316339	J.R. Rigby
<i>Aechmophorus clarkii</i>	XC143247	Andrew Spencer	<i>Ictinia mississippiensis</i>	XC669899	Russ Wigh
<i>Aechmophorus clarkii</i>	XC418571	Bobby Wilcox	<i>Ixbrychus exilis</i>	XC492421	Paul Driver
<i>Aechmophorus clarkii</i>	XC452390	Paul Marvin	<i>Ixbrychus exilis</i>	XC581228	Paul Marvin
<i>Aechmophorus clarkii</i>	XC641950	Paul Marvin	<i>Ixoreus naevius</i>	XC416081	Steve Hampton
<i>Aechmophorus occidentalis</i>	XC129074	Thomas G. Graves	<i>Lagopus leucura</i>	XC141894	Andrew Spencer
<i>Aechmophorus occidentalis</i>	XC527689	Thomas G. Graves	<i>Lagopus leucura</i>	XC152517	Davyd Betchkal
<i>Aechmophorus occidentalis</i>	XC527695	Thomas G. Graves	<i>Lagopus leucura</i>	XC363155	Frank Lambert
<i>Aechmophorus occidentalis</i>	XC527697	Thomas G. Graves	<i>Lagopus leucura</i>	XC756351	Bruce Lagerquist
<i>Aegolius acadicus</i>	XC546885	Lance A. M. Benner	<i>Lampornis clemenciae</i>	XC563006	Daniel Hincley
<i>Aegolius acadicus</i>	XC613765	Peter Ward and Ken Hall	<i>Lampornis clemenciae</i>	XC809118	Manuel Grosselet
<i>Aegolius funereus</i>	XC110187	Andrew Spencer	<i>Laterallus jamaicensis</i>	XC36145	Fabrice Schmitt

<i>Aegolius funereus</i>	XC233533	Steve Wilson	<i>Laterallus jamaicensis</i>	XC783437	Cristian Pinto Fernandez
<i>Aeronautes saxatalis</i>	XC470554	Thomas G. Graves	<i>Leiothlypis crissalis</i>	XC168577	Jerome Fischer
<i>Aeronautes saxatalis</i>	XC552939	Paul Marvin	<i>Leiothlypis crissalis</i>	XC34312	Andrew Spencer
					Yair Guillermo Molina
<i>Agapornis roseicollis</i>	XC346578	Peter Boesman	<i>Leptotila verreauxi</i>	XC420921	Martínez.
<i>Agapornis roseicollis</i>	XC453168	Paul Marvin	<i>Leptotila verreauxi</i>	XC838546	Jayrson Araujo De Oliveira
<i>Aix sponsa</i>	XC509715	Sunny Tseng	<i>Leucolia violiceps</i>	XC133184	Micah Riegner
<i>Aix sponsa</i>	XC509717	Sunny Tseng	<i>Leucolia violiceps</i>	XC445935	Richard E. Webster
<i>Alectoris chukar</i>	XC233760	Mouser Williams	<i>Leuconotopicus albolavatus</i>	XC540025	Bruce Lagerquist
<i>Alectoris chukar</i>	XC387754	Bruce Lagerquist	<i>Leuconotopicus albolavatus</i>	XC540025	Bruce Lagerquist
<i>Alopochen aegyptiaca</i>	XC546108	Albert Noorlander	<i>Leuconotopicus albolavatus</i>	XC614153	Peter Ward and Ken Hall
<i>Alopochen aegyptiaca</i>	XC620525	Francesco Sottile	<i>Leuconotopicus albolavatus</i>	XC737531	Paul Marvin
<i>Amazilia yucatanensis</i>	XC130831	Andrew Spencer	<i>Leuconotopicus arizonae</i>	XC322159	Paul Marvin
<i>Amazilia yucatanensis</i>	XC298921	Dan Lane	<i>Leuconotopicus arizonae</i>	XC323873	Richard E. Webster
<i>Amazona oratrix</i>	XC681814	Manuel Grosselet	<i>Leuconotopicus arizonae</i>	XC323875	Richard E. Webster
<i>Amazona oratrix</i>	XC804979	Manuel Grosselet	<i>Leuconotopicus arizonae</i>	XC522394	Jarrod Swackhamer
<i>Amazona viridigenalis</i>	XC320551	Paul Marvin	<i>Leuconotopicus borealis</i>	XC109888	Andrew Spencer
<i>Amazona viridigenalis</i>	XC320571	Paul Marvin	<i>Leuconotopicus borealis</i>	XC54339	Mike Nelson
<i>Ammospiza caudacuta</i>	XC55559	Andrew Spencer	<i>Leuconotopicus borealis</i>	XC54339	Mike Nelson
<i>Ammospiza leconteii</i>	XC598435	Peter Ward and Ken Hall	<i>Leuconotopicus borealis</i>	XC713000	Bruce Lagerquist
<i>Ammospiza maritima</i>	XC433071	Phil Brown	<i>Leuconotopicus villosus</i>	XC701063	Richard E. Webster
<i>Ammospiza maritima</i>	XC654371	William Whitehead	<i>Leuconotopicus villosus</i>	XC701065	Richard E. Webster
<i>Anas acuta</i>	XC453334	Paul Marvin	<i>Leuconotopicus villosus</i>	XC776033	Scott Olmstead
<i>Anas acuta</i>	XC786109	Paul Driver	<i>Leuconotopicus villosus</i>	XC841928	Sue Riffe
<i>Anas carolinensis</i>	XC173648	Paul Marvin	<i>Leucosticte australis</i>	XC87637	Andrew Spencer
<i>Anas carolinensis</i>	XC354707	Frank Lambert	<i>Leucosticte australis</i>	XC87646	Andrew Spencer
<i>Anas diazi</i>	XC663146	Manuel Grosselet	<i>Limnothlypis swainsonii</i>	XC423774	Aidan Place
<i>Anas diazi</i>	XC683209	Manuel Grosselet	<i>Limnothlypis swainsonii</i>	XC465064	John Middleton
<i>Anas fulvigula</i>	XC104626	Andrew Spencer	<i>Limosa fedoa</i>	XC307323	Paul Marvin
<i>Anas fulvigula</i>	XC192343	Paul Marvin	<i>Limosa fedoa</i>	XC574462	Manuel Grosselet
<i>Anas platyrhynchos</i>	XC630772	Paul Marvin	<i>Lophodytes cucullatus</i>	XC212480	Russ Wigh
<i>Anas rubripes</i>	XC142767	Martin St-Michel	<i>Lophodytes cucullatus</i>	XC74430	Todd Wilson
<i>Anas rubripes</i>	XC168801	Paul Driver	<i>Loxia sinesciuris</i>	XC204811	Andrew Spencer
<i>Anthus spragueii</i>	XC186346	Richard E. Webster	<i>Loxia sinesciuris</i>	XC548198	Richard E. Webster
<i>Anthus spragueii</i>	XC295527	Hal Mitchell	<i>Mareca americana</i>	XC519618	Manuel Grosselet
<i>Antigone canadensis</i>	XC606567	Peter Ward and Ken Hall	<i>Mareca americana</i>	XC519619	Manuel Grosselet
<i>Antigone canadensis</i>	XC625913	Richard Bradley	<i>Mareca strepera</i>	XC679027	Beatrix Saadi-Varchmin
<i>Antrrostomus arizonae</i>	XC553845	Scott Olmstead	<i>Mareca strepera</i>	XC845777	Jacobo Ramil Millarengo
<i>Antrrostomus arizonae</i>	XC651661	Bobby Wilcox	<i>Megaceryle alcyon</i>	XC451359	Paul Marvin
<i>Antrrostomus carolinensis</i>	XC555492	Ron Overholtz	<i>Megaceryle alcyon</i>	XC628808	Richard E. Webster
<i>Antrrostomus carolinensis</i>	XC568300	Russ Wigh	<i>Megaceryle torquata</i>	XC646540	Robson Silva e Silva
<i>Antrrostomus vociferus</i>	XC405768	Paul Marvin	<i>Megaceryle torquata</i>	XC837882	Jayrson Araujo De Oliveira
<i>Antrrostomus vociferus</i>	XC860759	Sue Riffe	<i>Megascops asio</i>	XC286959	Tim Spahr
<i>Aphelocoma californica</i>	XC454467	Lisa McMaster	<i>Megascops asio</i>	XC712961	Bruce Lagerquist
<i>Aphelocoma coerulescens</i>	XC161108	Paul Marvin	<i>Megascops kennicottii</i>	XC355668	Bruce Lagerquist
<i>Aphelocoma coerulescens</i>	XC371888	Bruce Lagerquist	<i>Megascops kennicottii</i>	XC540561	Lance A. M. Benner
<i>Aphelocoma coerulescens</i>	XC733475	PT xiao	<i>Megascops trichopsis</i>	XC347699	Jesse Fagan
<i>Aphelocoma coerulescens</i>	XC796364	Valerie Heemstra	<i>Megascops trichopsis</i>	XC351699	Frank Lambert
<i>Aphelocoma insularis</i>	XC27719	Andrew Spencer	<i>Melanerpes aurifrons</i>	XC143913	Andrew Spencer
<i>Aphelocoma insularis</i>	XC359507	Paul Marvin	<i>Melanerpes aurifrons</i>	XC297554	Ross Gallardy
<i>Aphelocoma insularis</i>	XC408450	Frank Lambert	<i>Melanerpes aurifrons</i>	XC305372	Paul Marvin
<i>Aphelocoma insularis</i>	XC89391	Steve Hampton	<i>Melanerpes aurifrons</i>	XC452716	Paul Marvin
<i>Aphelocoma wollweberi</i>	XC326271	Nick Komar	<i>Melanerpes carolinus</i>	XC225523	Peter Boesman
<i>Aphelocoma wollweberi</i>	XC776325	Scott Olmstead	<i>Melanerpes carolinus</i>	XC578524	Sue Riffe
<i>Aphelocoma woodhouseii</i>	XC452523	Paul Marvin	<i>Melanerpes carolinus</i>	XC624447	Bill Grantham
<i>Aphelocoma woodhouseii</i>	XC495164	Thomas G. Graves	<i>Melanerpes carolinus</i>	XC636507	Jasper Barnes
<i>Aphelocoma woodhouseii</i>	XC577097	Manuel Grosselet	<i>Melanerpes erythrocephalus</i>	XC254603	Jonathon Jongsma
<i>Aquila chrysaetos</i>	XC698030	Lars Edenius	<i>Melanerpes erythrocephalus</i>	XC313280	Hal Mitchell
<i>Aquila chrysaetos</i>	XC750025	Lars Edenius	<i>Melanerpes erythrocephalus</i>	XC477001	David Darrell-Lambert
<i>Aquila chrysaetos</i>	XC753804	Lars Edenius	<i>Melanerpes erythrocephalus</i>	XC698853	Matt Wistrand
<i>Aquila chrysaetos</i>	XC837084	Birger Hörnfeldt	<i>Melanerpes formicivorus</i>	XC649098	Paul Marvin
<i>Aratinga nenday</i>	XC104190	Andrew Spencer	<i>Melanerpes formicivorus</i>	XC656292	Paul Marvin
<i>Aratinga nenday</i>	XC196521	Gabriel Rosa	<i>Melanerpes formicivorus</i>	XC786993	Ed Pandolfino
<i>Archilochus alexandri</i>	XC132359	Richard E. Webster	<i>Melanerpes formicivorus</i>	XC856855	Sven Kransel
<i>Archilochus alexandri</i>	XC132692	Richard E. Webster	<i>Melanerpes lewis</i>	XC13659	Andrew Spencer
<i>Archilochus alexandri</i>	XC297544	Ross Gallardy	<i>Melanerpes lewis</i>	XC700388	Mark A. Ports
<i>Archilochus alexandri</i>	XC494996	Thomas G. Graves	<i>Melanerpes uropygialis</i>	XC354685	David Vander Pluym
<i>Archilochus colubris</i>	XC211131	Robert Benson	<i>Melanerpes uropygialis</i>	XC521997	Jarrod Swackhamer
<i>Archilochus colubris</i>	XC319184	Martin St-Michel	<i>Meleagris gallopavo</i>	XC617755	Manuel Grosselet
<i>Archilochus colubris</i>	XC673344	Christopher Moser-Purdy	<i>Meleagris gallopavo</i>	XC702183	Francesco Sottile
<i>Archilochus colubris</i>	XC758917	Manuel Grosselet	<i>Melospiza lincolnii</i>	XC558323	Ron Overholtz
<i>Archilochus colubris</i>	XC781005	Paul Driver	<i>Melospiza lincolnii</i>	XC574672	Aidan Place
<i>Ardea alba</i>	XC147337	Paul Marvin	<i>Melospiza lincolnii</i>	XC747200	Manuel Grosselet
<i>Ardea alba</i>	XC695589	amonmod	<i>Melospiza lincolnii</i>	XC691817	Simon Elliott
<i>Ardea alba</i>	XC705918	Sonothèque ADVL	<i>Mergus merganser</i>	XC94638	Jarek Matusiak
<i>Ardea alba</i>	XC794542	Geoff Carey	<i>Mergus merganser</i>	XC461181	Stein Ø. Nilsen
<i>Ardea herodias</i>	XC560546	Mark Nenadov	<i>Mergus serrator</i>	XC607514	Peter Stronach
<i>Ardea herodias</i>	XC578132	Ed Pandolfino	<i>Micrathene whitneyi</i>	XC363557	Scott Olmstead
<i>Asio flammeus</i>	XC545852	Luiz C. Silva	<i>Micrathene whitneyi</i>	XC555495	Ron Overholtz
<i>Asio flammeus</i>	XC557487	Jarek Matusiak	<i>Myiarchus crinitus</i>	XC137719	Jonathon Jongsma
<i>Asio otus</i>	XC793294	Dominique Guillerme	<i>Myiarchus crinitus</i>	XC844235	Sue Riffe
<i>Asio otus</i>	XC793296	Dominique Guillerme	<i>Myiodynastes luteiventris</i>	XC445503	Richard E. Webster
<i>Athene cunicularia</i>	XC104661	Andrew Spencer	<i>Myiopsitta monachus</i>	XC357408	Paul Marvin
		David Ricardo Rodríguez-Villamil			
<i>Athene cunicularia</i>	XC524491	Villamil	<i>Myiopsitta monachus</i>	XC452545	Paul Marvin
<i>Aythya affinis</i>	XC334315	Thomas Magarian	<i>Myiopsitta monachus</i>	XC669961	Manuel Grosselet
<i>Aythya affinis</i>	XC347797	Thomas Magarian	<i>Myiopsitta monachus</i>	XC682586	Manuel Grosselet
<i>Aythya americana</i>	XC104592	Andrew Spencer	<i>Nucifraga columbiana</i>	XC567739	Ron Overholtz
<i>Aythya americana</i>	XC206445	Jessie Barry	<i>Numenius americanus</i>	XC179500	Andrew Spencer
<i>Aythya collaris</i>	XC170973	Paul Driver	<i>Numenius americanus</i>	XC636979	Bruce Lagerquist
<i>Aythya collaris</i>	XC203611	Andrew Spencer	<i>Nyctanassa violacea</i>	XC487225	Paul Marvin
<i>Aythya valisineria</i>	XC169220	Paul Driver	<i>Nyctanassa violacea</i>	XC573260	Manuel Grosselet
<i>Aythya valisineria</i>	XC169224	Paul Driver	<i>Nycticorax nycticorax</i>	XC331173	Manuel Grosselet
<i>Baeolophus ridgwayi</i>	XC613815	Richard E. Webster	<i>Nycticorax nycticorax</i>	XC431999	Joost van Bruggen
<i>Bartramia longicauda</i>	XC143966	Laura Gooch	<i>Nyctidromus albigollis</i>	XC521299	Jarrod Swackhamer

<i>Bartramia longicauda</i>	XC656679	Matt Wistrand	<i>Nyctidromus albigollis</i>	XC743970	Jayrson Araujo De Oliveira
<i>Bonasa umbellus</i>	ML28156201	Jay McGowan	<i>Oporornis agilis</i>	XC475279	Scott Gravette
<i>Bonasa umbellus</i>	ML611940051	Daniel Jauvin	<i>Oporornis agilis</i>	XC480915	Matt Wistrand
<i>Botaurus lentiginosus</i>	XC233158	Harry Lehto	<i>Oreortyx pictus</i>	XC226935	Peter Boesman
<i>Botaurus lentiginosus</i>	XC601776	Peter Ward and Ken Hall	<i>Oreortyx pictus</i>	XC715988	Paul Marvin
<i>Branta canadensis</i>	XC722620	Stephan Risch	<i>Oxyura jamaicensis</i>	XC591763	Simon Elliott
<i>Branta canadensis</i>	XC775330	Nicolas Martinez	<i>Oxyura jamaicensis</i>	XC591765	Simon Elliott
<i>Branta canadensis</i>	XC844837	Michael Hurben	<i>Parabuteo unicinctus</i>	XC1325	Robin Carter
<i>Brotogeris chiriri</i>	XC744337	João Vitor Oliveira de Souza	<i>Parabuteo unicinctus</i>	XC755250	Patricio Mena Valenzuela
<i>Brotogeris chiriri</i>	XC816874	Jayrson Araujo De Oliveira	<i>Parakesia motacilla</i>	XC601743	Christopher McPherson
<i>Brotogeris versicolurus</i>	XC47713	Andrew Spencer	<i>Parakesia motacilla</i>	XC691611	Christopher McPherson
<i>Brotogeris versicolurus</i>	XC47714	Andrew Spencer	<i>Parakesia noveboracensis</i>	XC477981	Stanislas Wroza
<i>Bubo virginianus</i>	XC760068	Michael & Katie LaTour	<i>Parakesia noveboracensis</i>	XC752973	Sunny Tseng
<i>Bubo virginianus</i>	XC767278	Scott Olmstead	<i>Passer domesticus</i>	XC846053	Thierry THOMAS
<i>Bubulcus ibis</i>	XC108820	Andrew Spencer	<i>Passer domesticus</i>	XC861200	Jorge Leitão
<i>Bubulcus ibis</i>	XC192966	Paul Marvin	<i>Passer montanus</i>	XC655734	Samuel Jones
<i>Bubulcus ibis</i>	XC356329	Marco Dragonetti	<i>Passer montanus</i>	XC717520	Bobby Wilcox
<i>Bubulcus ibis</i>	XC495869	Joost van Bruggen	<i>Passerella iliaca</i>	XC557052	Ron Overholtz
<i>Bucephala albeola</i>	XC388268	Thomas Magarian	<i>Passerella iliaca</i>	XC562461	Steve Hampton
<i>Bucephala albeola</i>	XC710475	Richard E. Webster	<i>Patagioenas fasciata</i>	XC491894	Paul Marvin
<i>Bucephala clangula</i>	XC644304	Lars Edenius	<i>Patagioenas fasciata</i>	XC491896	Paul Marvin
<i>Bucephala clangula</i>	XC792699	Lars Edenius	<i>Patagioenas flavirostris</i>	XC499731	Richard E. Webster
<i>Bucephala islandica</i>	XC189404	Andrew Spencer	<i>Patagioenas flavirostris</i>	XC538453	Alain Malengreau
<i>Bucephala islandica</i>	XC83887	Patrik Åberg	<i>Patagioenas leucocephala</i>	XC101349	Andrew Spencer
<i>Buteo albonotatus</i>	XC604822	Richard E. Webster	<i>Patagioenas leucocephala</i>	XC145947	Paul Marvin
<i>Buteo albonotatus</i>	XC793837	Gregory Askew	<i>Pavo cristatus</i>	XC124017	pradnyavant mane
<i>Buteo brachyurus</i>	XC407410	Daniel de Jesus Garcia	<i>Pavo cristatus</i>	XC812476	Francesco Barberini
<i>Buteo brachyurus</i>	XC41473	Luiz Gabriel Mazzoni	<i>Perdix perdix</i>	XC591894	Simon Elliott
<i>Buteo jamaicensis</i>	XC638607	Bruce Lagerquist	<i>Perdix perdix</i>	XC651353	Uku Paal
<i>Buteo jamaicensis</i>	XC666007	Paul Marvin	<i>Perisoreus canadensis</i>	XC149242	Andrew Spencer
<i>Buteo lineatus</i>	XC361769	Bruce Lagerquist	<i>Perisoreus canadensis</i>	XC269086	Davyd Betchkal
<i>Buteo lineatus</i>	XC578105	Ed Pandolfino	<i>Petrochelidon fulva</i>	XC34141	Andrew Spencer
<i>Buteo plagiatus</i>	XC604803	Richard E. Webster	<i>Peucaea aestivalis</i>	XC567386	John A. Middleton Jr.
<i>Buteo plagiatus</i>	XC625830	Richard E. Webster	<i>Peucaea aestivalis</i>	XC712864	Brian Henderson
<i>Buteo platypterus</i>	XC454231	Miguel San Martin	<i>Peucaea botterii</i>	XC330308	Matt Baumann
<i>Buteo platypterus</i>	XC668893	Jim Berry	<i>Phalaenoptilus nuttallii</i>	XC317328	Lance A. M. Benner
<i>Buteo regalis</i>	XC419204	Paul Marvin	<i>Phalaenoptilus nuttallii</i>	XC490763	Lauren Harter
<i>Buteo regalis</i>	XC76663	Andrew Spencer	<i>Phalaropus tricolor</i>	XC294469	Paul Marvin
<i>Buteo swainsoni</i>	XC418250	Bobby Wilcox	<i>Phalaropus tricolor</i>	XC836128	Aluisio Ribeiro
<i>Buteo swainsoni</i>	XC438511	Julia Wittmann	<i>Phasianus colchicus</i>	XC744152	brickegidel
<i>Buteogallus anthracinus</i>	XC147311	Paul Marvin	<i>Phasianus colchicus</i>	XC799489	Regina Eickner
<i>Buteogallus anthracinus</i>	XC579265	Richard E. Webster	<i>Picoides arcticus</i>	XC210775	Paul Marvin
<i>Butorides virescens</i>	XC639384	Bobby Wilcox	<i>Picoides arcticus</i>	XC482563	Bruce Lagerquist
<i>Butorides virescens</i>	XC705567	Paul Driver	<i>Picoides arcticus</i>	XC663765	Whitney Neufeld-Kaiser
<i>Cairina moschata</i>	ML92424851	Paul Marvin	<i>Picoides arcticus</i>	XC78676	Andrew Spencer
<i>Cairina moschata</i>	ML92475411	Paul Marvin	<i>Picoides dorsalis</i>	XC102874	Andrew Spencer
<i>Callipepla californica</i>	XC299260	Paul Marvin	<i>Picoides dorsalis</i>	XC102878	Andrew Spencer
<i>Callipepla californica</i>	XC603751	Peter Ward and Ken Hall	<i>Picoides dorsalis</i>	XC362021	Frank Lambert
<i>Callipepla gambelii</i>	XC475181	Bobby Wilcox	<i>Picoides dorsalis</i>	XC613386	Doug Hynes
<i>Callipepla gambelii</i>	XC540563	Jarrod Swackhamer	<i>Pinicola enucleator</i>	XC267728	Davyd Betchkal
<i>Callipepla squamata</i>	XC255093	Richard E. Webster	<i>Pinicola enucleator</i>	XC30902	Allen T. Chartier
<i>Callipepla squamata</i>	XC255119	Richard E. Webster	<i>Pinicola enucleator</i>	XC369903	Eric DeFonso
<i>Calothorax lucifer</i>	XC297549	Ross Gallardy	<i>Pinicola enucleator</i>	XC424093	Terje Kolaas
<i>Calothorax lucifer</i>	XC297549	Ross Gallardy	<i>Piranga flava</i>	ML24627381	Paul Marvin
<i>Calypte anna</i>	XC132250	Richard E. Webster	<i>Piranga flava</i>	ML66835	William W. H. Gunn
<i>Calypte anna</i>	XC473410	bowtyler	<i>Piranga flava</i>	ML87917	Curtis Marantz
<i>Calypte anna</i>	XC501895	Paul Marvin	<i>Piranga flava</i>	XC657353	Leonardo Guzman Hernandez
<i>Calypte anna</i>	XC697495	Paul Marvin	<i>Piranga rubra</i>	XC558096	Ron Overholtz
<i>Calypte costae</i>	XC143788	Paul Marvin	<i>Piranga rubra</i>	XC650747	John A. Middleton Jr.
<i>Calypte costae</i>	XC390286	Paul Marvin	<i>Piranga rubra</i>	XC718200	Bobby Wilcox
<i>Campylorhynchus brunneicapillus</i>	XC702988	Paul Marvin	<i>Pitangus sulphuratus</i>	XC575562	Okamoto Keita Sin
<i>Canachites canadensis</i>	XC192149	Martin St-Michel	<i>Pitangus sulphuratus</i>	XC688651	Alán Palacios
<i>Canachites canadensis</i>	XC205576	Paul Marvin	<i>Pitangus sulphuratus</i>	XC831882	Christiana Fattorelli
<i>Canachites canadensis</i>	XC389927	Thomas Magarian	<i>Pitangus sulphuratus</i>	XC839479	Bernard Bousquet
<i>Canachites canadensis</i>	XC406266	Patrik Åberg	<i>Platalea ajaja</i>	XC173889	Paul Marvin
<i>Caracara plancus</i>	XC430769	Victor Antonelli	<i>Platalea ajaja</i>	XC451725	Paul Marvin
<i>Caracara plancus</i>	XC587538	Daniel Mello	<i>Plegadis chihi</i>	XC751188	Guillermo Vushurovich
<i>Cathartes aura</i>	ML442811061	Ronan Pangie	<i>Plegadis chihi</i>	XC754985	Franco Treboux
<i>Cathartes aura</i>	XC520287	Cristian Pinto	<i>Plegadis falcinellus</i>	XC314909	Marco Dragonetti
<i>Catherpes mexicanus</i>	XC728920	Scott Olmstead	<i>Plegadis falcinellus</i>	XC530553	Jordi Calvet
<i>Catherpes mexicanus</i>	XC794354	Eric DeFonso	<i>Podiceps auritus</i>	XC715920	Alan Dalton
<i>Centrocercus minimus</i>	XC100250	Andrew Spencer	<i>Podiceps auritus</i>	XC725086	Elias A. Ryberg
<i>Centrocercus minimus</i>	XC100250	Andrew Spencer	<i>Podiceps grisegena</i>	XC601774	Peter Ward and Ken Hall
<i>Centrocercus minimus</i>	XC100250	Andrew Spencer	<i>Podiceps grisegena</i>	XC804823	Uku Paal
<i>Centrocercus minimus</i>	XC100250	Andrew Spencer	<i>Podiceps nigricollis</i>	XC590654	Simon Elliott
<i>Centrocercus urophasianus</i>	XC368669	Sue Riffe	<i>Podiceps nigricollis</i>	XC601775	Peter Ward and Ken Hall
<i>Centrocercus urophasianus</i>	XC368674	Sue Riffe	<i>Podilymbus podiceps</i>	XC459166	Paul Marvin
<i>Centrocercus urophasianus</i>	XC634662	Scott Olmstead	<i>Podilymbus podiceps</i>	XC629177	Paul Marvin
<i>Centrocercus urophasianus</i>	XC77182	Andrew Spencer	<i>Podilymbus podiceps</i>	XC698503	Manuel Grosselet
<i>Chaetura pelagica</i>	XC180468	Dan Lane	<i>Podilymbus podiceps</i>	XC770459	Richard E. Webster
<i>Chaetura pelagica</i>	XC413369	Paul Marvin	<i>Poecile sclateri</i>	XC619624	Richard E. Webster
<i>Chaetura vauxi</i>	XC109774	Andrew Spencer	<i>Poliophtila caerulea</i>	XC331772	Andrew Spencer
<i>Chaetura vauxi</i>	XC150252	Paul Marvin	<i>Poliophtila caerulea</i>	XC392842	Manuel Grosselet
<i>Charadrius melodus</i>	XC328023	Patrick Turgeon	<i>Porphyrio martinica</i>	XC109039	Andrew Spencer
<i>Charadrius melodus</i>	XC494406	Will Sweet	<i>Porphyrio martinica</i>	XC147540	Robson Silva e Silva
<i>Charadrius montanus</i>	XC12209	Nathan Pieplow	<i>Porzana carolina</i>	XC477043	David Darrell-Lambert
<i>Charadrius montanus</i>	XC19091	Andrew Spencer	<i>Porzana carolina</i>	XC656414	Bruce Lagerquist
<i>Charadrius nivosus</i>	XC286696	Paul Marvin	<i>Progne subis</i>	XC649107	Paul Marvin
<i>Charadrius nivosus</i>	XC286814	Paul Marvin	<i>Progne subis</i>	XC675811	Scott Olmstead
<i>Charadrius vociferus</i>	XC601503	Christopher McPherson	<i>Psiloscops flammeolus</i>	XC13605	Andrew Spencer
<i>Charadrius vociferus</i>	XC754226	Manuel Grosselet	<i>Psiloscops flammeolus</i>	XC182640	Tim Avery
<i>Charadrius wilsonia</i>	XC551094	Isain Contreras Rodríguez	<i>Psittacara holochlorus</i>	XC277745	Paul Marvin
<i>Charadrius wilsonia</i>	XC574004	Manuel Grosselet	<i>Psittacara holochlorus</i>	XC900949	David Tatterstey
<i>Chloroceryle americana</i>	XC48818	Bernabe Lopez-Lanus	<i>Psittacara mitratus</i>	XC139485	Dan Lane

<i>Chloroceryle americana</i>	XC516956	Jacob Wijpkema	<i>Psittacara mitratus</i>	XC157990	Hans Matheve
<i>Chondestes grammacus</i>	XC423752	Ted Floyd	<i>Psittacara mitratus</i>	XC272935	Peter Boesman
<i>Chordeiles acutipennis</i>	XC109163	Paul Marvin	<i>Psittacula krameri</i>	XC707076	Richard E. Webster
<i>Chordeiles acutipennis</i>	XC574270	Paul Marvin	<i>Psittacula krameri</i>	XC267026	Andrew Spencer
<i>Chordeiles acutipennis</i>	XC582142	Paul Marvin	<i>Psittacula krameri</i>	XC759751	Romuald Mikusek
<i>Chordeiles gundlachi</i>	XC331763	Andrew Spencer	<i>Psittacula krameri</i>	XC812115	Paul Driver
<i>Chordeiles gundlachi</i>	XC331765	Andrew Spencer	<i>Psittacula krameri</i>	XC845916	Jorge Leitão
<i>Chordeiles minor</i>	XC333896	James Bradley	<i>Pycnonotus cafer</i>	XC460292	Peter Boesman
<i>Chordeiles minor</i>	XC660470	Bobby Wilcox	<i>Pycnonotus cafer</i>	XC741596	Sathyan Meppayur
<i>Circus hudsonius</i>	XC550984	Sue Riffe	<i>Pycnonotus jocosus</i>	XC547563	Andrew Spencer
<i>Circus hudsonius</i>	XC815811	Valerie Heemstra	<i>Pycnonotus jocosus</i>	XC769568	Ding Li Yong
<i>Cistothorus palustris</i>	XC722670	Barry Edmonston	<i>Pyrocephalus rubinus</i>	XC176958	Cleberton D. Bianchini
<i>Cistothorus stellaris</i>	XC659292	Paul Driver	<i>Pyrocephalus rubinus</i>	XC29069	Jason Beason
<i>Cistothorus stellaris</i>	XC659293	Paul Driver	<i>Pyrocephalus rubinus</i>	XC46384	Bernabe Lopez-Lanus
<i>Cistothorus stellaris</i>	XC685644	Meena Haribal	<i>Pyrocephalus rubinus</i>	XC788742	Marcela Morales sánchez
<i>Cistothorus stellaris</i>	XC815807	Valerie Heemstra	<i>Quiscalus quiscula</i>	XC786564	Paul Driver
<i>Clangula hyemalis</i>	XC106033	Ryan P. O'Donnell	<i>Rallus crepitans</i>	XC77512	Daniel Lane
<i>Clangula hyemalis</i>	XC203477	Andrew Spencer	<i>Rallus crepitans</i>	XC77531	Daniel Lane
<i>Clangula hyemalis</i>	XC323088	Peter Boesman	<i>Rallus elegans</i>	XC290118	J.R. Rigby
<i>Clangula hyemalis</i>	XC514046	Timo Janhonen	<i>Rallus elegans</i>	XC727691	Justin Lawson
<i>Coccyzus americanus</i>	XC100137	Mike Nelson	<i>Rallus limicola</i>	XC621187	Scott Crabtree
<i>Coccyzus americanus</i>	XC20962	Andrew Spencer	<i>Rallus limicola</i>	XC698488	Manuel Grosselet
<i>Coccyzus erythrophthalmus</i>	XC16526	Don Jones	<i>Rallus obsoletus</i>	XC543029	Jarrod Swackhamer
<i>Coccyzus erythrophthalmus</i>	XC16526	Don Jones	<i>Rallus obsoletus</i>	XC649092	Scott Olmstead
<i>Coccyzus minor</i>	XC265330	Andrew Spencer	<i>Recurvirostra americana</i>	XC554605	Thomas G. Graves
<i>Coccyzus minor</i>	XC590889	Simon Elliott	<i>Recurvirostra americana</i>	XC587206	Craig Robertson
<i>Colaptes auratus</i>	XC645833	Ted Floyd	<i>Rhynchophanes mccownii</i>	XC371731	Thomas Magarian
<i>Colaptes auratus</i>	XC777433	Valerie Heemstra	<i>Rhynchophanes mccownii</i>	XC371738	Thomas Magarian
<i>Colaptes chrysoides</i>	XC481160	Scott Olmstead	<i>Riparia riparia</i>	XC484331	Sebastian Andrejoff
<i>Colaptes chrysoides</i>	XC622425	Scott Crabtree	<i>Riparia riparia</i>	XC659405	Lars Edenius
<i>Colinus virginianus</i>	XC630289	Lawrence F Gardella	<i>Rostrhamus sociabilis</i>	XC454164	Rosendo Manuel Fraga
<i>Colinus virginianus</i>	XC703725	Antonio Xeira	<i>Rostrhamus sociabilis</i>	XC720696	Dante Buzzetti
<i>Columba livia</i>	XC726245	Olivier SWIFT	<i>Salpinctes obsoletus</i>	XC620784	Manuel Grosselet
<i>Columba livia</i>	XC726245	Olivier SWIFT	<i>Scolopax minor</i>	XC544586	Justin Watts
<i>Columbina inca</i>	XC268189	Richard E. Webster	<i>Scolopax minor</i>	XC709861	Joseph Fell
<i>Columbina inca</i>	XC623956	Manuel Grosselet	<i>Selasphorus calliope</i>	XC188263	Andrew Spencer
<i>Columbina passerina</i>	XC492787	Isain Contreras Rodríguez	<i>Selasphorus calliope</i>	XC188264	Andrew Spencer
<i>Columbina passerina</i>	XC693441	Peter Boesman	<i>Selasphorus platycercus</i>	XC132917	Richard E. Webster
<i>Coragyps atratus</i>	XC451477	Paul Marvin	<i>Selasphorus platycercus</i>	XC463254	Paul Marvin
<i>Coragyps atratus</i>	XC456651	David Monroy Rengifo	<i>Selasphorus rufus</i>	XC613904	Peter Ward and Ken Hall
<i>Corvus brachyrhynchos</i>	XC462767	Yaugen Slizh	<i>Selasphorus rufus</i>	XC76412	Andrew Spencer
<i>Corvus brachyrhynchos</i>	XC475165	Thomas Magarian	<i>Selasphorus sasin</i>	XC691195	Paul Marvin
<i>Corvus corax</i>	XC806240	Bobby Wilcox	<i>Selasphorus sasin</i>	XC691197	Paul Marvin
<i>Corvus corax</i>	XC807044	Ed Pandolfino	<i>Setophaga aestiva</i>	XC371864	Paolo Matteucci
<i>Corvus cryptoleucus</i>	XC456970	Paul Marvin	<i>Setophaga aestiva</i>	XC563515	Carlos Gonzalez
<i>Corvus cryptoleucus</i>	XC511416	Bobby Wilcox	<i>Setophaga discolor</i>	XC691783	Christopher McPherson
<i>Corvus ossifragus</i>	XC264970	Ted Floyd	<i>Setophaga graciae</i>	XC477833	Bobby Wilcox
<i>Corvus ossifragus</i>	XC745328	William Whitehead	<i>Setophaga graciae</i>	XC700830	Richard E. Webster
<i>Coturnicops noveboracensis</i>	XC103086	Andrew Spencer	<i>Setophaga kirtlandii</i>	XC419385	Sue Riffe
<i>Coturnicops noveboracensis</i>	XC729035	Chris Butler	<i>Setophaga kirtlandii</i>	XC419387	Sue Riffe
<i>Crotophaga sulcirostris</i>	XC327560	Manuel Grosselet	<i>Setophaga palmarum</i>	XC189607	Richard E. Webster
<i>Crotophaga sulcirostris</i>	XC623954	Manuel Grosselet	<i>Setophaga palmarum</i>	XC653737	Matt Wistrand
<i>Cyanocitta cristata</i>	XC555073	Lori Zabel	<i>Setophaga pensylvanica</i>	XC600741	Christopher McPherson
<i>Cyanocitta cristata</i>	XC721247	Thomas Ryder Payne	<i>Setophaga pensylvanica</i>	XC814843	Denis Provencher
<i>Cygnus buccinator</i>	XC298756	Antonio Xeira	<i>Sialia mexicana</i>	XC71747	Richard E. Webster
<i>Cygnus buccinator</i>	XC636462	Thomas Ryder Payne	<i>Sialia sialis</i>	XC408997	Frank Lambert
<i>Cygnus olor</i>	XC48742	Ian Davies	<i>Sialia sialis</i>	XC601011	Christopher McPherson
<i>Cygnus olor</i>	XC604181	Calum Mckellar	<i>Sialia sialis</i>	XC712412	Patrick J. Blake
<i>Cygnus olor</i>	XC728386	Simon Elliott	<i>Sitta carolinensis</i>	XC337748	Ted Floyd
<i>Cygnus olor</i>	XC764113	Bodo Sonnenburg	<i>Sitta carolinensis</i>	XC371116	Lance A. M. Benner
<i>Cyananthus latirostris</i>	ML121949	Curtis Marantz	<i>Spatula clypeata</i>	XC501879	Olivier SWIFT
<i>Cyananthus latirostris</i>	XC432720	Lauren Harter	<i>Spatula clypeata</i>	XC644498	Jarek Matusiak
<i>Cypseloides niger</i>	XC677270	Richard E. Webster	<i>Spatula cyanoptera</i>	XC22389	Israel Aragon
<i>Cypseloides niger</i>	XC677210	Richard E. Webster	<i>Spatula cyanoptera</i>	XC877014	Skyler Bol
<i>Cyrtonyx montezumae</i>	XC3983	Nathan Pieplow	<i>Spatula discors</i>	XC162091	Paul Marvin
<i>Cyrtonyx montezumae</i>	XC492136	Diana Doyle	<i>Spatula discors</i>	XC218547	Peter Boesman
<i>Dendragapus fuliginosus</i>	ML2393	Harry G. Lumsden	<i>Sphyrapicus nuchalis</i>	XC326115	Bruce Lagerquist
<i>Dendragapus fuliginosus</i>	XC559001	Ron Overholtz	<i>Sphyrapicus nuchalis</i>	XC354612	Thomas Magarian
<i>Dendragapus obscurus</i>	XC33714	Daniel Lane	<i>Sphyrapicus nuchalis</i>	XC354612	Thomas Magarian
<i>Dendragapus obscurus</i>	XC470937	Bruce Lagerquist	<i>Sphyrapicus nuchalis</i>	XC663246	Richard E. Webster
<i>Dendrocygna autumnalis</i>	XC564970	Isain Contreras Rodríguez	<i>Sphyrapicus ruber</i>	XC363352	Kristie Nelson
<i>Dendrocygna autumnalis</i>	XC858089	Valerie Heemstra	<i>Sphyrapicus ruber</i>	XC36976	Taylor Brooks
<i>Dendrocygna bicolor</i>	XC147332	Paul Marvin	<i>Sphyrapicus ruber</i>	XC408661	Frank Lambert
<i>Dendrocygna bicolor</i>	XC257267	John V. Moore	<i>Sphyrapicus ruber</i>	XC76213	Andrew Spencer
<i>Dryobates nuttallii</i>	XC161352	Paul Marvin	<i>Sphyrapicus thyroideus</i>	XC13889	Andrew Spencer
<i>Dryobates nuttallii</i>	XC349729	Paul Marvin	<i>Sphyrapicus thyroideus</i>	XC370020	Lance A. M. Benner
<i>Dryobates nuttallii</i>	XC408009	Frank Lambert	<i>Sphyrapicus thyroideus</i>	XC539025	Bruce Lagerquist
<i>Dryobates nuttallii</i>	XC703746	Paul Marvin	<i>Sphyrapicus thyroideus</i>	XC663254	Richard E. Webster
<i>Dryobates pubescens</i>	XC531280	Thomas Magarian	<i>Sphyrapicus varius</i>	XC21100	Andrew Spencer
<i>Dryobates pubescens</i>	XC531292	Thomas Magarian	<i>Sphyrapicus varius</i>	XC325526	Ross Gallardy
<i>Dryobates pubescens</i>	XC590054	William Whitehead	<i>Sphyrapicus varius</i>	XC388169	Martin St-Michel
<i>Dryobates pubescens</i>	XC673147	Paul Marvin	<i>Sphyrapicus varius</i>	XC612652	Peter Ward and Ken Hall
<i>Dryobates scalaris</i>	XC505919	Russ Wigh	<i>Spilopelia chinensis</i>	XC875469	Ray Tsu
<i>Dryobates scalaris</i>	XC522002	Jarrod Swackhamer	<i>Spilopelia chinensis</i>	XC879489	Geoff Carey
<i>Dryobates scalaris</i>	XC540657	Isain Contreras Rodríguez	<i>Spinus lawrencei</i>	XC315415	Lance A. M. Benner
<i>Dryobates scalaris</i>	XC617962	Richard E. Webster	<i>Spinus lawrencei</i>	XC483003	Lance A. M. Benner
<i>Dryocopus pileatus</i>	XC157763	Paul Driver	<i>Spinus pinus</i>	XC205802	Eric DeFonso
<i>Dryocopus pileatus</i>	XC402958	Bruce Lagerquist	<i>Spinus pinus</i>	XC544062	Steve Hampton
<i>Dryocopus pileatus</i>	XC566467	Matt Wistrand	<i>Spinus pinus</i>	XC574657	Richard E. Webster
<i>Dryocopus pileatus</i>	XC569933	Russ Wigh	<i>Spinus psaltria</i>	XC144120	Lauren Harter
<i>Dumetella carolinensis</i>	XC807482	Barry Edmonston	<i>Spinus psaltria</i>	XC624542	Richard E. Webster
<i>Dumetella carolinensis</i>	XC814892	Richard E. Webster	<i>Spinus tristis</i>	XC636512	Thomas Ryder Payne
<i>Dumetella carolinensis</i>	XC814895	Richard E. Webster	<i>Spinus tristis</i>	XC723797	Jim Berry
<i>Dumetella carolinensis</i>	XC818869	Bobby Wilcox	<i>Spinus tristis</i>	XC756999	Robert Benson
<i>Egretta caerulea</i>	XC395486	Paul Marvin	<i>Spizella pusilla</i>	XC807577	David A. Brinkman

<i>Egretta caerulea</i>	XC451872	Paul Marvin	<i>Streptopelia decaocto</i>	XC760695	Pere Josa
<i>Egretta rufescens</i>	XC130845	Andrew Spencer	<i>Streptopelia decaocto</i>	XC783411	Jorge Leitão
<i>Egretta rufescens</i>	XC452975	Paul Marvin	<i>Strix nebulosa</i>	XC655482	Lars Edenius
<i>Egretta thula</i>	XC481927	Paul Marvin	<i>Strix nebulosa</i>	XC884395	Ulf Elman
<i>Egretta thula</i>	XC654328	Dante Buzzetti	<i>Strix occidentalis</i>	ML274753161	Andrew Spencer
<i>Egretta tricolor</i>	XC102894	Andrew Spencer	<i>Strix varia</i>	XC727743	Barry Edmonston
<i>Egretta tricolor</i>	XC519779	Isain Contreras Rodríguez	<i>Strix varia</i>	XC801126	Anthony Gliozzo
<i>Elanoides forficatus</i>	XC405767	Paul Marvin	<i>Sturnus vulgaris</i>	XC197289	Paul Marvin
					Albert Lastukhin & Max lastukhin
<i>Elanoides forficatus</i>	XC531920	John A. Middleton Jr.	<i>Sturnus vulgaris</i>	XC233940	lastukhin
<i>Elanus leucurus</i>	XC565245	Steve Hampton	<i>Sturnus vulgaris</i>	XC361481	Thomas Magarian
<i>Elanus leucurus</i>	XC584969	Paul Marvin	<i>Sturnus vulgaris</i>	XC452776	Paul Marvin
<i>Empidonax fulvifrons</i>	XC160996	Paul Marvin	<i>Surnia ulula</i>	XC793932	Teet Sirotkin
<i>Empidonax fulvifrons</i>	XC315746	Nancy Hetrick	<i>Surnia ulula</i>	XC862737	Stein Ø. Nilsen
<i>Eudocimus albus</i>	XC163177	Paul Marvin	<i>Tachybaptus dominicus</i>	XC627755	Manuel Grosselet
<i>Eudocimus albus</i>	XC829401	PT xiao	<i>Tachybaptus dominicus</i>	XC661638	Manuel Grosselet
<i>Eugenes fulgens</i>	XC744810	Manuel Grosselet	<i>Tachybaptus dominicus</i>	XC704344	Jayrson Araujo De Oliveira
<i>Eugenes fulgens</i>	XC747195	Manuel Grosselet	<i>Tachybaptus dominicus</i>	XC800134	Manuel Grosselet
<i>Falco columbarius</i>	XC587990	Simon Elliott	<i>Tetraogallus himalayensis</i>	XC813673	Peter Boesman
<i>Falco columbarius</i>	XC731075	Lars Edenius	<i>Tetraogallus himalayensis</i>	XC813675	Peter Boesman
<i>Falco mexicanus</i>	XC109297	Nathan Pieplow	<i>Toxostoma bendirei</i>	XC408176	Frank Lambert
<i>Falco mexicanus</i>	XC386260	Thomas Magarian	<i>Toxostoma bendirei</i>	XC409670	Frank Lambert
<i>Falco peregrinus</i>	XC408644	Frank Lambert	<i>Toxostoma redivivum</i>	XC320588	Lance A. M. Benner
<i>Falco peregrinus</i>	XC545881	Thomas Magarian	<i>Toxostoma redivivum</i>	XC444656	Lance A. M. Benner
<i>Falco sparverius</i>	XC565033	Thomas G. Graves	<i>Toxostoma redivivum</i>	XC444658	Lance A. M. Benner
<i>Falco sparverius</i>	XC603740	Peter Ward and Ken Hall	<i>Toxostoma redivivum</i>	XC806203	Bobby Wilcox
<i>Fulica americana</i>	XC509714	Sunny Tseng	<i>Tringa melanoleuca</i>	XC236716	Iain
<i>Fulica americana</i>	XC546224	Richard E. Webster	<i>Tringa melanoleuca</i>	XC606570	Peter Ward and Ken Hall
<i>Gallinago delicata</i>	XC342368	Tero Linjama	<i>Tringa semipalmata</i>	XC564233	Sue Riffe
<i>Gallinula galeata</i>	XC460760	Paul Marvin	<i>Tringa semipalmata</i>	XC635271	Paul Marvin
<i>Gallinula galeata</i>	XC493683	Paul Marvin	<i>Tringa semipalmata</i>	XC651135	Paul Driver
<i>Gallus gallus</i>	XC689265	Ding Li Yong	<i>Tringa semipalmata</i>	XC723894	Molly Jacobson
<i>Gallus gallus</i>	XC773338	Jelle Scharringa	<i>Tringa solitaria</i>	XC211215	Davyd Betchkal
<i>Geococcyx californianus</i>	XC163982	Paul Marvin	<i>Tringa solitaria</i>	XC445577	Laura Stewart
<i>Geococcyx californianus</i>	XC254893	Richard E. Webster	<i>Troglodytes hiemalis</i>	XC814613	Christian Kerihuel
<i>Geococcyx californianus</i>	XC534824	Caleb Helsel	<i>Tympanuchus cupido</i>	XC469168	Ross Gallardy
<i>Geococcyx californianus</i>	XC610997	Richard E. Webster	<i>Tympanuchus cupido</i>	XC469173	Ross Gallardy
<i>Geranoaetus albicaudatus</i>	XC374799	Mary Beth Stowe	<i>Tympanuchus cupido</i>	XC685651	Meena Haribal
<i>Geranoaetus albicaudatus</i>	XC385597	Albert Lastukhin	<i>Tympanuchus cupido</i>	XC77187	Andrew Spencer
<i>Glaucidium gnoma</i>	XC202603	Lance A. M. Benner	<i>Tympanuchus pallidicinctus</i>	XC33958	Andrew Spencer
<i>Glaucidium gnoma</i>	XC646754	Alberto Lobato	<i>Tympanuchus pallidicinctus</i>	XC33960	Andrew Spencer
<i>Grus americana</i>	XC38536	Bill Evans	<i>Tympanuchus pallidicinctus</i>	XC33961	Andrew Spencer
<i>Grus americana</i>	XC533637	Sue Riffe	<i>Tympanuchus pallidicinctus</i>	XC33962	Andrew Spencer
<i>Gymnogyps californianus</i>	ML163901	Vincent Gerwe	<i>Tympanuchus phasianellus</i>	XC362541	Frank Lambert
<i>Gymnorhinus cyanocephalus</i>	XC215463	Kristie Nelson	<i>Tympanuchus phasianellus</i>	XC362548	Frank Lambert
<i>Gymnorhinus cyanocephalus</i>	XC362423	Frank Lambert	<i>Tympanuchus phasianellus</i>	XC557275	Paul Dickinsn
<i>Haematopus bachmani</i>	XC282104	Paul Marvin	<i>Tympanuchus phasianellus</i>	XC77227	Andrew Spencer
<i>Haematopus bachmani</i>	XC282178	Paul Marvin	<i>Tyrannus dominicensis</i>	XC357038	Paul Driver
<i>Haematopus palliatus</i>	XC571864	Manuel Grosselet	<i>Tyrannus dominicensis</i>	XC591013	Simon Elliott
<i>Haematopus palliatus</i>	XC572455	Isain Contreras Rodríguez	<i>Tyrannus forficatus</i>	XC323788	Terry Davis
<i>Haemorhous mexicanus</i>	XC691598	Christopher McPherson	<i>Vireo bellii</i>	XC661431	Richard E. Webster
<i>Haemorhous mexicanus</i>	XC720339	Thomas Ryder Payne	<i>Vireo flavifrons</i>	XC501230	Jacob Saucier
<i>Haemorhous mexicanus</i>	XC814493	Valerie Heemstra	<i>Vireo griseus</i>	XC452765	Paul Marvin
<i>Haliaeetus leucocephalus</i>	XC636910	Beverly Hallberg	<i>Vireo griseus</i>	XC684345	Brad Banner
<i>Haliaeetus leucocephalus</i>	XC703906	Steve Hampton	<i>Vireo griseus</i>	XC714441	Bruce Lagerquist
<i>Haliaeetus leucocephalus</i>	XC769877	Russ Wigh	<i>Vireo griseus</i>	XC742516	Robert Benson
<i>Haliaeetus leucocephalus</i>	XC779509	Steve Hampton	<i>Zenaida asiatica</i>	XC782417	Manuel Grosselet
		Jorge de Leon Cardozo &			
<i>Helmitheros vermivorum</i>	XC730179	Susan Hochgraf	<i>Zenaida asiatica</i>	XC785642	Sue Riffe
<i>Hesperiphona vespertina</i>	XC153406	Andrew Spencer	<i>Zenaida macroura</i>	XC613539	Peter Ward and Ken Hall
<i>Hesperiphona vespertina</i>	XC555496	Ron Overholtz	<i>Zenaida macroura</i>	XC696289	Manuel Grosselet
<i>Himantopus mexicanus</i>	XC587207	Craig Robertson			

Pan-European Common Bird Monitoring Scheme (PECBMS) Coordinators.

Scheme	Organisation	Co-ordinator
Austria	BirdLife Austria	Norbert Teufelbauer
Belgium	Aves-Natagora	Antoine Derouaux
Czechia	Institute of Environmental Studies, Faculty of Science, Charles University	Jiří Reif
Czechia	Czech Society for Ornithology	Petr Voříšek
Czechia	Czech Society for Ornithology	Zdeněk Vermouzek
Denmark	Danish Ornithological Society	Daniel Palm
Finland	Zoological Museum, Finnish Museum of Natural History	Aleksi Lehikoinen
France	Muséum national d'Histoire naturelle	Benoît Fontaine
France	Muséum national d'Histoire naturelle	Frédéric Jiguet
Ireland	BirdWatch Ireland	Lesley Lewis
Italy	Lombardy Foundation for the environment	Mattia Brambilla
Italy	Lega Italiana Protezione Uccelli (LIPU)	Laura Silva
Italy		Gianpiero Calvi
Netherlands	Sovon, Dutch Center for Field Ornithology	Chris van Turnhout
Norway	NINA Norwegian Institute for Nature Research	John Atle Kålås
Norway	NOF-BirdLife Norway	Ingar Jostein
	Polish Society for the Protection of Birds (OTOP) and Museum and	
Poland	Institute of Zoology, Polish Academy of Sciences	Tomasz Chodkiewicz
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Spain	Sociedad Española de Ornitología (SEO/BirdLife)	Juan Carlos del Moral
Spain-Catalonia	Institut Català d'Ornitologia	Sergi Herrando
Spain-Catalonia	Institut Català d'Ornitologia	Marc Anton
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UK	BTO	David Noble
UK	BTO	Dario Massimino
Czech Republic	PECBMS	Anna Gamero
Czech Republic	PECBMS	Alena Klvaňová
Germany		Sven Trautmann
Germany		Johannes Kamp

Appendix B: Chapter 4

Predictors of Δ_{syntopy} when restricted to pairs that share the same habitat type (n = 871 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bolded rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.075 (95% CI = 0.001, 0.347).

	Median	95% CI		pMCMC	
Intercept	0.176	-0.233	0.598	0.331	
Interspecifically territorial	0.263	0.012	0.521	0.044	*
Hybridising	0.080	-0.200	0.369	0.558	
Same intraspecific territory type	0.027	-0.159	0.217	0.750	
Patristic distance	0.068	-0.049	0.226	0.226	
Proportion shared axes	-0.055	-0.128	0.017	0.137	
Both cavity nesters	0.046	-0.018	0.111	0.142	
Intermediate habitat	-0.153	-0.450	0.141	0.302	
Complex habitat	-0.241	-0.516	0.031	0.075	
Mass difference	0.042	-0.048	0.130	0.350	
Bill difference	0.014	-0.067	0.097	0.757	
Both undergone range expansion	0.007	-0.172	0.190	0.971	
Both undergone range contraction	-0.040	-0.188	0.106	0.568	
Syntopy 1997-2000	-0.468	-0.531	-0.405	<0.0005	***

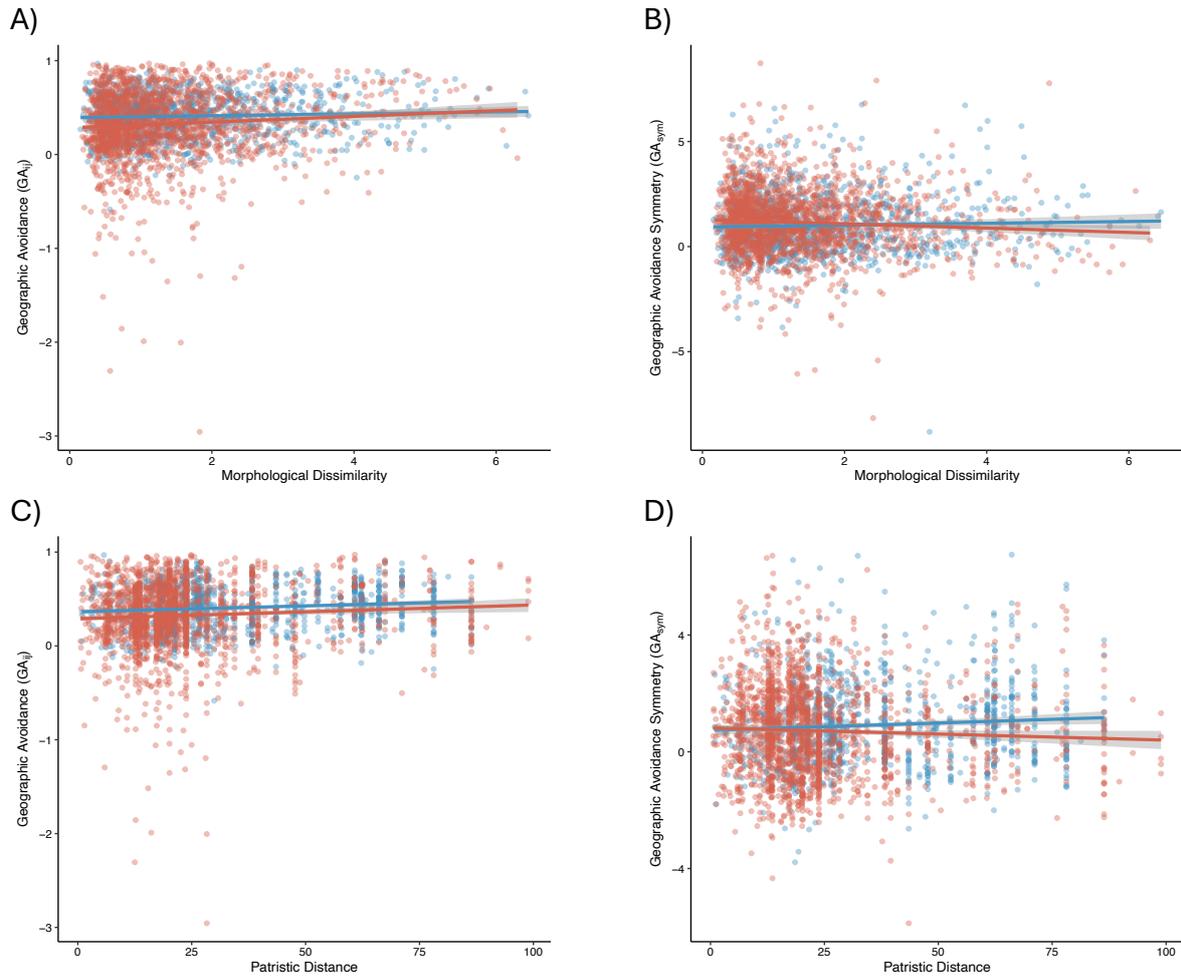
Significance codes: <0.05 *, <0.01 **, <0.001 ***

Predictors of Δ_{syntopy} when restricted to pairs that share the same intraspecific territory type (n = 1221 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are shown. Bolded rows indicate fixed effects with 95% credibility intervals that do not overlap 0. pMCMC values are from one chain (results are similar across all chains). The mean phylogenetic signal (λ) for this model was 0.239 (95% CI = 0.012, 0.643).

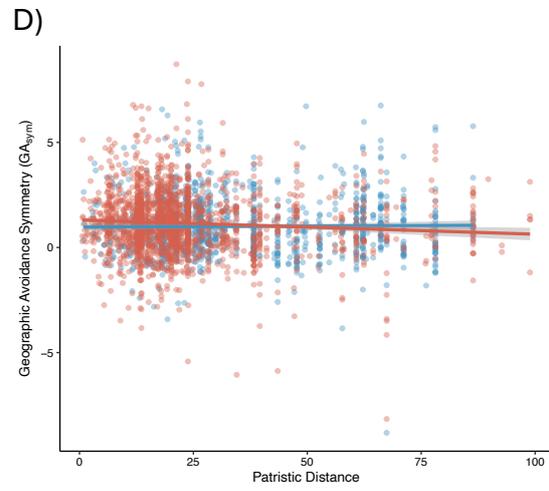
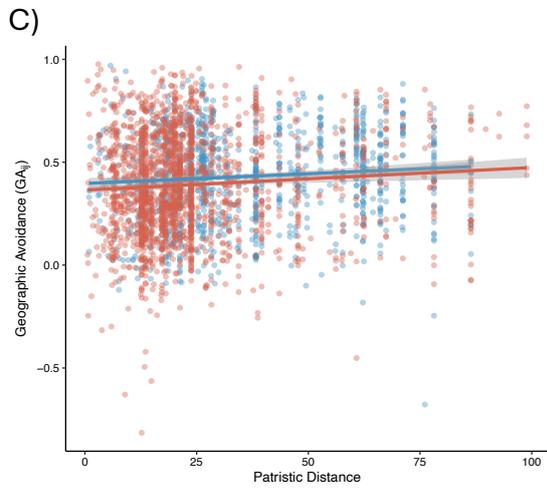
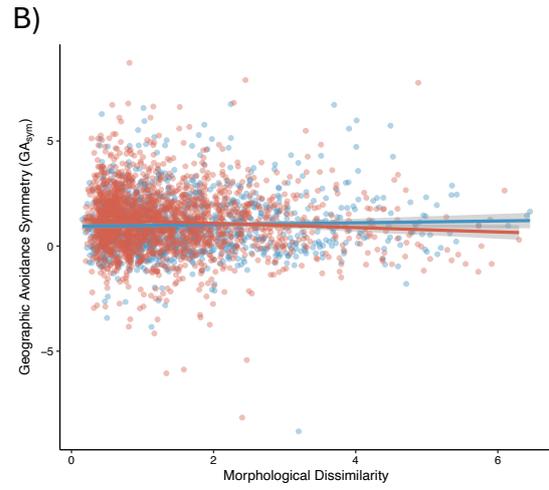
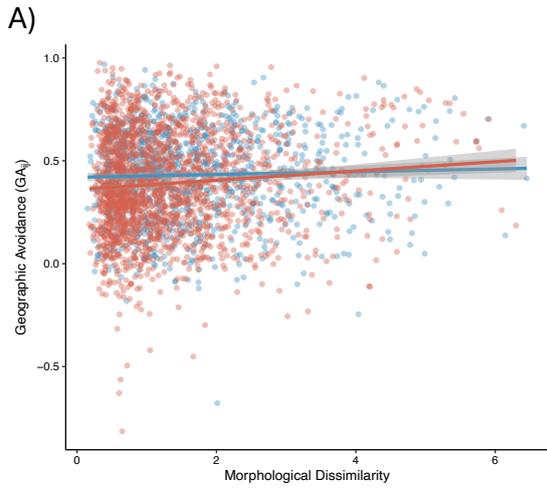
	Median	95% CI		pMCMC	
Intercept	-2.196	-3.356	-1.238	<0.0005	***
Interspecifically territorial	0.329	0.088	0.567	0.007	**
Hybridising	-0.037	-0.290	0.212	0.802	
Intraspecific territoriality 4	2.036	1.136	3.042	<0.0005	***
Intraspecific territoriality 5	2.146	1.290	3.138	<0.0005	***
Patristic distance	0.070	-0.161	0.276	0.419	
Proportion shared axes	0.041	-0.023	0.104	0.202	
Both cavity nesters	-0.035	-0.501	0.435	0.886	
Same habitat	0.154	0.040	0.267	0.011	*
Mass difference	0.047	-0.024	0.116	0.185	
Bill difference	0.000	-0.066	0.069	0.998	
Both undergone range expansion	0.067	-0.090	0.225	0.380	
Both undergone range contraction	0.083	-0.049	0.207	0.201	
Syntopy 1997-2000	-0.454	-0.506	-0.401	<0.0005	***

Significance codes: <0.05 *, <0.01 **, <0.001 ***

Appendix C: Chapter 5



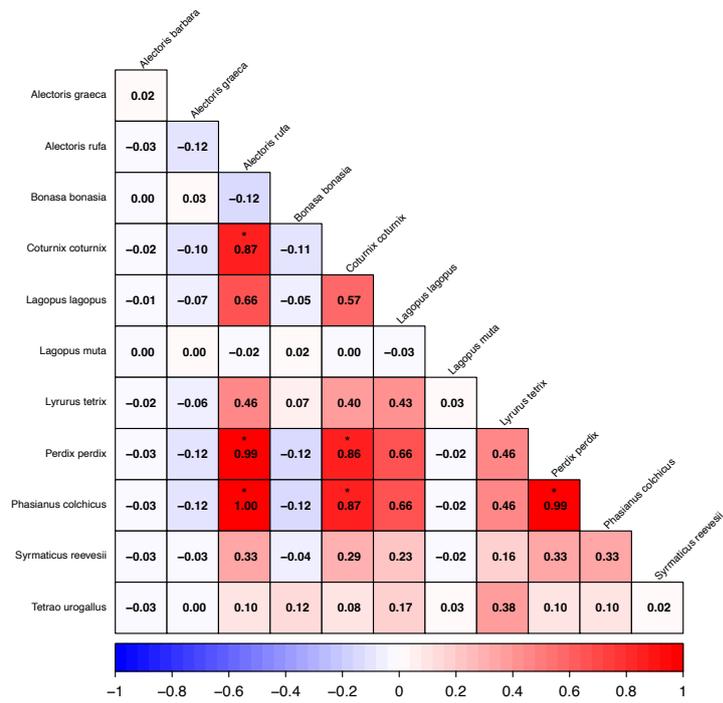
The effect of morphological dissimilarity (A, B) and patristic distance on Geographic Avoidance (GA_{ij}) (A, C) and GA_{ij} symmetry (GA_{sym}) (B, D). Lines and points are coloured by continent. Blue: Eurasia, Red: North America. Data from long clip.



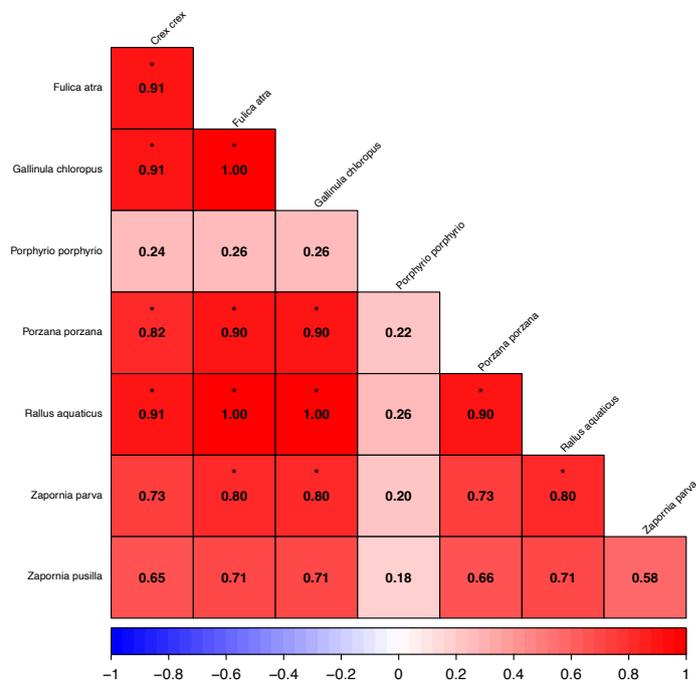
The effect of morphological dissimilarity (A, B) and patristic distance on Geographic Avoidance (GA_{ij}) (A, C) and GA_{ij} symmetry (GA_{sym}) (B, D). Lines and points are coloured by continent. Blue: Eurasia, Red: North America. Data from lat/long clip.

APPENDIX D: Chapter 6

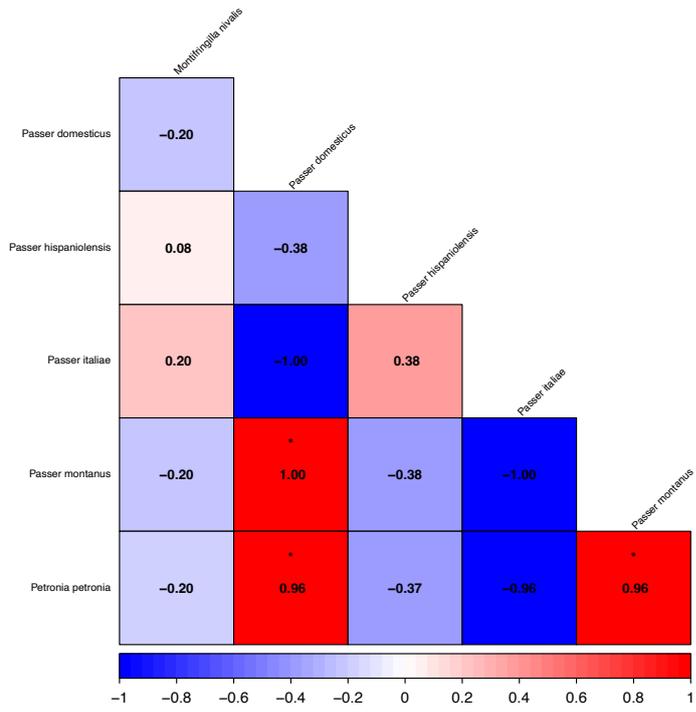
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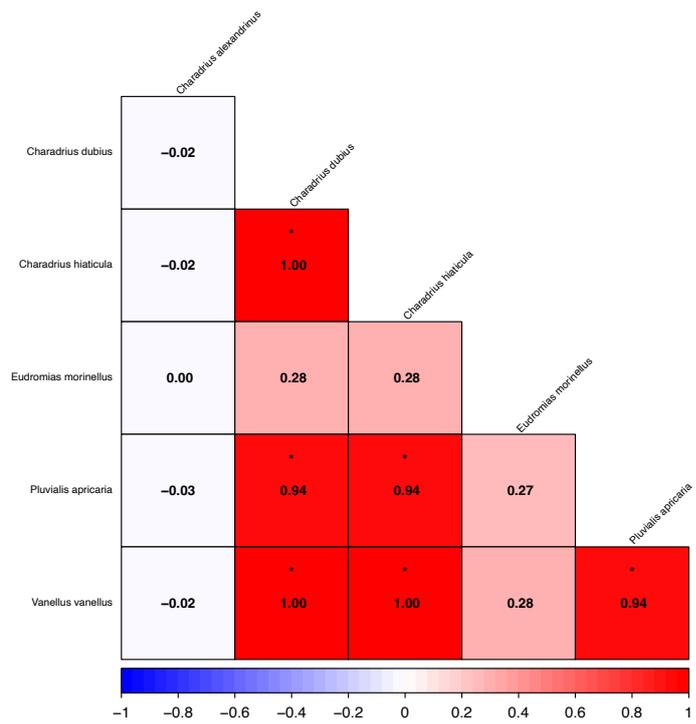
Rallidae



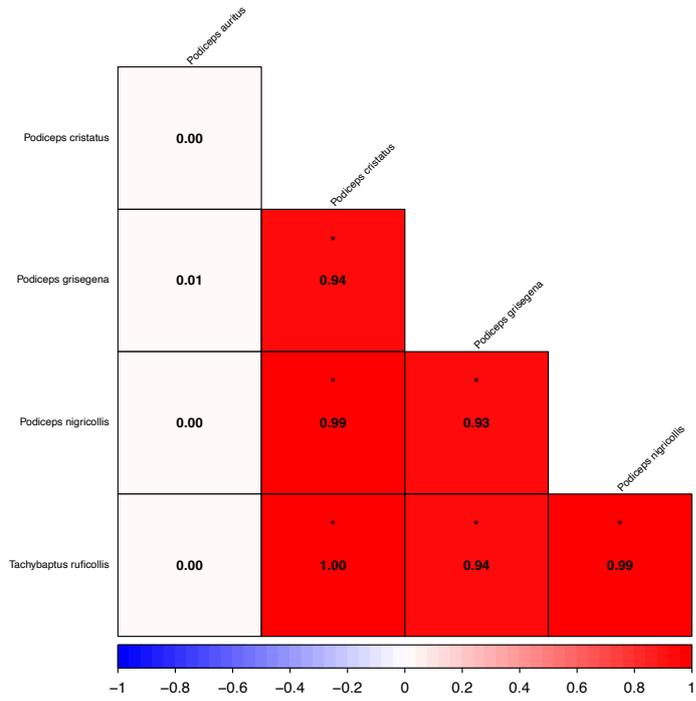
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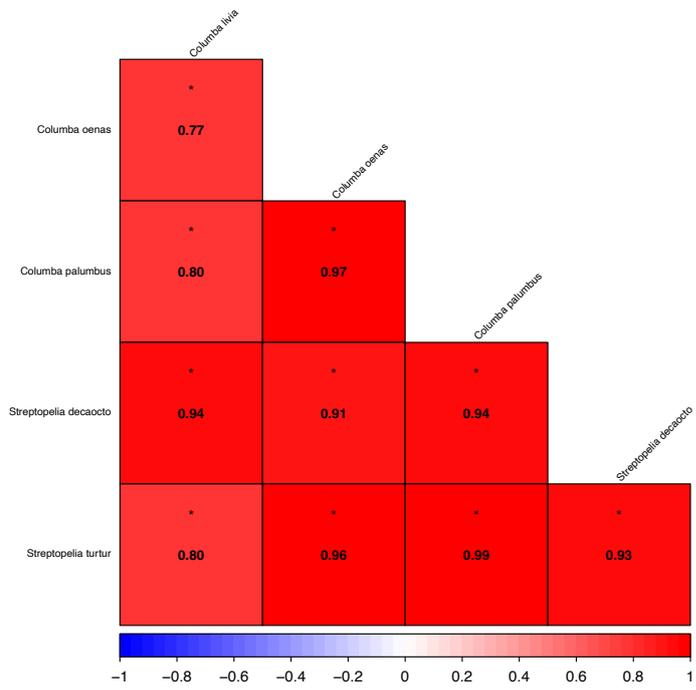
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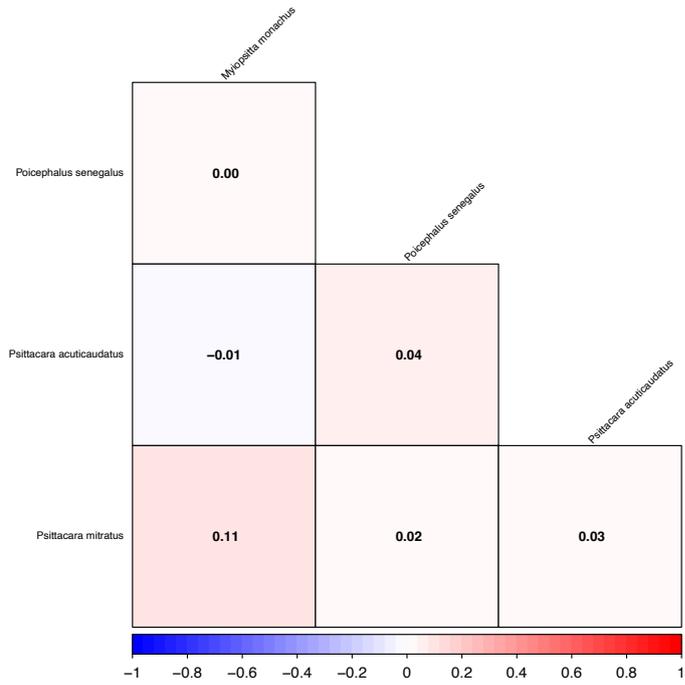
Podicipedidae



Columbidae

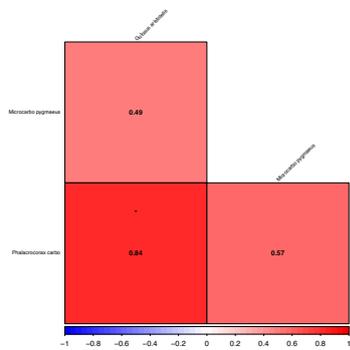


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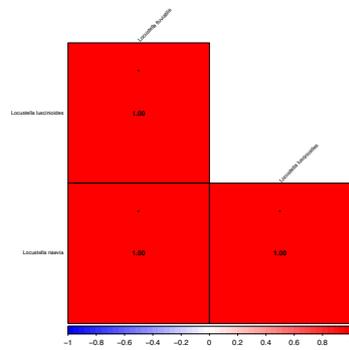


Phalacrocoracidae

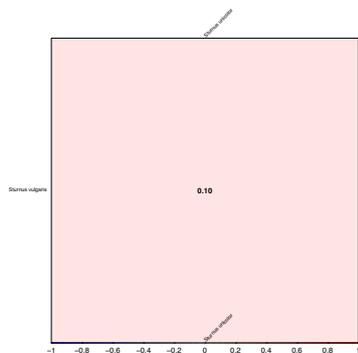
Locustellidae



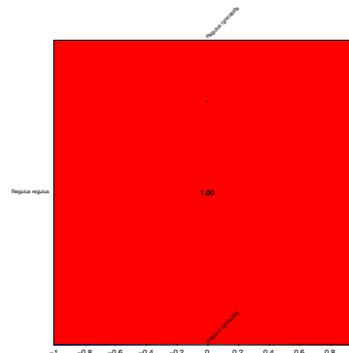
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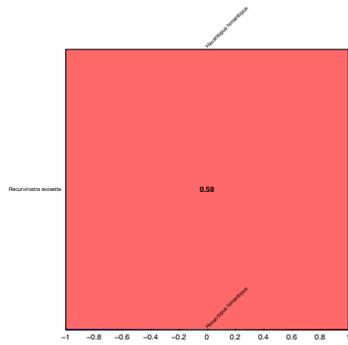
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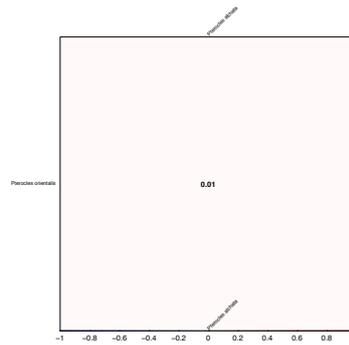
Recurvirostridae



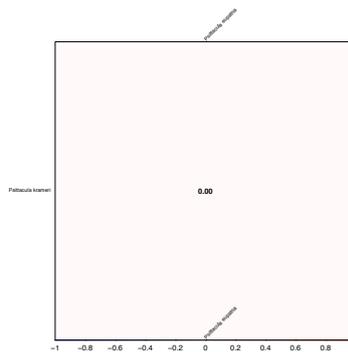
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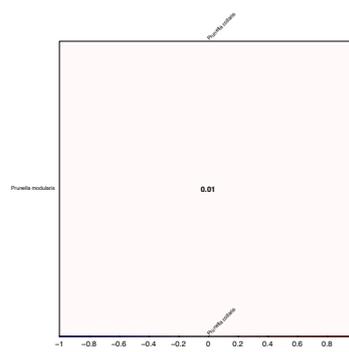
Psittaculidae



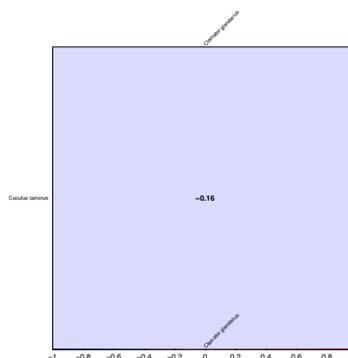
Prunellidae



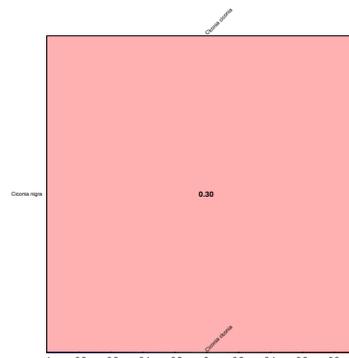
Cuculidae



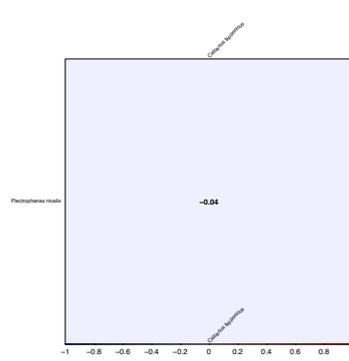
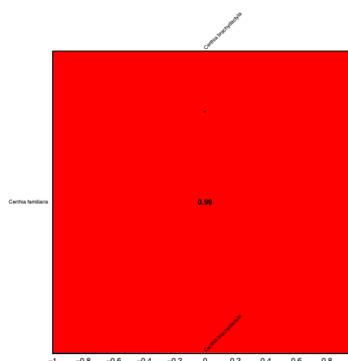
Ciconiidae



Certhiidae



Calcaridae



Residual association matrices for a variety of European families. Red indicates positive associations between species and blue indicates negative associations, after accounting for modelled environmental covariates. Asterisks indicate a posterior mean support level greater than 0.9, in that more than 90% of the MCMC iteration estimates had the same sign as the posterior mean.

