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

NESBIT, DANIEL,ANDREW

NESBIT, DANIEL,ANDREW (2025) *The impact of competition on global-change induced range shifts in birds* , Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/16360/

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.

Contents

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:

Daniel A. Nesbit: Conceptualisation (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Project administration- Supporting, Visualisation (lead); Writing – original draft (equal); Writing – review and editing (equal).

Madeline C. Cowen: Data curation (equal); Writing – original draft-Supporting, Writing – review and editing-Supporting.

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

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; Zuckerberg, 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, Atauchi, 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 Bücker, 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 Bücker, 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 occidentails 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. novaezelandiae*) (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.

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

Where N^y_1 is the number of records of species 1 in year y, N^y_2 is the number of records of species 2 in year y, $N^y_{1,2}$ is the number of eBird records of species 1 within 39.4km of species 2 within year y and $N^y_{2,1}$ 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) $$Mean\ sympatry = \frac{1}{10}\sum_{y=1}^{10} Sympatry_y$$

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 ($n^y_{1,2}$, $n^y_{2,1}$).

(Eq. 3) $$Syntopy_y = \frac{1}{2}\left(\frac{n^y_{1,2}}{N^y_1} + \frac{n^y_{2,1}}{N^y_2}\right)$$

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

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.

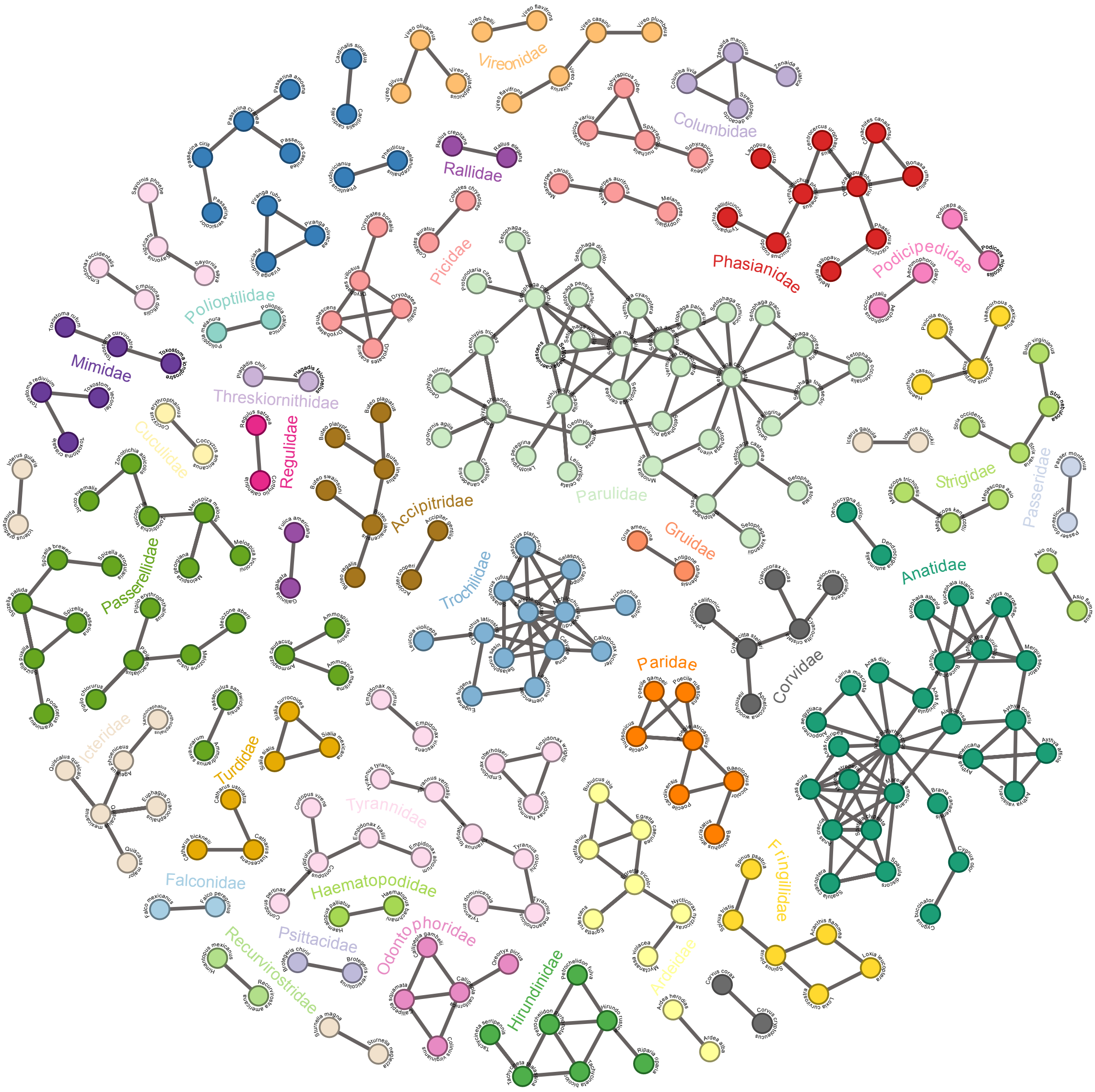


Figure 1. Network of North American hybridisation. Nodes represent species (coloured by family), and lines indicate recorded hybridisation in the wild. Non-hybridising pairs are not included.

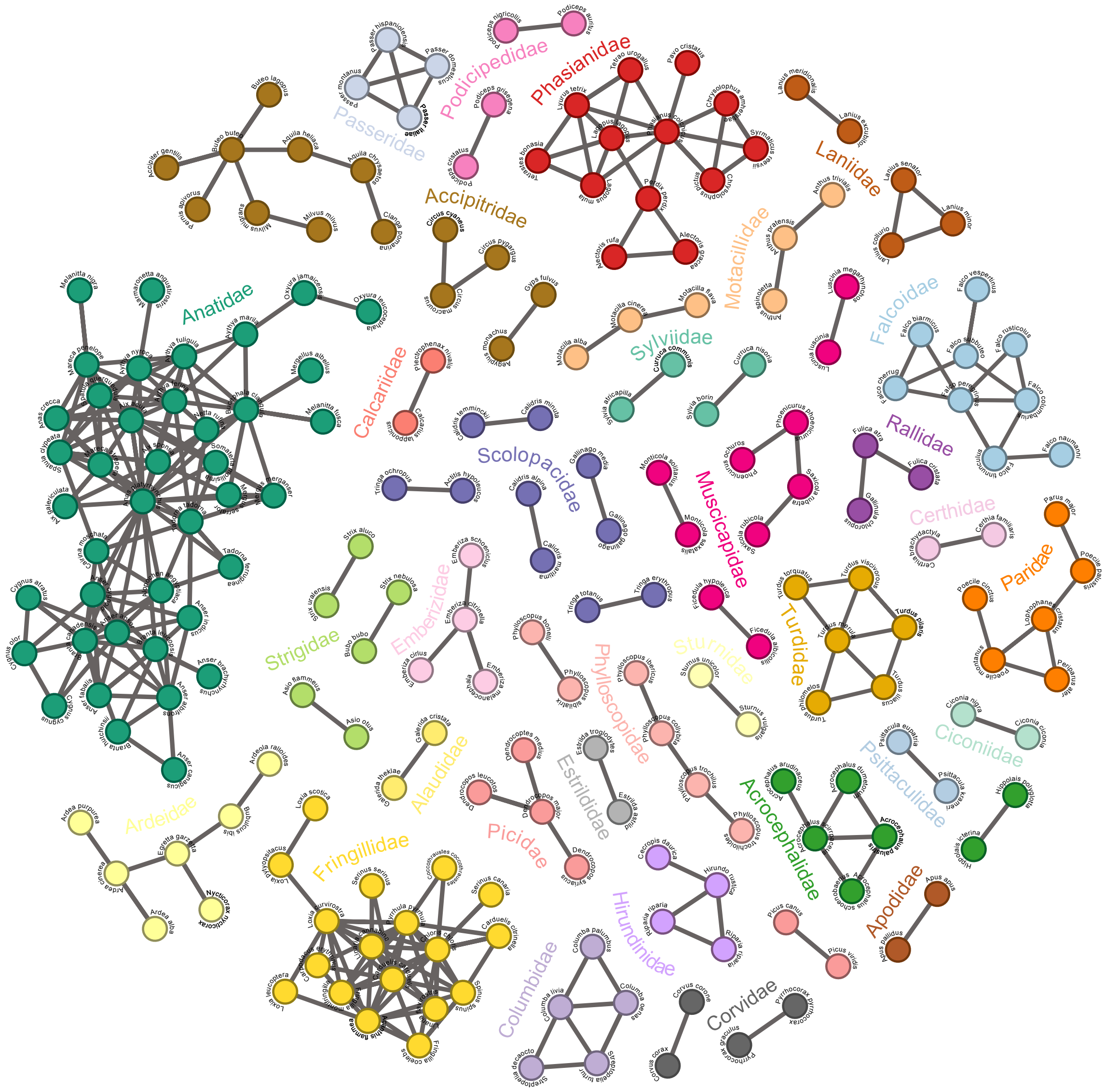
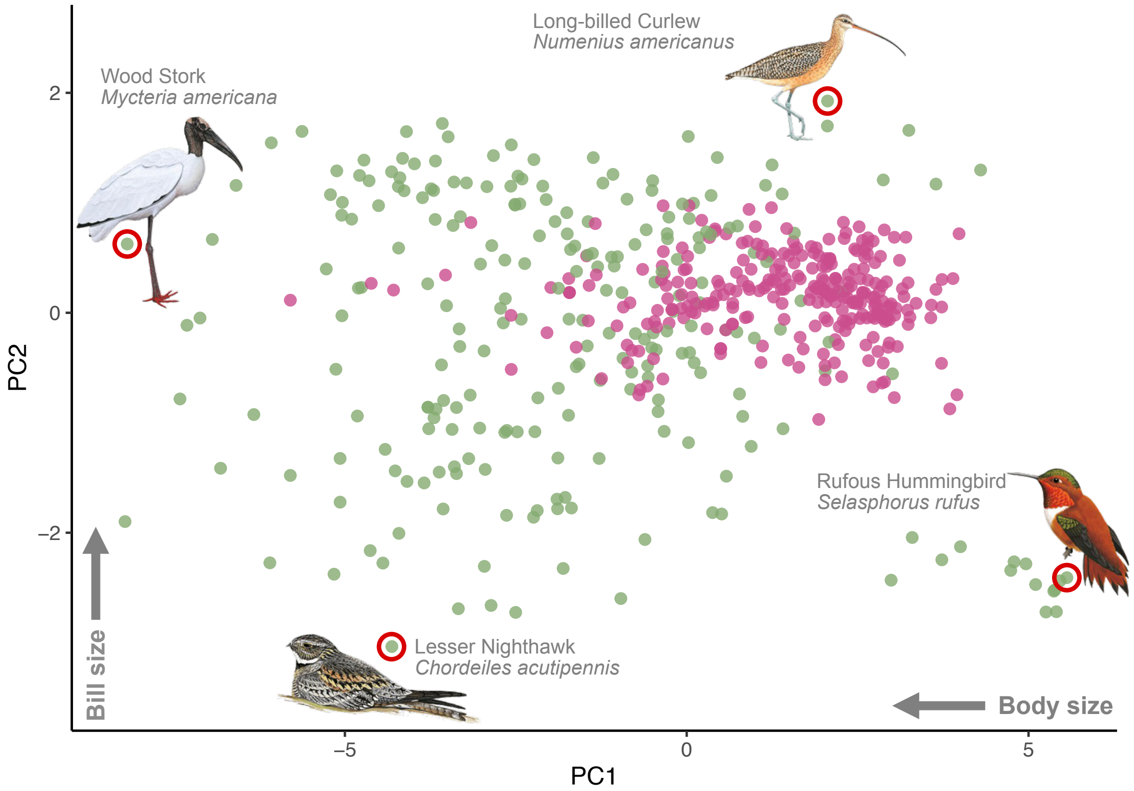


Figure 2. Network of European hybridisation. Nodes represent species (coloured by family), and lines indicate recorded hybridisation in the wild. Non-hybridising pairs are not included.

A) North American morpho-space



B) European morpho-space

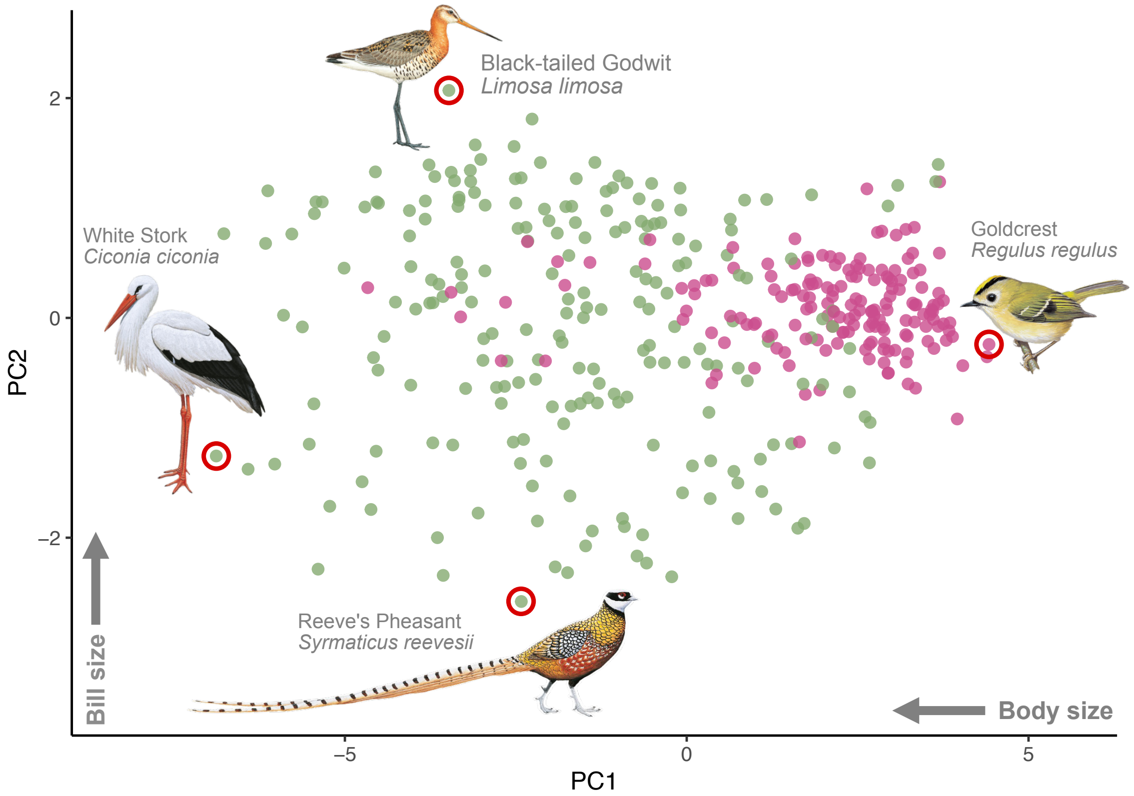
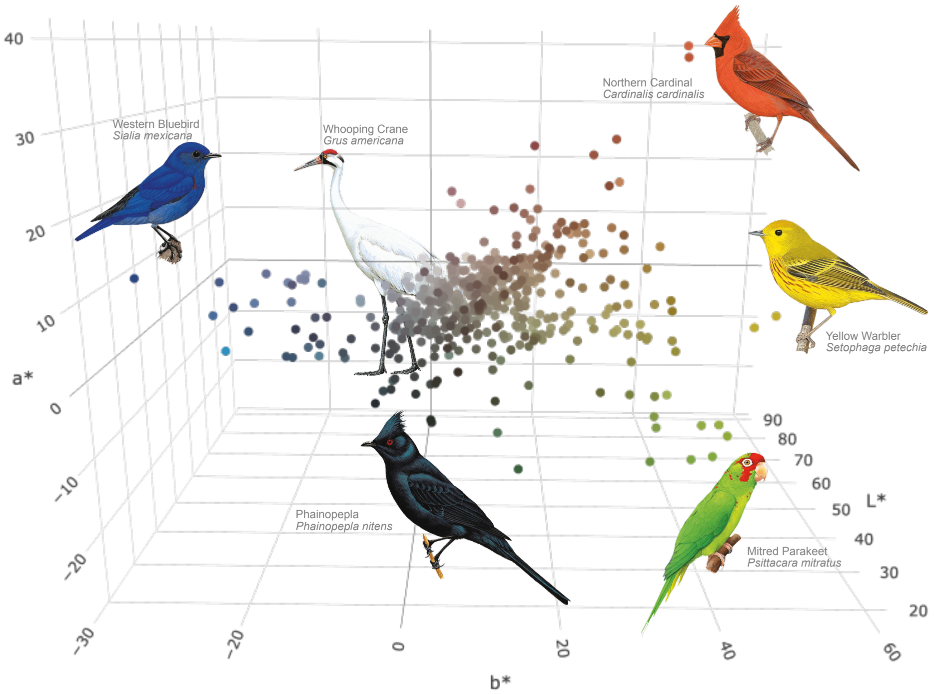


Figure 3. Principal component plots of North American (A) (n=524) and European (B) (n=386) species in morpho-space. Passerines are shown in pink, non-passerines in green. PCA were conducted separately between continents, so plots are not directly comparable.

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

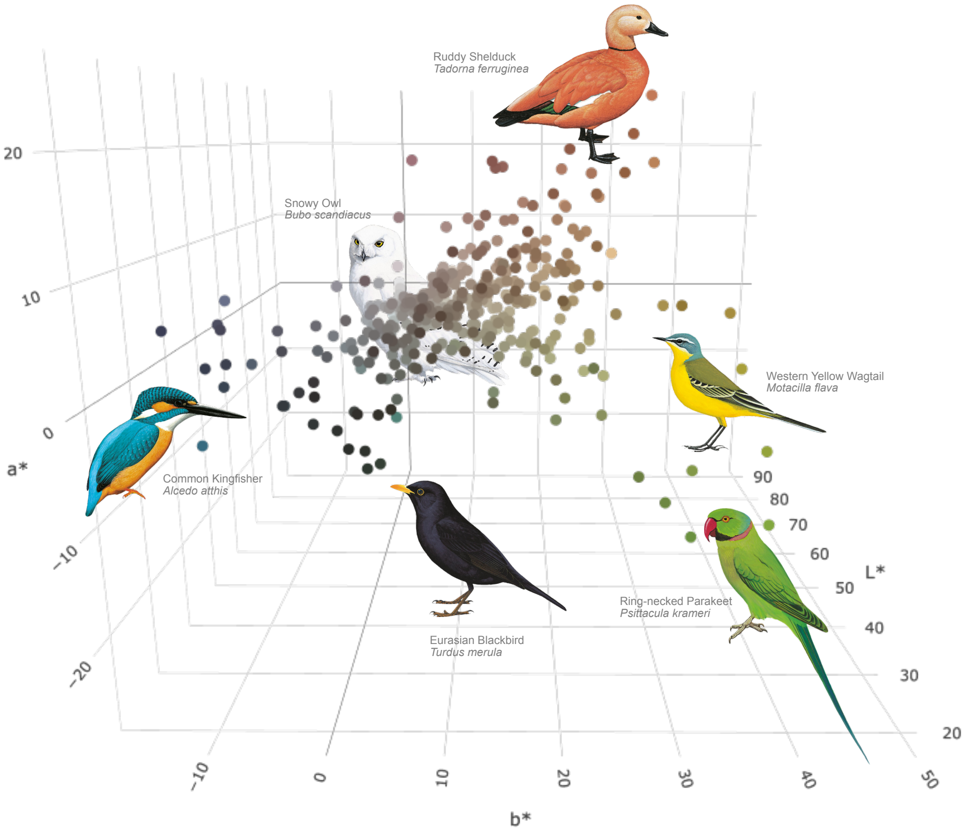
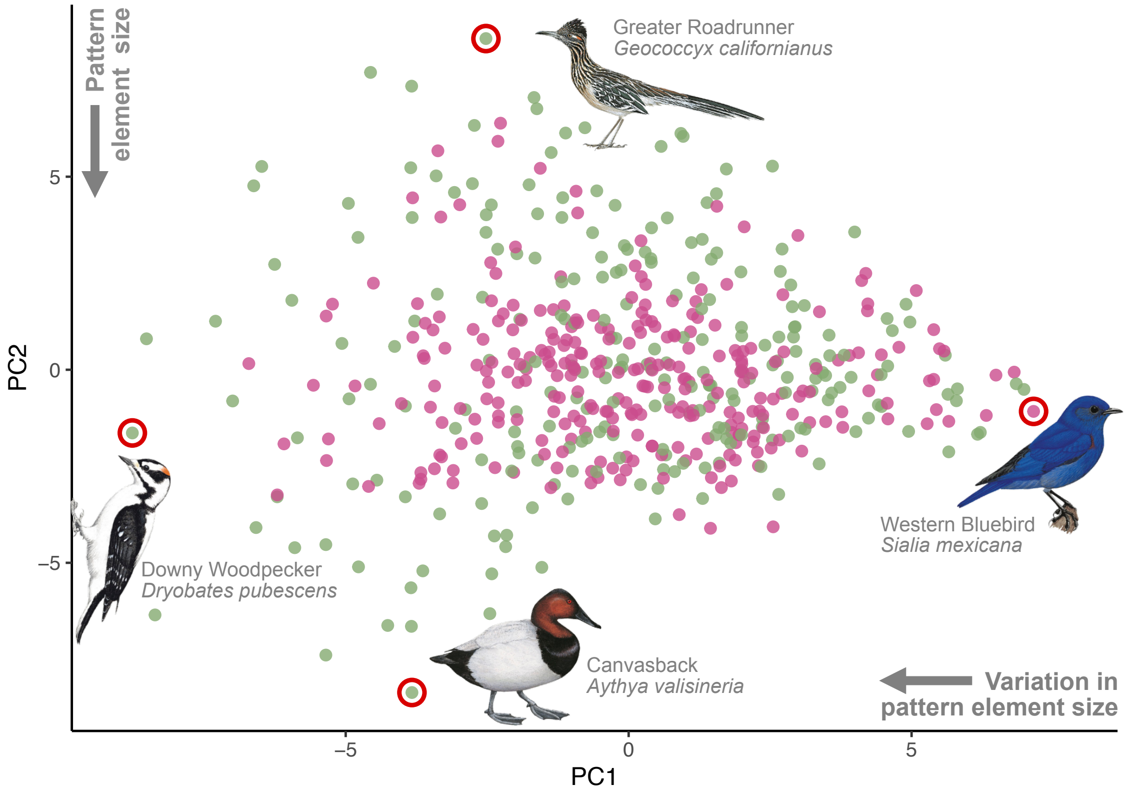


Figure 4. The average colour of North American (A)(n=524) and European birds (B) (n=386) plotted in CIELAB colour space, calculated as the average colour coordinates of 1000 random points on Birds of the World species illustrations. L* corresponds to lightness, a* is

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

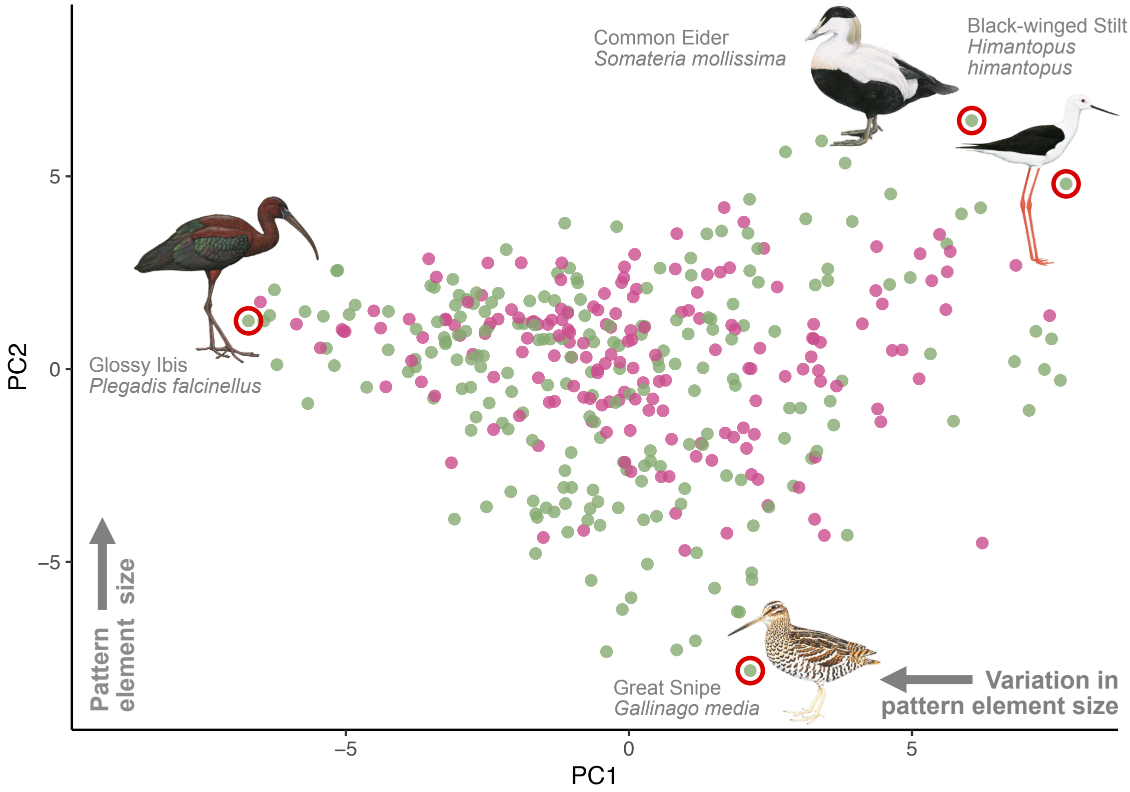
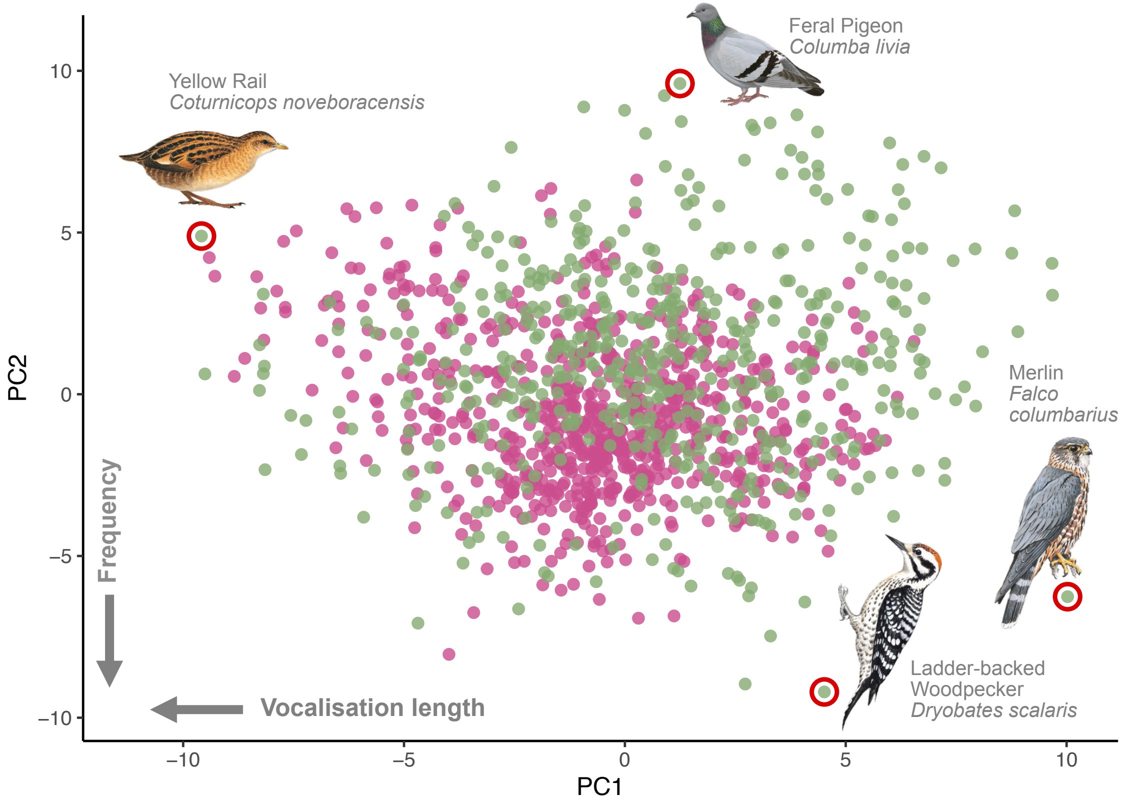


Figure 5. Principal component plots of North American (A) (n=524) and European (B) (n=386) species in pattern-space. Passerines are shown in pink, non-passerines in green. PCA were conducted separately between continents, so plots are not directly comparable. Illustrations: Cornell Lab of Ornithology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

A) North American vocal-space



B) European vocal-space

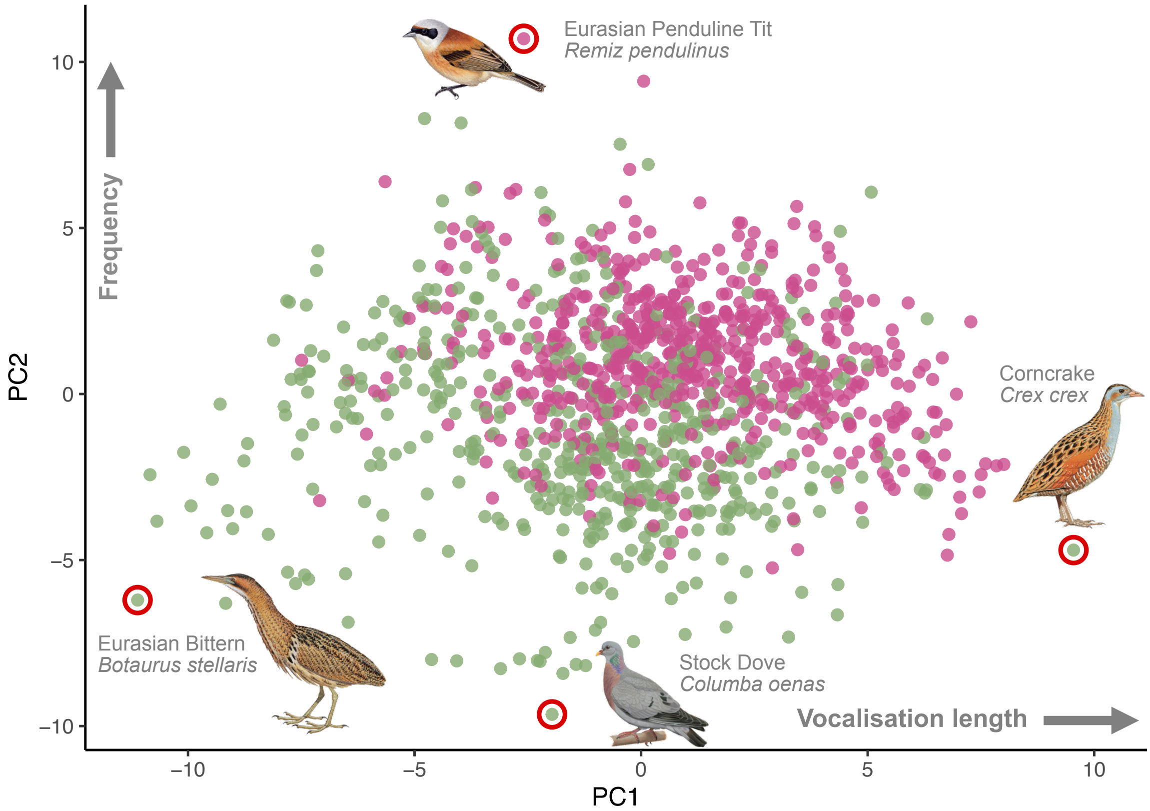


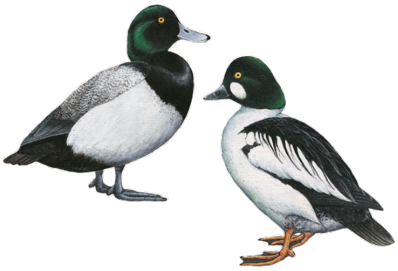
Figure 6. Principal component plots of North American (A) (n=524) and European (B) (n=386) species in vocal-space. Passerines are shown in pink, non-passerines in green. PCA were conducted separately between continents, so plots are not directly comparable. Each species has 2 or 4 vocalisations in vocal-space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

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

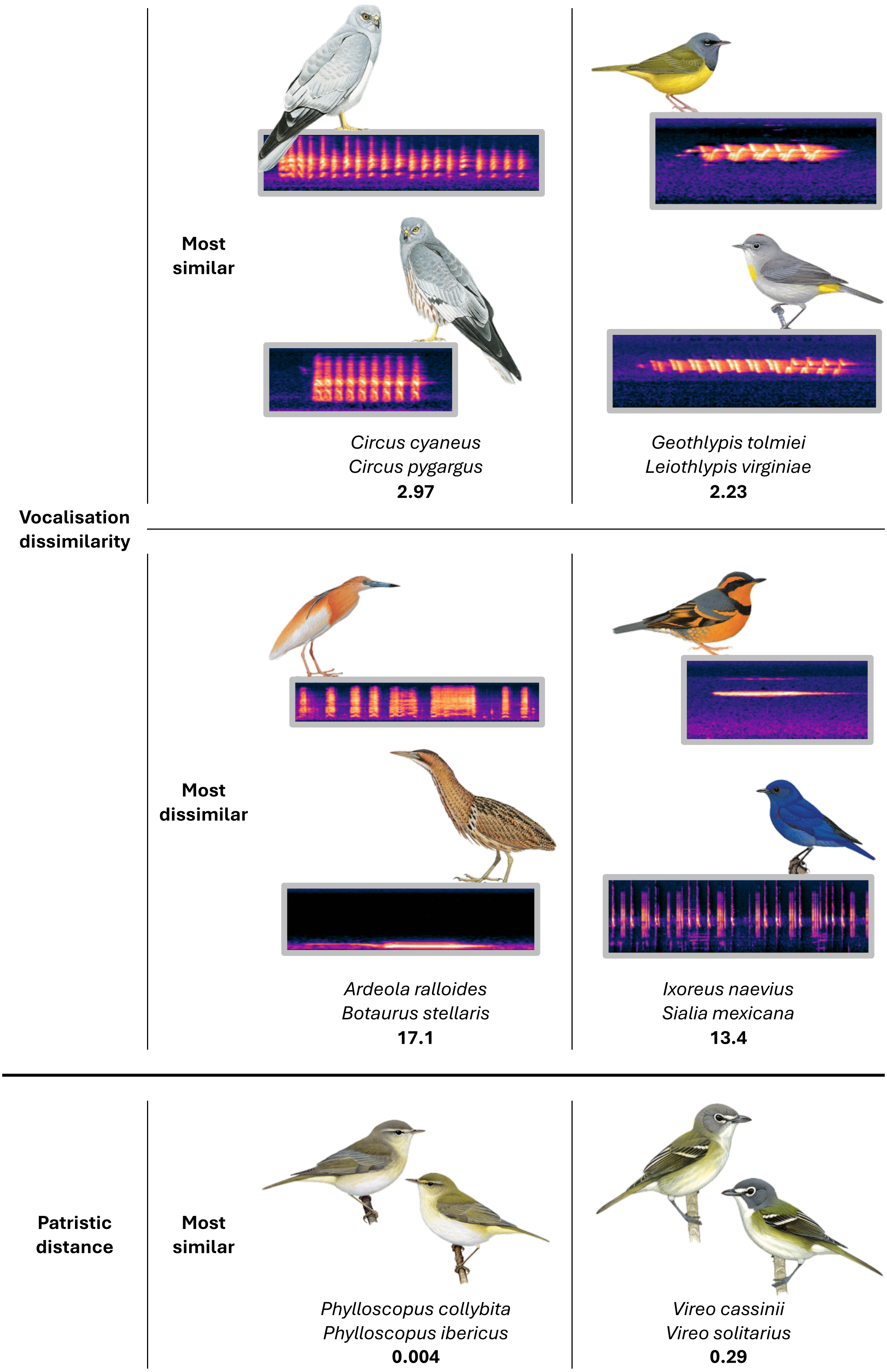
2.3 Results

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	**Most similar**	 *Lanius excubitor* *Lanius meridionalis* **0.15**	 *Catharus fuscescens* *Catharus ustulatus* **0.16**
	Most dissimilar	 *Coturnix coturnix* *Pavo cristatus* **6.97**	 *Corvus corax* *Pica nuttalli* **6.41**
Colour dissimilarity	**Most similar**	 *Aythya marila* *Bucephala clangula* **0.03**	 *Dryobates pubescens* *Dryobates villosus* **0.07**

	Most dissimilar	 *Cygnus cygnus* *Melanitta nigra* **10.9**	 *Anas rubripes* *Cygnus buccinator* **7.91**
Pattern dissimilarity	**Most similar**	 *Loxia pytyopsittacus* *Loxia scotica* **0.38**	 *Aegolius funereus* *Athene cunicularia* **0.69**
	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.

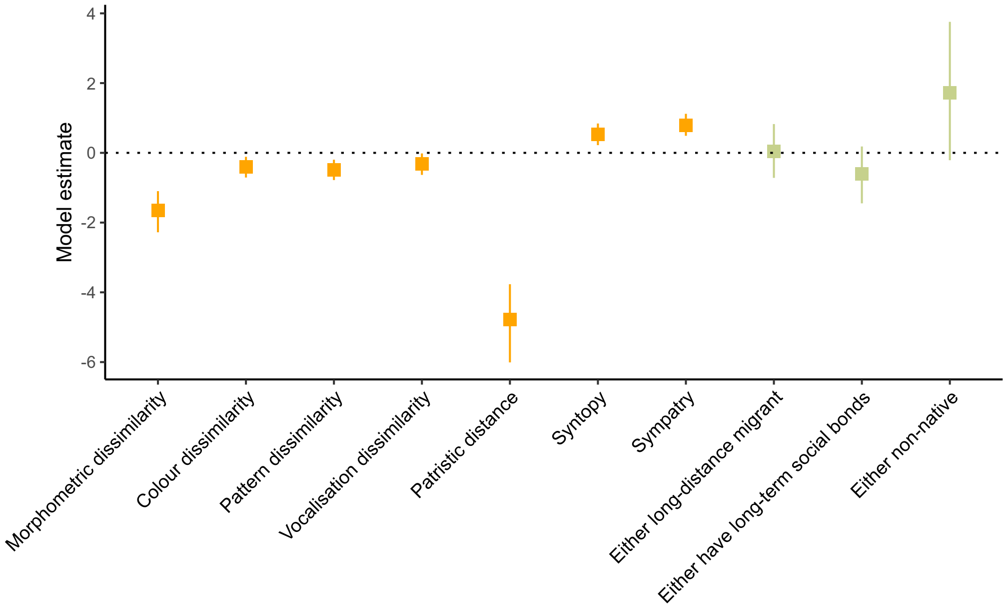
Migratory strategy did not influence hybridisation in any models (Tables 2-7, Figure 7, summarised in Table 8). Social bond length decreased the likelihood of hybridisation in North American passerines, but no other models (Table 2, Figure 7B, summarised in

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).

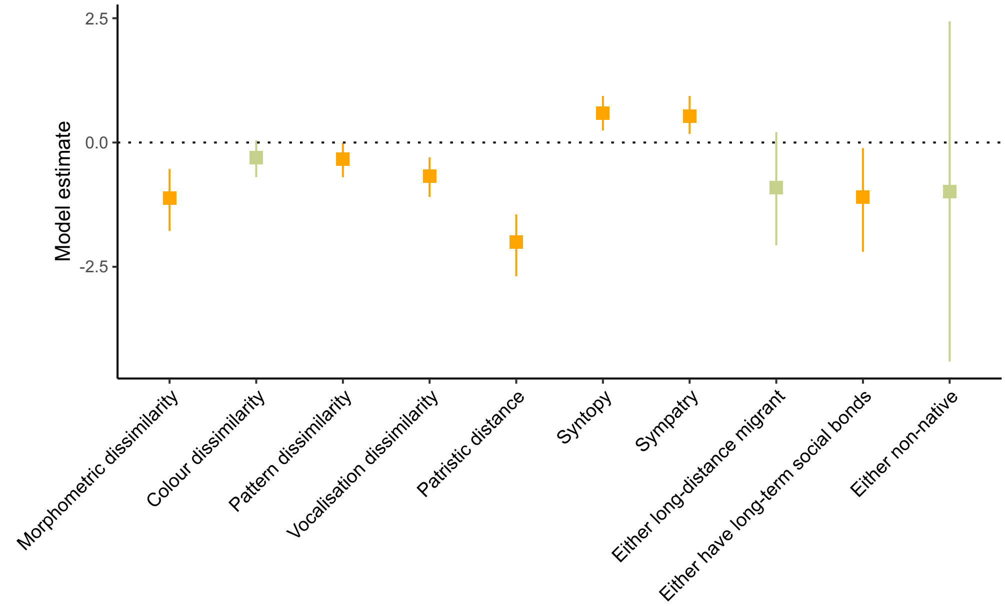
Syntopy increased the likelihood of hybridisation in models including all pairs and passerines but not in non-passerines in both North America and Europe (Table 2, 3, 5 & 6, Figure 7A, 7B, 7D, & 7E, summarised in Table 8). In North American models, sympatry increased the likelihood of hybridisation in 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).

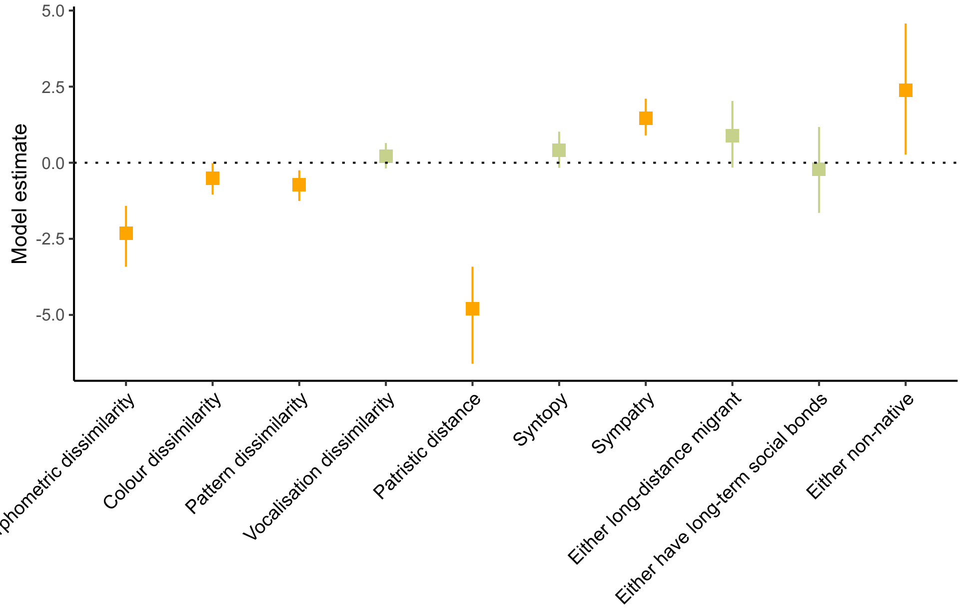
A) North America, all pairs



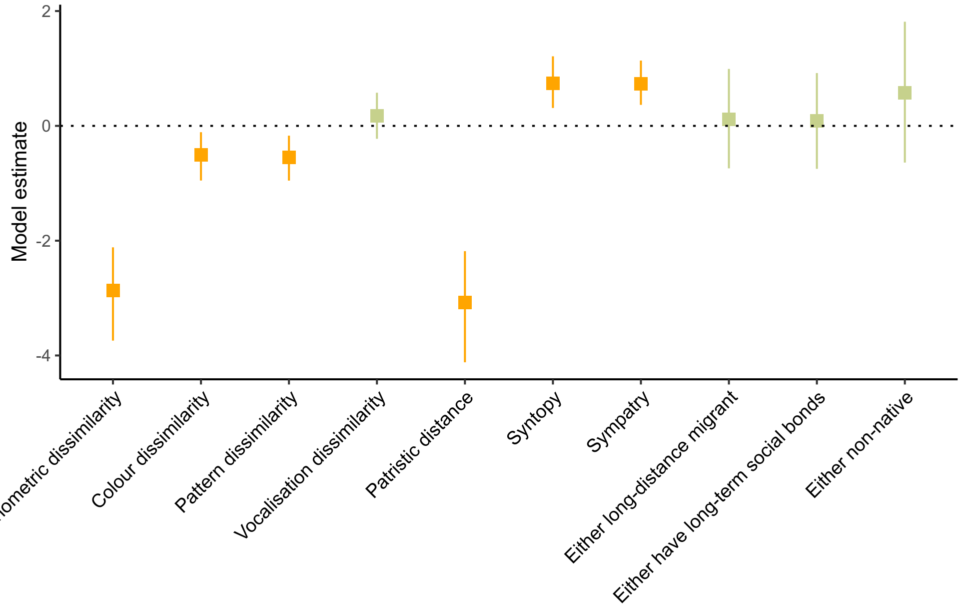
B) North America, passerines



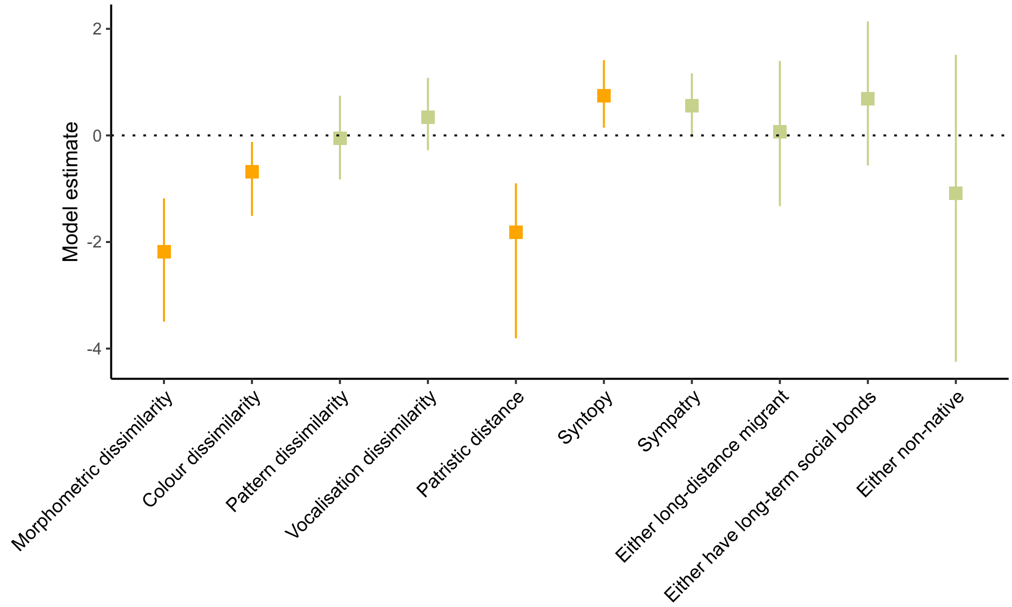
C) North America, non-passerines



D) Europe, all pairs



E) Europe, passerines



F) Europe, non-passerines

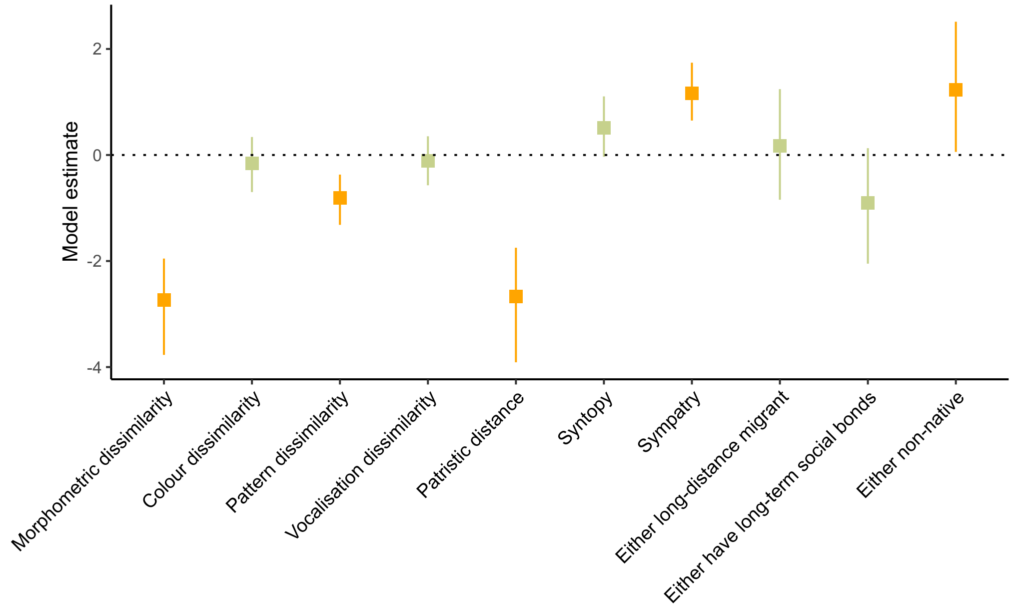


Figure 7: Predictors of hybridisation in North American (A, B, C, n=3339, 2189 and 1150, respectively) and European pairs (D, E, F, n=1647, 522, 1125, respectively). Plotted values are coefficient estimates from phylogenetic generalised linear mixed models with hybridisation as the response variable. 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

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***

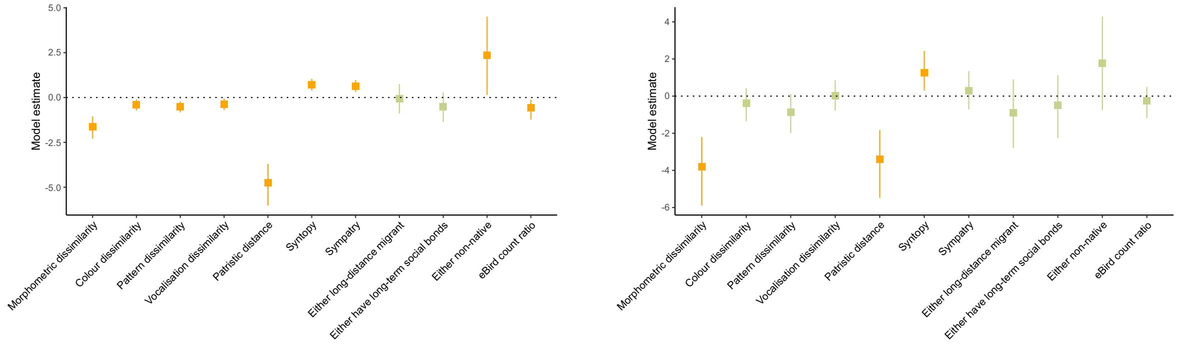
Model	Variables	Median	2.5%	97.5%	pMCMC	
Non-passerines	Intercept	-1.949	-5.005	1.452	0.253	
	Morphometric dissimilarity	**-2.739**	**-3.770**	**-1.954**	**<0.0005**	***
	Colour dissimilarity	-0.160	-0.699	0.340	0.529	
	Pattern dissimilarity	**-0.810**	**-1.317**	**-0.370**	**<0.0005**	***
	Vocalisation 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 (↑) indicate the variable increases the likelihood of hybridisation. Downward arrows (↓) 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			↑			↑

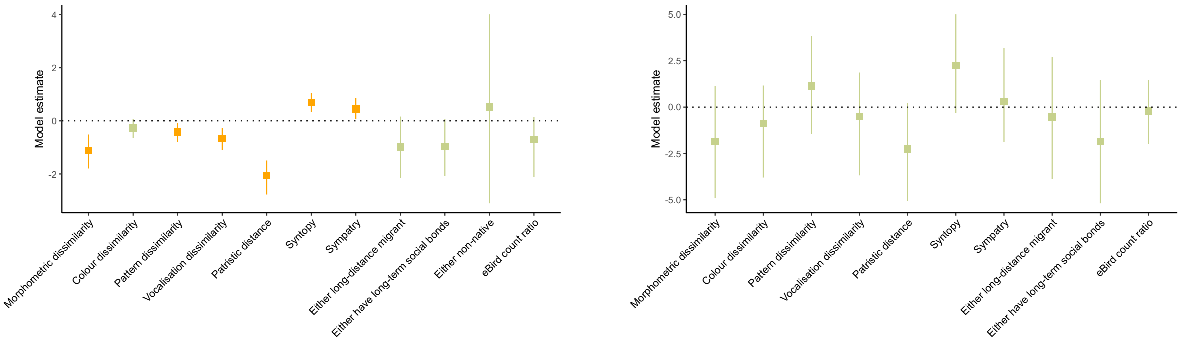
A) North America, all pairs, with eBird count ratios

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

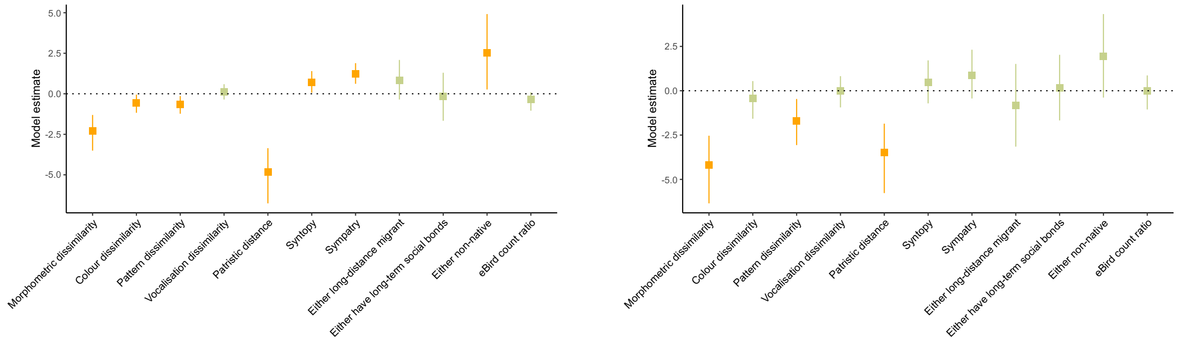


Figure 8: Predictors of Hybridisation in North American (A, B, C, n=3039, 1023 and 2016, respectively) and European pairs (D, E, F, n=243, 53, 190, respectively) subset to those with data for eBird count ratios. In the European passerine model (E) there were no pairs containing non-natives, as such, 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

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

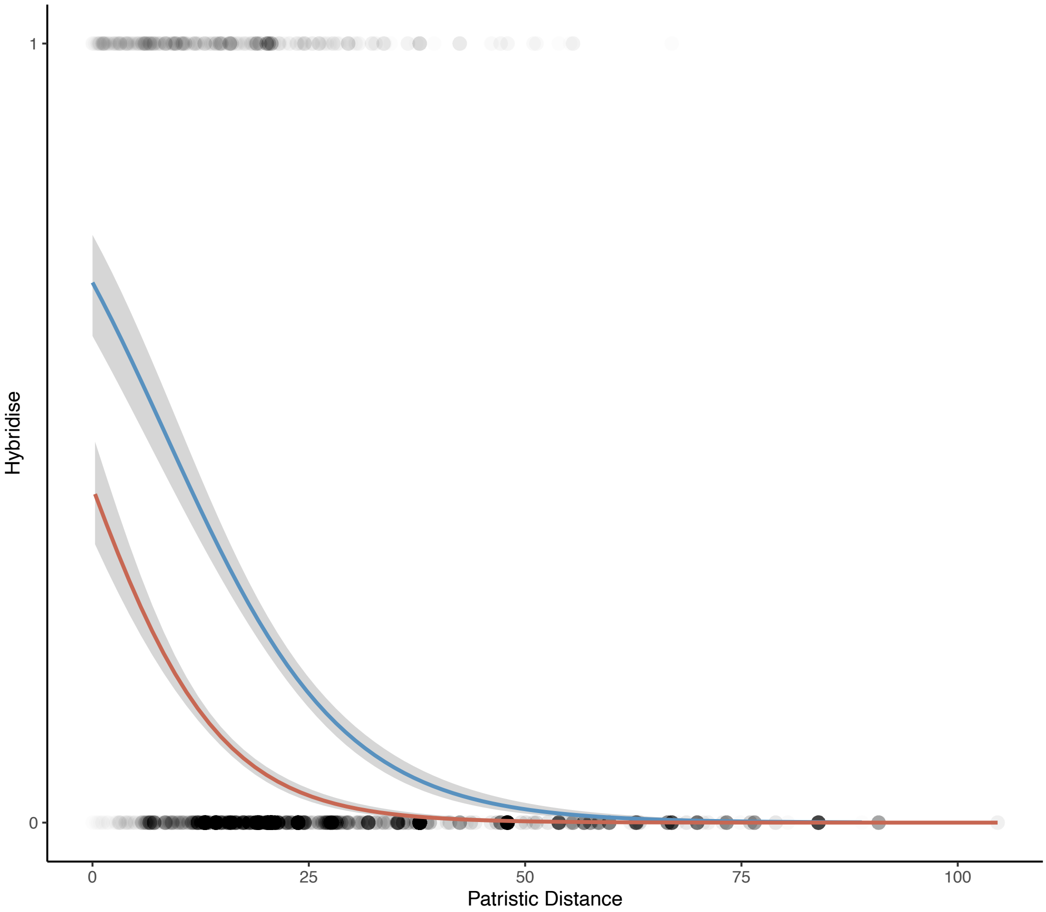


Figure 9. The relationship between patristic distance and hybridisation in European (blue line) (n=2203) and North American pairs (red line) (n=3647).

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), successionally (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. novaezelandiae*) (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 29/11*/2025 12*:14:00, 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) $$Accuracy = \frac{TP + TN}{\#\, pairs}$$

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

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

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

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

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 canadensi*s) 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/m^2 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).

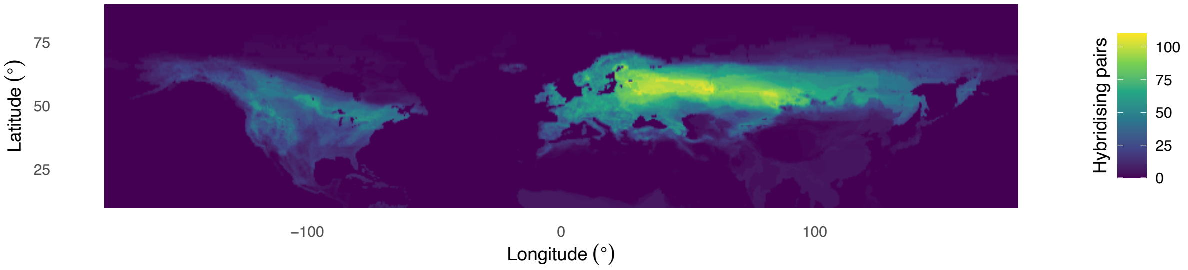
	Full Model	No synt, No symp	Full Model	No synt, No symp	Full Model	No synt, No symp
	Combined		Passerine		Non-passerine	
Accuracy	RFML	RFML	RFML	RFML	RFML	RFML
Precision	RFML	RFML	RFML	RFML	RFML	RFML
Sensitivity	PLMM	PLMM	PLMM	PLMM	PLMM	PLMM
Specificity	RFML	RFML	RFML	RFML	RFML	RFML
F1 Score	PLMM	PLMM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

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

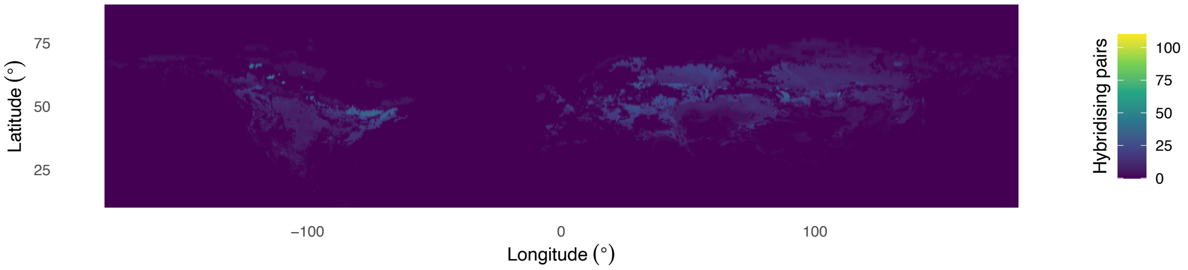
	Combined	Passerines	Non-passerines
Full Model	0.497	0.701	0.623
No synt, No symp	0.503	0.724	0.691

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%.

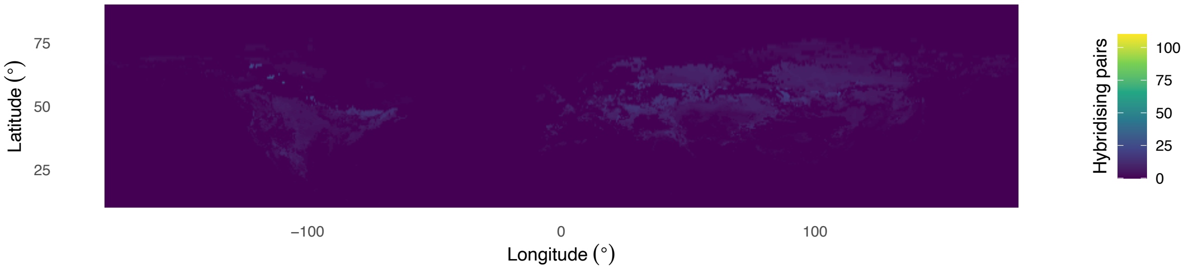
A) Actual hybrids, current



B) Actual hybrids, 2070, SSP370



C) Predicted hybrids, 2070, SSP370



D) Predicted and actual hybrids combined, 2070, SSP370

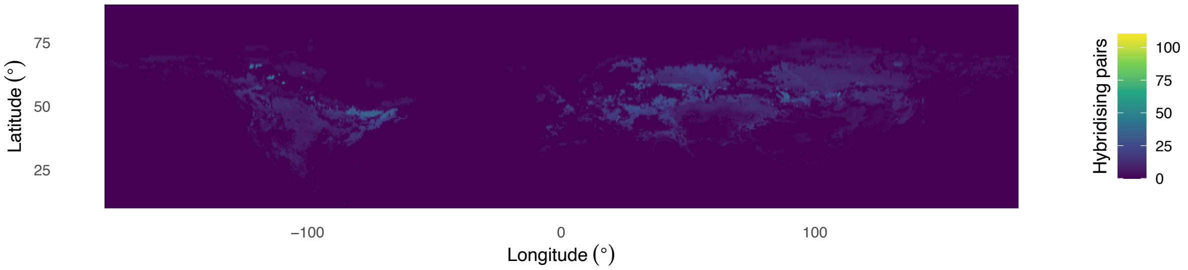


Figure 1. Spatial overlap of hybridising pairs, cell values correspond to the number of hybridising pairs that co-occur in said cell. Species can appear multiple times in different pair combinations. Maps only show sympatric areas for pairs. Hybrid predictions are made using random forest machine learning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

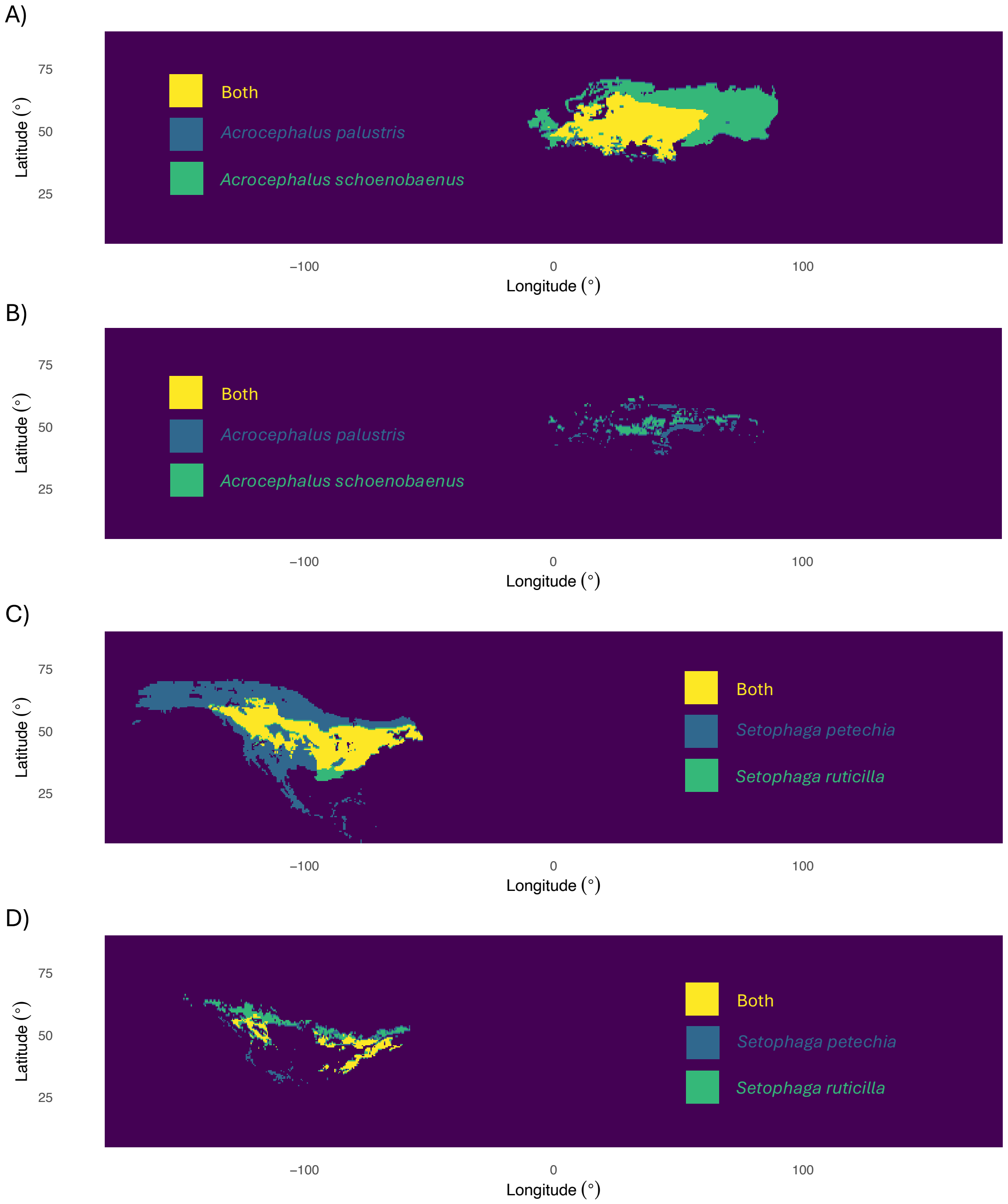


Figure 2. The current (A, C) and future distributions of two hybridising pairs; Marsh (*Acrocephalus palustris*) (blue) and Sedge Warbler (*A. schoenobaenus*) (green) and Yellow Warbler (*Setophaga petechia*) (blue) and American Redstart (*S. ruticilla*) (green) and their overlap (yellow). Marsh and 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.

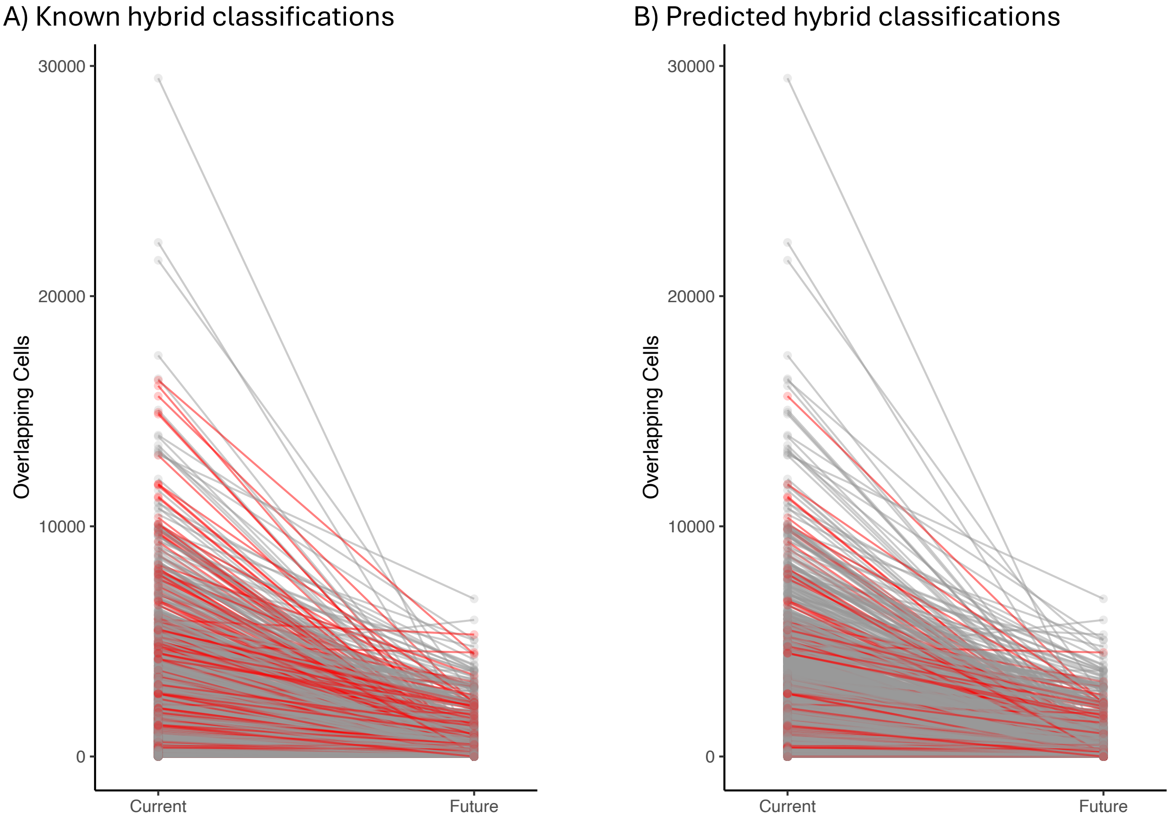


Figure 3. The number of overlapping 0.5° cells for pairs in their current distribution and in 2070 under an SSP370 projection. Red lines indicate hybridising pairs. Those with known hybridisation classifications (A) ($n=3929$, $n_{Hyb}= 420$) and those with predicted hybrid classifications (B) ($n=4969$,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

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

(*Curruca 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 Bücker, 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)
$$\frac{1}{Y}\sum_{i=1}^{Y}\frac{1}{R1{,}2_i}\sum_{\mathrm{k}=1}^{R1{,}2_i}\left(\frac{S1{,}2_k}{S1_k+S2_k-S1{,}2_k}\right)$$

Where S1,2k refers to the number of stops where species 1 and 2 co-occur in year i on route k. S1k and S2k refer to stops where species 1 and species 2 were recorded on route k, respectively. R1,2i 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 (Δsyntopy) 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)

$$\begin{cases} \frac{1}{Y}\sum_{i=1}^{Y}\frac{R1{,}2_i}{R1_i}, if\ \ R1_i < R2_i \\ \frac{1}{Y}\sum_{i=1}^{Y}\frac{R1{,}2_i}{R2_i}, if\ R2_i < R1_i \end{cases}$$

Where all terms are as above. We calculated the temporal change in sympatry (Δsympatry) 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.

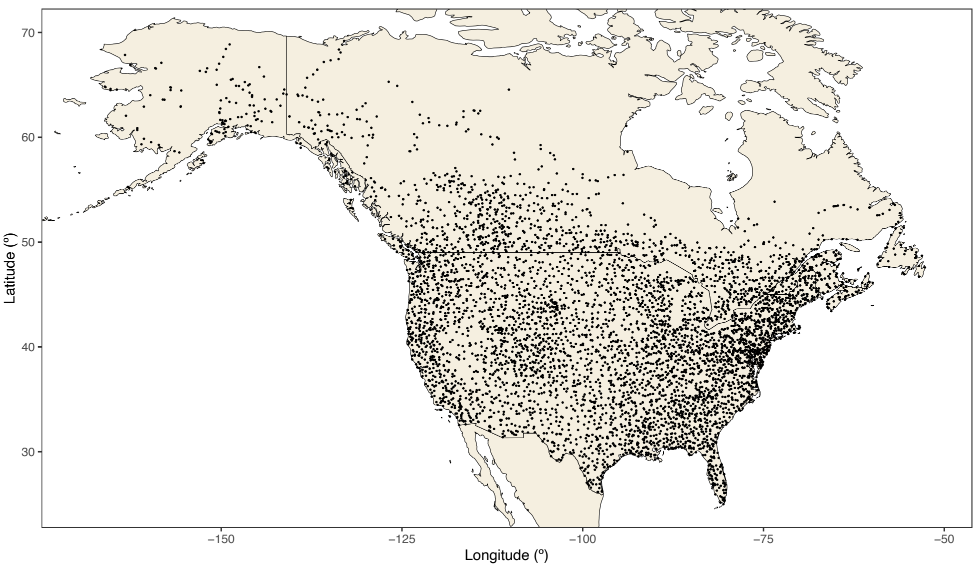


Figure 1. Location of all North American Breeding Bird Survey routes between 1966 and 2019 (n=5756), not every route is surveyed annually.

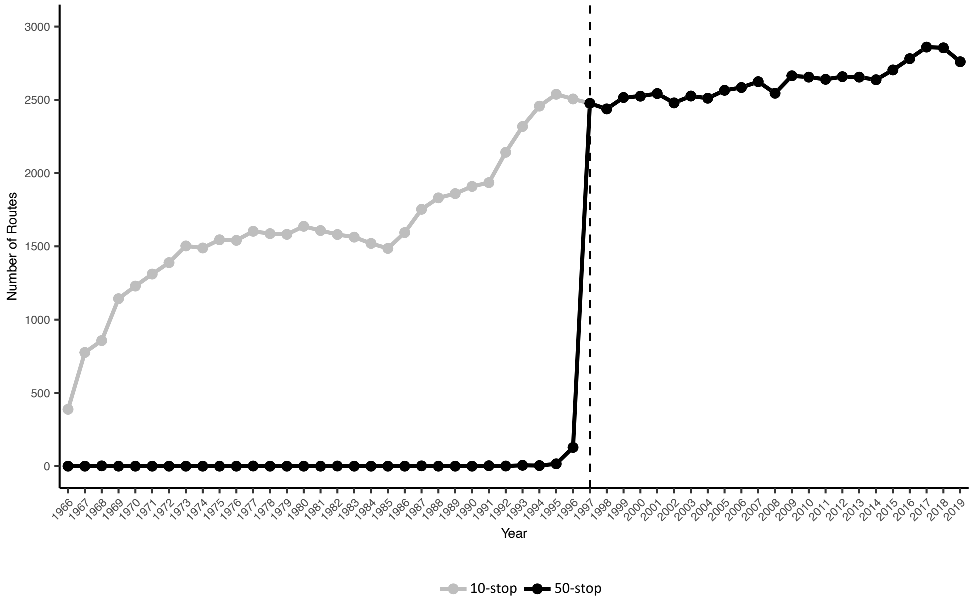


Figure 2. The number of North American BBS Routes with available data in each year. 10-stop data was used to calculate sympatry (grey). 50-stop data was used to calculate syntopy (black). Vertical dashed line denotes the first year (1997) in which both datasets contain all the same routes.

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.

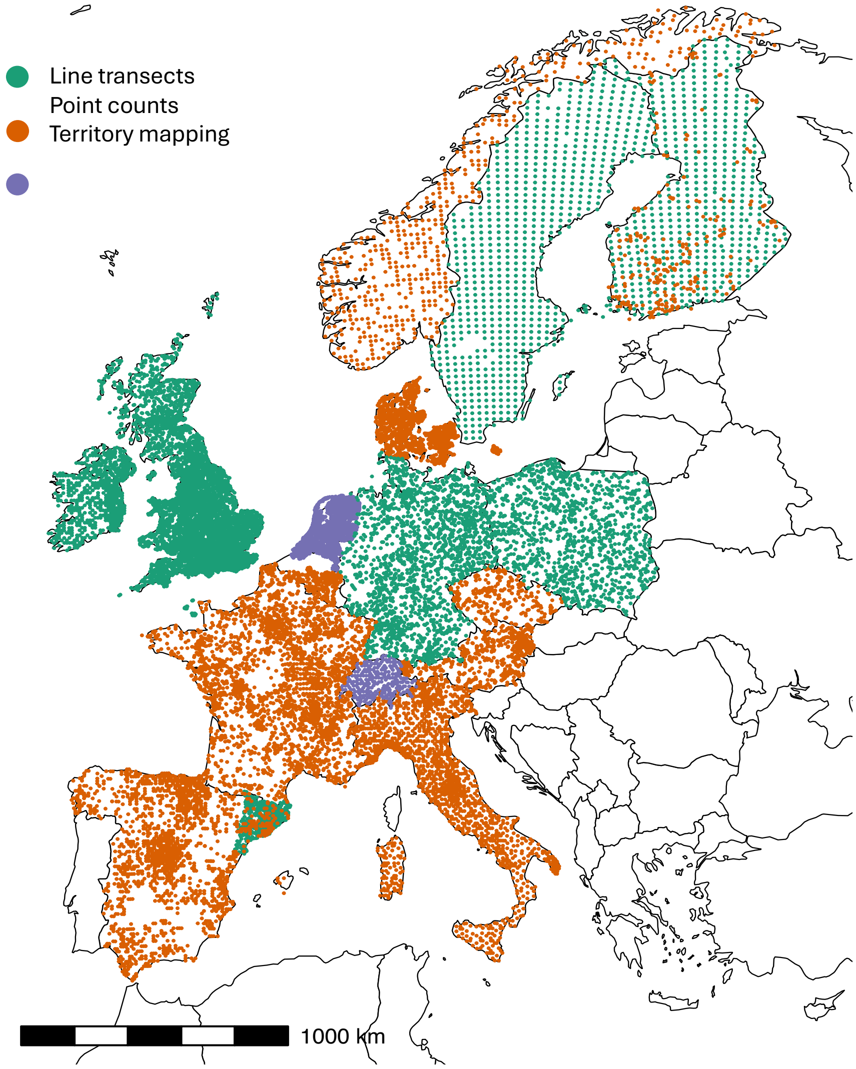


Figure 3. Distribution of Pan-European Common Bird Monitoring (PECBMS) sites and their survey methodology. Line transects (green), point counts (orange) and territory mapping (purple). Spain, Switzerland, Finland and Czech Republic were removed from analyses.

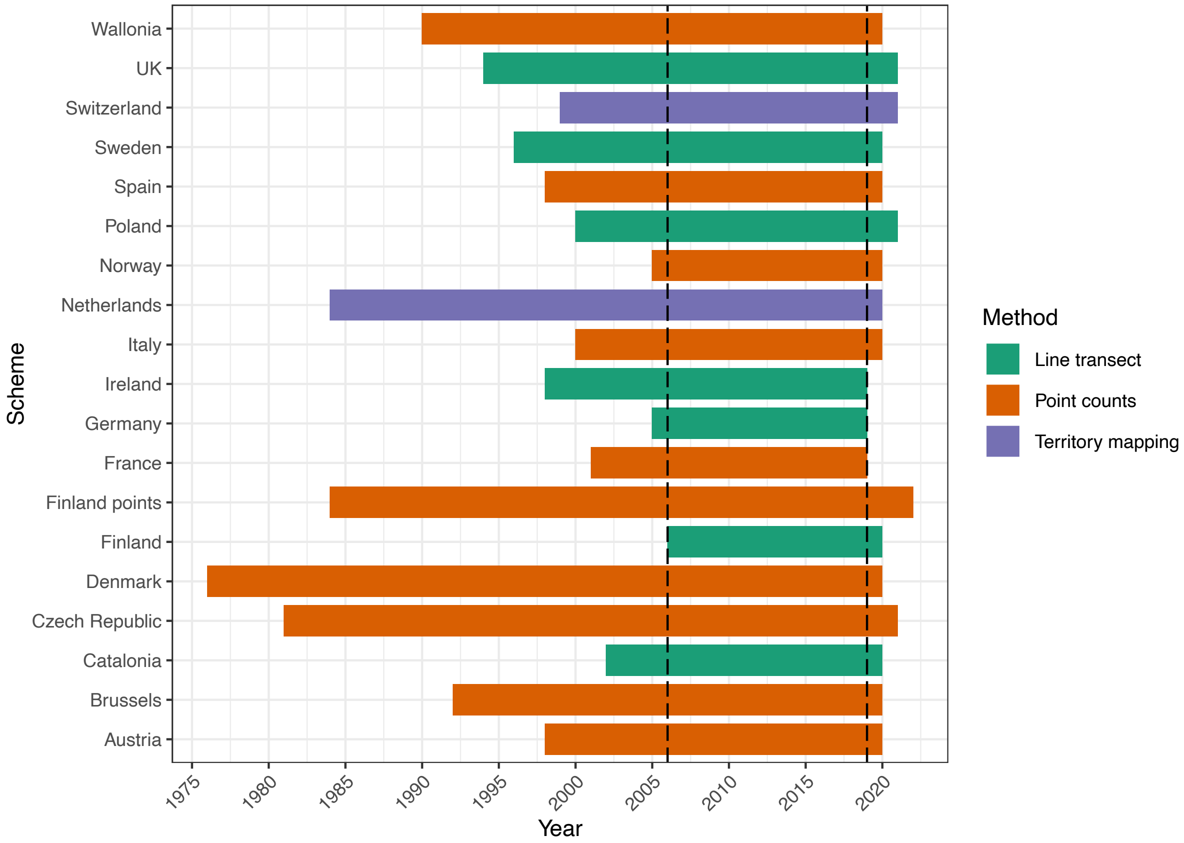


Figure 4. Duration of available survey schemes. Bar colour denotes survey method. Line transects (green), point counts (orange) and territory mapping (purple). Vertical dotted lines denote the time-period with data available for all schemes (2006-2019). Spain, Switzerland, Finland and Czech Republic 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
Acrocephalus paludicola & *Acrocephalus schoenobaenus*	
Acrocephalus palustris & *Acrocephalus scirpaceus*	Catchpole (1978)
Certhia brachydactyla & *Certhia familiaris*	Aggression but overlapping territories (Clouet and and Gerard, 2020)
Cyanistes caeruleus & *Parus major*	
Cyanistes caeruleus & *Periparus ater*	
Estrilda astrild & *Estrilda troglodytes*	
Ficedula albicollis & *Ficedula hypoleuca*	Alatalo, Gustafsson and Lundberg (1997)
Ficedula hypoleuca & *Phoenicurus phoenicurus*	
Fringilla coelebs & *Fringilla montifringilla*	Overlapping territories (Mikkonen, 1985)
Hippolais icterina & *Hippolais polyglotta*	(Secondi, Faivre and Kreutzer, 1999)
Lophophanes cristatus & *Periparus ater*	
Lophophanes cristatus & *Poecile montanus*	
Lophophanes cristatus & *Poecile palustris*	
Loxia curvirostra & *Loxia pytyopsittacus*	
Luscinia luscinia & *Luscinia megarhynchos*	Sorjonen (1986)
Passer domesticus & *Passer hispaniolensis*	
Passer domesticus & *Passer italiae*	
Passer hispaniolensis & *Passer italiae*	
Periparus ater & *Poecile palustris*	
Phylloscopus bonelli & *Phylloscopus sibilatrix*	Aggression, but overlapping territories (Luepold, Carlotti and Pasinelli, 2024)
Phylloscopus collybita & *Phylloscopus ibericus*	
Phylloscopus collybita & *Phylloscopus trochilus*	Sæther (1983)
Phylloscopus ibericus & *Phylloscopus trochilus*	
Sturnus unicolor & *Sturnus vulgaris*	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 I*ndices 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	Species 2	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

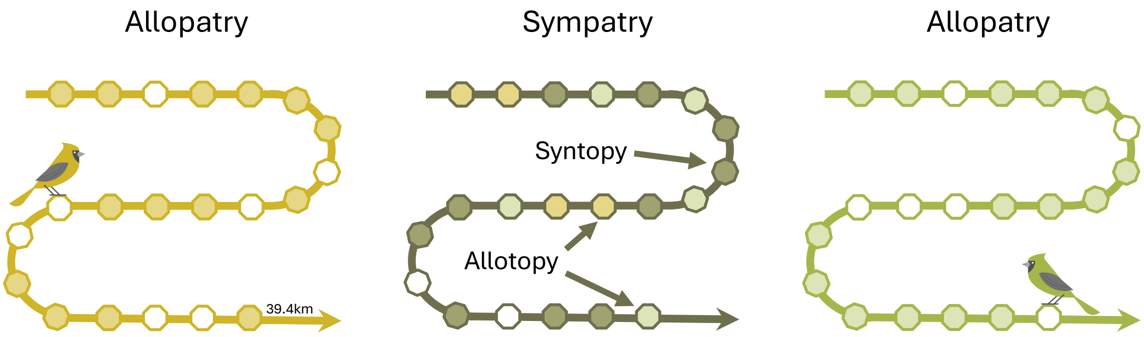
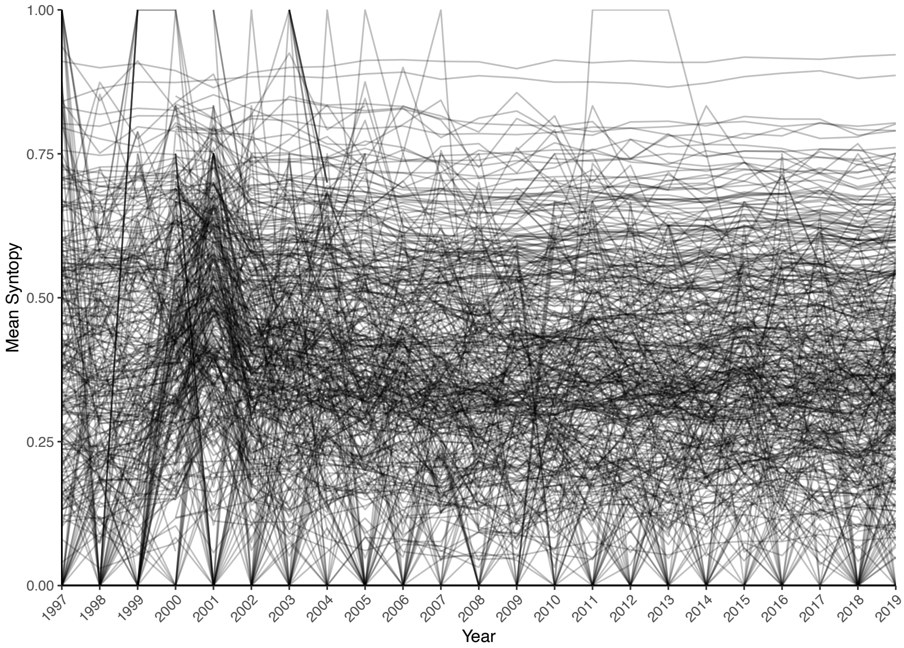


Figure 5. Schematic diagram of North American Breeding Bird Survey (NABBS) routes in Sympatry (dark green) and Allopatry (yellow and light green). Octagons represent syntopic (dark green) and allotopic (yellow, light green) NABBS stops at each route. Filled Octagons indicate species presence. Routes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

A) Syntopy



B) Sympatry

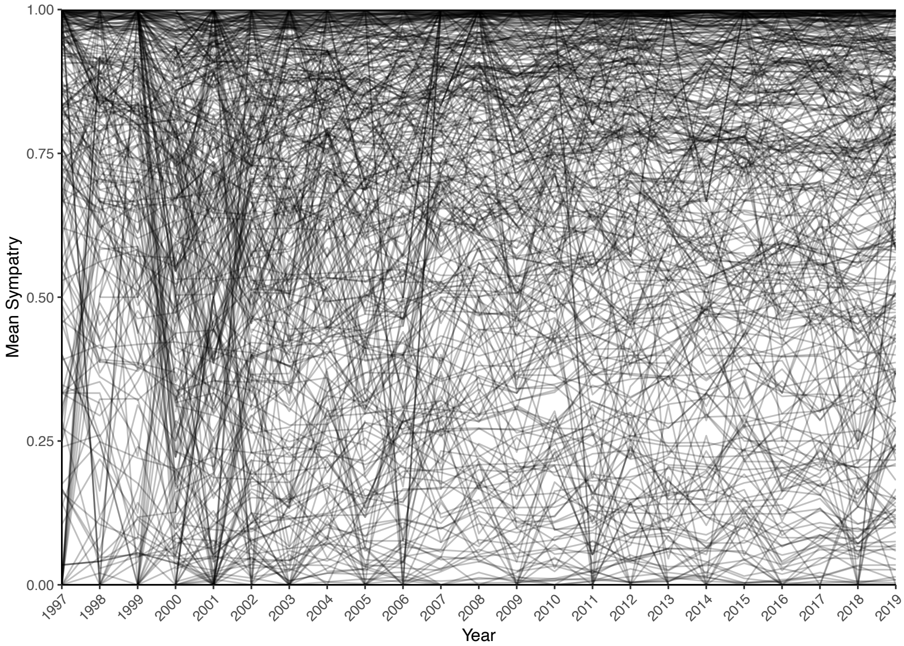


Figure 6. Mean syntopy (A) and mean sympatry (B) between 1997 and 2019 for European pairs (n=418). Each line corresponds to a pair. For rarer species, found at fewer sites, or years with fewer sites surveyed, it is possible that all the sites they occur at are within 40km of the other member of their 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 Δsyntopy (Appendix B). We found no effect of hybridisation on Δsyntopy (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 Δsyntopy (pMCMC < 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 Δsympatry. As mass difference increased, Δsympatry decreased. Contrastingly, as bill length difference increased, Δsympatry increased. As with syntopy analyses, we found no effect of either hybridisation or an interaction between interspecific territoriality and hybridisation on Δsympatry (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).

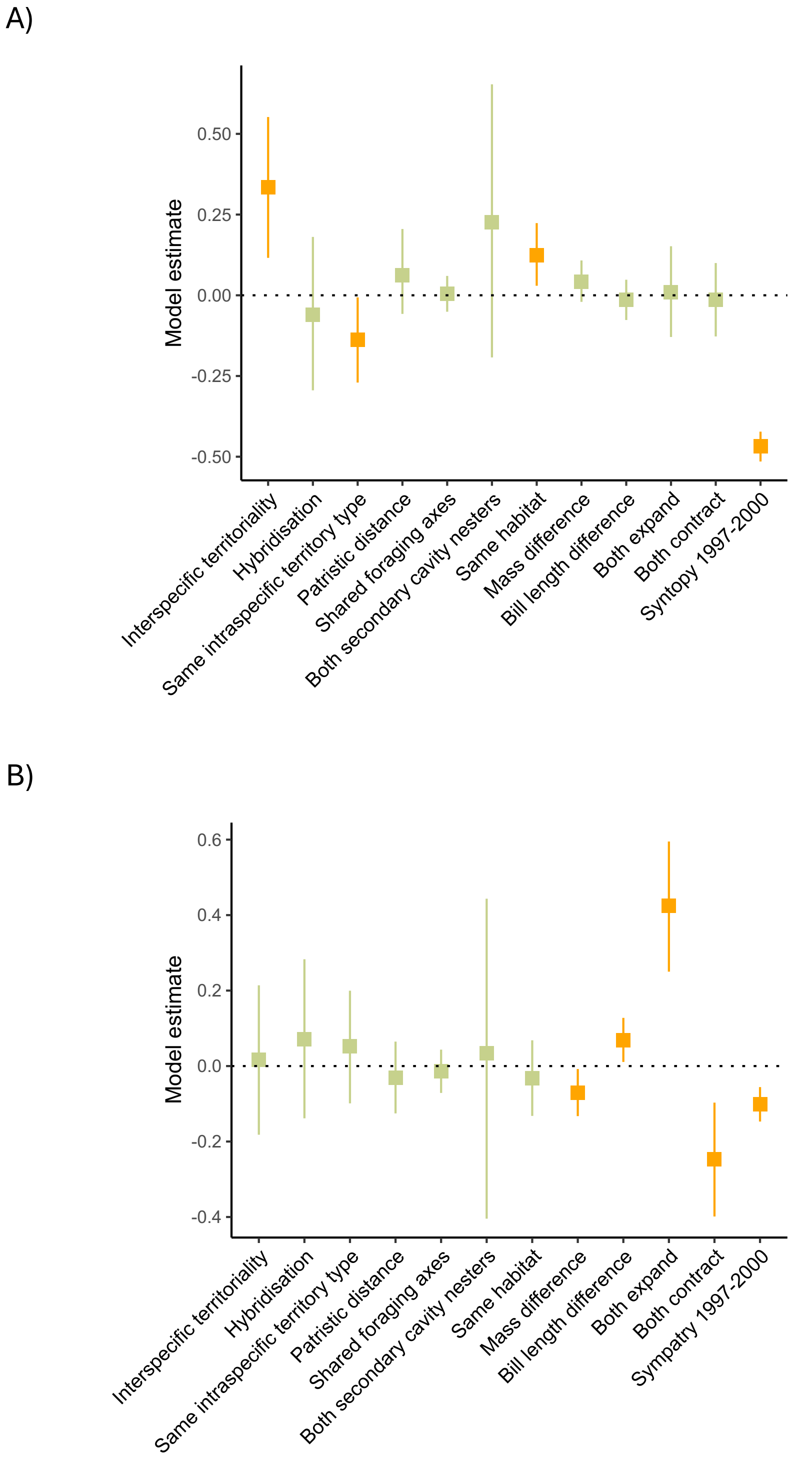


Figure 7: Predictors of Δsyntopy (A) and Δsympatry (B) in North American pairs. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed models with Δsyntopy and Δsympatry as the response variables. Points correspond to the median and error bars represent the 95% credibility 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 (Δsyntopy) 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	
Δsyntopy North America	Intercept	0.046	-0.319	0.415	0.773	
	Interspecific territoriality	**0.335**	**0.116**	**0.552**	**0.001**	**
	Hybridisation	-0.061	-0.294	0.181	0.613	
	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 (Δsympatry) 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	
Δsympatry North America	Intercept	0.016	-0.265	0.287	0.885	
	Interspecific territoriality	0.017	-0.182	0.214	0.857	
	Hybridisation	0.071	-0.138	0.283	0.509	
	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**	***

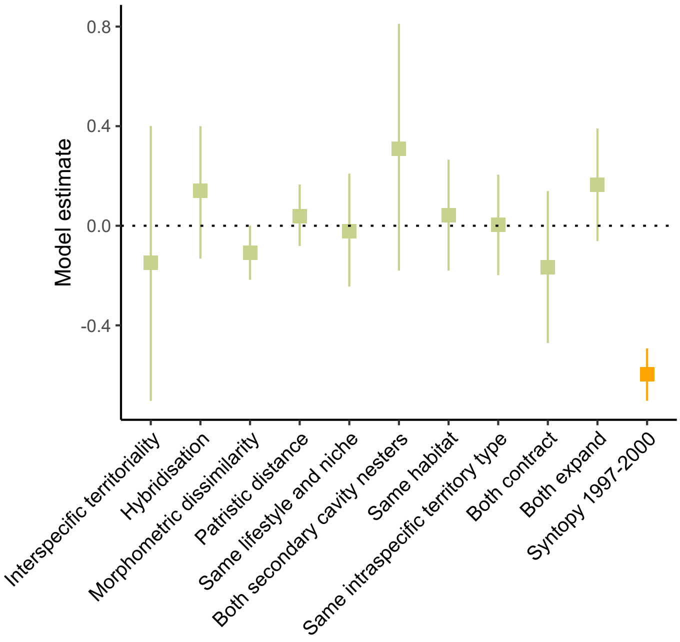
Table 6. Predictors of the change in syntopy between 1997–2000 and 2016–2019 (Δsyntopy) for European pairs from phylogenetic linear mixed models (n = 418 species pairs). The median coefficient estimates from the posterior distribution, as well as 95% credibility intervals and MCMC derived p-values are 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	
Δsyntopy 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 (Δsympatry) 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	
Δsympatry 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)

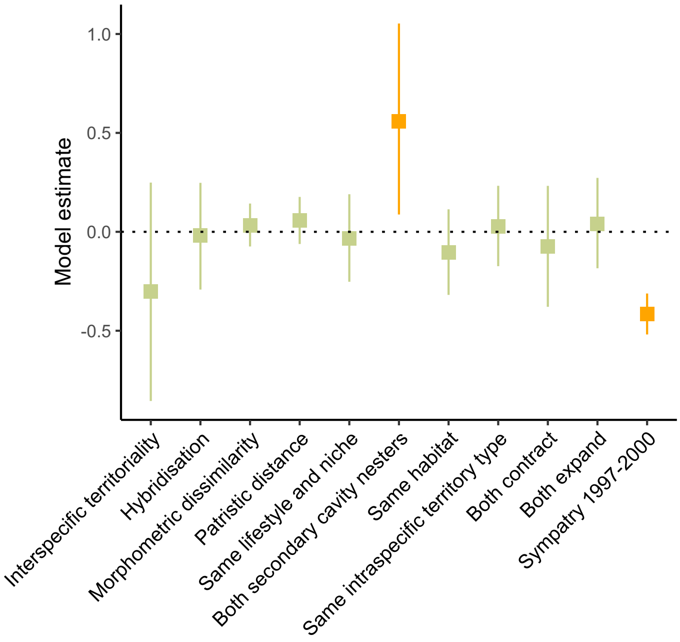


Figure 8: Predictors of Δsyntopy (A) and Δsympatry (B) between 1997-2000 and 2016-2019 in European pairs. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed models with Δsyntopy and Δsympatry as the response variables. Points correspond to the median and error bars 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 Δsyntopy. 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 (Wisz *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; Wisz *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 (reveiwed 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:

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

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:

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

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

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:

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

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

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

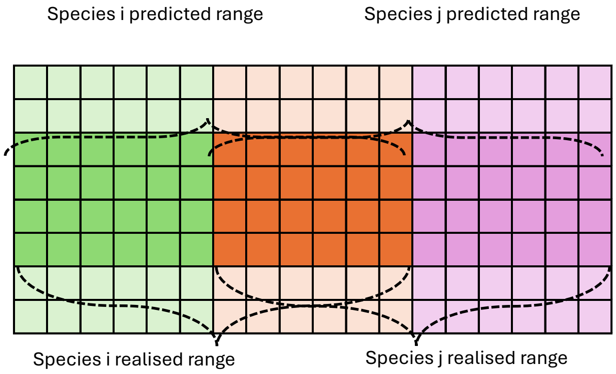
We collated data on several ecological and life history traits of species to test if they were related to geographic avoidance and avoidance symmetry. The first of these variables was interspecific territoriality, which was included as territoriality can lead to species coexistence and exclusion, at 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.

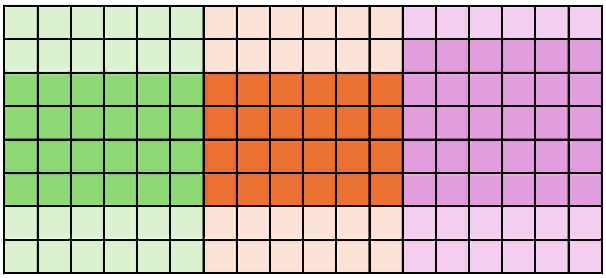
A)



PO_{ij}	48
RO_{ij}	24
PR_i	96
RR_i	48
PR_j	96
RR_j	48

GA_{ij}	GA_i	GA_j	GA_{sym}
0.00	1.00	1.00	9.21

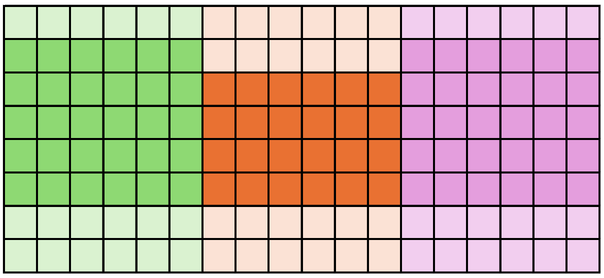
B)



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

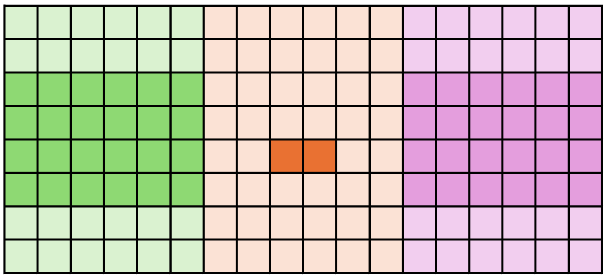
C)



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)

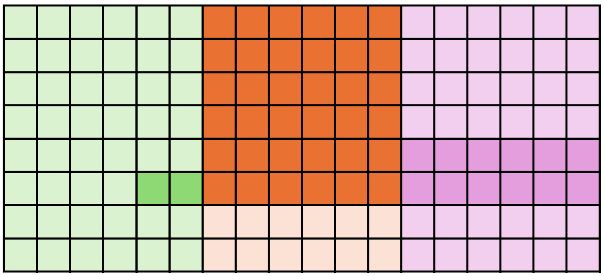


PO_{ij}	48
RO_{ij}	2
PR_i	96
RR_i	26
PR_j	96
RR_j	26

GA_{ij}	GA_i	GA_j	GA_{sym}
0.92	0.08	0.08	6.73

E)

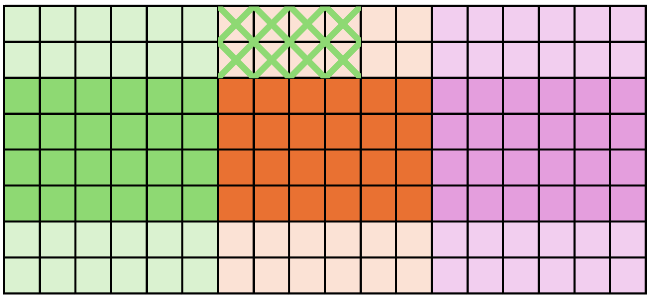
PO_{ij}	48



RO_{ij}	36
PR_i	96
RR_i	38
PR_j	36
RR_j	48

GA_{ij}	GA_i	GA_j	GA_{sym}
-4.14	18	3	-1.61

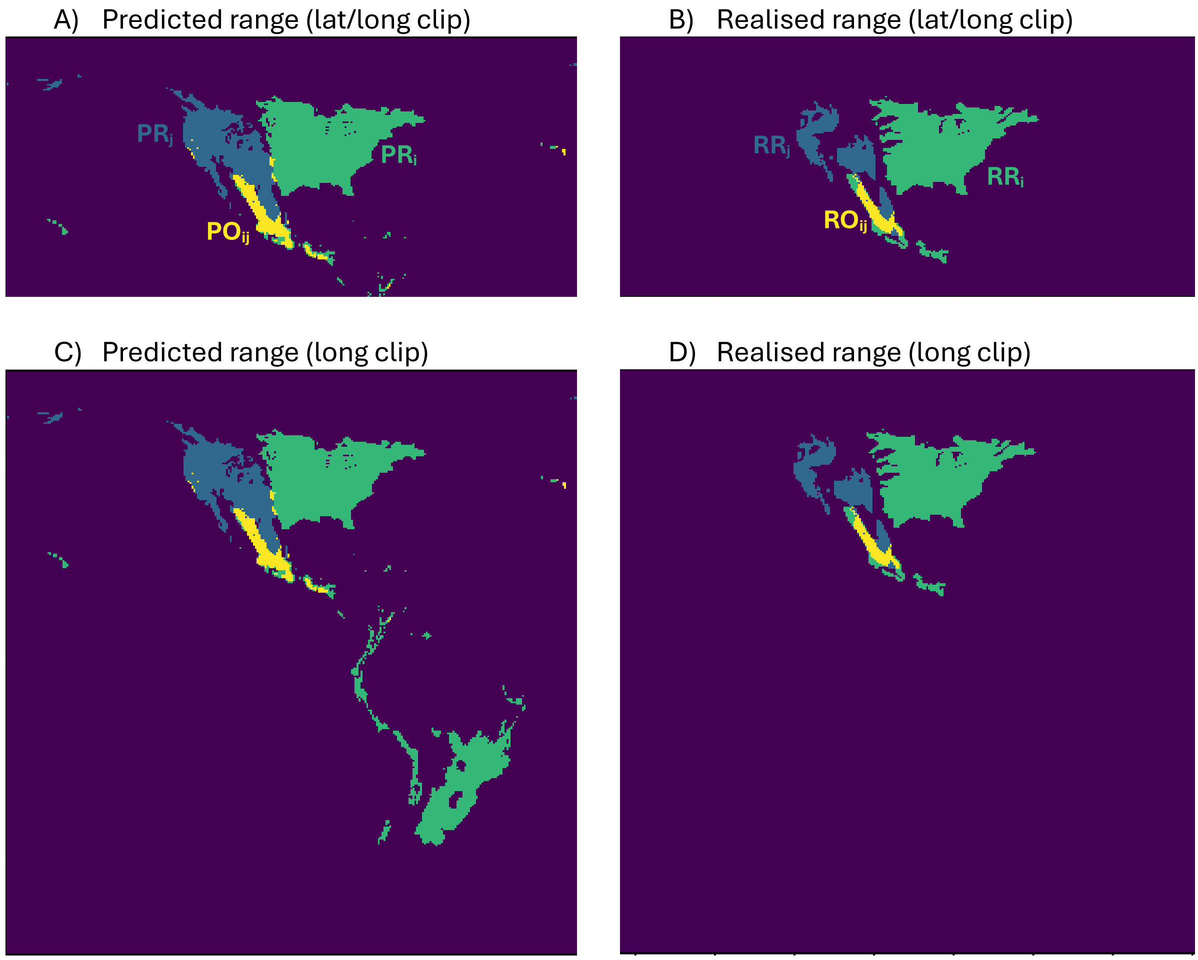
F)



PO_{ij}	48
RO_{ij}	24
PR_i	96
RR_i	56
PR_j	96
RR_j	48

GA_{ij}	GA_i	GA_j	GA_{sym}
0.14	0.75	1	1.10

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).



A) Predicted range (lat/long clip)

B) Realised range (lat/long clip)

C) Predicted range (long clip)

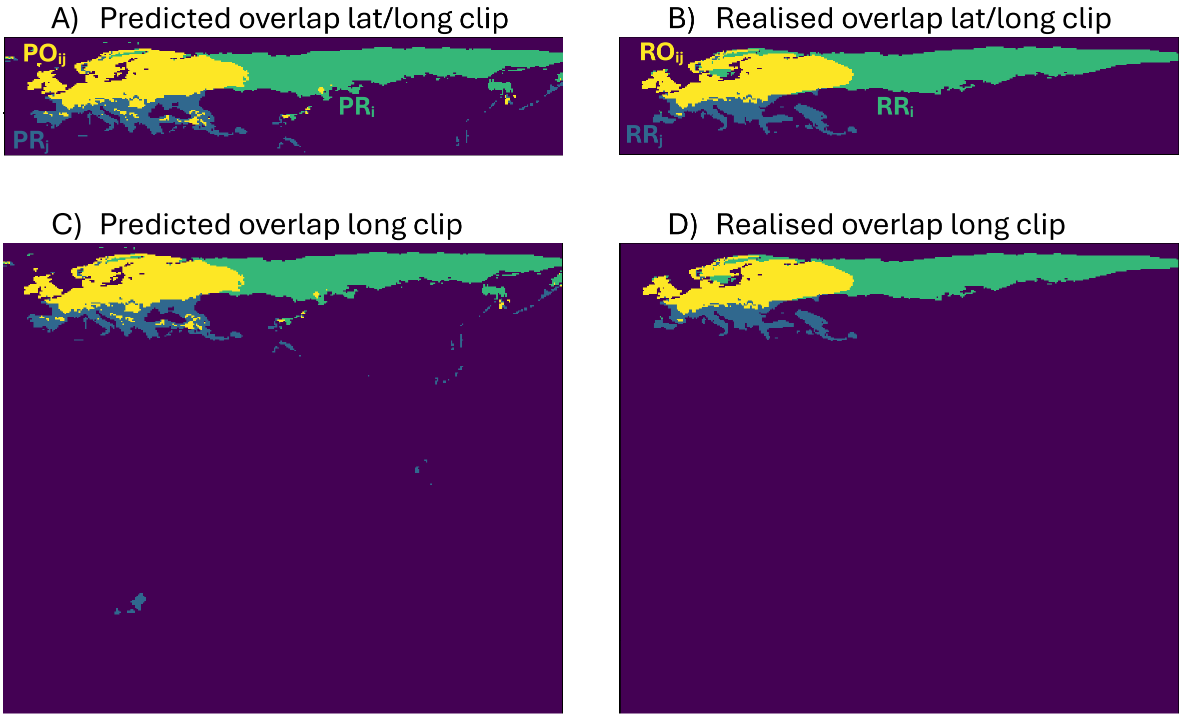
D) Realised range (long clip)

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
🟦 Species j
🟪 Neither
🟨 Overlap

PR_i	3483
RR_i	3080
PR_j	2151
RR_j	1126
PO_{ij}	414
RO_{ij}	214

GA_{ij}	GA_i	GA_j	GA_{sym}
0.34	0.55	0.98	0.25


A) Predicted overlap lat/long clip

B) Realised overlap lat/long clip

C) Predicted overlap long clip

D) Realised overlap long clip

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
- 🟦 Species j
- 🟪 Neither
- 🟨 Overlap

PR_i	8743
RR_i	8053
PR_j	5456
RR_j	8053
PO_{ij}	3664
RO_{ij}	3115

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.

🟧 Predicted range

🟥 Realised range

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 (*Lymnocryptes 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_{ij} does GA_{sym}, 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).

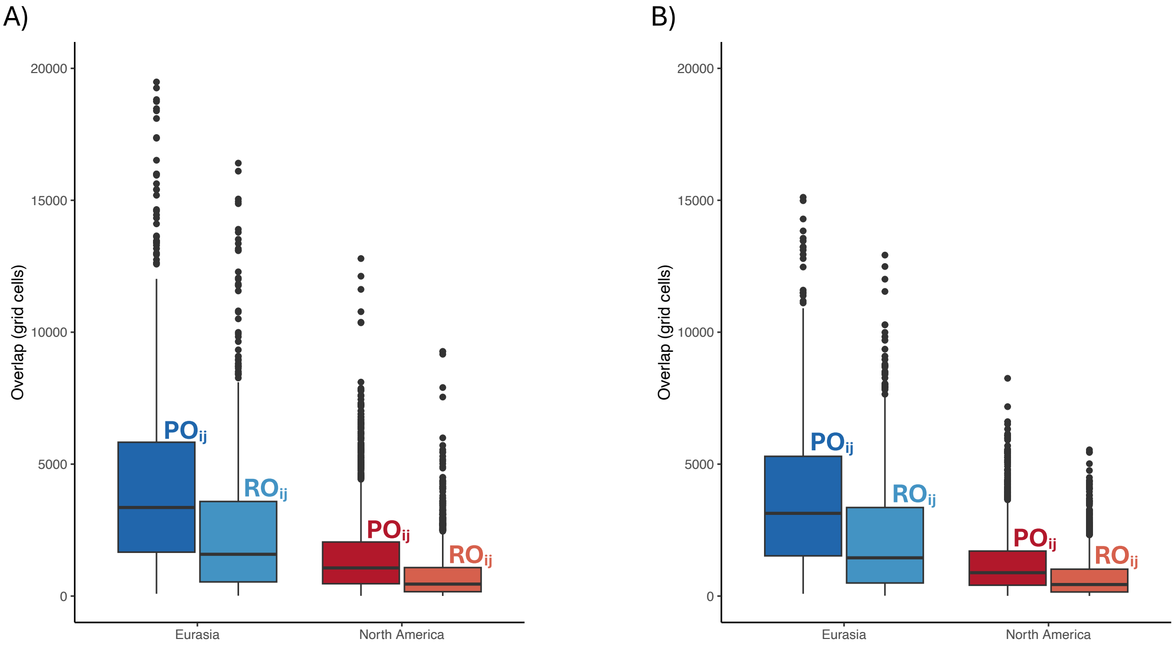


Figure 5: Average number of predicted (PO_{ij}, darker shade) and realised (RO_{ij}, lighter shade) overlapping grid cells for species i and species j in Eurasia (blue) and North America (red). Boxes represent median and interquartile range, while whiskers indicate maximum and minimum values excluding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

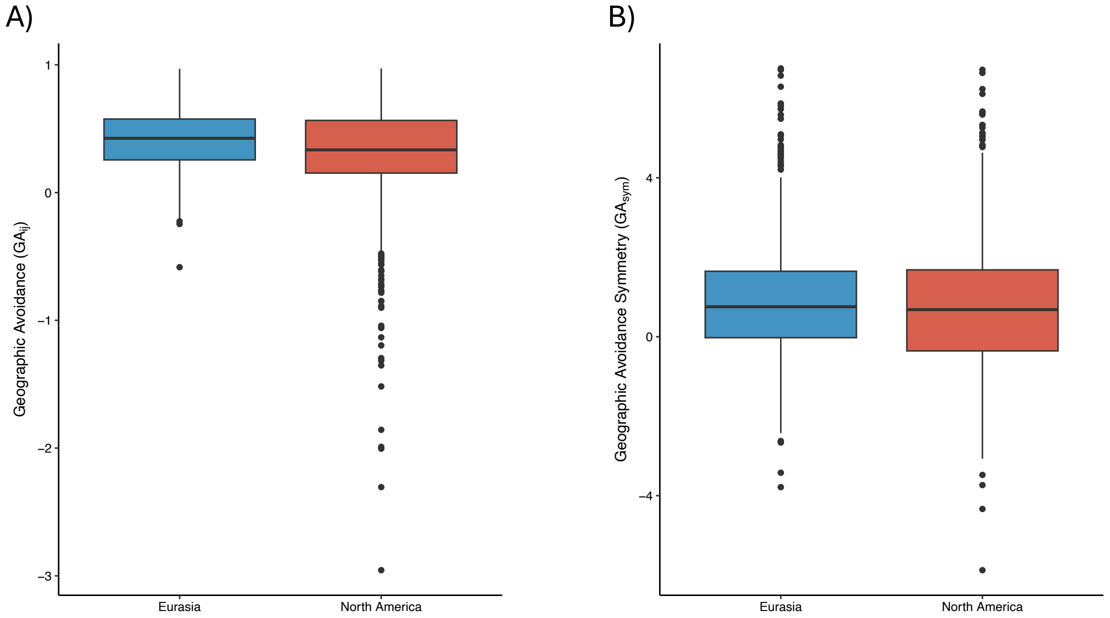


Figure 6. Geographic Avoidance (GA_{ij}) (A) and GA_{ij} symmetry (GA_{sym}) for Eurasia (blue) and North America (red). Boxes represent median and interquartile range, while whiskers indicate maximum and minimum values excluding outliers. Data from long clip.

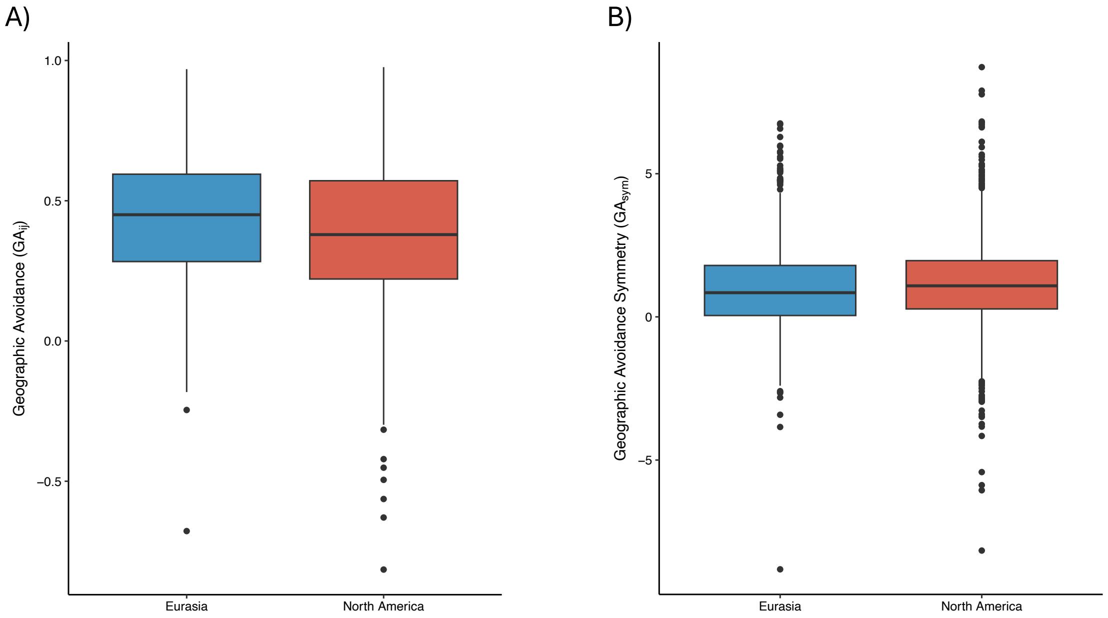


Figure 7. Geographic Avoidance (GA_{ij}) (A) and GA_{ij} symmetry (GA_{sym}) for Eurasia (blue) and North America (red). Boxes represent median and interquartile range, while whiskers indicate maximum and minimum values excluding outliers. Data from lat/long clip.

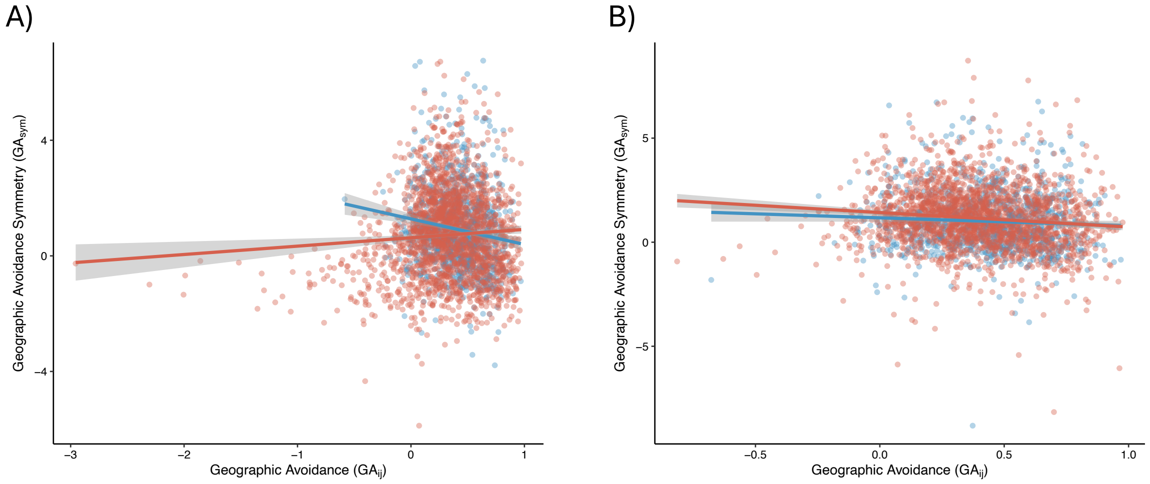


Figure 8. Geographic avoidance (GA_{ij}) and avoidance symmetry (GA_{sym}) for Europe (blue) and North America (red). A) data from long clip. B) data from lat/long clip.

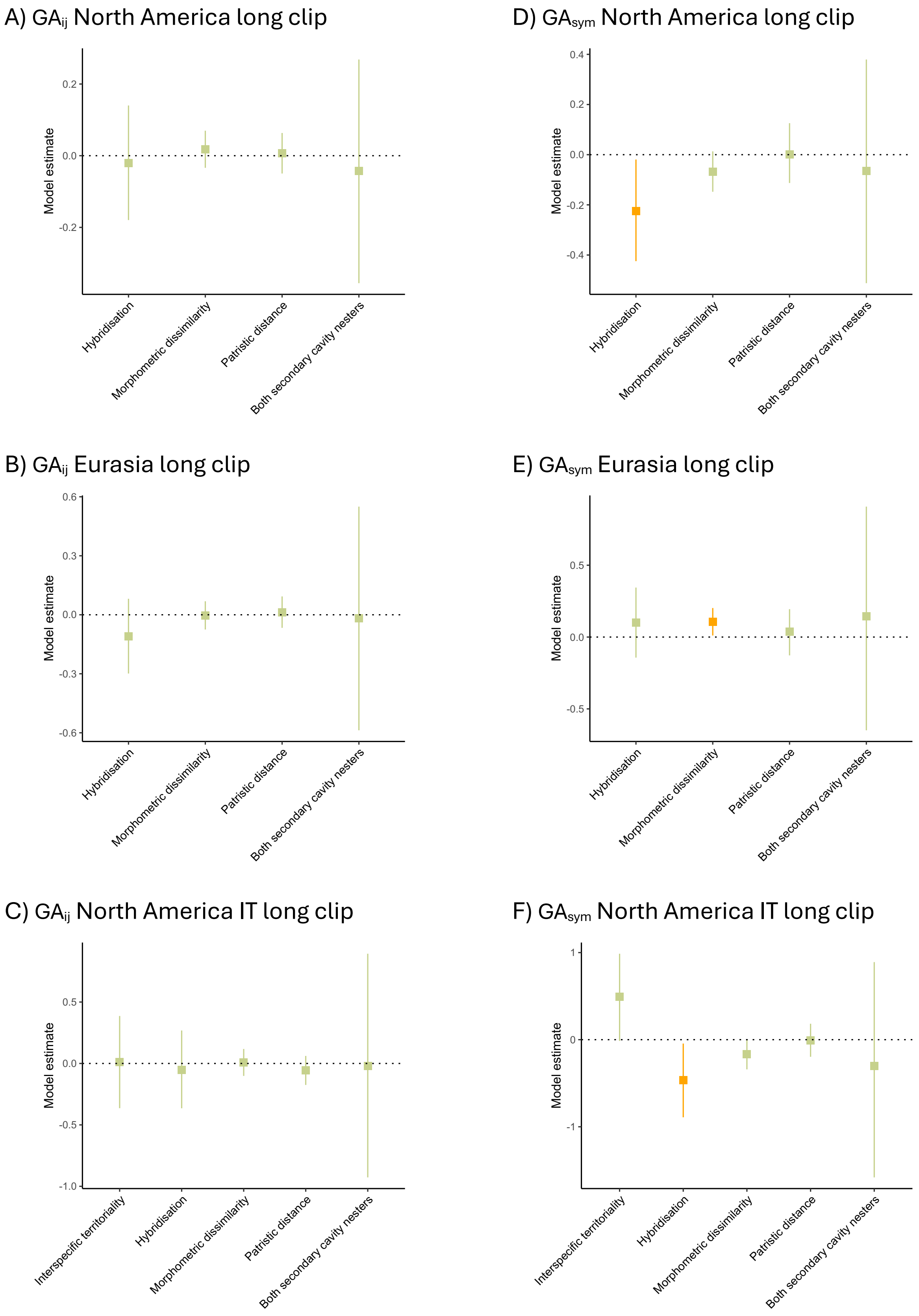
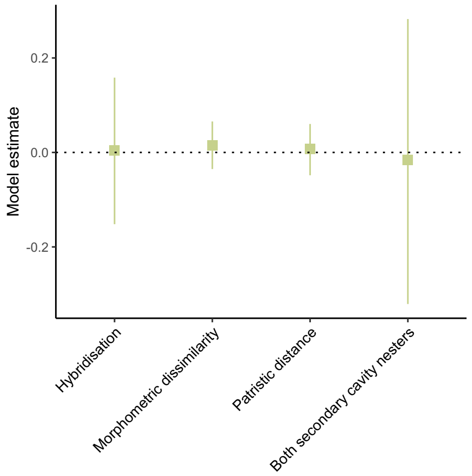


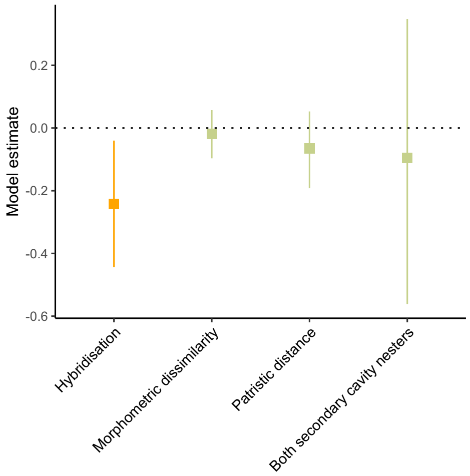
Figure 9: Predictors of the Geographic Avoidance (GA$_{ij}$) (A,C,E) and GA$_{ij}$ symmetry (GA$_{sym}$) (B,D,F) in North America (A,B,E,F) and Eurasia (C,D) using data from longitudinal clips. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed model with GA$_{ij}$ and GA$_{asym}$ 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.

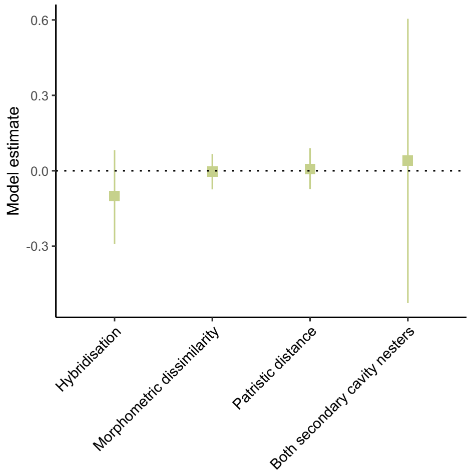
A) GA$_{ij}$ North America lat/long clip



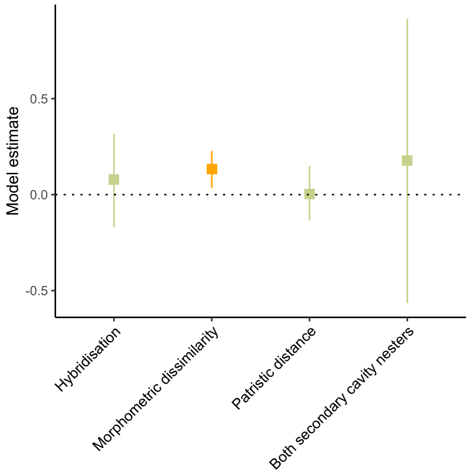
F) GA$_{sym}$ North America lat/long clip



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

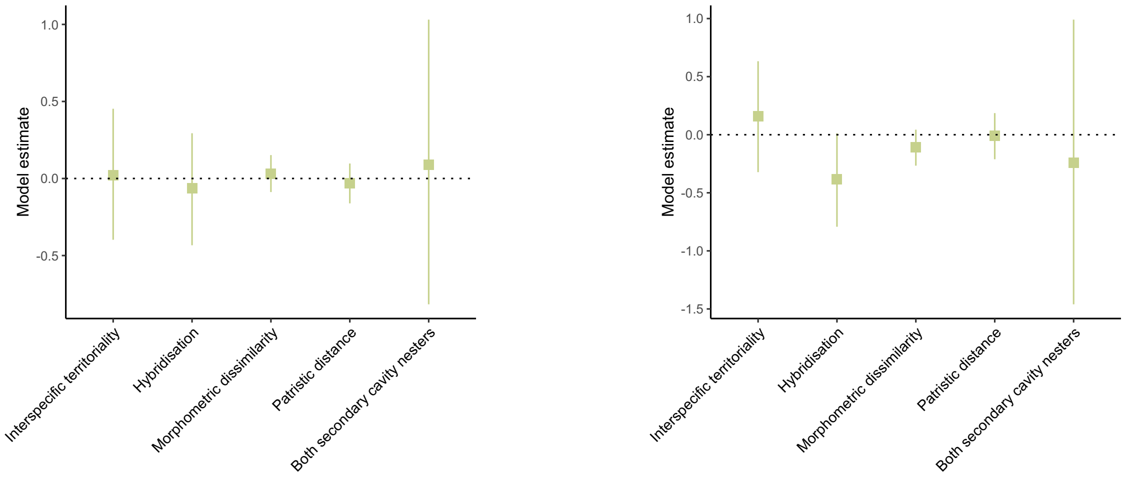


Figure 10: Predictors of the Geographic Avoidance (GA_{ij}) (A,C,E) and GA_{ij} symmetry (GA_{sym}) (B,D,F) in North America (A,B,E,F) and Eurasia (C,D) using data from lat/long clips. Plotted values are coefficient estimates from a phylogenetic generalized linear mixed model with GA_{ij} and GA_{asym} 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	
North America GA_{ij} long clip	**Intercept**	**0.341**	**0.270**	**0.429**	**<0.0005**	***
	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		Median	2.5%	97.5%	pMCMC	
Eurasia GA_{ij} long clip	**Intercept**	**0.421**	**0.329**	**0.509**	**<0.0005**	***
	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		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	
North America GA_{ij} lat/long clip	**Intercept**	**0.399**	**0.333**	**0.475**	**<0.0005**	***
	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		Median	2.5%	97.5%	pMCMC	
Eurasia GA_{ij} lat/long clip	**Intercept**	**0.443**	**0.352**	**0.53**	**<0.0005**	***
	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		Median	2.5%	97.5%	pMCMC	
North America Passerine subset GA_{ij} lat/long clip	**Intercept**	**0.269**	**0.063**	**0.487**	**0.020**	*
	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		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		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		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		Median	2.5%	97.5%	pMCMC
North America teritory 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 Bücker, 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, $GA_{Townsed's}$=0.62, GA_{Hermit}=0.49, GA_{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).

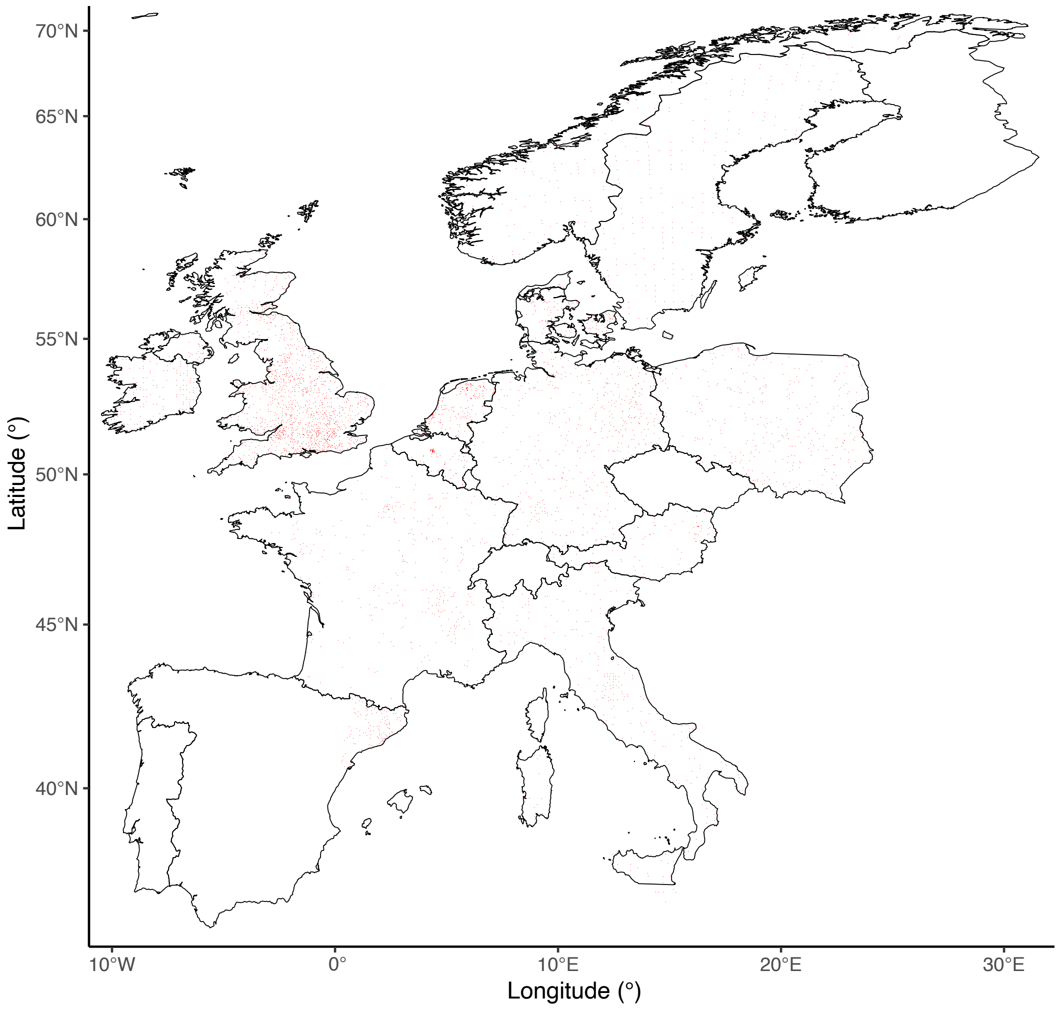


Figure 1. Map of thinned Pan-European Common Bird Monitoring Scheme (PECBMS) sites in 2015 used in models (n=4367). Red 1km cells indicate a survey site is present within said cell. Sites were randomly thinned to allow models to run. Portuguese data was unavailable and Spanish (bar Catalonian), Finnish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

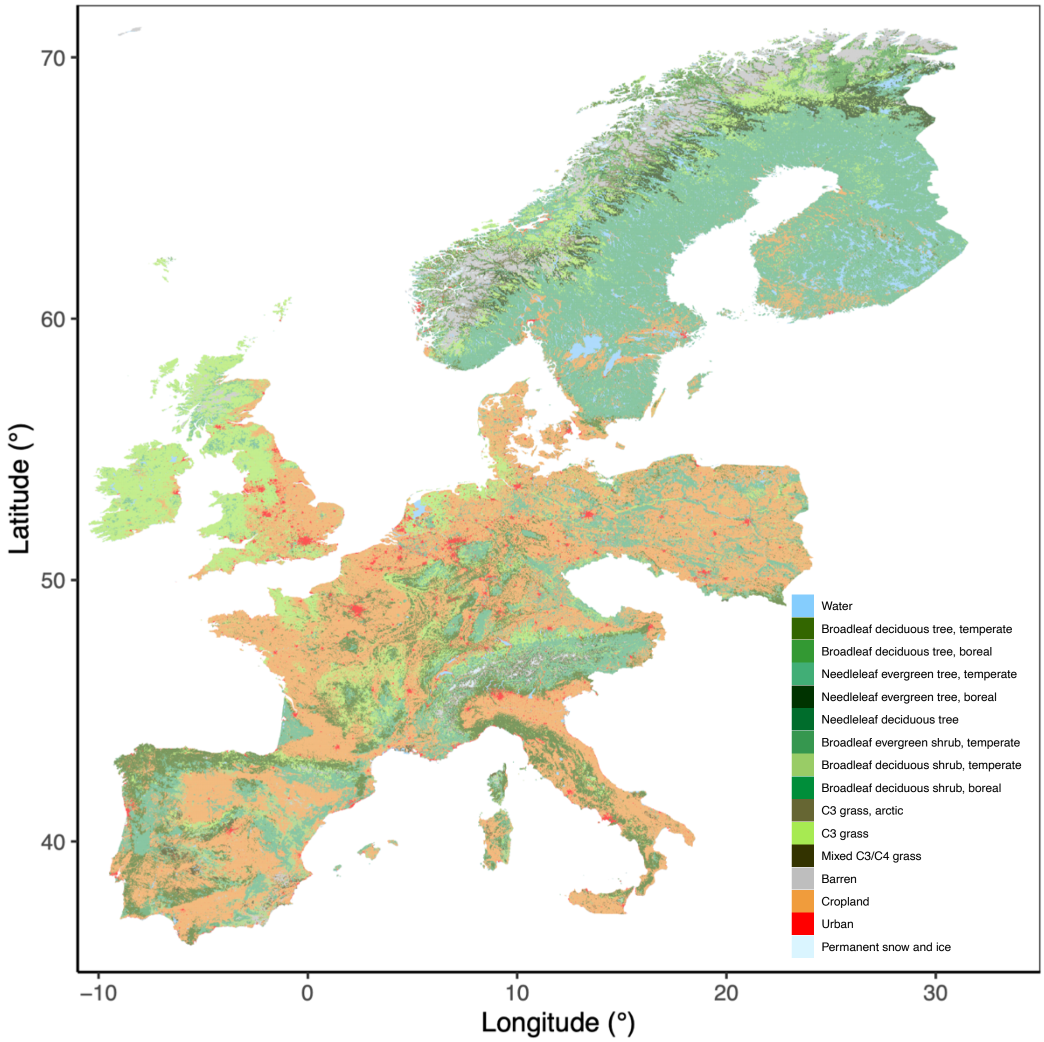


Figure 2. Map of Chen *et al.* (2022) land use/land cover (LULC) 20 plant functional types (PFTs) across Europe for 2015. Not all 20 PFTs occur in Europe.

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

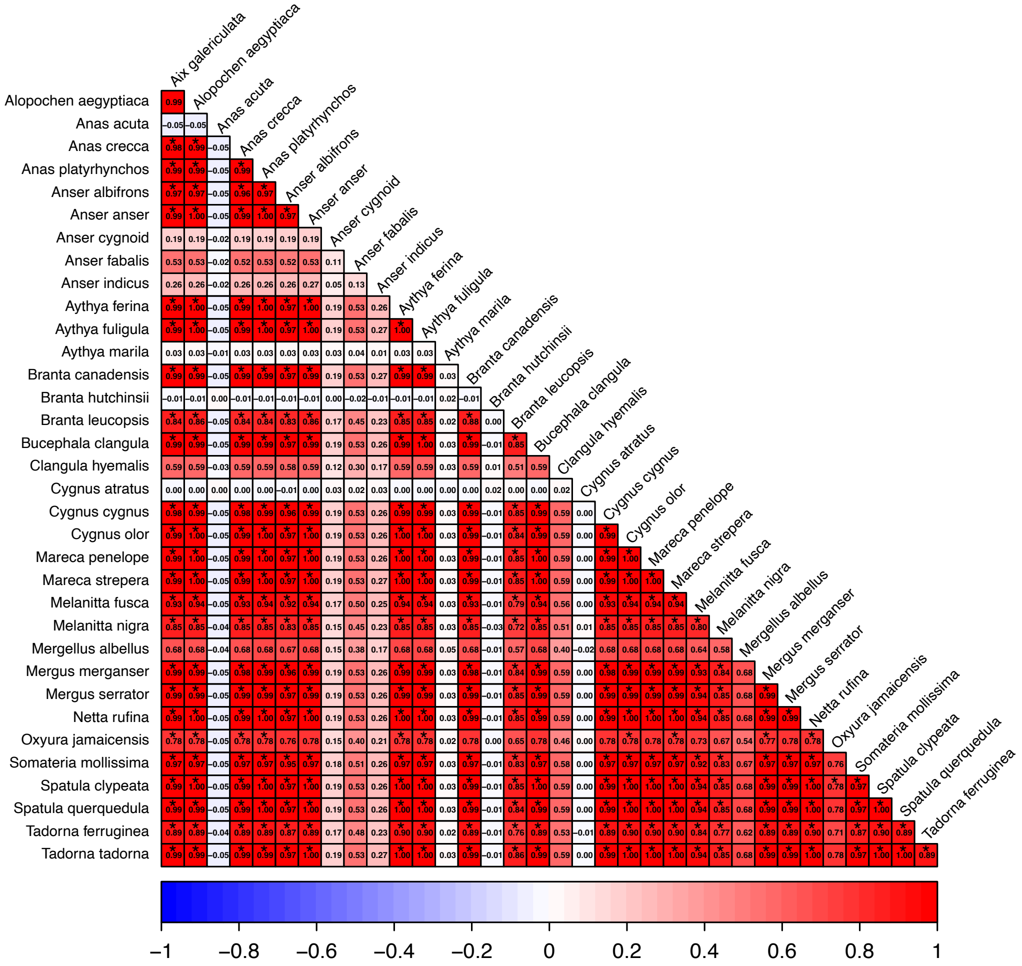
6.3.1 Residual associations

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.

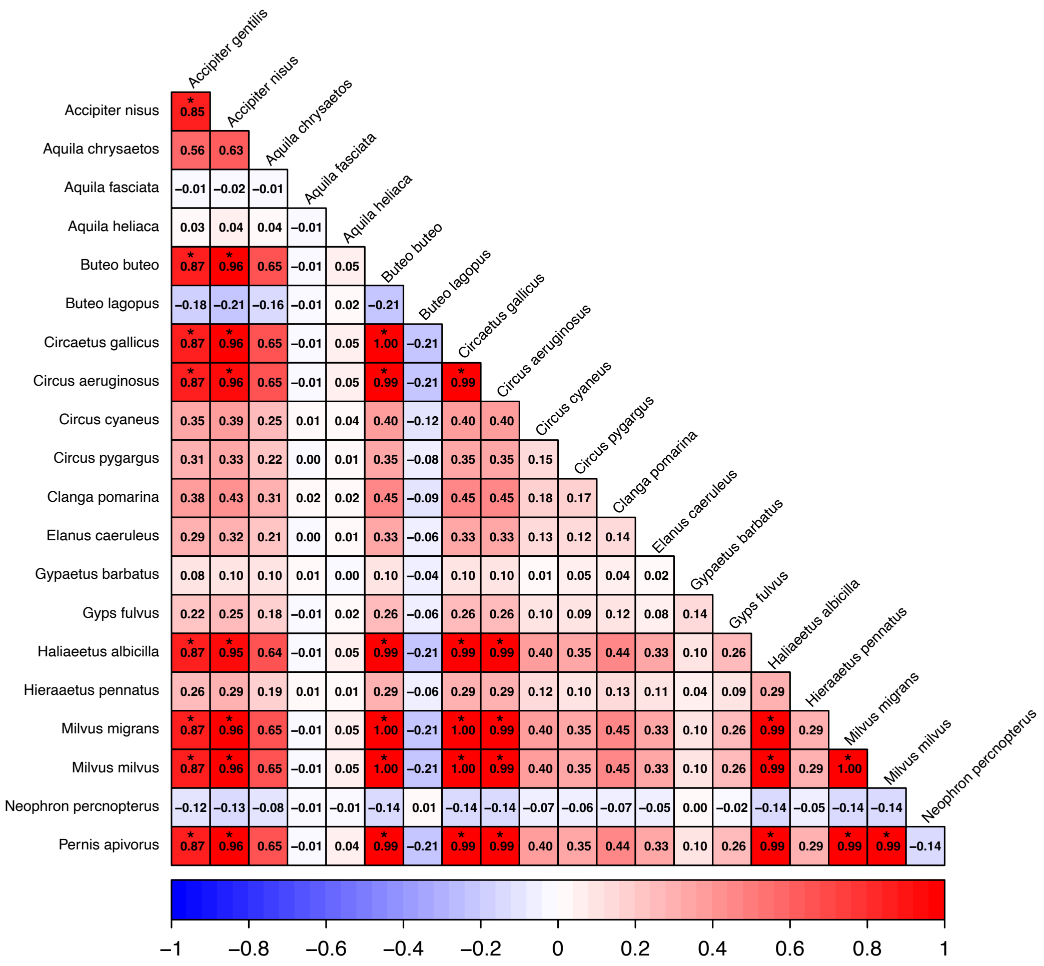
We also found evidence that hybridising species pairs are more likely to have support for the posterior mean >0.9 than non-hybridising pairs. However, this was only the case for the model including all pairs (Figure 5, Table 4). The model containing passerine pairs with interspecific territoriality classifications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

Anatidae



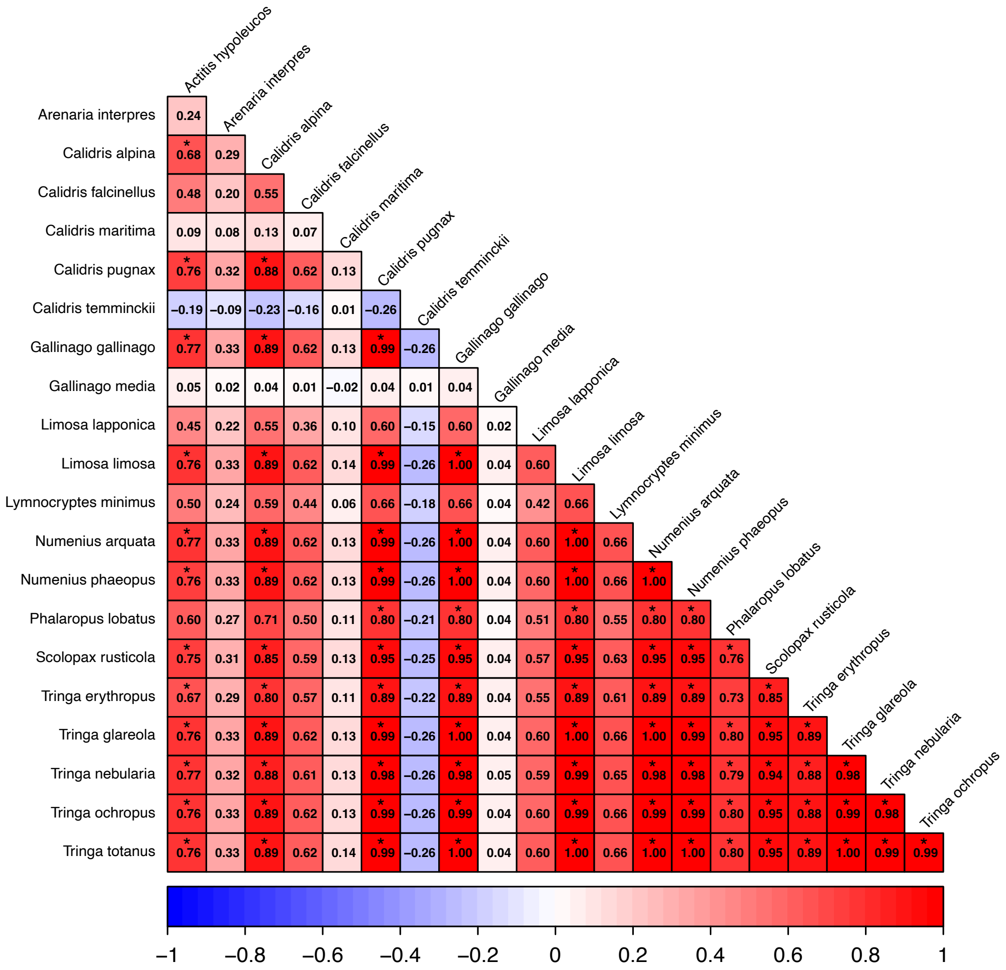
	Aix galericulata	Alopochen aegyptiaca	Anas acuta	Anas crecca	Anas platyrhynchos	Anser albifrons	Anser anser	Anser cygnoid	Anser fabalis	Anser indicus	Aythya ferina	Aythya fuligula	Aythya marila	Branta canadensis	Branta hutchinsii	Branta leucopsis	Bucephala clangula	Clangula hyemalis	Cygnus atratus	Cygnus cygnus	Cygnus olor	Mareca penelope	Mareca strepera	Melanitta fusca	Melanitta nigra	Mergellus albellus	Mergus merganser	Mergus serrator	Netta rufina	Oxyura jamaicensis	Somateria mollissima	Spatula clypeata	Spatula querquedula	Tadorna ferruginea
Alopochen aegyptiaca	0.99
Anas acuta	−0.05	−0.05
Anas crecca	*0.98	*0.99	−0.05
Anas platyrhynchos	*0.99	*0.99	−0.05	*0.99
Anser albifrons	*0.97	*0.97	−0.05	*0.96	*0.97
Anser anser	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97
Anser cygnoid	0.19	0.19	−0.02	0.19	0.19	0.19	0.19
Anser fabalis	0.53	0.53	−0.02	0.52	0.53	0.52	0.53	0.11
Anser indicus	0.26	0.26	−0.02	0.26	0.26	0.26	0.27	0.05	0.13
Aythya ferina	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.26
Aythya fuligula	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.27	*1.00
Aythya marila	0.03	0.03	−0.01	0.03	0.03	0.03	0.03	0.03	0.04	0.01	0.03	0.03
Branta canadensis	*0.99	*0.99	−0.05	*0.99	*0.99	*0.97	*0.99	0.19	0.53	0.27	*0.99	*0.99	0.03
Branta hutchinsii	−0.01	−0.01	0.00	−0.01	−0.01	−0.01	−0.01	0.00	−0.02	−0.01	−0.01	−0.01	0.02	−0.01
Branta leucopsis	*0.84	*0.86	−0.05	*0.84	*0.84	*0.83	*0.86	0.17	0.45	0.23	*0.85	*0.85	0.02	*0.88	0.00
Bucephala clangula	*0.99	*0.99	−0.05	*0.99	*0.99	*0.97	*0.99	0.19	0.53	0.26	*0.99	*1.00	0.03	*0.99	−0.01	*0.85
Clangula hyemalis	0.59	0.59	−0.03	0.59	0.59	0.58	0.59	0.12	0.30	0.17	0.59	0.59	0.03	0.59	0.01	0.51	0.59
Cygnus atratus	0.00	0.00	0.00	0.00	0.00	−0.01	0.00	0.03	0.02	0.03	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.02
Cygnus cygnus	*0.98	*0.99	−0.05	*0.98	*0.99	*0.96	*0.99	0.19	0.53	0.26	*0.99	*0.99	0.03	*0.99	−0.01	*0.85	*0.99	0.59	0.00
Cygnus olor	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.26	*1.00	*1.00	0.03	*0.99	−0.01	*0.84	*0.99	0.59	0.00	*0.99
Mareca penelope	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.26	*1.00	*1.00	0.03	*0.99	−0.01	*0.85	*1.00	0.59	0.00	*0.99	*1.00
Mareca strepera	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.27	*1.00	*1.00	0.03	*0.99	−0.01	*0.85	*1.00	0.59	0.00	*0.99	*1.00	*1.00
Melanitta fusca	*0.93	*0.94	−0.05	*0.93	*0.94	*0.92	*0.94	0.17	0.50	0.25	*0.94	*0.94	0.03	*0.93	−0.01	*0.79	*0.94	0.56	0.00	*0.93	*0.94	*0.94	*0.94
Melanitta nigra	*0.85	*0.85	−0.04	*0.85	*0.85	*0.83	*0.85	0.15	0.45	0.23	*0.85	*0.85	0.03	*0.85	−0.03	*0.72	*0.85	0.51	0.01	*0.85	*0.85	*0.85	*0.85	*0.80
Mergellus albellus	0.68	0.68	−0.04	0.68	0.68	0.67	0.68	0.15	0.38	0.17	0.68	0.68	0.05	0.68	−0.01	0.57	0.68	0.40	−0.02	0.68	0.68	0.68	0.68	0.64	0.58
Mergus merganser	*0.99	*0.99	−0.05	*0.98	*0.99	*0.96	*0.99	0.19	0.53	0.26	*0.99	*0.99	0.03	*0.98	−0.01	*0.84	*0.99	0.59	0.00	*0.98	*0.99	*0.99	*0.99	*0.93	*0.84	0.68
Mergus serrator	*0.99	*0.99	−0.05	*0.99	*0.99	*0.97	*0.99	0.19	0.53	0.26	*0.99	*0.99	0.03	*0.99	−0.01	*0.85	*0.99	0.59	0.00	*0.99	*0.99	*0.99	*0.99	*0.94	*0.85	0.68	*0.99
Netta rufina	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.26	*1.00	*1.00	0.03	*0.99	−0.01	*0.85	*0.99	0.59	0.00	*0.99	*1.00	*1.00	*1.00	*0.94	*0.85	0.68	*0.99	*0.99
Oxyura jamaicensis	*0.78	*0.78	−0.05	*0.78	*0.78	0.76	0.78	0.15	0.40	0.21	*0.78	*0.78	0.02	0.78	0.00	0.65	0.78	0.46	0.00	0.78	*0.78	0.78	*0.78	0.73	0.67	0.54	*0.77	0.78	*0.78
Somateria mollissima	*0.97	*0.97	−0.05	*0.97	*0.97	*0.95	*0.97	0.18	0.51	0.26	*0.97	*0.97	0.03	*0.97	−0.01	*0.83	*0.97	0.58	0.00	*0.97	*0.97	*0.97	*0.97	*0.92	*0.83	0.67	*0.97	*0.97	*0.97	0.76
Spatula clypeata	*0.99	*1.00	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.26	*1.00	*1.00	0.03	*0.99	−0.01	*0.85	*1.00	0.59	0.00	*0.99	*1.00	*1.00	*1.00	*0.94	*0.85	0.68	*0.99	*0.99	*1.00	*0.78	*0.97
Spatula querquedula	*0.99	*0.99	−0.05	*0.99	*1.00	*0.97	*1.00	0.19	0.53	0.26	*1.00	*1.00	0.03	*0.99	−0.01	*0.84	*0.99	0.59	0.00	*0.99	*1.00	*1.00	*1.00	*0.94	*0.85	0.68	*0.99	*0.99	*1.00	0.78	*0.97	*1.00
Tadorna ferruginea	*0.89	*0.89	−0.04	*0.89	*0.89	*0.87	*0.89	0.17	0.48	0.23	*0.90	*0.90	0.02	*0.89	−0.01	*0.76	*0.89	0.53	−0.01	*0.89	*0.90	*0.90	*0.90	*0.84	*0.77	0.62	*0.89	*0.89	*0.90	0.71	*0.87	*0.90	*0.89
Tadorna tadorna	*0.99	*0.99	−0.05	*0.99	*0.99	*0.97	*1.00	0.19	0.53	0.27	*1.00	*1.00	0.03	*0.99	−0.01	*0.86	*0.99	0.59	0.00	*0.99	*1.00	*1.00	*1.00	*0.94	*0.85	0.68	*0.99	*0.99	*1.00	0.78	*0.97	*1.00	*1.00	*0.89

Accipitridae



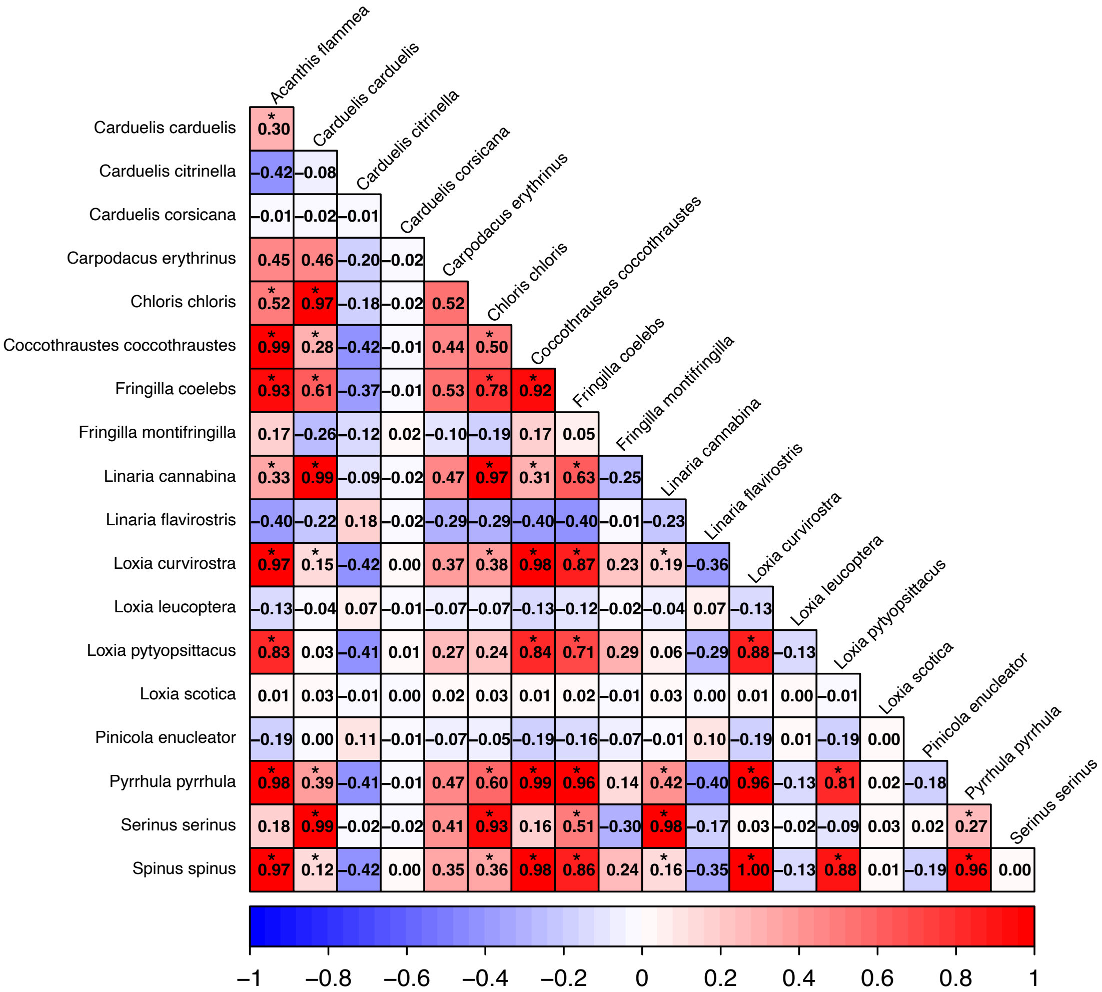
	Accipiter gentilis	Accipiter nisus	Aquila chrysaetos	Aquila fasciata	Aquila heliaca	Buteo buteo	Buteo lagopus	Circaetus gallicus	Circus aeruginosus	Circus cyaneus	Circus pygargus	Clanga pomarina	Elanus caeruleus	Gypaetus barbatus	Gyps fulvus	Haliaeetus albicilla	Hieraaetus pennatus	Milvus migrans	Milvus milvus	Neophron percnopterus
Accipiter nisus	*0.85																			
Aquila chrysaetos	0.56	0.63																		
Aquila fasciata	–0.01	–0.02	–0.01																	
Aquila heliaca	0.03	0.04	0.04	–0.01																
Buteo buteo	*0.87	*0.96	0.65	–0.01	0.05															
Buteo lagopus	–0.18	–0.21	–0.16	–0.01	0.02	–0.21														
Circaetus gallicus	*0.87	*0.96	0.65	–0.01	0.05	*1.00	–0.21													
Circus aeruginosus	*0.87	*0.96	0.65	–0.01	0.05	*0.99	–0.21	*0.99												
Circus cyaneus	0.35	0.39	0.25	0.01	0.04	0.40	–0.12	0.40	0.40											
Circus pygargus	0.31	0.33	0.22	0.00	0.01	0.35	–0.08	0.35	0.35	0.15										
Clanga pomarina	0.38	0.43	0.31	0.02	0.02	0.45	–0.09	0.45	0.45	0.18	0.17									
Elanus caeruleus	0.29	0.32	0.21	0.00	0.01	0.33	–0.06	0.33	0.33	0.13	0.12	0.14								
Gypaetus barbatus	0.08	0.10	0.10	0.01	0.00	0.10	–0.04	0.10	0.10	0.01	0.05	0.04	0.02							
Gyps fulvus	0.22	0.25	0.18	–0.01	0.02	0.26	–0.06	0.26	0.26	0.10	0.09	0.12	0.08	0.14						
Haliaeetus albicilla	*0.87	*0.95	0.64	–0.01	0.05	*0.99	–0.21	*0.99	*0.99	0.40	0.35	0.44	0.33	0.10	0.26					
Hieraaetus pennatus	0.26	0.29	0.19	0.01	0.01	0.29	–0.06	0.29	0.29	0.12	0.10	0.13	0.11	0.04	0.09	0.29				
Milvus migrans	*0.87	*0.96	0.65	–0.01	0.05	*1.00	–0.21	*1.00	*0.99	0.40	0.35	0.45	0.33	0.10	0.26	*0.99	0.29			
Milvus milvus	*0.87	*0.96	0.65	–0.01	0.05	*1.00	–0.21	*1.00	*0.99	0.40	0.35	0.45	0.33	0.10	0.26	*0.99	0.29	*1.00		
Neophron percnopterus	–0.12	–0.13	–0.08	–0.01	–0.01	–0.14	0.01	–0.14	–0.14	–0.07	–0.06	–0.07	–0.05	0.00	–0.02	–0.14	–0.05	–0.14	–0.14	
Pernis apivorus	*0.87	*0.96	0.65	–0.01	0.04	*0.99	–0.21	*0.99	*0.99	0.40	0.35	0.44	0.33	0.10	0.26	*0.99	0.29	*0.99	*0.99	–0.14

Scolopacidae



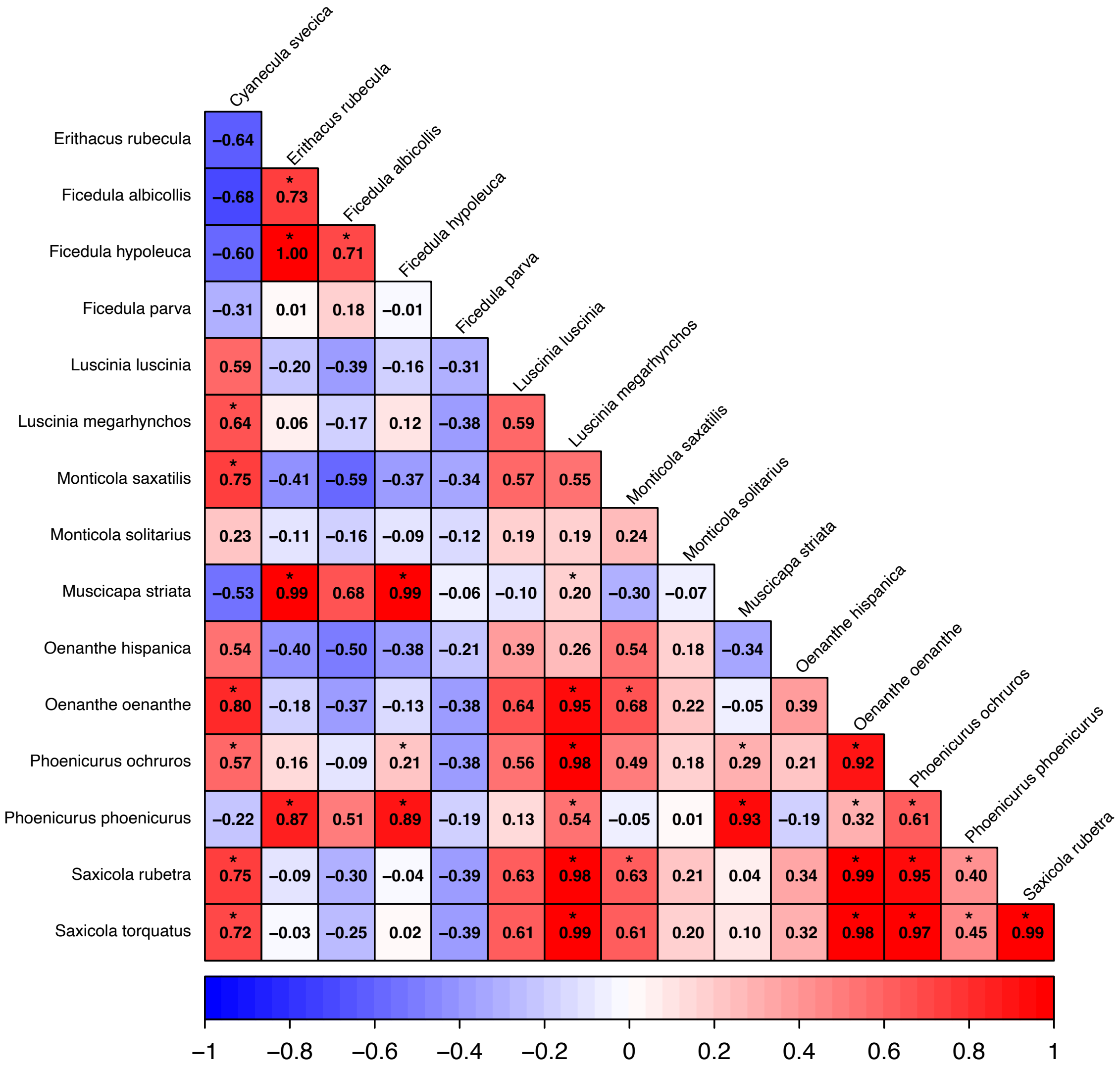
	Actitis hypoleucos	Arenaria interpres	Calidris alpina	Calidris falcinellus	Calidris maritima	Calidris pugnax	Calidris temminckii	Gallinago gallinago	Gallinago media	Limosa lapponica	Limosa limosa	Lymnocryptes minimus	Numenius arquata	Numenius phaeopus	Phalaropus lobatus	Scolopax rusticola	Tringa erythropus	Tringa glareola	Tringa nebularia	Tringa ochropus
Arenaria interpres	0.24																			
Calidris alpina	* 0.68	0.29																		
Calidris falcinellus	0.48	0.20	0.55																	
Calidris maritima	0.09	0.08	0.13	0.07																
Calidris pugnax	* 0.76	0.32	* 0.88	0.62	0.13															
Calidris temminckii	−0.19	−0.09	−0.23	−0.16	0.01	−0.26														
Gallinago gallinago	* 0.77	0.33	* 0.89	0.62	0.13	* 0.99	−0.26													
Gallinago media	0.05	0.02	0.04	0.01	−0.02	0.04	0.01	0.04												
Limosa lapponica	0.45	0.22	0.55	0.36	0.10	0.60	−0.15	0.60	0.02											
Limosa limosa	* 0.76	0.33	* 0.89	0.62	0.14	* 0.99	−0.26	* 1.00	0.04	0.60										
Lymnocryptes minimus	0.50	0.24	0.59	0.44	0.06	0.66	−0.18	0.66	0.04	0.42	0.66									
Numenius arquata	* 0.77	0.33	* 0.89	0.62	0.13	* 0.99	−0.26	* 1.00	0.04	0.60	* 1.00	0.66								
Numenius phaeopus	* 0.76	0.33	* 0.89	0.62	0.13	* 0.99	−0.26	* 1.00	0.04	0.60	* 1.00	0.66	* 1.00							
Phalaropus lobatus	0.60	0.27	0.71	0.50	0.11	* 0.80	−0.21	* 0.80	0.04	0.51	* 0.80	0.55	* 0.80	* 0.80						
Scolopax rusticola	* 0.75	0.31	* 0.85	0.59	0.13	* 0.95	−0.25	* 0.95	0.04	0.57	* 0.95	0.63	* 0.95	* 0.95	* 0.76					
Tringa erythropus	* 0.67	0.29	* 0.80	0.57	0.11	* 0.89	−0.22	* 0.89	0.04	0.55	* 0.89	0.61	* 0.89	* 0.89	0.73	* 0.85				
Tringa glareola	* 0.76	0.33	* 0.89	0.62	0.13	* 0.99	−0.26	* 1.00	0.04	0.60	* 1.00	0.66	* 1.00	* 0.99	* 0.80	* 0.95	* 0.89			
Tringa nebularia	* 0.77	0.32	* 0.88	0.61	0.13	* 0.98	−0.26	* 0.98	0.05	0.59	* 0.99	0.65	* 0.98	* 0.98	* 0.79	* 0.94	* 0.88	* 0.98		
Tringa ochropus	* 0.76	0.33	* 0.89	0.62	0.13	* 0.99	−0.26	* 0.99	0.04	0.60	* 0.99	0.66	* 0.99	* 0.99	* 0.80	* 0.95	* 0.88	* 0.99	* 0.98	
Tringa totanus	* 0.76	0.33	* 0.89	0.62	0.14	* 0.99	−0.26	* 1.00	0.04	0.60	* 1.00	0.66	* 1.00	* 1.00	* 0.80	* 0.95	* 0.89	* 1.00	* 0.99	* 0.99

Fringillidae



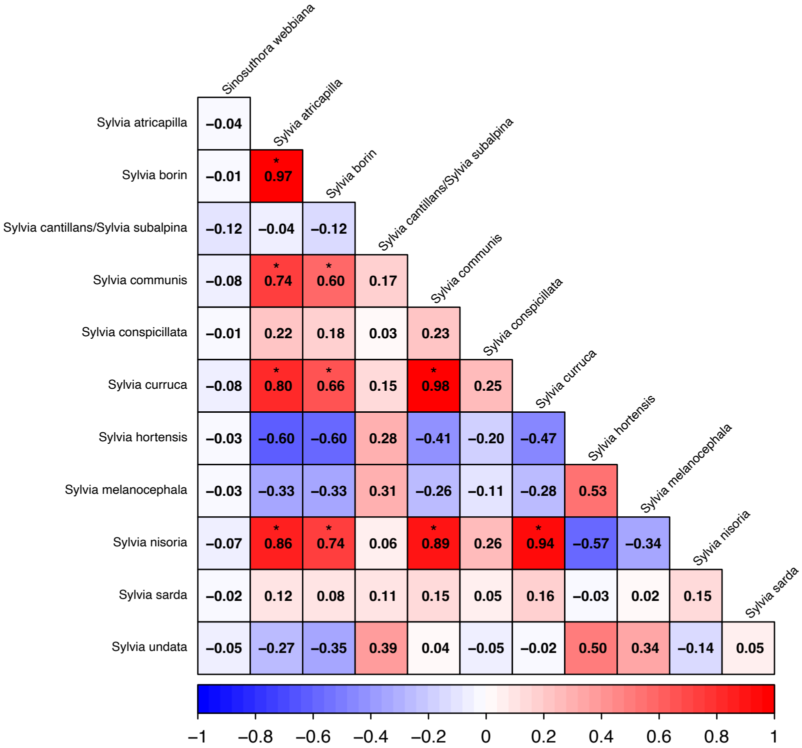
	Acanthis flammea	Carduelis carduelis	Carduelis citrinella	Carduelis corsicana	Carpodacus erythrinus	Chloris chloris	Coccothraustes coccothraustes	Fringilla coelebs	Fringilla montifringilla	Linaria cannabina	Linaria flavirostris	Loxia curvirostra	Loxia leucoptera	Loxia pytyopsittacus	Loxia scotica	Pinicola enucleator	Pyrrhula pyrrhula	Serinus serinus
Carduelis carduelis	* 0.30																	
Carduelis citrinella	−0.42	−0.08																
Carduelis corsicana	−0.01	−0.02	−0.01															
Carpodacus erythrinus	0.45	0.46	−0.20	−0.02														
Chloris chloris	* 0.52	* 0.97	−0.18	−0.02	0.52													
Coccothraustes coccothraustes	* 0.99	* 0.28	−0.42	−0.01	0.44	* 0.50												
Fringilla coelebs	* 0.93	* 0.61	−0.37	−0.01	0.53	* 0.78	* 0.92											
Fringilla montifringilla	0.17	−0.26	−0.12	0.02	−0.10	−0.19	0.17	0.05										
Linaria cannabina	* 0.33	* 0.99	−0.09	−0.02	0.47	* 0.97	* 0.31	* 0.63	−0.25									
Linaria flavirostris	−0.40	−0.22	0.18	−0.02	−0.29	−0.29	−0.40	−0.40	−0.01	−0.23								
Loxia curvirostra	* 0.97	* 0.15	−0.42	0.00	0.37	* 0.38	* 0.98	* 0.87	0.23	* 0.19	−0.36							
Loxia leucoptera	−0.13	−0.04	0.07	−0.01	−0.07	−0.07	−0.13	−0.12	−0.02	−0.04	0.07	−0.13						
Loxia pytyopsittacus	* 0.83	0.03	−0.41	0.01	0.27	0.24	* 0.84	* 0.71	0.29	0.06	−0.29	* 0.88	−0.13					
Loxia scotica	0.01	0.03	−0.01	0.00	0.02	0.03	0.01	0.02	−0.01	0.03	0.00	0.01	0.00	−0.01				
Pinicola enucleator	−0.19	0.00	0.11	−0.01	−0.07	−0.05	−0.19	−0.16	−0.07	−0.01	0.10	−0.19	0.01	−0.19	0.00			
Pyrrhula pyrrhula	* 0.98	* 0.39	−0.41	−0.01	0.47	* 0.60	* 0.99	* 0.96	0.14	* 0.42	−0.40	* 0.96	−0.13	* 0.81	0.02	−0.18		
Serinus serinus	0.18	* 0.99	−0.02	−0.02	0.41	* 0.93	0.16	* 0.51	−0.30	* 0.98	−0.17	0.03	−0.02	−0.09	0.03	0.02	* 0.27	
Spinus spinus	* 0.97	* 0.12	−0.42	0.00	0.35	* 0.36	* 0.98	* 0.86	0.24	* 0.16	−0.35	* 1.00	−0.13	* 0.88	0.01	−0.19	* 0.96	0.00

Muscicapidae



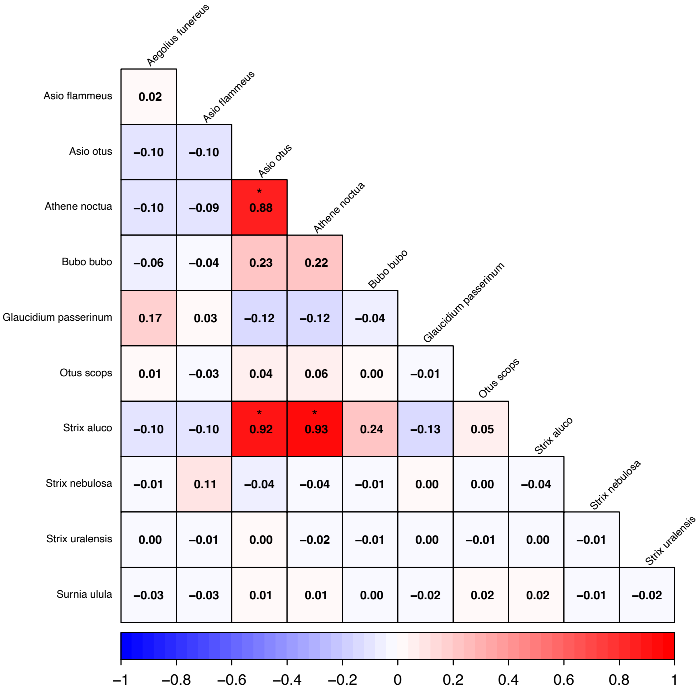
	Cyanecula svecica	Erithacus rubecula	Ficedula albicollis	Ficedula hypoleuca	Ficedula parva	Luscinia luscinia	Luscinia megarhynchos	Monticola saxatilis	Monticola solitarius	Muscicapa striata	Oenanthe hispanica	Oenanthe oenanthe	Phoenicurus ochruros	Phoenicurus phoenicurus	Saxicola rubetra
Erithacus rubecula	−0.64														
Ficedula albicollis	−0.68	*0.73													
Ficedula hypoleuca	−0.60	*1.00	*0.71												
Ficedula parva	−0.31	0.01	0.18	−0.01											
Luscinia luscinia	0.59	−0.20	−0.39	−0.16	−0.31										
Luscinia megarhynchos	*0.64	0.06	−0.17	0.12	−0.38	0.59									
Monticola saxatilis	*0.75	−0.41	−0.59	−0.37	−0.34	0.57	0.55								
Monticola solitarius	0.23	−0.11	−0.16	−0.09	−0.12	0.19	0.19	0.24							
Muscicapa striata	−0.53	*0.99	0.68	*0.99	−0.06	−0.10	*0.20	−0.30	−0.07						
Oenanthe hispanica	0.54	−0.40	−0.50	−0.38	−0.21	0.39	0.26	0.54	0.18	−0.34					
Oenanthe oenanthe	*0.80	−0.18	−0.37	−0.13	−0.38	0.64	*0.95	*0.68	0.22	−0.05	0.39				
Phoenicurus ochruros	*0.57	0.16	−0.09	*0.21	−0.38	0.56	*0.98	0.49	0.18	*0.29	0.21	*0.92			
Phoenicurus phoenicurus	−0.22	*0.87	0.51	*0.89	−0.19	0.13	*0.54	−0.05	0.01	*0.93	−0.19	*0.32	*0.61		
Saxicola rubetra	*0.75	−0.09	−0.30	−0.04	−0.39	0.63	*0.98	*0.63	0.21	0.04	0.34	*0.99	*0.95	*0.40	
Saxicola torquatus	*0.72	−0.03	−0.25	0.02	−0.39	0.61	*0.99	0.61	0.20	0.10	0.32	*0.98	*0.97	*0.45	*0.99

Sylviidae



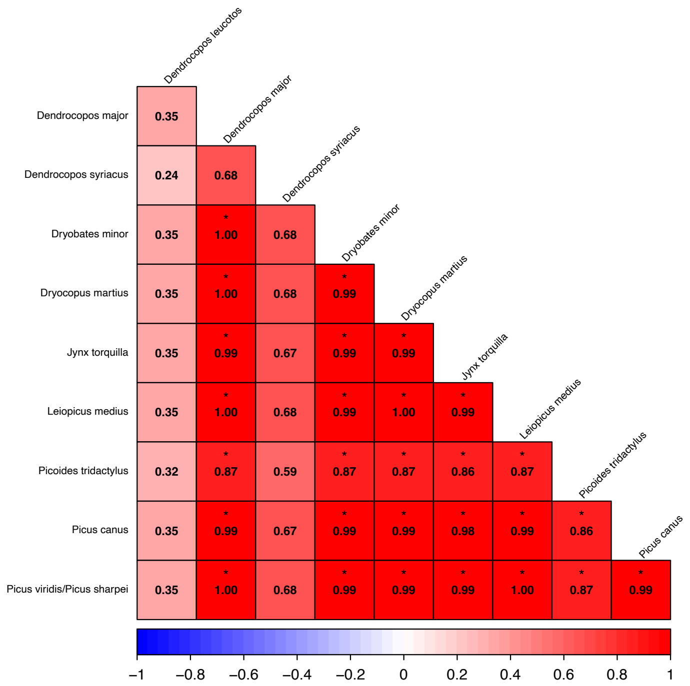
	Sinosuthora webbiana	Sylvia atricapilla	Sylvia borin	Sylvia cantillans/Sylvia subalpina	Sylvia communis	Sylvia conspicillata	Sylvia curruca	Sylvia hortensis	Sylvia melanocephala	Sylvia nisoria	Sylvia sarda
Sylvia atricapilla	−0.04										
Sylvia borin	−0.01	* 0.97									
Sylvia cantillans/Sylvia subalpina	−0.12	−0.04	−0.12								
Sylvia communis	−0.08	* 0.74	* 0.60	0.17							
Sylvia conspicillata	−0.01	0.22	0.18	0.03	0.23						
Sylvia curruca	−0.08	* 0.80	* 0.66	0.15	* 0.98	0.25					
Sylvia hortensis	−0.03	−0.60	−0.60	0.28	−0.41	−0.20	−0.47				
Sylvia melanocephala	−0.03	−0.33	−0.33	0.31	−0.26	−0.11	−0.28	0.53			
Sylvia nisoria	−0.07	* 0.86	* 0.74	0.06	* 0.89	0.26	* 0.94	−0.57	−0.34		
Sylvia sarda	−0.02	0.12	0.08	0.11	0.15	0.05	0.16	−0.03	0.02	0.15	
Sylvia undata	−0.05	−0.27	−0.35	0.39	0.04	−0.05	−0.02	0.50	0.34	−0.14	0.05

Strigidae



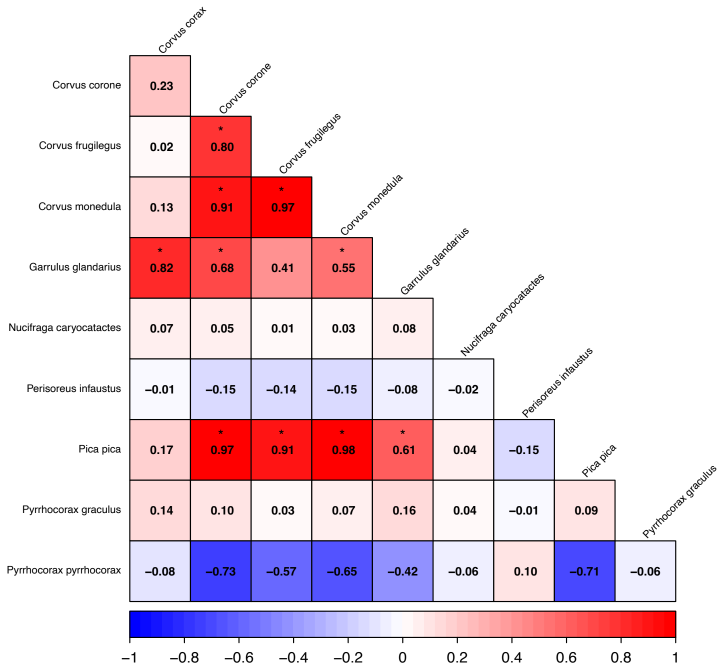
	Aegolius funereus	Asio flammeus	Asio otus	Athene noctua	Bubo bubo	Glaucidium passerinum	Otus scops	Strix aluco	Strix nebulosa	Strix uralensis
Asio flammeus	0.02									
Asio otus	−0.10	−0.10								
Athene noctua	−0.10	−0.09	* 0.88							
Bubo bubo	−0.06	−0.04	0.23	0.22						
Glaucidium passerinum	0.17	0.03	−0.12	−0.12	−0.04					
Otus scops	0.01	−0.03	0.04	0.06	0.00	−0.01				
Strix aluco	−0.10	−0.10	* 0.92	* 0.93	0.24	−0.13	0.05			
Strix nebulosa	−0.01	0.11	−0.04	−0.04	−0.01	0.00	0.00	−0.04		
Strix uralensis	0.00	−0.01	0.00	−0.02	−0.01	0.00	−0.01	0.00	−0.01	
Surnia ulula	−0.03	−0.03	0.01	0.01	0.00	−0.02	0.02	0.02	−0.01	−0.02

Picidae



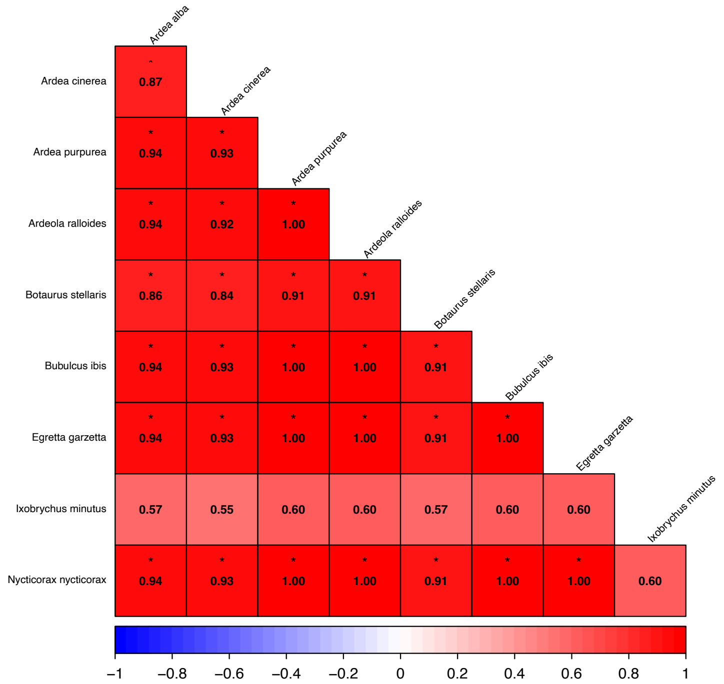
	Dendrocopos leucotos	Dendrocopos major	Dendrocopos syriacus	Dryobates minor	Dryocopus martius	Jynx torquilla	Leiopicus medius	Picoides tridactylus	Picus canus
Dendrocopos major	0.35								
Dendrocopos syriacus	0.24	0.68							
Dryobates minor	0.35	* 1.00	0.68						
Dryocopus martius	0.35	* 1.00	0.68	* 0.99					
Jynx torquilla	0.35	* 0.99	0.67	* 0.99	* 0.99				
Leiopicus medius	0.35	* 1.00	0.68	* 0.99	* 1.00	* 0.99			
Picoides tridactylus	0.32	* 0.87	0.59	* 0.87	* 0.87	* 0.86	* 0.87		
Picus canus	0.35	* 0.99	0.67	* 0.99	* 0.99	* 0.98	* 0.99	* 0.86	
Picus viridis/Picus sharpei	0.35	* 1.00	0.68	* 0.99	* 0.99	* 0.99	* 1.00	* 0.87	* 0.99

Corvidae



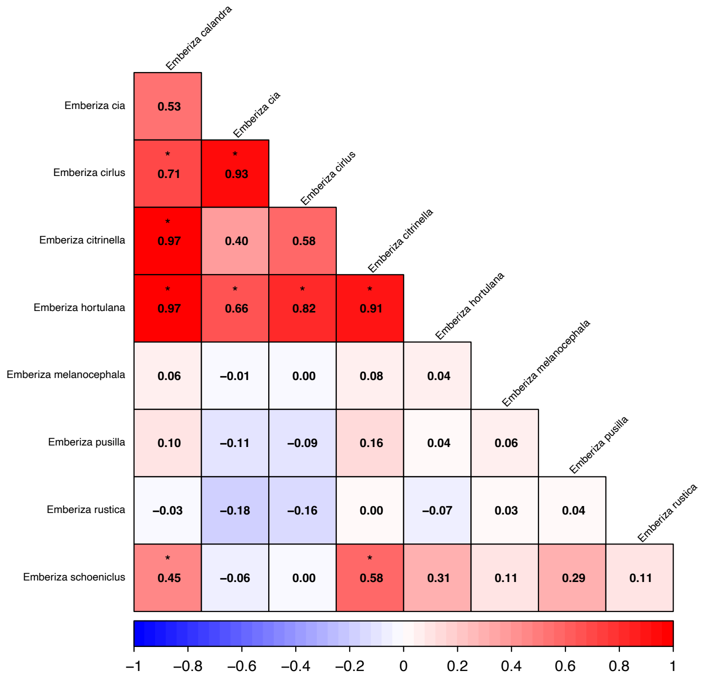
	Corvus corax	Corvus corone	Corvus frugilegus	Corvus monedula	Garrulus glandarius	Nucifraga caryocatactes	Perisoreus infaustus	Pica pica	Pyrrhocorax graculus
Corvus corone	0.23								
Corvus frugilegus	0.02	* 0.80							
Corvus monedula	0.13	* 0.91	* 0.97						
Garrulus glandarius	* 0.82	* 0.68	0.41	* 0.55					
Nucifraga caryocatactes	0.07	0.05	0.01	0.03	0.08				
Perisoreus infaustus	−0.01	−0.15	−0.14	−0.15	−0.08	−0.02			
Pica pica	0.17	* 0.97	* 0.91	* 0.98	* 0.61	0.04	−0.15		
Pyrrhocorax graculus	0.14	0.10	0.03	0.07	0.16	0.04	−0.01	0.09	
Pyrrhocorax pyrrhocorax	−0.08	−0.73	−0.57	−0.65	−0.42	−0.06	0.10	−0.71	−0.06

Ardeidae



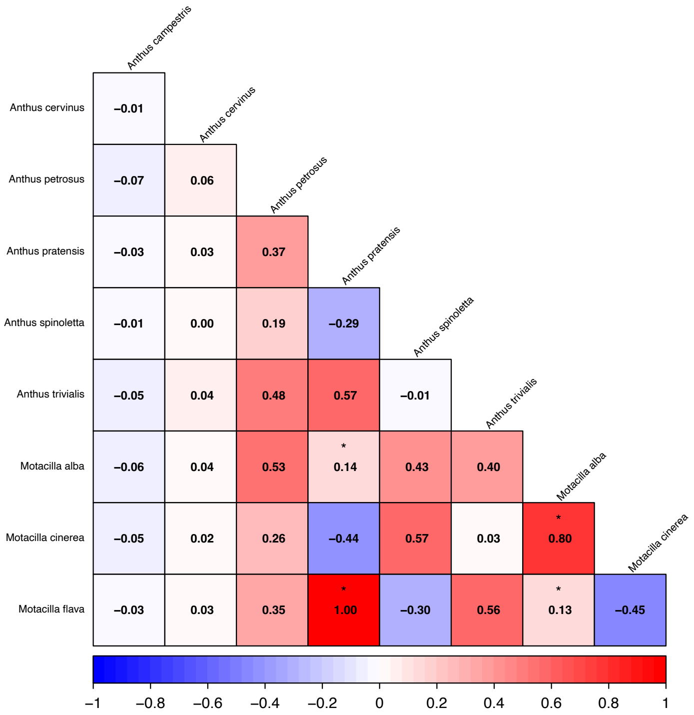
	Ardea alba	Ardea cinerea	Ardea purpurea	Ardeola ralloides	Botaurus stellaris	Bubulcus ibis	Egretta garzetta	Ixobrychus minutus
Ardea cinerea	^ 0.87							
Ardea purpurea	* 0.94	* 0.93						
Ardeola ralloides	* 0.94	* 0.92	* 1.00					
Botaurus stellaris	* 0.86	* 0.84	* 0.91	* 0.91				
Bubulcus ibis	* 0.94	* 0.93	* 1.00	* 1.00	* 0.91			
Egretta garzetta	* 0.94	* 0.93	* 1.00	* 1.00	* 0.91	* 1.00		
Ixobrychus minutus	0.57	0.55	0.60	0.60	0.57	0.60	0.60	
Nycticorax nycticorax	* 0.94	* 0.93	* 1.00	* 1.00	* 0.91	* 1.00	* 1.00	0.60

Emberizidae



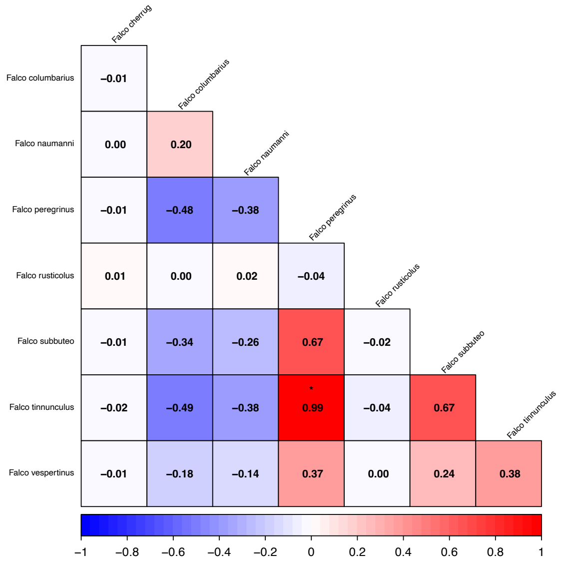
	Emberiza calandra	Emberiza cia	Emberiza cirlus	Emberiza citrinella	Emberiza hortulana	Emberiza melanocephala	Emberiza pusilla	Emberiza rustica
Emberiza cia	0.53							
Emberiza cirlus	* 0.71	* 0.93						
Emberiza citrinella	* 0.97	0.40	0.58					
Emberiza hortulana	* 0.97	* 0.66	* 0.82	* 0.91				
Emberiza melanocephala	0.06	−0.01	0.00	0.08	0.04			
Emberiza pusilla	0.10	−0.11	−0.09	0.16	0.04	0.06		
Emberiza rustica	−0.03	−0.18	−0.16	0.00	−0.07	0.03	0.04	
Emberiza schoeniclus	* 0.45	−0.06	0.00	* 0.58	0.31	0.11	0.29	0.11

Motacillidae



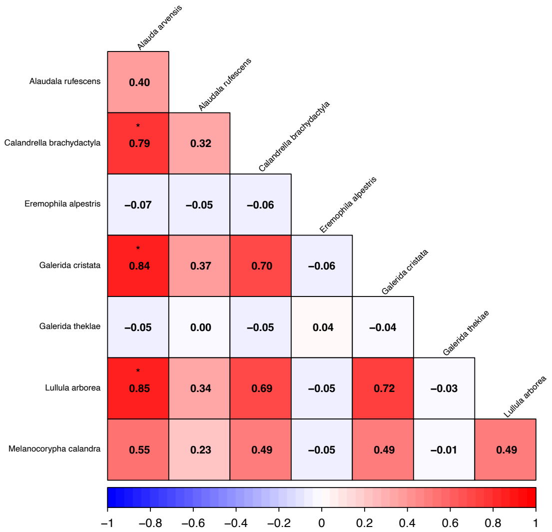
	Anthus campestris	Anthus cervinus	Anthus petrosus	Anthus pratensis	Anthus spinoletta	Anthus trivialis	Motacilla alba	Motacilla cinerea
Anthus cervinus	−0.01							
Anthus petrosus	−0.07	0.06						
Anthus pratensis	−0.03	0.03	0.37					
Anthus spinoletta	−0.01	0.00	0.19	−0.29				
Anthus trivialis	−0.05	0.04	0.48	0.57	−0.01			
Motacilla alba	−0.06	0.04	0.53	* 0.14	0.43	0.40		
Motacilla cinerea	−0.05	0.02	0.26	−0.44	0.57	0.03	* 0.80	
Motacilla flava	−0.03	0.03	0.35	* 1.00	−0.30	0.56	* 0.13	−0.45

Falconidae



	Falco cherrug	Falco columbarius	Falco naumanni	Falco peregrinus	Falco rusticolus	Falco subbuteo	Falco tinnunculus
Falco columbarius	−0.01						
Falco naumanni	0.00	0.20					
Falco peregrinus	−0.01	−0.48	−0.38				
Falco rusticolus	0.01	0.00	0.02	−0.04			
Falco subbuteo	−0.01	−0.34	−0.26	0.67	−0.02		
Falco tinnunculus	−0.02	−0.49	−0.38	* 0.99	−0.04	0.67	
Falco vespertinus	−0.01	−0.18	−0.14	0.37	0.00	0.24	0.38

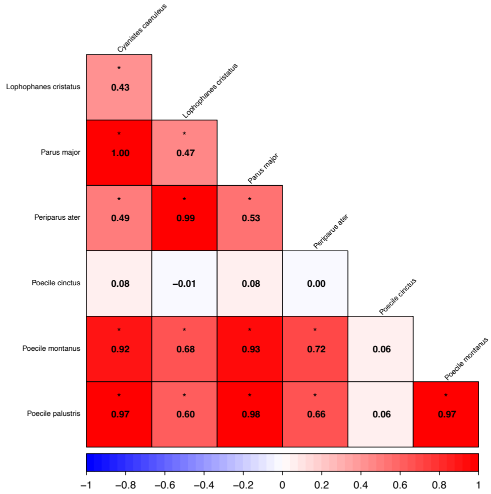
Alaudidae

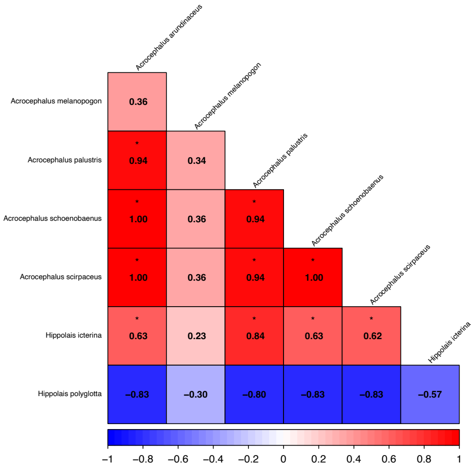


	Alauda arvensis	Alaudala rufescens	Calandrella brachydactyla	Eremophila alpestris	Galerida cristata	Galerida theklae	Lullula arborea
Alaudala rufescens	0.40						
Calandrella brachydactyla	* 0.79	0.32					
Eremophila alpestris	−0.07	−0.05	−0.06				
Galerida cristata	* 0.84	0.37	0.70	−0.06			
Galerida theklae	−0.05	0.00	−0.05	0.04	−0.04		
Lullula arborea	* 0.85	0.34	0.69	−0.05	0.72	−0.03	
Melanocorypha calandra	0.55	0.23	0.49	−0.05	0.49	−0.01	0.49

Paridae

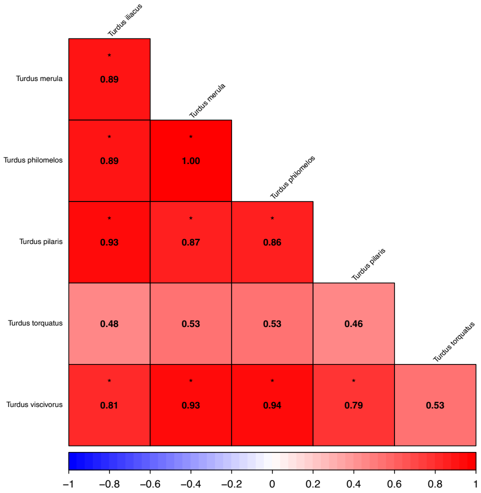
Acrocephalidae

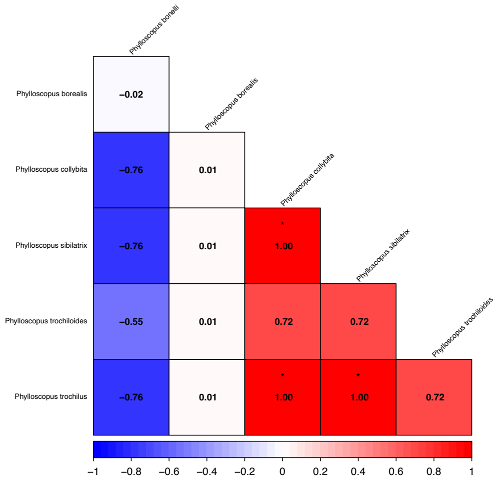




Turdidae

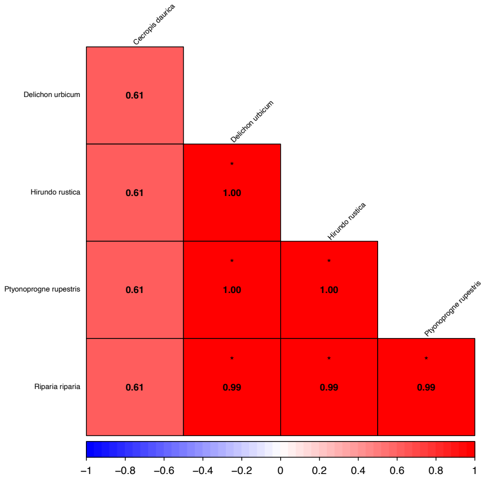
Phylloscopidae

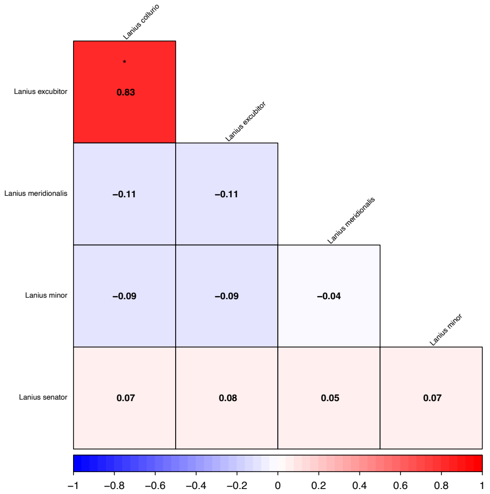




Hirundinidae

Laniidae





Apodidae

Threskiornithidae

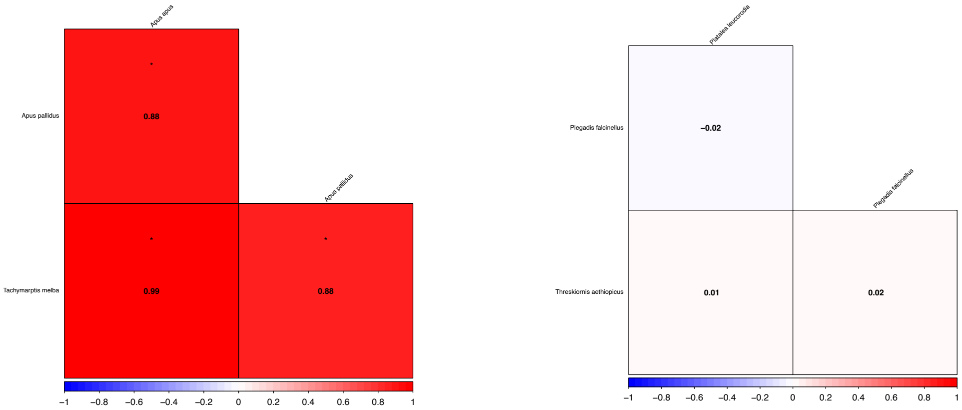


Figure 3. Residual association matrices for a variety of European families. Matricies not shown here can be found in Appendix D. Red indicates positive associations between species and blue indicates negative associations, after accounting for modelled environmental covariates. Asterices indicate a posterior 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 JSDMs, 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	
All pairs	**Intercept**	**2.784**	**1.578**	**3.749**	**0.001**	**
	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 JSDMs, 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	
Passerines with interspecific territoriality predictions	Intercept	0.370	-3.466	3.748	0.883	
	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 JSDMs, 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	
All pairs	Intercept	-0.587	-4.434	3.306	0.804	
	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 JSDMs, 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	
Passengers with interspecific territoriality predictions	Intercept	-0.7728	-4.061	3.519	0.715	
	Interspecific territoriality	0.6041	-2.190	3.457	0.650	
	Hybridisation	1.6451	-0.168	3.670	0.092	
	Morphometric dissimilarity	-0.7543	-1.798	0.137	0.088	
	Patristic distance	-0.1103	-1.354	1.111	0.855	
	Same lifestyle & niche	-0.5161	-2.319	1.086	0.533	
	Same habitat type	**1.660**	**0.135**	**3.438**	**0.026**	*

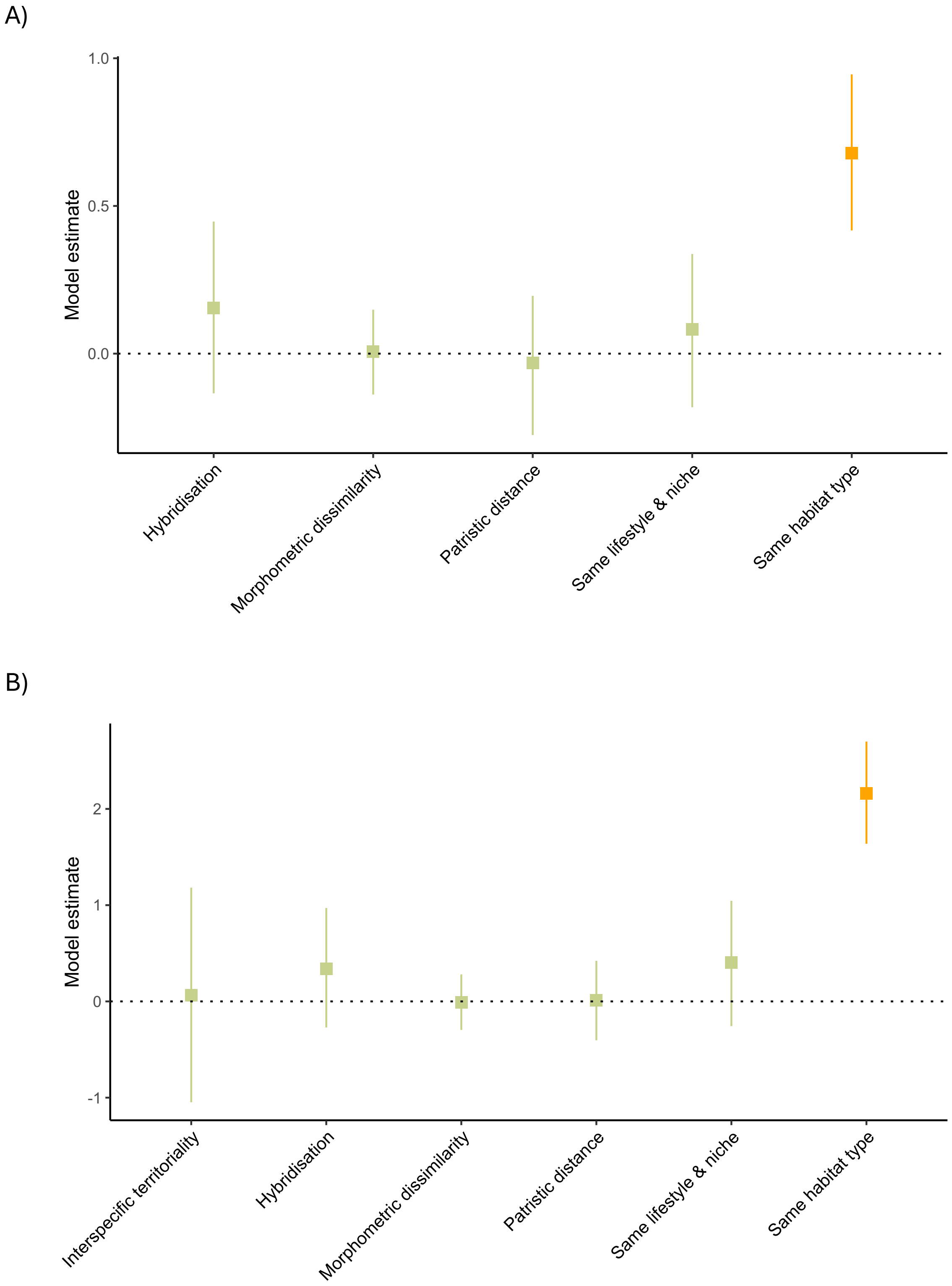


Figure 4: Predictors of residual associations in European pairs (A) (n=698) and European passerines with available predicted interspecific territoriality classifications (B) (n=168). Plotted values are coefficient estimates from phylogenetic generalised linear mixed models. Points correspond to the median 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.

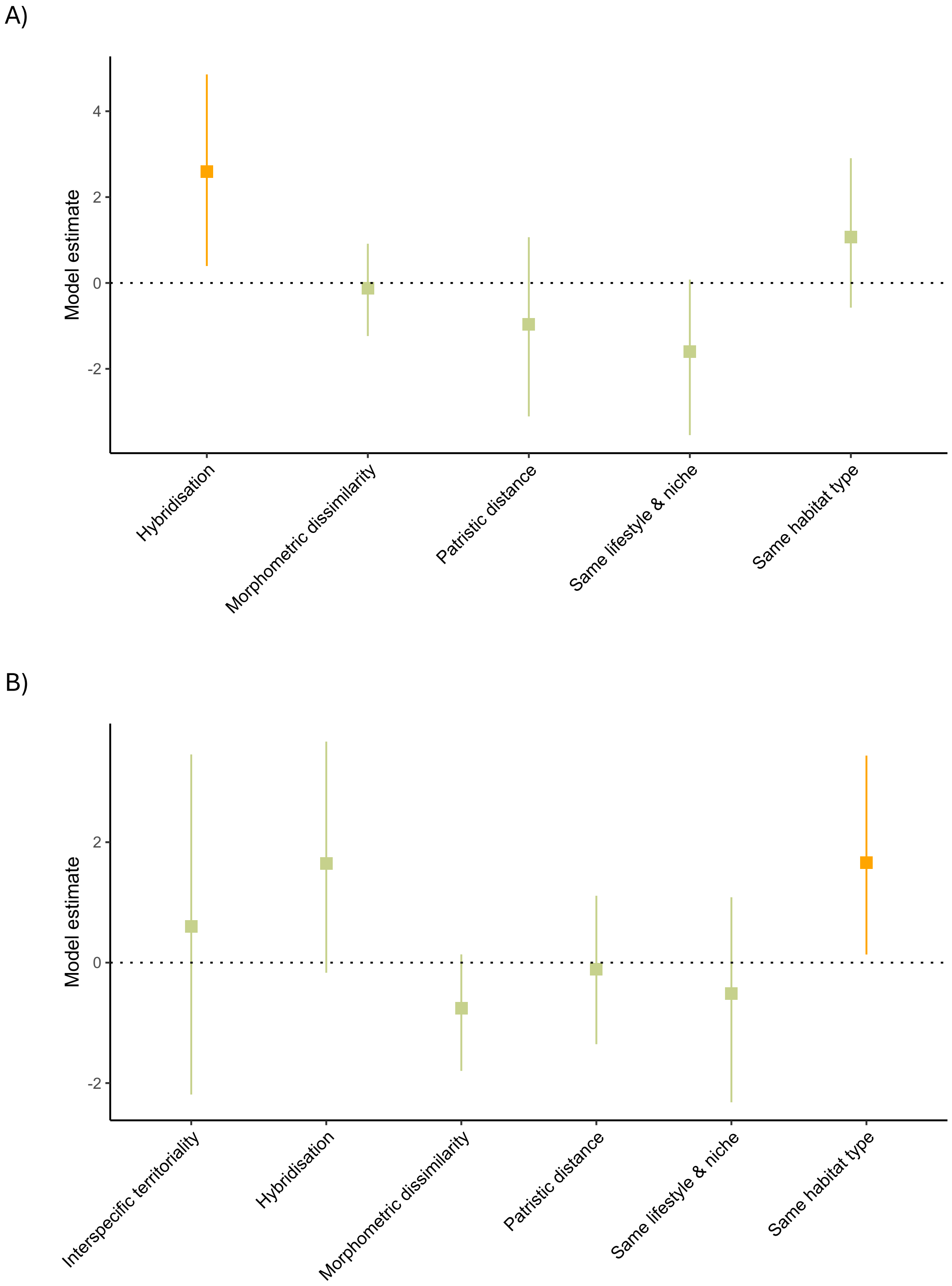


Figure 5: Predictors of support for the posterior means of residual associations in European pairs being greater than 0.9 (A) (n=698) and European passerines with available predicted interspecific territoriality classifications (B) (n=168). Plotted values are coefficient estimates from phylogenetic generalised 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 JSDMs, but higher when predicted by SSDMs on the southern coast of England and the Italian Alps (Figure 6).

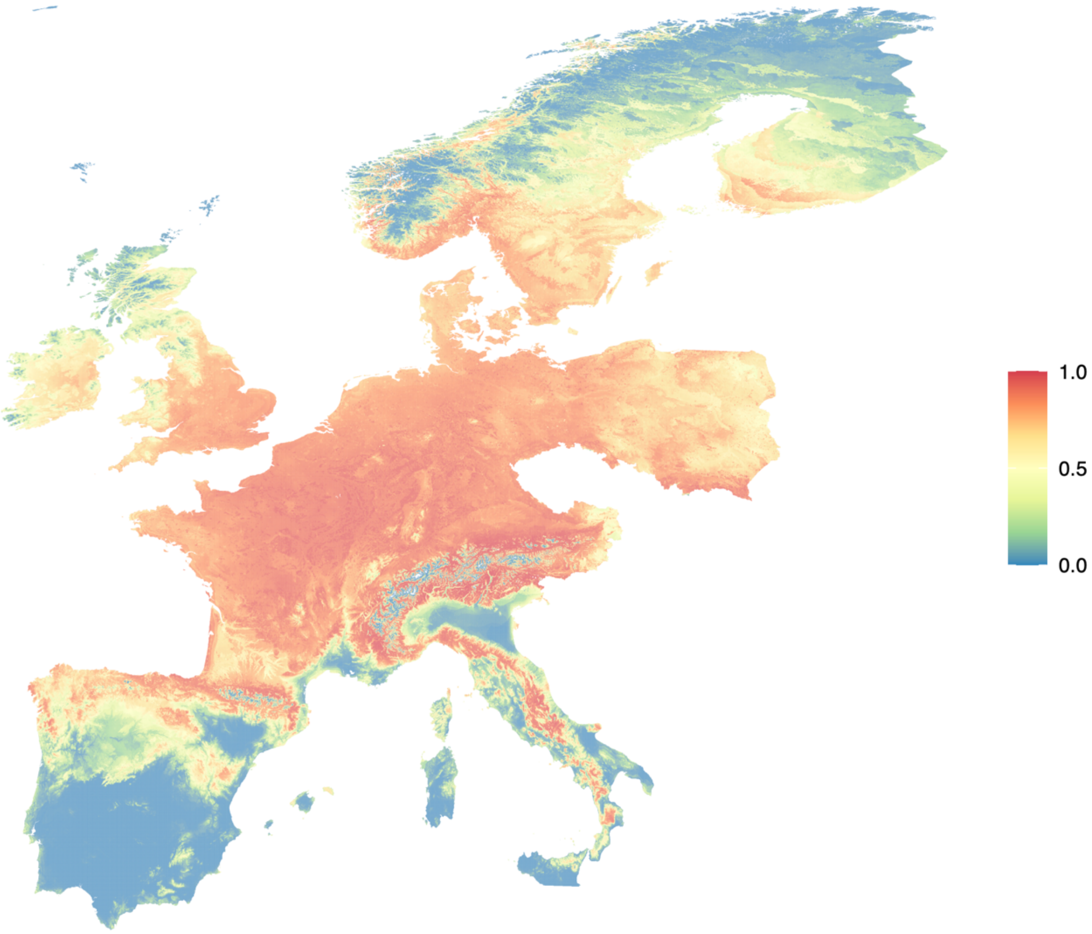
Table 6. Model fit estimates for four species of *Phylloscopus* warbler from a HSMC Joint Species Distribution Model (JSDM) and an identical HMSC Single Species Distribution Model (SSDM) but run on individual species. Estimates include Root Square Mean Error (RSME), Area Under the ROC Curve (AUC) and Tjur's R^2

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

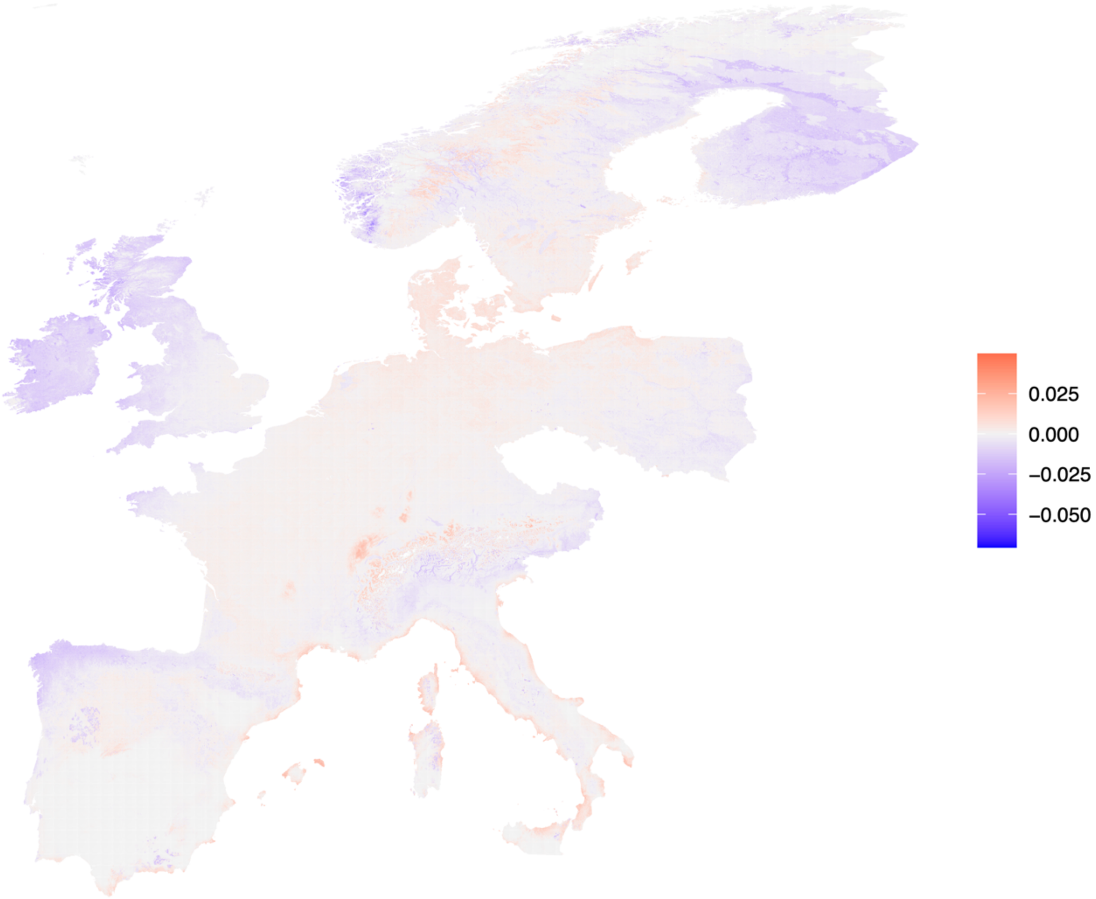
Table 7. Metrics comparing spatial predictions across western Europe for four species of *Phylloscopus* warbler from Joint Species Distribution Models (JSDMs) and Single Species Distribution Models (SSDMs). Mean difference, Root Square Mean Error (RSME) and correlation utilise probability of occurrence 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
P. collybita	-0.00159	0.007	0.999	0.991
P. trochilus	-0.00024	0.005	0.999	0.992
P. sibilatrix	0.01043	0.016	0.024	0.991
P. bonelli	0.00009	0.010	0.998	0.909

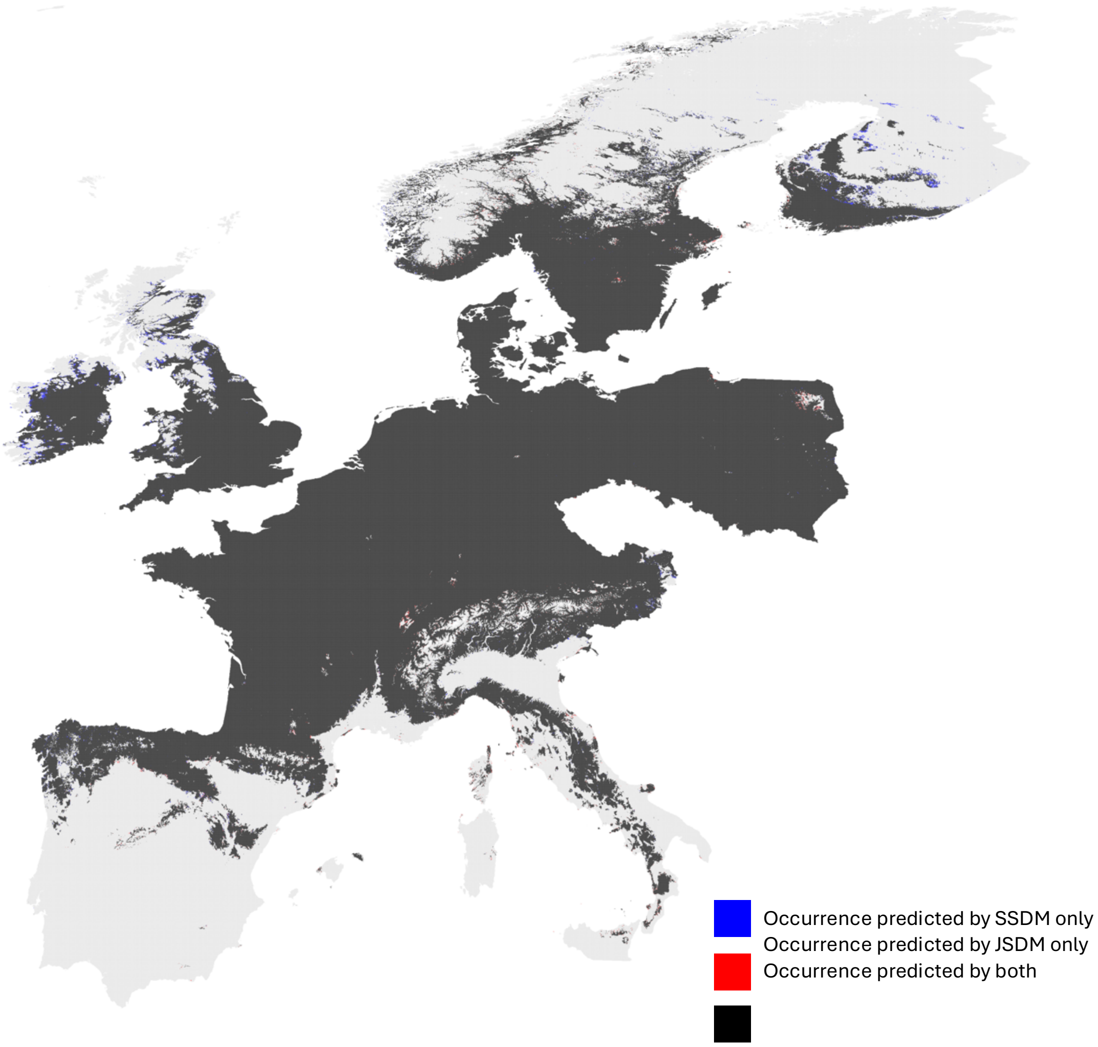
Phylloscopus collybita JSDM



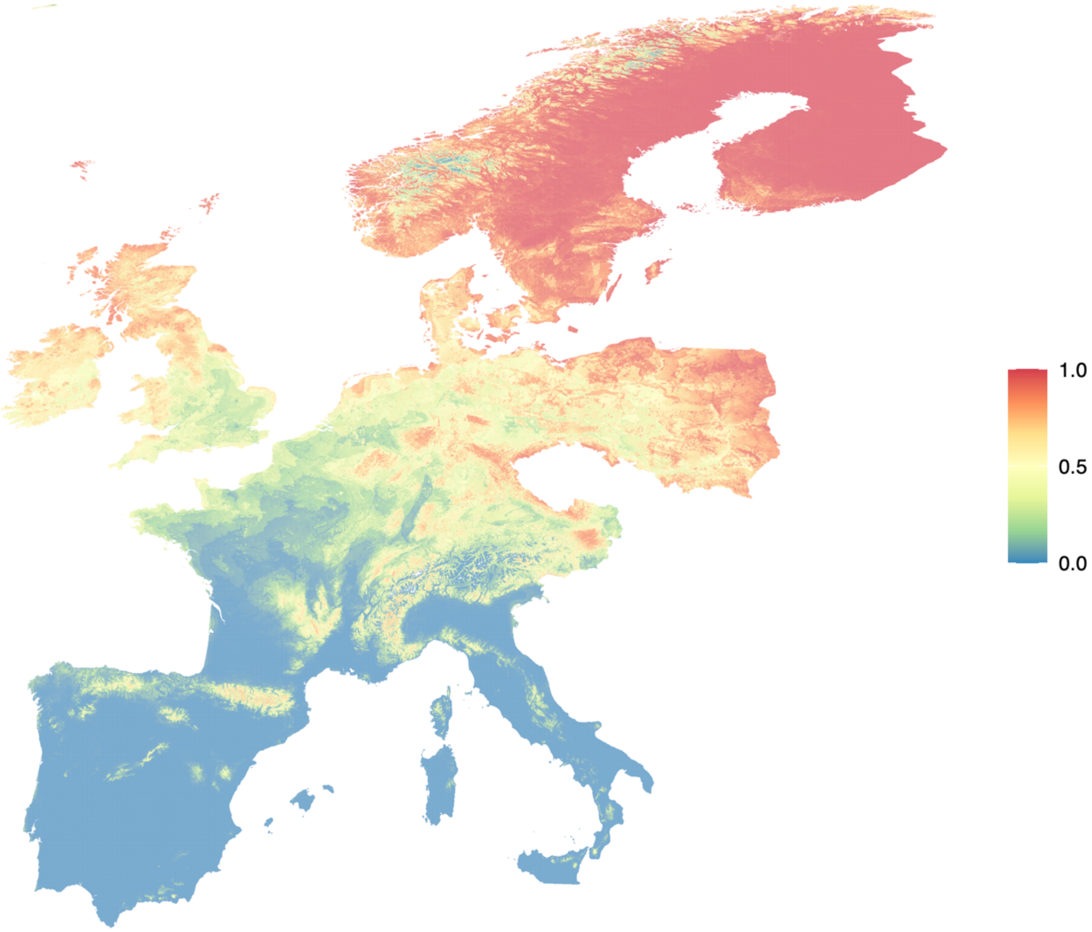
Phylloscopus collybita JSDM occurrence probability minus SSDM occurrence probability



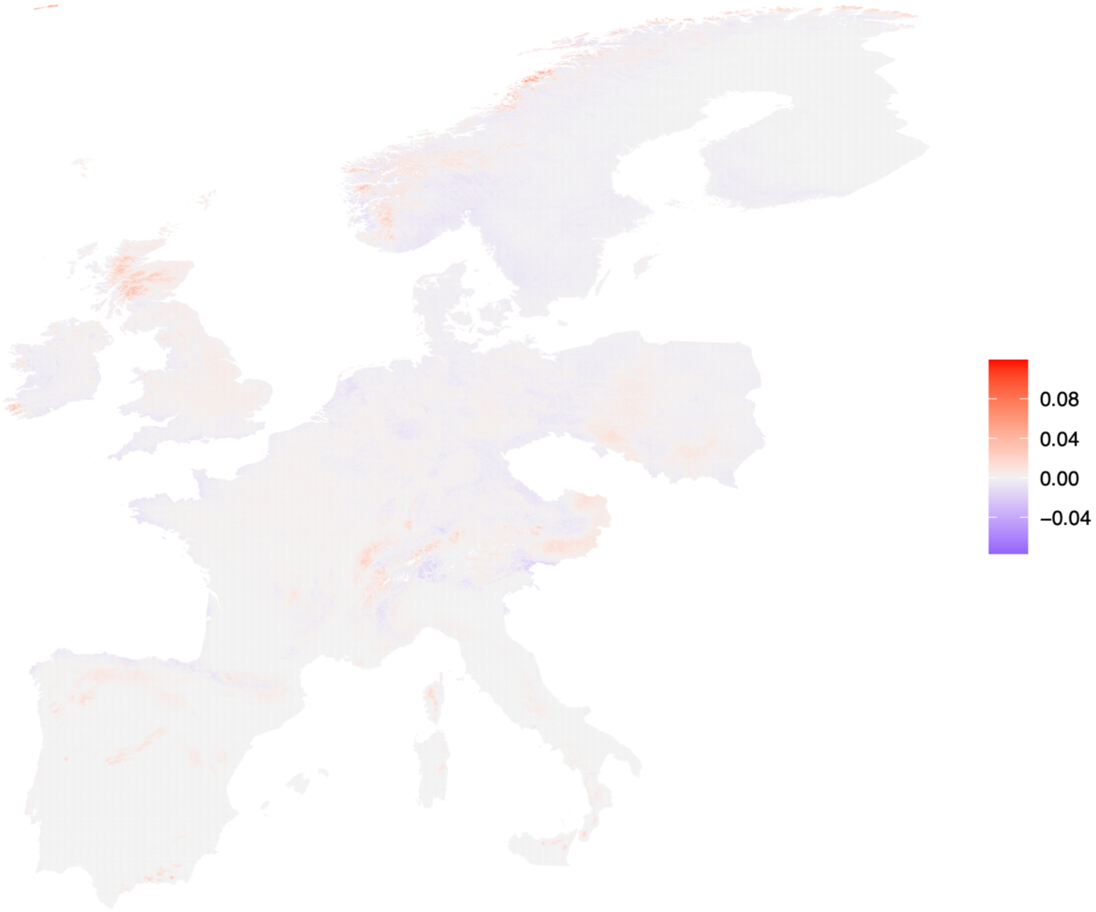
Phylloscopus collybita predicted presence-absence difference



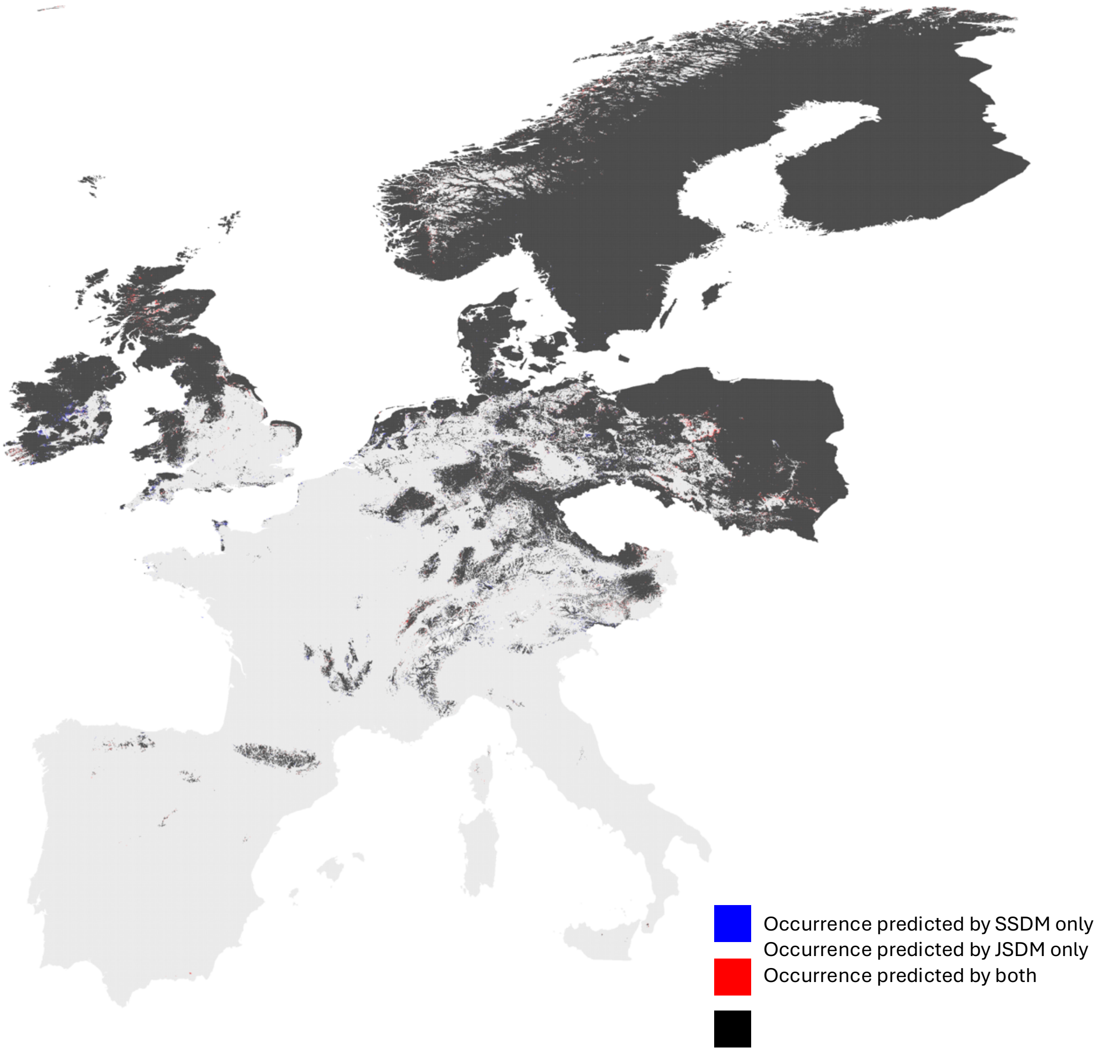
Phylloscopus trochilus JSDM



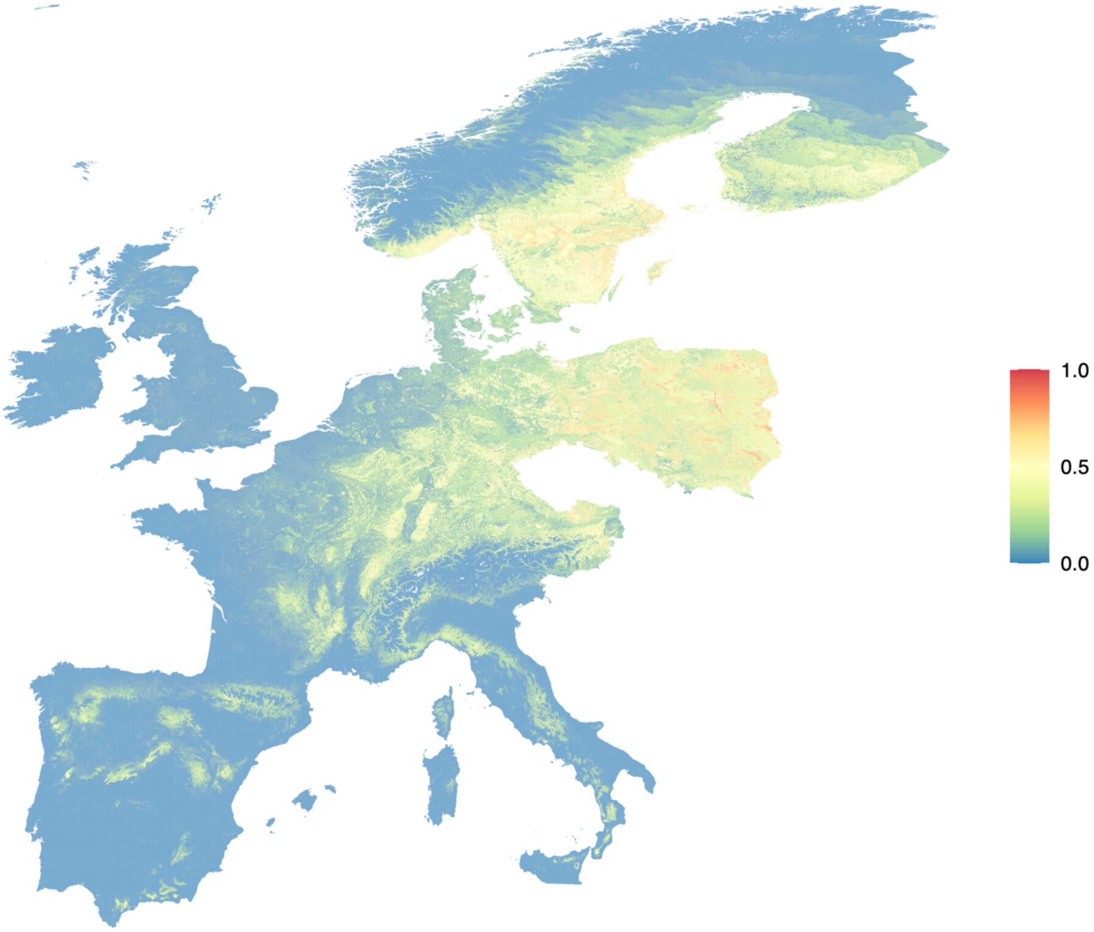
Phylloscopus trochilus JSDM occurrence probability minus SSDM occurrence probability



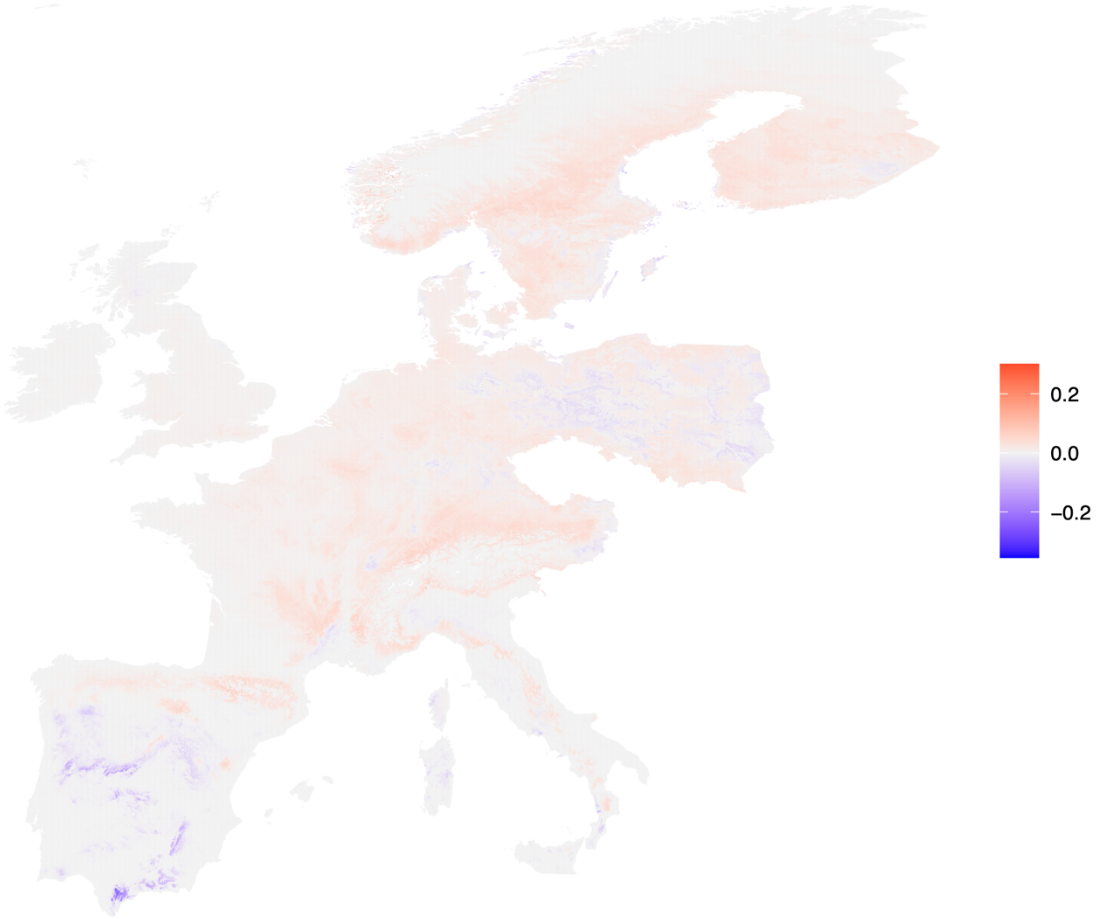
Phylloscopus trochilus predicted presence-absence difference



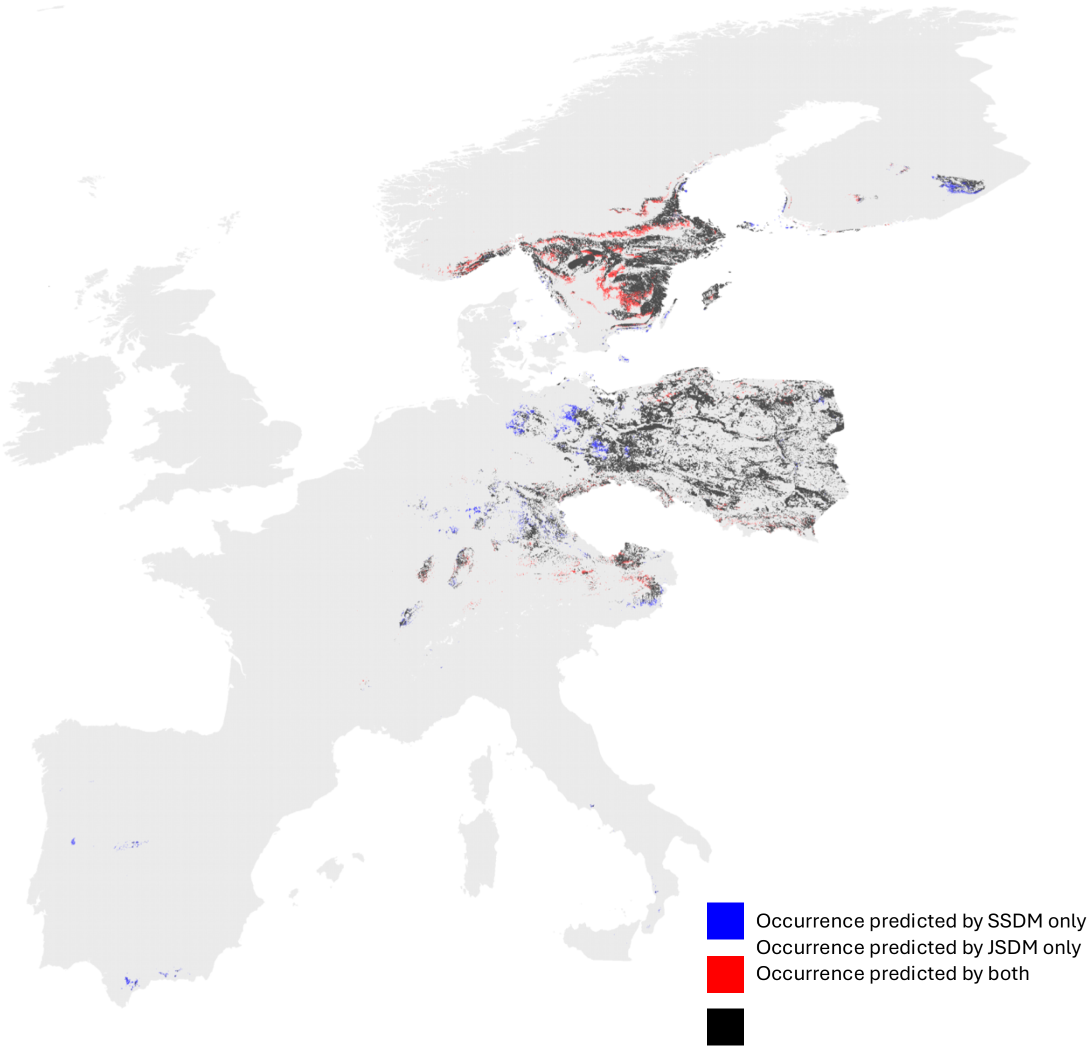
Phylloscopus sibilatrix JSDM



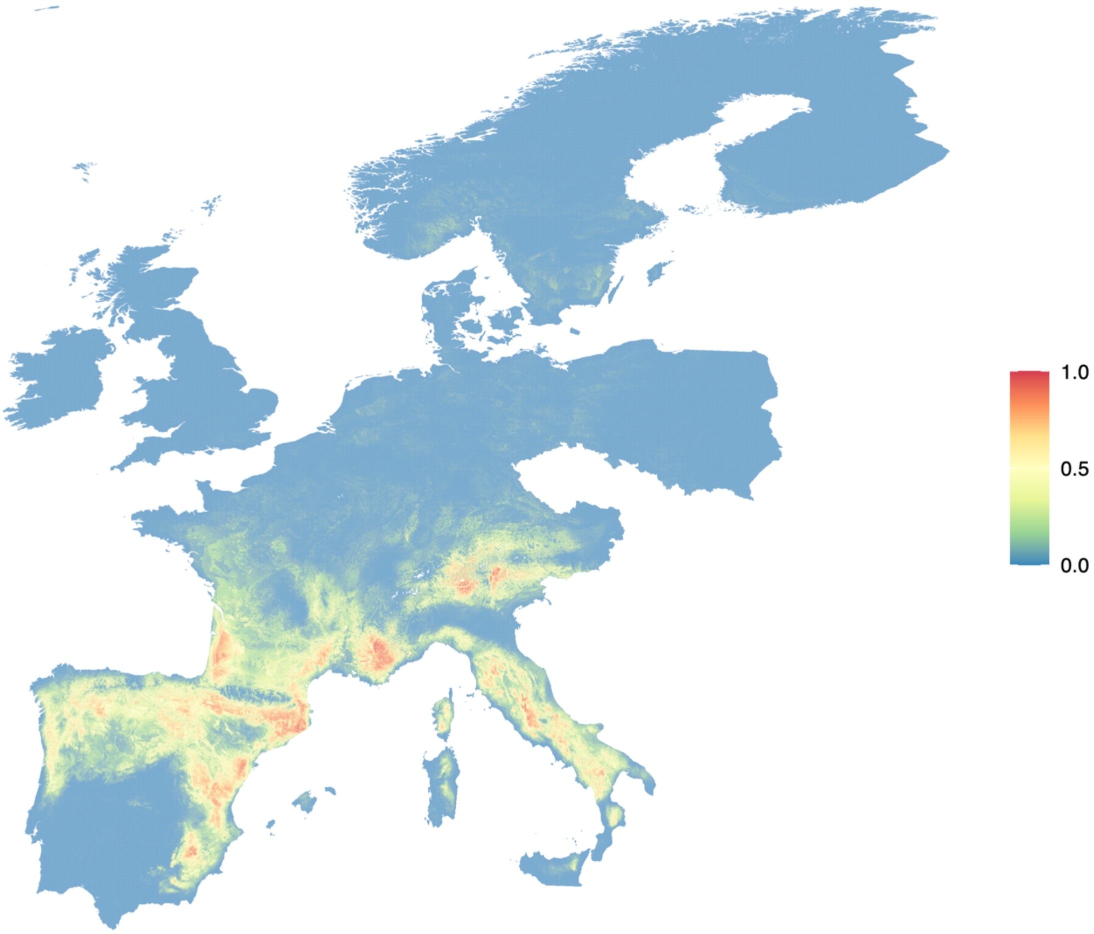
Phylloscopus sibilatrix JSDM occurrence probability minus SSDM occurrence probability



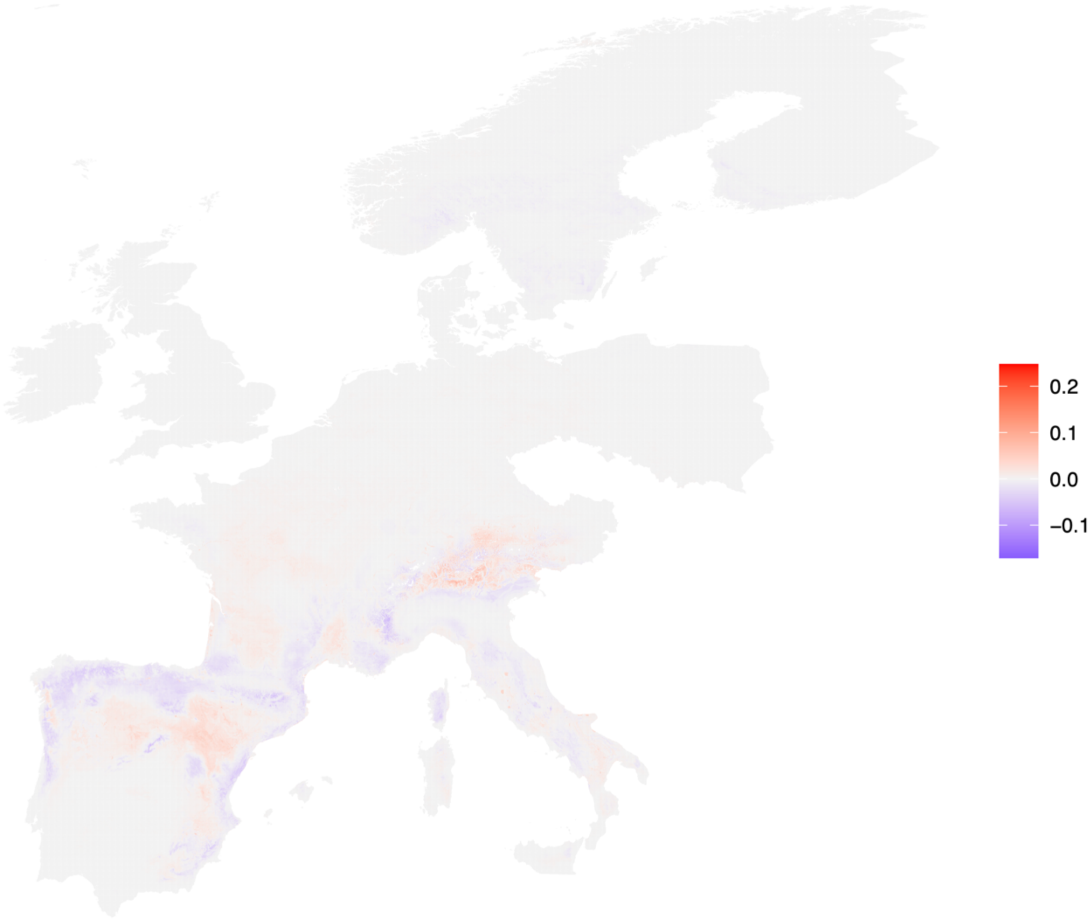
Phylloscopus sibilatrix predicted presence-absence difference

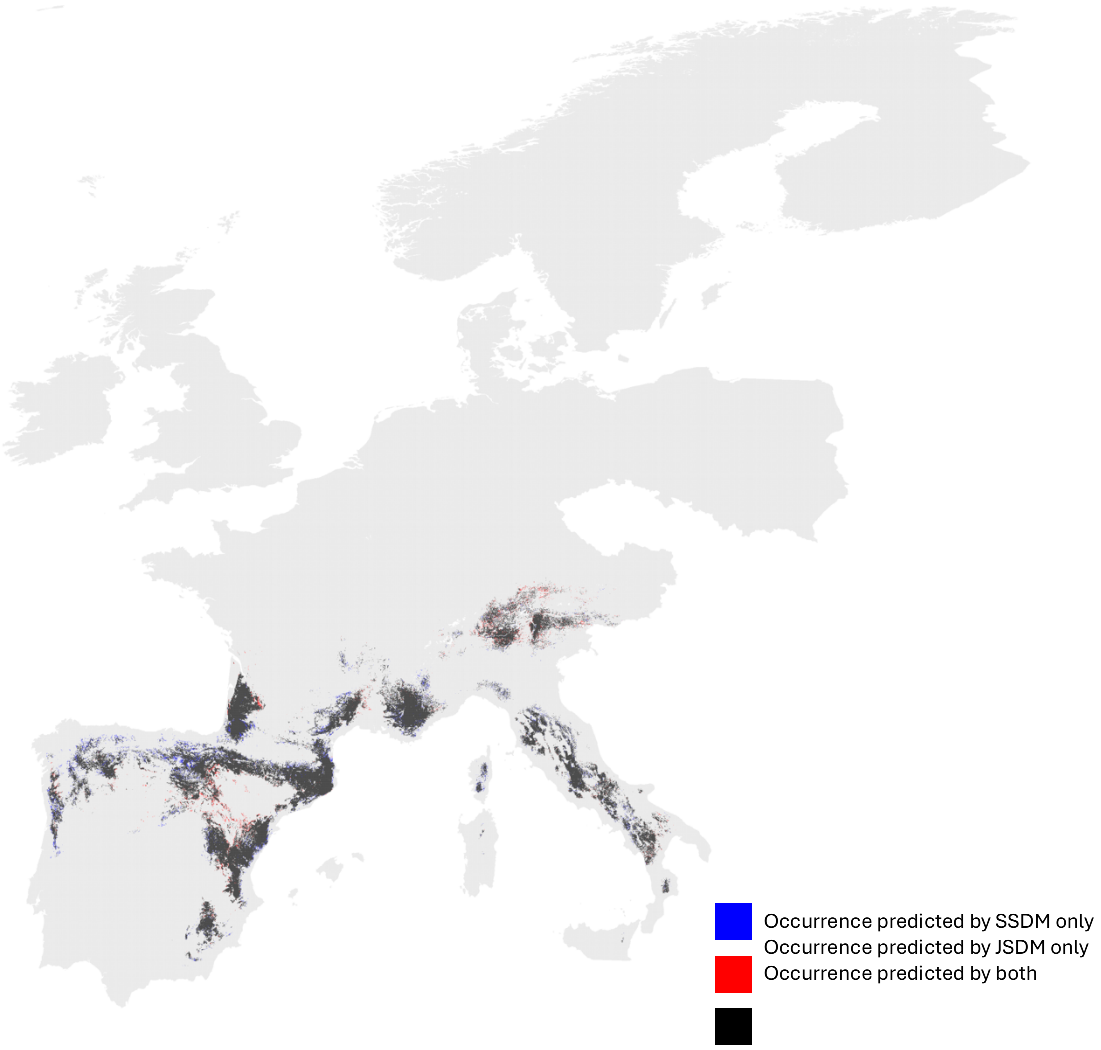


Phylloscopus bonelli JSDM



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).

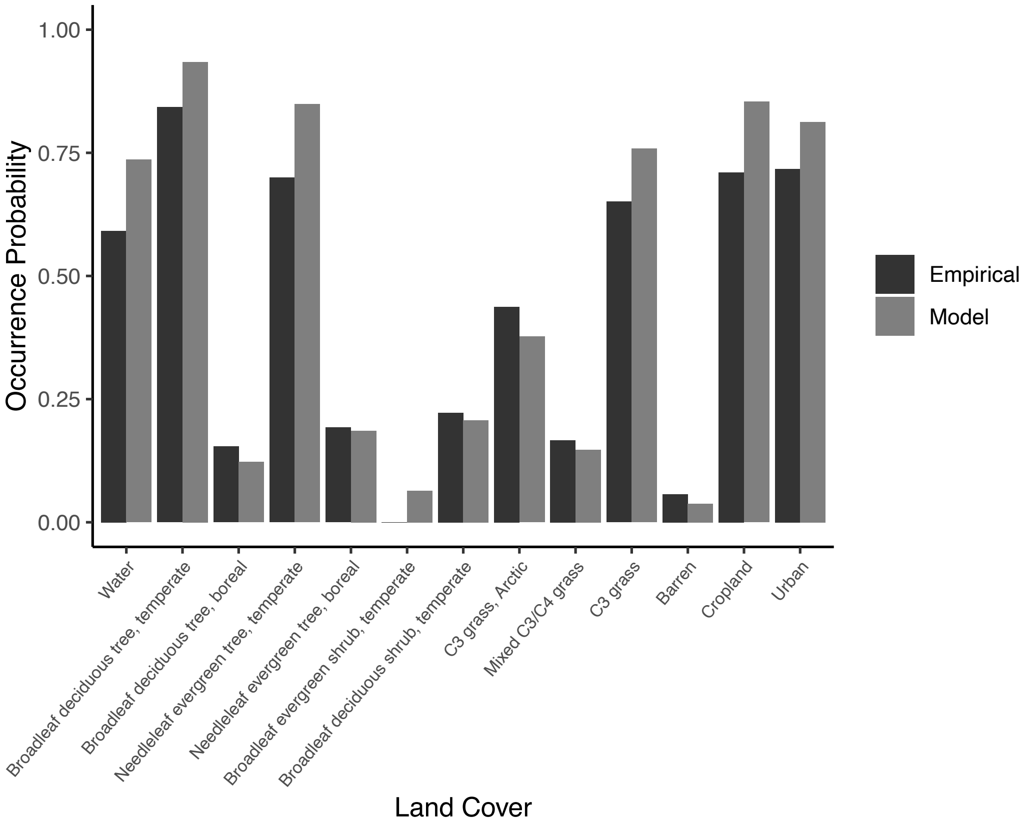
Our species data were at a 1km resolution, which may still be too coarse to capture biotic interactions, particularly negative ones (Araújo and Rozenfeld, 2014; Zurell, Pollock and Thuiller, 2018). For instance, Vallé *et al.* (2024) found negative species associations to be more prevalent in models 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).

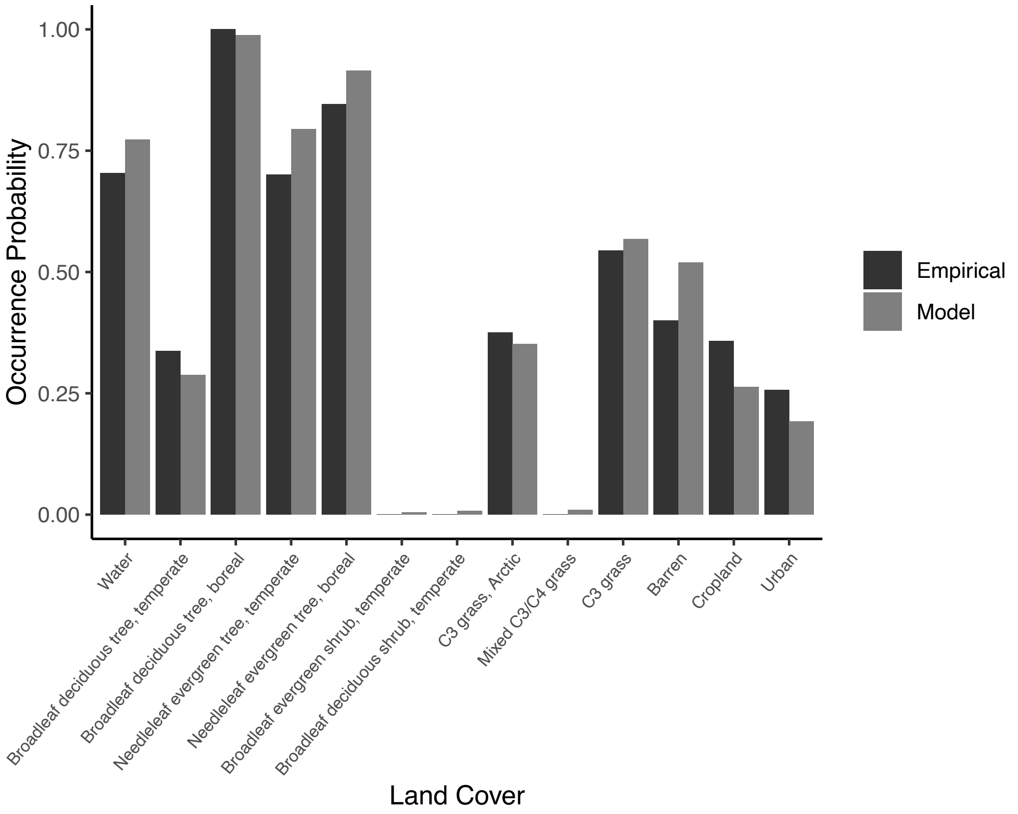
It could be argued that the predictor variables we included in our PLMMs are all indicative of negative species interactions. While that may be the case, we had assumed there would be a more even mix of positive and negative residual associations, that negative associations would be more indicative of 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 JSDMs) 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 JSDMs 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.

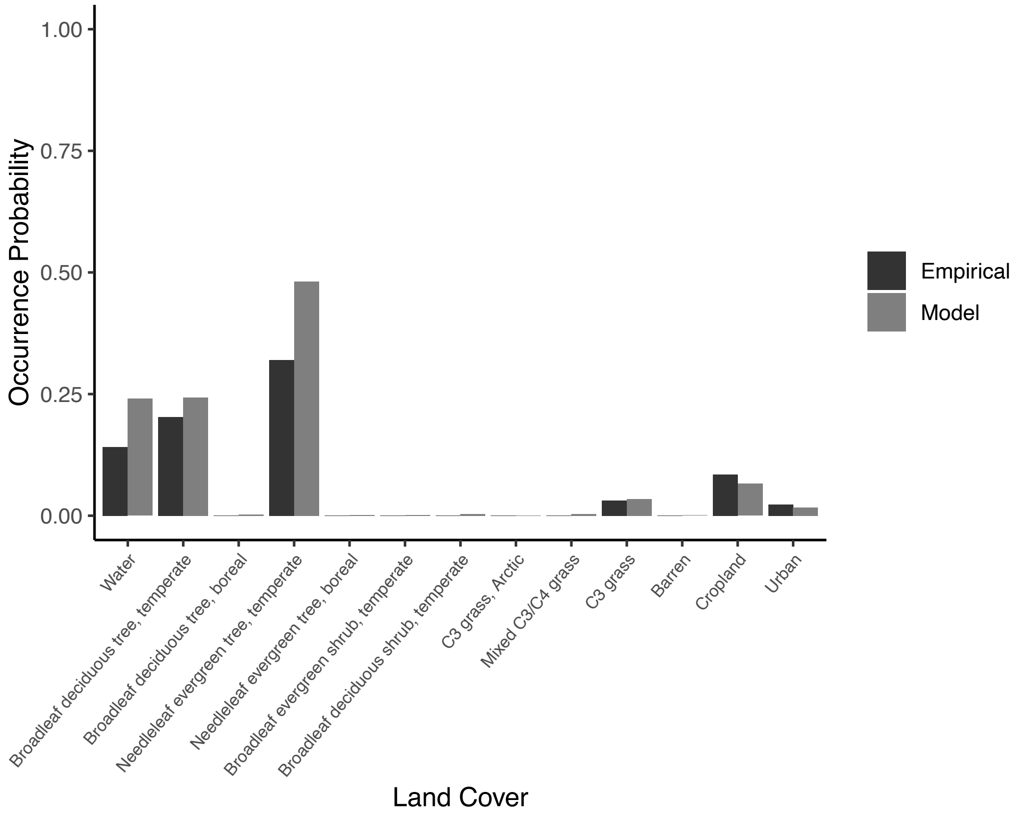


Phylloscopus collybita



Phylloscopus trochilus

Phylloscopus sibilatrix



Phylloscopus bonelli

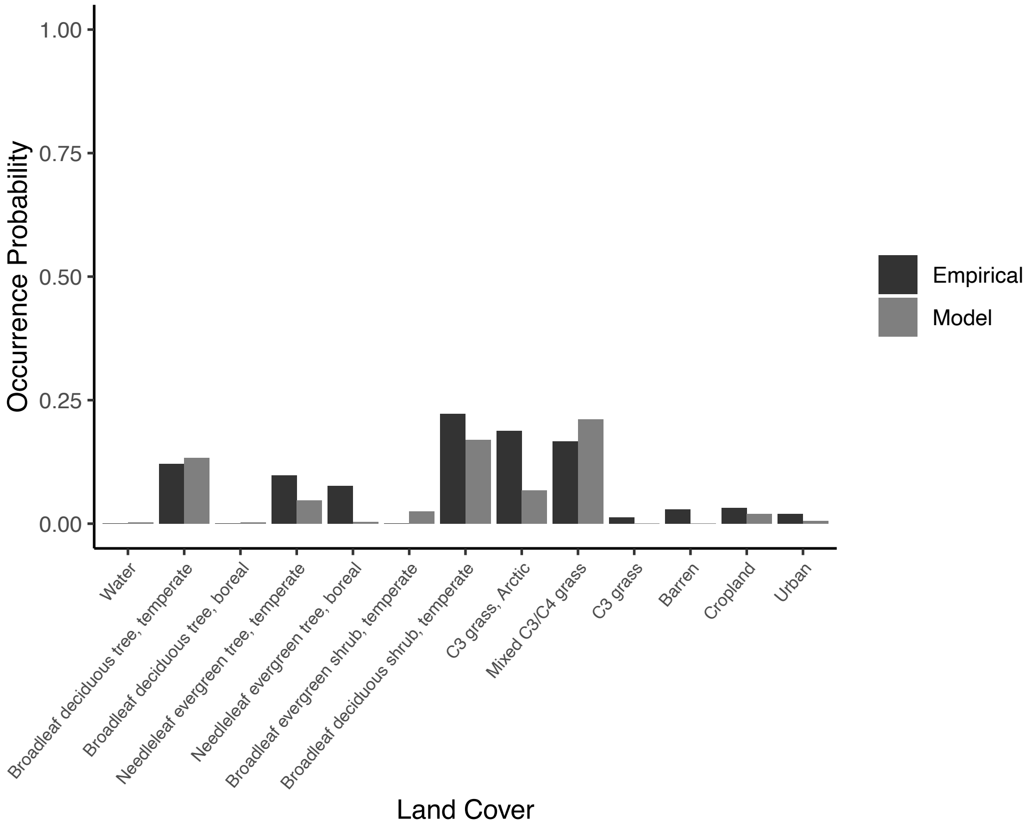


Figure 7. Observed (dark grey bars) and predicted (light grey bars) occurrence probabilities for four *Phylloscopus* warblers across various land use/land cover (LULC) types in Europe. Empirical observations are extracted from 4367 Pan-European Common Bird Monitoring Scheme (PECBMS) survey cells.

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 Bücker, 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 Δsyntopy. 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 Δsympatry, which again could be the result of habitat filtering (Polo and Carrascal, 1999b). Bill length difference in North American pairs increased Δsympatry, 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 Δsyntopy was only marginally negative; only two of the four PLMM chains had a pMCMC<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 Bücker, 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 Δsympatry. 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 JSDMs 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 JSDMs, 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 (JDSDMs) and HMSC JSDMs 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.

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.

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 consepcific 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.

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.

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 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.

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’, Sciencee, 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 couse 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.

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.

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.

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.

Lamichhaney, 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.

Luddem, 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/geographicalecol0000maca (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.

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.

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) ‘clootl: 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 communites?’, 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.

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 Committee2021’, 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.

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 Kreutzer, 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.

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 Introgreesion 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.

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 hypocnemis 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
Acanthis flammea	XC216985	Janne Bruun	*Gulosus aristotelis*	XC914590	Aku Kalliomäki
Acanthis flammea	XC687649	Niels Van Doninck	*Gypaetus barbatus*	XC144936	Fernand Deroussen
Acanthis flammea	XC710795	Lars Edenius	*Gypaetus barbatus*	XC569323	Stanislas Wroza
Acanthis flammea	XC712649	Lars Edenius	*Gyps fulvus*	XC423956	Stanislas Wroza
Accipiter gentilis	XC756188	brickegickel	*Gyps fulvus*	XC542056	Pere Josa
Accipiter gentilis	XC817762	Lars Edenius	*Gyps fulvus*	XC653855	Eduardo Realinho
Accipiter nisus	XC665236	Eetu Paljakka	*Gyps fulvus*	XC915617	Sven Normant
Accipiter nisus	XC744165	Romuald Mikusek	*Haematopus ostralegus*	XC831730	W. Agster
Acrocephalus arundinaceus	XC811727	Ulf Elman	*Haematopus ostralegus*	XC942096	Arjun Dutta
Acrocephalus arundinaceus	XC813097	Lukas Thiess	*Haliaeetus albicilla*	XC619160	Stein Ø. Nilsen
Acrocephalus arundinaceus	XC813205	Peter Boesman	*Haliaeetus albicilla*	XC745843	Lars Edenius
Acrocephalus arundinaceus	XC815947	Guy Kirwan	*Hieraaetus pennatus*	XC430828	Joost van Bruggen
Acrocephalus dumetorum	XC811764	Dag Österlund	*Hieraaetus pennatus*	XC668479	Eduardo Realinho
Acrocephalus dumetorum	XC813038	Marcus Fransson	*Himantopus himantopus*	XC828544	BirdingAlbufera
Acrocephalus dumetorum	XC814045	Anders Westman	*Himantopus himantopus*	XC905801	Albert Lastukhin
Acrocephalus dumetorum	XC842258	Ulf Elman	*Hippolais icterina*	XC659733	Bodo Sonnenburg
Acrocephalus melanopogon	XC793095	Stanislas Wroza	*Hippolais icterina*	XC750858	Ulf Elman
Acrocephalus melanopogon	XC872907	Thierry Thomas	*Hippolais icterina*	XC800661	Stanislas Wroza
Acrocephalus melanopogon	XC879400	Manuel Oudard	*Hippolais icterina*	XC815416	Thomas Bergman
Acrocephalus melanopogon	XC891244	Bernard Bousquet	*Hippolais polyglotta*	XC560575	Jorge Leitão
Acrocephalus paludicola	XC480838	Dries Van de Loock	*Hippolais polyglotta*	XC560590	Jorge Leitão
Acrocephalus paludicola	XC561499	Jarek Matusiak	*Hippolais polyglotta*	XC909833	Jacobo Ramil Millarengo
Acrocephalus paludicola	XC688954	Romuald Mikusek	*Hippolais polyglotta*	XC910101	Olivier Swift, Hélène Cartaud
Acrocephalus paludicola	XC692253	Romuald Mikusek	*Hirundo rustica*	XC823733	Francesco Sottile
Acrocephalus palustris	XC862700	Mats Rellmar	*Hirundo rustica*	XC877300	João Tomás
Acrocephalus palustris	XC871930	Mauro Fioretto	*Hirundo rustica*	XC903563	Stanislas Wroza
Acrocephalus palustris	XC883779	Johan Roeland	*Hirundo rustica*	XC910186	Uku Paal
Acrocephalus palustris	XC892416	Alain Malengreau	*Iduna opaca*	XC414658	Stanislas Wroza
Acrocephalus schoenobaenus	XC870841	Alain Malengreau	*Iduna opaca*	XC414663	Stanislas Wroza
Acrocephalus schoenobaenus	XC871701	Alain Malengreau	*Iduna opaca*	XC467771	Thijs Fijen
Acrocephalus schoenobaenus	XC884922	Olivier Swift	*Iduna opaca*	XC798474	Azens
Acrocephalus schoenobaenus	XC895063	Martin Billard	*Ixobrychus minutus*	XC656126	Lorenzo Maffezzoli
Acrocephalus scirpaceus	XC862813	Olivier Swift	*Ixobrychus minutus*	XC836679	Esperanza Poveda
Acrocephalus scirpaceus	XC863306	Chèvremont Fabian	*Jynx torquilla*	XC769997	Michel Veldt
Acrocephalus scirpaceus	XC897725	Lee Alder	*Jynx torquilla*	XC902613	Ulf Elman
Acrocephalus scirpaceus	XC901326	Susanne Kuijpers	*Lagopus lagopus*	XC591861	Simon Elliott
Actitis hypoleucos	XC815419	Thomas Bergman	*Lagopus lagopus*	XC652923	Thomas Bergman
Actitis hypoleucos	XC824403	Romuald Mikusek	*Lagopus lagopus*	XC798642	Uku Paal
Actitis hypoleucos	XC834283	Paolo Zucca	*Lagopus lagopus*	XC900335	Uku Paal
Actitis hypoleucos	XC861917	Peter Stronach	*Lagopus muta*	XC26647	Patrik Åberg
Aegithalos caudatus	XC645359	Regina Eidner	*Lagopus muta*	XC340677	Tero Linjama
Aegithalos caudatus	XC707059	Shamgar Brook	*Lagopus muta*	XC420429	Stein Ø. Nilsen
Aegolius funereus	XC708202	Thomas Bergman	*Lagopus muta*	XC835510	Petter Westberg
Aegolius funereus	XC837555	Romuald Mikusek	*Lanius collurio*	XC560390	Stanislas Wroza
Aegypius monachus	XC144935	Fernand Deroussen	*Lanius collurio*	XC700280	Dominique Guillerme
Aegypius monachus	XC915625	Sven Normant	*Lanius collurio*	XC731753	Marc Anderson
Aix galericulata	XC389998	Jarek Matusiak	*Lanius collurio*	XC803339	Lars Edenius
Aix galericulata	XC389999	Jarek Matusiak	*Lanius excubitor*	XC649962	Johan Södercrantz
Aix sponsa	XC509715	Sunny Tseng	*Lanius excubitor*	XC712619	Lars Edenius
Aix sponsa	XC63109	Jonathon Jongsma	*Lanius excubitor*	XC838997	Leander Khil
Alauda arvensis	XC890349	Olivier Swift	*Lanius excubitor*	XC855983	Mats Rellmar
Alauda arvensis	XC893507	Krzysztof Deoniziak	*Lanius meridionalis*	XC150493	Paulo Alves
Alauda arvensis	XC895628	Agris Celmins	*Lanius meridionalis*	XC727014	Magnus Wadstein
Alauda arvensis	XC896982	Martin Billard	*Lanius meridionalis*	XC767941	Stanislas Wroza
Alaudala rufescens	XC730308	Stanislas Wroza	*Lanius meridionalis*	XC795282	Étienne Leroy
Alaudala rufescens	XC730310	Stanislas Wroza	*Lanius minor*	XC295984	Marco Dragonetti
Alaudala rufescens	XC730383	Stanislas Wroza	*Lanius minor*	XC342809	Lars Buckx
Alaudala rufescens	XC756693	SonoNatura	*Lanius minor*	XC813442	Peter Boesman
Alcedo atthis	XC845635	Johannes Dag Mayer	*Lanius minor*	XC904703	David Darrell-Lambert
Alcedo atthis	XC936832	Johannes Dag Mayer	*Lanius senator*	XC561941	François Grimal
Alectoris barbara	ML71168	Arnoud B. van den Berg	*Lanius senator*	XC722557	SonoNatura
Alectoris barbara	XC134392	Fernand Deroussen	*Lanius senator*	XC754423	Stein Ø. Nilsen
Alectoris barbara	XC347457	Tero Linjama	*Lanius senator*	XC797821	Xavier Riera
Alectoris barbara	XC901725	Andrew Harrop	*Leiothrix lutea*	ML14175	William V. Ward
Alectoris graeca	XC182904	Manuel Schweizer	*Leiothrix lutea*	ML445568141	Sujith S
Alectoris graeca	XC247001	Jerome Fischer	*Leiothrix lutea*	ML580194941	Benjamin Costello
Alectoris graeca	XC416855	Jerome Fischer	*Leiothrix lutea*	ML600224591	Ray Tsu
Alectoris graeca	XC730580	Stanislas Wroza	*Limosa lapponica*	XC654136	Lars Edenius
Alectoris rufa	XC265614	david m	*Limosa lapponica*	XC807724	Thomas Bergman
Alectoris rufa	XC334156	Jordi Calvet	*Limosa lapponica*	XC913545	Thomas Bergman
Alectoris rufa	XC372530	Stanislas Wroza	*Limosa lapponica*	XC915090	Thomas Bergman
Alectoris rufa	XC794515	Stuart Fisher	*Limosa limosa*	XC722732	Lars Edenius
Alopochen aegyptiaca	XC546108	Albert Noorlander	*Limosa limosa*	XC740254	Uku Paal
Alopochen aegyptiaca	XC620525	Francesco Sottile	*Limosa limosa*	XC740270	Uku Paal
Amandava amandava	XC545983	Peter Ericsson	*Limosa limosa*	XC818972	Azens
Amandava amandava	XC552807	Bram Piot	*Linaria cannabina*	XC802274	Thomas Bergman
Amandava amandava	XC824847	He Wenjin	*Linaria cannabina*	XC876858	João Tomás
Amandava amandava	XC840610	Bram Piot	*Linaria cannabina*	XC899180	Paul Kelly
Anas acuta	XC712335	Jack Berteau	*Linaria cannabina*	XC906691	Olivier Swift
Anas acuta	XC721976	Lars Edenius	*Linaria flavirostris*	XC364664	Elias A. Ryberg
Anas crecca	XC668192	Ireneusz Oleksik	*Linaria flavirostris*	XC470797	Dries Van de Loock
Anas crecca	XC732343	Marc Anderson	*Linaria flavirostris*	XC638923	Lars Edenius
Anas platyrhynchos	XC755991	Romuald Mikusek	*Linaria flavirostris*	XC638934	Lars Edenius
Anas platyrhynchos	XC774431	Irish Wildlife Sounds	*Locustella fluviatilis*	XC861724	András Schmidt
Anser albifrons	XC644998	Joost van Bruggen	*Locustella fluviatilis*	XC908882	Eric Söderman
Anser albifrons	XC698271	András Schmidt	*Locustella luscinioides*	XC740299	Uku Paal
Anser albifrons	XC712047	Joost van Bruggen	*Locustella luscinioides*	XC813023	Lukas Thiess
Anser albifrons	XC878146	Lars Mogensen	*Locustella naevia*	XC900840	Martin Billard
Anser anser	XC792700	Lars Edenius	*Locustella naevia*	XC900843	Martin Billard

Anser anser	XC803358	Lars Edenius
Anser anser	XC896889	Lars Edenius
Anser anser	XC914627	Lennart Jeppsson
Anser brachyrhynchus	XC521246	Ireneusz Oleksik
Anser brachyrhynchus	XC601551	Will Scott
Anser canagicus	XC185372	Andrew Spencer
Anser canagicus	XC486631	Jens Kirkeby
Anser cygnoides	XC635985	Simon Kiesé
Anser cygnoides	XC765912	Stanislas Wroza
Anser fabalis	XC109681	Jelmer Poelstra
Anser fabalis	XC676859	Thomas Bergman
Anser indicus	XC526948	James Lidster
Anser indicus	XC635939	David Darrell-Lambert
Anthus berthelotii	XC134391	Fernand Deroussen
Anthus berthelotii	XC374980	Peter Boesman
Anthus berthelotii	XC764548	Stein Ø. Nilsen
Anthus berthelotii	XC782278	Rubén Barone
Anthus campestris	XC801392	Manceau Lionel
Anthus campestris	XC813237	Peter Boesman
Anthus campestris	XC839904	Corentin Rivière
Anthus campestris	XC897500	Tero Linjama
Anthus cervinus	XC139099	Fernand Deroussen
Anthus cervinus	XC345769	Tero Linjama
Anthus cervinus	XC382130	Jens Kirkeby
Anthus cervinus	XC424100	Terje Kolaas
Anthus petrosus	XC146046	julien Rochefort
Anthus petrosus	XC263958	Terje Kolaas
Anthus petrosus	XC610047	Lars Edenius
Anthus petrosus	XC667502	Irish Wildlife Sounds
Anthus pratensis	XC779776	Erik Normark
Anthus pratensis	XC831852	Agris Celmins
Anthus pratensis	XC831853	Agris Celmins
Anthus pratensis	XC857639	Beatrix Saadi-Varchmin
Anthus spinoletta	XC716570	Xavier Riera
Anthus spinoletta	XC730538	Stanislas Wroza
Anthus spinoletta	XC734861	Magnus Hellström
Anthus spinoletta	XC839878	Romuald Mikusek
Anthus trivialis	XC855476	Jack Berteau
Anthus trivialis	XC879350	Stein Ø. Nilsen
Anthus trivialis	XC895016	Christian Kerihuel
Anthus trivialis	XC897400	Jacobo Ramil Millarengo
Apus apus	XC810578	Susanne Kuijpers
Apus apus	XC817637	João Tomás
Apus caffer	ML5989	Myles E. W. North
Apus caffer	XC677525	Esperanza Poveda
Apus pallidus	XC557421	Jorge Leitão
Apus pallidus	XC763779	Guillaume Bigayon
Apus unicolor	XC164524	Antero Lindholm
Apus unicolor	XC657346	Paulo Alves
Aquila adalberti	XC148645	Patrik Åberg
Aquila adalberti	XC420390	José Carlos Sires
Aquila adalberti	XC699619	SonoNatura
Aquila adalberti	XC864217	SonoNatura
Aquila chrysaetos	XC341722	Tero Linjama
Aquila chrysaetos	XC453324	Lars Edenius
Aquila chrysaetos	XC753803	Lars Edenius
Aquila chrysaetos	XC820295	Hans Norelius
Aquila fasciata	ML411897521	Fast As Falcon
Aquila fasciata	XC781530	Peter Boesman
Aquila heliaca	XC582823	Jarek Matusiak
Aquila heliaca	XC731082	brickegickel
Ardea alba	XC615283	Stanislas Wroza
Ardea alba	XC681080	Uku Paal
Ardea alba	XC738072	Marcin Sołowiej
Ardea alba	XC776170	Irish Wildlife Sounds
Ardea cinerea	XC857972	Martin Billard
Ardea cinerea	XC881881	Esperanza Poveda
Ardea cinerea	XC882189	Christian Vemmelund Helligsø
Ardea cinerea	XC897660	Paul Kelly
Ardea purpurea	ML568281661	Anonymous
Ardea purpurea	XC485377	Joost van Bruggen
Ardea purpurea	XC903478	Stanislas Wroza
Ardea purpurea	XC903564	Stanislas Wroza
Ardeola ralloides	XC577793	Cedric Mroczko
Ardeola ralloides	XC836622	Esperanza Poveda
Arenaria interpres	XC815489	Sonothèque ADVL
Arenaria interpres	XC815490	Sonothèque ADVL
Arenaria interpres	XC827973	Jorge Leitão
Arenaria interpres	XC895259	Francesco Sottile
Asio flammeus	XC718743	Lars Edenius
Asio flammeus	XC731000	Lars Edenius
Asio otus	XC793292	Dominique Guillerme
Asio otus	XC793294	Dominique Guillerme
Athene noctua	XC883232	Anthony Roux
Athene noctua	XC891838	András Schmidt
Athene noctua	XC908597	Martin Billard
Athene noctua	XC915445	Esperanza Poveda
Aythya ferina	XC769846	Dominique Guillerme
Aythya ferina	XC797060	Alan Dalton
Aythya fuligula	XC644316	Lars Edenius
Lophophanes cristatus	XC780340	Lars Edenius
Lophophanes cristatus	XC790414	Lars Edenius
Lophophanes cristatus	XC804854	Uku Paal
Lophophanes cristatus	XC896344	Jacobo Ramil Millarengo
Loxia curvirostra	XC831945	Lars Edenius
Loxia curvirostra	XC837909	Lars Edenius
Loxia curvirostra	XC864185	András Schmidt
Loxia curvirostra	XC901928	Lars Edenius
Loxia leucoptera	XC338457	Piotr Szczypinski
Loxia leucoptera	XC484760	Teet Sirotkin
Loxia leucoptera	XC602666	Christopher McPherson
Loxia leucoptera	XC89151	Patrik Åberg
Loxia pytyopsittacus	XC403068	Hans Matheve
Loxia pytyopsittacus	XC829642	Lars Edenius
Loxia pytyopsittacus	XC893254	Lars Edenius
Loxia pytyopsittacus	XC900834	Johan Forssell
Loxia scotica	XC544934	Peter Stronach
Loxia scotica	XC715938	Andrew Harrop
Loxia scotica	XC892394	Peter Stronach
Loxia scotica	XC906960	Peter Stronach
Lullula arborea	XC712592	Joost van Bruggen
Lullula arborea	XC722492	Lars Edenius
Lullula arborea	XC723523	Olivier Swift, Sylvain REYT
Lullula arborea	XC852698	Rob van Bemmelen
Luscinia luscinia	XC654939	maxander
Luscinia luscinia	XC727140	Lennart Jeppsson
Luscinia luscinia	XC803654	Johannes Sander
Luscinia luscinia	XC903880	Jocce Ekstrom
Luscinia megarhynchos	XC803656	Johannes Sander
Luscinia megarhynchos	XC901015	Grzegorz Lorek
Luscinia megarhynchos	XC908425	Leconte Michel
Luscinia megarhynchos	XC909501	Mats Rellmar
Luscinia svecica	XC707296	Antonio Xeira
Luscinia svecica	XC731887	SonoNatura
Luscinia svecica	XC884116	Maarten Sluijter
Luscinia svecica	XC899983	Jörgen Pisch
Lymnocryptes minimus	XC723297	Lars Edenius
Lymnocryptes minimus	XC799634	Lars Edenius
Lyrurus tetrix	XC711208	Baltasar Pinheiro
Lyrurus tetrix	XC758859	Lars Edenius
Lyrurus tetrix	XC758861	Lars Edenius
Lyrurus tetrix	XC805524	Lars Edenius
Mareca penelope	XC767302	Irish Wildlife Sounds
Mareca penelope	XC882155	David Darrell-Lambert
Mareca strepera	XC679027	Beatrix Saadi-Varchmin
Mareca strepera	XC871361	Paul Kelly
Marmaronetta angustirostris	XC780493	Santiago Caballero Carrera
Marmaronetta angustirostris	XC784480	Santiago Caballero Carrera
Melanitta fusca	XC448663	Patrik Åberg
Melanitta fusca	XC817948	Alan Dalton
Melanitta nigra	XC902773	david thorns
Melanitta nigra	XC915469	Thomas Bergman
Melanocorypha calandra	XC510598	Marco Dragonetti
Melanocorypha calandra	XC730261	Stanislas Wroza
Melanocorypha calandra	XC730301	Stanislas Wroza
Melanocorypha calandra	XC880726	Luis Gracia
Mergellus albellus	XC563997	Lars Edenius
Mergellus albellus	XC610927	Lars Edenius
Mergus merganser	XC644424	Lars Edenius
Mergus merganser	XC759927	Simon Elliott
Mergus serrator	XC607514	Peter Stronach
Mergus serrator	XC762330	Simon Elliott
Merops apiaster	XC824573	Grzegorz Lorek
Merops apiaster	XC900856	João Tomás
Microcarbo pygmaeus	XC168146	Andre et Odile Boucher
Microcarbo pygmaeus	XC296075	Marco Dragonetti
Milvus migrans	XC796153	Beatrix Saadi-Varchmin
Milvus migrans	XC899786	Jorge Leitão
Milvus milvus	XC829695	Olivier Swift
Milvus milvus	XC879195	Olivier Swift
Monticola saxatilis	XC296005	Marco Dragonetti
Monticola saxatilis	XC649771	Jordi Calvet
Monticola saxatilis	XC730219	Stanislas Wroza
Monticola saxatilis	XC833863	Martin Billard
Monticola solitarius	XC265241	Michele Viganò
Monticola solitarius	XC417708	Stanislas Wroza
Monticola solitarius	XC881595	Francesco Sottile
Monticola solitarius	XC99691	Jordi Calvet
Montifringilla nivalis	XC141184	Fernand Deroussen
Montifringilla nivalis	XC186477	Michele Peron
Montifringilla nivalis	XC355444	maudoc
Montifringilla nivalis	XC486810	Audevard Aurélien
Motacilla alba	XC598489	Tanguy Loïs
Motacilla alba	XC656706	Uku Paal
Motacilla alba	XC656713	Uku Paal
Motacilla alba	XC722531	Jens Kirkeby
Motacilla cinerea	XC682324	Jacobo Ramil MIllarengo
Motacilla cinerea	XC757193	Lars Lachmann
Motacilla cinerea	XC797916	brickegickel
Motacilla cinerea	XC904381	Cedric Mroczko

Aythya fuligula	XC644396	Lars Edenius
Aythya marila	ML137835	Gerrit Vyn
Aythya marila	ML444104281	Reid Hildebrandt
Aythya nyroca	XC296088	Marco Dragonetti
Aythya nyroca	XC528021	Jan Daniels-Trautner
Bombycilla garrulus	XC597940	Lars Edenius
Bombycilla garrulus	XC861580	Peter Stronach
Botaurus stellaris	XC465220	Gregorio Para
Botaurus stellaris	XC720112	Manuel Grosselet
Branta canadensis	XC646159	Lars Edenius
Branta canadensis	XC715941	Agris Celmins
Branta canadensis	XC787100	Susanne Kuijpers
Branta canadensis	XC909895	Uku Paal
Branta hutchinsii	ML135491	William W. H. Gunn
Branta hutchinsii	ML203928861	Josep del Hoyo
Branta hutchinsii	XC361080	Paul Marvin
Branta hutchinsii	XC838299	Seth Beaudreault (Toolik Field Station)
Branta leucopsis	XC549292	Lars Edenius
Branta leucopsis	XC724651	Uku Paal
Branta leucopsis	XC763873	Uku Paal
Branta leucopsis	XC903305	Lars Edenius
Bubo bubo	XC836565	Thierry Thomas
Bubo bubo	XC896167	Bram Vogels
Bubo scandiacus	XC343144	Tero Linjama
Bubo scandiacus	XC343145	Tero Linjama
Bubulcus ibis	XC356329	Marco Dragonetti
Bubulcus ibis	XC495869	Joost van Bruggen
Bubulcus ibis	XC76666	Marco Dragonetti
Bubulcus ibis	XC831486	Jordi Calvet
Bucanetes githagineus	XC164199	Tero Linjama
Bucanetes githagineus	XC855968	Mats Rellmar
Bucephala clangula	XC234677	dmitry yakubovich
Bucephala clangula	XC641760	Lars Edenius
Burhinus oedicnemus	XC896992	Martin Billard
Burhinus oedicnemus	XC914574	Thierry Thomas
Burhinus oedicnemus	XC923183	Jordi Calvet
Burhinus oedicnemus	XC934316	Peter Ertl
Buteo buteo	XC878780	João Tomás
Buteo buteo	XC895030	Martin Billard
Buteo lagopus	XC665960	Lars Edenius
Buteo lagopus	XC747268	Lars Edenius
Cairina moschata	ML92424851	Paul Marvin
Cairina moschata	ML92475411	Paul Marvin
Calandrella brachydactyla	XC806185	Pere Josa
Calandrella brachydactyla	XC813260	Peter Boesman
Calandrella brachydactyla	XC813265	Peter Boesman
Calandrella brachydactyla	XC839296	Corentin Rivière
Calcarius lapponicus	XC567566	Lars Edenius
Calcarius lapponicus	XC580134	Niels Van Doninck
Calcarius lapponicus	XC639055	Peter Stronach
Calcarius lapponicus	XC688953	Lars Edenius
Calidris alpina	XC739138	Uku Paal
Calidris alpina	XC833015	Michaël Bridoux
Calidris alpina	XC852842	Rob van Bemmelen
Calidris alpina	XC908418	Lars Edenius
Calidris falcinellus	XC654231	Lars Edenius
Calidris falcinellus	XC911575	Niclas Backstrom
Calidris maritima	XC186400	Stein Ø. Nilsen
Calidris maritima	XC321244	Tim de Boer
Calidris maritima	XC322089	Rob van Bemmelen
Calidris maritima	XC423507	Johan Råghall
Calidris minuta	XC383563	Terje Kolaas
Calidris minuta	XC383564	Terje Kolaas
Calidris pugnax	XC765283	Stanislas Wroza
Calidris pugnax	XC852294	Jordi Calvet
Calidris temminckii	XC765454	Stanislas Wroza
Calidris temminckii	XC809521	Frode Falkenberg
Caprimulgus europaeus	XC809979	Olivier Swift
Caprimulgus europaeus	XC957127	Jarek Matusiak
Caprimulgus ruficollis	XC724307	Antonio Xeira
Caprimulgus ruficollis	XC905834	SonoNatura
Carduelis carduelis	XC854554	David Pennington
Carduelis carduelis	XC883327	João Tomás
Carduelis carduelis	XC884098	Christian Kerihuel
Carduelis carduelis	XC894563	Jorge Leitão
Carduelis citrinella	XC246416	Jordi Calvet
Carduelis citrinella	XC315443	Jerome Fischer
Carduelis citrinella	XC372554	Jerome Fischer
Carduelis citrinella	XC730229	Stanislas Wroza
Carduelis corsicana	XC349876	Tero Linjama
Carduelis corsicana	XC624722	Charlie Bodin
Carduelis corsicana	XC662052	Marta Celej
Carduelis corsicana	XC662053	Marta Celej
Carpodacus erythrinus	XC743414	Romuald Mikusek
Carpodacus erythrinus	XC863138	Mats Rellmar
Carpodacus erythrinus	XC904579	Lars Edenius
Carpodacus erythrinus	XC912797	Hans Matheve
Cecropis daurica	XC485355	Lars Lachmann
Cecropis daurica	XC723730	Geoff Carey
Cercotrichas galactotes	XC670255	Jonathan Bryant
Cercotrichas galactotes	XC692573	Santiago Caballero Carrera
Cercotrichas galactotes	XC831603	Esperanza Poveda
Motacilla flava	XC745680	Lars Edenius
Motacilla flava	XC793956	Jacobo Ramil Millarengo
Motacilla flava	XC838987	Regina Eidner
Motacilla flava	XC881967	Olivier Swift
Muscicapa striata	XC598245	Niels Van Doninck
Muscicapa striata	XC727741	Paolo Zucca
Muscicapa striata	XC780925	Bas
Muscicapa striata	XC877767	Maarten Sluijter
Myiopsitta monachus	XC622769	jesus carrion
Myiopsitta monachus	XC669961	Manuel Grosselet
Myiopsitta monachus	XC678007	Guilherme Renzo Rocha Brito
Myiopsitta monachus	XC682586	Manuel Grosselet
Neophron percnopterus	XC650774	Eduardo Realinho
Neophron percnopterus	XC654205	Eduardo Realinho
Netta rufina	XC404318	Pascal Christe
Netta rufina	XC407509	Francesco Sottile
Netta rufina	XC644652	Audevard Aurélien
Netta rufina	XC769720	Michel Veldt
Nucifraga caryocatactes	XC736823	Lars Edenius
Nucifraga caryocatactes	XC818171	Lars Edenius
Nucifraga caryocatactes	XC843797	Richard Brahmstaedt
Nucifraga caryocatactes	XC906816	Frode Falkenberg
Numenius arquata	XC830500	Lars Edenius
Numenius arquata	XC832849	Agris Celmins
Numenius phaeopus	XC735243	Lars Edenius
Numenius phaeopus	XC741684	Lars Edenius
Numenius phaeopus	XC799611	Niels Van Doninck
Numenius phaeopus	XC801501	Olivier Swift
Numida meleagris	XC280506	Peter Boesman
Numida meleagris	XC507927	Tim Cockcroft
Nycticorax nycticorax	XC903475	Stanislas Wroza
Nycticorax nycticorax	XC921344	Sébastien Arriubergé
Oenanthe hispanica	XC343294	Agostinho Tomás
Oenanthe hispanica	XC416420	Jordi Calvet
Oenanthe hispanica	XC730459	Stanislas Wroza
Oenanthe hispanica	XC794843	João Tomás
Oenanthe leucura	XC538884	Xavier Riera
Oenanthe leucura	XC692725	Santiago Caballero Carrera
Oenanthe leucura	XC730407	Stanislas Wroza
Oenanthe leucura	XC840125	Pere Josa
Oenanthe oenanthe	XC759707	Ulf Elman
Oenanthe oenanthe	XC769226	Michel Veldt
Oenanthe oenanthe	XC769227	Michel Veldt
Oenanthe oenanthe	XC898202	Jochem verweij
Oriolus oriolus	XC708637	Agris Celmins
Oriolus oriolus	XC739166	Grzegorz Lorek
Oriolus oriolus	XC743901	Romuald Mikusek
Oriolus oriolus	XC809026	Bodo Sonnenburg
Otis tarda	XC721833	Lars Lachmann
Otis tarda	XC721834	Lars Lachmann
Otus scops	XC905326	Christian Kerihuel
Otus scops	XC910434	Antoine Salmon
Oxyura jamaicensis	XC591765	Simon Elliott
Oxyura jamaicensis	XC603727	Peter Ward and Ken Hall
Oxyura leucocephala	XC132436	Fernand Deroussen
Oxyura leucocephala	XC462959	Geoffrey Monchaux
Pandion haliaetus	XC826075	Olli Juhnke
Pandion haliaetus	XC924318	Lars Edenius
Panurus biarmicus	XC955702	Jarek Matusiak
Panurus biarmicus	XC955703	Jarek Matusiak
Parus major	XC881427	Michel Veldt
Parus major	XC899545	Beatrix Saadi-Varchmin
Parus major	XC899637	Lennart Jeppsson
Parus major	XC902756	Olivier Swift
Passer domesticus	XC879927	Paul Kelly
Passer domesticus	XC881740	Olivier Swift
Passer domesticus	XC896493	Martin Billard
Passer domesticus	XC899351	Jack Berteau
Passer hispaniolensis	XC309787	Cedric Mroczko
Passer hispaniolensis	XC334279	Yoann Blanchon
Passer hispaniolensis	XC905912	João Tomás
Passer hispaniolensis	XC913059	Stephan Risch
Passer italiae	XC727597	Francesco Sottile
Passer italiae	XC906612	Frederic Lionel
Passer italiae	XC906614	Frederic Lionel
Passer italiae	XC907069	Mats Rellmar
Passer montanus	XC800953	Daniele Baroni
Passer montanus	XC813881	Susanne Kuijpers
Passer montanus	XC814643	Uku Paal
Passer montanus	XC815513	Susanne Kuijpers
Pavo cristatus	XC812476	Francesco Barberini
Pavo cristatus	XC902565	Kalle Nibbenhagen
Perdix perdix	XC651353	Uku Paal
Perdix perdix	XC897003	Martin Billard
Periparus ater	XC891510	Frederic Lionel
Periparus ater	XC902395	Thomas Bergman
Periparus ater	XC904730	Jorge Leitão
Periparus ater	XC910374	Johan Södercrantz
Perisoreus infaustus	XC611732	Lars Edenius
Perisoreus infaustus	XC652996	Thomas Bergman
Perisoreus infaustus	XC680829	Lars Edenius
Perisoreus infaustus	XC751019	Lars Edenius

Cercotrichas galactotes	XC831605	Esperanza Poveda
Certhia brachydactyla	XC899288	David Pennington
Certhia brachydactyla	XC901386	Jorge Leitão
Certhia brachydactyla	XC901387	Jorge Leitão
Certhia brachydactyla	XC905013	Olivier Swift
Certhia familiaris	XC808139	Lars Edenius
Certhia familiaris	XC878886	Baltasar Pinheiro
Certhia familiaris	XC893809	Azens
Certhia familiaris	XC904077	Corentin Rivière
Cettia cetti	XC907063	Mats Rellmar
Cettia cetti	XC963920	Jack Berteau
Cettia cetti	XC964596	Friedrich Richard
Cettia cetti	XC965043	Jack Berteau
Charadrius alexandrinus	XC338266	José Carlos Sires
Charadrius alexandrinus	XC817932	Sonothèque ADVL
Charadrius dubius	XC813186	Lars Edenius
Charadrius dubius	XC815926	Albert Lastukhin
Charadrius hiaticula	XC653537	Elias A. Ryberg
Charadrius hiaticula	XC653595	Elias A. Ryberg
Charadrius morinellus	XC440167	Stein Ø. Nilsen
Charadrius morinellus	XC570939	Lars Edenius
Chersophilus duponti	XC216990	Cristian Pérez-Granados
Chersophilus duponti	XC235394	Luis Gracia
Chersophilus duponti	XC315238	Jarmo Pirhonen
Chersophilus duponti	XC536806	Sean Ronayne
Chloris chloris	XC814746	Martin Billard
Chloris chloris	XC834605	Esperanza Poveda
Chloris chloris	XC879027	João Tomás
Chloris chloris	XC898912	Nicolas Martinez
Chrysolophus amherstiae	XC473878	Albert Lastukhin
Chrysolophus amherstiae	XC916157	Peter Boesman
Chrysolophus pictus	XC37540	David Farrow
Chrysolophus pictus	XC908427	Xingyu Li
Ciconia ciconia	XC878180	Мітла Андрій Володимирович
Ciconia ciconia	XC878788	João Tomás
Ciconia nigra	XC795530	Sven Normant
Ciconia nigra	XC96963	Edmunds Racinskis
Cinclus cinclus	XC687370	Lars Edenius
Cinclus cinclus	XC700209	Stanislas Wroza
Cinclus cinclus	XC700213	Stanislas Wroza
Cinclus cinclus	XC883370	Teet Sirotkin
Circaetus gallicus	XC40049	Doug Knapp
Circaetus gallicus	XC587198	Eduardo Realinho
Circus aeruginosus	XC859056	João Tomás
Circus aeruginosus	XC884134	João Tomás
Circus cyaneus	XC341267	Tero Linjama
Circus cyaneus	XC670733	Stanislas Wroza
Circus macrourus	XC471461	Stanislas Wroza
Circus macrourus	XC643655	Hans Matheve
Circus pygargus	XC433734	José Carlos Sires
Circus pygargus	XC573274	Jarek Matusiak
Cisticola juncidis	XC930481	Esperanza Poveda
Cisticola juncidis	XC962299	Hans Matheve
Clamator glandarius	XC708536	Sergi Carreras
Clamator glandarius	XC724315	Alexander Schlatmann
Clamator glandarius	XC877435	João Tomás
Clamator glandarius	XC877437	João Tomás
Clanga pomarina	XC329332	Łukasz Bednarz
Clanga pomarina	XC563265	Zbigniew Kajzer
Clangula hyemalis	XC106033	Ryan P. O'Donnell
Clangula hyemalis	XC203477	Andrew Spencer
Clangula hyemalis	XC514046	Timo Janhonen
Clangula hyemalis	XC820344	Johan Willner
Coccothraustes coccothraustes	XC626792	brickegickel
Coccothraustes coccothraustes	XC707043	Lars Edenius
Coccothraustes coccothraustes	XC710720	Török Tamás
Coccothraustes coccothraustes	XC712663	Alan Dalton
Colinus virginianus	XC138625	Paul Marvin
Colinus virginianus	XC567479	Dare Šere
Coloeus monedula	XC856321	Thierry Thomas
Coloeus monedula	XC904574	Martin Billard
Columba bollii	XC270048	Peter Boesman
Columba bollii	XC530191	Mats Rellmar
Columba livia	XC270097	Timo Schnabel
Columba livia	XC92264	Herman van der Meer
Columba oenas	XC738668	Simon Elliott
Columba oenas	XC747109	Simon Elliott
Columba palumbus	XC915274	Susanne Kuijpers
Columba palumbus	XC920599	Lars Edenius
Coracias garrulus	XC661132	Camille Monnet
Coracias garrulus	XC770236	Michel Veldt
Corvus corax	XC791383	Marcin Urbański
Corvus corax	XC800465	Nicolas Martinez
Corvus corax	XC880900	Lars Edenius
Corvus corax	XC880911	Lars Edenius
Corvus corone	XC815510	Susanne Kuijpers
Corvus corone	XC856556	Martin Billard
Corvus corone	XC878485	Anthony Roux
Corvus corone	XC893406	Pere Josa
Pernis apivorus	XC329631	Kaspars Funts
Pernis apivorus	XC666557	P. Venema
Pernis apivorus	XC668502	Sophie Neill
Pernis apivorus	XC826297	Lars Edenius
Petronia petronia	XC651365	Marta Celej
Petronia petronia	XC692717	Santiago Caballero Carrera
Petronia petronia	XC783481	Jacobo Ramil Millarengo
Petronia petronia	XC783482	Jacobo Ramil Millarengo
Phalacrocorax carbo	XC646784	Agris Celmins
Phalacrocorax carbo	XC737064	Irish Wildlife Sounds
Phalacrocorax carbo	XC776010	Paul Kelly
Phalacrocorax carbo	XC841971	Jorge Leitão
Phalaropus lobatus	XC342920	Tero Linjama
Phalaropus lobatus	XC420149	Stein Ø. Nilsen
Phalaropus lobatus	XC487653	Stanislas Wroza
Phalaropus lobatus	XC514049	Timo Janhonen
Phasianus colchicus	XC640749	Tanguy Loïs
Phasianus colchicus	XC929867	Bram Piot
Phoenicopterus roseus	XC267542	Andrew Spencer
Phoenicopterus roseus	XC899996	Paul Coiffard
Phoenicurus ochruros	XC832033	Francisco Molinero
Phoenicurus ochruros	XC844168	Frederic Lionel
Phoenicurus ochruros	XC857226	Grzegorz Lorek
Phoenicurus ochruros	XC898801	Nicolas Martinez
Phoenicurus phoenicurus	XC899515	Lars Mogensen
Phoenicurus phoenicurus	XC911881	Antonio Xeira
Phoenicurus phoenicurus	XC913428	Martin Billard
Phoenicurus phoenicurus	XC913449	Thomas Bergman
Phylloscopus bonelli	XC769307	Michel Veldt
Phylloscopus bonelli	XC799404	João Tomás
Phylloscopus bonelli	XC819672	Jacobo Ramil Millarengo
Phylloscopus bonelli	XC892813	Frederic Lionel
Phylloscopus borealis	XC401786	Karl-Birger Strann
Phylloscopus borealis	XC652032	Lukas Pelikan
Phylloscopus borealis	XC785236	Teet Sirotkin
Phylloscopus borealis	XC896729	Zbigniew Kajzer
Phylloscopus canariensis	XC626845	Olivier Swift, Ludivine Delamare
Phylloscopus canariensis	XC934197	Jose
Phylloscopus collybita	XC879588	Susanne Kuijpers
Phylloscopus collybita	XC900042	Thomas Bergman
Phylloscopus collybita	XC904320	Martin Billard
Phylloscopus collybita	XC908343	Olivier Swift, Hélène Cartaud
Phylloscopus ibericus	XC794962	Jacobo Ramil Millarengo
Phylloscopus ibericus	XC894453	Pere Josa
Phylloscopus ibericus	XC896346	Jacobo Ramil Millarengo
Phylloscopus ibericus	XC909268	Pere Josa
Phylloscopus sibilatrix	XC729301	Bastian Forkel
Phylloscopus sibilatrix	XC769998	Michel Veldt
Phylloscopus sibilatrix	XC840441	Rob van Bemmelen
Phylloscopus sibilatrix	XC911177	W. Agster
Phylloscopus trochiloides	XC802971	Jens Kirkeby
Phylloscopus trochiloides	XC810536	Romuald Mikusek
Phylloscopus trochiloides	XC813612	Peter Boesman
Phylloscopus trochiloides	XC913921	Lars Edenius
Phylloscopus trochilus	XC801762	Lars Edenius
Phylloscopus trochilus	XC855110	David Pennington
Phylloscopus trochilus	XC905213	Azens
Phylloscopus trochilus	XC913109	Thomas Bergman
Pica pica	XC862133	Olivier Swift, Manuel Grosselet
Pica pica	XC872510	Paul Kelly
Pica pica	XC879895	Susanne Kuijpers
Pica pica	XC897040	Sławomir Karpicki
Picoides tridactylus	XC715987	Thomas Bergman
Picoides tridactylus	XC738886	Thomas Bergman
Picus canus	XC878809	András Schmidt
Picus canus	XC882147	Lars Edenius
Picus viridis	XC882026	Jean Pierre Sciolla
Picus viridis	XC927450	Martin Billard
Pinicola enucleator	XC684582	Lars Edenius
Pinicola enucleator	XC778268	Lars Edenius
Pinicola enucleator	XC895559	Maarten Sluijter
Pinicola enucleator	XC895942	Maarten Sluijter
Platalea leucorodia	XC596491	Tristan Guillebot de Nerville
Platalea leucorodia	XC768150	Stanislas Wroza
Plectrophenax nivalis	XC350489	Tero Linjama
Plectrophenax nivalis	XC379430	Stein Ø. Nilsen
Plectrophenax nivalis	XC425901	Terje Kolaas
Plectrophenax nivalis	XC425902	Terje Kolaas
Plegadis falcinellus	XC530553	Jordi Calvet
Plegadis falcinellus	XC890702	Bernard Bousquet
Pluvialis apricaria	XC745635	Lars Edenius
Pluvialis apricaria	XC789865	Simon Elliott
Pluvialis apricaria	XC818974	Azens
Pluvialis apricaria	XC831715	W. Agster
Podiceps auritus	XC375396	Stein Ø. Nilsen
Podiceps auritus	XC715920	Alan Dalton
Podiceps cristatus	XC130588	maudoc
Podiceps cristatus	XC773246	Bernard Bousquet
Podiceps cristatus	XC790749	Stanislas Wroza

Corvus frugilegus	XC770891	Michel Veldt
Corvus frugilegus	XC780915	Jorge Leitão
Corvus frugilegus	XC783382	Stuart Fisher
Corvus frugilegus	XC883859	Alain Malengreau
Corvus splendens	XC254340	az dipu
Corvus splendens	XC322403	Thomas Lüthi
Corvus splendens	XC357593	Oscar Campbell
Corvus splendens	XC446886	Audevard Aurélien
Coturnix coturnix	XC915429	Lars Edenius
Coturnix coturnix	XC915737	Joost van Bruggen
Crex crex	XC803640	Frode Falkenberg
Crex crex	XC918715	Dag Österlund
Cuculus canorus	XC710111	Alain Malengreau
Cuculus canorus	XC917958	Arjun Dutta
Curruca balearica	XC410968	Jerome Fischer
Curruca balearica	XC411039	Jerome Fischer
Curruca balearica	XC411067	Jerome Fischer
Curruca balearica	XC411330	Jerome Fischer
Curruca cantillans	XC807728	Dare Šere
Curruca cantillans	XC907144	Peter Carr
Curruca communis	XC898903	Krzysztof Deoniziak
Curruca communis	XC898982	Olivier Swift
Curruca communis	XC900942	Martin Billard
Curruca communis	XC904596	Niels Krabbe
Curruca conspicillata	XC470756	Geoffrey Monchaux
Curruca conspicillata	XC537227	Charlie Bodin
Curruca conspicillata	XC793044	Stanislas Wroza
Curruca conspicillata	XC793047	Stanislas Wroza
Curruca conspicillata	XC819009	Paul Coiffard
Curruca curruca	XC800988	Daniele Baroni
Curruca curruca	XC809662	Dominique Guillerme
Curruca curruca	XC826101	Esperanza Poveda
Curruca curruca	XC899224	Bodo Sonnenburg
Curruca hortensis	XC801094	João Tomás
Curruca hortensis	XC802317	SonoNatura
Curruca hortensis	XC845162	julien Birard
Curruca iberiae	XC722937	Xavier Riera
Curruca iberiae	XC791461	Maxence Fouillade
Curruca melanocephala	XC792298	SonoNatura
Curruca melanocephala	XC900159	David Pennington
Curruca melanocephala	XC917380	Alain Verneau
Curruca nisoria	XC801193	Bodo Sonnenburg
Curruca nisoria	XC807274	Frank DD4WH
Curruca nisoria	XC816689	Grzegorz Lorek
Curruca nisoria	XC845030	Lukas Thiess
Curruca nisoria	XC905521	Délfin Gonzalez
Curruca sarda	XC246980	Jerome Fischer
Curruca sarda	XC370650	Jerome Fischer
Curruca sarda	XC471853	Stanislas Wroza
Curruca sarda	XC666367	Marta Celej
Curruca undata	XC483891	David Bissett
Curruca undata	XC530015	Stanislas Wroza
Curruca undata	XC794772	Jacobo Ramil Millarengo
Curruca undata	XC844566	Martin Billard
Cursorius cursor	XC149578	Frank Lambert
Cursorius cursor	XC164193	Tero Linjama
Cyanistes caeruleus	XC893737	Guillaume Wetzel
Cyanistes caeruleus	XC894018	Tanguy Loïs
Cyanistes caeruleus	XC898570	Jorge Leitão
Cyanistes caeruleus	XC898938	Paul Kelly
Cyanistes teneriffae	XC367032	Thomas Lüthi
Cyanistes teneriffae	XC458948	Twan Mols
Cyanistes teneriffae	XC530210	Mats Rellmar
Cyanistes teneriffae	XC796196	Sidnei Dantas
Cyanopica cooki	XC341189	José Carlos Sires
Cyanopica cooki	XC414693	Stanislas Wroza
Cyanopica cooki	XC747540	Jorge Leitão
Cyanopica cooki	XC747830	Jorge Leitão
Cygnus atratus	XC297979	Timo Schnabel
Cygnus atratus	XC674006	Marc Anderson
Cygnus cygnus	XC791765	Lars Edenius
Cygnus cygnus	XC795335	Lars Edenius
Cygnus olor	XC764112	Bodo Sonnenburg
Cygnus olor	XC861052	Paul Kelly
Cygnus olor	XC864373	Paul Kelly
Cygnus olor	XC879427	Olivier Swift
Delichon urbicum	XC598648	Simon Elliott
Delichon urbicum	XC726339	Jorge Leitão
Delichon urbicum	XC792837	João Tomás
Delichon urbicum	XC792855	João Tomás
Dendrocopos leucotos	XC680685	Jerome Fischer
Dendrocopos leucotos	XC689011	Romuald Mikusek
Dendrocopos leucotos	XC713501	Lars Edenius
Dendrocopos leucotos	XC719600	Uku Paal
Dendrocopos major	XC622683	Lars Edenius
Dendrocopos major	XC895779	Lennart Jeppsson
Dendrocopos major	XC911171	W. Agster
Dendrocopos major	XC926178	Samir Hellal
Dendrocopos syriacus	XC480290	Albert Lastukhin
Dendrocopos syriacus	XC528724	Jarek Matusiak
Dendrocopos syriacus	XC667315	András Schmidt
Dendrocopos syriacus	XC770414	Michel Veldt
Dendrocoptes medius	XC859063	Maarten Sluijter
Dendrocoptes medius	XC862406	Martin Billard
Dendrocoptes medius	XC877498	Guilherme Melo
Podiceps cristatus	XC801357	Chèvremont Fabian
Podiceps grisegena	XC26934	Patrik Åberg
Podiceps grisegena	XC804818	Uku Paal
Podiceps nigricollis	XC26932	Patrik Åberg
Podiceps nigricollis	XC590654	Simon Elliott
Poecile cinctus	XC401785	Karl-Birger Strann
Poecile cinctus	XC750044	Lars Edenius
Poecile cinctus	XC752844	Lars Edenius
Poecile cinctus	XC807539	Thomas Bergman
Poecile montanus	XC818372	Thomas Bergman
Poecile montanus	XC880573	Bodo Sonnenburg
Poecile montanus	XC896685	Zbigniew Kajzer
Poecile montanus	XC896794	Lars Edenius
Poecile palustris	XC864410	Bodo Sonnenburg
Poecile palustris	XC864410	Bodo Sonnenburg
Poecile palustris	XC893807	Azens
Poecile palustris	XC913905	Elias A. Ryberg
Poicephalus senegalus	XC447381	Étienne Leroy
Poicephalus senegalus	XC523303	Joost van Bruggen
Poicephalus senegalus	XC719437	Peter Boesman
Poicephalus senegalus	XC719438	Peter Boesman
Porphyrio porphyrio	XC505960	Jordi Calvet
Porphyrio porphyrio	XC546992	Vincent Palomares
Porphyrio porphyrio	XC702417	Stanislas Wroza
Porphyrio porphyrio	XC799681	Pere Josa
Porzana porzana	XC900764	Mats Olsson
Porzana porzana	XC917901	Uku Paal
Prunella collaris	XC569165	Stanislas Wroza
Prunella collaris	XC569172	Stanislas Wroza
Prunella collaris	XC625477	Marcel Gil Velasco
Prunella collaris	XC688398	Stanislas Wroza
Prunella modularis	XC581070	Arjun Dutta
Prunella modularis	XC881318	Martin Billard
Prunella modularis	XC902691	Paul Kelly
Prunella modularis	XC912899	Romuald Mikusek
Psittacara mitratus	XC707076	Richard E. Webster
Psittacara mitratus	XC931278	Jorge Leitão
Psittacula eupatria	XC628895	Stanislas Wroza
Psittacula eupatria	XC628898	Stanislas Wroza
Psittacula eupatria	XC628899	Stanislas Wroza
Psittacula eupatria	XC628900	Stanislas Wroza
Psittacula krameri	XC694156	Eduardo Realinho
Psittacula krameri	XC933414	Jarek Matusiak
Psittacula krameri	XC933415	Jarek Matusiak
Psittacula krameri	XC933415	Jarek Matusiak
Pterocles alchata	XC142059	Jordi Calvet
Pterocles alchata	XC924210	Jordi Calvet
Pterocles orientalis	XC730394	Stanislas Wroza
Pterocles orientalis	XC730396	Stanislas Wroza
Ptyonoprogne rupestris	XC657489	Camille Monnet
Ptyonoprogne rupestris	XC893409	Pere Josa
Pyrrhocorax graculus	XC569238	Stanislas Wroza
Pyrrhocorax graculus	XC769199	Frank Lambert
Pyrrhocorax graculus	XC820207	João Tomás
Pyrrhocorax graculus	XC898787	Daniele Baroni
Pyrrhocorax pyrrhocorax	XC288230	Antonio Xeira
Pyrrhocorax pyrrhocorax	XC584324	Stanislas Wroza
Pyrrhocorax pyrrhocorax	XC596499	Simon Elliott
Pyrrhocorax pyrrhocorax	XC735115	Irish Wildlife Sounds
Pyrrhula pyrrhula	XC690409	Lars Edenius
Pyrrhula pyrrhula	XC696696	Lars Edenius
Pyrrhula pyrrhula	XC780464	Lars Edenius
Pyrrhula pyrrhula	XC903130	Corentin Rivière
Rallus aquaticus	XC689678	Stanislas Wroza
Rallus aquaticus	XC789677	Mats Olsson
Rallus aquaticus	XC859387	Pere Josa
Rallus aquaticus	XC879688	João Tomás
Recurvirostra avosetta	XC698221	Olivier Swift, Hélène Cartaud
Recurvirostra avosetta	XC883880	Pere Josa
Regulus ignicapilla	XC893407	Pere Josa
Regulus ignicapilla	XC900900	Ireneusz Oleksik
Regulus ignicapilla	XC902782	Lars Edenius
Regulus ignicapilla	XC913156	Romuald Mikusek
Regulus regulus	XC569378	Stanislas Wroza
Regulus regulus	XC570588	Paul Holt
Regulus regulus	XC831497	Mats Rellmar
Regulus regulus	XC902433	Elias A. Ryberg
Remiz pendulinus	XC770244	Michel Veldt
Remiz pendulinus	XC828602	Kuzey Cem Kulaçoğlu
Remiz pendulinus	XC884995	João Tomás
Remiz pendulinus	XC902668	Stephan Risch
Riparia riparia	XC659405	Lars Edenius
Riparia riparia	XC666843	Domagoj Tomičić
Saxicola dacotiae	XC153273	Herman van Oosten
Saxicola dacotiae	XC346441	Tero Linjama
Saxicola rubetra	XC797269	Grzegorz Lorek
Saxicola rubetra	XC803189	Lars Edenius
Saxicola rubetra	XC808861	Lars Edenius
Saxicola rubetra	XC908625	Martin Billard
Saxicola rubicola	XC716408	Christian Kerihuel
Saxicola rubicola	XC789119	João Tomás
Saxicola rubicola	XC799490	Regina Eidner
Saxicola rubicola	XC909121	Mercier Christophe
Scolopax rusticola	XC397413	Ruud van Beusekom
Scolopax rusticola	XC922073	Teet Sirotkin

Dendrocoptes medius	XC913132	Romuald Mikusek
Dryobates minor	XC709565	Alan Dalton
Dryobates minor	XC712215	Lars Edenius
Dryobates minor	XC739164	Uku Paal
Dryobates minor	XC742967	Pontus Wennesjö
Dryocopus martius	XC839151	Lars Edenius
Dryocopus martius	XC839284	Lars Edenius
Dryocopus martius	XC902134	Ulf Elman
Dryocopus martius	XC911632	Jelle Scharringa
Egretta garzetta	XC774430	Irish Wildlife Sounds
Egretta garzetta	XC790717	Stanislas Wroza
Egretta garzetta	XC841128	Ray Tsu
Egretta garzetta	XC856824	Jorge Leitão
Elanus caeruleus	XC351398	José Carlos Sires
Elanus caeruleus	XC352476	José Carlos Sires
Emberiza calandra	XC835054	Esperanza Poveda
Emberiza calandra	XC864606	Frederic Lionel
Emberiza calandra	XC882055	João Tomás
Emberiza calandra	XC899277	David Pennington
Emberiza cia	XC467766	Thijs Fijen
Emberiza cia	XC722554	SonoNatura
Emberiza cia	XC724311	brickegickel
Emberiza cia	XC865950	Azens
Emberiza cirlus	XC799684	Jacobo Ramil Millarengo
Emberiza cirlus	XC831373	Francesco Sottile
Emberiza cirlus	XC882008	Azens
Emberiza cirlus	XC892785	Martin Billard
Emberiza citrinella	XC819013	Grzegorz Lorek
Emberiza citrinella	XC826623	Jack Berteau
Emberiza citrinella	XC879349	Jarek Matusiak
Emberiza citrinella	XC895089	Martin Billard
Emberiza hortulana	XC795809	Stephan Börnecke
Emberiza hortulana	XC802483	João Tomás
Emberiza hortulana	XC902403	Grzegorz Lorek
Emberiza hortulana	XC903923	Lars Edenius
Emberiza melanocephala	XC729335	Leconte Michel
Emberiza melanocephala	XC741120	Agris Celmins
Emberiza melanocephala	XC801378	Stephan Risch
Emberiza melanocephala	XC813175	Domagoj Tomičić
Emberiza pusilla	XC484445	Fraser Simpson
Emberiza pusilla	XC571116	Ulf Hansson
Emberiza pusilla	XC779437	Erik Normark
Emberiza pusilla	XC809482	Kasper Wieck
Emberiza rustica	XC655533	Olavi Hinkkanen
Emberiza rustica	XC815431	Lars Edenius
Emberiza rustica	XC900006	Thomas Bergman
Emberiza rustica	XC904018	Lars Edenius
Emberiza schoeniclus	XC790740	Stanislas Wroza
Emberiza schoeniclus	XC791229	Marcin Urbański
Emberiza schoeniclus	XC792702	Stuart Fisher
Emberiza schoeniclus	XC796332	Albert Lastukhin
Eremophila alpestris	XC485435	Stanislas Wroza
Eremophila alpestris	XC571278	Lars Edenius
Erithacus rubecula	XC865221	Jean Pierre Sciolla
Erithacus rubecula	XC897347	W. Agster
Erithacus rubecula	XC897396	Jacobo Ramil Millarengo
Erithacus rubecula	XC906740	Mats Rellmar
Estrilda astrild	XC640274	Jacobo Ramil MIllarengo
Estrilda astrild	XC719273	Nicolas Martinez
Estrilda astrild	XC748911	Jacobo Ramil Millarengo
Estrilda astrild	XC750258	Jacobo Ramil Millarengo
Estrilda troglodytes	XC164462	Fernand Deroussen
Estrilda troglodytes	XC719131	Peter Boesman
Estrilda troglodytes	XC719132	Peter Boesman
Estrilda troglodytes	XC957262	Julien Birard
Euodice malabarica	XC471526	Stanislas Wroza
Euodice malabarica	XC838993	Piqué Simon
Falco biarmicus	ML615715308	Shane Sumasgutner
Falco biarmicus	ML89506	Justin Schuetz
Falco biarmicus	XC101188	James and David Bradley
Falco biarmicus	XC398048	Peter Boesman
Falco cherrug	XC412094	Frank Lambert
Falco cherrug	XC491256	Peter Boesman
Falco columbarius	XC731075	Lars Edenius
Falco columbarius	XC896663	Tero Linjama
Falco eleonorae	XC854572	Wim Jacobs
Falco eleonorae	XC893157	Alain Malengreau
Falco naumanni	XC383877	maudoc
Falco naumanni	XC579422	Jordi Calvet
Falco peregrinus	XC748303	Irish Wildlife Sounds
Falco peregrinus	XC896686	Sven Normant
Falco rusticolus	XC189210	Andrew Spencer
Falco rusticolus	XC709104	Lars Edenius
Falco rusticolus	XC710854	Dag Österlund
Falco rusticolus	XC713307	Lars Edenius
Falco subbuteo	XC586296	Hugo Wieleman
Falco subbuteo	XC796706	Lars Edenius
Falco tinnunculus	XC822020	Dominique Guillerme
Serinus canaria	XC722081	SonoNatura
Serinus canaria	XC722083	SonoNatura
Serinus canaria	XC722084	SonoNatura
Serinus canaria	XC831509	Mats Rellmar
Serinus serinus	XC725616	Uku Paal
Serinus serinus	XC812475	Romuald Mikusek
Serinus serinus	XC875263	João Tomás
Serinus serinus	XC900917	Martin Billard
Sinosuthora webbiana	XC241076	Michael Grunwell
Sinosuthora webbiana	XC464672	Martin Sutherland
Sinosuthora webbiana	XC722418	Common Jeff（麻杰夫）
Sinosuthora webbiana	XC889840	Geoff Carey
Sitta europaea	XC897314	Lennart Jeppsson
Sitta europaea	XC897670	Jacobo Ramil Millarengo
Sitta europaea	XC927958	Ulf Elman
Sitta europaea	XC938013	Francesco Sottile
Somateria mollissima	XC383544	Terje Kolaas
Somateria mollissima	XC549046	Lars Edenius
Spatula clypeata	XC644500	Jarek Matusiak
Spatula clypeata	XC863292	João Tomás
Spatula querquedula	XC544441	Hans Matheve
Spatula querquedula	XC650914	Lars Edenius
Spinus spinus	XC594919	Simon Elliott
Spinus spinus	XC793450	Lars Edenius
Spinus spinus	XC799041	Romuald Mikusek
Spinus spinus	XC871416	Xavier Riera
Streptopelia decaocto	XC843476	Joost van Bruggen
Streptopelia decaocto	XC881441	Michel Veldt
Streptopelia turtur	XC862628	Olivier Swift
Streptopelia turtur	XC902789	Olivier Swift
Strix aluco	XC845803	SonoNatura
Strix aluco	XC936220	Martin Billard
Strix nebulosa	XC343167	Tero Linjama
Strix nebulosa	XC655482	Lars Edenius
Strix uralensis	XC705899	Lars Edenius
Strix uralensis	XC750071	Agris Celmins
Strix uralensis	XC797469	Ulf Elman
Strix uralensis	XC884935	Ulf Elman
Sturnus unicolor	XC642973	Marcel Gil Velasco
Sturnus unicolor	XC665188	Jorge Leitão
Sturnus unicolor	XC683425	Jacobo Ramil MIllarengo
Sturnus unicolor	XC752912	David Tattersley
Sturnus vulgaris	XC543800	Thomas Bergman
Sturnus vulgaris	XC604977	Simon Elliott
Sturnus vulgaris	XC652012	Uku Paal
Sturnus vulgaris	XC712625	Olivier Swift, Ludivine Delamare
Surnia ulula	XC793932	Teet Sirotkin
Surnia ulula	XC862737	Stein Ø. Nilsen
Sylvia atricapilla	XC858846	Jacobo Ramil Millarengo
Sylvia atricapilla	XC880829	Jean Pierre Sciolla
Sylvia atricapilla	XC904739	Thomas Bergman
Sylvia atricapilla	XC905957	Grzegorz Lorek
Sylvia borin	XC836965	Jack Berteau
Sylvia borin	XC904341	Martin Billard
Sylvia borin	XC906128	Ulf Elman
Sylvia borin	XC906390	Azens
Syrmaticus reevesii	XC360690	Stanislas Wroza
Syrmaticus reevesii	XC360691	Stanislas Wroza
Tachybaptus ruficollis	XC634413	Peter Boesman
Tachybaptus ruficollis	XC720814	Ulf Elman
Tachymarptis melba	XC544109	Jordi Calvet
Tachymarptis melba	XC569487	Beatrix Saadi-Varchmin
Tadorna ferruginea	XC683992	Geoff Carey
Tadorna ferruginea	XC778623	Valentin Monnoy
Tadorna ferruginea	XC835668	Martin Billard
Tadorna ferruginea	XC872210	Johannes Dag Mayer
Tadorna tadorna	XC735778	Irish Wildlife Sounds
Tadorna tadorna	XC882474	Jean Courtin
Tadorna tadorna	XC909997	Uku Paal
Tadorna tadorna	XC936128	Arjun Dutta
Tarsiger cyanurus	XC606234	Niels Van Doninck
Tarsiger cyanurus	XC644039	Agris Celmins
Tarsiger cyanurus	XC661672	Lukas Thiess
Tarsiger cyanurus	XC912128	Michel Watelet
Tetrao urogallus	XC473720	Simon Ernst
Tetrao urogallus	XC611477	Stanislas Wroza
Tetrao urogallus	XC639001	Stanislas Wroza
Tetrao urogallus	XC641981	Stanislas Wroza
Tetrastes bonasia	XC779196	Lars Edenius
Tetrastes bonasia	XC814145	Cedric Mroczko
Tetrastes bonasia	XC881064	Lars Edenius
Tetrastes bonasia	XC904071	Corentin Rivière
Tetrax tetrax	XC363911	Stanislas Wroza
Tetrax tetrax	XC722329	SonoNatura
Thectocercus acuticaudatus	XC189895	Andrew Spencer
Thectocercus acuticaudatus	XC189896	Andrew Spencer
Thectocercus acuticaudatus	XC635097	Dante Buzzetti
Thectocercus acuticaudatus	XC879279	Dante Buzzetti

Falco tinnunculus	XC876577	João Tomás	*Threskiornis aethiopicus*	XC278223	Andrew Spencer
Falco vespertinus	XC770207	Michel Veldt	*Threskiornis aethiopicus*	XC429511	Frank Lambert
Falco vespertinus	XC813402	Peter Boesman	*Threskiornis aethiopicus*	XC505935	Lynette Rudman
Ficedula albicollis	XC653221	brickegickel	*Threskiornis aethiopicus*	XC651807	Nature sounds by Simply Birding
Ficedula albicollis	XC653222	brickegickel	*Tichodroma muraria*	XC512330	Thomas Armand
Ficedula albicollis	XC655679	W. Agster	*Tichodroma muraria*	XC569274	Stanislas Wroza
Ficedula albicollis	XC723932	Ireneusz Oleksik	*Tichodroma muraria*	XC573620	Sean Ronayne
Ficedula hypoleuca	XC802629	bert de bruin	*Tichodroma muraria*	XC698260	András Schmidt
Ficedula hypoleuca	XC803215	Mats Rellmar	*Tringa erythropus*	XC564369	Lars Edenius
Ficedula hypoleuca	XC806550	Alan Dalton	*Tringa erythropus*	XC915323	Thomas Bergman
Ficedula hypoleuca	XC908488	Jacek Mucha	*Tringa glareola*	XC903314	Lars Edenius
Ficedula parva	XC736819	Lars Edenius	*Tringa glareola*	XC906765	Francesco Sottile
Ficedula parva	XC743060	Romuald Mikusek	*Tringa nebularia*	XC900331	Uku Paal
Ficedula parva	XC804988	Mikael Litsgård	*Tringa nebularia*	XC917906	Esperanza Poveda
Ficedula parva	XC807830	Lars Edenius	*Tringa ochropus*	XC803363	Lars Edenius
Fringilla coelebs	XC897397	Jacobo Ramil Millarengo	*Tringa ochropus*	XC808190	Lars Edenius
Fringilla coelebs	XC908632	Martin Billard	*Tringa totanus*	XC884810	Olivier Swift
Fringilla coelebs	XC908812	Olivier Swift	*Tringa totanus*	XC890808	Christian Bøggild
Fringilla coelebs	XC909647	Carlos Pereira	*Tringa totanus*	XC898939	Paul Kelly
Fringilla montifringilla	XC653538	Agris Celmins	*Tringa totanus*	XC906104	Thomas Bergman
Fringilla montifringilla	XC675120	Albert Lastukhin	*Troglodytes troglodytes*	XC916801	Olivier Swift
Fringilla montifringilla	XC731505	Marc Anderson	*Troglodytes troglodytes*	XC928304	Jorge Leitão
Fringilla montifringilla	XC861643	Nicolas Martinez	*Turdus iliacus*	XC808871	Lars Edenius
Fulica atra	XC715239	Susanne Kuijpers	*Turdus iliacus*	XC881694	Eric Roualet
Fulica atra	XC881746	Paul Kelly	*Turdus iliacus*	XC901039	Kai Rantala
Fulica atra	XC893840	Susanne Kuijpers	*Turdus iliacus*	XC903924	Lars Edenius
Fulica atra	XC902418	Jack Berteau	*Turdus merula*	XC815531	Agris Celmins
Fulica cristata	XC306654	Hans Matheve	*Turdus merula*	XC900559	Lennart Jeppsson
Fulica cristata	XC431996	Joost van Bruggen	*Turdus merula*	XC906491	Olivier Swift
Fulica cristata	XC860421	Dries Van de Loock	*Turdus merula*	XC907818	Olivier Swift
Fulica cristata	XC908546	Nelson Conceição	*Turdus philomelos*	XC831495	Agris Celmins
Galerida cristata	XC832503	Stein Ø. Nilsen	*Turdus philomelos*	XC879352	Alain Malengreau
Galerida cristata	XC839414	Corentin Rivière	*Turdus philomelos*	XC897346	W. Agster
Galerida cristata	XC864276	SonoNatura	*Turdus philomelos*	XC899778	Jorge Leitão
Galerida cristata	XC864607	Frederic Lionel	*Turdus pilaris*	XC635213	Stanislas Wroza
Galerida theklae	XC463869	Jordi Calvet	*Turdus pilaris*	XC686589	Niels Van Doninck
Galerida theklae	XC730352	Stanislas Wroza	*Turdus pilaris*	XC727604	Lars Edenius
Galerida theklae	XC779770	Luis Gracia	*Turdus pilaris*	XC834617	Grégoire Chauvot
Galerida theklae	XC900368	Christian Kerihuel	*Turdus torquatus*	XC593279	Simon Elliott
Gallinago gallinago	XC633300	Krzysztof Deoniziak	*Turdus torquatus*	XC721589	Loan Delpit
Gallinago gallinago	XC729310	Lars Edenius	*Turdus torquatus*	XC724232	Romuald Mikusek
Gallinago media	XC201361	Stein Ø. Nilsen	*Turdus torquatus*	XC837014	Petter Westberg
Gallinago media	XC325087	Terje Kolaas	*Turdus viscivorus*	XC718033	Manuel Grosselet
Gallinula chloropus	XC894656	Lars Mogensen	*Turdus viscivorus*	XC788562	Jacobo Ramil Millarengo
Gallinula chloropus	XC895059	Martin Billard	*Turdus viscivorus*	XC807826	Lars Edenius
Gallinula chloropus	XC902620	Lars Mogensen	*Turdus viscivorus*	XC879652	Christian Vemmelund Helligsø
Gallinula chloropus	XC905071	Vandousselaere Patrick	*Tyto alba*	XC948997	SonoNatura
Garrulus glandarius	XC856324	Thierry Thomas	*Tyto alba*	XC952015	SonoNatura
Garrulus glandarius	XC881809	Esperanza Poveda	*Tyto alba*	XC952969	Friedrich Richard
Garrulus glandarius	XC884360	Thomas Bergman	*Tyto alba*	XC962216	Hans Matheve
Garrulus glandarius	XC902468	Jack Berteau	*Upupa epops*	XC897074	SonoNatura
Geronticus eremita	XC361510	José Carlos Sires y Eloisa Matheu	*Upupa epops*	XC917761	Regina Eidner
Geronticus eremita	XC361523	José Carlos Sires y Eloisa Matheu	*Vanellus vanellus*	XC638538	Thomas Bergman
Glareola pratincola	XC379455	Stanislas Wroza	*Vanellus vanellus*	XC880717	Olivier Swift
Glareola pratincola	XC758522	Dries Van de Loock	*Vanellus vanellus*	XC881982	Olivier Swift
Glaucidium passerinum	XC883372	Teet Sirotkin	*Vanellus vanellus*	XC898816	Thomas Bergman
Glaucidium passerinum	XC902777	David Darrell-Lambert	*Zapornia parva*	XC732543	Tero Linjama
Grus grus	XC723192	Lars Edenius	*Zapornia parva*	XC900252	Krzysztof Deoniziak
Grus grus	XC836029	Hannu Varkki	*Zapornia pusilla*	XC656129	Yannick Jacob
Gulosus aristotelis	XC588002	Simon Elliott	*Zapornia pusilla*	XC745918	Marcin Sołowiej

Recording credits for audio files of North American species downloaded from Xeno canto (XC) and the Macaulay Library (ML).

Species	File	Recordist	Species	File	Recordist
Acanthis flammea	XC383642	Terje Kolaas	*Himantopus mexicanus*	XC778463	Paul Driver
Acanthis flammea	XC589966	Seth Beaudreault, Toolik Field Station	*Hirundo rustica*	XC129647	Thomas G. Graves
Accipiter cooperii	XC603733	Peter Ward and Ken Hall	*Hirundo rustica*	XC446455	Ed Pandolfino
Accipiter cooperii	XC609230	Matt Wistrand	*Histrionicus histrionicus*	XC181783	Andrew Spencer
Accipiter gentilis	XC59174	Tayler Brooks	*Histrionicus histrionicus*	XC351801	Bruce Lagerquist
Accipiter gentilis	XC818169	Lars Edenius	*Hylocichla mustelina*	XC692210	Christopher McPherson
Accipiter striatus	XC285549	Paul Driver	*Hylocichla mustelina*	XC739057	Bobby Wilcox
Accipiter striatus	XC791005	Pedro Rinaldi	*Hylocichla mustelina*	XC771930	Paul Driver
Acridotheres tristis	XC659209	Sunny Tseng	*Hylocichla mustelina*	XC818020	Bobby Wilcox
Acridotheres tristis	XC729094	Greg Irving	*Icterus gularis*	XC318526	Paul Marvin
Acridotheres tristis	XC812211	Geoff Carey	*Icterus gularis*	XC359069	Paul Marvin
Acridotheres tristis	XC812212	Geoff Carey	*Icterus pectoralis*	XC224640	Peter Boesman
Actitis macularius	XC183594	Ian Cruickshank	*Icterus pectoralis*	XC363554	Roland Rumm
Actitis macularius	XC232641	Paul Marvin	*Ictinia mississippiensis*	XC316339	J.R. Rigby
Aechmophorus clarkii	XC143247	Andrew Spencer	*Ictinia mississippiensis*	XC669899	Russ Wigh
Aechmophorus clarkii	XC418571	Bobby Wilcox	*Ixobrychus exilis*	XC492421	Paul Driver
Aechmophorus clarkii	XC452390	Paul Marvin	*Ixobrychus exilis*	XC581228	Paul Marvin
Aechmophorus clarkii	XC641950	Paul Marvin	*Ixoreus naevius*	XC416081	Steve Hampton
Aechmophorus occidentalis	XC129074	Thomas G. Graves	*Lagopus leucura*	XC141894	Andrew Spencer
Aechmophorus occidentalis	XC527689	Thomas G. Graves	*Lagopus leucura*	XC152517	Davyd Betchkal
Aechmophorus occidentalis	XC527695	Thomas G. Graves	*Lagopus leucura*	XC363155	Frank Lambert
Aechmophorus occidentalis	XC527697	Thomas G. Graves	*Lagopus leucura*	XC756351	Bruce Lagerquist
Aegolius acadicus	XC546885	Lance A. M. Benner	*Lampornis clemenciae*	XC563006	Daniel Hinckley
Aegolius acadicus	XC613765	Peter Ward and Ken Hall	*Lampornis clemenciae*	XC809118	Manuel Grosselet
Aegolius funereus	XC110187	Andrew Spencer	*Laterallus jamaicensis*	XC36145	Fabrice Schmitt

Aegolius funereus	XC233533	Steve Wilson
Aeronautes saxatalis	XC470554	Thomas G. Graves
Aeronautes saxatalis	XC552939	Paul Marvin
Agapornis roseicollis	XC346578	Peter Boesman
Agapornis roseicollis	XC453168	Paul Marvin
Aix sponsa	XC509715	Sunny Tseng
Aix sponsa	XC509717	Sunny Tseng
Alectoris chukar	XC233760	Mouser Williams
Alectoris chukar	XC387754	Bruce Lagerquist
Alopochen aegyptiaca	XC546108	Albert Noorlander
Alopochen aegyptiaca	XC620525	Francesco Sottile
Amazilia yucatanensis	XC130831	Andrew Spencer
Amazilia yucatanensis	XC298921	Dan Lane
Amazona oratrix	XC681814	Manuel Grosselet
Amazona oratrix	XC804979	Manuel Grosselet
Amazona viridigenalis	XC320551	Paul Marvin
Amazona viridigenalis	XC320571	Paul Marvin
Ammospiza caudacuta	XC55559	Andrew Spencer
Ammospiza leconteii	XC598435	Peter Ward and Ken Hall
Ammospiza maritima	XC433071	Phil Brown
Ammospiza maritima	XC654371	William Whitehead
Anas acuta	XC453334	Paul Marvin
Anas acuta	XC786109	Paul Driver
Anas carolinensis	XC173648	Paul Marvin
Anas carolinensis	XC354707	Frank Lambert
Anas diazi	XC663146	Manuel Grosselet
Anas diazi	XC683209	Manuel Grosselet
Anas fulvigula	XC104626	Andrew Spencer
Anas fulvigula	XC192343	Paul Marvin
Anas platyrhynchos	XC630772	Paul Marvin
Anas rubripes	XC142767	Martin St-Michel
Anas rubripes	XC168801	Paul Driver
Anthus spragueii	XC186346	Richard E. Webster
Anthus spragueii	XC295527	Hal Mitchell
Antigone canadensis	XC606567	Peter Ward and Ken Hall
Antigone canadensis	XC625913	Richard Bradley
Antrostomus arizonae	XC553845	Scott Olmstead
Antrostomus arizonae	XC651661	Bobby Wilcox
Antrostomus carolinensis	XC555492	Ron Overholtz
Antrostomus carolinensis	XC568300	Russ Wigh
Antrostomus vociferus	XC405768	Paul Marvin
Antrostomus vociferus	XC860759	Sue Riffe
Aphelocoma californica	XC454467	Lisa McMaster
Aphelocoma coerulescens	XC161108	Paul Marvin
Aphelocoma coerulescens	XC371888	Bruce Lagerquist
Aphelocoma coerulescens	XC733475	PT xiao
Aphelocoma coerulescens	XC796364	Valerie Heemstra
Aphelocoma insularis	XC27719	Andrew Spencer
Aphelocoma insularis	XC359507	Paul Marvin
Aphelocoma insularis	XC408450	Frank Lambert
Aphelocoma insularis	XC89391	Steve Hampton
Aphelocoma wollweberi	XC326271	Nick Komar
Aphelocoma wollweberi	XC776325	Scott Olmstead
Aphelocoma woodhouseii	XC452523	Paul Marvin
Aphelocoma woodhouseii	XC495164	Thomas G. Graves
Aphelocoma woodhouseii	XC577097	Manuel Grosselet
Aquila chrysaetos	XC698030	Lars Edenius
Aquila chrysaetos	XC750025	Lars Edenius
Aquila chrysaetos	XC753804	Lars Edenius
Aquila chrysaetos	XC837084	Birger Hörnfeldt
Aratinga nenday	XC104190	Andrew Spencer
Aratinga nenday	XC196521	Gabriel Rosa
Archilochus alexandri	XC132359	Richard E. Webster
Archilochus alexandri	XC132692	Richard E. Webster
Archilochus alexandri	XC297544	Ross Gallardy
Archilochus alexandri	XC494996	Thomas G. Graves
Archilochus colubris	XC211131	Robert Benson
Archilochus colubris	XC319184	Martin St-Michel
Archilochus colubris	XC673344	Christopher Moser-Purdy
Archilochus colubris	XC758917	Manuel Grosselet
Archilochus colubris	XC781005	Paul Driver
Ardea alba	XC147337	Paul Marvin
Ardea alba	XC695589	amonmod
Ardea alba	XC705918	Sonothèque ADVL
Ardea alba	XC794542	Geoff Carey
Ardea herodias	XC560546	Mark Nenadov
Ardea herodias	XC578132	Ed Pandolfino
Asio flammeus	XC545852	Luiz C. Silva
Asio flammeus	XC557487	Jarek Matusiak
Asio otus	XC793294	Dominique Guillerme
Asio otus	XC793296	Dominique Guillerme
Athene cunicularia	XC104661	Andrew Spencer
Athene cunicularia	XC524491	David Ricardo Rodríguez-Villamil
Aythya affinis	XC334315	Thomas Magarian
Aythya affinis	XC347797	Thomas Magarian
Aythya americana	XC104592	Andrew Spencer
Aythya americana	XC206445	Jessie Barry
Aythya collaris	XC170973	Paul Driver
Aythya collaris	XC203611	Andrew Spencer
Aythya valisineria	XC169220	Paul Driver
Aythya valisineria	XC169224	Paul Driver
Baeolophus ridgwayi	XC613815	Richard E. Webster
Bartramia longicauda	XC143966	Laura Gooch

Laterallus jamaicensis	XC783437	Cristian Pinto Fernandez
Leiothlypis crissalis	XC168577	Jerome Fischer
Leiothlypis crissalis	XC34312	Andrew Spencer
Leptotila verreauxi	XC420921	Yair Guillermo Molina Martínez.
Leptotila verreauxi	XC838546	Jayrson Araujo De Oliveira
Leucolia violiceps	XC133184	Micah Riegner
Leucolia violiceps	XC445935	Richard E. Webster
Leuconotopicus albolarvatus	XC540025	Bruce Lagerquist
Leuconotopicus albolarvatus	XC540025	Bruce Lagerquist
Leuconotopicus albolarvatus	XC614153	Peter Ward and Ken Hall
Leuconotopicus albolarvatus	XC737531	Paul Marvin
Leuconotopicus arizonae	XC322159	Paul Marvin
Leuconotopicus arizonae	XC323873	Richard E. Webster
Leuconotopicus arizonae	XC323875	Richard E. Webster
Leuconotopicus arizonae	XC522394	Jarrod Swackhamer
Leuconotopicus borealis	XC109888	Andrew Spencer
Leuconotopicus borealis	XC54339	Mike Nelson
Leuconotopicus borealis	XC54339	Mike Nelson
Leuconotopicus borealis	XC713000	Bruce Lagerquist
Leuconotopicus villosus	XC701063	Richard E. Webster
Leuconotopicus villosus	XC701065	Richard E. Webster
Leuconotopicus villosus	XC776033	Scott Olmstead
Leuconotopicus villosus	XC841928	Sue Riffe
Leucosticte australis	XC87637	Andrew Spencer
Leucosticte australis	XC87646	Andrew Spencer
Limnothlypis swainsonii	XC423774	Aidan Place
Limnothlypis swainsonii	XC465064	John Middleton
Limosa fedoa	XC307323	Paul Marvin
Limosa fedoa	XC574462	Manuel Grosselet
Lophodytes cucullatus	XC212480	Russ Wigh
Lophodytes cucullatus	XC74430	Todd Wilson
Loxia sinesciuris	XC204811	Andrew Spencer
Loxia sinesciuris	XC548198	Richard E. Webster
Mareca americana	XC519618	Manuel Grosselet
Mareca americana	XC519619	Manuel Grosselet
Mareca strepera	XC679027	Beatrix Saadi-Varchmin
Mareca strepera	XC845777	Jacobo Ramil Millarengo
Megaceryle alcyon	XC451359	Paul Marvin
Megaceryle alcyon	XC628808	Richard E. Webster
Megaceryle torquata	XC646540	Robson Silva e Silva
Megaceryle torquata	XC837882	Jayrson Araujo De Oliveira
Megascops asio	XC286959	Tim Spahr
Megascops asio	XC712961	Bruce Lagerquist
Megascops kennicottii	XC355668	Bruce Lagerquist
Megascops kennicottii	XC540561	Lance A. M. Benner
Megascops trichopsis	XC347699	Jesse Fagan
Megascops trichopsis	XC351699	Frank Lambert
Melanerpes aurifrons	XC143913	Andrew Spencer
Melanerpes aurifrons	XC297554	Ross Gallardy
Melanerpes aurifrons	XC305372	Paul Marvin
Melanerpes aurifrons	XC452716	Paul Marvin
Melanerpes carolinus	XC225523	Peter Boesman
Melanerpes carolinus	XC578524	Sue Riffe
Melanerpes carolinus	XC624447	Bill Grantham
Melanerpes carolinus	XC636507	Jasper Barnes
Melanerpes erythrocephalus	XC254603	Jonathon Jongsma
Melanerpes erythrocephalus	XC313280	Hal Mitchell
Melanerpes erythrocephalus	XC477001	David Darrell-Lambert
Melanerpes erythrocephalus	XC698853	Matt Wistrand
Melanerpes formicivorus	XC649098	Paul Marvin
Melanerpes formicivorus	XC656292	Paul Marvin
Melanerpes formicivorus	XC786993	Ed Pandolfino
Melanerpes formicivorus	XC856855	Sven Kransel
Melanerpes lewis	XC13659	Andrew Spencer
Melanerpes lewis	XC700388	Mark A. Ports
Melanerpes uropygialis	XC354685	David Vander Pluym
Melanerpes uropygialis	XC521997	Jarrod Swackhamer
Meleagris gallopavo	XC617755	Manuel Grosselet
Meleagris gallopavo	XC702183	Francesco Sottile
Melospiza lincolnii	XC558323	Ron Overholtz
Melospiza lincolnii	XC574672	Aidan Place
Melozone fusca	XC747200	Manuel Grosselet
Mergus merganser	XC691817	Simon Elliott
Mergus merganser	XC94638	Jarek Matusiak
Mergus serrator	XC461181	Stein Ø. Nilsen
Mergus serrator	XC607514	Peter Stronach
Micrathene whitneyi	XC363557	Scott Olmstead
Micrathene whitneyi	XC555495	Ron Overholtz
Myiarchus crinitus	XC137719	Jonathon Jongsma
Myiarchus crinitus	XC844235	Sue Riffe
Myiodynastes luteiventris	XC445503	Richard E. Webster
Myiopsitta monachus	XC357408	Paul Marvin
Myiopsitta monachus	XC452545	Paul Marvin
Myiopsitta monachus	XC669961	Manuel Grosselet
Myiopsitta monachus	XC682586	Manuel Grosselet
Nucifraga columbiana	XC567739	Ron Overholtz
Numenius americanus	XC179500	Andrew Spencer
Numenius americanus	XC636979	Bruce Lagerquist
Nyctanassa violacea	XC487225	Paul Marvin
Nyctanassa violacea	XC573260	Manuel Grosselet
Nycticorax nycticorax	XC331173	Manuel Grosselet
Nycticorax nycticorax	XC431999	Joost van Bruggen
Nyctidromus albicollis	XC521299	Jarrod Swackhamer

Bartramia longicauda	XC656679	Matt Wistrand
Bonasa umbellus	ML28156201	Jay McGowan
Bonasa umbellus	ML611940051	Daniel Jauvin
Botaurus lentiginosus	XC233158	Harry Lehto
Botaurus lentiginosus	XC601776	Peter Ward and Ken Hall
Branta canadensis	XC722620	Stephan Risch
Branta canadensis	XC775330	Nicolas Martinez
Branta canadensis	XC844837	Michael Hurben
Brotogeris chiriri	XC744337	João Vitor Oliveira de Souza
Brotogeris chiriri	XC816874	Jayrson Araujo De Oliveira
Brotogeris versicolurus	XC47713	Andrew Spencer
Brotogeris versicolurus	XC47714	Andrew Spencer
Bubo virginianus	XC760068	Michael & Katie LaTour
Bubo virginianus	XC767278	Scott Olmstead
Bubulcus ibis	XC108820	Andrew Spencer
Bubulcus ibis	XC192966	Paul Marvin
Bubulcus ibis	XC356329	Marco Dragonetti
Bubulcus ibis	XC495869	Joost van Bruggen
Bucephala albeola	XC388268	Thomas Magarian
Bucephala albeola	XC710475	Richard E. Webster
Bucephala clangula	XC644304	Lars Edenius
Bucephala clangula	XC792699	Lars Edenius
Bucephala islandica	XC189404	Andrew Spencer
Bucephala islandica	XC83887	Patrik Åberg
Buteo albonotatus	XC604822	Richard E. Webster
Buteo albonotatus	XC793837	Gregory Askew
Buteo brachyurus	XC407410	Daniel de Jesus Garcia
Buteo brachyurus	XC41473	Luiz Gabriel Mazzoni
Buteo jamaicensis	XC638607	Bruce Lagerquist
Buteo jamaicensis	XC666007	Paul Marvin
Buteo lineatus	XC361769	Bruce Lagerquist
Buteo lineatus	XC578105	Ed Pandolfino
Buteo plagiatus	XC604803	Richard E. Webster
Buteo plagiatus	XC625830	Richard E. Webster
Buteo platypterus	XC454231	Miguel San Martin
Buteo platypterus	XC668893	Jim Berry
Buteo regalis	XC419204	Paul Marvin
Buteo regalis	XC76663	Andrew Spencer
Buteo swainsoni	XC418250	Bobby Wilcox
Buteo swainsoni	XC438511	Julia Wittmann
Buteogallus anthracinus	XC147311	Paul Marvin
Buteogallus anthracinus	XC579265	Richard E. Webster
Butorides virescens	XC639384	Bobby Wilcox
Butorides virescens	XC705567	Paul Driver
Cairina moschata	ML92424851	Paul Marvin
Cairina moschata	ML92475411	Paul Marvin
Callipepla californica	XC299260	Paul Marvin
Callipepla californica	XC603751	Peter Ward and Ken Hall
Callipepla gambelii	XC475181	Bobby Wilcox
Callipepla gambelii	XC540563	Jarrod Swackhamer
Callipepla squamata	XC255093	Richard E. Webster
Callipepla squamata	XC255119	Richard E. Webster
Calothorax lucifer	XC297549	Ross Gallardy
Calothorax lucifer	XC297549	Ross Gallardy
Calypte anna	XC132250	Richard E. Webster
Calypte anna	XC473410	bowtyler
Calypte anna	XC501895	Paul Marvin
Calypte anna	XC697495	Paul Marvin
Calypte costae	XC143788	Paul Marvin
Calypte costae	XC390286	Paul Marvin
Campylorhynchus brunneicapillus	XC702988	Paul Marvin
Canachites canadensis	XC192149	Martin St-Michel
Canachites canadensis	XC205576	Paul Marvin
Canachites canadensis	XC389927	Thomas Magarian
Canachites canadensis	XC406266	Patrik Åberg
Caracara plancus	XC430769	Victor Antonelli
Caracara plancus	XC587538	Daniel Mello
Cathartes aura	ML442811061	Ronan Pangie
Cathartes aura	XC520287	Cristian Pinto
Catherpes mexicanus	XC728920	Scott Olmstead
Catherpes mexicanus	XC794354	Eric DeFonso
Centrocercus minimus	XC100250	Andrew Spencer
Centrocercus minimus	XC100250	Andrew Spencer
Centrocercus minimus	XC100250	Andrew Spencer
Centrocercus minimus	XC100250	Andrew Spencer
Centrocercus urophasianus	XC368669	Sue Riffe
Centrocercus urophasianus	XC368674	Sue Riffe
Centrocercus urophasianus	XC634662	Scott Olmstead
Centrocercus urophasianus	XC77182	Andrew Spencer
Chaetura pelagica	XC180468	Dan Lane
Chaetura pelagica	XC413369	Paul Marvin
Chaetura vauxi	XC109774	Andrew Spencer
Chaetura vauxi	XC150252	Paul Marvin
Charadrius melodus	XC328023	Patrick Turgeon
Charadrius melodus	XC494406	Will Sweet
Charadrius montanus	XC12209	Nathan Pieplow
Charadrius montanus	XC19091	Andrew Spencer
Charadrius nivosus	XC286696	Paul Marvin
Charadrius nivosus	XC286814	Paul Marvin
Charadrius vociferus	XC601503	Christopher McPherson
Charadrius vociferus	XC754226	Manuel Grosselet
Charadrius wilsonia	XC551094	Isain Contreras Rodríguez
Charadrius wilsonia	XC574004	Manuel Grosselet
Chloroceryle americana	XC48818	Bernabe Lopez-Lanus

Nyctidromus albicollis	XC743970	Jayrson Araujo De Oliveira
Oporornis agilis	XC475279	Scott Gravette
Oporornis agilis	XC480915	Matt Wistrand
Oreortyx pictus	XC226935	Peter Boesman
Oreortyx pictus	XC715988	Paul Marvin
Oxyura jamaicensis	XC591763	Simon Elliott
Oxyura jamaicensis	XC591765	Simon Elliott
Parabuteo unicinctus	XC1325	Robin Carter
Parabuteo unicinctus	XC755250	Patricio Mena Valenzuela
Parkesia motacilla	XC601743	Christopher McPherson
Parkesia motacilla	XC691611	Christopher McPherson
Parkesia noveboracensis	XC477981	Stanislas Wroza
Parkesia noveboracensis	XC752973	Sunny Tseng
Passer domesticus	XC846053	Thierry THOMAS
Passer domesticus	XC861200	Jorge Leitão
Passer montanus	XC655734	Samuel Jones
Passer montanus	XC717520	Bobby Wilcox
Passerella iliaca	XC557052	Ron Overholtz
Passerella iliaca	XC562461	Steve Hampton
Patagioenas fasciata	XC491894	Paul Marvin
Patagioenas fasciata	XC491896	Paul Marvin
Patagioenas flavirostris	XC499731	Richard E. Webster
Patagioenas flavirostris	XC538453	Alain Malengreau
Patagioenas leucocephala	XC101349	Andrew Spencer
Patagioenas leucocephala	XC145947	Paul Marvin
Pavo cristatus	XC124017	pradnyavant mane
Pavo cristatus	XC812476	Francesco Barberini
Perdix perdix	XC591894	Simon Elliott
Perdix perdix	XC651353	Uku Paal
Perisoreus canadensis	XC149242	Andrew Spencer
Perisoreus canadensis	XC269086	Davyd Betchkal
Petrochelidon fulva	XC34141	Andrew Spencer
Peucaea aestivalis	XC567386	John A. Middleton Jr.
Peucaea aestivalis	XC712864	Brian Henderson
Peucaea botterii	XC330308	Matt Baumann
Phalaenoptilus nuttallii	XC317328	Lance A. M. Benner
Phalaenoptilus nuttallii	XC490763	Lauren Harter
Phalaropus tricolor	XC294469	Paul Marvin
Phalaropus tricolor	XC836128	Aluisio Ribeiro
Phasianus colchicus	XC744152	brickegickel
Phasianus colchicus	XC799489	Regina Eidner
Picoides arcticus	XC210775	Paul Marvin
Picoides arcticus	XC482563	Bruce Lagerquist
Picoides arcticus	XC663765	Whitney Neufeld-Kaiser
Picoides arcticus	XC78676	Andrew Spencer
Picoides dorsalis	XC102874	Andrew Spencer
Picoides dorsalis	XC102878	Andrew Spencer
Picoides dorsalis	XC362021	Frank Lambert
Picoides dorsalis	XC613386	Doug Hynes
Pinicola enucleator	XC267728	Davyd Betchkal
Pinicola enucleator	XC30902	Allen T. Chartier
Pinicola enucleator	XC369903	Eric DeFonso
Pinicola enucleator	XC424093	Terje Kolaas
Piranga flava	ML24627381	Paul Marvin
Piranga flava	ML66835	William W. H. Gunn
Piranga flava	ML87917	Curtis Marantz
Piranga flava	XC657353	Leonardo Guzman Hernandez
Piranga rubra	XC558096	Ron Overholtz
Piranga rubra	XC650747	John A. Middleton Jr.
Piranga rubra	XC718200	Bobby Wilcox
Pitangus sulphuratus	XC575562	Okamoto Keita Sin
Pitangus sulphuratus	XC688651	Alán Palacios
Pitangus sulphuratus	XC831882	Christiana Fattorelli
Pitangus sulphuratus	XC839479	Bernard Bousquet
Platalea ajaja	XC173889	Paul Marvin
Platalea ajaja	XC451725	Paul Marvin
Plegadis chihi	XC751188	Franco Vushurovich
Plegadis chihi	XC754985	Guillermo Treboux
Plegadis falcinellus	XC314909	Marco Dragonetti
Plegadis falcinellus	XC530553	Jordi Calvet
Podiceps auritus	XC715920	Alan Dalton
Podiceps auritus	XC725086	Elias A. Ryberg
Podiceps grisegena	XC601774	Peter Ward and Ken Hall
Podiceps grisegena	XC804823	Uku Paal
Podiceps nigricollis	XC590654	Simon Elliott
Podiceps nigricollis	XC601775	Peter Ward and Ken Hall
Podilymbus podiceps	XC459166	Paul Marvin
Podilymbus podiceps	XC629177	Paul Marvin
Podilymbus podiceps	XC698503	Manuel Grosselet
Podilymbus podiceps	XC770459	Richard E. Webster
Poecile sclateri	XC619624	Richard E. Webster
Polioptila caerulea	XC331772	Andrew Spencer
Polioptila caerulea	XC392842	Manuel Grosselet
Porphyrio martinica	XC109039	Andrew Spencer
Porphyrio martinica	XC147540	Robson Silva e Silva
Porzana carolina	XC477043	David Darrell-Lambert
Porzana carolina	XC656414	Bruce Lagerquist
Progne subis	XC649107	Paul Marvin
Progne subis	XC675811	Scott Olmstead
Psiloscops flammeolus	XC13605	Andrew Spencer
Psiloscops flammeolus	XC182640	Tim Avery
Psittacara holochlorus	XC277745	Paul Marvin
Psittacara holochlorus	XC900949	David Tattersley
Psittacara mitratus	XC139485	Dan Lane

Chloroceryle americana	XC516956	Jacob Wijpkema
Chondestes grammacus	XC423752	Ted Floyd
Chordeiles acutipennis	XC109163	Paul Marvin
Chordeiles acutipennis	XC574270	Paul Marvin
Chordeiles acutipennis	XC582142	Paul Marvin
Chordeiles gundlachii	XC331763	Andrew Spencer
Chordeiles gundlachii	XC331765	Andrew Spencer
Chordeiles minor	XC333896	James Bradley
Chordeiles minor	XC660470	Bobby Wilcox
Circus hudsonius	XC550984	Sue Riffe
Circus hudsonius	XC815811	Valerie Heemstra
Cistothorus palustris	XC722670	Barry Edmonston
Cistothorus stellaris	XC659292	Paul Driver
Cistothorus stellaris	XC659293	Paul Driver
Cistothorus stellaris	XC685644	Meena Haribal
Cistothorus stellaris	XC815807	Valerie Heemstra
Clangula hyemalis	XC106033	Ryan P. O'Donnell
Clangula hyemalis	XC203477	Andrew Spencer
Clangula hyemalis	XC323088	Peter Boesman
Clangula hyemalis	XC514046	Timo Janhonen
Coccyzus americanus	XC100137	Mike Nelson
Coccyzus americanus	XC20962	Andrew Spencer
Coccyzus erythropthalmus	XC16526	Don Jones
Coccyzus erythropthalmus	XC16526	Don Jones
Coccyzus minor	XC265330	Andrew Spencer
Coccyzus minor	XC590889	Simon Elliott
Colaptes auratus	XC645833	Ted Floyd
Colaptes auratus	XC777433	Valerie Heemstra
Colaptes chrysoides	XC48160	Scott Olmstead
Colaptes chrysoides	XC622425	Scott Crabtree
Colinus virginianus	XC630289	Lawrence F Gardella
Colinus virginianus	XC703725	Antonio Xeira
Columba livia	XC726245	Olivier SWIFT
Columba livia	XC726245	Olivier SWIFT
Columbina inca	XC268189	Richard E. Webster
Columbina inca	XC623956	Manuel Grosselet
Columbina passerina	XC492787	Isain Contreras Rodríguez
Columbina passerina	XC693441	Peter Boesman
Coragyps atratus	XC451477	Paul Marvin
Coragyps atratus	XC456651	David Monroy Rengifo
Corvus brachyrhynchos	XC462767	Yaugen Slizh
Corvus brachyrhynchos	XC475165	Thomas Magarian
Corvus corax	XC806240	Bobby Wilcox
Corvus corax	XC807044	Ed Pandolfino
Corvus cryptoleucus	XC456970	Paul Marvin
Corvus cryptoleucus	XC511416	Bobby Wilcox
Corvus ossifragus	XC264970	Ted Floyd
Corvus ossifragus	XC745328	William Whitehead
Coturnicops noveboracensis	XC103086	Andrew Spencer
Coturnicops noveboracensis	XC729035	Chris Butler
Crotophaga sulcirostris	XC327560	Manuel Grosselet
Crotophaga sulcirostris	XC623954	Manuel Grosselet
Cyanocitta cristata	XC555073	Lori Zabel
Cyanocitta cristata	XC721247	Thomas Ryder Payne
Cygnus buccinator	XC298756	Antonio Xeira
Cygnus buccinator	XC636462	Thomas Ryder Payne
Cygnus olor	XC48742	Ian Davies
Cygnus olor	XC604181	Calum Mckellar
Cygnus olor	XC728386	Simon Elliott
Cygnus olor	XC764113	Bodo Sonnenburg
Cynanthus latirostris	ML121949	Curtis Marantz
Cynanthus latirostris	XC432720	Lauren Harter
Cypseloides niger	XC677207	Richard E. Webster
Cypseloides niger	XC677210	Richard E. Webster
Cyrtonyx montezumae	XC3983	Nathan Pieplow
Cyrtonyx montezumae	XC492136	Diana Doyle
Dendragapus fuliginosus	ML2393	Harry G. Lumsden
Dendragapus fuliginosus	XC559001	Ron Overholtz
Dendragapus obscurus	XC33714	Daniel Lane
Dendragapus obscurus	XC470937	Bruce Lagerquist
Dendrocygna autumnalis	XC564970	Isain Contreras Rodríguez
Dendrocygna autumnalis	XC858089	Valerie Heemstra
Dendrocygna bicolor	XC147332	Paul Marvin
Dendrocygna bicolor	XC257267	John V. Moore
Dryobates nuttallii	XC161352	Paul Marvin
Dryobates nuttallii	XC349729	Paul Marvin
Dryobates nuttallii	XC408009	Frank Lambert
Dryobates nuttallii	XC703746	Paul Marvin
Dryobates pubescens	XC531280	Thomas Magarian
Dryobates pubescens	XC531292	Thomas Magarian
Dryobates pubescens	XC590054	William Whitehead
Dryobates pubescens	XC673147	Paul Marvin
Dryobates scalaris	XC505919	Russ Wigh
Dryobates scalaris	XC522002	Jarrod Swackhamer
Dryobates scalaris	XC540657	Isain Contreras Rodríguez
Dryobates scalaris	XC617962	Richard E. Webster
Dryocopus pileatus	XC157763	Paul Driver
Dryocopus pileatus	XC402958	Bruce Lagerquist
Dryocopus pileatus	XC566467	Matt Wistrand
Dryocopus pileatus	XC569933	Russ Wigh
Dumetella carolinensis	XC807482	Barry Edmonston
Dumetella carolinensis	XC814892	Richard E. Webster
Dumetella carolinensis	XC814895	Richard E. Webster
Dumetella carolinensis	XC818869	Bobby Wilcox
Egretta caerulea	XC395486	Paul Marvin

Psittacara mitratus	XC157990	Hans Matheve
Psittacara mitratus	XC272935	Peter Boesman
Psittacara mitratus	XC707076	Richard E. Webster
Psittacula krameri	XC267026	Andrew Spencer
Psittacula krameri	XC759751	Romuald Mikusek
Psittacula krameri	XC812115	Paul Driver
Psittacula krameri	XC845916	Jorge Leitão
Pycnonotus cafer	XC460292	Peter Boesman
Pycnonotus cafer	XC741596	Sathyan Meppayur
Pycnonotus jocosus	XC547563	Andrew Spencer
Pycnonotus jocosus	XC769568	Ding Li Yong
Pyrocephalus rubinus	XC176958	Cleberton D. Bianchini
Pyrocephalus rubinus	XC29069	Jason Beason
Pyrocephalus rubinus	XC46384	Bernabe Lopez-Lanus
Pyrocephalus rubinus	XC788742	Marcela Morales sánchez
Quiscalus quiscula	XC786564	Paul Driver
Rallus crepitans	XC77512	Daniel Lane
Rallus crepitans	XC77531	Daniel Lane
Rallus elegans	XC290118	J.R. Rigby
Rallus elegans	XC727691	Justin Lawson
Rallus limicola	XC621187	Scott Crabtree
Rallus limicola	XC698488	Manuel Grosselet
Rallus obsoletus	XC543029	Jarrod Swackhamer
Rallus obsoletus	XC649092	Scott Olmstead
Recurvirostra americana	XC554605	Thomas G. Graves
Recurvirostra americana	XC587206	Craig Robertson
Rhynchophanes mccownii	XC371731	Thomas Magarian
Rhynchophanes mccownii	XC371738	Thomas Magarian
Riparia riparia	XC484331	Sebastian Andrejeff
Riparia riparia	XC659405	Lars Edenius
Rostrhamus sociabilis	XC454164	Rosendo Manuel Fraga
Rostrhamus sociabilis	XC720696	Dante Buzzetti
Salpinctes obsoletus	XC620784	Manuel Grosselet
Scolopax minor	XC544586	Justin Watts
Scolopax minor	XC709861	Joseph Fell
Selasphorus calliope	XC188263	Andrew Spencer
Selasphorus calliope	XC188264	Andrew Spencer
Selasphorus platycercus	XC132917	Richard E. Webster
Selasphorus platycercus	XC463254	Paul Marvin
Selasphorus rufus	XC613904	Peter Ward and Ken Hall
Selasphorus rufus	XC76412	Andrew Spencer
Selasphorus sasin	XC691195	Paul Marvin
Selasphorus sasin	XC691197	Paul Marvin
Setophaga aestiva	XC371864	Paolo Matteucci
Setophaga aestiva	XC563515	Carlos Gonzalez
Setophaga discolor	XC691783	Christopher McPherson
Setophaga graciae	XC477833	Bobby Wilcox
Setophaga graciae	XC700830	Richard E. Webster
Setophaga kirtlandii	XC419385	Sue Riffe
Setophaga kirtlandii	XC419387	Sue Riffe
Setophaga palmarum	XC189607	Richard E. Webster
Setophaga palmarum	XC653737	Matt Wistrand
Setophaga pensylvanica	XC600741	Christopher McPherson
Setophaga pensylvanica	XC814843	Denis Provencher
Sialia mexicana	XC71747	Richard E Webster
Sialia sialis	XC408997	Frank Lambert
Sialia sialis	XC601011	Christopher McPherson
Sialia sialis	XC712412	Patrick J. Blake
Sitta carolinensis	XC337748	Ted Floyd
Sitta carolinensis	XC371116	Lance A. M. Benner
Spatula clypeata	XC501879	Olivier SWIFT
Spatula clypeata	XC644498	Jarek Matusiak
Spatula cyanoptera	XC22389	Israel Aragon
Spatula cyanoptera	XC877014	Skyler Bol
Spatula discors	XC162091	Paul Marvin
Spatula discors	XC218547	Peter Boesman
Sphyrapicus nuchalis	XC326115	Bruce Lagerquist
Sphyrapicus nuchalis	XC354612	Thomas Magarian
Sphyrapicus nuchalis	XC354612	Thomas Magarian
Sphyrapicus nuchalis	XC663246	Richard E. Webster
Sphyrapicus ruber	XC363352	Kristie Nelson
Sphyrapicus ruber	XC36976	Tayler Brooks
Sphyrapicus ruber	XC408661	Frank Lambert
Sphyrapicus ruber	XC76213	Andrew Spencer
Sphyrapicus thyroideus	XC13889	Andrew Spencer
Sphyrapicus thyroideus	XC370020	Lance A. M. Benner
Sphyrapicus thyroideus	XC539025	Bruce Lagerquist
Sphyrapicus thyroideus	XC663254	Richard E. Webster
Sphyrapicus varius	XC21100	Andrew Spencer
Sphyrapicus varius	XC325526	Ross Gallardy
Sphyrapicus varius	XC388169	Martin St-Michel
Sphyrapicus varius	XC612652	Peter Ward and Ken Hall
Spilopelia chinensis	XC875469	Ray Tsu
Spilopelia chinensis	XC879489	Geoff Carey
Spinus lawrencei	XC315415	Lance A. M. Benner
Spinus lawrencei	XC483003	Lance A. M. Benner
Spinus pinus	XC205802	Eric DeFonso
Spinus pinus	XC544062	Steve Hampton
Spinus pinus	XC574657	Richard E. Webster
Spinus psaltria	XC144120	Lauren Harter
Spinus psaltria	XC624542	Richard E. Webster
Spinus tristis	XC636512	Thomas Ryder Payne
Spinus tristis	XC723797	Jim Berry
Spinus tristis	XC756999	Robert Benson
Spizella pusilla	XC807577	David A. Brinkman

Egretta caerulea	XC451872	Paul Marvin
Egretta rufescens	XC130845	Andrew Spencer
Egretta rufescens	XC452975	Paul Marvin
Egretta thula	XC481927	Paul Marvin
Egretta thula	XC654328	Dante Buzzetti
Egretta tricolor	XC102894	Andrew Spencer
Egretta tricolor	XC519779	Isain Contreras Rodríguez
Elanoides forficatus	XC405767	Paul Marvin
Elanoides forficatus	XC531920	John A. Middleton Jr.
Elanus leucurus	XC565245	Steve Hampton
Elanus leucurus	XC584969	Paul Marvin
Empidonax fulvifrons	XC160996	Paul Marvin
Empidonax fulvifrons	XC315746	Nancy Hetrick
Eudocimus albus	XC163177	Paul Marvin
Eudocimus albus	XC829401	PT xiao
Eugenes fulgens	XC744810	Manuel Grosselet
Eugenes fulgens	XC747195	Manuel Grosselet
Falco columbarius	XC587990	Simon Elliott
Falco columbarius	XC731075	Lars Edenius
Falco mexicanus	XC109297	Nathan Pieplow
Falco mexicanus	XC386260	Thomas Magarian
Falco peregrinus	XC408644	Frank Lambert
Falco peregrinus	XC545881	Thomas Magarian
Falco sparverius	XC565033	Thomas G. Graves
Falco sparverius	XC603740	Peter Ward and Ken Hall
Fulica americana	XC509714	Sunny Tseng
Fulica americana	XC546224	Richard E. Webster
Gallinago delicata	XC342368	Tero Linjama
Gallinula galeata	XC460760	Paul Marvin
Gallinula galeata	XC493683	Paul Marvin
Gallus gallus	XC689265	Ding Li Yong
Gallus gallus	XC773338	Jelle Scharringa
Geococcyx californianus	XC163982	Paul Marvin
Geococcyx californianus	XC254893	Richard E. Webster
Geococcyx californianus	XC534824	Caleb Helsel
Geococcyx californianus	XC610997	Richard E. Webster
Geranoaetus albicaudatus	XC374799	Mary Beth Stowe
Geranoaetus albicaudatus	XC385597	Albert Lastukhin
Glaucidium gnoma	XC202603	Lance A. M. Benner
Glaucidium gnoma	XC646754	Alberto Lobato
Grus americana	XC38536	Bill Evans
Grus americana	XC533637	Sue Riffe
Gymnogyps californianus	ML163901	Vincent Gerwe
Gymnorhinus cyanocephalus	XC215463	Kristie Nelson
Gymnorhinus cyanocephalus	XC362423	Frank Lambert
Haematopus bachmani	XC282104	Paul Marvin
Haematopus bachmani	XC282178	Paul Marvin
Haematopus palliatus	XC571864	Manuel Grosselet
Haematopus palliatus	XC572455	Isain Contreras Rodríguez
Haemorhous mexicanus	XC691598	Christopher McPherson
Haemorhous mexicanus	XC720339	Thomas Ryder Payne
Haemorhous mexicanus	XC814493	Valerie Heemstra
Haliaeetus leucocephalus	XC636910	Beverly Hallberg
Haliaeetus leucocephalus	XC703906	Steve Hampton
Haliaeetus leucocephalus	XC769877	Russ Wigh
Haliaeetus leucocephalus	XC779509	Steve Hampton
Helmitheros vermivorum	XC730179	Jorge de Leon Cardozo & Susan Hochgraf
Hesperiphona vespertina	XC153406	Andrew Spencer
Hesperiphona vespertina	XC555496	Ron Overholtz
Himantopus mexicanus	XC587207	Craig Robertson

Streptopelia decaocto	XC760695	Pere Josa
Streptopelia decaocto	XC783411	Jorge Leitão
Strix nebulosa	XC655482	Lars Edenius
Strix nebulosa	XC884395	Ulf Elman
Strix occidentalis	ML274753161	Andrew Spencer
Strix varia	XC727743	Barry Edmonston
Strix varia	XC801126	Anthony Gliozzo
Sturnus vulgaris	XC197289	Paul Marvin
Sturnus vulgaris	XC233940	Albert Lastukhin & Max lastukhin
Sturnus vulgaris	XC361481	Thomas Magarian
Sturnus vulgaris	XC452776	Paul Marvin
Surnia ulula	XC793932	Teet Sirotkin
Surnia ulula	XC862737	Stein Ø. Nilsen
Tachybaptus dominicus	XC627755	Manuel Grosselet
Tachybaptus dominicus	XC661638	Manuel Grosselet
Tachybaptus dominicus	XC704344	Jayrson Araujo De Oliveira
Tachybaptus dominicus	XC800134	Manuel Grosselet
Tetraogallus himalayensis	XC813673	Peter Boesman
Tetraogallus himalayensis	XC813675	Peter Boesman
Toxostoma bendirei	XC408176	Frank Lambert
Toxostoma bendirei	XC409670	Frank Lambert
Toxostoma redivivum	XC320588	Lance A. M. Benner
Toxostoma redivivum	XC444656	Lance A. M. Benner
Toxostoma redivivum	XC444658	Lance A. M. Benner
Toxostoma redivivum	XC806203	Bobby Wilcox
Tringa melanoleuca	XC236716	Iain
Tringa melanoleuca	XC606570	Peter Ward and Ken Hall
Tringa semipalmata	XC564233	Sue Riffe
Tringa semipalmata	XC635271	Paul Marvin
Tringa semipalmata	XC651135	Paul Driver
Tringa semipalmata	XC723894	Molly Jacobson
Tringa solitaria	XC211215	Davyd Betchkal
Tringa solitaria	XC445577	Laura Stewart
Troglodytes hiemalis	XC814613	Christian Kerihuel
Tympanuchus cupido	XC469168	Ross Gallardy
Tympanuchus cupido	XC469173	Ross Gallardy
Tympanuchus cupido	XC685651	Meena Haribal
Tympanuchus cupido	XC77187	Andrew Spencer
Tympanuchus pallidicinctus	XC33958	Andrew Spencer
Tympanuchus pallidicinctus	XC33960	Andrew Spencer
Tympanuchus pallidicinctus	XC33961	Andrew Spencer
Tympanuchus pallidicinctus	XC33962	Andrew Spencer
Tympanuchus phasianellus	XC362541	Frank Lambert
Tympanuchus phasianellus	XC362548	Frank Lambert
Tympanuchus phasianellus	XC557275	Paul Dickinsn
Tympanuchus phasianellus	XC77227	Andrew Spencer
Tyrannus dominicensis	XC357038	Paul Driver
Tyrannus dominicensis	XC591013	Simon Elliott
Tyrannus forficatus	XC323788	Terry Davis
Vireo bellii	XC661431	Richard E. Webster
Vireo flavifrons	XC501230	Jacob Saucier
Vireo griseus	XC452765	Paul Marvin
Vireo griseus	XC684345	Brad Banner
Vireo griseus	XC714441	Bruce Lagerquist
Vireo griseus	XC742516	Robert Benson
Zenaida asiatica	XC782417	Manuel Grosselet
Zenaida asiatica	XC785642	Sue Riffe
Zenaida macroura	XC613539	Peter Ward and Ken Hall
Zenaida macroura	XC696289	Manuel Grosselet

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	Lombary 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
Poland	Polish Society for the Protection of Birds (OTOP) and Museum and Institute of Zoology, Polish Academy of Sciences	Tomasz Chodkiewicz
Spain	Sociedad Española de Ornitologia (SEO/BirdLife)	Virginia Escandell
Spain	Sociedad Española de Ornitologia (SEO/BirdLife)	Juan Carlos del Moral
Spain-Catalonia	Institut Catala d'Ornitologia	Sergi Herrando
Spain-Catalonia	Institut Catala d'Ornitologia	Marc Anton
Sweden	Lund University, Department of Biology	Åke Lindström
Switzerland	Schweizerische Vogelwarte Sempach - Swiss Ornithological Institute	Hans Schmid
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 $\Delta_{syntopy}$ 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**	***

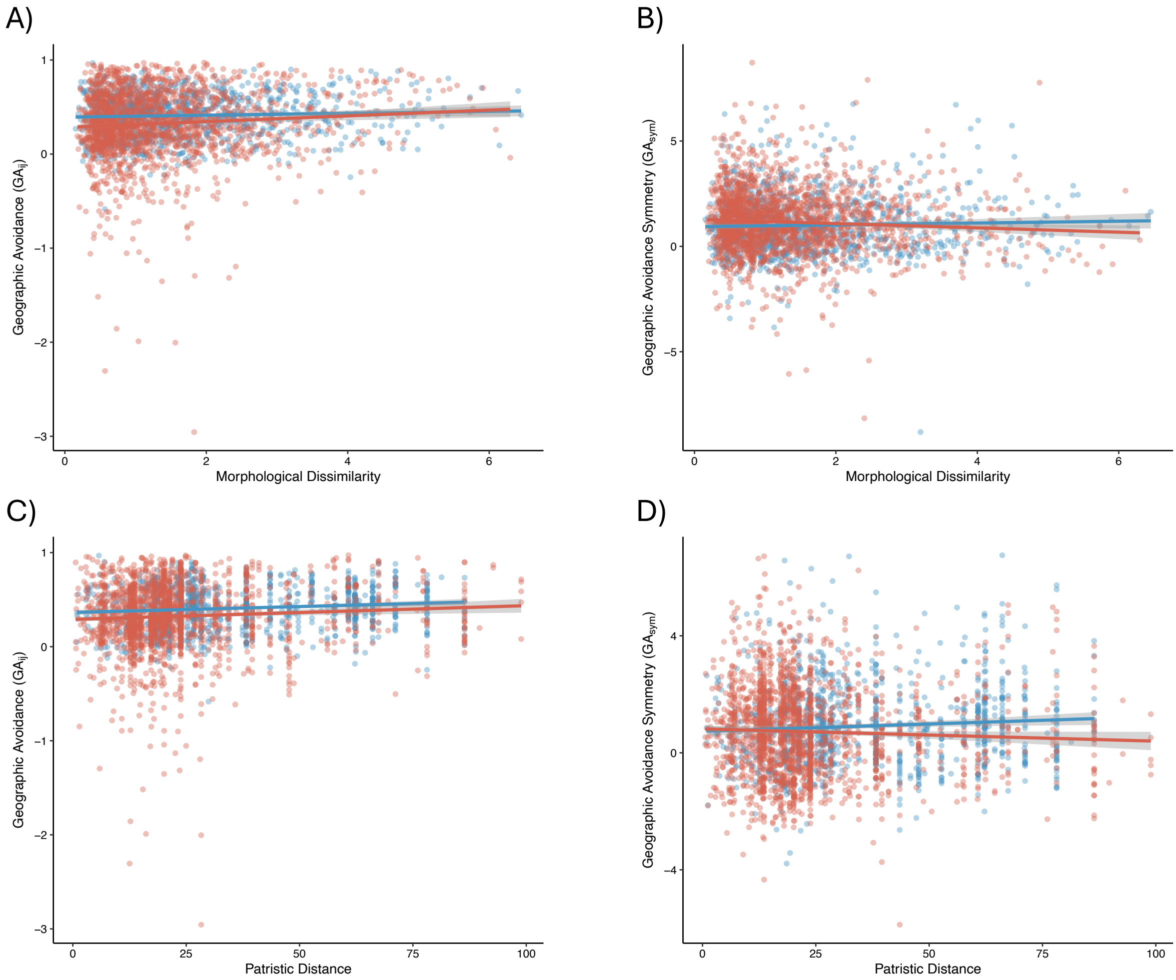
Significance codes: <0.05 *, <0.01 **, <0.001 ***

Predictors of $\Delta_{syntopy}$ 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).

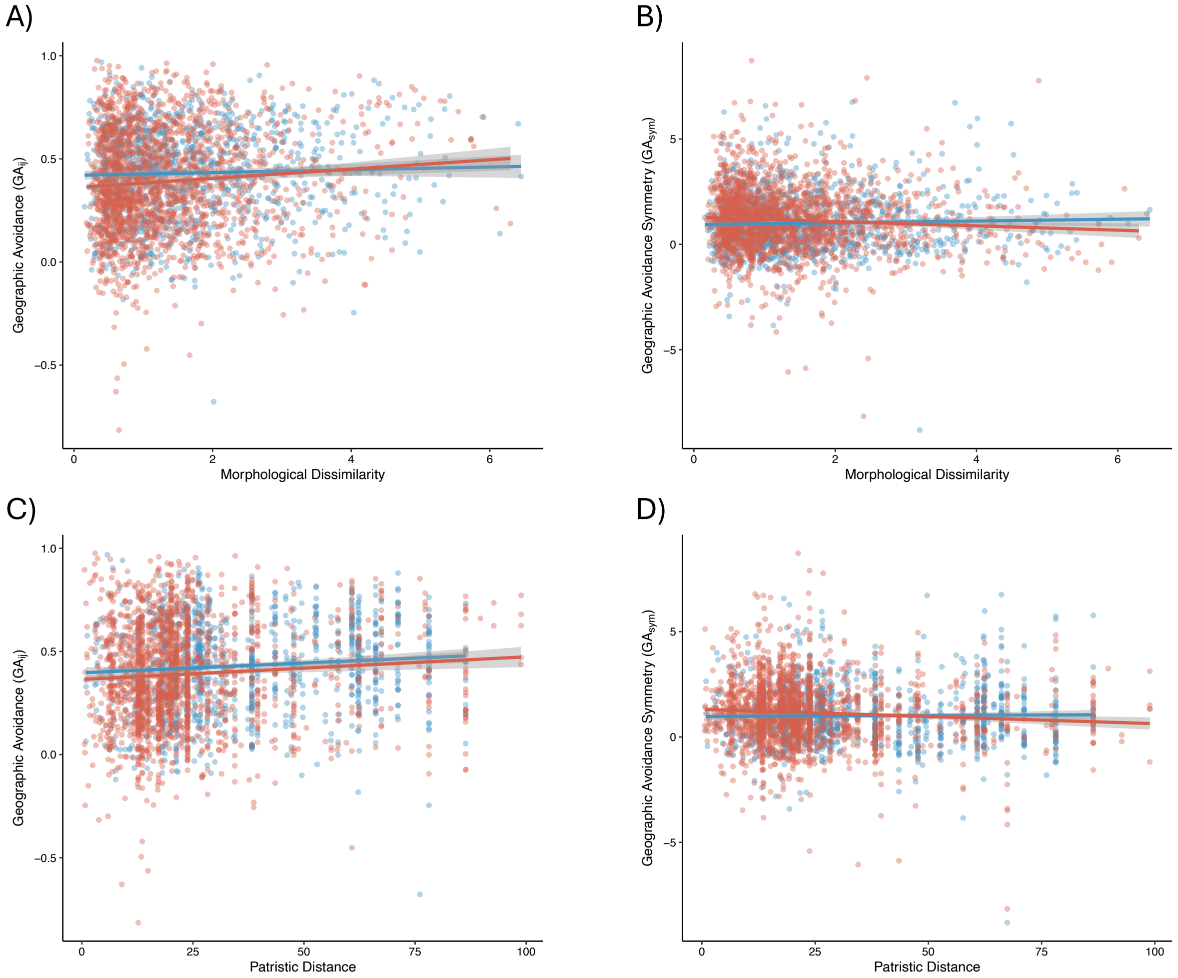
	Median	95% CI		pMCMC	
Intercept	**-2.196**	**-3.356**	**-1.238**	**<0.0005**	***
Interspecifically territorial	**0.329**	**0.088**	**0.567**	**0.007**	**
Hybridising	-0.037	-0.290	0.212	0.802	
Intraspecific territoriality 4	**2.036**	**1.136**	**3.042**	**<0.0005**	***
Intraspecific territoriality 5	**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



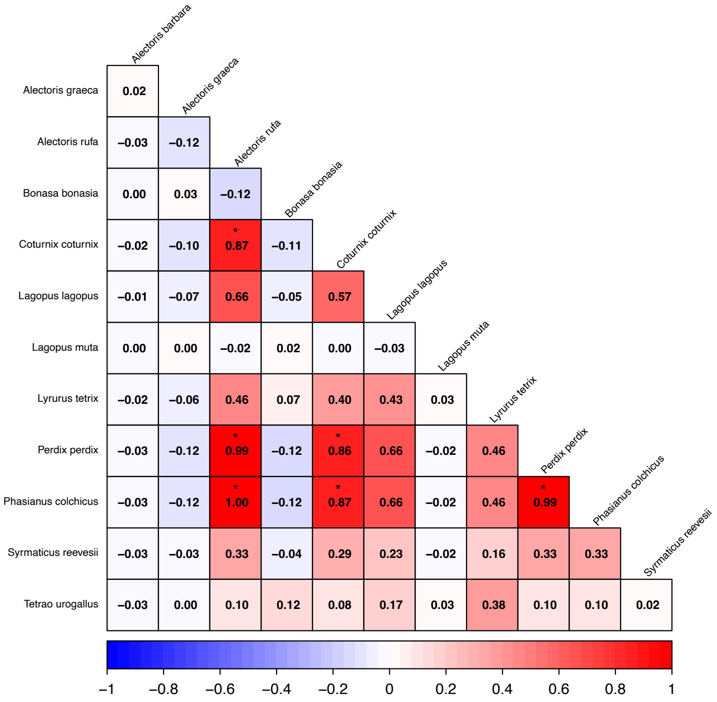
The effect of morphological dissimilarity (A, B) and patristic distance on Geographic Avoidance (GA_{ij}) (A, C) and GA_{ij} symmetry (GA_{sym}) (B, D). Lines and points are coloured by continent. Blue: Eurasia, Red: North America. Data from long clip.



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.

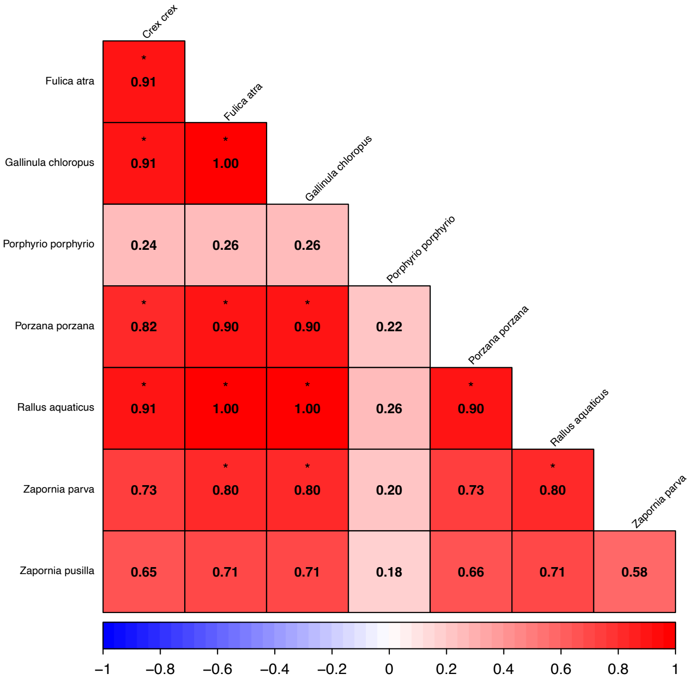
APPENDIX D: Chapter 6

Phasianidae



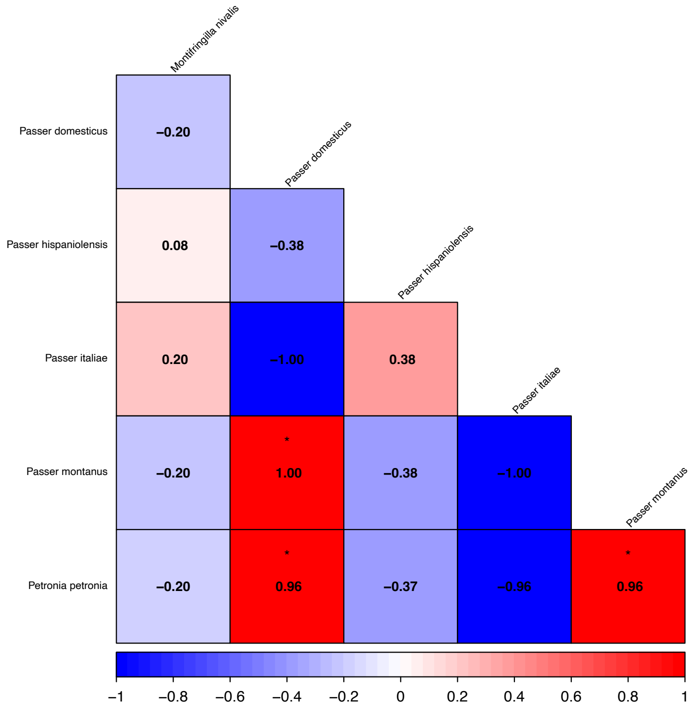
	Alectoris barbara	Alectoris graeca	Alectoris rufa	Bonasa bonasia	Coturnix coturnix	Lagopus lagopus	Lagopus muta	Lyrurus tetrix	Perdix perdix	Phasianus colchicus	Syrmaticus reevesii
Alectoris graeca	0.02										
Alectoris rufa	−0.03	−0.12									
Bonasa bonasia	0.00	0.03	−0.12								
Coturnix coturnix	−0.02	−0.10	* 0.87	−0.11							
Lagopus lagopus	−0.01	−0.07	0.66	−0.05	0.57						
Lagopus muta	0.00	0.00	−0.02	0.02	0.00	−0.03					
Lyrurus tetrix	−0.02	−0.06	0.46	0.07	0.40	0.43	0.03				
Perdix perdix	−0.03	−0.12	* 0.99	−0.12	* 0.86	0.66	−0.02	0.46			
Phasianus colchicus	−0.03	−0.12	* 1.00	−0.12	* 0.87	0.66	−0.02	0.46	* 0.99		
Syrmaticus reevesii	−0.03	−0.03	0.33	−0.04	0.29	0.23	−0.02	0.16	0.33	0.33	
Tetrao urogallus	−0.03	0.00	0.10	0.12	0.08	0.17	0.03	0.38	0.10	0.10	0.02

Rallidae

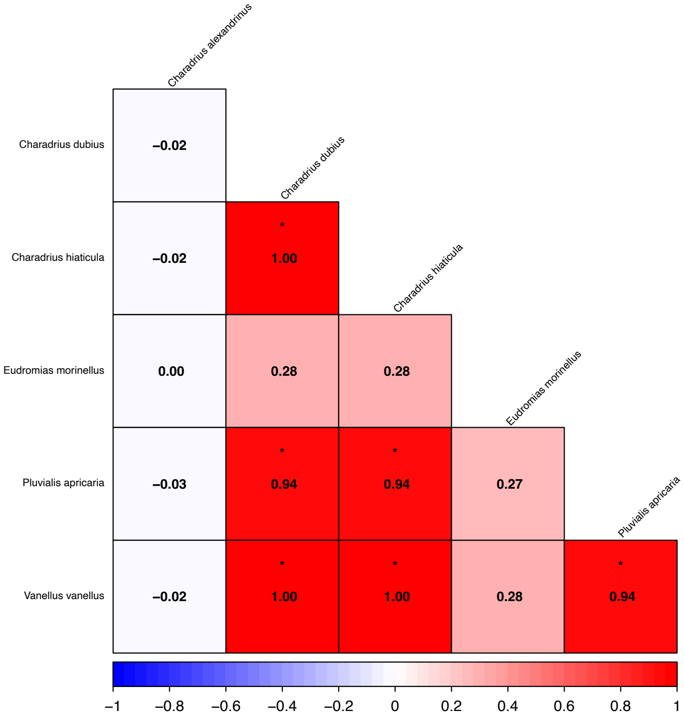


	Crex crex	Fulica atra	Gallinula chloropus	Porphyrio porphyrio	Porzana porzana	Rallus aquaticus	Zapornia parva
Fulica atra	* 0.91						
Gallinula chloropus	* 0.91	* 1.00					
Porphyrio porphyrio	0.24	0.26	0.26				
Porzana porzana	* 0.82	* 0.90	* 0.90	0.22			
Rallus aquaticus	* 0.91	* 1.00	* 1.00	0.26	* 0.90		
Zapornia parva	0.73	* 0.80	* 0.80	0.20	0.73	* 0.80	
Zapornia pusilla	0.65	0.71	0.71	0.18	0.66	0.71	0.58

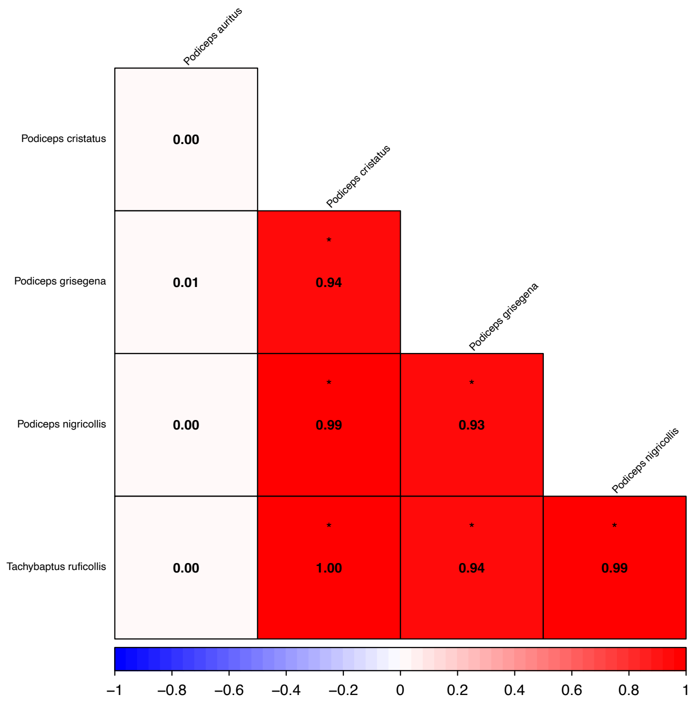
Passeridae



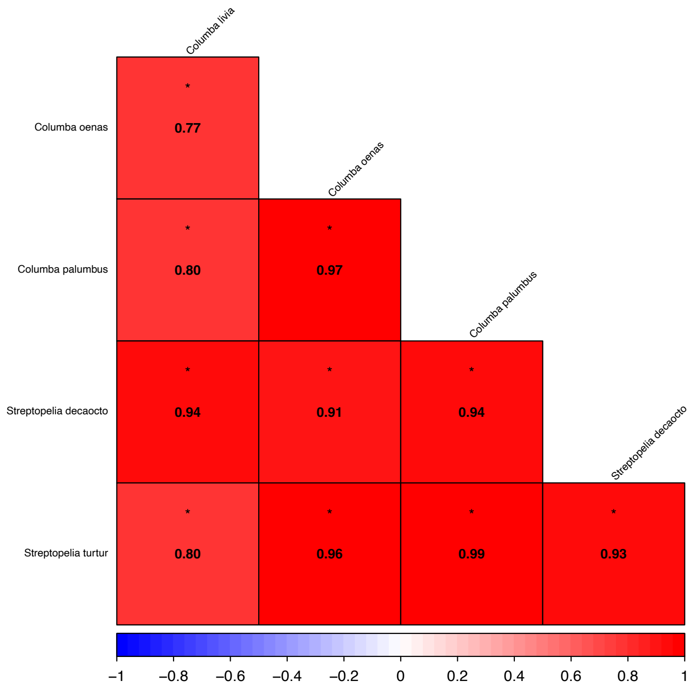
Charadriidae



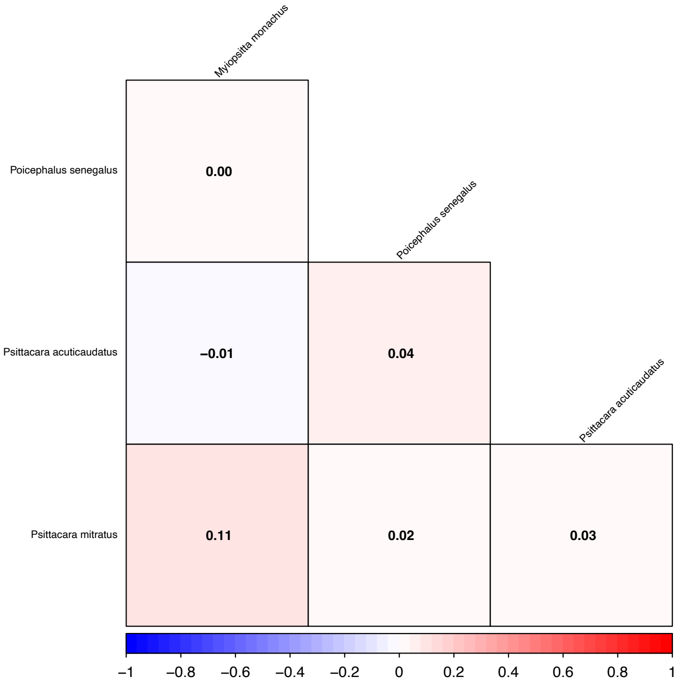
Podicipedidae



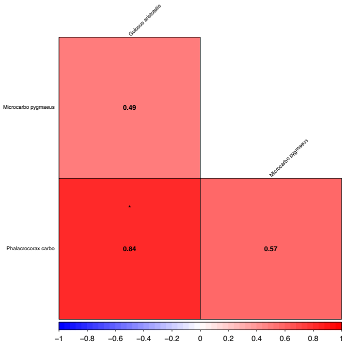
Columbidae



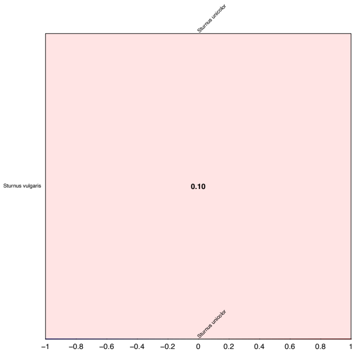
Psittacidae



Phalacrocoracidae

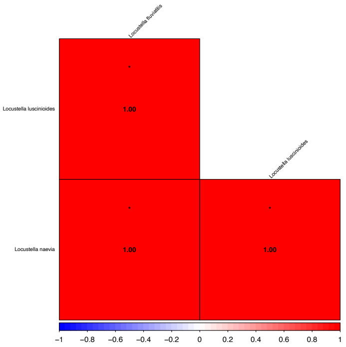


Sturnidae

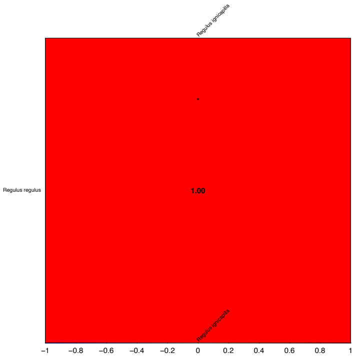


Recurvirostridae

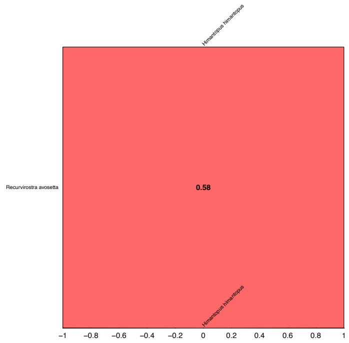
Locustellidae

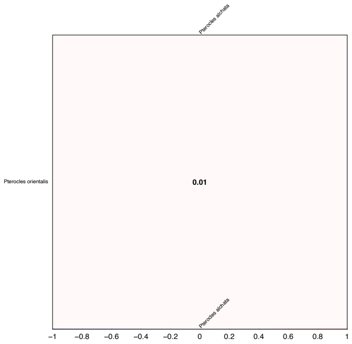


Regulidae



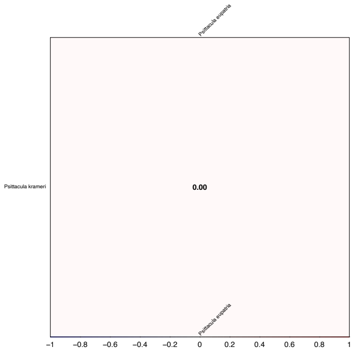
Pteroclidae

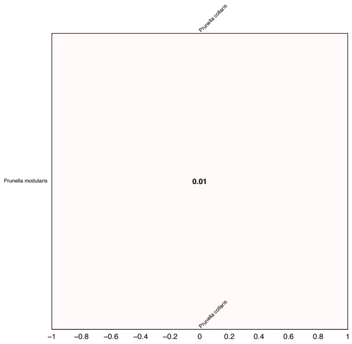




Psittaculidae

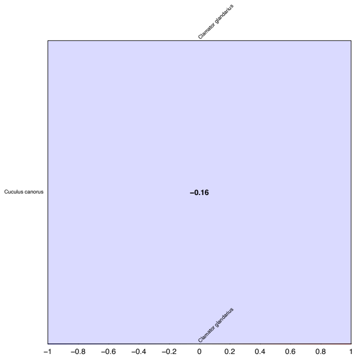
Prunellidae

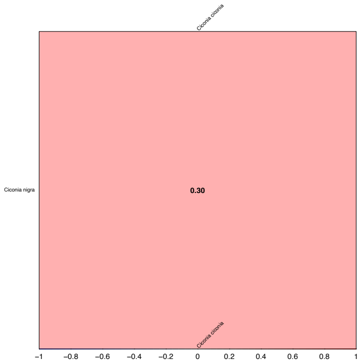




Cuculidae

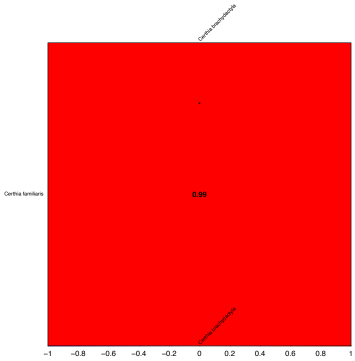
Ciconiidae

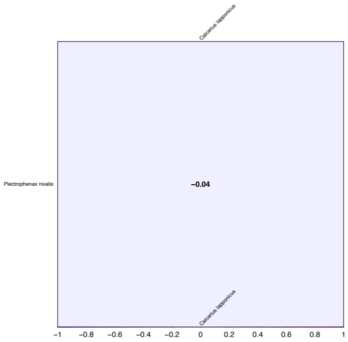




Certhiidae

Calcariidae





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. 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.