The Role of Social and Ecological Processes on Phenotypic Evolution in Birds

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ABSTRACT

The broad concept of "biodiversity" can be roughly separated into two related components: trait diversity and species richness. Despite the fact that one or both of these types of biodiversity underlie much of ecology, evolution, and conservation, however, it remains largely unknown how traits and speciation dynamics can interact, particularly at a large scale. My thesis uses modern phylogenetic comparative methods and a new global database of avian morphological traits to quantify and predict the drivers of biodiversity across the world's birds, focusing particularly on the relative roles of ecological and social traits to understanding broad evolutionary patterns.

In Chapter 2 I present a survey of avian functional traits, focusing on eight measurements of the beaks, wings, tails, and tarsi of 42,334 individuals representing 10,023 extant and recently extinct species. The global trait distribution of avian communities is consistent with a competition-based model of community assembly, and I find no evidence of environmental filtering at the biome level. The traits exhibited within avian orders tend to become more dissimilar as species richness increases, with the notable exception of the *Passeriformes*, an order containing around 60% of the total avian species richness but occupying a region of morphospace expected of a clade two orders of magnitude smaller. The *Passeriformes* also possess remarkable vocal morphology and behavior, and thus I spend the next three chapters of this thesis focused on the role of social processes in avian evolution.

In Chapter 3, I use detailed morphological and vocal trait data from the suboscine family *Furnariidae* to demonstrate that social traits evolve faster and with less regularity than ecological traits. I then in Chapter 4 examine the social and ecological drivers of female song in birds, a widespread trait whose persistence challenges traditional sexual selection theory. I find that the separate drivers of male and female song can be explained by social selection theory, a framework which encompasses all social interactions above and beyond competition for mating opportunities. In Chapter 5 I apply this concept of social selection to macroevolutionary studies, using sex-specific song behaviors to separately investigate the roles of social and sexual selection on speciation and extinction rates. I demonstrate that lineages with male-only song (sexual selection) diversify faster than lineages with both male and female song (social selection). This result suggests that social selection theory may inform the controversial relationship between sexual selection and diversification.

Finally, in Chapter 6 I look at the role of dispersal in modulating these speciation and extinction rates. Using data from the wing morphologies of 26,043 individuals from 6,028 species, I test the "intermediate dispersal hypothesis," hitherto only examined at small scales, across the order *Passeriformes*, revealing that the highest rates of diversification are indeed found in lineages with an intermediate capacity for flight. When birds that defend year-round territories are considered separately from non-territorial birds, however, the intermediate dispersal hypothesis only holds for territorial birds, demonstrating the importance of considering the ecological context of traits in macroevolutionary studies.

Together, my results present evidence that both social and ecological processes facilitate the generation and maintenance of biodiversity in birds.

DECLARATION

The work presented in this thesis is my own, with the following acknowledgements:

The biometric data presented in chapter 2 were collected by many individuals, including myself (26%), Monte Neate-Clegg (11%), Nico Alioravainen (10%), Hannah MacGregor (9%), Claire Vincent (7%), Sam Jones (7%), Bianca Darski (4%), Tom Bregman (4%), Chris Trisos (3%), Nicolas Soulages (2%), Sarah Rosenberg-Wohl (2%), Phil Chapman (1%), Eden Cottee-Jones (1%), and Ben Daly (1%). The analyses in this chapter were designed with the help of Dr. Alex Pigot (University of Groningen) and Dr. Uri Roll (University of Oxford), the latter of whom provided the data on biome membership.

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CHAPTER 1: GENERAL INTRODUCTION.

Variation in life on Earth is distributed unevenly across both space and time. There are 6,000 species of passerines but just a single oilbird (del Hoyo 1992-2011); 1,200 species of bats and 2,000 species of rodents but only five species of monotremes (Nowak 1999); 2,000 species of cichlids (Kocher 2004) and an “inordinate” number of beetles (Raikow and Bledsoe 2000) but also thousands of monotypic taxa. There are many, many more species of plants and animals found in the tropics than in the temperates, across both marine and terrestrial environments (Tomašových et al. 2016, Cardillo, Orme and Owens 2005b, Wiens, Pyron and Moen 2011, Mittelbach et al. 2007). Some of these species distribution patterns are well-explained, such as Darwin’s finches in the Galapagos (Grant and Grant 2008), but most are not. Why are some taxa so species-rich? And why can so many species co-exist in certain places on earth?

Biodiversity is generally quantified in these terms of species richness, but there are also other metrics. A classic example of such a metric from community ecology are the terms “alpha diversity” and “beta diversity,” wherein the former measures local species richness and the latter measures the heterogeneity between communities (Whittaker 1972). In conservation, a reasonable goal for prioritization might be to conserve the greatest possible proportion of a clade’s phylogenetic history by considering a species’ “evolutionary distinctness” (Jetz et al. 2014). Thus, a monotypic species would have higher evolutionary distinctness than a group of closely-related species, and thus conserving the monotypic species and one of the closely-related species would maximize the amount of “biodiversity” preserved.

These metrics use the species boundary as a proxy for ecological differences, but these two concepts are not always perfectly linked. That is, phylogenetic history is not the only process determining a species' function in its environment (Pyron et al. 2015). The ability of fish to expand their ranges, for example, is not phylogenetically conserved (Comte, Murienne and Grenouillet 2014). Mammal niches are more closely related to species' environments than their evolutionary histories (Cooper, Freckleton and Jetz 2011). Sparrow bill size depends on the temperature of the wintering grounds (Danner and Greenberg 2015). When studying concepts such as ecosystem services (Daily and Matson 2008) or human cultural valuation of birds (Tidemann and Gosler 2010), it is important to directly measure the relevant characteristics of the organisms.

Biodiversity and functional traits

The word "trait" has many meanings, from Darwin's understanding of a trait as a proxy for organism performance (Darwin 1859) to uses in psychology, philosophy, and beyond. Over the past decade, however, the ecological community has coalesced on the term "functional trait" when describing aspects, attributes, or features of organisms. Violle et al. (2007) defined functional traits as "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction, and survival, the three components of individual performance." This has since been restated more succinctly as properties of an organism "considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties" (Díaz et al. 2013).

Functional traits allow the relationship between an organism and its environment to be explicitly quantified (Díaz and Cabido 2001). Thus, they can be used to predict the response of species to habitat loss (Newbold et al. 2014), measure a species niche (Winemiller et al. 2015, Violle and Jiang 2009), understand community assembly and species coexistence (Kraft, Godoy and Levine 2015, Adler et al. 2013, Laughlin et al. 2012, Barnagaud et al. 2014, McGill et al. 2006), study the latitude species gradient (Lamanna et al. 2014), or define ecosystem services (Díaz et al. 2004, Díaz et al. 2013), with important applications in fields such as biogeography (Violle et al. 2014) and conservation (Newbold et al. 2012, Laughlin 2014, Burivalova et al. 2015).

Studies of functional traits have been especially popular in plants, thanks to the availability of large datasets (which in turn exist due to the ease of collecting, storing, and digitizing plant specimens) (Kattge et al. 2011). For example, a recent survey of the wood density, leaf area, and maximum height of 3 million trees from 140,000 global locations has found clear trade-offs in traits between competition and growth, presenting evidence that intraspecific competition is more influential in determining these strategies than interspecific competition (Kunstler et al. 2016). Another study using the same database considered six traits from 46,085 vascular plant species and found similar trade-offs between leaf construction and overall plant growth (Díaz et al. 2016). That is, the occupation of plant trait space is strongly clumped, with different regions of space corresponding to different competitive strategies.

Avian functional traits

Global surveys of animal functional traits are rarer than those of plants, though many animal taxa would be appropriate for such an analysis. In particular, birds, class *Aves*, feathered egg-laying tetrapods descended from therapod dinosaurs (Gill 2006), are wellsuited for broad-scale comparative analyses. They are distributed globally and, at just over 10,000 species (del Hoyo 1992-2011), present a sample size large enough for detailed analyses but small enough to feasibly survey. In part due to human cultural fascination of birds, there is an tremendous amount of global avian scientific and ethnobiological knowledge, which in the past decade has been represented in an extensive survey of avian ecology and behavior (del Hoyo 1992-2011), a global phylogeny (Jetz et al. 2012), and a compilation of range maps (BirdLife International and NatureServe 2011), as well as many museums with vast numbers of specimens (Suarez and Tsutsui 2004) and countless field guides and scientific papers on all aspects of avian biology. Birds play an important role in the maintenance of healthy ecosystems, including functioning as seed dispersers (Jordano 1995), pollinators (Cruden 1972), and scavengers that consume dead animal material, including, in some cultures, humans (Acharya et al. 2009). According to the International Union for the Conservation of Nature “Red List,” over 13% of all bird species are threatened or endangered (IUCN 2015), a number that is likely to rise over the next century (Barnosky et al. 2011). In order to preserve these species and their ecological functions, it is necessary to quantify the role of a species in its environment and to understand what processes drive avian phenotypic evolution and maintain species boundaries.

These 10,000 species of birds comprise approximately one third of all extant tetrapods (IUCN 2015), but this species richness is distributed unevenly across taxa. Though there are around 37 orders of birds, a single order, *Passeriformes* (“passerines”), contains over 60% of the total avian species richness (del Hoyo 1992-2011). Passerines represent one of the youngest avian orders, and it is generally thought that the passerines originated in Australia (Barker et al. 2004), though their modern distribution spans all continents except

Antarctica. In particular, the passerine suborder *Tyranni* (the “suboscines”) in South America is in part responsible for the hyperdiverse avian communities on either side of the Andes (Derryberry et al. 2011). The passerines are traditionally diagnosed by the arrangement of their feet, with an enlarged hallux (single hind toe) and so-called “tendon passerine” that enables perching and is noteworthy for its “simplicity and economy of structure” (Raikow and Bledsoe 2000). It seems unlikely that foot morphology could be causally linked to an increased speciation rate (Raikow 1986), and although passerines tend to be small, a relationship between body size and lineage diversification (Cardillo et al. 2005a, Etienne et al. 2012b), which is itself controversial (Burbrink and Myers 2014, Owens, Bennett and Harvey 1999), would not explain why out of all the small-bodied birds only the passerines radiated.

Passerines do, however, have an additional noteworthy feature: complex vocal behavior. Most members of the suborder *Passeri* (“oscines”) have elaborate syrinxes (vocal organs, analogous to the human larynx), and many sing songs that are learned from conspecifics (Raikow and Bledsoe 2000). Avian song has many functions, including the classic sexually-selected roles of mate attraction and male-male competition (Catchpole and Slater 2008, Gill 2006). This suggests a potential link: could high levels of sexual selection be responsible for the disproportionate species richness found in the passerines?

Sexual selection and speciation

The extent to which sexual selection can accelerate the process of speciation is highly contentious. Darwin termed sexual selection as “the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction”

(Darwin 1871), which has since been simplified to "the evolution of traits associated with competition for mates" (Shuker 2010). In theory, the divergence of sexual traits between two populations, either stochastically or due to different signaling environments, should facilitate reproductive isolation upon secondary sympatry (West-Eberhard 1983, Doorn, Edelaar and Weissing 2009, Gage et al. 2002b, M'Gonigle et al. 2012). Lineages with high levels of sexual selection would thus require less time in allopatry before completing the speciation cycle (Grant and Grant 1997), resulting in higher species richness.

There certainly is evidence that high levels of sexual selection can drive speciation. A study of populations of the jumping spider *Habronattus pugillis* (from the family *Salticidae*, known for elaborate courtship displays) shows that selection on the genes controlling divergent male traits vastly exceeds rates of neutral evolution in mitochondrial genes (Masta and Maddison 2002). Guppy populations translocated to a low-predator environment evolved bright orange coloration within three generations, with corresponding rapid genetic divergence (Gordon et al. 2015); in another population of guppies, 20 generations in a low-predator environment with limited dispersal was long enough for sexually-selected color variation to present a reproductive barrier despite no evidence of ecological divergence (Labonne and Hendry 2010). In Amazonian frogs, *Physalaemus petersi*, population-level genetic introgression was inversely correlated with mating call divergence after controlling for inter-population geographic distance (Boul et al. 2007). In mormyrid fishes, traits related to the sexually-selected electrical communication system evolve much faster than ecological traits such as morphology or trophic ecology (Arnegard et al. 2010), and within passerine birds, intraspecific plumage dichromatism is correlated with interspecific plumage divergence (Seddon et al. 2013b). In addition to bouts of apparently arbitrary signal divergence, sexual traits can also rapidly evolve in response to differences in the ambient environment, such as selection for habitat-dependent acoustic properties in birds (Nemeth et al. 2013, Slabbekoorn and Smith 2002, Tobias et al. 2010, Wilkins, Seddon and Safran 2013) or for color contrasts under different light environments in fish (Fuller 2002, Seehausen et al. 2008, Boughman 2001).

A 2011 meta-analysis of comparative studies of sexual selection and speciation found a small but significant overall effect of sexual selection on diversification (Kraaijeveld, Kraaijeveld-Smit and Maan 2011). For example, levels of feather ornamentation in bird genera correlate with species richness (Moller and Cuervo 1998), and avian taxa with promiscuous mating systems are more species-rich (Mitra, Landel and Pruett-Jones 1996). Levels of plumage dichromatism and song complexity predicts clade species richness in antbirds (family *Thamnophilidae*), particularly when subspecies are considered (Seddon, Merrill and Tobias 2008), and it has even been suggested that the well-documented relationship between body size and diversification rate (Cardillo et al. 2005a, Etienne et al. 2012b) is better predicted by sexual selection in birds (Owens et al. 1999). On the other hand, genetic models of strong female-choice sexual selection suggest that strong mate preferences can facilitate gene flow and thus impede ecological divergence (Servedio and Bürger 2014). A survey of testes size, sexual size dimorphism, and sexual dichromatism across 1,031 species of birds found no correlation between clade-level sexual selection and species richness (Morrow, Pitcher and Arnqvist 2003). Sexual size dimorphism and testes size in 480 mammalian genera, size dimorphism and mating frequency in 105 butterfly genera, and size dimorphism in 148 spider genera all failed to correlate with species richness (Gage et al. 2002b). Furthermore, when the dispersal abilities of birds are explicitly controlled for, sexual dichromatism does not predict avian diversification rate (Huang and Rabosky 2014). Sexual selection apparently can affect speciation dynamics, but the extent to which is does remains unclear.

Some of this controversy can likely be attributed to shortcomings in the methodology. Studies that compare species richness across higher-order taxa such as genera or families assume that the entire clade experiences a single, constant level of sexual selection (Kraaijeveld et al. 2011, Ritchie 2007); this is rarely, if ever, true. Present levels of sexual selection and ornamentation may not reflect the state at time of speciation (Badyaev and Hill 2003, Wiens 2001, Price and Eaton 2014), and accurately estimating extinction rates is difficult without an extensive fossil record (Kraaijeveld et al. 2011). Other studies may rely on signals where human and species' perceptions may not be the same, such as discounting the UV spectrum when considering avian plumage (Dale et al. 2015). Furthermore, there is currently substantial criticism of popular methods for estimating shifts in speciation and extinction rates (Davis, Midford and Maddison 2013, Rabosky and Goldberg 2015), potentially invalidating previously-reported results.

It is also possible that sexual selection is not the best framework for considering the effect of social processes on macroevolutionary dynamics. Sexual selection is not a perfect theory. Elaborate secondary sexual characteristics that are apparently neutral or detrimental to an individual's survival are both common and adaptive in female animals, above and beyond sex-role reversal and genetic correlation (LeBas 2006, Tobias, Montgomerie and Lyon 2012b, Kraaijeveld and Komdeur 2007). When some species of birds come into contact, their songs become *more* similar, not less (Tobias et al. 2014, Tobias and Seddon 2009, Kirschel, Blumstein and Smith 2009). There are many sound reasons to preserve the current model of sexual selection and/or to expand it to fit modern empirical evidence (Clutton-Brock 2010, Hosken, Alonzo and Wedell 2016). There is, however, an alternative to sexual selection that has become increasingly popular in the recent literature: social selection.

Social selection

In 1983, West-Eberhard introduced the term “social selection” to mean “differential reproductive success…due to differential success in social competition, whatever the resource at stake” (West-Eberhard 1983), noting that many traits typically grouped under the vague term “mate recognition” were in fact used for social competition, over resources that were not obviously related to mating, such as parent-offspring conflict and interspecies competition. The signals used in these conflicts all display attributes similar to classically “sexual” traits and different attributes from ecological traits, such as exaggeration and rapid divergence; a sexual/non-sexual divide thus seemed empirically more artificial than a social/ecological distinction (West-Eberhard 1983).

This idea was largely ignored at the time, though in the mid-2000s there was a surge of criticism of sexual selection, including a 2006 *Nature* paper advocating game-theoretical approaches to mating and cooperative behavior (Roughgarden, Oishi and Akçay 2006). Of particular concern was the frequency, and apparent adaptive value, of ornamentation in females.

Ornaments can be defined as “any signal trait that is elaborated to such a degree that its cost is greater than required by efficacy,” but this is usually shortened to “any trait that can reasonably be said to be conspicuous” (both definitions from Kraaijeveld, Kraaijeveld-

Smit and Komdeur (2007)). In theory, ornaments can only be present in the sex favored by the operant sex ratio (OSR) and/or with fewer costs to reproduction (Andersson 1994). Aside from a small number of cases of sex role reversal (Price et al. 2008), this is generally the male. Background levels of female ornamentation are traditionally consigned to “genetic correlation” (Lande 1980), under the assumption that an ornament expressed in both sexes is an evolutionary compromise between the male’s higher optimum and the female’s lower optimum until genetic or epigenetic mutations arise allowing for differential expression of the trait (Kraaijeveld et al. 2007).

Though shared genetic architecture explains much of the correlation between male and female ornamentation (Dale et al. 2015, Bonduriansky and Chenoweth 2009), female ornamentation is in many cases adaptive. Female ornamentation is often gained secondarily (Wiens 2001, Irwin 1994, Burns 1998) and has been shown to serve many roles including resource defense, territory defense, mutual mate choice, pair bond maintenance, social dominance, and sexual mimicry (reviewed in Kraaijeveld et al. (2007) and Tobias et al. (2012b)). Sexual selection in its traditional form does not explain the phenomenon of mutual ornamentation, but all of the aforementioned functions of female ornaments do fall under the umbrella of social selection. It is now reasonably common to frame ornamentation in terms of social selection (Keen et al. 2016, McEntee et al. 2016, Dey et al. 2015, Webb et al. 2016), but the processes driving female ornamentation remain largely unknown (Dale et al. 2015, Bath et al. 2015).

Social selection theory can also be used to explain why some social signals converge rather than diverge upon secondary sympatric contact. Character displacement is traditionally framed in terms of “ecological character displacement,” where the traits of one or both closely-related species in a zone of sympatry diverge so as lessen interspecific competition (Brown and Wilson 1956, Grant and Grant 2006), as an alternative to competitive exclusion. "Reproductive character displacement," however, is also widely recognized, wherein traits used in mate recognition also diverge upon secondary sympatry so as to reinforce the species boundary and prevent hybridization (Grant and Grant 2010, Stre et al. 1997). There is, however, a third type of character displacement, termed "agonistic character displacement" (ACD) by Grether et al (2009). ACD is "the process of phenotypic evolution in a population caused by interference competition…which results in shifts in traits that affect the rate, intensity or outcome of interspecific aggression" (Grether et al. 2009). That is, ACD operates on competitive social interactions. Though Grether et al do not explicitly state this, ACD falls under the umbrella of social selection.

There are not many published examples of ACD, though it is a recently-defined concept; more examples are likely to be discovered as the idea increases in popularity and awareness. In addition to the 33 examples raised by Grether et al (2009), evidence for ACD includes wing coloration of damselflies (Drury and Grether 2014) and territorial displays in *Hypocnemis* antbirds (Tobias and Seddon 2009). The most prominent example comes from ovenbirds, family *Furnariidae,* in which species overlap predicts *convergence,* rather than divergence, in songs (Tobias et al. 2014). Sexual selection, in which ornaments are explained by competition for mates or mating opportunities, does not explain why social signals sometimes converge between closely-related species. Social selection, a broader view that encompasses fitness gained by any social competitive interactions regardless of the resource in dispute, does predict both the divergence of reproductive traits and either the convergence or the divergence of aggressive behaviors and ornaments. That is, if the benefit of an accurate signaling pathway (i.e., by successfully defending a territory from competitors) is outweighed by the cost of maintaining that signal, than those signals are likely to converge, even if the competitors are from members of another species.

Avian song as a social signal

Many definitions of avian "song" explicitly require complexity and/or functions in mate attraction or male-male competition (Read and Weary 1992, del Hoyo 1992-2011, Gill 2006), but the most basic definition, and the one used here, is simply as a long-range acoustic signal (Tobias et al. 2016). Though the oscine passerines (suborder *Passeri* in the order *Passeriformes*) are often called "songbirds" and are sometimes considered to be the only lineage to sing (Odom et al. 2014), that seems a needlessly limited criterion. First, plenty of non-avian creatures are said to sing, such as gibbons (Geissmann 1984), mice (Campbell et al. 2010), humpback whales (Noad et al. 2000), and bats (Boughman and Wilkinson 1998), not to mention humans. Second, vocal ornaments such as those found in hummingbirds (Ficken et al. 2000), barred owls (Odom and Mennill 2012), parrots (Pepperberg 1994), hoopoes (Martín-Vivaldi et al. 1999), and suboscine passerines (Kroodsma and Konishi 1991) fulfill nearly identical functions as those in the oscines. This definition of song does not include short, simple vocalizations commonly known as "calls," serving roles including contact calls, alarm calls, or begging calls (Logue and Hall 2014, Odom et al. 2014).

Song is an ideal ornament for comparative analyses. Unlike other behavioral signals, such as the pair-bond dances of estrildid finches (Soma and Garamszegi 2015) or the leks of manakins or birds of paradise (Endler and Thery 1996, Pruett-Jones and Pruett-Jones 1990), song is widespread across avian clades (Catchpole and Slater 2008). Furthermore, the auditory perception of humans is apparently similar to that of birds (Williams and Nottebohm 1985), which avoids problems presented by the UV spectrum when studying the other widespread social/sexual avian ornament, plumage coloration (Dale et al. 2015, Delhey and Peters 2008, Endler and Mielke 2005). Plumage coloration also has a strong ecological component, crypsis, and it can be difficult to determine if a given pattern functions as a social signal, as camouflage, or as both (Wallace 1889, Hill 2006). The presence and absence of song is also easily dichotomized into a binary variable, as it is presented in Chapters 4 and 5, allowing for clear standardization across many taxa and permitting analytical techniques that would be either too intensive or entirely impossible with more complicated types of data.

Ecological drivers of speciation and extinction

Sexual selection is, of course, not the only process that can affect diversification rates. The most obvious example, the latitude species gradient, is also one of the most controversial; the greater numbers of species in the tropics could be a result of environmental drivers (Givnish 1999, Butlin 2012), differences in niche width and range size (Salisbury et al. 2012), high levels of tropical mutualisms (Schemske et al. 2009), or simple niche conservatism and the amount of time clades have spent in the tropics (Hawkins et al. 2007) (though see (Rabosky 2009a) or Rabosky (2009b) for critiques of this view). It could even be the case that diversification rates are greatest at high latitudes and that these species subsequently enter the tropics (Weir and Schluter 2007). The unique biogeography of Amazonia and the Andes has been implicated in the particular species richness of the

Neotropics (Hoorn et al. 2010, Pomara, Ruokolainen and Young 2014), though most inter-tropic comparisons remain speculative due to the lack of replicability, as there is only one Neotropics. Other ecological processes posited to drive speciation and extinction events include small body size (Etienne et al. 2012b, Cardillo et al. 2005a), climatic niche evolution (Cooney, Seddon and Tobias 2016), and feeding guild generalization (Vamosi, Armbruster and Renner 2014).

An important aspect of a species' ecology and evolution is its ability to disperse. Dispersal, or the movement of an organism in relation to its birth and breeding sites (Greenwood and Harvey 1982), is a major driver of gene flow between populations and of the ability to explore new habitats. This in turn has biological implications for individuals and populations ranging from disease dynamics (Mack et al. 2000) to predation risk (Bonte et al. 2012). In particular, the genetic diversity of an individual's potential mates as well as the probability of encountering insurmountable geographic barriers, and thus the speciation and extinction dynamics of the population, is dependent on individual dispersal abilities (Kokko and López-Sepulcre 2006). Dispersal can, however, be very difficult to measure accurately (Nichols et al. 2001, Paradis et al. 1998), and much is unknown about how dispersal affects macroecological and macroevolutionary dynamics (Ronce 2007).

In 1976, Diamond et al. published a study of speciation in the Solomon Islands that separately considered birds that could not cross water, birds that could reach nearby but not remote islands, and long-distance dispersers that could reach all islands, finding that the so-called "great speciators" nearly all belonged to the intermediate dispersal category (Diamond, Gilpin and Mayr 1976). Three decades later, an experimental study of *Pseudomonas fluorescens* found that intermediate dispersal rates facilitated high niche differentiation, leading to both high genetic diversity and highly productive populations (Venail et al. 2008). Species with limited mobility typically have small ranges, which present little opportunity for vicariance and increase extinction vulnerability (Losos and Parent 2009, Vamosi and Vamosi 2010, Salisbury et al. 2012). On the other hand, highly mobile populations will surmount most barriers to isolation and thus will maintain high levels of genetic admixture (Claramunt et al. 2011, Weeks and Claramunt 2014, Coyne and Orr 2004). Thus, it has been posited that the highest levels of diversification might be found in intermediate dispersers.

This so-called "intermediate dispersal hypothesis" (IDH) has become increasingly popular, but the evidence for it is mixed and is often presented as a post-hoc explanation for inconsistent results. For example, a study of Hawaiian angiosperms (Price and Wagner 2004) correlated lineage species richness with certain modes of avian seed dispersal, but not others, and not with pollination mode, which has been implicated as a key driver of diversification in other angiosperm studies (Eriksson and Bremer 1992, Ricklefs and Renner 1994, Dodd, Silvertown and Chase 1999); the authors briefly cite the IDH to explain the contradiction but then focus on allopatric and parapatric speciation processes. Studies of the wing morphology of the suboscine family *Furnariidae* (Claramunt et al. 2011) and of birds in the Australasian islands (Weeks and Claramunt 2014) found an inverse relationship between dispersal and speciation, the opposite relationship to what other studies have shown (Phillimore et al. 2006); these discrepancies too are attributed to the IDH, despite the fact that the results are clearly monotonic.

Studies of the IDH encounter the same methodological challenges as studies of sexual selection's effect on speciation/extinction: species-level traits are difficult to correlate to clade-level processes. It is hard to accurately assess a single value of dispersal for a genus or a family, for example in island species originating as long-distance dispersers but subsequently rapidly lose their dispersal abilities (Price and Wagner 2004, Mayr and Diamond 2002). This phenomenon can be seen clearly in birds, where many island species have evolved flightlessness (Wright, Steadman and Witt 2016). Furthermore, dispersal, unlike some metrics of sexual selection, is an undeniably quantitative trait, and most modern methodologies can only correlate shifts in diversification rates to binary or categorical states (FitzJohn 2010). Furthermore, what techniques linking diversification with quantitative variables do exist – notably QuaSSE (Quantitative State Speciation and Extinction, (FitzJohn 2010)) and BAMM (Bayesian Analyses of Macroevolutionary Mixtures, (Rabosky et al. 2014)) – have fallen under recent scrutiny (see Chapter 7, General Conclusions).

Analytic controversies aside, the largest barrier to studying the IDH is the difficulty in accurately measuring dispersal across a large number of species. Birds, however, solve this problem nicely due to the close correlation between dispersal and wing morphology. The “hand-wing index,” defined as the ratio of Kipp’s distance (the length between the first secondary covert flight feather and the longest primary covert flight feather in a closed wing) to the unflattened wing chord (Claramunt et al. 2011), is a measure of the aspect ratio of the wing and of the bird’s ability to fly long distances, i.e., to disperse (Pennycuick 2008). The index can be easily obtained from live birds and museum specimens and can be standardly measured in all birds with flight feathers, which is nearly all species. Furthermore, avian dispersal varies from highly sedentary tinamous to terns that circumnavigate the globe annually; even within passerines, swallows migrate across continents whereas most furnariids are year-round residents of tiny territories (del Hoyo

1992-2011). If some of the controversy surrounding the IDH results from sampling only one part of the curve, a global survey of birds would capture the entire spectrum of the dispersal-speciation relationship.

Summary of outstanding questions and outline of thesis

Biodiversity can be measured both in terms of the number of species and the variation in traits between those species. My research investigates the role of social and ecological processes on avian evolution by focusing on phenotypic trait evolution and addressing three main themes.

1) A global survey of avian functional traits.

In Chapter 2, I present the first comprehensive survey of avian functional traits, a dataset comprising eight morphological measurements of the beaks, tails, wings, and tarsi of 42,334 individuals from 10,023 extant and recently-extinct avian species. The spatial and taxonomic breadth of this data allows tests of fundamental ecological and evolutionary processes hitherto only considered on small scales, some of which I explore. In particular, I find that global avian community trait composition is consistent with a competition-based model of species coexistence, with a clear separation in trait packing between Old World (Africa, Eurasia, and Australia) and New World (North and South America) communities. I demonstrate that avian traits are determined by species’ diet, phylogenetic history, and broad habitat type, but I find little evidence of environmental filtering. I also establish that avian order species richness is generally correlated with explorations of new regions of morphospace, with the exception of the order *Passeriformes*, in which species occupy an area of trait space far more densely than expected.

2) The influence of social selection on speciation and extinction.

With the most speciose – and the mostly unexpectedly speciose – avian order also possessing elaborate morphology specialized for vocal ornaments, global avian diversity suggests a potential link between sexual selection and speciation. To investigate this question, in Chapter 3 I first use 279 lineages from the family *Furnariidae* to establish that vocal traits can evolve faster and less predictably than morphological traits such as beak shape. In Chapter 4 I then challenge traditional assumptions about female ornaments and demonstrate across 10,257 avian species that female song is not only adaptive but driven by different ecological and social processes than male song. Female song thus is not explained by traditional theories of sexual selection but does fit the model of social selection. Finally, in Chapter 5 I use 6,601 species to show that the separate consideration of male-only song from species in which both males and female sing allows for a clearer understanding of the relationship between sexual selection and speciation. Namely, lineages under high levels of sexual selection (male-only song) have the highest rates of lineage diversification, whereas lineages shaped by social selection (male and female song) have intermediate levels of lineage diversification. Thus, my research suggests that the explicit analysis of female ornaments, long ignored as maladaptive, might elucidate the controversy surrounding studies of sexual selection and speciation.

3) The role of dispersal in avian diversification.

In Chapter 6, I use the wing morphology data from Chapter 2 to explicitly test the intermediate dispersal hypothesis (IDH) across the most species-rich avian order, the *Passeriformes*. Like the proposed link between sexual selection and speciation, the relationship between dispersal and speciation has strong theoretical evidence but mixed empirical evidence. In particular, previous studies of the IDH have focused on small sample sizes, especially island taxa, and have used imprecise methodologies to estimate lineage diversification rates. Here, I use several different metrics of diversification to test the IDH across 6,028 species of birds, taking into account the main macroecological correlates of avian dispersal and several other proposed drivers of avian speciation. I find that the relationship between dispersal and diversification depends upon the lineage and the ecological context, demonstrating the importance of understanding the macroecological context before undertaking macroevolutionary analyses.

CHAPTER 2: COMPETITION AND THE GLOBAL DISTRIBUTION OF AVIAN FUNCTIONAL TRAITS.

Abstract

Functional traits, or characteristics of an organism related to its role within the environment, present a framework for quantifying a species niche. By pinpointing an individual's location in trait space, it is possible to explicitly calculate how similar it is to other species and thus to calculate the density of niche space within a community. There have been a number of recent global analyses of plant functional traits, but it is not yet known how animal communities assemble on a broad scale. Two common and opposite hypothesis for community assemblage are a competition-based model, in which the existence of one set of traits excludes the co-occurrence of similar traits, and environmental filtering, in which only certain combinations of traits can exist in a given environment. Furthermore, at a species level, it is generally unknown whether and to what extent these traits are determined by evolutionary history (phylogeny), ecological use (diet), or environmental context (biome). Here I present a survey of eight key morphological measurements of the bills, tails, wings, and tarsi of 42,334 individual birds across 10,023 extant and recently-extinct avian species in order to test the forces shaping the global distribution of avian traits. I use the metric "functional dispersion" to measure the clustering of traits, establishing that avian community composition is consistent with a competition-based model of community assemblage. Furthermore, there is a strong biogeographic signature within the variation of avian community density, with New World trait distributions being generally more compact. I also demonstrate that avian orders become

more spread out with increasing clade richness, with the notable exception of the passerines, order *Passeriformes*. Finally, I show that increasing dietary specialization, but not biome specialization, has a filtering effect on species traits above and beyond phylogenetic history. Thus, I suggest that it is the evolutionary context of species' niches, rather than environmental filtering processes, that primarily determines the global distribution of avian biodiversity.

Introduction

A classic ecological quandary asks whether a community's trait composition is driven primarily by interspecific competition or environmental filtering, the former resulting in coexisting species being less alike than expected by chance and the latter in coexisting species that are more alike (Diaz, Cabido and Casanoves 1998, Lebrija-Trejos et al. 2010, Ricklefs 2012). Functional traits – defined by Díaz and Cabido (2001) as "characteristics of an organism considered relevant to its response to the environment and/or its effects on ecosystem functioning" – can be used to explicitly quantify species' roles in the environment, thus providing a metric to measure species' similarity (Kunstler et al. 2016, Díaz et al. 2016, Violle et al. 2007). Understanding the trait-based processes facilitating co-existence is especially relevant as human behavior increasingly drives range shift via habitat fragmentation and climatic instability (Vitousek et al. 1997, Barnosky et al. 2011, Sala et al. 2000), as conservation models require insight in which species can coincide.

Alternatively, this competition-versus-filtering debate could be framed as "niche expansion" versus "niche packing" with respect to increases in species richness. Under the niche expansion model, species richness is increased by the addition of species belonging to novel regions of functional morphospace, with competitive exclusion preventing overlap in previously-occupied space (Karr and James 1975, Macarthur 1965). Under the niche packing model, increased species richness is associated with denser occupancy of functional morphospace, with unoccupied regions of morphospace unavailable due to environmental and/or phylogenetic constraints (Macarthur 1965, Karr and James 1975, Hubbell 2001, Klopfer and MacArthur 1961). This is of particular interest to the study of the temporal build-up of biodiversity – is the species richness of clades driven by radiations in key adaptations (expansion) or by refinement of the existing morphospace (packing)? (Ricklefs 2012)

Furthermore, it is generally unknown how the density of functional trait space varies biogeographically (Lamanna et al. 2014). A recent study by Pigot, Trisos and Tobias (2016b) examined the variation in species richness and functional traits across a Neotropical elevational gradient and found strong support for high species richness leading to niche packing. Similarly, a comprehensive survey of diet and habitat specialization of the world’s birds by Belmaker et al (2012) found a strong relationship between specialization and species richness even after accounting for differences in the productivity of the region. Furthermore, a global study of herbivore insect diet found high levels of dietary specialization in the tropics (Forister et al. 2015). That is, species in areas with high richness appear to occupy narrower niches, allowing for the packing found by Pigot et al. (2016b), and thus both functional trait density and species richness would be expected to display a strong spatial signature.

Natural selection, however, acts at the level of the individual, not at the level of the community (Darwin 1859). An organism’s form will be determined to some extent by its evolutionary history (Peterson, Soberón and Sánchez-Cordero 1999, Losos 2008), but what other processes drive morphological adaptations? If an environmental filtering process were occurring, one would expect organisms in similar environments to have similar combinations of traits (Diaz et al. 1998, Lebrija-Trejos et al. 2010, Winemiller et al. 2015). Likewise, organisms with corresponding ecological roles, such as similar diets, might also resemble one another more closely than species with different functions, i.e., convergent evolution (Man and Price 1992, Miles and Ricklefs 1984). On the other hand, there could be a many-to-one mapping of form to function, such as with jaws of *Labridae* fish (wrasses) obtaining similar biomechanical properties via many different morphologies (Wainwright et al. 2005), or a one-to-many relationship, such as continental Anolis lizards showing near-identical morphologies (form) to those in the Greater Antilles despite occupying very different niches (functions) (Irschick et al. 1997). These processes have rarely been examined across many different taxa, particularly as such analyses require independent trait and ecological data, as well as accurate range maps and phylogenetic information.

Functional trait methodology has recently become incredibly popular in basic evolutionary biology as well as applied conservation and agricultural sciences (Chaves and Oliveira 2004, Wood et al. 2015, Brown et al. 2013, Díaz and Cabido 2001, Lavorel and Garnier 2002, Díaz et al. 2004). Most global studies to date, however, have focused on plants (Garnier, Navas and Grigulis 2015, Díaz et al. 2016, Kattge et al. 2011, Kunstler et al. 2016, Jetz et al. 2016). Birds present a perfect system for functional trait analyses on a broad scale. They have radiated to inhabit all major ecosystems on earth, from the Arctic tundra to the Ecuadorian rainforest to the Namibian desert. They are of great cultural and economic importance, from crop pollination and pest control to the pet trade and religious symbology

(Luck, Hunt and Carter 2015, Tidemann and Gosler 2010, Greenberg et al. 2000). Due in part to birds' popular appeal, there are well-documented life history (del Hoyo 1992-2011) and phylogenetic (Jetz et al. 2012) data available. Furthermore, with around 10,000 recognized species, the clade is speciose enough provide large sample sizes across a wide range of environments and ecological functions, but small enough to be both logistically and computationally feasible to survey.

Here I present the first global survey of functional traits in extant and recently-extinct birds. I quantify avian biodiversity along eight morphometric axes related to resource acquisition (beaks) (Schoener 1965), locomotion (tarsus, wings, and tail) (Miles and Ricklefs 1984), dispersal ability (wing morphology) (Claramunt et al. 2011), and overall body size, which together have been recently shown to be excellent predictors of avian ecological function (Pigot et al. in prep, Pigot et al. 2016b). This dataset spans 42,334 individuals across 10,023 species, allowing for the first time an investigation of the form and function of the world's birds to gain a better understanding of the fundamental evolutionary processes shaping the world's avian communities. I will first offer a description of the data, mapping the variation in morphology across space and time and testing whether avian order richness more closely follows an expansion or a packing model. I will then consider the functional distributions of the world's avian communities, using simulations to discover if trait assemblages are more consistent with an environmental filtering model or a competition-based model. Finally, I will explicitly test the effects of diet, biome, habitat, and phylogeny on determining avian morphology.

Materials and Methods

Data collection

Eight continuous biometric traits were collected from 42,334 museum specimens and live birds from 10,023 extant and recently-extinct avian species representing 39 orders, 224 families, and 2180 genera. I considered the definition of “trait” provided in Flynn et al. (2009) – “a measurable aspect of an organism which impacts its interaction with the environment” – and selected measurements relevant to a bird’s diet, body size, and locomotion (Miles and Ricklefs 1984, Grant and Grant 2006, Schoener 1965). I used dial calipers to measure bill culmen length from the tip to the intersection of the bill and the skull, bill length from the distal edge of the nares to the tip, bill width at the distal edge of the nares, bill depth at the distal edge of the nares, and tarsus length from the notch at the ankle to the third crease at the start of the toes, all to the nearest 0.1 mm, as well as Kipp’s distance (Claramunt et al. 2011) to the nearest 0.5 mm. To the nearest 0.5 mm I measured also unflattened wing chord (using a metal ruler with a perpendicular stop) and tail length from the tip of the longest retrix to the point at which the two central retrices protrude from the skin (using a flexible clear plastic tail ruler). Hand-wing index, or the ratio of Kipp’s distance to the total wing chord, is a common proxy for dispersal (Claramunt et al. 2011) and therefore was used in these analyses instead of raw Kipp’s distance. More details on these protocols can be found in papers based on subsets of this data (Pigot et al. in prep, Pigot et al. 2016b, Trisos, Petchey and Tobias 2014, Derryberry et al. 2011, Matthews et al. 2015). Where possible, I sampled two males and two females in good condition from the nominate subspecies, excluding all juveniles and potential hybrids. Any museum specimen that was the sole representative of its species was measured twice before the data was entered. While measuring, I spot-checked each week's data for obvious errors (e.g., a measurement an order of magnitude greater than the conspecifics', letters or symbols in the place of number) before importation to the main dataset. After measuring was complete, I examined the records of any species traits where the variance in measurements was greater than 20% of species mean, flagging potential problems and removing them from this analysis. Other outliers were flagged by collaborators and removed following approval by myself or Dr. Joseph Tobias.

To control for collinearity between the traits and for phylogenetic relationships between the species, I performed a phylogenetically-corrected principal components analyses on the log-transformed traits by using the command "phyl.pca" in the R package *phytools* (Revell 2009, Revell 2012) on 100 randomly-selected gene-based phylogenetic trees from the Hackett backbone of the Global Bird Tree (Jetz et al. 2012) for the 6,418 species in our sample for which high-quality phylogenetic information is available. The calculated weights from each of 100 trees were averaged and then applied across all 10,023 species to determine each principal component axis (PC).

Functional dispersion, here abbreviated "FD," is a measure of the density of traits for a given subset of species, defined as the mean distance of the subset's species' multidimensional traits to the subset's traits' centroid (Laliberté and Legendre 2010). High FD indicates a dense traitspace, or a set of similar species; low FD indicates a sparse traitspace, or a set of dissimilar species. FD was chosen as a metric of trait divergence due to its insensitivity to subset richness and general robustness to outliers (Mason et al. 2013, Tardif and Shipley 2015, Laliberté and Legendre 2010). FD was calculated in all instances without abundance weights using the command “fdisp” in the R package *fd* (Laliberté and Legendre 2010).

Order Functional Dispersion

FD was calculated for each of the 38 taxonomic orders, and I ran linear models to compare order FD and logged species richness. As a single order, *Passeriformes* (“passerines”), contains approximately 60% of the total avian species richness, I also ran a separate model excluding this order.

Community simulations

Breeding range GIS shape files for 9,660 species were obtained from (BirdLife International and NatureServe 2011); by intersecting these ranges with a 1°x1° grid and excluding grid cells containing > 50% water cover and/or fewer than 10 species, I obtained a presence-absence matrix for 12,137 grid cells, here considered global avian communities. These cells were classified as “New World” if they fell between 180°W to 30°W (North and South America), “Old World West” if between 30°W to 60°E (Europe, Africa, the Middle East, and Russia up to the eastern edge of the Caspian Sea), and “Old World East” if between 60°E to 180°E (central, east, south, and southeast Asia, Australia, and Oceania). I then simulated null communities for each value of species richness between 2 and the maximum community richness of 919 by randomly selecting a null “community” of that richness from the set of all birds and calculating the FD of that community, repeated 1,000 times for each richness value. As this procedure does not take into account either phylogenetic non-independence or spatial autocorrelation, the comparison of the simulated and realized results remains descriptive rather than an explicit test.

Macroecological models

For the 6,418 species for which high-quality phylogenetic data are available (Jetz et al. 2012), I obtained a three-way habitat classification from Tobias et al. (2016), which categorized each species as living in "dense" (closed-canopy forests), "semi-open" (open-canopy woodland and shrubland), or "open" (grasslands and deserts) habitats. Using the R package *MCMCglmm* (Hadfield 2010b) and the 100 phylogenetic trees used to compute the principal components, I tested the difference in each of the eight PCs across these three habitat types. I ran each chain for 550,000 iterations (55,000 for each tree), discarding the first 50,000 (5,000 for each tree) as burn-in, with flat, non-informative priors.

Dietary classification data have been published for 9,611 of these 10,023 species (Wilman et al. 2014). This resource lists the percent (to the nearest 10%) of each species' diet for 10 guilds (invertebrates, vertebrate ectotherms, vertebrate endotherms, vertebrate fish, vertebrate other, scavenging, fruits, nectar, seeds, and plants). Previous work (Pigot et al. in prep) has shown that the relationship between diet and functional traits varies depending on which PC axis is considered, with a close relationship in some axes but little correlation in others. Therefore, to test whether diet has a filtering effect on functional traits, I calculated the variance in each of the principal components for each of the 10% bins within each of the 10 dietary categories. I then ran a linear model on these trait variances, with dietary category and decile richness as additional fixed effects, to test if the trait variance decreased with increased dietary specialization.

Finally, I intersected the aforementioned breeding range shape files with shape files representing the 14 World Wildlife Fund global biomes (Olson et al. 2001), determining for each bird the proportion of the range to fall within each biome. To test whether there is an environmental filtering effect on traits, here measured as species biome specialization, I again calculated the variance in each of the principal components for each decile of biome membership ($0\% \leq x < 10\%$, $10\% \leq x < 20\%$, etc). I ran a linear model on the trait variance, with biome identity and decile richness as additional fixed effects, to test if trait variance decreased with increased biome specialization.

Results

Overall

The functional trait space of birds ranges from the small bills of *Zoonavena sylavatica* (White-rumped Spinetail, the smallest bill culmen measured) to the long tails of *Rheinardia ocellata* (Crested Argus, the longest tail measured) to the pointy wings of *Cypsiurus parvus* (African Palm Swift, the highest HWI measured). Intraspecific variation and sex differences account for 7% and less than 0.2%, respectively, of the total variation in traits. Interspecifically, however, 45% of the variation in traits is found between orders, 25% between families, and 17% between genera.

The first principal component (PC1) a measure roughly corresponding to body size formed by weighting all traits in approximately equal measure (with slightly more emphasis on tarsus and bill length and slightly less on tail length), represents 61% of the variation in traits (Table 2.1). PC1 reaches its maximum with *Leptoptilos dubius* (the Greater Adjutant, a large stork found in India and Cambodia) and its minimum with *Myiornis ecaudatus* (the

Table 2.1: Principal components loadings of the eight biometric traits, corrected for phylogenetic non-independence.

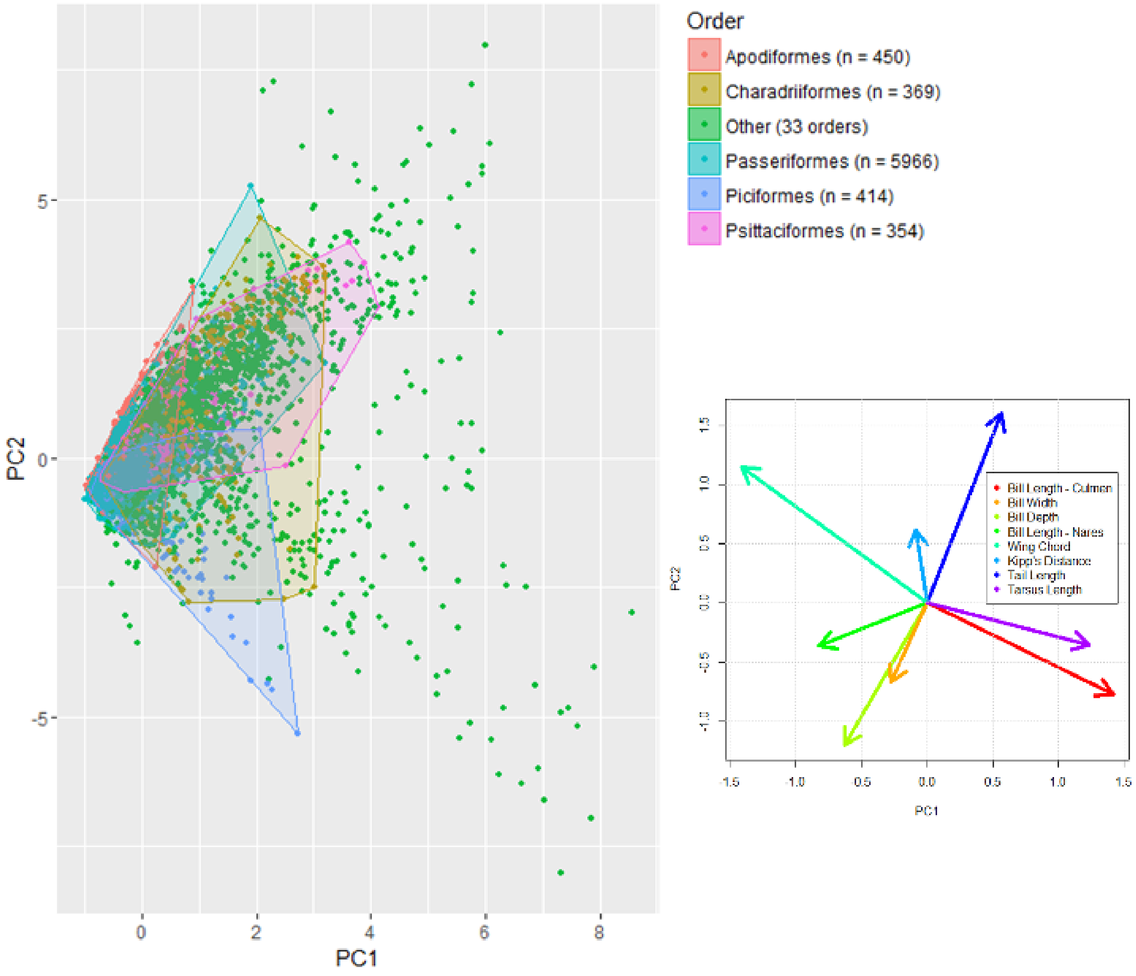
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Bill length (culmen)	0.15	0.02	-0.01	-0.01	0.01	0.00	-0.01	0.01
Bill length (from nares)	0.14	0.02	-0.02	0.00	0.02	0.01	0.00	0.00
Bill width	0.06	0.01	-0.01	0.06	-0.12	-0.08	-0.01	0.00
Bill depth	0.13	0.02	0.00	0.03	-0.01	-0.02	0.01	0.00
Tarsus length	0.14	0.00	0.01	-0.01	-0.06	0.01	0.02	0.00
Wing chord	0.12	0.00	-0.01	0.02	-0.03	0.03	0.01	0.00
Hand-wing index	0.02	0.01	0.00	0.01	0.00	0.00	0.00	0.00
Tail length	0.10	-0.02	0.02	-0.02	0.02	0.00	-0.01	0.00

Table 2.2: Bayesian phylogenetic generalized linear mixed models predicting each principal components axis by evolutionary history and three-way habitat type (open, semi-open, and closed). 95% confidence intervals are shown, with non-significant variables in dark grey.

	Phylogeny			Habitat - semi-open		Habitat - open		Habitat R2	total R2
	Coefficient	CI	R2	Coefficient	CI	Coefficient	CI		
PC1	0.44	(0.39,0.51)	0.28	0.00	(-0.07,0.07)	0.14	(0.14,0.05)	0.07	0.35
PC2	0.64	(0.06,0.72)	0.32	-0.10	(-0.16,-0.04)	-0.24	(-0.33,-0.13)	0.11	0.43
PC3	0.43	(0.37,0.49)	0.28	0.03	(-0.03,0.09)	-0.07	(-0.16,0.01)	0.04	0.32
PC4	0.45	(0.40,0.51)	0.21	0.01	(-0.05,0.09)	-0.74	(-0.17,0.03)	0.13	0.34
PC5	0.72	(0.64,0.81)	0.38	0.05	(-0.02,0.12)	-0.13	(-0.24,-0.04)	0.07	0.45
PC6	0.55	(0.48,0.62)	0.33	0.06	(-0.01,0.12)	0.07	(-0.01,0.18)	0.09	0.41
PC7	1.35	(1.24,1.49)	0.53	-0.10	(-0.17,-0.03)	-0.08	(-0.19,0.01)	0.07	0.61
PC8	0.78	(0.68,0.86)	0.37	-0.09	(-0.15,-0.02)	-0.25	(-0.34,-0.14)	0.10	0.46

Figure 2.1: Distribution of all avian species values of a) PC1 versus PC2 and b) PC2 versus PC3. Convex hulls of traits for the five most speciose orders are displayed, and the composition of the trait axes is included in the lower right.

A.



B.

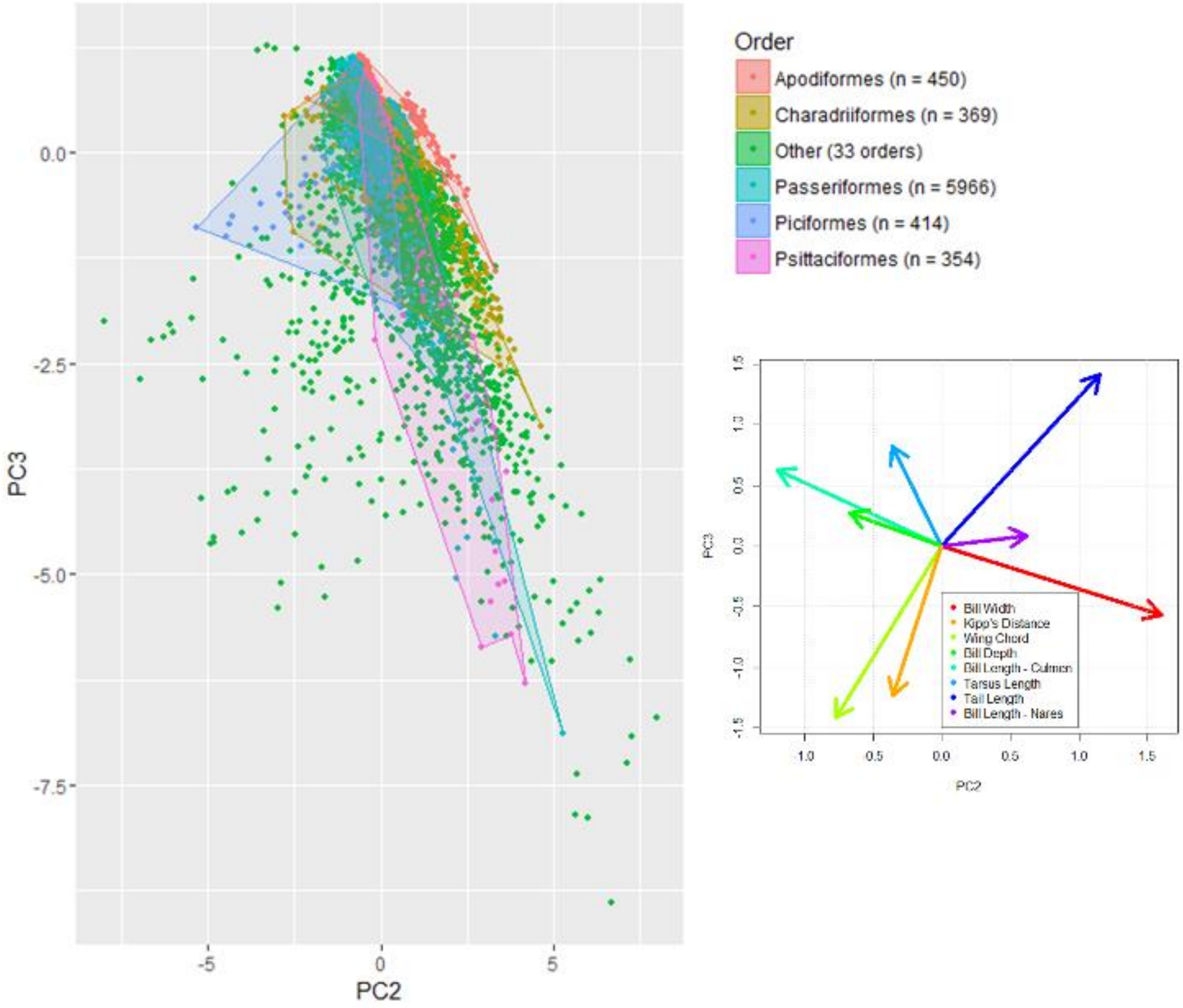
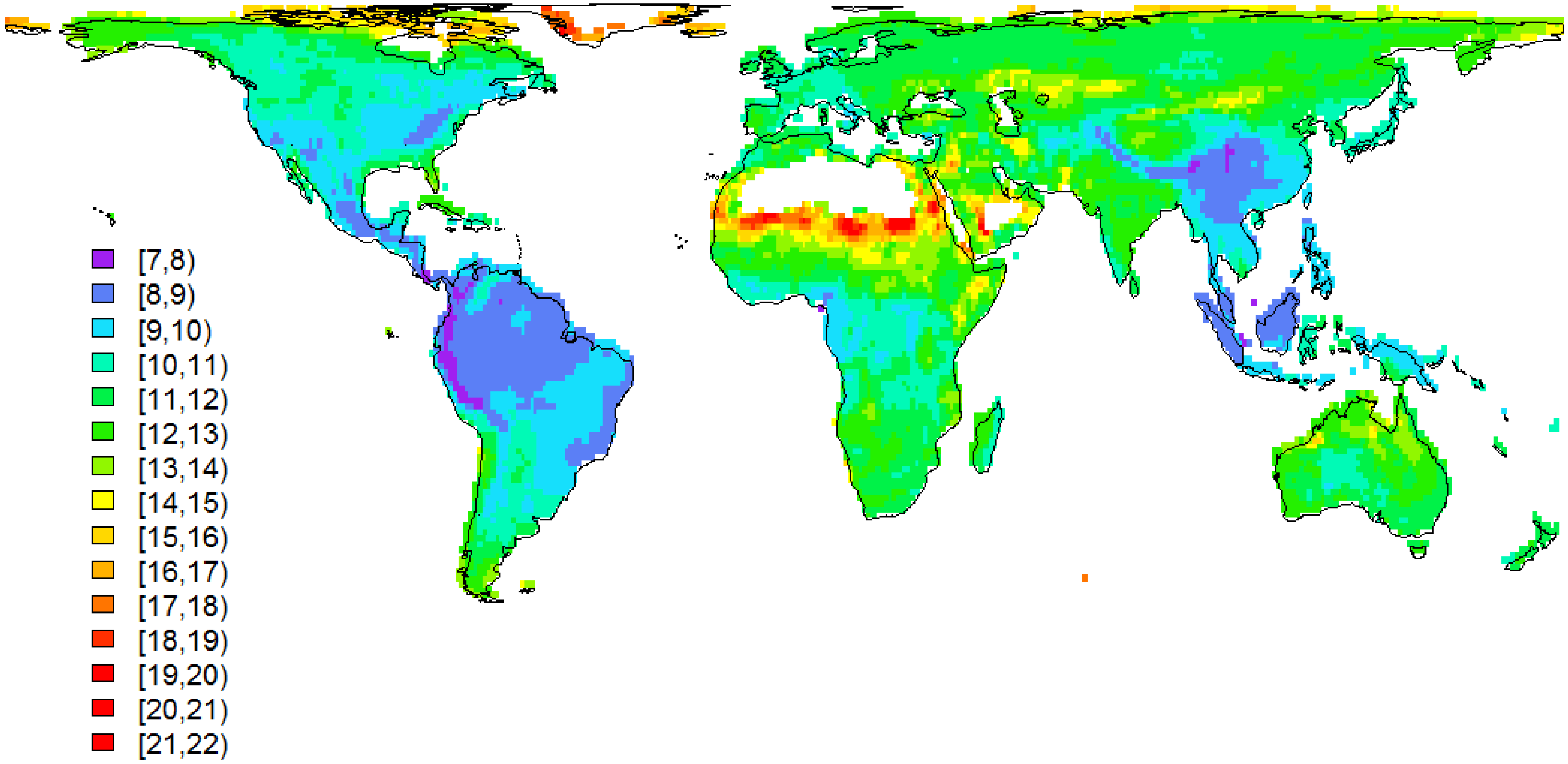
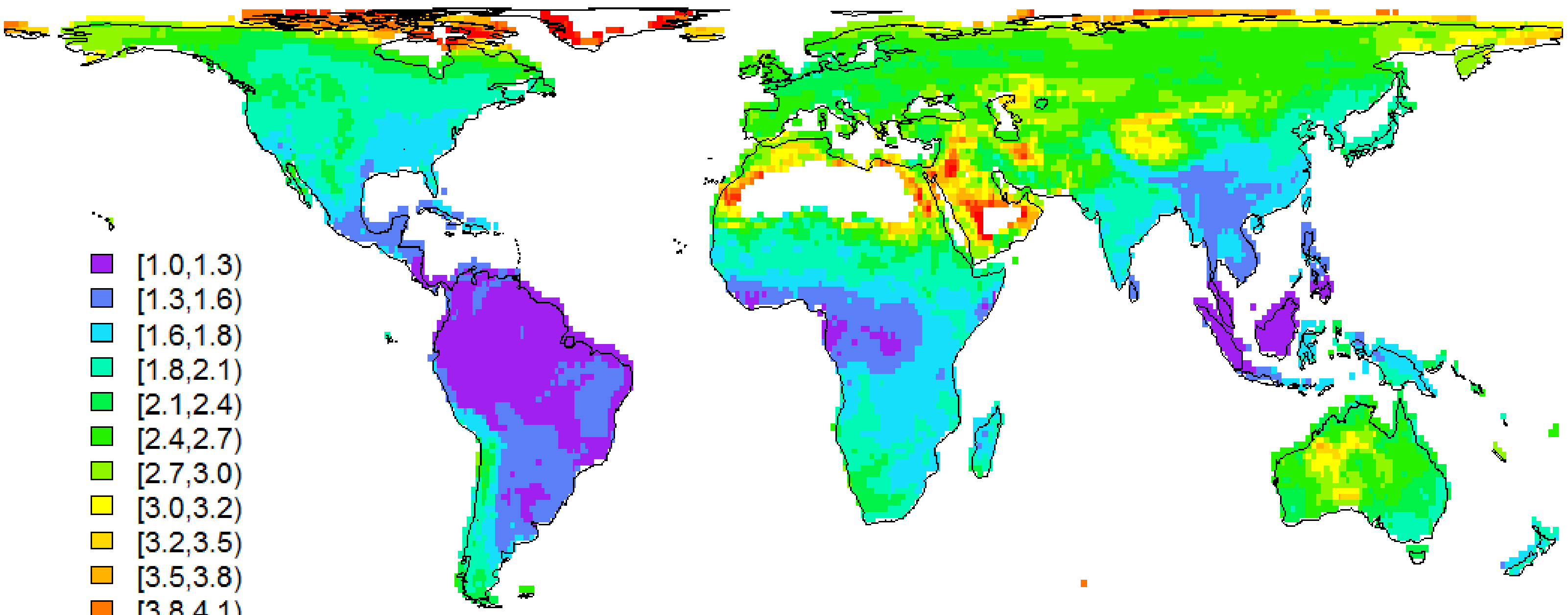

Order
Apodiformes (n = 450)
Charadriiformes (n = 369)
Other (33 orders)
Passeriformes (n = 5966)
Piciformes (n = 414)
Psittaciformes (n = 354)
PC3
PC2
0.0
-2.5
-5.0
-7.5
-5
0
5
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
1.0
0.5
0.0
0.5
1.0
1.5
Bill Width
Kipp's Distance
Wing Chord
Bill Depth
Bill Length - Culmen
Tarsus Length
Tail Length
Bill Length - Nares

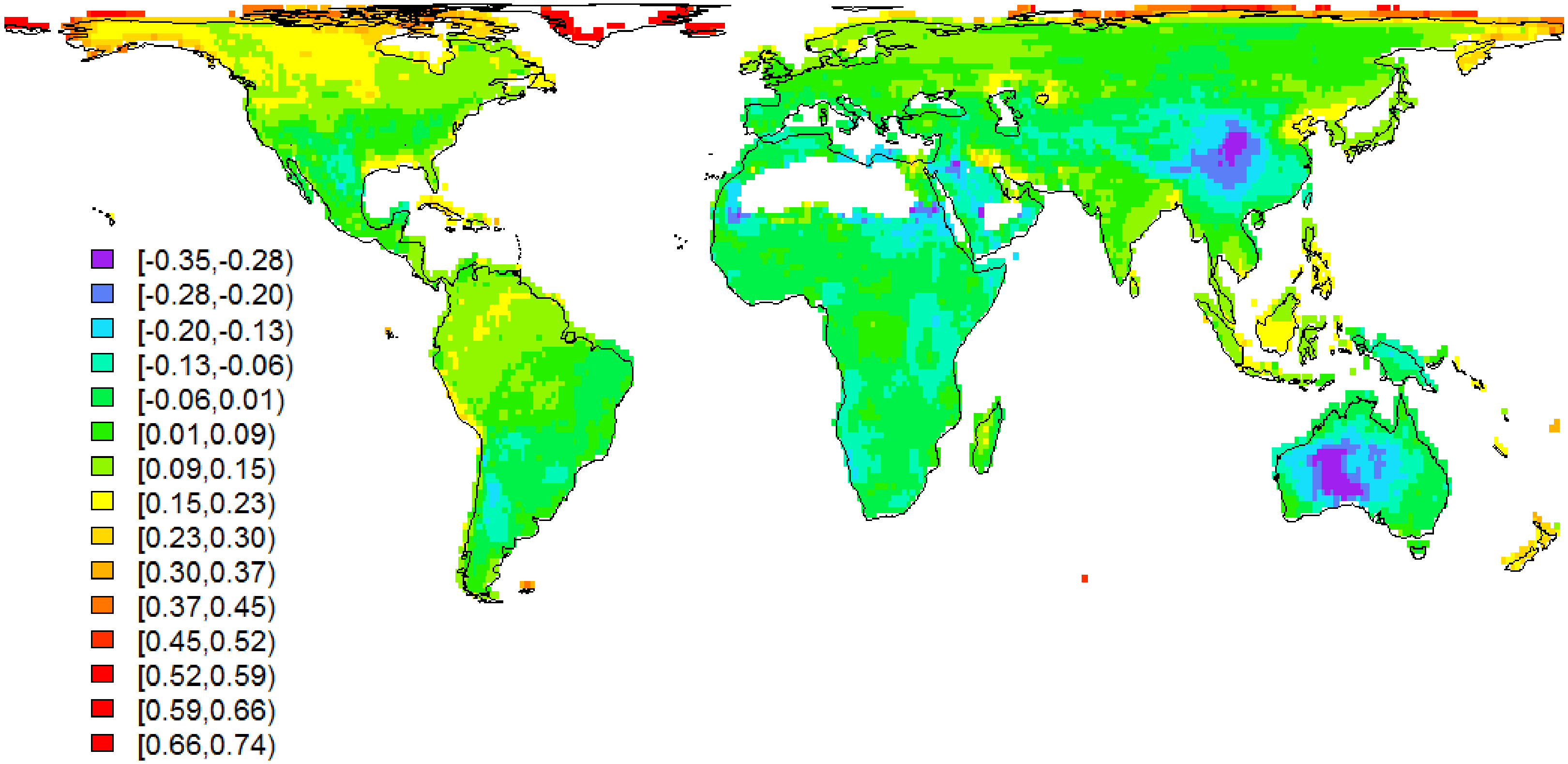
Figure 2.2: Average community values of a) PC1, b) PC2, and c) PC3.
A.



B.


[1.0,1.3)
[1.3,1.6)
[1.6,1.8)
[1.8,2.1)
[2.1,2.4)
[2.4,2.7)
[2.7,3.0)
[3.0,3.2)
[3.2,3.5)
[3.5,3.8)
[3.8,4.1)
[4.1,4.4)
[4.4,4.7)
[4.7,4.9)
[4.9,5.2)

C.

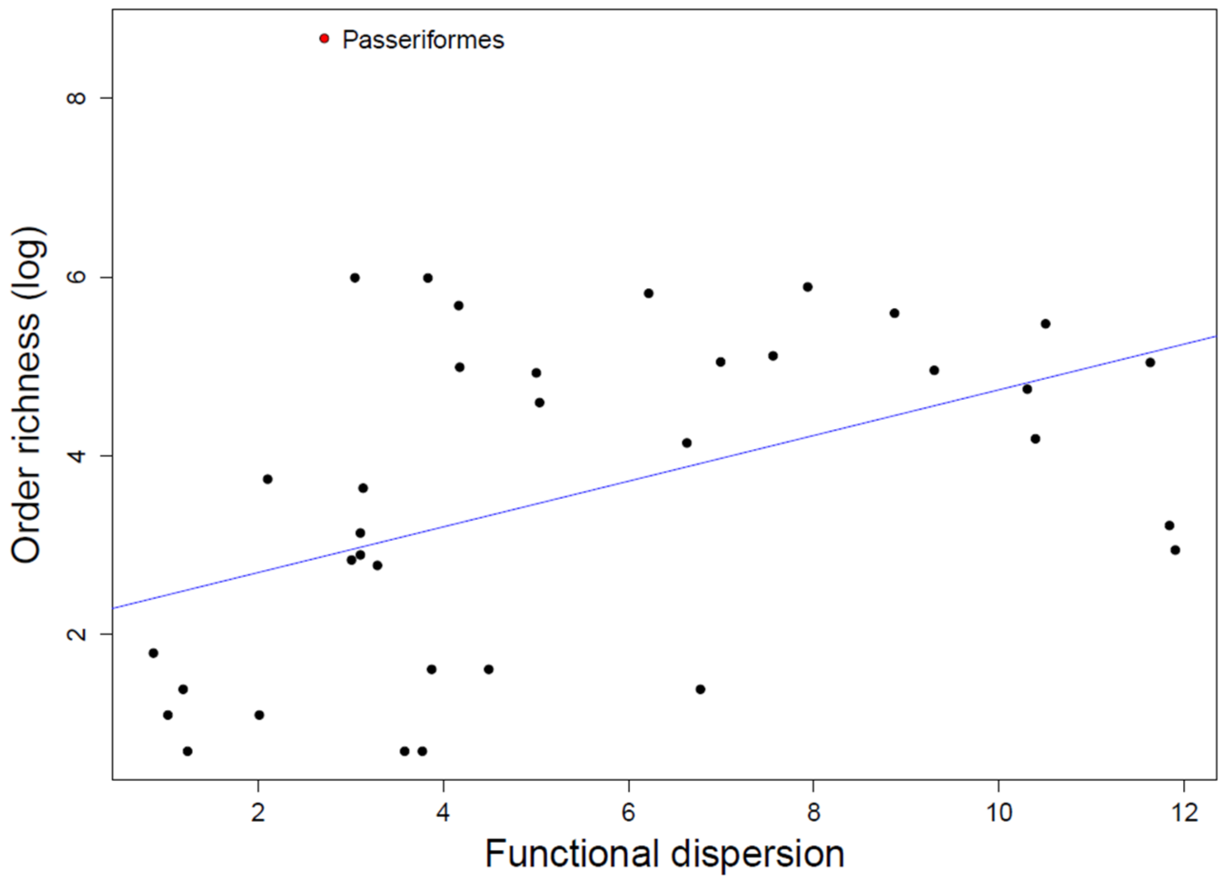

[-0.35,-0.28)
[-0.28,-0.20)
[-0.20,-0.13)
[-0.13,-0.06)
[-0.06,0.01)
[0.01,0.09)
[0.09,0.15)
[0.15,0.23)
[0.23,0.30)
[0.30,0.37)
[0.37,0.45)
[0.45,0.52)
[0.52,0.59)
[0.59,0.66)
[0.66,0.74)

Short-tailed Pygmy Tyrant, the smallest passerine) (Figure 2.1a). PC1 is highest in the Sahara and Arctic and lowest in the Neotropics, Southeast Asia, China, and Appalachia (Figure 2.2a). PC2, representing 9% of the variation in traits, is a measure of beak shape controlled for body size, formed primarily by bill length, width, and depth (Table 2.1). The lowest value of PC2 is *Pelecanus conspicillatus* (Australian Pelican) and the highest is *Gypaetus barbatus* (Bearded Vulture) (Figure 2.1a-b). PC2 is lowest in the tropics and highest in the Arctic and deserts (Sahara, Australian, Arabian) (Figure 2.2b). PC3, in turn, is most closely related to tail length, followed by tarsus length and Kipp's distance, representing 8% of the variation (Table 2.1). The lowest value of PC3 is *Apteryx mantelli* (North Island Brown Kiwi) and the highest is *Rheinardia ocellata* (Crested Argus) (Figure 2.2b). PC3 is again highest in the Arctic, but lowest in the world's deserts (notably Gobi and Australian) (Figure 2.2c).

Order Functional Dispersion

Order FD is generally correlated species richness, meaning that larger orders are generally less dense (have higher FD). The passerines (order *Passeriformes*), however, are a clear outlier ($R^2 = 0.14$, slope = 0.22, p = 0.027 with passerines; $R^2 = 0.23$, slope = 0.26, p = 0.004 without passerines) (Figure 2.3). Indeed, the 5,829 species of passerines in this survey had an FD of 2.71 but would be modeled to have an FD of 25.4, meaning the trait packing is over 9 times denser than expected. Conversely, an order with an FD of 2.71 would be modeled to have a richness of 17.7 species; the passerines contain 300 times more species than expected given their functional trait distribution. Alternatively, the passerine FD per

Figure 2.3: Order richness as a function of clade FD. The passerines, order *Passeriformes*, are marked in red. Shown in blue is the line of best fit with the passerines excluded, with an $R^2 = 0.23$ and a slope = 0.26 ($p = 0.004$).



species is 0.0005, which is 16 times smaller than the next tightest order, the *Apodiformes* (swifts, 450 species).

Community simulations

Globally, the lowest levels of FD – that is, the most tightly packed communities – are found along the Andes, the Appalachians, central Mexico, and China, with low levels found in the tropics of Central and South America, Southeast Asia, and to a lesser extent the Afrotropics. The highest levels of FD, and thus the most spread-out communities, are found in the deserts of the world (Sahara, Atacama, Arabia, Namib, Gobi, and the Australian Outback) as well as parts of the Arctic (Figure 2.4).

Avian communities display a similar funnel-shaped distribution of FD to that predicted by the simulations of random communities, but the values of FD are much higher (Figure 2.5). This is consistent with a competition-based model of community composition, one in which there is a higher FD (sparser packing) because species occupying similar regions of trait space do not co-exist. Furthermore, for a given species richness, the values of FD display a strong biogeographic signature. Of the 3,716 New World communities, 261 (11%) were above the simulated maximum FD, whereas 2,676 (64%) of the 4,155 Old World West and 2,079 (51%) of 4,098 Old World East communities were above the simulated maximum. Furthermore, all 11 of the communities *below* the simulated FD minimum – that is, showing an even tighter packing than expected by chance – were in the New World. As these communities are neither spatially nor phylogenetically independent, further analyses of this pattern were not conducted.

Figure 2.4: Map of global avian community FD. Cool colors (purples and blues) denote low FD (tight packing of traitspace), while warm colors (oranges and reds) denote high FD (loose packing of traitspace). Cells are determined by a presence-absence grid of 9,660 avian ranges and a 1°x1° grid; cells with < 10 birds or > 50% water are excluded.

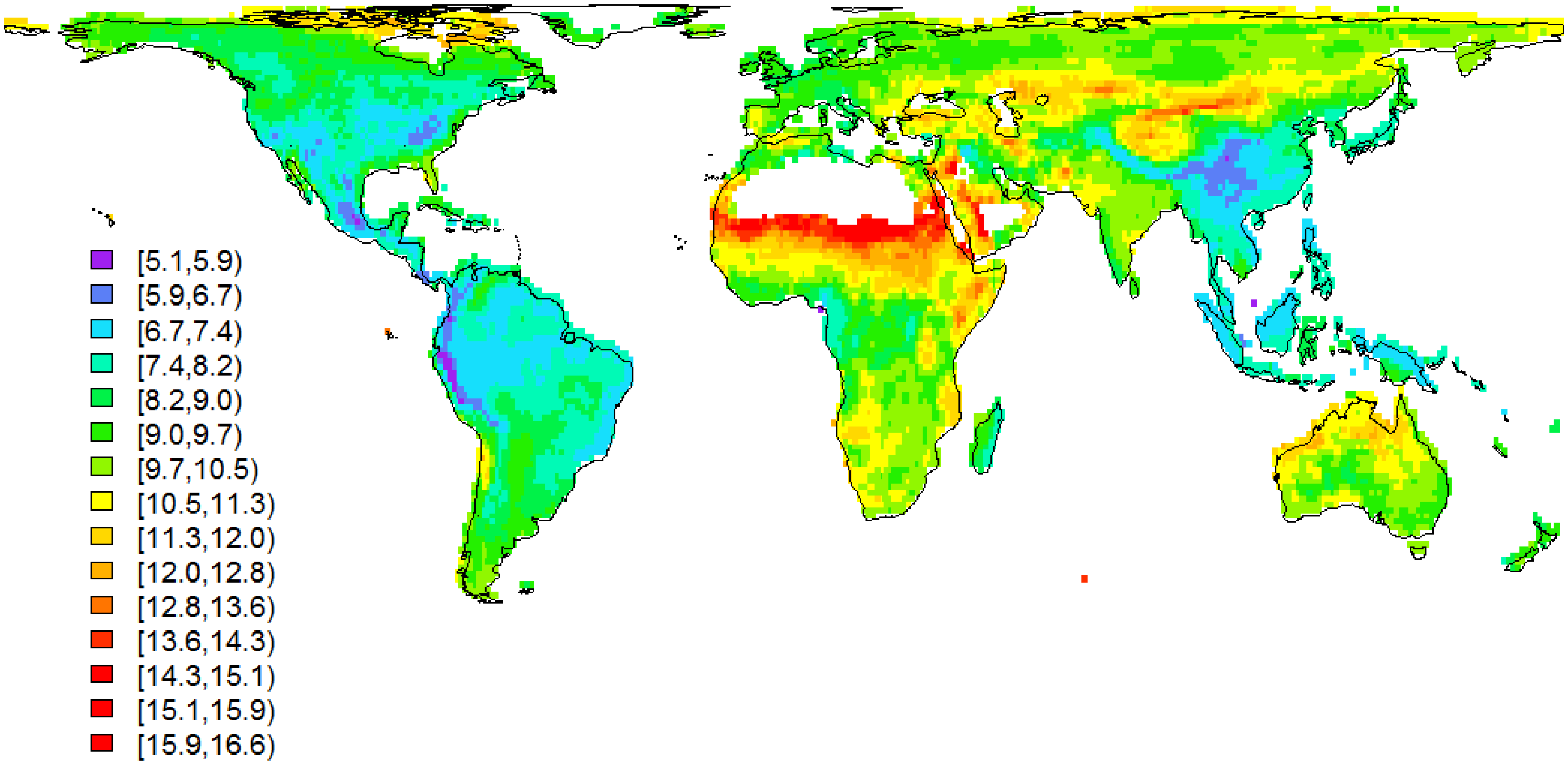


Figure 2.5: Global avian community FD. Communities are determined by a presence-absence grid of 9660 avian breeding ranges and a 1°x1° grid. Red denotes the upper and lower bounds of 1,000 simulated communities for each richness drawn from the global avian species pool. Here "New World" is defined as 180°W to 30°W, "Old World West" as 30°W to 60°E, and "Old World East" as 60°E to 180°E.

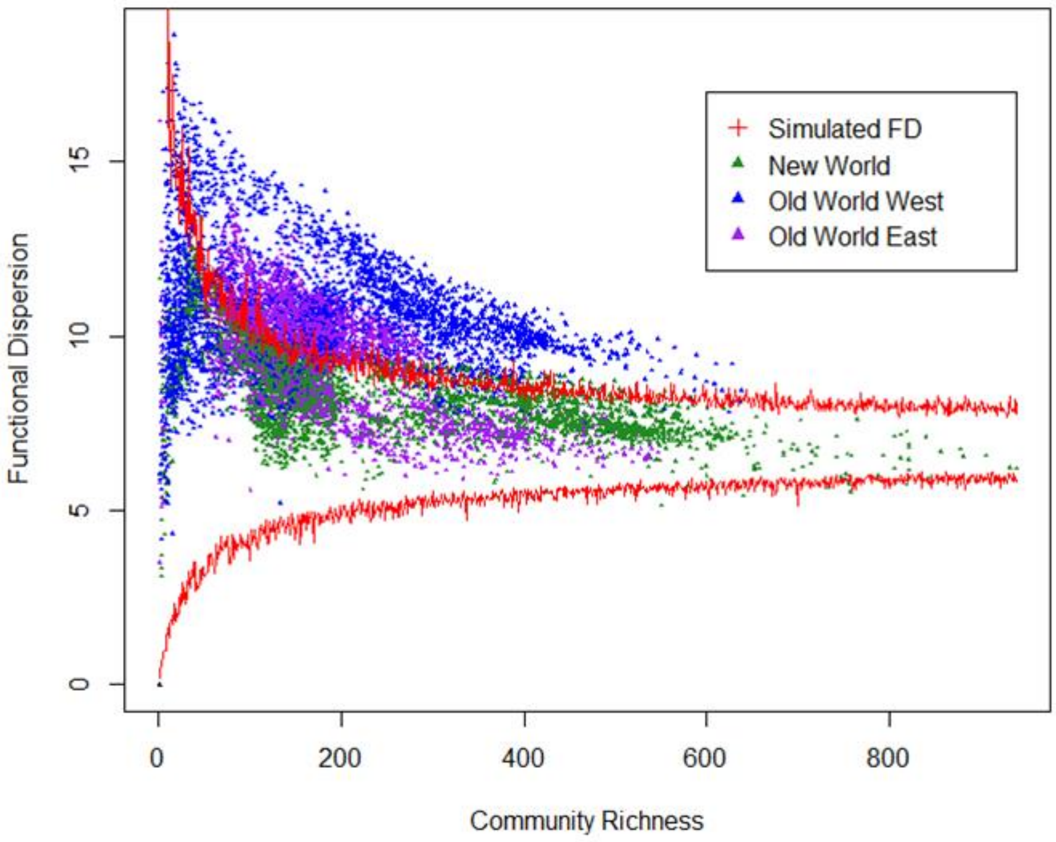


Table 2.3: Variation in each PC axis (columns) as a function of dietary specialization in deciles, with dietary category and decile richness as additional fixed effects (rows). A negative slope for dietary specialization represents how quickly the variance in traits decreases with increased dietary specialization. Slopes under dietary category refer to the difference in model intercept between that category and the reference, “Diet – Vertebrates, fish.” Coefficients highlighted in grey are not significantly different from 0 at the 95% confidence level.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Model intercept	1.20	1.77	1.08	1.44	1.45	1.80	1.33	2.60
Dietary specialization	-0.04	-0.03	-0.06	-0.08	-0.05	-0.04	-0.08	-0.08
Dietary category								
Diet - Fruit	-0.06	-0.71	-0.10	0.03	-0.19	-0.85	0.35	-1.26
Diet - Invertebrates	-0.05	-0.79	0.13	-0.07	-0.11	-0.69	0.07	-1.15
Diet - Nectar	-0.06	-0.71	-0.10	0.03	-0.19	-0.85	0.35	-1.26
Diet - Plants	-0.20	-0.89	0.06	0.20	0.10	-0.10	0.69	-1.08
Diet - Scavengers	-0.54	-1.10	-0.49	-0.65	-0.61	-1.05	-0.43	-0.82
Diet - Seeds	-0.37	-0.91	-0.34	0.15	-0.39	-0.90	-0.22	-1.44
Diet - Vertebrates, ectotherms	-0.40	-0.89	-0.20	-0.39	-0.46	-1.02	-0.25	-1.41
Diet - Vertebrates, endotherms	-0.43	-1.05	-0.41	-0.49	-0.49	-1.09	-0.25	-0.89
Diet - Vertebrates, other	-0.40	-0.97	-0.03	-0.33	-0.27	-0.78	0.33	-1.38
Decile richness	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 2.4: Variation in each principal componenets axis (columns) as a functional of biome specialization in deciles, with biome identity and decile richness as additional fixed effects (rows). A negative slope for dietary specialization represents how quickly the variance in traits decreases with increased biome specialization. Slopes under biome identity refer to the difference in model intercept between that category and the reference, "(sub-) tropical moist broadleaf forests." Coefficients highlighted in grey are not significantly different from 0 at the 95% confidence level.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Model intercept	1.17	0.67	1.19	1.00	0.74	1.13	-0.16	0.12
Biome specialization	-0.03	0.04	-0.02	0.00	0.03	-0.02	0.17	0.12
Biome identity								
B2 ([sub-] tropical dry broadleaf forests)	-0.05	-0.11	-0.08	0.09	0.02	-0.05	-0.38	-0.06
B3 ([sub-] tropical coniferous forests)	-0.16	-0.14	0.62	-0.11	-0.31	-0.11	-0.41	-0.35
B4 (temperate broadleaf/mixed forests)	0.25	0.69	-0.25	0.03	0.62	0.03	2.85	2.42
B5 (temperate coniferous forests)	-0.05	-0.38	0.05	-0.06	-0.18	0.19	-0.23	0.09
B6 (boreal forests)	0.05	-0.45	-0.35	0.29	-0.33	0.20	-0.39	0.39
B7 (tropical grasslands)	0.06	0.01	-0.28	0.08	-0.02	0.00	0.00	0.01
B8 (temperate grasslands)	0.14	-0.01	-0.37	0.21	-0.05	0.48	0.69	0.25
B9 (flooded grasslands)	0.79	-0.24	-0.47	0.90	0.17	0.00	0.13	0.37
B10 (montane grasslands)	-0.12	-0.20	-0.27	0.10	-0.02	-0.23	-0.12	-0.09
B11 (tundra)	0.01	-0.05	-0.37	0.33	-0.09	0.85	-0.33	1.86
B12 (mediterranean)	0.12	-0.07	-0.31	0.11	0.03	0.02	-0.20	0.47
B13 (deserts)	0.08	-0.06	-0.17	0.09	-0.07	0.05	-0.29	0.16
B14 (mangroves)	0.24	0.58	0.80	-0.02	0.44	0.18	-0.11	-0.09
Decile richness	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Macroecological models

Phylogeny explains between 21% (PC4) and 53% (PC7) of the variation in biometric traits; habitat type explains another ~10% (PCs 4, 5, 7, and 8) (Table 2.2). Diet has a filtering effect on traits; as dietary specialization increases, the variance in traits decreases, for all PCs (Table 2.3). This is not true for biome membership, however; in only PC1 does trait variation decrease with increased biome specialization (Table 2.4). This is again consistent with the hypothesis that trait distributions are not primarily driven by environmental processes.

Discussion

Until recently, competition-based models of species coexistence relied on phylogenetic relationships as a proxy for niche overlap, with higher rates of competition among those species that were closely related (Mayfield and Levine 2010). Such models, however, ignored taxa with low rates of niche conservatism, as well as competitive interactions between convergent species (Godoy, Kraft and Levine 2014). Functional traits provide a method for quantifying a species' role in its environment without relying on the so-called "competition-relatedness hypothesis" (Cahill et al. 2008). My results are consistent with a competition-based model of species coexistence, as avian communities were generally less dense than expected by chance and as biome membership had little effect on the distribution of avian functional traits.

The concept of a biome, a broad categorical classification based on plant types (Olson et al. 2001), is useful in many contexts, such as in studying convergent evolution on plant functional traits (Moncrieff, Bond and Higgins 2016). Though I find that habitat type has a slight filtering effect on avian traits, it is only in PC1, body size, that there is evidence for convergence in avian functional traits within a biome. That is, in a given location birds generally occupy all possible ecological niches, varying in their density of occupation rather than the volume of morphospace they fill. This is consistent with a recent study of niche packing along an elevational gradient (Pigot et al. 2016b), which found a much greater increase in trait density, rather than morphospace volume, as species richness increased.

Instead, avian traits are closely determined by dietary specialization; an encouraging result, given the assumptions that the traits presented here are "functional." A separate study of these traits (Pigot et al. in prep) has found that a random forest model correctly assigns traits to dietary guilds 74% of the time, with > 80% accuracy when omnivores are excluded. Thus, avian morphology is related to its phylogenetic history, diet, habitat type, and the traits of its competitors, but, except for body size, not to the environment.

As the traits presented here are at the species level, any population-level effects of character displacement are masked. If the functional traits of closely related species diverged in sympatry to facilitate coexistence (Grant and Grant 2006, Pfennig and Pfennig 2009), one would expect to see even higher levels of FD within a given community. Furthermore, the eight traits presented here do not capture the entirety of an avian niche; in particular, divergence in song is enough to maintain species boundaries even in species that are apparently morphologically and ecologically identical (McEntee et al. 2016). As song is a crucial aspect of the lives of many species of birds, facilitating mate recognition and both intra- and inter-sexual competition (West-Eberhard 1983), and as acoustic properties of vocal traits are reasonably easy to measure, it is perhaps worth considering that stable distinctions in song patterns might indicate fundamental differences in niche, even if the exact ecological contrast remains opaque.

Though FD and clade richness are generally positively related, the passerines are an outlier. Something about the most species-rich clade of birds enables them to be packed more tightly into functional trait space, by an order of magnitude, than other orders. Indeed, order has over 300 times more species than expected given the portion of total trait space occupied by the passerines. The passerines are not the only globally distributed avian order – others include the *Charadriiformes* (shorebirds, 369 species), *Anseriformes* (ducks, geese, and swans, 160 species), and *Accipitriformes* (diurnal raptors, 251 species) – so this pattern is not due solely to the environmental variety available to form species niches. Nor is this difference solely due to clade age; although the passerines date back to the Cretaceous, they are consistently placed among the younger avian orders (Ericson et al. 2014). It is possible that passerines have significantly smaller ranges and/or poorer dispersal abilities (Claramunt et al. 2011), which would mean that fewer passerine species geographically co-exist than other orders based on richness, and thus lead to a misleadingly dense distribution of global traits. It is also possible that passerines are able to co-exist due to variation in some trait not measured here, such as song ((Seddon et al. 2013b), though see (Tobias et al. 2014)).

Other than the passerines, however, the general increase of order FD with order richness is consistent with time-based and environment-based models of avian diversification, particularly within the framework of niche expansion. For example, a recent survey of the geographic conditions of 7,657 species of birds linked the rate of climatic niche evolution with species diversification, demonstrating that either clades diversify when exposed to new environments or that diversification promotes adaptation (Cooney et al.

2016). Even though I found no evidence for environmental filtering across all birds, different environments almost certainly require different traits within a single clade; clades that encounter the most different types of climates would thus display both an increase in richness and an increase in trait diversity. Furthermore, if avian clade richness is also determined by the amount of time available to diversify, as demonstrated in Hawkins et al. (2007), and if traits evolve according to Brownian as is typically assumed (see for example (Ackerly 2009)), older clades would have both higher species richness and a wider trait distribution.

Geographically, the smallest community FD, and thus the tightest concentration of traits, is seen the tropics (the areas of highest avian species richness). Given the funnel-shaped distribution of simulated communities and the finite boundaries of avian traitspace, this is not surprising – beyond a certain point, sampling a large number of traits will by definition lead to a higher density of those traits in trait space, specifically converging on the FD of all birds. Of greater interest are the large FD values in the world's most extreme environments: the major deserts, the Tibetan Plateau, and the Arctic. Environmental filtering models would predict that only a small subset of functional traits would be able to persist in such challenging conditions (Poff 1997), which would lead to smaller FD – the opposite of what is seen here. Instead, there seems to be less leeway for species coexistence, and thus less tolerance for competition, consistent with the idea that harsher environments lead to larger ecological niches (Klopfer and MacArthur 1960). Of course, this pattern is dependent on the traits selected as "functional traits"; a survey of heat stress adaptations and nocturnality, for example, would likely yield greater levels of trait convergence in the world's deserts.

There are, however, a few regions of both high and low community FD that do not easily correlate with species richness. The Smoky Mountains in the USA, the Himalayas, and much of China have very low FD, whereas the grasslands of Mongolia and Kazakhstan have high FD. In part, this could be a signature of climate stability, as the parts of the continental US with higher FD correspond to the areas that were covered by glaciers during the last glacial period (Jackson et al. 2000). A further biogeographic analysis explicitly examining potential climatic drivers of avian trait distributions would be warranted, particularly in the face of extreme climate change, high levels of species extinctions, and rapid range shifts (Barnosky et al. 2011).

The apparent dissimilarity in functional composition between Old World and New World avian communities is intriguing, though ultimately unsurprising. 93% of the New World communities fall within the simulated range of community FD, compared with 36% of Old World West and 49% of Old World East communities, the rest having higher FD than predicted by chance. That is, the trait distributions of avian communities in North and South America are apparently denser than those of Africa, Eurasia, and Australia. The Neotropics are home to several avian clades that have undergone recent radiations, including the families *Tyrannidae, Furnariidae, Thraupidae,* and *Trochilidae* (Ricklefs 2002, Hawkins et al. 2007), suggesting that the Neotropics might promote rapid speciation and thus a high tolerance for coexistence (Cardillo et al. 2005b), and/or that these Neotropical clades have been *in situ* for longer than comparable clades in the Old World (Hawkins et al. 2007). The Andes mountains, a comparatively young range, and the Amazonian network of meandering rivers present significant geographic barriers to many Neotropical birds (Smith et al. 2014), whereas such barriers are largely absent in other tropical settings, particularly the

Afrotropics. Thus, the Andean uplift (Bates et al. 2008), the dispersal abilities of the birds that happen to have settled in the Neotropics (Smith et al. 2014) along with social traits potentially amenable to coexistence (Tobias et al. 2014), and the climatic history of the Neotropics (Oswald et al. 2016, Steadman, Oswald and Rincón 2015) together could potentially explain why New World communities are apparently more amenable to the coexistence of functionally similar species.

Alternatively, this pattern could be the result of smaller ranges in the Neotropics; at a 1°x1° spatial scale, it is possible that two closely-related birds occurring in the same cell are indeed allopatric, causing a misleadingly dense distribution of traits. The same geographic disparities that might be speeding up speciation could also lead to small range sizes, though one might wonder why the Malaysian and Indonesian islands would not present a similar signature of range-driven density. Given the coarse resolution of many current avian distribution maps, particularly in understudied tropical regions, it is not possible at this time to test these ideas on a broad scale. It is also conceivable, though less likely, that there is an environmental filtering effect in the New World rather than the Old World, perhaps due to differences in seasonality (Hawkins et al. 2007) or migratory patterns (Greenberg 2005, Cresswell, Boyd and Stevens 2008, Salewski, Bairlein and Leisler 2003).

Here, I present a survey of avian functional traits, demonstrating that avian community assembly is consistent with a competition-based model. These results are particularly important within the context of modern climate change. Just as evolutionary distinctiveness presents a useful metric for conservation decisions, allowing practitioners to preserve the greatest amount of evolutionary history and genetic diversity, a trait-based approach to conservation would facilitate the preservation of ecosystem function. For example, a recent survey of frugivorous birds and seed dispersal networks found that frugivore functional irreplaceability was predicted by beak morphology, but not by properties of the networks (Pigot et al. in review). Furthermore, a trait-based approach to species invasions may inform their management and help to predict future species interactions (Blackburn et al. 2011, Blackburn, Lockwood and Cassey 2009, Pyšek and Richardson 2008). As the links between morphological form and ecological function become clearer and as large global trait datasets become more common, the extant distribution of functional traits will increase the understanding of evolutionary processes.

Chapter 3: The tempo and mode of phenotypic evolution in a diverse Neotropical bird radiation.

Abstract.

Understanding variation in the tempo and mode of phenotypic evolution is a critical component of diversification studies. While it has long been theorized that social and ecological pressures can have contrasting effects how on traits evolve, few studies have directly compared rates. In particular, it is only recently that macroevolutionary methodology, accurate phylogenetic trees, and sufficiently large databases of traits have existed so as to allow a broad level of analysis. Using a diverse and well-studied radiation of Neotropical birds, the *Furnariidae* ("ovenbirds"), and a comprehensive survey of biometric (ecological) and song (social) traits, I quantify the tempo and mode of the evolution of these traits and examine the evidence for character displacement among closely-related species within this clade. As has been found in many other study systems, I demonstrate that social and ecological trait evolution is de-coupled in ovenbirds, with ecological traits evolving much more slowly and in a much more phylogenetically constrained pattern than social traits. Additionally, I establish that contemporary levels of sympatry have no effect on recent ecological and social trait divergence. Thus, I determine that social and ecological selective pressures need not act in parallel, suggesting that social traits can potentially facilitate rapid diversification.

Introduction.

The phenomenon of rapid species radiations is well described but poorly understood (Gavrilets and Vose 2005, Irschick et al. 1997, Valente, Phillimore and Etienne 2015). The classic explanation for these bursts of speciation and/or trait divergence is disruptive selection in the presence of novel ecological opportunities (Lovette, Bermingham and Ricklefs 2002, Grant and Grant 2008, Losos et al. 1998, Schluter 2000). Another biological factor often implicated in generating and maintaining this species richness, however, is sexual selection (Arnegard et al. 2010, Arnold et al. 2016, Wagner, Harmon and Seehausen 2012). Differences in sexual traits could either themselves be a driver of rapid diversification (Grant and Grant 2010, Boul et al. 2007, Masta and Maddison 2002, Mendelson and Shaw 2005, Ritchie 2007, Seddon et al. 2013a), with ecological traits diverging more slowly after initial reproductive separation, or could simply facilitate prezygotic barriers to reproduction and prevent hybridization upon secondary sympatry (Arnegard et al. 2010). The extent to which these processes occur, however, remains unknown.

Though these signals are typically termed “sexual,” a more appropriate framework might be that of social selection, or evolutionary processes acting on intraspecific interactions (Tobias et al. 2012b, Tobias and Seddon 2009, West-Eberhard 1979, West-Eberhard 1983). Social selection theory is particularly advantageous because it does not distinguish between the multiple purposes a signaling trait can have, such as mate attraction and territory defense, which is a major problem in comparing sexual and ecological traits (Arnegard et al. 2010, Tobias et al. 2010, Tobias et al. 2012a, Tobias and Seddon 2009, Wilkins et al. 2013). Furthermore, theories of character displacement, discussed below, differentiate between reproductive traits, which are always predicted to diverge, and agonistic traits, which could either converge or diverge (Grether et al. 2009); this distinction is difficult to explain under traditional sexual selection theory, but is easily allowed if signals are always considered "social" rather than strictly sexual. As such, the term "social" here will refer to traits with sexual and/or non-sexual social functions.

Tempo and mode

If ecological and social traits were to have demonstrably different effects on diversification dynamics, they would need to be able to evolve separately (Arnegard et al. 2010, Blomberg, Garland and Ives 2003, Macagno, Moczek and Pizzo 2016). One way to establish this criterion would be a direct comparison of the tempo and mode of the social and ecological traits. If social signals evolve faster and with less adherence to the Brownian motion patterns predicted by the clade's phylogenetic structure, these signals could be a potential driver of diversification. In contrast, if ecological traits evolve faster and/or less predictably, speciation might be more strongly propelled by competition for ecological resources and adaptation to different environments. Finally, if social and ecological traits evolve in concert within a clade, then these two types of traits could not be said to have contrasting effects on the clade's radiation.

Character displacement

The concept of character displacement was first introduced by Darwin under the name "divergence of character" (Darwin 1859) and formally defined by Brown and Wilson (1956) as "species populations show[ing] displacement where they occur together and convergence where they do not." Within this framework, two closely-related species occupying a similar niche in sympatry would diverge faster than expected in response to interspecific competition (Grant and Grant 2006, Pfennig and Pfennig 2010, Schoener 1965). In contrast, the opposite pattern is predicted by environmental filtering, wherein the ecological traits of sympatric populations would be more similar, as the shared environment would drive the populations' traits toward similar evolutionary optima (Adler et al. 2013, Diaz et al. 1998).

Analogous arguments can be made for social traits, with one additional hypothesis. If hybridization between two populations leads to less fit offspring, the signals that are used to attract mates would be expected to diverge in sympatry (Grant and Grant 2010). This is often called "reproductive character displacement" (RCD), as opposed to the "ecological character displacement" (ECD) described in the previous paragraph. If these social signals are used in agonistic interactions, however, such as competition over ecological resources, these traits could conceivably either diverge or converge. In this so-called "agonistic character displacement" (ACD), diverging traits would indicate that interspecific signals are too costly to maintain and respond to, given the amount of actual interspecific competition over the relevant resource (Grether et al. 2009). On the other hand, converging agonistic traits would suggest that there is enough interspecific competition over the relevant resource to merit a single signal for both intra- and inter-specific competitive interactions. Furthermore, as in ecological traits, the environment may have a filtering effect on social traits, such that the signals of sympatric populations converge in response to a shared environmental optimum (Endler 1992, Seehausen et al. 2008).

Thus, there are several competing hypotheses regarding social and ecological trait divergence. In ecological traits, the degree of sympatry will relate to trait divergence either positively (ECD), negatively (environmental filtering), or not at all. For social traits, the three possible relationships between traits and sympatry are again positive (RCD and/or ACD divergence), negative (ACD convergence and/or environmental filtering), or no correlation. An analysis of ovenbird traits by Tobias et al. (2014) considered sympatry as a binary variable (species ranges either had some degree of overlap or no overlap) and found evidence of convergent character displacement in social traits but no displacement in ecological traits, concluding that this was an example of ACD. This study, however, did not consider any other potential predictors of trait displacement beyond this binary variable and the time since speciation, such as the species' environments, habitats, or social behaviors. Furthermore, all possible combinations of species pairs were considered, which raises the potential for phylogenetic pseudo-replication and obscures the fact that most character displacement hypotheses focus on closely-related species, rather than deep time relationships, due to the difficulty in estimating ancestral range overlap.

The study

Ovenbirds, from the family *Furnariidae,* are suboscine passerines found throughout South and Central America. Like other suboscine birds, ovenbirds exhibit little to no song learning (Ricklefs 2002). The clade is entirely insectivorous, with chiefly dull brown coloration but an enormous diversity of habitat type, beak morphology, and song structure (del Hoyo 1992-2011, Tobias et al. 2012a). Though ovenbirds have often been neglected in favor of clades with temperate radiations and/or more charismatic sexual dimorphism, their ecological diversity and reliable response to playback field studies make them an ideal taxon for many comparative analyses (Tobias et al. 2012a). In particular, the high species richness of the clade (270 lineages) is large enough for considerable statistical power but small enough that extensive biometric and song data collection is feasible, and there is a high-quality phylogeny available for the entire radiation (Derryberry et al. 2011). Furthermore, as ovenbirds are found throughout the Neotropics, with generally very small range sizes, meaningful environmental comparisons between species can be considered.

Here, I examine a large dataset of social (song) and ecological (biometric) traits in a recent radiation of Neotropical passerines, the ovenbirds, to directly compare the correlates and trajectories of social and ecological selection. First, I evaluate the tempo and mode of these two evolutionary pathways to determine if ecological and social pressures act in parallel. Second, I calculate levels of recent phenotypic trait divergence in a framework explicitly designed to minimize phylogenetic pseudo-replication and test the extent to which range sympatry, similarity of habitat, and social functions influence social and ecological character displacement.

Materials and Methods.

Data

Following the procedures detailed in Chapter 2, eight biometric measurements were obtained for 270 species from museum specimens and live birds: total bill length, bill length from the anterior tip of the nares, bill width and depth at the anterior tip of the nares, unflattened wing chord length, Kipp’s distance (Claramunt et al. 2011), tarsus length, and tail length. A total of 2415 adult specimens in good condition were measured (1-84 specimens per species, mean ± SD 8.94 ± 7.33), wherever possible sampling at least two males and two females per species.

Fourteen acoustic measurements were obtained from Tobias et al. (2014) for these 270 species: peak frequency, pace, mean maximum frequency, mean minimum frequency, mean bandwidth, song duration, number of notes, variance in note peak frequency across entire song, variance in note bandwidth across entire song, upper frequency bound of the notes, chance in pace between the first and second tercile of the songs, change in pace between the second and third tercile of the songs, mean note duration, and variance in note duration. These measurements came from 1855 high-quality male song recordings, ranging from 1 to 46 samples per species (mean ± SD, 6.44 ± 5.08). Further details of the data collection methodology can be found in the supplements to Tobias et al. (2014). As with Arnegard et al. (2010)'s study of electric signals in mormyrid fish, ovenbird biometric and song structure traits are unlikely to be subject to the same selective pressures, though beak shape does strongly limit the types of songs that can be produced (Derryberry et al. 2012). This is in contrast to other avian strategies for sexual signaling, such as body postures that have been co-opted from foraging movements (Derryberry et al. 2012) or plumage patterns or morphology, which can be simultaneously under positive selection for sexual signaling and negative selection for predator avoidance (Wallace 1889, Hill 2006).

All phylogenetic analyses used the single maximum-likelihood *furnariid* phylogenetic tree published in Derryberry et al. (2011), hereafter "the phylogeny."

To reduce dimensionality, a phylogenetically-controlled principal components analyses (Revell 2009) was performed separately on the biometric and acoustic traits after log-transforming all variables (Table 3.1a-b). The first acoustic PC, which is primarily a measure of pace, the number of notes, and duration, explains 66% of the total variation in ovenbird songs, while the second acoustic PC explains an additional 11% variation and is largely determined by song duration, number of notes, and variation in bandwidth. For the biometric traits, the first PC explains 51% of the total variation and is generally a proxy for body size, while the second PC explains 18% of the variation and is primarily a measure of dispersal ability.

Tempo and mode

For each of the first two principal component of the acoustic and biometric variables, evolutionary rates under a Brownian motion model were calculated and compared using maximum-likelihood methods, with intra-species variation accounted for to minimize Type I error, using the methodology outlined in Adams (2012). To test the goodness-of-fit for the Brownian Motion model, I used the "fitContinuous" function in R's "geiger" package, evaluating the likelihood of four evolutionary models: the null model, Brownian motion (Felsenstein 1973) ("BM"); a model of Brownian motion reverting to a trait mean, Ornstein-Uhlenbeck (Butler and King 2004) ("O-U"); an early-burst model with rapid initial trait evolution followed by stasis (Harmon et al. 2010) ("EB"); and finally a model that allowed the acceleration or deceleration of trait evolution over time (Pagel 1999) ("delta"). To evaluate the degree of phylogenetic signal, Pagel's λ (Pagel 1999) and Blomberg's K (Blomberg et al. 2003) were calculated using the "phylosig" function of the R package "phytools" (Revell 2012).

Character displacement

Range maps were obtained from BirdLife species distribution datasets (BirdLife International and NatureServe 2011) for 215 of the 270 species. Using the R package maptools (Bivand et al. 2016), each of these 215 ranges were intersected with the other 214 ranges, and the amount of range overlap was calculated as a percentage of each species range. That is, for each pair of species A and B, two numbers were recorded: the percent of species A's range that overlaps species B's range and the percent of species B's range overlaps species A's range.

Each of these ranges were then intersected with WorldClim data (Hijmans et al. 2005) to compute mean temperatures, mean precipitation rates, mean annual temperature ranges, and mean annual precipitation ranges for each species. All four climatic variables were log-transformed. Species information on territorial behavior ("territoriality") and social pair bonding ("sociality") were obtained from Tobias et al. (2016) and re-leveled such that 0 denoted the absence of the behavior, 1 weak behavior (seasonal pair bonds and seasonal territory defense), and 2 strong behavior (multi-year pair bonds or multi-year territory defense). The species-level habitat classification detailed in Chapter 2 was also re-leveled such that 0 represented dense habitat, 1 "semi-open" habitat, and 2 open habitat. For each possible species pair, and for each of the four climatic variables, two social behaviors, and one habitat score, I calculated the absolute value of the differences in species values.

Finally, pairwise distances between each species were calculated using the "cophenetic.phylo" command in the R package *ape* 3.5 (Paradis, Claude and Strimmer 2004). Thus, nine variables could be attached to every possible species pair (A, B): time since the most recent common ancestor; the percent of species A's range that contains species B; scores of 0, 1, or 2 for disparity in each of habitat, territoriality, and sociality; and values for differences in average range temperature, precipitation, temperature variability, and precipitation variability.

To control for phylogenetic pseudo-replication, and because I wish to test the factors influencing character displacement of closely-related species (i.e., recently-split lineages), I followed the procedure used by Cooper et al. (2012) to select pairs of recently-diverged lineages. To determine each set of pairs, I selected as a focal individual a species at random from the phylogenetic tree and paired it with a random descendent of its most recent ancestral node; this node was then removed from the phylogeny before the next pair was selected so as not to repeat any evolutionary history within diverging branches. This was repeated until no more species were available (see Figure 3.1). Any set containing fewer than 10 pairs was discarded.

For each set of species pairs, I then ran a linear model predicting the absolute value of the differences in each of the four traits (song PC1, song PC2, biometric PC1, biometric PC2) as a function of the nine predictor variables. The simulation to select species pairs was run 1,000 times, with results reported as the average of these 1,000 linear models. To verify these results, two more sets of linear models were run; one, following Tobias et al. (2014), allowing the relationship between trait divergence and time to vary with the degree of range overlap, and the second excluding all variables except the interaction between time and range overlap.

Figure 3.1: Illustration of species pair selection. 1) A species is selected at random as the focal individual. 2) The focal individual is traced back to its most recent branching point (orange node). 3) A second species is selected at random from all other descendants of the most recent branching point (blue species). This forms the species pair. 4) All descendants of the orange node are removed from the tree. 5) A new focal species is selected from the reduced tree.

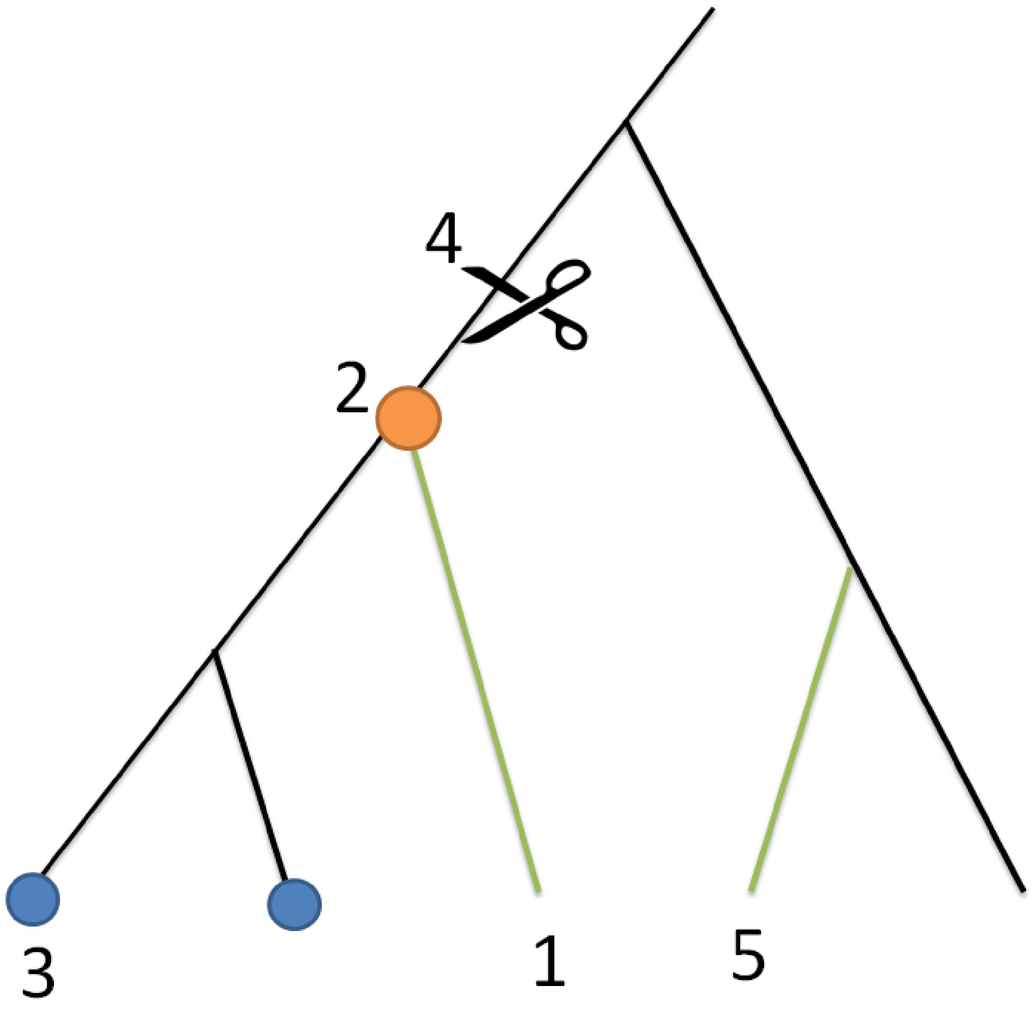
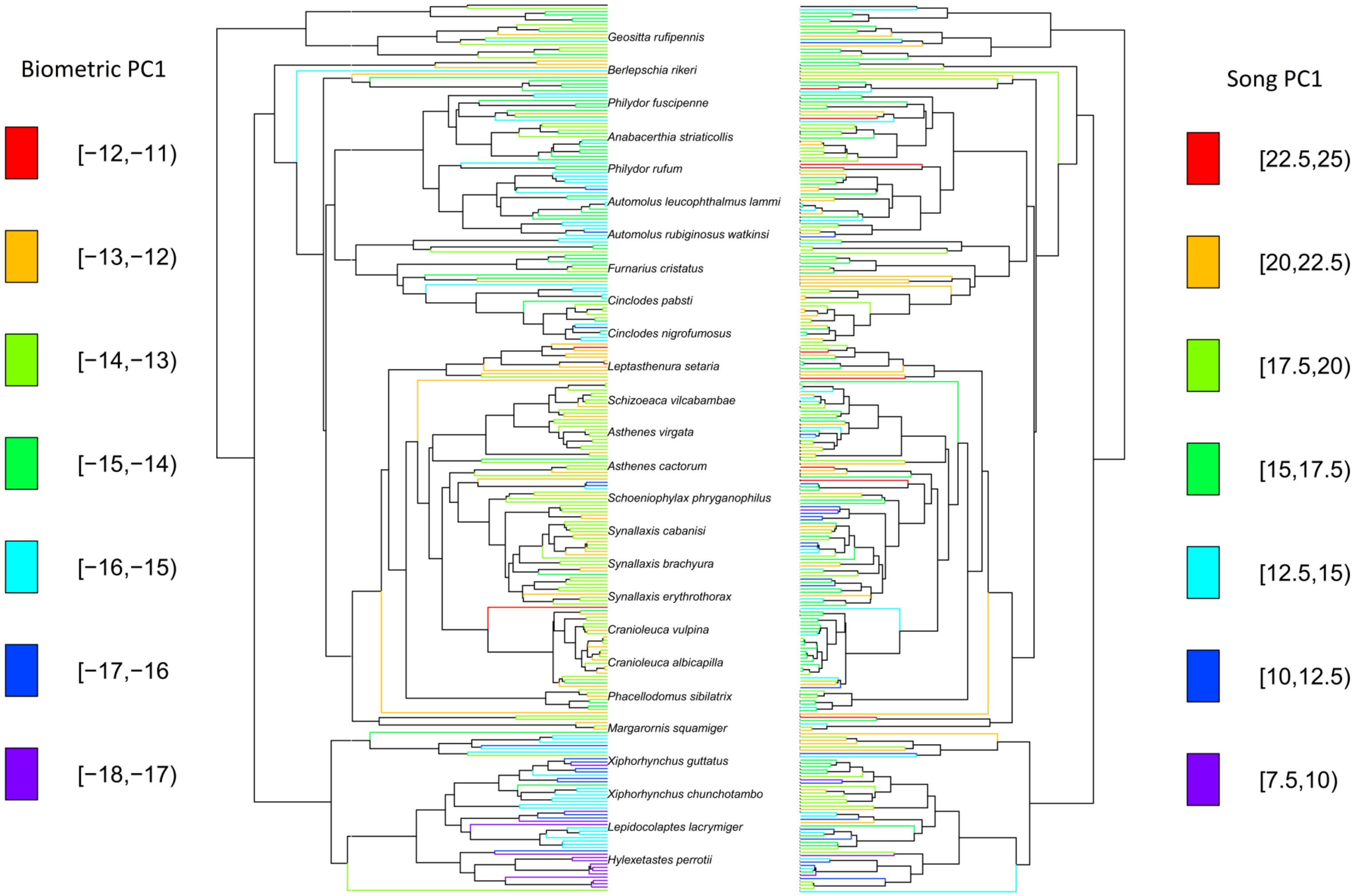


Figure 3.2: Biometric and song evolution in the ovenbirds. Biometric PC1 is displayed on the left and song PC1 on the right. Every tenth species name is displayed.



Results.

Tempo and mode

Song traits were modeled to evolve faster than biometric traits, with the first song principal component evolving at approximately 29.3 times the rate of the first biometric principal component and 357.2 times the rate of the second biometric principal component (Figure 3.2). Song PC2 was modeled to evolve approximately 5.7 times as fast as biometric PC1 and 69 times as fast as biometric PC2. All six pairwise differences in rates were highly significant, with $p << 0.001$ (Table 3.2).

Values of λ, wherein values close to 1 suggest perfect Brownian motion (strong phylogenetic signal) and values close to 0 suggest no correlation between species (no phylogenetic signal) (Pagel 1999), suggest that biometric traits have a stronger phylogenetic signal than song traits (Table 3.3). Similarly, biometric values of K (Blomberg et al. 2003) are greater than 1, indicating that species resemble one another more than expected under Brownian motion (have a stronger phylogenetic signal), whereas the song values of K are very low, demonstrating little phylogenetic signal (Table 3.3).

Of the four macroevolutionary models tested, Brownian motion was the most likely process for biometric PC1, whereas an O-U model (Brownian motion reverting to a long-term mean) was weakly considered the best process for biometric PC2 and strongly considered the best process for both song principal components (Table 3.3). Delta models, which permit the acceleration or deceleration of trait evolution over time, were also supported over pure Brownian motion for biometric PC2 and song PCs 1 and 2, but not as strongly as O-U models. Though there are known biases toward O-U models when, as here, intraspecific variation is not considered (Cooper et al. 2016b), these results still suggest that morphological evolution has stronger phylogenetic constraints than song evolution.

Table 3.1a: Principal components loadings of the eight biometric traits, corrected for phylogenetic non-independence.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Bill culmen length	-0.86	-0.14	0.36	0.20	0.24	0.13	0.00	-0.01
Bill length from nares	-0.87	-0.11	0.35	0.10	-0.23	-0.20	-0.01	0.00
Bill width	-0.70	-0.10	-0.21	-0.56	0.18	-0.18	-0.26	-0.09
Bill depth	-0.78	-0.12	-0.16	-0.50	0.04	0.01	0.26	0.18
Tarsus length	-0.77	0.10	-0.34	0.06	-0.23	0.33	-0.28	0.18
Wing chord length	-0.76	-0.24	-0.28	-0.17	-0.23	0.29	0.15	-0.31
HWI	0.34	-0.94	-0.04	0.02	-0.01	0.00	-0.03	0.03
Tail length	-0.58	-0.04	-0.68	0.40	0.08	-0.14	0.05	0.00
PC variance	0.51	0.18	0.13	0.09	0.03	0.03	0.02	0.01
Cumulative variance	0.51	0.70	0.82	0.91	0.94	0.97	0.99	1.00

Table 3.1b: Principal components loadings of the fourteen song traits, corrected for phylogenetic non-independence.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14
Peak frequency	0.03	-0.41	-0.59	-0.01	0.11	0.09	-0.03	0.63	0.17	0.09	-0.04	0.08	0.14	0.01
Pace	0.76	0.32	-0.12	0.04	0.50	-0.13	0.00	0.05	-0.16	-0.01	-0.02	-0.04	0.01	0.00
Mean maximum frequency	0.07	-0.48	-0.68	0.12	0.10	0.05	-0.01	0.41	0.13	0.24	-0.16	-0.03	-0.04	-0.08
Mean minimum frequency	0.07	-0.17	-0.33	-0.35	0.02	0.11	-0.01	0.79	0.19	-0.22	-0.01	-0.04	-0.09	0.04
Mean bandwidth	0.03	-0.54	-0.61	0.39	0.12	-0.01	0.00	-0.06	0.01	0.40	-0.12	0.00	-0.01	0.02
Song duration	-0.06	0.64	-0.47	0.16	-0.57	0.05	-0.02	-0.02	0.07	0.01	0.01	-0.04	0.01	0.00
Number of notes	0.52	0.71	-0.43	0.16	-0.04	-0.07	-0.02	0.02	-0.07	-0.01	0.00	0.03	-0.01	0.00
Variance in peak frequency	-0.01	-0.15	-0.53	-0.83	-0.05	-0.06	0.00	-0.03	-0.03	0.02	0.01	0.00	0.00	0.00
Variance in bandwidth	0.07	-0.65	-0.66	0.35	0.06	0.01	0.01	-0.03	-0.01	-0.08	0.04	0.00	0.00	0.00
Upper frequency bound	0.10	-0.37	-0.39	-0.14	-0.15	0.00	0.11	-0.18	0.05	-0.39	-0.68	0.01	0.01	0.00
Mean note duration	-0.83	-0.32	0.14	0.04	-0.38	0.05	0.06	0.06	-0.19	0.01	-0.01	0.00	0.00	0.00
Change in pace 1st to 2nd tercile	0.27	-0.42	0.26	0.11	-0.32	-0.73	-0.20	0.03	0.03	-0.01	0.00	0.00	0.00	0.00
Change in pace 2nd to 3rd tercile	0.28	0.13	0.00	0.05	-0.03	-0.42	0.84	0.01	0.09	0.02	0.03	0.00	0.00	0.00
Variance in note duration	-0.99	0.08	-0.05	0.01	0.06	-0.03	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
PC variance	0.66	0.11	0.09	0.06	0.04	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Cumulative variance	0.66	0.77	0.86	0.92	0.96	0.97	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00

Table 3.2: The tempo of the first two song and biometric principal components. Calculated rates are listed along the diagonal (light grey). For each pairwise comparison, listed in white is the difference in log likelihood between a model where the two variables evolve independently and a model constraining the variables to evolve at the same rate. Any difference in likelihood above 3.84 is significant at the $\alpha = 0.05$ level.

	Song PC1	Song PC2	Biometric PC1	Biometric PC2
Song PC1	1.786	177.4	559.8	1203.4
Song PC2		0.345	182.5	760.9
Biometric PC1			0.061	331.4
Biometric PC2				0.005

Table 3.3: The evolutionary mode of the first two song and biometric principal components. λ refers to Pagel's lambda (Pagel 1999) and *K* to Blomberg's *K* (Blomberg et al 2003), both measures of trait phylogenetic signal. Listed are the likelihood values for four possible modes of evolution: Brownian motion ("BM"), Brownian motion reverting to a trait mean (Ornstein-Uhlenbeck, "OU"), an early-burst model ("EB"), and a model allowing acceleration of the trait over time ("Delta"). Brownian motion is the null model; listed for OU, EB, and Delta models is the change in likelihood between that model and Brownian motion. Any difference in likelihood above 3.84 is significant at the α = 0.05 level and is denoted by dark grey. The best model for each trait is highlighted in light grey.

	λ	K	BM	OU	Δ OU	EB	Δ EB	Delta	Δ Delta
Song PC1	0.798	0.217	-723.8	-687.3	36.5	-723.8	0.0	-704.5	19.3
Song PC2	0.846	0.274	-502.0	-471.7	30.3	-502.0	0.0	-484.1	17.9
Biometric PC1	0.967	1.189	-267.9	-267.6	0.3	-267.9	0.0	-267.7	0.2
Biometric PC2	0.931	1.278	61.4	68.4	7.1	61.4	0.0	66.3	4.9

Table 3.4: Trait divergence in song and biometric principal components 1 and 2 as predicted by range overlap, time since divergence, and disparity in habitat, social behavior, and climate. Results are of linear models averaged across 1,000 simulated sets of species pairs. Significant coefficient estimates ($p < 0.05$) are highlighted in grey.

	Biometric PC1				Biometric PC2			
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	31.20	1.22	27.85	0.00	21.47	1.15	20.41	0.00
Time	-0.01	0.04	-0.19	0.50	0.01	0.04	0.22	0.50
Range overlap	0.24	2.27	0.16	0.50	0.02	2.15	0.06	0.51
Habitat disparity	-0.20	1.20	-0.18	0.51	-0.44	1.14	-0.42	0.49
Sociality disparity	0.38	2.35	0.31	0.49	0.57	2.22	0.44	0.48
Territoriality disparity	1.19	1.52	0.88	0.39	1.14	1.44	0.89	0.40
Disparity in mean temperature	-0.12	0.18	-0.74	0.43	-0.07	0.17	-0.47	0.48
Disparity in mean temperature variability	0.16	0.21	0.87	0.40	0.19	0.19	1.13	0.34
Disparity in mean precipitation	0.00	0.00	-0.08	0.53	0.00	0.00	-0.24	0.52
Disparity in mean precipitation variability	0.00	0.01	0.19	0.53	0.00	0.01	0.16	0.53

	Song PC1				Song PC2			
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	2.39	0.87	3.02	0.05	41.36	1.20	38.02	0.00
Time	0.01	0.03	0.22	0.52	-0.01	0.04	-0.14	0.51
Range overlap	-0.19	1.62	-0.08	0.54	-0.67	2.24	-0.28	0.53
Habitat disparity	-0.06	0.86	-0.09	0.51	-0.08	1.20	-0.08	0.52
Sociality disparity	-0.49	1.70	-0.40	0.44	0.06	2.35	0.13	0.53
Territoriality disparity	0.65	1.09	0.78	0.39	0.94	1.51	0.66	0.44
Disparity in mean temperature	0.07	0.13	0.55	0.48	-0.13	0.17	-0.78	0.41
Disparity in mean temperature variability	-0.10	0.15	-0.81	0.40	0.13	0.20	0.70	0.43
Disparity in mean precipitation	0.00	0.00	0.84	0.41	0.00	0.00	0.02	0.51
Disparity in mean precipitation variability	0.00	0.01	-0.11	0.57	0.00	0.01	0.14	0.52

Table 3.5: Trait divergence in song and biometric principal components 1 and 2 as predicted by range overlap, time since divergence, and disparity in habitat, social behavior, and climate, with the coefficient estimate for range overlap allowed to vary with time (interaction term). Results are of linear models averaged across 1,000 simulated sets of species pairs. Significant coefficient estimates ($p < 0.05$) are highlighted in grey.

	Biometric PC1				Biometric PC2			
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	31.22	1.21	27.93	0.00	21.46	1.14	20.56	0.00
Time	-0.01	0.05	-0.17	0.49	0.01	0.05	0.21	0.50
Range overlap	0.61	4.04	0.10	0.50	0.63	3.88	0.07	0.50
Habitat disparity	-0.15	1.17	-0.14	0.52	-0.40	1.10	-0.40	0.51
Sociality disparity	0.46	2.30	0.34	0.49	0.65	2.17	0.47	0.47
Territoriality disparity	1.15	1.56	0.85	0.41	1.08	1.48	0.85	0.41
Disparity in mean temperature	-0.12	0.17	-0.75	0.41	-0.07	0.16	-0.48	0.47
Disparity in mean temperature variability	0.17	0.20	0.93	0.39	0.20	0.19	1.19	0.32
Disparity in mean precipitation	0.00	0.00	-0.10	0.54	0.00	0.00	-0.27	0.53
Disparity in mean precipitation variability	0.00	0.01	0.20	0.53	0.00	0.01	0.18	0.54
Time * Range	-0.02	0.20	0.01	0.52	-0.03	0.19	-0.03	0.51

	Song PC1				Song PC2			
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	2.35	0.85	2.97	0.05	41.39	1.20	38.16	0.00
Time	0.01	0.04	0.41	0.47	-0.01	0.05	-0.24	0.50
Range overlap	-0.20	2.89	0.16	0.54	-0.84	4.06	-0.35	0.51
Habitat disparity	-0.07	0.82	-0.12	0.53	-0.02	1.17	-0.03	0.54
Sociality disparity	-0.60	1.61	-0.46	0.43	0.19	2.28	0.14	0.53
Territoriality disparity	0.77	1.10	0.90	0.38	0.84	1.55	0.63	0.44
Disparity in mean temperature	0.06	0.12	0.53	0.48	-0.12	0.17	-0.74	0.41
Disparity in mean temperature variability	-0.11	0.14	-0.85	0.40	0.13	0.20	0.74	0.42
Disparity in mean precipitation	0.00	0.00	0.84	0.41	0.00	0.00	0.02	0.53
Disparity in mean precipitation variability	0.00	0.01	-0.14	0.57	0.00	0.01	0.14	0.53
Time * Range	0.00	0.14	-0.27	0.50	0.02	0.20	0.22	0.52

Table 3.6: Trait divergence in song and biometric principal components 1 and 2 as predicted by range overlap and time since divergence, with the coefficient estimate for range overlap allowed to vary with time (interaction term). Results are of linear models averaged across 1,000 simulated sets of species pairs. Significant coefficient estimates ($p < 0.05$) are highlighted in grey.

	Biometric PC1				Biometric PC2			
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	31.48	0.75	44.03	0.00	21.87	0.71	32.58	0.00
Time	0.00	0.04	-0.01	0.50	0.02	0.04	0.44	0.48
Range overlap	0.38	3.63	0.16	0.50	0.11	3.42	0.10	0.49
Time * Range	-0.01	0.17	0.03	0.52	-0.01	0.16	-0.02	0.52
	Song PC1				Song PC2			
	Estimate	SE	t value	p value	Estimate	SE	t value	p value
(Intercept)	2.49	0.53	4.97	0.00	41.64	0.73	60.58	0.00
Time	0.02	0.03	0.97	0.39	-0.01	0.04	-0.22	0.49
Range overlap	0.40	2.53	0.20	0.54	-1.15	3.55	-0.30	0.52
Time * Range	-0.04	0.12	-0.45	0.48	0.03	0.16	0.26	0.52

Character displacement

Remarkably, no predictor variable was found to be related to any of the pairwise differences in principal component, even time (Tables 3.4-6) That is, I find no evidence of either convergent or divergent species-level character displacement, suggesting some combination of (a) the competition-based processes of character displacement are sufficiently modulated by environmental filtering so as to produce no pattern, (b) character displacement only operates at the level of more distantly related species, and/or (c) the primary forces shaping recent ovenbird phenotypic evolution are not any of the variables tested here.

Discussion.

The capacity of social traits to evolve rapidly is often implicated in bursts of species radiations, but this assumption is rarely tested empirically. Here, I demonstrate that social traits have evolved much faster than ecological traits in ovenbirds, with less adherence to the family's phylogenetic structure. Furthermore, I find no evidence of either convergence or divergence in social and ecological traits in relational to the degree of range sympatry among closely-related species.

Tempo and mode

Ovenbird song traits evolve faster and with less phylogenetic signal than biometric traits. This is in line with many other studies of signal evolution, which have found that behavioral (Blomberg et al. 2003) and/or sexual (Arnegard et al. 2010) traits evolve more rapidly, suggesting that such traits can be important early drivers of diversification (Ritchie

2007). Social signaling plays a key role in preventing hybridization among genetically compatible populations; particularly as I found no evidence of character displacement in the song traits of recently-diverged lineages, rapidly evolving song could facilitate a faster process of speciation (Tobias and Seddon 2009, Arnegard et al. 2010, Ritchie 2007, Owens et al. 1999).

In theory, ecological and environmental variables should constrain both social (Bradbury and Vehrencamp 2011, Derryberry 2009, Cummings 2007) and ecological (Losos et al. 1998, Schluter 2000, Lovette et al. 2002) traits, especially in the case of song, which is at least in part dependent on the shape of the beak (Podos, Huber and Taft 2004a, Podos, Southall and Rossi-Santos 2004b). Indeed, a study of the ovenbird subfamily *Dendrocolaptinae* (the woodcreepers) found strong evidence for correlated song and beak evolution (Derryberry et al. 2012). Despite these evolutionary restrictions, it seems that song is a more flexible trait, constrained less by phylogenetic history than are the biometric variables.

Character displacement

The theory of population-level character displacement is well-described, but the extent of its applicability remains unknown, particularly at the species level. Most of the evidence for character displacement is restricted to a small number of species, often a single pair (Grant and Grant 2010, Grant and Grant 2006, Stre et al. 1997, Pfennig and Pfennig 2009, Schluter and McPhail 1992). Furthermore, the relatively recent concept of agonistic character displacement, ACD, can be used to predict both convergence and divergence in signaling traits (Grether et al. 2009). I find no evidence of character displacement occurring in recently-speciated groups of ovenbirds, a result that could indicate several evolutionary patterns.

It could be that the process of character displacement occurs not among recently-diverged lineages, as is typically suggested, but instead across deeper time, as suggested by Tobias et al. (2014). It could instead or additionally be that environmental filtering processes counteract any character displacement, together creating this null result. Furthermore, the main driver of recent trait divergence in ovenbirds could be an ecological or social difference not captured by any of the nine predictor variables tested here (time since speciation, proportion of range overlap, difference in habitat categorization, four environmental variables, and two measures of social behavior). It could of course instead be that these traits are determined by a random, neutral process (Hubbell 2001).

Finally, most studies of character displacement consider the phenomenon as operating at the level of the population rather than across the entire species. That is, it is the traits of the sympatric population that should be different from the allopatric populations (Brown and Wilson 1956, Grant and Grant 2006, Kirschel et al. 2009, Pfennig, Rice and Martin 2006, Pfennig and Pfennig 2009, Schluter and McPhail 1992). The lack of family-wide character displacement in this dataset does not preclude the process from occurring within species between allopatric and sympatric populations, though this is a harder phenomenon to test. Most museum specimens are not documented well enough to provide location data accurate enough to determine whether a given set of biometric traits is allopatric or sympatric; geo-tagged song recordings, however, together with field measurements and recently-collected specimens could provide the level of detail to test population-level divergence across this family.

Conclusions

Here, I establish that social traits evolve more rapidly and with less predictability than ecological traits in the avian family *Furnariidae*, suggesting that rapid signal evolution could facilitate species radiations. Contrary to a recent analysis of *furnariid* character displacement across deep time, however, I find that precise measures of range sympatry and methodology designed to minimize phylogenetic pseudo-replication in recently-diverged lineages reveal no evidence of either convergence or divergence in social and ecological traits. This result suggests that neither a competition-based hypothesis of character displacement nor environmental filtering dominates trait evolution at the interspecific, recent scale. As more trait datasets become available and as well-resolved high-confidence phylogenies continue to be published, more broad-scale studies of phenotypic trait evolution such as this will be possible, allowing empirical evidence to evaluate well-established but rarely tested theories of character displacement and the relative roles of social and ecological selection.

CHAPTER 4: CONTRASTING SELECTION ON MALES AND FEMALE AND THE EVOLUTION OF SONG IN BIRDS.

Summary

Explaining dramatic differences between the sexes in phenotypes and behaviors has long been a major focus of evolutionary biology (Darwin 1871). Of critical interest has been the evolution of elaborate ornamentation, i.e., traits neutral or detrimental to survival. Although traditionally explained by female-choice sexual selection and/or male-male competition (Tobias et al. 2012b, Andersson 1994), the widespread occurrence of mutual ornamentation – i.e., conspicuous traits, such as song, found in both sexes (Langmore 1998, Evans and Pinxten 1998) – challenges this view. In particular, whether the same processes shape the evolution of ornamentation in males versus females remains controversial (Kraaijeveld and Komdeur 2007, Tobias et al. 2012b). Here, I conduct the first test of the drivers of evolution of song in males versus females within a global comparative framework for the world's birds (10,257 species), addressing the roles of ecology, social behavior, habitat, and climate. My phylogenetic models reveal that song in both sexes is associated with territory defense, body mass, and migratory patterns. However, I find that while male song is strongly predicted by habitat type, female song is associated with diet, temperature, and social bond stability (i.e., the presence or absence of pair bonding). Not only does this study provide the first broad-scale comparative evidence that ornaments such as song evolve along different trajectories in males versus females, it can help explain the predominance of species with female ornaments in the tropics and southern hemisphere.

Introduction

Female ornaments have long been assumed to arise through genetic correlation, with selection operating only in males but arising in females because they share most of their genome with males (Lande 1980, Rice 1984, Darwin 1871). Although this idea received initial support from both theoretical models (Lande 1980) and empirical studies (Price 1996, Potti and Canal 2011), recent research confirms the importance of selection for variation in female ornamentation among species (Odom et al. 2014, Amundsen 2000, Tobias et al. 2012b, Rosvall 2011, Clutton-Brock and Huchard 2013, Cain and Rosvall 2014, Dale et al. 2015). Opinions are divided about whether the pressures driving the evolution of female ornaments are the same as those for males – that is, primarily developing due to competition for mating opportunities – or are different due to fundamental differences between the sexes in the costs of reproduction. In particular, although males are thought to maximize fitness through access to mates, females may maximize fitness by defending resources associated with fecundity, including resources required to raise offspring (Trivers 1972, Bateman 1948). Few studies, however, have tested these hypotheses in a comparative framework, and it remains unclear whether ornaments evolve under contrasting selective processes in males and females (Kraaijeveld and Komdeur 2007, Odom et al. 2014). Furthermore, if selection pressures favoring ornaments differ between the sexes, it has not yet been established whether those drivers are related to competition for resources inherently ecological (e.g., food or foraging territories) (Stankowich and Caro 2009, West-Eberhard 1983, Arcese, Stoddard and Hiebert 1988, Baptista et al. 1993, Cain and Langmore 2015) or social (e.g., group membership, pair bonds, or parental care) (Rosvall 2011, Kraaijeveld and Komdeur 2007, Cooney and Cockburn 1995, Garamszegi et al. 2006).

Birds, with their high phenotypic and species diversity, global distribution, and well-studied phylogeny, life history and behavior, provide an ideal study system for large-scale comparative analysis (Kissling, Sekercioglu and Jetz 2012, Odom et al. 2014, Jetz and Rubenstein 2011, Dale et al. 2015). The main challenge to any comparative approach aiming to be representative, however, is how to reproducibly and objectively quantify sexual traits across a large number of species. Ornamentation can vary drastically among species even within a single clade, and it can be difficult to determine which morphologies or strategies are analogous. Color, one of the most obvious sexual signals, is hard to measure consistently across many species (Delhey and Peters 2008), and cues that are conspicuous to birds – e.g., UV reflectance (Stoddard and Prum 2011) – may be opaque to human vision (Endler and Mielke 2005). Songs can be even more intricate and thus ambiguous within a multi-species standardization. Furthermore, many of these ornaments simultaneously undergo natural selection unrelated to mate attraction, such as cryptic feather patterns for predator avoidance (Hill 2006, Wallace 1889). Consequently, most studies of avian ornamentation have thus far been restricted to relatively small samples of species, limited in scope either geographically (Garamszegi et al. 2006, Diamond and Terborgh 1968) or taxonomically (Badyaev, Hill and Weckworth 2002, Pavlova, Pinxten and Eens 2005, Price 2009, Odom et al. 2014), making it difficult to reach general conclusions about the role of sexual selection on avian ornaments.

By focusing on the binary trait of song presence, however, I am able to circumvent many of these difficulties. The presence or absence of song – defined here to mean a complex vocalization used by adult birds in mate attraction and/or territory defense – is a trait standardized across the entire bird tree and is known for all but the most obscure of species (del Hoyo 1992-2011). Furthermore, the presence of song, unlike morphological characteristics or more specific auditory cues, is relatively unencumbered by non-sexual selective pressures (Odom et al. 2014, Garamszegi et al. 2006, Langmore 1998). Here, using broadly-defined social and ecological characters and key environmental variables, I examine the global biogeographic and phylogenetic distribution of male and female song, examine the drivers of this pattern, and then assess the co-evolution of the key correlates of female and male song.

Results and Discussion

Phylogenetic and biogeographic distribution of male and female song

Song has evolved multiple times across the avian tree of life (Figure 4.1). I found that 8284 species of birds (85%) have male song and 2959 species (30%) have female song. Just 31 species (< 1%) have only female song, and thus 30% of all bird species have song in both sexes and 55% of all species have song in males only. Despite the wide distribution of song across the avian tree (Figure 4.1), there is substantial phylogenetic signal, though it deviates significantly from that expected under an evolutionary model of Brownian motion (Pagel's $\lambda = 0.8544$, $p < 0.001$ for female song; Pagel's $\lambda = 0.9146$, $p < 0.001$ for male song). For example, 95% of the passerines (5903 of 6189 species) exhibit male song and 27% (1663 of 6189) exhibit female song, whereas just 23% of the Anseriformes (38 of 168 species) exhibit male song and 2% (3 of 168) exhibit female song.

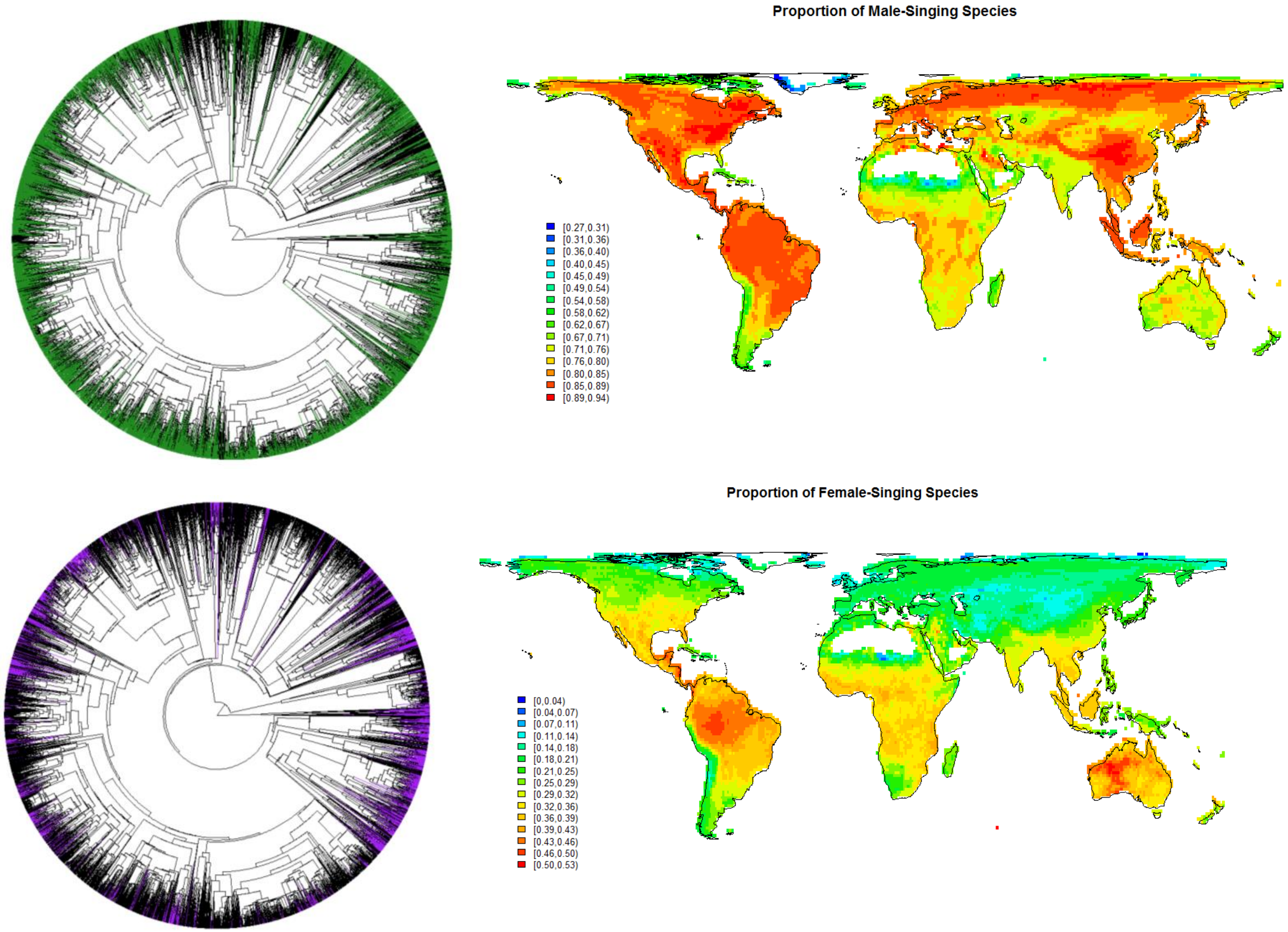


Figure 4.1: Phylogenetic structure (left) and biogeography (right) of male (top) and female song (bottom). In (top left), green denotes lineages with male song (*n* = 8284) and black lineages without male song (*n* = 1450), and in (bottom left), purple denotes lineages

with female song (*n* = 2959) and black lineages without female song (*n* = 6775). Phylogeny includes 9734 species from (Jetz et al. 2012). In (right), each grid cell represents 110 km x 110 km, with cells containing < 50% landmass or < 20 bird species excluded (white). Colors indicate the proportion of birds breeding in that location with (top) male song and (bottom) female song, ranging from dark blue (low proportions, 0.27 – 0.31 for male song and 0.00 – 0.04 for female song) to red (0.89 – 0.94 for male song and 0.50 – 0.53 for female song).

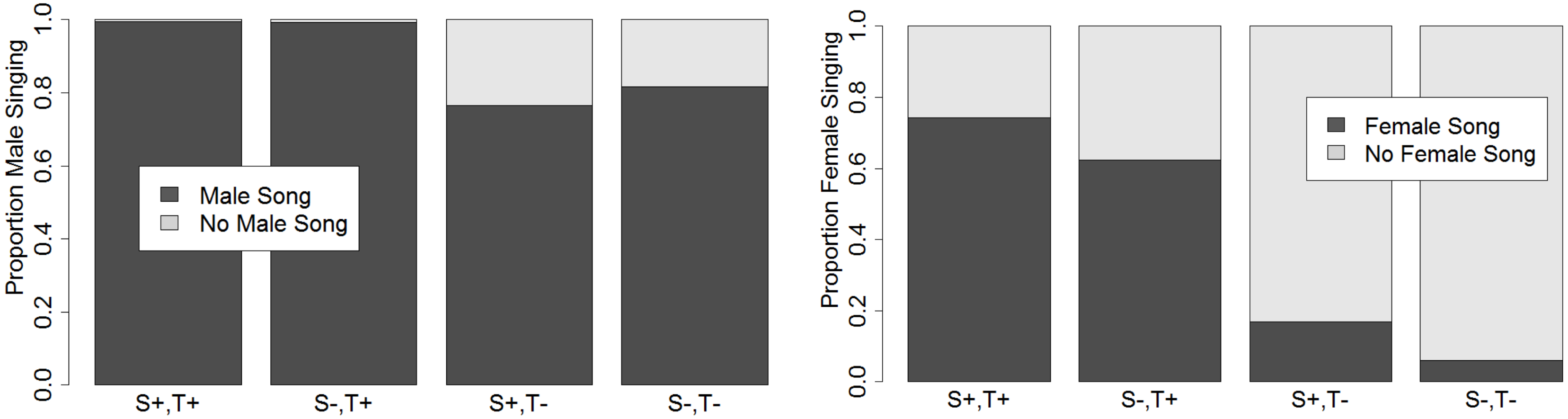


Figure 4.2: Proportions of (a) male and (b) female song in species partitioned by social stability and territoriality. Each column represents a species category: from left to right, species with both territoriality and social stability, species with territoriality but no social stability, species with social stability but no territoriality, and species with neither social stability nor territoriality. Dark gray represents the portion of species within the category that have (a) male or (b) female song.

Just as the occurrence of male and female song is not distributed evenly throughout the avian phylogenetic tree, I found strong sex differences in the global biogeography of song (Figure 4.1). Specifically, male song is fairly evenly distributed throughout the northern latitudes, East and Southeast Asia, and the New World, but is less prominent in the southern latitudes (Australia, New Zealand, and southern South America), the Middle East, the Tibetan plateau, the Caucasus, and throughout Africa. Conversely, the proportions of species producing female song are highest in the Amazon basin and Western Australia and lowest in the northern latitudes. My finding that song is unequally distributed across the globe in the two sexes, accords with previous studies conducted at smaller taxonomic and geographic scales (Odom et al. 2014, Garamszegi et al. 2006, Langmore 1998), and provides an opportunity to identify the environmental and social drivers of ornament evolution.

Predictors of male and female song

Song in males is primarily driven by female mate choice and male-male competition over territories and mate acquisition (Tobias et al. 2012b, Darwin 1871, West-Eberhard 1983, Kraaijeveld and Komdeur 2007, Clutton-Brock 2007). The function of widespread female ornamentation, however, when acknowledged at all, is much less clear. Female song has been shown to be both an ornament and an armament (Tobias and Seddon 2009); proposed roles of female song include territory defense (Ulmar Grafe, Bitz and Wink 2004, Hall and Peters 2008, Illes and Yunes-Jimenez 2009), mate-guarding (Ulmar Grafe et al. 2004), synchronization of breeding (Hall 2009), male mate selection (Jones and Hunter 1993, Langmore 1998), and the defense of non-territorial ecological resources against female competitors (Marshall-Ball and Slater 2004, Tobias et al. 2012b, Cain and Langmore

2015). These hypotheses can be broadly divided into two categories within the framework of social selection (Tobias et al. 2012b): intrasexual competition over or intersexual selection on mating resources (Clutton-Brock 2007), and intra- and inter-sexual competition over ecological resources (LeBas 2006, Kraaijeveld and Komdeur 2007, Cain and Langmore 2015), both of which can be influenced by further extrinsic factors (i.e. abiotic conditions, such as climate and habitat).

To test the relative importance of these functions, I used Bayesian binary-response mixed-effect models to examine the roles of these factors in the evolution of male and female song. I found that territoriality was paramount to the evolution of both male and female song; both male and female birds with strong year-round territory defense were the most likely to sing, with an intermediate probability for seasonal or weak territory defense (pMCMC < 0.001) and a very low probability for no territoriality ($p < 0.001$). Within male birds, the next strongest predictor of song was migratory behavior, with migratory species more likely to sing than partially- or non-migratory species ($p = 0.002$). With female song, however, the next strongest predictors of song were diet (with more song found in frugivorous, nectivorous, or insect-eating birds than omnivores or consumers of vertebrates or plants, $p < 0.001$) and pair bonding behavior, with seasonal bonds showing much lower levels of female song ($p = 0.001$) than either year-round bonds or a solitary lifestyle. Migration plays a significant though small role in predicting female song, though with *partially* migratory species, rather than fully migratory, displaying the highest levels of female song.

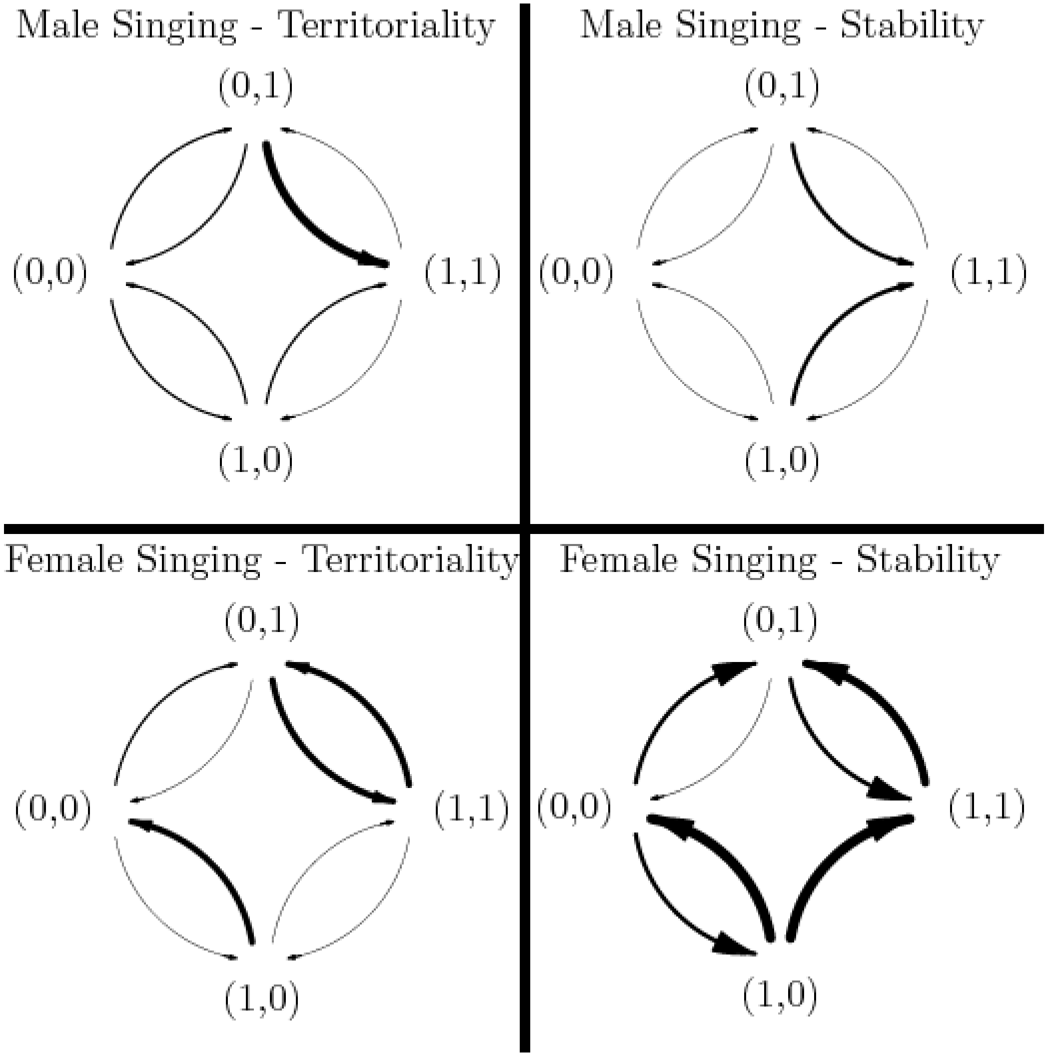
Once these two strong intrinsic predictors are accounted for, two extrinsic variables are linked with song behavior; birds which nest in open habitat, as opposed to dense or semi-

Table 4.1: Results of a generalized linear mixed model testing the effects of intrinsic and extrinsic predictors of male song (left) and female song (right) across all birds. Model used a Markov-chain Monte-Carlo algorithm (MCMCglmm) with phylogeny as a random effect averaged across 100 trees. Significant results are shaded in grey.

	MALE SONG						FEMALE SONG					
	z	2.5% CL	97.5% CI	% Change	SD	p-value	z	2.5% CL	97.5% CI	% Change	SD	p-value
Intercept	4.965	3.305	6.613	-	-	0.001	0.623	-0.981	2.201	-	-	0.499
Intrinsic Fixed Effect												
Migration (part migratory, ref = full)	-0.061	-0.341	0.223	-0.6	0.152	0.675	**0.348**	**0.087**	**0.608**	**2.5**	**0.128**	**0.010**
Migration (fully migratory)	**0.732**	**0.309**	**1.158**	**7.5**	**0.221**	**0.002**	0.141	-0.221	0.504	1.0	0.196	0.460
Diet (animals, ref = plants)	0.229	-0.103	0.562	2.3	0.180	0.190	-	-	-	-	-	-
Diet (plants and animals)	-0.264	-1.156	0.616	-2.7	0.451	0.571	-	-	-	-	-	-
Diet (fruit and nectar)	-	-	-	-	-	-	**1.128**	**0.533**	**1.728**	**8.2**	**0.315**	**0.002**
Diet (invertebrates)	-	-	-	-	-	-	**0.979**	**0.441**	**1.520**	**7.1**	**0.287**	**0.002**
Diet (omnivorous)	-	-	-	-	-	-	0.527	-0.377	1.447	3.8	0.496	0.264
Diet (plants)	-	-	-	-	-	-	0.903	-0.277	1.053	6.6	0.335	0.304
Dietary specialism (general, ref = sp)	-0.240	-0.985	0.512	-2.4	0.389	0.535	0.327	-0.336	1.000	2.4	0.354	0.347
Dietary specialism (omnivore)	0.461	-0.703	0.045	4.7	0.688	0.084	0.845	-0.196	1.897	6.1	0.547	0.119
Body mass	**-0.249**	**-0.468**	**-0.025**	**-2.5**	**0.113**	**0.031**	**0.287**	**0.097**	**0.479**	**2.1**	**0.100**	**0.005**
Territoriality (seasonal/weak)	**-2.312**	**-2.848**	**-1.794**	**-23.6**	**0.279**	**0.001**	**-2.302**	**-2.498**	**-2.107**	**-16.7**	**0.108**	**0.001**
Territoriality (none, ref = strong)	**-3.432**	**-4.016**	**-2.851**	**-35.1**	**0.313**	**0.001**	**-3.466**	**-3.848**	**-3.030**	**-25.2**	**0.211**	**0.001**
Mating system (cooperative breeding)	-0.351	-0.705	0.006	-3.6	0.193	0.059	0.174	-0.071	0.416	1.3	0.131	0.176
Social stability (seasonal bonds)	0.056	-0.201	0.316	0.6	0.141	0.683	**-0.916**	**-1.140**	**-0.687**	**-6.7**	**0.119**	**0.002**
Social stability (solitary, ref = stable)	0.547	-0.056	1.158	5.6	0.320	0.085	-0.640	-1.335	0.048	-4.7	0.366	0.070
Extrinsic Fixed Effect												
Mean annual temperature	0.079	-0.120	0.275	0.8	0.098	0.446	0.170	-0.007	0.346	1.2	0.097	0.065
Annual temperature range	0.240	-0.017	0.494	2.5	0.132	0.072	**0.319**	**0.111**	**0.525**	**2.3**	**0.111**	**0.004**

Mean annual precipitation	0.034	-0.149	0.215	0.3	0.092	0.719	0.019	-0.123	0.160	0.1	0.073	0.793
Annual precipitation range	-0.001	-0.155	0.153	0.0	0.082	0.940	0.035	-0.076	0.145	0.3	0.061	0.500
Median range latitude	0.013	-0.119	0.148	0.1	0.066	0.855	-0.001	-0.006	0.004	0.0	0.003	0.653
Habitat (semi-open)	-0.052	-0.304	0.206	-0.5	0.128	0.695	0.159	-0.019	0.335	1.2	0.089	0.085
Habitat (open, ref = closed)	**-0.444**	**-0.779**	**-0.101**	**-4.5**	**0.174**	**0.012**	-0.077	-0.339	0.192	-0.6	0.143	0.573
Random Effect				Partial R2						Partial R2		
Phylogeny (n = 6377)	6	6	6	0.746	-	-	6	6	6	0.746	-	-
Summary statistics												
DIC	1639	-	-	-	-	-	2937	-	-	-	-	-
R2	0.885	-	-	-	-	-	0.906	-	-	-	-	-

Figure 4.3 (left): Diagram showing median relative transition rates, *q*, between states, as determined by BayesTraits. Arrow width varies in proportion to the log of *q*. Clockwise from upper left, transitions among states of (a) male song and territoriality, (b) male song and social stability, (c) female song and social stability, and (d) female song and territoriality. (0,0) is the absence of both traits, (1,0) is the presence of respective song trait but absence of the other trait, (0,1) is the absence of the respective song trait but the presence of the other trait, and (1,1) is the presence of both traits. **Table 4.2** (right): Relative transition rates (q ± SD) between male/female song and territoriality or social stability. qXY denotes the transition from state X to state Y. State 1 is no song, no ecological trait; 2 is no song with the ecological trait; 3 is song but no ecological trait, and 4 is song and the ecological trait.



Relative transitions rates (q) of song and territoriality or stability, ± SD			
		Male	Female
Territoriality	q12	0.517 ± 0.338	0.530 ± 0.063
	q13	0.951 ± 0.086	0.116 ± 0.022
	q21	0.953 ± 0.085	0.520 ± 0.054
	q24	3.129 ± 0.366	1.791 ± 0.122
	q31	0.952 ± 0.083	0.955 ± 0.596
	q34	0.954 ± 0.083	0.217 ± 0.183
	q42	0.194 ± 0.021	1.792 ± 0.123
	q43	0.195 ± 0.021	0.115 ± 0.020
Stability	q12	0.591 ± 0.605	0.332 ± 0.392
	q13	1.299 ± 0.618	1.109 ± 0.262
	q21	0.077 ± 0.013	0.111 ± 0.022
	q24	1.770 ± 0.219	1.036 ± 0.075
	q31	0.929 ± 0.432	35.657 ± 33.091
	q34	1.118 ± 0.442	55.330 ± 33.863
	q42	0.237 ± 0.028	1.997 ± 0.148
	q43	0.077 ± 0.012	0.045 ± 0.051

open, are less likely to have male song (p = 0.012), and birds whose ranges face higher annual temperature ranges are more likely to have female song (p = 0.004). Though mutual ornamentation has been generally poorly studied (Kraaijeveld and Komdeur 2007), female bird song in particular tends to suffer from a geographic bias, as the highest proportions of female song are found in the tropics and the southern hemisphere (Figure 4.1), areas less intensely surveyed during the heyday of European and North American field biology (Langmore 1998, Brunton and Li 2006). My phylogenetically-controlled linear models, however, reveal these patterns not to be a function of latitude, but rather of phylogeny and, to a small extent, temperature variability, underscoring the role of intrinsic life histories in determining ornamentation.

Similarly, the intrinsic factors of migration and body mass act on male and female song in separate directions, highlighting the difference in roles that the two sexes' songs play. Male song is most prevalent in fully migratory species – species with shorter breeding seasons at higher latitudes that must attract mates quickly in order to reproduce (Irwin 2000, Kokko 1999, Collins et al. 2009). Conversely, female song prevails in partially-migratory species, where there is a balance between the need to defend established territories and the need to maintain pair bonds. Male song is inversely correlated with body mass, a pattern reflecting life history differences between passerines and non-passerines. Female song, however, is positively correlated with body mass; all other variables being equal, larger birds are more likely to sing. This could be explained by differential costs related to predation, as smaller female birds may more strongly value crypsis and thus benefit more from not singing than their larger counterparts. While evidence for this hypothesis remains circumstantial, other experiments have demonstrated differential correlations between ornamentation and nest predation in male and female warbles and finches (Martin and Badyaev 1996), and the plumage under male-choice sexual selection in female cardinals is in the underwings so as to counteract the higher predation rates on brightly-colored female birds (Jawor et al. 2003). Furthermore, female songs tend to be less elaborate than those of the male conspecifics, sung at lower frequencies so as to avoid detection by predators (Rubenstein and Lovette 2009). Similar themes of predator avoidance can be seen in the relationship between male song and primary habitat type, with song being least prevalent in open habitat – that is, the type of habitat where singing is most likely to attract predators. Interestingly, I find no relationship between cooperative breeding and female song, a link that has been found in mutual plumage ornamentation in passerine birds (Dale et al. 2015).

If female song, as a mutual ornament, merely represented an evolutionary stepping-stone prior to sexual decoupling (Kraaijeveld et al. 2007), I would expect less predictive power for the female song models than those for male song. I find the opposite pattern, however: my linear models have an estimated conditional R^2-value (as defined in (Nakagawa and Schielzeth 2013)) of 0.906 for female song, which is slightly higher than the R^2 of 0.885 for male song. This shows that female song, rather than being a phylogenetic by-product of the biologically more important male song, is not only predicted by slightly different variables than male song, but also has a marginally stronger relationship to those variables.

Co-evolution of male and female song with life history traits

This regression analysis, although highly instructive about the intrinsic and extrinsic factors correlated with the evolution of song, cannot provide any information about the presence or direction of causality. To investigate how life history and song have co-evolved, I used the Discrete function in BayesTraits (Pagel and Meade 2006) to investigate the two variables most commonly linked to song, territory defense and pair bonding. These analyses reveal that female song has co-evolved with both territoriality (LHR = 123, $p < 0.0001$) and social stability (LHR = 29, $p < 0.0001$), but that male song has only co-evolved with territoriality (LHR = 83, $p < 0.0001$) (Table 4.1). This is in line with the linear models, as social stability was not found to be a correlate of male song, and as the coefficients for territoriality as a predictor of male and female song were commensurate.

The transitions among states of male song and territoriality are remarkably symmetric, with the exception of the rapid acquisition of song once territoriality has evolved (Figure 4.4, Table 4.2). In particular, the state of both male song and territoriality is especially stable, with rates of losing one or the other trait being essentially equal (average $q = 0.194$ transitions per lineage per million years for losing song versus $q = 0.195$ transitions per lineage per million years for losing territoriality) and being one-fifth most of the other rates in the transition matrix. In other words, territoriality tends to precede the evolution of male song in birds, highlighting a causal link in this relationship.

Within female song, however, the transitions between song and territoriality are much more pronounced. Species are over three times as likely to acquire female song after gaining territoriality ($q = 1.791$) than they are to lose that territoriality ($q = 0.520$); conversely, if a species has female song but not territoriality, the species is nearly five times as likely to lose the female song ($q = 0.955$) than to gain territoriality ($q = 0.217$), and even in the case of both song and territoriality, the species is sixteen times more likely to first lose female song ($q = 1.792$) rather than to first lose territoriality ($q = 0.115$). That is to say, female song is typically evolved after the acquisition of territory defense and will usually not be lost until after the species becomes non-territorial. Similarly, female song is rapidly lost if evolved in the absence of territoriality, whereas switching between song and no song once territoriality is evolved is common.

Female song and social stability have an even stronger co-evolutionary relationship than female song and territoriality. As with territoriality, once the life history trait is evolved, species are nearly ten times more likely to evolve female song ($q = 1.036$) than they are to lose social stability ($q = 0.111$). Female song without social stability is particularly unstable, though the species is slightly less likely to lose female song ($q = 36$) than it is to gain social stability ($q = 55$). In other words, once the life history trait is evolved, female song often follows, though in the case of social stability, and unlike territoriality, it is possible that the species acquires female song before pair bonding. Once the species has both evolved female song and social stability, it is nearly forty-five times more likely to first lose female song ($q = 2.00$) than to first lose social stability ($q = 0.045$). That is, species almost always must lose female song before they can lose pair bonding. In contrast, male song has no evolutionary relationship with pair bonding. The same trait here causes two different evolutionary trajectories, underscoring the different roles of and selective pressures for male and female song.

As the calculation of transition rates requires the computation of all node states, one can reconstruct ancestral states in the BayesTraits frame. With a high degree of confidence (probabilities of 93% and 92% respectively), I can conclude that territoriality and social stability are basal avian characteristics. Song, however, appears to be derived in both sexes. These analyses disagree with studies that posit female song as an ancestral trait, notably a survey in Odom et al. (2014) of 1,141 bird species from 32 families and a study of European birds in Garamszegi et al. (2006), both of which focus primarily on passerines. My study considered 100 phylogenetic trees of the 6,670 bird species for which there are currently genetic-based phylogenies; as knowledge of avian genetics and historical relationships grows, and as computational methodologies provide increasing certainty in these types of predictions, these discrepancies can be more definitively resolved. Though the BayesTraits models cannot be run on trees with unresolved polytomies, such as those present in the full 9,993-species phylogenetic trees, the power of my gene-tree sample size is bolstered by the similarities in results in the linear models when run on the genetics trees and the full trees, as well as by the overall concordance among models run under several different assumptions (Supplementary Analyses).

Taken together, these results reveal that ecological resources, namely territories, are of fundamental importance to the evolution of female song, particularly in conjunction with long-term pair bonds, whereas male song has a reduced relationship with these ecological resources and with extrinsic factors as a whole. That is, while male song borders on omnipresent throughout the order and across the globe, female song is more sensitive to environmental and life-history drivers, presumably a function of the many roles of female ornamentation. Sexual selection is predicted to favor ornamental traits that are most conspicuous, least costly, and provide the most honest assessment of signals (Andersson 1994, West-Eberhard 1983). Thus, avian song is expected in situations where the signaling would be useful (for example, where there are territories to be defended or mates to be guarded), effective (for example, in habitats conducive to the vocal strategies employed), and where the benefits outweigh the costs (for example, in birds without major predators).

As females face different costs and benefits in reproduction, it is not surprising that the evolution and maintenance of female signals follows a different evolutionary path than those of male signals. Specifically, female song is more clearly defined by territory defense and pair bonding, the two major functions of song.

Experimental Procedures

Data collection

Data were collected for 10,335 species of birds on the occurrence of singing in each sex, along with information on seven core behavioral, ecological, and environmental traits: territoriality, social stability, mating system, migratory movement, diet and dietary specialism, and habitat. Species were classified as having male song if males of the species were reported to regularly sing and as having female song if females of the species were reported to regularly sing. “Singing” included songs in choruses and duets as well as independent song but excluded vocalizations including contact calls, alarm calls, and flight calls. Intrinsic traits of species were categorized with respect to degree of territoriality (non-territorial, weakly territorial or permanently territorial); social bond stability (solitary, seasonal bond or permanent bond); type of mating system (cooperative or non-cooperative); and movement (non-migratory, partially migratory or migratory), as well as the extrinsic variable of habitat (open, semi-open and dense). The primary source of information used to assign species to these categories were the detailed species accounts provided in Handbook of the Birds of the World series (del Hoyo 1992-2011), supplemented by a wide range of family- and region-specific bird identification books and journal articles as well as decades of field observations by NS and JAT. Further details on this data collection can be found in

(Tobias et al. 2016). Data on median latitude was calculated from global range polygons (BirdLife International and NatureServe 2011), while extrinsic environmental data (mean annual temperature, temperature range, annual precipitation and precipitation range) were extracted from the Worldclim database (Hijmans et al. 2005). Phylogenetic trees were obtained from the Global Bird Tree (Jetz et al. 2012). Species with few life-history data or with poor range maps were excluded, and species that could not be reconciled with the 6,670 species in the Global Bird Tree were omitted, leaving a total of 6,377 species for the comparative analysis.

Comparative analyses

Mixed models were performed using Bayesian binary-response mixed-effect models with logit link using a Markov-chain Monte Carlo algorithm, implemented in the *R* package MCMCglmm with phylogeny as a random factor (Hadfield 2010b). A total of 5,500,000 iterations were run – 55,000 on each of 100 bird trees – with the first 500,000 iterations discarded as burn-in and sampling every 5000 iterations, with a Gelman prior for random effects (Gelman et al. 2008). All continuous variables were rescaled to have a mean of 0 and a variance of 1 so as to be directly comparable. All models were implemented in *R* version 2.15.2. Plots of the sampled output were visually inspected to check model convergence and to ensure proper mixing, and two other independent sets of models were run to verify overall model accuracy.

Co-evolutionary analyses

Once the two most important predictors were established, associations between these traits and male and female song were investigated using Pagel's Discrete algorithm with MCMC, implemented in BayesTraits (Pagel and Meade 2006) across 100 phylogenetic trees restricted to species with available genetic data (n = 6,670). Using a likelihood ratio test, correlated evolution for each of the four combinations (female song and territoriality, female song and social bonds, male song and territoriality, male song and social bonds) was established; evolutionary transitions between the four possible states of each of the four combinations were then calculated. For purposes of this calculation, the ternary territoriality and sociality categorizations were collapsed into a binary system, with seasonal bonds collapsed with pair bonds (as opposed to no bonds) and weak territoriality collapsed with strong territoriality (as opposed to no territorial defense).

Sensitivity analyses

Sensitivity analyses were conducted in the following ways: (1) a full set of models examining the drivers of female song only among species that sing – that is, considering mutual song as an extension of singing behavior, so that each variable only tests the predictive power of female song itself, rather than of both overall singing behavior and mutual song; (2) a full set of models re-run with the 31 sex-role-reversed species excluded; (3) two runs of the BayesTraits simulations were run and checked for consistency; and (4) models examining the correlates of male and female song across the entire 9993-species tree were run. These results are all reported in Appendix 1.

CHAPTER 5: SEXUAL SELECTION, SOCIAL SELECTION, AND SPECIATION: AVIAN LINEAGES DIVERSIFY MOST RAPIDLY WHEN ORNAMENTATION IS MALE-BIASED RATHER THAN MUTUAL.

Abstract.

Sexual selection has long been proposed to accelerate speciation in animals, yet previous comparative studies have mainly focused on sexual dimorphism as an index of sexual selection. This approach assumes that monomorphism indicates low levels of sexual selection, perhaps incorrectly, as many lineages have elaborate traits expressed in both sexes. The extent to which speciation rates are influenced by mutual sexual selection, or related forms of social selection acting on both sexes, is therefore poorly understood. Here, I focus on the presence or absence of vocal ornaments (song) in birds to assess the relative importance of selection on male-only versus mutual ornaments in lineage diversification at global scales (N = 6601 species). I find that species with vocal ornaments diversify at faster rates, and that this effect is maximized when ornamentation is male-biased. Mutually ornamented species, by contrast, diversify at intermediate rates. These findings are consistent with the view that diversification rates are increased when sexual selection acts asymmetrically on males because of contrasting sex roles and unidirectional mate choice. However, I also conclude that mutual forms of sexual and social selection can drive similar, though weaker, increases in diversification, suggesting that greater care is required when interpreting patterns of selection and diversification in monomorphic lineages.

Introduction.

Divergence in sexual traits or behaviors can result in reproductive isolation between two recently-diverged populations (Mendelson, Martin and Flaxman 2014, Darwin 1871). Alternatively, traits under high levels of sexual selection may inhibit the speciation process by facilitating sexual encounters even after the populations have ecologically diverged. Despite decades of research, the extent and direction of the link between sexual selection and speciation remain controversial (West-Eberhard 1983, Butlin 2012, Panhuis et al. 2001, Price 1998, Turelli, Barton and Coyne 2001, Huang and Rabosky 2014, Gage et al. 2002a). While some studies find experimental (Rice and Hostert 1993, Jowers et al. 2014, Morgans, Cooke and Ord 2014, Selz et al. 2014) or comparative (Seddon et al. 2013b, Seddon et al. 2008, Masta and Maddison 2002, Boul et al. 2007, Cooney et al. 2015) support for sexually-selected traits accelerating lineage diversification, others suggest either no relationship (Kraaijeveld et al. 2011, Ritchie 2007, Phillimore et al. 2006, Morrow et al. 2003) or the opposite pattern (Servedio and Bürger 2014). In theory, differences in the sexually-selected signaling traits of two isolated populations, either under different environmental conditions or due to simple stochasticity, allow for the rapid development of reproductive isolation in cases of secondary sympatry or incomplete geographic segregation. Thus, species with highly plastic sexual traits might in theory be able to speciate faster than species lacking such traits. Consistent with this are the proliferation of large clades of highly charismatic species, nearly identical ecologically but taxonomically separable by an elaborate trait (Rundell and Price 2009, Schluter 2000, Tobias et al. 2014, Wagner et al. 2012).

To date, however, a key component of social signaling has been overlooked in studies of the rule of sexual selection in lineage diversification: mutual ornamentation, the presence of extravagant traits in both sexes. Sexually dimorphic ornamentation – the elaboration of traits unrelated or detrimental to survival, typically in the male – has been amply demonstrated to be the result of male-male competition and/or female choice (Andersson 1994, Clutton-Brock 2007), falling under the traditional purview of "sexual selection." The customary explanation for male-like secondary sexual traits expressed in females is genetic correlation (Darwin 1871, Lande 1980, Rice 1984), the idea that these traits are favored in males due to their role in male intrasexual competition or female choice (Bateman 1948, Trivers 1972) and that in females these same traits are non-adaptive and expressed only due to the shared genetic history with males (Potti and Canal 2011, Lande and Arnold 1985). The prevalence of these traits, however, coupled with evidence that mutual ornamentation has been gained and lost many times throughout evolutionary history (Wiens 2001), entreats a more adaptive explanation. In 1914, Huxley introduced the idea of "mutual mate choice", and in 1983 West-Eberhard coined the term "social selection." These two concepts frame the many roles of female ornamentation, with mechanisms for the acquisition and/or maintenance of these traits ranging from male-choice sexual selection to the need to defend ecological resources from conspecifics (Kraaijeveld and Komdeur 2007, Clutton-Brock 2009, Clutton-Brock and Huchard 2013, Tobias et al. 2012b, West-Eberhard 1983, Jones and Hunter 1993). These studies, however, have not yet permeated all aspects of sexual selection science, including omission from the sexual selection – speciation framework.

If the selective pressures on female ornaments are similar to those on males, female ornamentation would have an additive effect, if any, on any sexually-selected speciation trends. Given the ample evidence, however, that female song evolves under non-sexual social selection (see Chapter 4) (Garamszegi et al. 2006, Odom et al. 2014, Tobias et al. 2012b), the proposed speciation cycle linking male trait exaggeration and lineage diversification would be slowed or absent in monomorphic species, as the evolutionary pressures maintaining the role of female song would restrain the trait from reaching its dimorphic optimum and/or would engage with a separate association with the processes of speciation and extinction. Specifically, non-sexual social traits may play a reduced role in reproductive isolation, and, indeed, are known to converge upon population contact so as to better facilitate competition over ecological resources (Tobias and Seddon 2009). All studies to date, however, have ignored the potential confounding effect of mutual ornamentation, either by using monomorphism as a proxy for the lack of ornamentation or by assuming that all male ornaments are under similar selective pressures, regardless of whether this ornament is also present in females.

Here, I address this gap in the literature by considering the relationship between lineage diversification and song, a trait produced by males and/or females, across a large, well-sampled clade, birds. Male birdsong is a well-established index of sexual selection (Logue and Hall 2014, Mason, Shultz and Burns 2014, Price 1998, Read and Weary 1992, Tobias et al. 2010), and much is known about avian behavior, environment, breeding ranges, and phylogenetic history (Jetz et al. 2012, del Hoyo 1992-2011). Furthermore, recent advances in methodology for measuring speciation and extinction rates across large clades, including BAMM (Rabosky et al. 2014) and BiSSE (Maddison, Midford and Otto 2007), as well as strong evidence that less computationally-intensive methods of estimating diversification rates give consistent results (Jetz et al. 2012), allow for the relationship between sexual selection and lineage diversification to be explicitly and rigorously tested.

Because speciation-extinction models are easily biased by rare traits and/or small sample sizes (Davis et al. 2013), any mutually ornamented trait considered must be fairly prevalent in order to achieve statistically accurate results; furthermore, this trait needs to be found across many different clades, so as to balance the vast phylogenetic and geographic differences among diversification rates (Jetz et al. 2012). Avian song satisfies both of these conditions, and although female song is less common than male song it is nonetheless also found throughout the phylogenetic tree and across the globe (Odom et al. 2014, Garamszegi et al. 2006, Langmore 1998). The presence or absence of song is also relatively straightforward to quantify within birds, as it is known for nearly all species (del Hoyo 1992-2011) and is not subject to the human prejudices inherent in categorizing, for example, traits related to avian color dimorphism (Delhey and Peters 2008, Endler and Mielke 2005) or to more complicated acoustic measures (Mason et al. 2014). Although the spectral and temporal properties of song structure are strongly shaped by environmental variation, the simple presence or absence of song, unlike some other sexual traits, depends very little on the environment (Chapter 4), overcoming the common confounding force of ecological selection shaping signal divergence (Endler 1992, Wilkins et al. 2013, Maan and Seehausen 2011). Moreover, by selecting a binary trait, I am able to harness the computational power of BiSSE and MuSSE models (Binary State Speciation and Extinction and Multiple State Speciation and Extinction: (Maddison et al. 2007)) rather than being restricted to the much more time-intensive QuaSSE algorithms (Quantitative State Speciation and Extinction: (FitzJohn 2010)).

Using a dataset of the vocal traits of 6601 avian species, together with information on their geographic range, life history, and phylogeny, I am able to test predictions on the relationship between sexual selection and speciation in birds while taking into account potential confounding effects of mutual ornaments. I predict that male-only song – that is, a trait targeted by sexual selection – will be linked with the highest rates of lineage diversification, whereas the socially-selected mutual ornament of female song will display a distinct, muted relationship with lineage diversification. Furthermore, I predict that these effects are robust to the effects of phylogeny, life history, and geography, the three main potential correlates of both diversification and song that could be underlying any observed pattern. This is the first study, to my knowledge, to quantitatively demonstrate a relationship between mutual ornamentation and speciation on a broad scale. By separating monomorphic and dimorphic ornamentation, I not only help to substantiate the controversial relationship between sexual selection and speciation, but I also provide a potential explanation for why the controversy exists and highlight the need for the consideration of female ornamentation in future studies.

Materials and Methods.

Data were collected for 10,335 species of birds on the presence or absence of male song, female song, territoriality, and social stability according to methods detailed in Tobias et al. (2016). Specifically, species were classified as having male song if they produced complex vocalizations apparently related to sexual selection (as opposed to, e.g., warning or begging calls), the definition in del Hoyo (1992-2011); species were categorized as having female song if females were observed in free-ranging populations to produce complex vocalizations similar to those of males and/or apparently related to sexual selection, either independently or as a duet with a male. A small number of sex-role-reversed species (N = 37) were found to have female song but not male song; these were excluded from all analyses. Species with permanent or semi-permanent territories were classed as having "territory defense"; species that maintained permanent or seasonal pair bonds were classed as having "social stability." The majority of this species-level information came from *The Handbook of the Birds of the World* (del Hoyo 1992-2011), supplemented by sources such as family monographs; regional handbooks; consultations with expert field biologists and ornithologists; online resources such as Birds of America Online, the Macaulay Library, Xeno-canto, and the Internet Bird Collection; and a thorough literature search. Following the publication of recent clade-level studies of female song, namely (Odom et al. 2014, Price, Lanyon and Omland 2009, Logue and Hall 2014), my datasets were compared, with a small of species entries (n = 2) changed so as to be in accordance with these studies.

One hundred phylogenetic trees for the 6,670 species for which there are genetic data were obtained from the Global Bird Tree (Jetz et al. 2012) by randomly selecting 100 maximal likelihood trees from the Hackett backbone, and range information for 10,000 species was obtained from BirdLife International (BirdLife International and NatureServe 2011), for a total of 6,601 species with existing vocal, life history, phylogenetic, and distributional data.

To first determine the relationship between avian song and diversification rates, without taking into account the potential confounding effect of mutual ornamentation, I ran

Binary State Speciation and Extinction (“BiSSE”) models across the 100 phylogenetic trees using the package *diversitree* (Maddison et al. 2007) in R version 3.1.0 to test for differences in diversification rates between species with and without male song. BiSSE uses a birth-death model of diversification to estimate character-dependent speciation and extinction rates, allowing me to account for frequent evolutionary transition between the presence and absence of song. To then test my main prediction, that mutually-ornamented lineages would display an intermediate level of diversification, I employed Multiple State Speciation and Extinction (“MuSSE”, (FitzJohn 2010)) models, using the command “musse.multitrait” and allowing male and female song to evolve independently in the models so as to avoid the bias inherent in constraining mutual song and male-only song into a ranked categorical variable.

To test if these two models were consistent across the major divisions of birds, I re-ran each of the BiSSE and MuSSE models on trees limited to, respectively, passerines (order *Passeriformes*, roughly half the diversity of the world’s birds), non-passerines (all other birds), oscines (sub-order *Passeri,* the so-called “songbirds”), and sub-oscines (sub-order *Tyranni*, ~1,000 species of passerines with a unique syrinx structure).

As ornaments are closely linked to species life history (Dale et al. 2015) and as both social and ecological traits can have an effect on speciation (Maan and Seehausen 2011, Wilkins et al. 2013), I then explicitly tested the role of territoriality and social stability in lineage diversification, both separately using BiSSE models and in conjunction with song using MuSSE models.

Furthermore, as the environment has well-described, if not well-understood, effect on both signal evolution (Wilkins et al. 2013, Endler 1992, Maan and Seehausen 2011) and on overall patterns of speciation and extinction (Cardillo et al. 2005b, Jetz et al. 2012, Goldberg, Lancaster and Ree 2011), I ran a separate set of models considering only the species found in each of the 14 terrestrial biomes (Olson et al. 2001). In addition, speciation rates tend to vary across latitude (Weir and Schluter 2007), as does mutual ornamentation (Dale et al. 2015) and female song (Odom et al. 2014), suggesting that any relationship with diversification rates may be driven by underlying latitudinal gradients. To address this, I also classified each species as "tropical" if more than 50% of its range fell between 23° S and 23° N or "temperate" otherwise, then ran an additional set of models separately for each of these two categories.

Finally, to confirm that these results are not a statistical artifact of known biases in BiSSE-type models (Rabosky and Goldberg 2015, Davis et al. 2013), I employed two common estimators of tip-level diversification rates. Using Rabosky et al.'s Bayesian Analysis of Macroevolutionary Mixtures – "BAMM" (Rabosky 2014) – methodology, I randomly selected 25 of the 100 trees used in these analyses to estimate speciation and extinction methods. I estimated priors using the command "setBAMMpriors" in the R package *BAMMtools*, then ran the C++ "BAMM" program for $5.5\text{x}10^6$ generations, using the recommended defaults for the MCMC frequency and burn-in parameters. I also used the "DR" (diversification rate) estimation methodology presented by Jetz et al at the time of publication of the avian bird tree (Jetz et al. 2012), in which $DR_i = (\sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}})^{-1}$ for species i where N_i is the number of edges on the path from species i to the root and l_j is the length of edge j, calculating separate estimates for all species on each of the 100 phylogenetic trees.

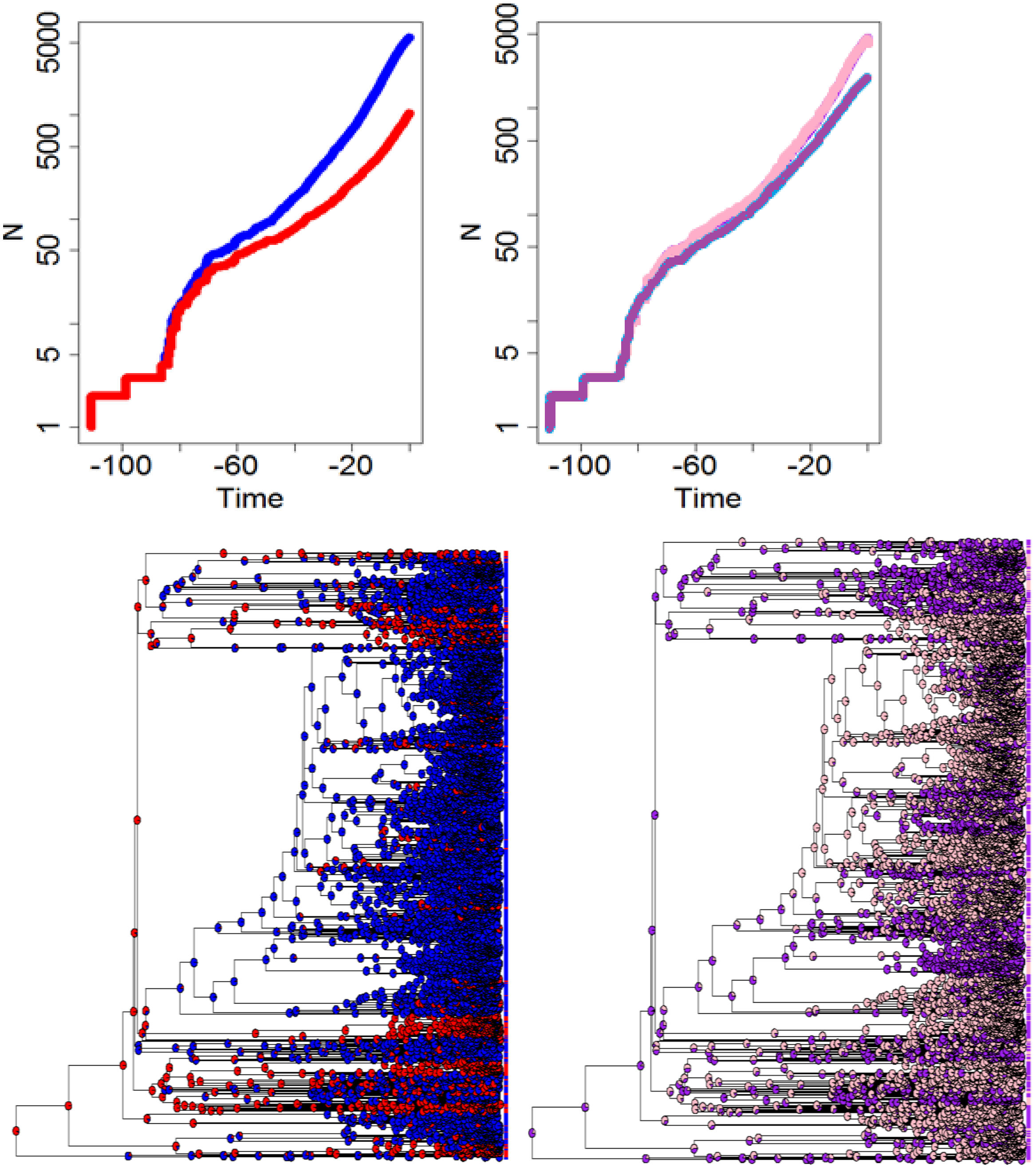
As these methods of estimating tip-level diversification are dependent solely on the phylogenetic structure, usual phylogenetic mixed modeling methods such as *MCMCglmm* (Hadfield 2010a, Hadfield and Nakagawa 2010) and phylogenetic generalized least squares (Revell 2010) fail to produce any variance to test after phylogeny is included as a random effect . Therefore, I was forced to test the relationship between song and diversification rate using mixed models with order and family as nested random effects, using the natural log of the diversification rates as the response variable with song and latitude as the fixed effects with the *R* package *nlme* and the command "lme" (Pinheiro et al. 2016).

Results.

The evolutionary history of song

Song is present in 85% of all extant avian species, with 35% percent of those (30% of the total avifauna) displaying mutual song. Song is not, however, the ancestral state for birds (median $\rho = 0.99$ for male song, $\rho = 0.91$ for female song, across 100 trees), with both male and female song appearing approximately 90 million years ago (age = 90.1 ± 9.5 SD million years). That is, the first song was a mutual ornament and appeared approximately one-third of the way into the evolutionary history of modern birds (Figure 5.1).

Figure 5.1: Phylogenetic state reconstruction of song. Above: Lineage-through-time plots of male (left) and female (right) song. Below: Ancestral state reconstructions of male (left) and female (song), calculated using the all-rates-different model in the command “ace” in the R package *ape*. Blue denotes the presence of male song, red denotes the absence of male song, pink denotes the presence of female song, and purple denotes the absence of female song.



The effect of song on speciation

Ornamented lineages – lineages with song – display diversification rates over twice as high as those found in species lacking song ($\overline{d_0}$= 0.048, $\overline{d_1}$= 0.104, $\bar{p}$ < 0.0001), a broad and crude confirmation of the hypothesis that increased sexual selection is linked to higher levels of net species diversification (Figure 5.2).

When mutual ornamentation is considered in the analyses, this result becomes more pronounced. Lineages in which song is an ornament used primarily in mate attraction – that is, in which song is found solely in the males and is driven by sexual selection – display the highest rates of diversification ($\bar{d}_M$ = 0.134), with the lowest rates found in species with no song ($\bar{d}_M$ = 0.077, $\bar{p}$ < 0.0001) and intermediate rates found in species in which song occurs in both males and females ($\bar{d}_{MF}$ = 0.090, $\bar{p}$ < 0.0001) (Figure 5.3).

The overall result linking the presence of avian song to higher rates of diversification is limited to non-passerine clades, as passerine lineages, overall and within both the oscines and the suboscines, display no observable pattern ($\bar{p}_{passerine}$ = 0.159, $\bar{p}_{oscines}$ = 0.101, and $\bar{p}_{suboscine}$ = 0.128) (Figure 5.4). As non-singing clades are rare within the passerines (229 of 5817 species, or 3.9%), oscines (175 of 4558 species, or 3.8%), and sub-oscines (54 of 1259 species, or 4.3%), this pattern is almost certainly a known statistical artifact of BiSSE-type models (Davis et al. 2013).

Furthermore, when the female ornament is considered as distinct from the sexually selected male-only song, the relationship found in all birds – with mutually-ornamented lineages displaying intermediate levels of diversification – remains consistent across the passerines, non-passerines, and suboscines, with no significant relationship in the oscines ($\bar{p}_{oscine}$ = 0.353) (Figure 5.4).

Figure 5.2: Average diversification rates of avian lineages with song (green) and without song (orange) across 100 trees. Diversification rate is measured in events per lineage per million years.

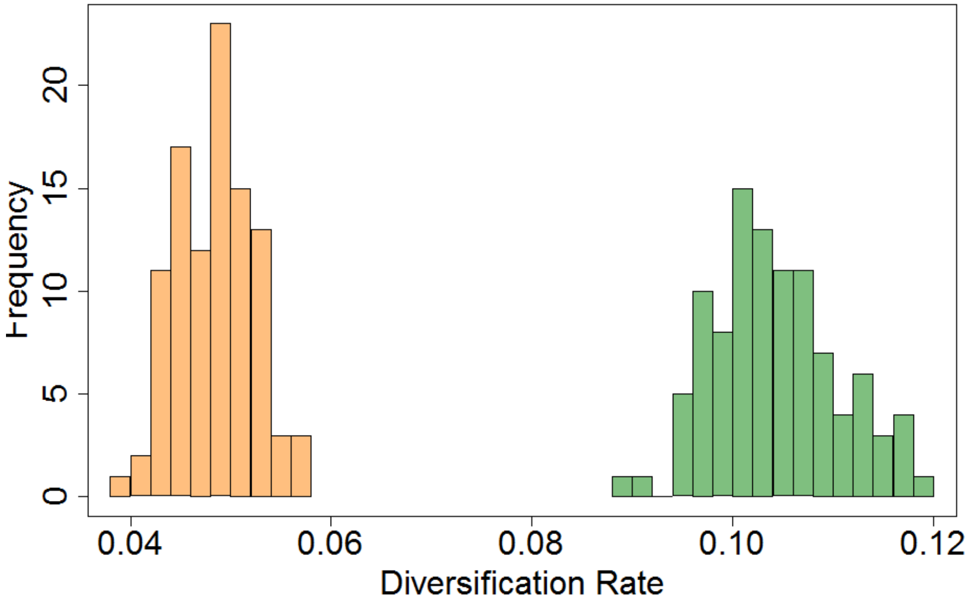


Figure 5.3: Average diversification rates of lineages with male-only song (purple), mutual song (green), and no song (red) across 100 phylogenetic trees. Rates are measured in events per lineage per million years.

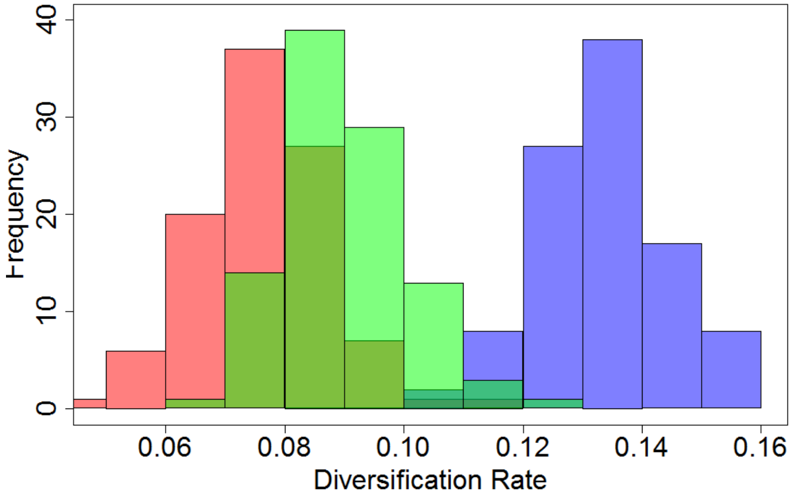
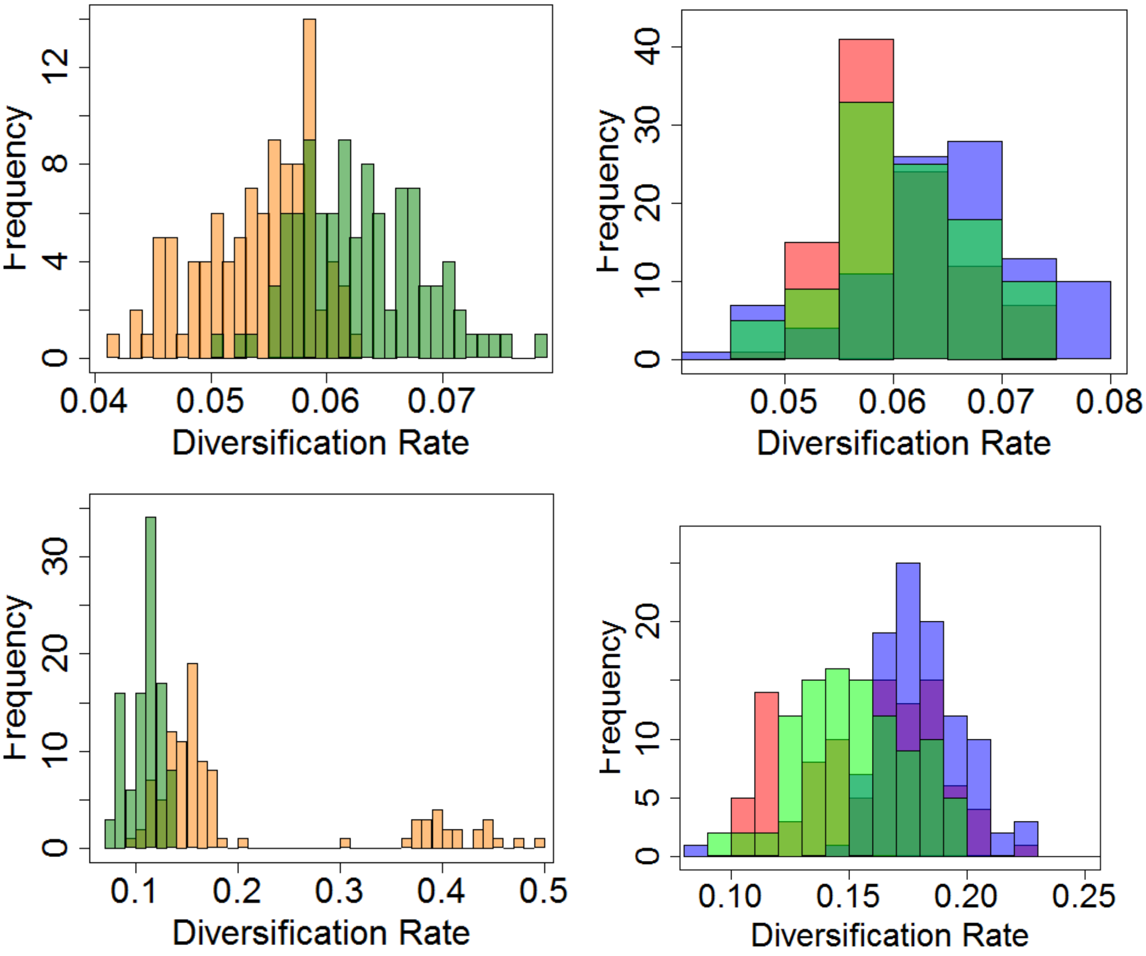
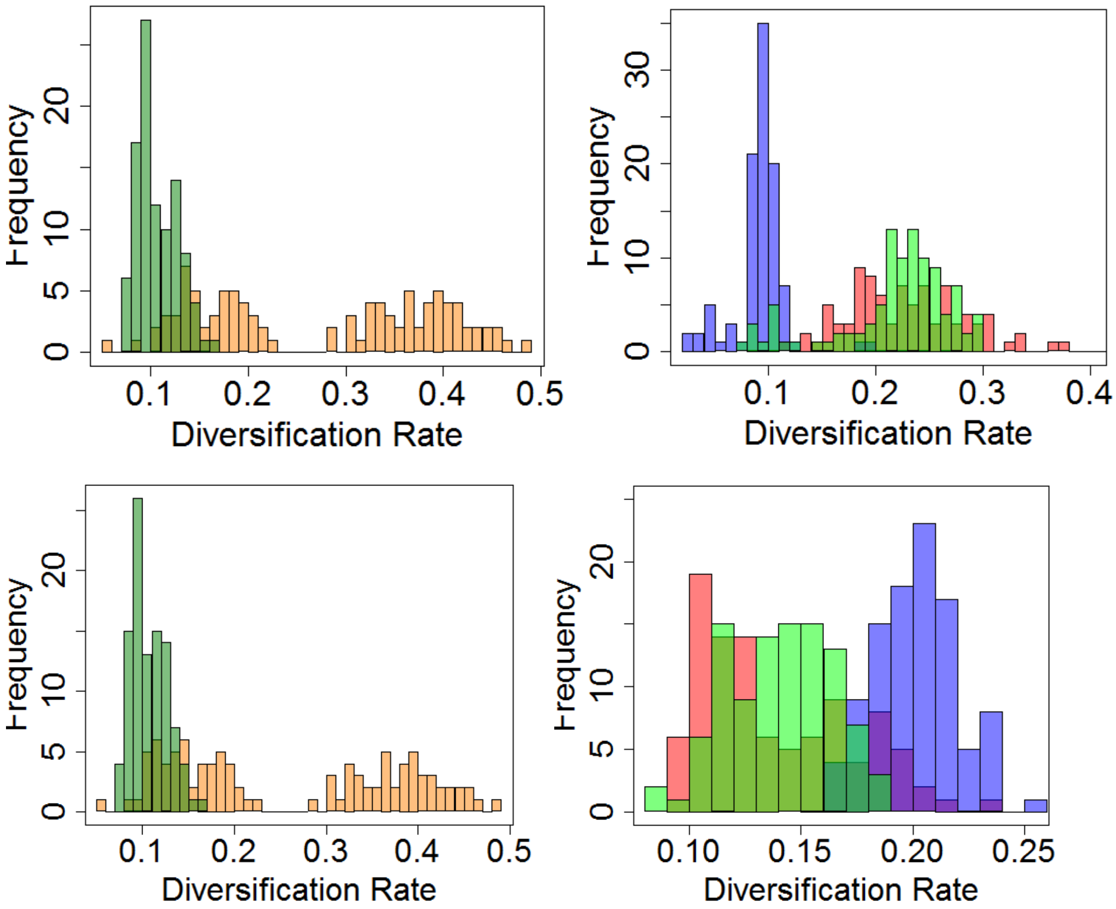


Figure 5.4: Average diversification rates of lineage by song status and clade. From top to bottom, graphs show non-passerines, passerines, oscines, and sub-oscines, with the left column contrasting the presence (green) and absence (orange) of song and the right column showing differences between lineages with male-only song (purple), mutual song (green), and no song (red). All rates in events per lineage per million years.

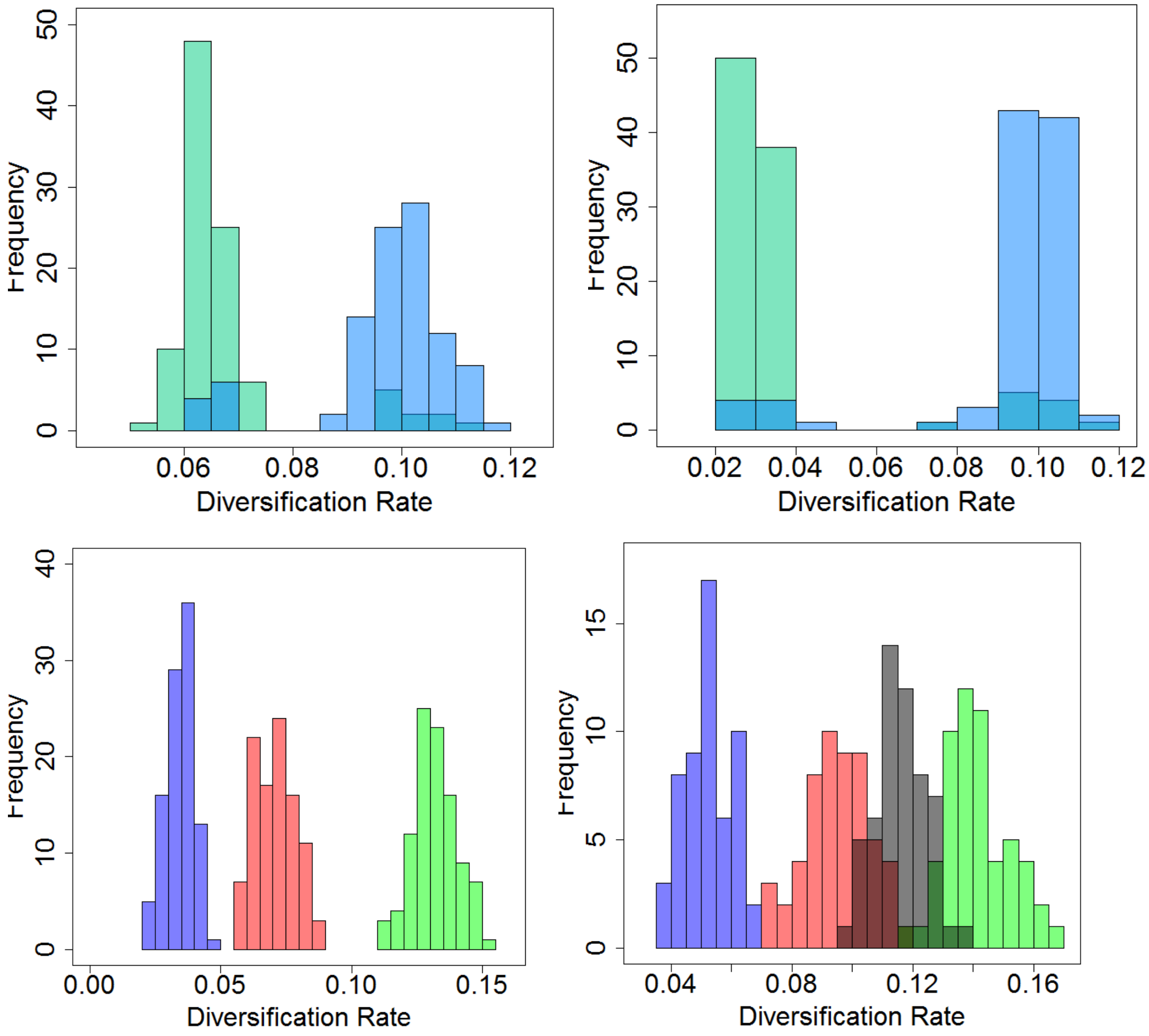




Other potential drivers of speciation: life-history traits and biogeographic factors

As female and male song is closely linked to several life history traits, principally the social traits territory defense ("territoriality") and pair bonding ("social stability") behaviors (Chapter 4), I wanted to examine the possibility that it could be these traits, rather than song itself, driving the relationship with lineage diversification. I first explicitly tested the relationship between territoriality, social stability, and diversification, without considering the song status of the lineage, using BiSSE. Territoriality was linked to a decrease in diversification rates ($\bar{d}_0$ = 0.10 events per lineage per million years, $\bar{d}_1$ = 0.04 events per lineage per million years, $\bar{p} < 0.001$), whereas social stability had no significant effect on diversification rate ($\bar{p} = 0.297$) (Figure 5.5).

Figure 5.5: The effect of song and life history traits on lineage diversification. Clockwise from upper left: average diversification rates for lineages with (green) and without (blue) territoriality; average diversification rates for lineages with (green) and without (blue) social stability; average diversification rates for lineages with male-only song and territoriality (green), mutual song and territoriality (grey), with neither song nor territoriality (red), and territoriality but no song (purple); and average diversification rates for lineage with both territoriality and song (green), neither territoriality nor song (red), and territoriality but no song (purple).



I then ran MuSSE models to consider the evolution of territoriality simultaneously with the evolution of song. The highest diversification rates were found in lineages with both territoriality and song ($\bar{d}$ = 0.134); there was no difference between lineages with neither trait ($\bar{d}$ = 0.071) and lineages with song but not territoriality ($\bar{d}$ = 0.074); and the lowest diversification rates were found in lineages with territoriality but no song ($\bar{d}$ = 0.035) (Figure 5.5).

Finally, I ran MuSSE models comparing the six possible combinations of song (male-only, mutual, and none) and territoriality (present or absent) finding the highest diversification rates in clades with male-only song and territoriality ($\bar{d}$ = 0.142), the second-highest in clades with mutual song and territoriality ($\bar{d}$ = 0.116), the second-lowest in clades with neither song nor territoriality ($\bar{d}$ = 0.096), and the lowest in clades with territoriality but not song ($\bar{d}$ = 0.053), with the remaining two categories (mutual or male-only song with no territoriality) excluded due to paucity in nature (Figure 5.5).

That speciation and extinction rates vary with latitude is a core, if not yet well-understood, theme of speciation studies (Cardillo et al. 2005b, Hawkins et al. 2012, Schemske et al. 2009). As mutual song is biased toward the tropics (Chapter 4), it is important to attempt to distinguish the effect of biogeography from that of sexual and social pressures. To do this, I first re-ran the main BiSSE and MuSSE models for each of the 14 WWF terrestrial biomes (Olson et al. 2001), assigning to each biome all of the birds whose breeding range (BirdLife International and NatureServe 2011) overlaps the biome at the scale of a 110x110km equal-area grid cell. In only three biomes (temperate coniferous forests, temperate grasslands, and deserts) was there no significant difference in diversification rates between lineages with and without song in the BiSSE models, and in no biome were rates of clades without song higher than those with song (Table 5.1). When considering male-only and mutual song as separate categories in the MuSSE models, singing lineages in all biomes had higher diversification rates than non-singing lineages, though three biomes had the highest diversification rates for species with *mutual* song and the remaining eleven biomes displayed the expected pattern of highest diversification rates in male-only singing species (Table 5.2).

To test explicitly for a tropic/temperate bias, I categorized any bird whose median breeding range latitude fell between 23.4°N and 23.4°S as “tropical” and the remaining birds as “temperate” and re-ran the speciation and extinction models a final time. Though tropical lineages did have higher diversification rates than temperate lineages, species with song consistently and significantly displayed higher diversification rates than species lacking song in the BiSSE models ($\overline{p_{trop}} < 0.001$ and $\overline{p_{temp}} = 0.038$). Furthermore, in the MuSSE models, diversification rates were again highest for lineages with male-only song in both the tropics and the temperates ($\overline{d_{trop}} = 0.116$ and $\overline{d_{temp}} = 0.112$), intermediate for lineages with mutual song ($\overline{d_{trop}} = 0.114$ and $\overline{d_{temp}} = 0.074$), and lowest for lineages with no song ($\overline{d_{trop}} = 0.067$ and $\overline{d_{temp}} = 0.048$) (all $\bar{p} < 0.001$) (Figure 5.6).

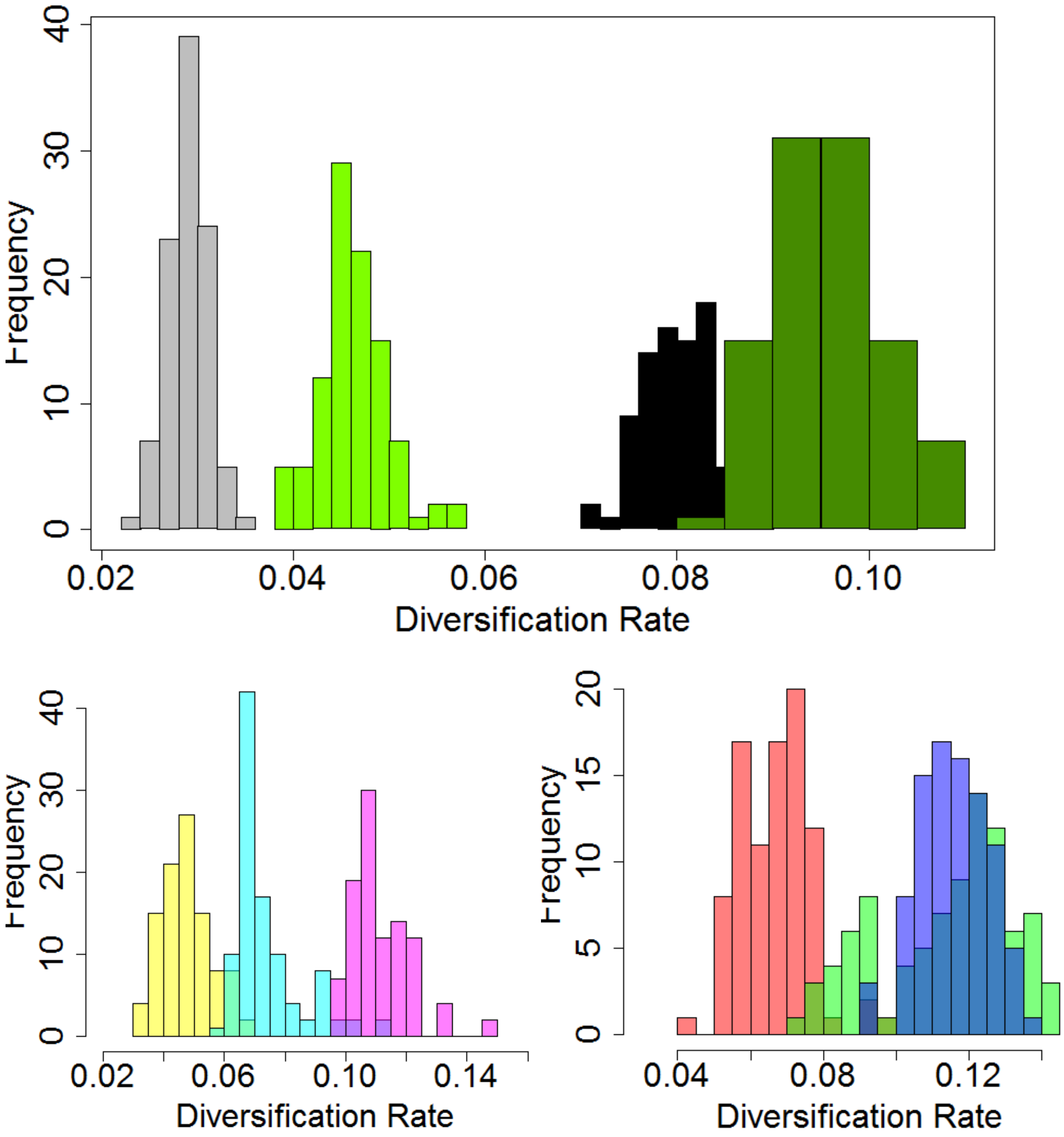
Table 5.1: The prevalence of and the diversification rates of lineages with and without song across 14 World Wildlife Fund terrestrial biomes. Pairs of diversification rates whose differences are statistically insignificant are highlighted in blue. Diversification rate is measured in events per lineage per million years and averaged across 100 trees.

Biome	Prevalence of Mutual Song	Prevalence of All Song	Diversification Rate - No Song	Diversification Rate - Song	Biome Description
1	0.325	0.868	0.051	0.095	(Sub-)Tropical moist broadleaf forests
2	0.338	0.858	0.040	0.087	(Sub-)Tropical dry broadleaf forests
3	0.314	0.865	0.037	0.068	(Sub-)Tropical coniferous forests
4	0.314	0.865	0.037	0.068	Temperate broadleaf/mixed forests
5	0.238	0.851	0.030	0.081	Temperate coniferous forests
6	0.166	0.788	0.023	0.071	Boreal forests
7	0.335	0.852	0.044	0.083	Tropical grasslands
8	0.245	0.791	0.036	0.073	Temperate grasslands
9	0.305	0.823	0.044	0.070	Flooded grasslands
10	0.294	0.855	0.046	0.081	Montane grasslands
11	0.162	0.768	0.023	0.064	Tundra
12	0.270	0.756	0.037	0.061	Mediterranean
13	0.294	0.837	0.042	0.083	Deserts
14	0.348	0.801	0.033	0.049	Mangrove

Table 5.2: The prevalence of and the diversification rates of lineages without song, with male and female song, and with male-only song across 14 World Wildlife Fund terrestrial biomes. Biomes for which lineages with mutual song had higher diversification rates than male-only singers are highlighted in orange. Diversification rate is measured in events per lineage per million years and averaged across 100 trees.

Biome	Diversification Rate – No Song	Diversification Rate – Mutual Song	Diversification Rate – Male-Only Song
1	0.081	0.113	0.126
2	0.062	0.079	0.135
3	0.060	0.132	0.130
4	0.060	0.132	0.130
5	0.035	0.126	0.104
6	0.041	0.063	0.094
7	0.070	0.070	0.129
8	0.045	0.059	0.097
9	0.067	0.047	0.123
10	0.073	0.084	0.135
11	0.053	0.048	0.093
12	0.044	0.082	0.087
13	0.059	0.070	0.135
14	0.017	0.131	0.071

Figure 5.6: Average lineage diversification rates for above: tropical lineages with song (dark green), temperate lineages with song (black), tropical lineages without song (light green), and temperate lineages without song (grey); below left: temperate lineages without song (yellow), with mutual song (blue), and male-only song (purple); below right: tropical lineages without song (red), with mutual song (green), and male-only song (blue). All rates in events per lineage per million years.



Other estimates of diversification

Models relying on the algorithms employed by BiSSE-type models (including BiSSE (Maddison et al. 2007), MuSSE and QuaSSE (FitzJohn 2010), and GeoSSE (Goldberg et al. 2011)) have recently come under heavy criticism for high type I error (Davis et al. 2013, Ng and Smith 2014, Rabosky and Goldberg 2015). Therefore, to independently confirm the validity of my results, I repeated my analyses using the program Bayesian Analyses of Macroevolutionary Mixtures, “BAMM,” (Rabosky 2013, Rabosky 2014, Rabosky and Goldberg 2015) and a rough species-level approximation of diversification rate determined by averaging branch lengths, “DR” (Jetz et al. 2012). These methods have the additional benefit of being able to integrate latitudinal variation in speciation rates directly into the model, rather than resorting to broad geographic categorical variables as a proxy. It is worth noting, however, that two estimates of diversification rates are not particularly well correlated, with $R \approx 0.5$ for each of the 25 trees in common between the two methods.

Both of these methods confirmed the main results presented here. Across 25 trees, diversification rates estimated using BAMM were found to be correlated with male-only song ($p = 0.027$), with no difference between lineages with mutual song and no song ($p = 0.335$). Similarly, higher diversification rates estimated using the DR method were also found in lineages with male-only song ($p = 0.036$), with no difference between lineages with mutual song and no song ($p = 0.118$).

Discussion.

My finding that male bird song is linked to higher levels of speciation adds to the growing body of evidence that sexual selection can accelerate the process of lineage diversification. In theory, sexually selected traits can create prezygotic reproductive barriers upon secondary sympatry, allowing coexistence in two recently-diverged populations (Doorn et al. 2009, Gröning and Hochkirch 2008). This would accelerate the so-called “speciation cycle” (Grant and Grant 1997) and facilitate alpha diversity, though the experimental and comparative evidence remains ambiguous (West-Eberhard 1983, Butlin 2012, Huang and Rabosky 2014, Kraaijeveld et al. 2011, Selz et al. 2014). Avian song is a classic sexual trait, driven by competition for mates between and within the sexes (Grant and Grant 2008, Price 1998, Read and Weary 1990, Read and Weary 1992, West-Eberhard 1979, Darwin 1871). It is found throughout the avian tree (del Hoyo 1992-2011), and its presence or absence is easily quantified, allowing for speciation and extinction models to move beyond assumptions that diversification rates are constant over time or restrictions that higher order clades have a single trait value (Maddison et al. 2007).

Furthermore, my finding that mutual ornaments are associated with intermediate levels of diversification – that is, that species operating under high levels of social, but not necessarily sexual, selection – highlights for the first time the importance of distinguishing social from sexual selection when considering the impact of selection on diversification. Specifically, failing to consider mutual ornamentation obscures underlying evolutionary processes, likely contributing to the confusion surrounding this topic. Monomorphism is typically assumed to indicate low levels of sexual selection (Dale et al. 2015), whereas in truth elaborate female ornaments perform a variety of functions falling under the purview of social selection (Tobias et al. 2012b) that may be mediating steps in the speciation cycle. Importantly, these roles may be different from the functions of male ornaments, thus affecting the types of selection operating on the species as a whole.

Female and male song arose simultaneously in birds (Figure 5.1), likely due to genetic correlation (Kraaijeveld et al. 2007), but in many species female birds use song for different purposes than their male counterparts (Cain and Langmore 2015, Cooney and Cockburn 1995, Evans and Pinxten 1998, Garamszegi et al. 2006, Langmore 1998, Odom et al. 2014). These opposing selective pressures in the evolution and retention of mutual song are visible from the modern-day geographic and phylogenetic distribution of female song Chapter 4) and can perhaps be best understood in the framework of social selection (West-Eberhard 1979, Tobias et al. 2012b). Thus, even if there is selection acting to, for example, differentiate male songs in different populations to prevent hybridization (Delmore and Irwin 2014), there might also be stabilizing pressure for convergence in the territory defense songs of species occupying similar niches (Tobias et al. 2014), and as a result the ability of song to modulate lineage diversification is less pronounced (Wilkins et al. 2013). Furthermore, song can be linked with high diversification rates even after accounting for the effects of territoriality (Figure 5.5). This, together with the fact that territoriality has the opposite relationship with diversification rates than song (and that pair bonding, another social trait closely linked to song, has no relationship with lineage diversification), indicates that it might be the plastic nature of the signal morphospace, rather than an intrinsic behavioral characteristic, that enables these populations to differentiate.

Despite the recent controversies in methodologies used to estimate speciation and extinction rates (Ng and Smith 2014, Davis et al. 2013, Rabosky and Goldberg 2015), the finding that three independent analyses yield similar results – results that are robust to taxonomic scale, confounding behavioral factors, and geographic variation – strongly indicates that social and sexual selection play an important role in facilitating avian diversification. Importantly, my findings suggest that failure to account for the types of non-sexual social selection that generally operate on female ornaments may explain the contradictory conclusions of previous studies (Butlin 2012, Servedio and Bürger 2014, Huang and Rabosky 2014, Kraaijeveld et al. 2011, Ritchie 2007, Seddon et al. 2013b, Seddon et al. 2008).

Though the selection of a binary trait presents many computational advantages, the main drawback of my study is my inability to quantify the many roles of male and female bird song (Andersson 1994, Slabbekoorn 2004), and thus my inability to present a definitive causal explanation for the demonstrated link between avian song and lineage diversification. Future work – experimental, comparative, and theoretical – with explicit consideration of mutual ornamentation is needed to determine the relationship between sexual selection and biodiversity. It is possible, for example, that the particulars of avian sexual selection and hybridization (Short 1972, Grant and Grant 1997) render this finding inapplicable to other animal clades, or that signals with different ecological and social functions, such as dichromatism and other visual ornaments (Cooney et al. 2015), have a different relationship with the speciation cycle.

Signals such as song are crucial to avian intra- and inter-specific interactions, including mate choice, species recognition, and territory defense, and their sex-specific roles have important consequences for the origin and maintenance of species boundaries. The diversity of ornamental traits throughout the animal kingdom – and the charisma of the species possessing these elaborate ornaments – has long suggested that a relationship between ornamentation and the origin and maintenance of biodiversity, and social traits provide a convenient, albeit controversial, framework to understand this link. My findings support the idea that sexual signals accelerate species diversification processes and highlight the crucial role that non-sexual social traits play in understanding the relationship between animal traits and species boundaries.

CHAPTER 6: DISPERSAL AND DIVERSIFICATION IN PASSERINE BIRDS: A TEST OF THE INTERMEDIATE DISPERSAL HYPOTHESIS.

Abstract.

The role of dispersal in shaping patterns of diversity is controversial, with some studies showing positive effects of high levels of dispersal ability on species richness but others the converse. In theory, species with both extremely high and extremely low dispersive abilities could have low levels of diversity. It follows, therefore, that lineages with intermediate capacity for dispersal will have the highest levels of diversification, though this “intermediate dispersal hypothesis” (IDH) has not been verified empirically on a large scale. Here, I conduct a test of the IDH across the *Passeriformes* (“passerines”), the order containing ~ 60% of the world’s birds, using wing morphology measurements from 26,043 individuals across 6,028 species, finding weak but significant support for this hump-shaped model. Within the suborder *Passeri* (the oscines, so-called “songbirds”), I find much stronger support for the IDH, whereas the suborder *Tyranni* demonstrates a monotonically increasing relationship. Furthermore, when I separately consider birds that defend year-round territories from those that do not, territorial birds fit a hump-shaped model whereas non-territorial birds fit the monotonically increasing model. These relationships hold true across the macroecological correlates of passerine dispersal as well as across other common predictors of avian speciation. I conclude that dispersal behaviour is an important driver of avian diversification, but that the applicability of the IDH varies with the ecological traits of the lineages in question.

Introduction.

Dispersal, or the movement of an organism in relation to its birth and breeding sites (Greenwood and Harvey 1982), shapes many observed ecological and evolutionary processes (Ronce 2007). Dispersal affects gene flow between populations (Mayr 1963), the size of a species range (Rosenzweig 1995, Losos and Parent 2009, MacArthur and Wilson 1967), inbreeding depression (Roze and Rousset 2003), the speed at which species can explore new habitats (Kovach et al. 2015), extinction risk (Agnarsson, Cheng and Kuntner 2014, Kokko and López-Sepulcre 2006), energy consumption and predation risks (Bonte et al. 2012), and disease dynamics (Mack et al. 2000), all of which have important consequences for biodiversity and conservation. Much of the current spatial structure of communities and species distributions is shaped by dispersal processes, and dispersal ability is a key though oft-overlooked component of a species ecological niche (Shaw and Kokko 2015, Pigot and Tobias 2015).

Of particular importance is the role of dispersal in the processes of speciation and extinction. Highly mobile populations are less likely to become genetically isolated, as geographic barriers fail to block genetic admixture (Coyne and Orr 2004, Gavrilets 2014, Gavrilets and Vose 2005, Claramunt et al. 2011, Weeks and Claramunt 2014, Belliure et al. 2000). On the other hand, poor dispersers are unlikely to ever surmount barriers to movement, providing little opportunity for range expansion or division, which has the effect of both inhibiting speciation and promoting extinction (Kisel and Barraclough 2010, Rosenzweig 1995, Phillimore et al. 2006, Bocxlaer et al. 2010, Dodd et al. 1999, Vamosi and Vamosi 2010, Levin 2006). The “intermediate dispersal hypothesis” (IDH) combines these two opposing theories and predicts that dispersers from both extremes will display low rates of lineage diversification, with the highest levels of speciation and/or lowest levels of extinction found in "intermediate" populations with neither high nor low dispersal abilities (Claramunt et al. 2011, Venail et al. 2008). That is, the species with the highest diversification rates will be those with populations that can be separated by geographic barriers such as mountains ranges or oceans but that are not so poor dispersers that they will rarely encounter such barriers and/or will be highly sensitive to local extinction.

The causes and consequences of dispersal are poorly understood, particularly on a global level. Dispersal ability is difficult to measure (Nichols et al. 2001, Paradis et al. 1998); and the best dispersal data available focuses on the pollination syndromes of plants (Vamosi and Vamosi 2010, Levin 2006, Gillespie et al. 2012). Field studies are limited to studying dispersal that takes place within the study area (Paradis et al. 1998), and macroevolutionary models are typically unable to into account confounding factors that co-vary with dispersal ability, such as speciation rate and geographic range size (Pigot and Tobias 2015). Much of the current evidence for the IDH comes from bacteria (Venail et al. 2008), and what evidence there is for the IDH in eukaryotes is decidedly mixed (Eriksson and Bremer 1992, Ricklefs and Renner 1994, Dodd et al. 1999, Claramunt et al. 2011, Weeks and Claramunt 2014, Price and Wagner 2004, Phillimore et al. 2006).

The flying abilities of volant creatures, however, allow for a clearly-defined relationship between behavior, morphology, and dispersal. Avian dispersal is closely linked to wing shape (Claramunt et al. 2011, Lockwood, Swaddle and Rayner 1998), so that avian dispersal can be estimated from simple measurements of both live birds and museum specimens. Furthermore, birds are widely distributed globally, with a well-described phylogenies based on molecular sequencing data (Jetz et al. 2012, Prum et al. 2015, Jarvis et al. 2014) and a wealth of information available about their life histories (del Hoyo 1992-2011). Using newly-available methodology (Rabosky et al. 2014, FitzJohn 2010), it is now possible to simultaneously consider the macroecological context for the dispersal-diversification relationship.

Here, I test the IDH by presenting a global survey of the distribution of dispersal ability across space and time in the largest avian order, the *Passeriformes*, a speciose and diverse clade containing both island and continental lineages. With data on the wing morphologies of over 26,000 individuals from over 6,000 species of passerines, I am able to explicitly test hypotheses of the evolutionary causes of dispersal that have hitherto been restricted to single geographic areas (Weeks and Claramunt 2014, Linder et al. 2014, Agnarsson et al. 2014), small sample sizes (Claramunt et al. 2011, Phillimore et al. 2006, Paradis et al. 1998), and/or imprecise estimations of speciation and extinction rates (Phillimore et al. 2006). By focusing on the passerines, with their elaborate vocal morphology, I sidestep most issues about the relationship, or lack thereof, between sexual selection and speciation (Huang and Rabosky 2014, Kraaijeveld et al. 2011, Maan and Seehausen 2011, Masta and Maddison 2002, Morrow et al. 2003, Panhuis et al. 2001), as well as any other characteristics that may have caused a single avian order to contain over half of the class species richness (Phillimore et al. 2006). Furthermore, an analysis of the entire passerine clade allows me to explicitly compare the dispersal patterns of the oscines versus the suboscines, as dispersal is an oft-cited reason for different biogeographic patterns between the two sub-orders (Kennedy et al. 2014). Finally, by incorporating both a macroecological and macroevolutionary perspective, I am able to separate the effect of dispersal from the confounding effects of other potential drivers of diversification dynamics.

Materials and Methods.

Data Collection.

The Kipps distance (distance from longest feather of the closed wing to first secondary, (Claramunt et al. 2011)) and unflattened wing chord were measured to the nearest 0.5 mm in 26,043 museum specimens and live birds representing 6028 extant and recently-extinct species from the order *Passeriformes* ("passerines"), mean 4.29 specimens per species. Wherever possible, two adult males and two adult females in good condition from the nominate subspecies were measured; any juveniles, identified as such either on the specimen label or by the measurer, were excluded. The "hand-wing index", HWI, a proxy for flight ability (Claramunt et al. 2011), was then calculated by dividing the Kipp's distance by the wing chord and multiplying by 100. Low HWI indicates inefficient flight and thus poor dispersal; high HWI indicates effective flight and high dispersal. HWI was log-transformed for all of these analyses.

Ecological Correlates.

In order to control for non-dispersive drivers of the IDH, I tested the following potential correlates of avian dispersal ability: habitat, body mass, migration, range size, diet, song, territoriality, latitude, and island status. Details for the habitat, migration, song, and territoriality can be found in Chapter 4, but briefly: each species was categorized with respect to degree of territoriality (non-territorial, weakly territorial or permanently territorial); movement (non-migratory, partially migratory or migratory); habitat (open, semi-open and dense); and song (no song, male and female song, or male-only song).

Body mass data was obtained from (Dunning 2007). Range size was computed by intersecting global range polygons (BirdLife International and NatureServe 2011), with a 1°x1° grid and counting the number of grid cells overlapped by each range; median range latitude was also extracted from these polygons. These ranges were then intersected with shapefiles of the global continents in ArcGIS 10; any bird whose range was contained entirely within the continents was classified as "continental", entirely not within the continents as "island", and "both" otherwise. Dietary data was taken from Wilman et al. (2014) and re-categorized as "frugivores", "insectivores", "nectarivores", "granivores/plants", and "omnivores" so as better to reflect passerine dietary composition; any species scored as at least 60% one of these categories in (Wilman et al. 2014) was classified as that category here and was otherwise classified as an omnivore. Phylogenetic trees were obtained from the Global Bird Tree (Jetz et al. 2012). Species with few life-history data or with poor range maps were excluded, and species that could not be reconciled with the 6,670 species in the Global Bird Tree were omitted, leaving a total of 3239 passerine species for the comparative analysis.

Mixed models were performed using Bayesian binary-response mixed-effect models with logit link using a Markov-chain Monte Carlo algorithm, implemented in the R package MCMCglmm with phylogeny as a random factor (Hadfield 2010b). A total of 5,500,000 iterations were run – 55,000 on each of 100 bird trees – with the first 500,000 iterations discarded as burn-in and sampling every 5000 iterations, with a Gelman prior for random effects (Gelman et al. 2008). All continuous variables were rescaled to have a mean of 0 and a variance of 1 so as to be directly comparable. All models were implemented in R version 3.2.3. Plots of the sampled output were visually inspected to check model convergence and to ensure proper mixing, and two other independent sets of models were run to verify overall model accuracy.

Speciation and Extinction Models.

The relationship between speciation and extinction rates was quantified using the program "QuaSSE" ("Quantitative State Speciation and Extinction") (FitzJohn 2010) , implemented using the package *diversitree* in R version 3.2.3. These algorithms were run on the 4001 passerine species for which there are high-quality gene-based phylogenies and were run across 25 randomly-selected trees. For each tree, I ran models in which the relationship between HWI and lineage diversification rate (speciation rate – extinction rate) was constrained to be (1) constant, (2) logistic ("monotonic"), and (3) Gaussian ("hump-shaped").

As island-dwelling species likely represent clades which rapidly transitioned from high to low dispersal ability (Wright et al. 2016), and thus might spuriously link high diversification rates with poor dispersal (Owens et al. 1999), I then re-ran these QuaSSE analyses with the 32 island-restricted species excluded. Finally, I ran these analyses separately on the suborders *Passeri* (the "oscines") and *Tyranni* (the "suboscines") and then separately on species with permanent year-round territorial behavior (the strongest predictor of dispersal ability in birds) and species with weak or seasonal territorial behavior.

There is a known tendency towards Type I error in the so-called "BiSSE-type" models, including QuaSSE (Davis et al. 2013, Rabosky and Goldberg 2015). Therefore, to validate these models, I also employed two common estimators of tip-level diversification rates. Using Rabosky et al.'s Bayesian Analysis of Macroevolutionary Mixtures ("BAMM"

(Rabosky et al. 2014)) methodology, I calculated speciation and extinction values for the species in each of the 25 trees used in the QuaSSE analyses. I estimated priors using the command "setBAMMpriors" in the R package *BAMMtools*, then ran the C++ "BAMM" program for 5.5x10^6 generations, using the recommended defaults for the MCMC frequency and burn-in parameters. I also used the "DR" (diversification rate) estimation methodology presented by Jetz et al at the time of publication of the avian bird tree (Jetz et al. 2012), in which $DR_i = (\sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}})^{-1}$ for species *i* where N_i is the number of edges on the path from species *i* to the root and l_j is the length of edge *j*, calculating separate estimates for all species on all 100 of the phylogenetic trees used throughout this study.

For each of these metrics, I tested tip-level diversification rates against HWI in a generalized linear mixed model framework using the R package *MCMCglmm* (Hadfield 2010b) using the same methodology as described above. To retain analogy to the models possible in QuaSSE, I tested the BAMM and DR rates against HWI linearly and then against a Gaussian distribution that reached its peak (mean) at the HWI corresponding to the highest species diversification rate and where one standard deviation to either side of the mean encompassed 67% of the HWIs.

Though these tip-based metrics are not as informative as the QuaSSE analyses, they do allow multivariate correlations. Therefore, for my penultimate set of models I tested dispersal ability as a predictor of the BAMM and DR lineage diversification rates against the six correlates of dispersal ability – habitat, migration, range size, diet, territoriality, and latitude – to determine if the relationship between dispersal and diversification is an artefact of a correlate of dispersal. Finally, I compared dispersal as a predictor of diversification alongside several other known or suspected correlates of speciation, namely latitude

(Rolland et al. 2014), climate (Chejanovski and Wiens 2014, Lawson and Weir 2014), feeding guild generalization (Cardoso et al. 2011, Paine 1966, Kissling et al. 2012) , male and female song (Chapter 5), and body mass (Agnarsson et al. 2014, Pabijan, Wollenberg and Vences 2012).

Results.

Overall

Though males and females generally differ in their dispersal abilities (Greenwood and Harvey 1982), male and female hand-wing indices were different at a 0.05 significance threshold in only 9.5% of species and at a 0.01 significance threshold in 4.6% of species, with a fairly even split between species with larger female HWI (n = 2239) and species with larger male HWI (n = 2633). Less than 1% of intraspecific variance was explained by sex differences, compared with 96% of interspecific variance explained by species differences. Therefore, each species HWI value represents the average of all sampled adults, including 13% (3417 of 26043) of individuals for which sex could not be determined.

Passerine HWI ranged from 0.96 in the Superb Lyrebird (*Menura novaehollandiae*) to 58.12 in the White-throated Swallow (*Hirundo albigularis*), with an overall mean passerine HWI of 18.28 and a median of 17.35 (Figure 6.1). Average community dispersal ability was highest in species that bred in the northern latitudes and lowest in the tropics

Figure 6.1: Passerine dispersal ability (HWI, logged) plotted on a phylogenetic tree obtained from (Jetz et al. 2012). Hot colors (reds and oranges) denote high dispersal; cold colors (blues and purples) denote low dispersal. Every third family (38 of 114) is labelled.

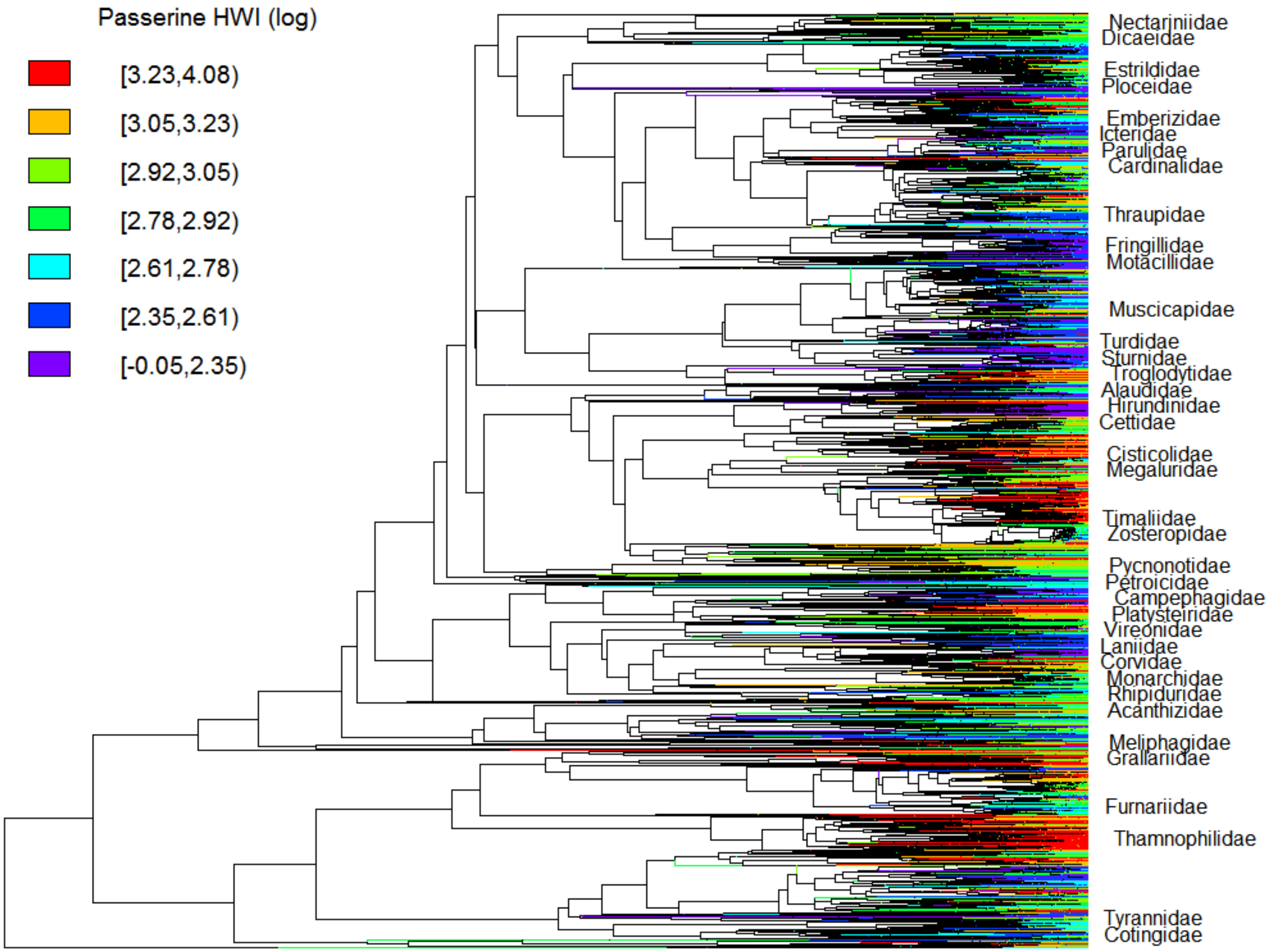
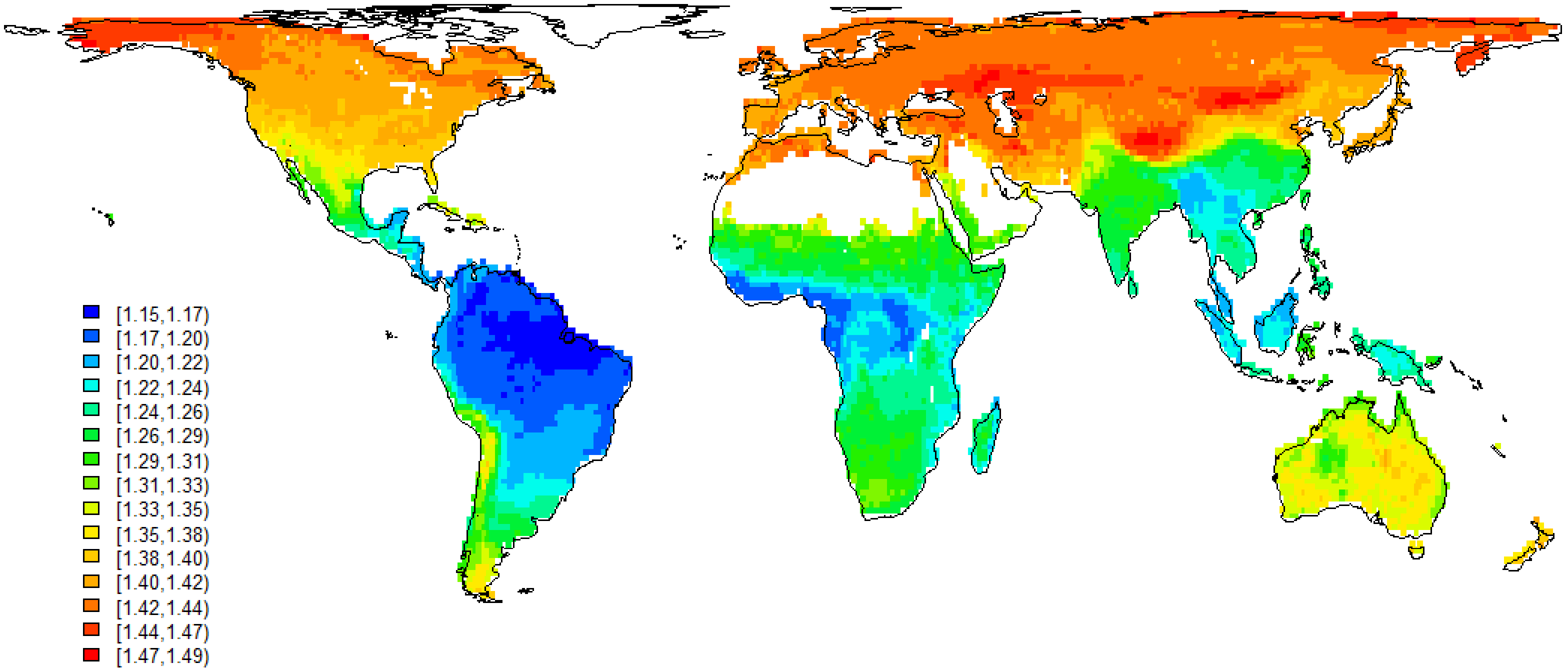
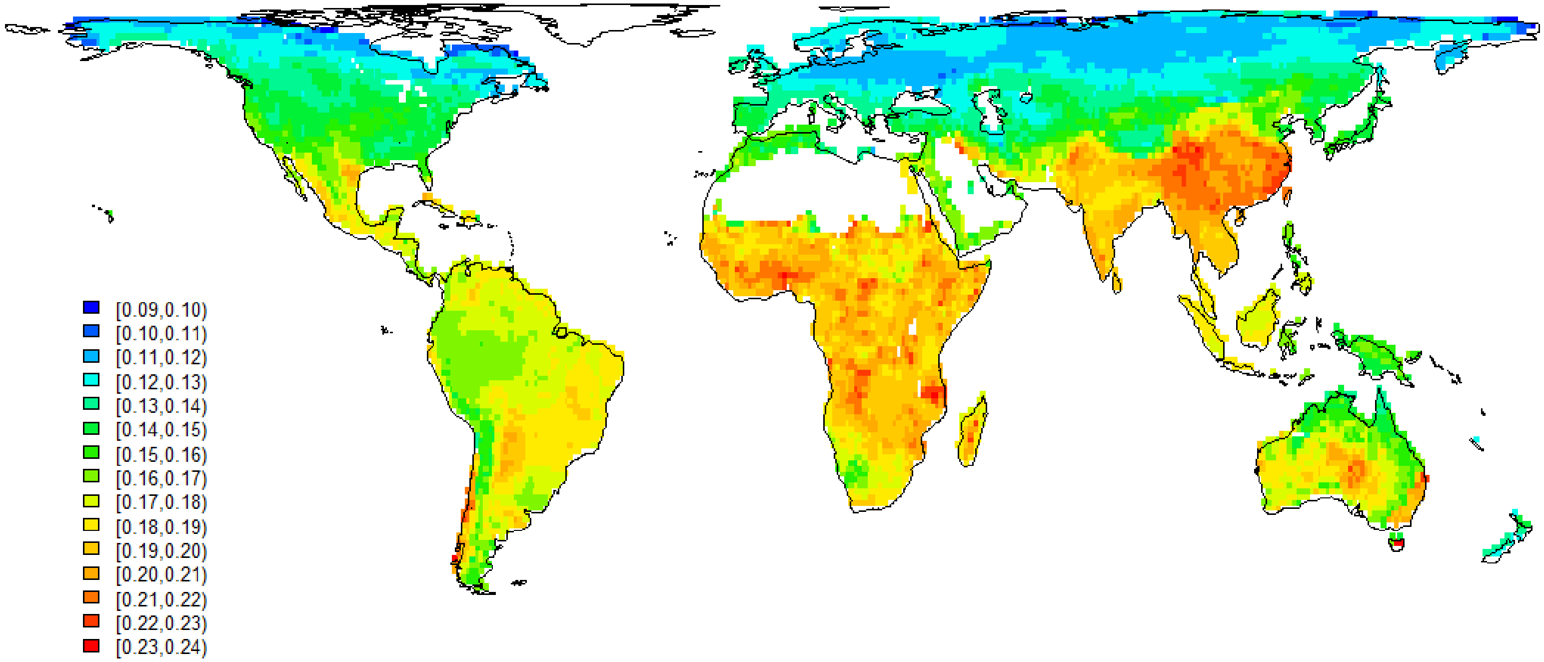


Figure 6.2: Global distribution of passerine HWI (logged) community [a] mean and [b] standard deviation. Each grid cell represents 1°x1°, or approximately 110 km x 110 km, and each value is computed from all birds whose breeding range (BirdLife International and NatureServe 2011) intersects that cell.

[A]



[B]


[0.09,0.10)
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[0.21,0.22)
[0.22,0.23)
[0.23,0.24)

(Figure 6.2a), likely reflecting differences in wing morphology for migratory species. Within avian communities, the variance in dispersal was highest in the Afrotropics, Australia, India, and China, but low in the Neotropics (Figure 2b), indicating that dispersal abilities may be driven by phylogeny and biogeographic history rather than environmental history. Indeed, the HWI and phylogeny are closely related, with Pagel's $\lambda = 0.936$.

Macroecology

Of the potential ecological correlates of dispersal tested, territoriality was the strongest predictor of dispersal ability, with moderate roles for habitat type, migration, diet, and latitude (Table 6.1). Though range size was significantly positively correlated with dispersal ability ($p = 0.024$), its effect size ($z = 0.049$) was tiny, with an increase of 1 standard deviation of range size leading on average to an increase of 0.05 standard deviations of HWI. Tested in absence of any other predictors, however, the effect size of range doubled ($z = 0.119$, $p < 0.001$), indicating that some of the conventional relationship between dispersal and range size is in fact better explained by other ecological factors.

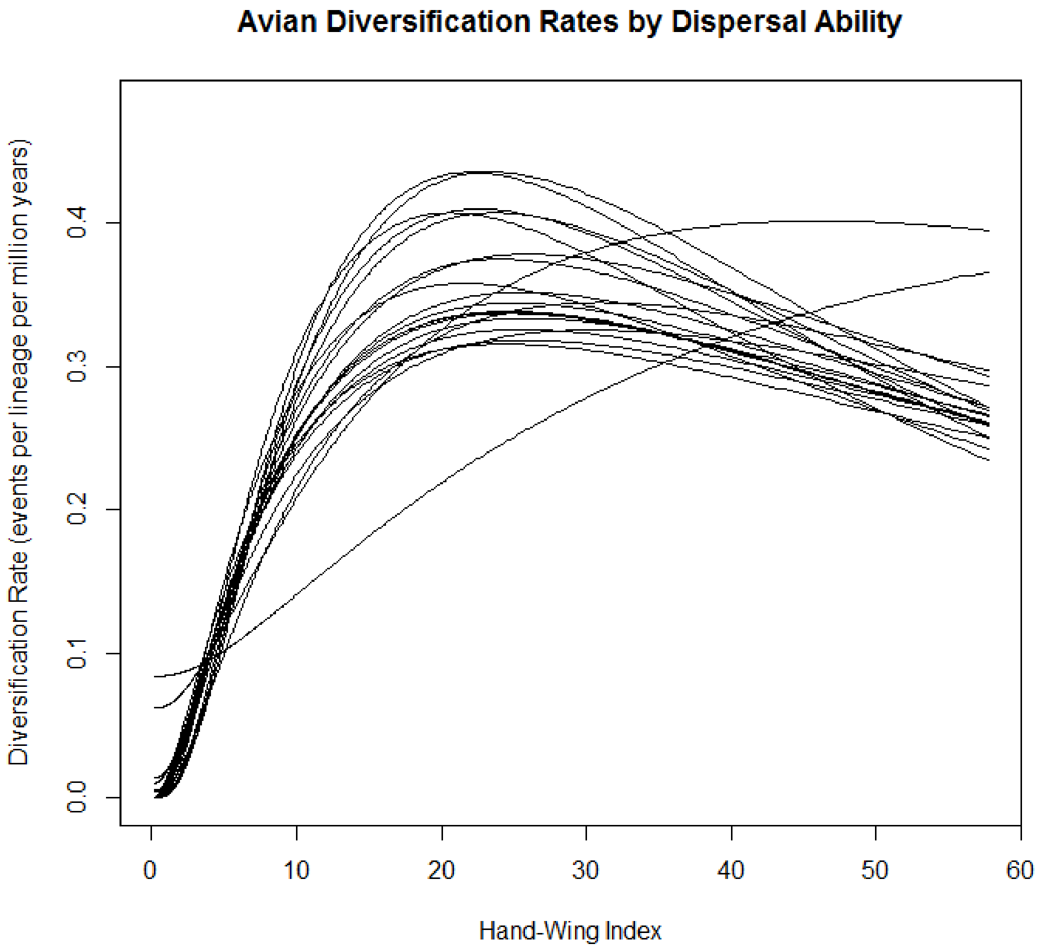
Macroevolution

In support of the IDH, the highest diversification rates were in lineages with intermediate levels of dispersal. Across all trees, both monotonic and hump-shaped curves models fit the relationship between HWI and lineage diversification better than a constant model, with the hump-shaped relationship on average best out of the three (average log likelihood -12544.3 for constant, -12520.4 for monotonic, and -12518.3 for hump-shaped, p[hump-shaped > monotonic] = 0.040). This relationship is parameterized by

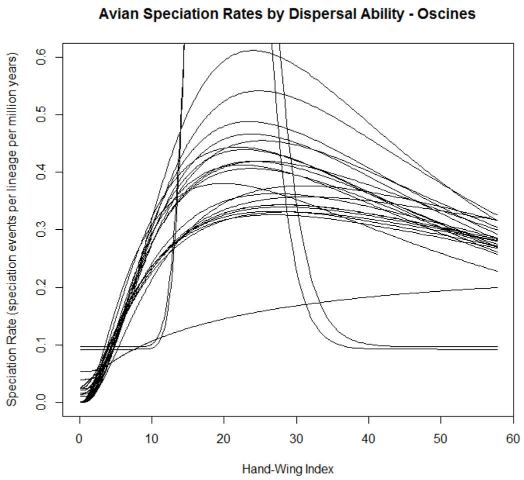
Table 6.1: Macroecological summary of HWI. Bayesian phylogenetic mixed model (BPMM) fitted as generalized linear mixed-effects models (GLMM) with gaussian error. Grey denotes predictors with statistically significant effects ($p < 0.05$), i.e. with 95% credible limits (CL) that do not span 0 in both models. DIC is the deviance information criterion, and R^2 is the variance explained by both fixed and random factors.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value estimate
Intercept	-0.346	-0.961	0.202	-	-	0.232
Habitat (semi-open)	-0.014	-0.105	0.076	-0.5	0.047	0.808
Habitat (open)	0.171	0.031	0.312	6.5	0.071	0.008
Mass	-0.036	-0.091	0.022	-1.4	0.029	0.200
Migration	0.162	0.106	0.214	6.2	0.028	<0.001
Range Size	0.049	0.009	0.091	1.9	0.021	0.024
Diet (invertivores)	-0.184	-0.335	-0.021	-7.0	0.083	0.032
Diet (nectarivores)	0.050	-0.292	0.385	1.9	0.178	0.794
Diet (omnivores)	0.176	-0.064	0.431	6.7	0.127	0.152
Diet (granivores)	-0.225	-0.454	0.003	-8.6	0.118	0.054
Song (none)	0.187	-0.052	0.418	7.2	0.122	0.132
Song (male-only)	0.044	-0.065	0.165	1.7	0.059	0.466
Territory (seasonal/weak)	0.266	0.140	0.381	10.2	0.062	<0.001
Territory (none)	0.650	0.451	0.817	24.9	0.094	<0.001
Latitude	0.153	0.102	0.204	5.8	0.027	<0.001
Continental	-0.139	-0.393	0.143	-5.3	0.140	0.310
Island	0.107	-0.410	0.591	4.1	0.258	0.676
Random effects				σ^2 %		
Phylogeny (n = 3239)	0.404	0.325	0.493	10.1	-	-
Summary statistics						
DIC	7357	-	-	-	-	-
R^2	0.751	-	-	-	-	-

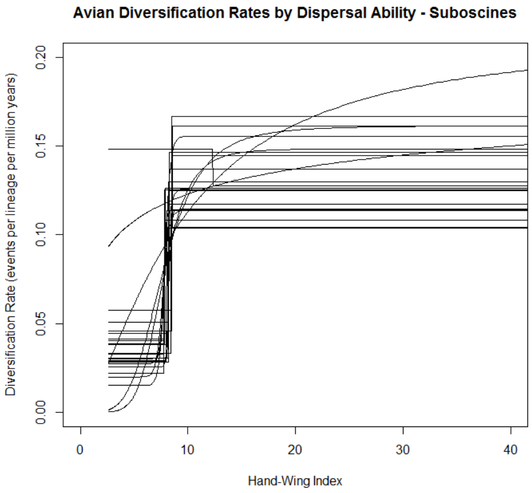
Figure 6.3: Predicted QuaSSE lineage diversification rates by HWI across (a) all passerine birds, (b) suborder *Passeri* (oscines), (c) suborder *Tyranni* (sub-oscines), (d) territorial birds, and (e) non-territorial birds. Each line represents one phylogenetic tree from (Jetz et al. 2012).



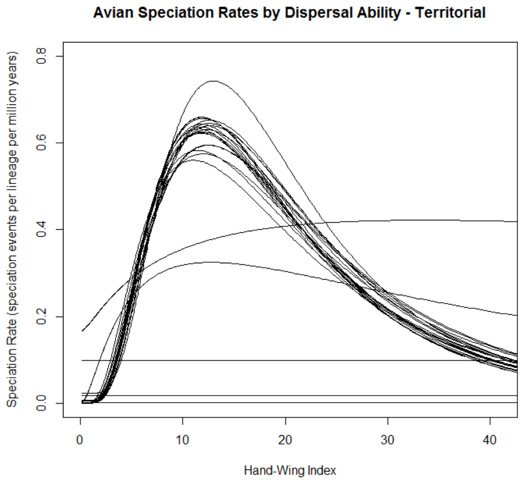
[A]


Avian Speciation Rates by Dispersal Ability - Oscines

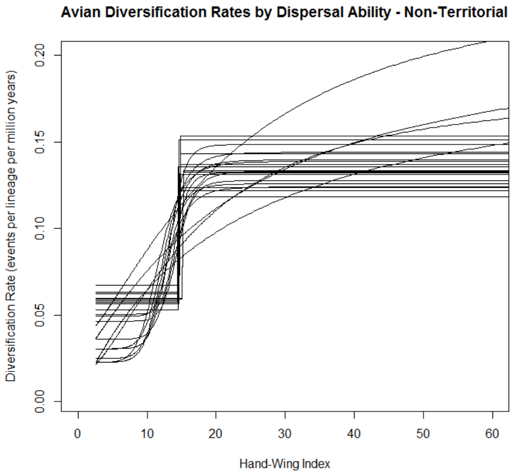
[B]


Avian Diversification Rates by Dispersal Ability - Suboscines

[C]


Avian Speciation Rates by Dispersal Ability - Territorial

[D]


Avian Diversification Rates by Dispersal Ability - Non-Territorial

[E]

an equation which predicts a lineage diversification rate of 0.01 events/lineage/million years for the poorest dispersers and 0.26 events/lineage/million years for good dispersers, with a peak of 0.34 events/lineage/million years for birds with a HWI around 25 (Figure 6.3a).

When island-dwelling species were excluded from these analyses, hump-shaped models were a slightly better fit (average log likelihood -1243780 for constant, -12404.9 for monotonic, and -12399.5 for hump-shaped, p[hump-shaped > monotonic] = 0.001). Similarly, this relationship holds true in the suborder *Passeri* (average log likelihood -9756.7 for constant, -9729.0 for monotonic, and -9725.7 for hump-shaped, p[hump-shaped > monotonic] = 0.010) and birds with strong year-round territorial displays (average log likelihood -4388.2 for constant, -4379.5 for monotonic, and -4367.5 for hump-shaped, p[hump-shaped > monotonic] < 0.001), but it is not true in the *Tyranni* (average log likelihood -2784.2 for constant, -2769.4 for monotonic, and -2774.3 for hump-shaped, p[monotonic > hump-shaped] = 0.002) or for birds with weak, seasonal, or no territory defense behaviors (average log likelihood -8514.2 for constant, -8462.4 for monotonic, and -8472.1 for hump-shaped, p[hump-shaped > monotonic] < 0.001).

Lineage diversification rates as calculated by BAMM were not significantly predicted by HWI in either model (p = 0.144 for monotonic and p = 0.102 for hump-shaped), and in the DR method, both the monotonic and the hump-shaped estimates of HWI were reasonably good predictors of lineage diversification, with no statistical difference between the two models (DIC = 10079 for monotonic, DIC = 10081 for hump-shaped; p = 0.022 for monotonic and p = 0.040 for hump-shaped).

This result is not robust when HWI is tested alongside the six correlates of HWI (p = 0.060 monotonic, p = 0.102 hump-shaped), though when the two least powerful predictors in

Table 6.2: The effect of dispersal on speciation along with other common predictors of avian speciation. The model shown estimates a hump-shaped relationship between dispersal diversification calculated by the “DR” method; the monotonic relationship between dispersal and DR and the hump-shaped and monotonic BAMM models are included in the supplementary materials.

		Bayesian phylogenetic mixed model (BPMM)				
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value estimate
Intercept	-0.424	-1.256	0.456	-	-	0.346
HWI	0.062	0.009	0.117		0.028	0.026
Song - none	-0.037	-0.280	0.197		0.124	0.770
Song - male-only	0.018	-0.092	0.142		0.030	0.826
Latitude	0.022	-0.027	0.071		0.026	0.398
Range Size	-0.063	-0.099	-0.011		0.022	0.018
Mass	-0.031	-0.090	0.038		0.033	0.356
Continental	-0.107	-0.361	0.177		0.140	0.452
Island	-0.144	-0.653	0.410		0.268	0.594
Territory (seasonal/weak)	-0.038	-0.169	0.078		0.065	0.568
Territory (strong)	0.112	-0.106	0.296		0.103	0.266
Habitat (semi-open)	0.107	0.019	0.195		0.046	0.018
Habitat (open)	0.299	0.163	0.432		0.071	< 0.001
Feeding Specialization	-0.027	-0.072	0.023		0.024	0.270
Passeri	-0.156	-1.171	0.898		0.543	0.770
Random effects				σ^2 %		
Phylogeny (n = 3247)	0.687	0.542	0.848	23.8	-	-
Summary statistics						
DIC	8272	-	-	-	-	-
R^2	0.656	-	-	-	-	-

Table 6.3: The effect of dispersal on speciation along with the six macroecological correlates of HWI. The model shown estimates a hump-shaped relationship between dispersal diversification calculated by the "DR" method; the monotonic relationship between dispersal and DR and the hump-shaped and monotonic BAMM models are included in the supplementary materials.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value estimate
Intercept	-0.552	-1.144	-0.008	-	-	0.058
HWI	0.047	-0.007	0.104	3.8	0.029	0.102
Latitude	-0.004	-0.060	0.049	-0.3	0.029	0.882
Range Size	-0.067	-0.109	-0.029	-5.5	0.021	0.001
Territory (seasonal/weak)	-0.039	-0.148	0.072	-3.2	0.058	0.528
Territory (strong)	0.077	-0.115	0.243	6.4	0.094	0.394
Habitat (semi-open)	0.113	0.019	0.204	9.3	0.048	0.016
Habitat (open)	0.308	0.170	0.452	25.4	0.072	0.001
Migration	0.055	0.009	0.113	4.5	0.027	0.044
Diet (insectivores)	-0.053	-0.215	0.106	-4.4	0.084	0.550
Diet (nectarivores)	0.250	-0.130	0.623	20.6	0.195	0.208
Diet (omnivores)	0.172	-0.068	0.420	14.2	0.128	0.184
Diet (granivores)	0.028	-0.238	0.235	2.3	0.123	0.812
Random effects				σ^2 %		
Phylogeny (n = 3277)	0.627	0.503	0.734	22.1	-	-
Summary statistics						
DIC	8341	-	-	-	-	-
R^2	0.648	-	-	-	-	-

the correlates model are sequentially dropped (latitude and diet), HWI does show a relationship with dispersal (p = 0.016 monotonic, p = 0.032 hump-shaped). When tested against other common predictors of speciation, HWI remained a key correlate of diversification as estimated by DR (p = 0.014 monotonic, p = 0.026 hump-shaped). Indeed, when tested together, the only other two predictors of diversification were habitat and range size. Birds in open habitats had higher diversification rates than those in dense habitats, with intermediate rates found in semi-open habitats. Range size was negatively correlated with diversification rates after controlling for HWI. That is, good dispersers tend to have large ranges, but for a given flight ability, birds with larger-than-average ranges had lower diversification rates. Diet was the only tested variables that significantly predicted the BAMM rates.

Discussion.

I found overall moderate support for the intermediate dispersal hypothesis, demonstrating that in passerine birds, the highest levels of lineage diversification are found in birds with intermediate flight abilities. These results are consistent with the conclusions of previous studies of dispersal and diversification in small groups of birds, such as a study of the family *Furnariidae* (Claramunt et al. 2011) and one of Australasian island birds (Weeks and Claramunt 2014) that both found decreasing speciation rates at high levels of dispersal. For low levels of dispersal, an increase in flight ability increases the likelihood of population separation and decreases the likelihood of extinction (Kisel and Barraclough 2010, Rosenzweig 1995, Phillimore et al. 2006, Bocxlaer et al. 2010, Dodd et al. 1999, Vamosi and Vamosi 2010, Levin 2006), which is seen in the low levels of diversification found in poor dispersers. This patterns tapers off, however, with very high levels of dispersal inhibiting diversification (Agnarsson et al. 2014).

Macroecological implications

Of particular note is the relationship between passerine flight ability and lineage diversification even after controlling for range size. Many studies of dispersal and speciation fail to distinguish between dispersal and range size, even explicitly using dispersal as a proxy for range size (Vamosi and Vamosi 2010, Kisel and Barraclough 2010). This study, however, demonstrates that range size has a *negative* relationship with diversification after controlling for dispersal ability. That is, for a given level of dispersal, birds with larger ranges will have slightly lower rates of diversification than those with smaller ranges (Table 6.2). If HWI were a poor estimate of actual, rather than potential, dispersal, this could simply be a signature of intermediate dispersal hypothesis, again suggesting that very high levels of dispersal, and thus very large ranges, lead to lower diversification rates. Alternatively, a smaller range for an identical dispersal ability suggests a more specialized ecological niche, which might be linked to higher rates of speciation (Janz, Nylin and Wahlberg 2006, Rundell and Price 2009).

The strongest macroecological correlate of dispersal ability is territoriality, with poor dispersers tending to defend year-long territories (Table 6.1). Resource defense is most important when an individual cannot fly away from the competitors and is most effective when the individual is familiar with the location (Clarke, Sæther and Røskaft 1997, Greenwood and Harvey 1982, Kokko and López-Sepulcre 2006). The suboscines are generally strongly territorial; as they dominate the Neotropical avifauna, this is seemingly the reason for the slightly lower average community dispersal in the New World tropics than the Old World (Figure 6.1a) Furthermore, the oscines in the Old World tropics, particularly the Afrotropics, have seasonal migratory patterns more complex than the north-south winter-summer archetype that dominates New World migration; these two facts together likely explain the higher variation in dispersal abilities seen in the Afrotropics (Figure 6.1b).

An important outstanding question in dispersal studies focuses on the speed at which dispersal can evolve (Ronce 2007, Laroche et al. 2016). Experiments artificially selecting for dispersal have been highly effective (Ronce 2007), and in some species dispersal can be changed by a mutation in a single gene (Roff 1986, Haag et al. 2005). I found that phylogeny explained approximately 10% of the variation in HWI, whereas the entire model explained just over 75% of the variation, indicating that dispersal is closely tied to the species' life history and less related to its evolutionary history. Furthermore, the relationship between dispersal, geography, and lineage diversification is particularly interesting. If dispersal evolved slowly, and thus was highly phylogenetically conserved, one might expect to see the dispersal-diversification pattern mirroring the geographic patterns of species richness. That is, regions with high species richness would contain many species with the dispersal abilities of those lineages exhibiting the highest rates of lineage diversification, namely intermediate levels. Instead, dispersal increases with latitude, closely mirroring the migratory patterns of birds; although the birds that speciate the fastest have intermediate levels of dispersion, flight ability apparently subsequently evolves to match other traits, leaving pockets of high species richness but generally low dispersal abilities.

Macroevolution differences in ecological and phylogenetic context

That the oscine and suboscine passerines contain different relationships between dispersal and diversification is not surprising, as 1161 of the 1239 suboscines (94%) have a HWI less than 25, the approximate peak for lineage diversification. Thus, the suboscines fall primarily along the first half of the hump-shaped model seen across all birds; it is only the oscine passerines that have dispersal abilities large enough to depress speciation rates.

The differentiation between territorial and non-territorial species is more puzzling, as it is the strongly territorial birds that generally have smaller HWIs but yet are the ones with the hump-shaped relationship between dispersal and diversification. Territoriality is a major life history trait, affecting both intraspecific social interactions and the relationship between an individual and space (Clarke et al. 1997, Temeles 1994). That excellent dispersers in territorial species experience a decline in diversification rates, but excellent dispersers in non-territorial species do not, may reflect the different relationships between dispersal and ecological resources in territorial and non-territorial species. For example, strongly territorial species may be at higher risk of extinction, even in instances of high dispersal, as territoriality lowers the effective population size (Bush et al. 1977). It may also be that a strong correlate of territoriality, such as social and sexual selection (see Chapters 4 and 5) or migratory behavior (Belliure et al. 2000) may be mediating this relationship. In particular, migratory species generally display high levels of philopatry (Weatherhead and Forbes 1994); high levels of movement only enable gene flow if the birds breed with a different population than those they were born with. Alternatively, it could be that restricting a phylogenetic tree based on a tip-level state produces spurious results; instead of examining the speciation and extinction rates at all points in the tree with a particular territorial behavior, this method instead only examines the evolutionary history of species that are currently territorial. If territoriality is not well phylogenetically conserved, rapid transitions between states could be skewing these tip-based results, particularly as non-territorial lineages have an overall higher diversification rate than territorial lineages (Chapter 5).

Dispersal, range size, and habitat were the only significant predictors of lineage diversification across passerines. Unlike Phillimore et al. (2006), I found no relationship between lineage diversification and feeding generalization, though generalization was measured at a family level in Phillimore et al. (2006) whereas it is here presented at the species level. Lineage diversification rates increase with the openness of the habitat, possibly reflecting the importance of geographic context in considering movement ecology (Weeks and Claramunt 2014). For a given flight ability, species occupying dense habitats may be more vulnerable to fragmentation, and thus extinction, than those occupying more open habitats, where movement is easier. That is, for a given flight ability, movement is still more energetically demanding in a dense habitat than an open habitat, suggesting that birds with a given wing shape may fly less in dense habitats and thus disperse less despite the potential suggested by their morphology.

Methodological limitations

The method used to present the primary results of this paper – QuaSSE, Quantitative State Speciation and Extinction (FitzJohn 2010) – allows for the simultaneous inference of trait states, speciation rates, and extinction rates. This allows an analysis of trait-dependent macroevolution to use the entirety of phylogenetic information presented, rather than just the tip states, as well as to incorporate a trait's continuous variation in a way that clade-level analyses (e.g., analyses of family richness, or sister-species) cannot (FitzJohn 2010). This method, however, has fallen under recent criticism. In particular, rare traits (< 10% of the total sample) tend to be assigned superfluous shifts to higher speciation rates (Beaulieu and O'Meara 2016); it is possible that some proportion of the high diversification rates assigned to high HWIs are a mere by-product of the paucity of species with high HWIs. Furthermore, QuaSSE does not allow for rate shifts caused by some additional, unrelated trait, resulting in a high chance of Type I error (Rabosky and Goldberg 2015). The DR method used in (Jetz et al. 2012) is unable to distinguish between a monotonic and a hump-shaped model, though both are statistically significant; the BAMM method (Rabosky et al. 2014) suggests that no trait, besides insectivory, can be linked to avian speciation and extinction. Whether the former discrepancy is caused by QuaSSE's increased precision or its potential for Type I error is unknown, though the fact that BAMM finds no trait to be correlated with diversification in our data despite dozens of studies to the contrary (for example, (Claramunt et al. 2011, Weeks and Claramunt 2014, Phillimore et al. 2006, Barnagaud et al. 2014, Belmaker and Jetz 2015, Belmaker et al. 2012, Kissling et al. 2012)) suggests an incongruence beyond the scope of this chapter.

Conclusions

Here, I present a test of the intermediate dispersal hypothesis using flight information from nearly every species of a large, global, and diverse order of birds, the *Passeriformes*. Using several different metrics of speciation and extinction, I find evidence for high levels of lineage diversification at intermediate levels of dispersal. These results are, however, somewhat mixed, dependent both on the social behavior of the species and on the methodology used. As avian phylogenies become increasingly detailed (Prum et al. 2015), as methodology improves for linking traits with lineage diversification (Laurent, Robinson-Rechavi and Salamin 2015), and as more fossil evidence can be used to calibrate phylogenies and to provide a more accurate measure of extinction rates (Mayr 2016), more accurate models will reveal the relationship between ecology and speciation/extinction underlying patterns of biodiversity today.

CHAPTER 7: GENERAL DISCUSSION.

Summary

In Chapter 2, I presented a global survey of avian functional traits. I showed that avian communities generally have a less dense occupancy of trait space than expected by chance, consistent with a competition-based model of community assemblage. At the species level, I similarly found little evidence for filtering effect of biome specialization, instead establishing that morphological traits are determined by species' evolutionary histories, diet, and general habitat type. Furthermore, I demonstrated that the trait density of avian orders generally decreases with increased species richness, indicating that the build-up of species richness is facilitated by radiations in new sections of morphospace. The passerines (order *Passeriformes*), however, were a clear exception to this pattern, containing 300 times more species than would be expected based on their occupancy of trait space. The remainder of the thesis was devoted to further understanding the social and ecological processes which could be driving these uneven patterns of species richness.

In Chapter 3, I used the morphological traits from Chapter 2 and a published analysis of song traits from the family *Furnariidae* to establish that social traits evolve faster and less predictably than ecological traits.

In Chapter 4, I demonstrated that female song is both widespread and adaptive across the avian tree, with different factors, both intrinsic and extrinsic, driving the evolution of song in the two sexes. Male song was most closely related to territory defense, whereas female song was mainly driven by both territory defense and pair-bonding behavior. Moreover, body size was negatively correlated with male song (likely reflecting the signatures of the passerines, which are some of the smallest birds and have very high levels of song) but positively correlated with female song (possibly suggesting a trade-off between the conspicuousness of the signal and the need for crypsis to avoid predators). Separate adaptive trajectories for male and female song are inconsistent with classic models of sexual selection, but they are consistent with the more inclusive model of social selection.

In Chapter 5, I used a three-way consideration of avian song (no song, male and female song, and male-only song) to separately test the effects of sexual and social selection on diversification rates across the avian tree. The relationship between sexual selection and speciation highly controversial, with mixed results both between and within taxa, but female ornamentation and social selection have been routinely ignored in these types of analyses. I found that lineages with male-only song (sexual selection) diversified the fastest and that lineages with no song (neither sexual nor social selection) diversified the slowest; lineages with both male and female song (social selection) displayed intermediate levels of diversification. This pattern held true for both passerines and non-passerines, as well as in both the tropics and the temperates. I concluded that the explicit consideration of non-sexual social selection, measured by the presence of female ornamentation, may clarify some of the controversy between sexual selection and speciation.

Finally, in Chapter 6, I returned to the passerines to test the role of dispersal in mediating speciation and extinction dynamics. The “intermediate dispersal hypothesis” (IDH) predicts that the highest diversification rates will be found in lineages with intermediate dispersal abilities, but the evidence thus far for the IDH is both limited and mixed. Using three different metrics of diversification, I found weak evidence for the IDH across all birds, but very strong evidence for the IDH in territorial birds and in the suborder *Passeri* (the “oscine” passerines). Non-territorial birds and the suborder *Tyranni* (“suboscines”), however, exhibited a monotonically-increasing relationship between dispersal and diversification. Therefore, I concluded that flight ability does shape patterns of avian species richness, but that the nature of this relationship depends on the ecological context of the dispersal events.

Directions for future work: Biometric traits

Trait packing

The trait packing patterns presented in Chapter 2 were primarily descriptive. Many avian communities occupy morphospace less densely than one would expect by chance, and that density does appear to have a biogeographic signature, but what biotic and abiotic processes facilitate species co-existence? This question has been examined many times at local levels (e.g., Pigot et al. 2016b, Wiens et al. 2011, Anacker and Strauss 2014), and recent advances in plant functional trait databases have allowed botanical trait co-existence to be examined globally (Kunstler et al. 2016, Díaz et al. 2016), but these questions have yet to be addressed in avian communities on a broad scale.

At least four methodological improvements would need to be made to Chapter 2’s descriptions of community FD before it could be used to test any hypotheses. The first would be the selection of an appropriate null model. Communities are not drawn from the entire global species pool; whether a species could conceivably be found in a particular location depends on, among other variables, its clade’s biogeographic history and dispersal abilities. The second methodological improvement would involve controlling for the phylogenetic non-independence of communities. The most obvious avian example is the passerine/non-passerine split; as discussed in Chapter 2, the reason(s) that a single avian order contains 60% of the world's species richness while occupying an unexpectedly small portion of trait space are yet unknown. If each community's trait packing density is simply a signature of the community's passerine richness, these patterns would be the result of phylogenetic pseudo-replication and thus would not address any underlying processes.

The third methodological improvement would control for spatial autocorrelation. Communities close together in space are not independent; they will share many of the same species and face similar environments (Legendre 1993, Dormann et al. 2007). Finally, the ideal analysis of this data would incorporate intraspecific variation. Each species is not a single point in morphospace but instead a distribution of points, and any analysis using trait density to estimate niche overlap should account for the fact that some species' niches will be wider than others (Jung et al. 2014, Ackerly and Cornwell 2007).

Once these four limitations have been resolved, however, these functional traits could be used to explicitly examine ecological processes of community assembly. Recently, Miller et al (2016) published a review of metrics to test phylogenetic clustering and overdispersion along with an R package, *metricTester*, to implement the most accurate of the simulation strategies. This study would provide an excellent starting point to realistically measure the global trait distributions of avian communities.

Functional traits in conservation

As human behavior increasingly drives habitat fragmentation and climatic instability (Vitousek et al. 1997, Barnosky et al. 2011, Sala et al. 2000), preserving ecosystem biodiversity and function has become critically important. To do this, ecosystem biodiversity and function must be effectively measured. Conservation scientists need to quantify the ecological processes present in communities and to measure species interactions with the biotic and abiotic environments in order to make informed decisions (Winemiller et al. 2015, Scherer et al. 2016). Functional traits can provide a standardized framework to quantify a species niche and thus to study species coexistence and interspecific variation (Adler et al. 2013, Mark et al. 2002). For example, as climate change causes range shifts, species will be forced into unprecedented contact (Root et al. 2003, Parmesan 2006), and conservation decisions will thus need to be made based on whether species can coexist. In additional, increased globalization has contributed to the spread of invasive species, which can disrupt agricultural industries and put native species at great risk of extinction (Pimental 2001); a trait-based approach to understanding which species could invade which communities would help in the management of these alien species (Blackburn et al. 2009).

Furthermore, functional traits can be used to calculate a species-level metric of “functional diversity” or “functional distinctness” (Tilman et al. 1997, Cadotte, Carscadden and Mirotchnick 2011, Thuiller et al. 2014, Cardinale et al. 2012). Like “evolutionary distinctiveness,” which quantifies the degree of unique evolutionary history contained in a single species (Jetz et al. 2014), functional distinctness would measure the uniqueness of species’ morphological traits. This metric could then be used as a proxy for the functional irreplaceability within a community (Bregman, Sekercioglu and Tobias 2014, Cottee-Jones et al. 2015) or to better understand human cultural valuation of birds (Tidemann and Gosler 2010), and thus inform conservation decisions.

Co-evolution of morphology and song

The main trade-off of any macroecological study is breadth versus depth; there are 14 continuous song variables presented for 270 species in Chapter 3, but only two binary variables presented for 10,257 species in Chapters 4 and 5. One potential direction for future data collection would be to use publicly available online libraries of avian song recordings (e.g., xeno-canto, Cornell University's Macaulay Library) to collate surveys of song traits at the level of detail that has been done for the ovenbirds (family *Furnariidae*) (Tobias et al. 2014) or by Mason et al. for the tanagers (family *Thraupidae*) (Mason et al. 2014). With such data, one could then test, for example, the extent to which song and beak shape co-evolve (Tobias et al. 2010, Derryberry et al. 2012, Podos et al. 2004a), or whether the agonistic character displacement (Grether et al. 2009) found in ovenbirds (Tobias et al. 2014) holds true across other radiations of birds and/or are modulated by clade-level properties such as song learning or territory defense.

Other uses for the data

The global survey of avian functional traits presented in Chapter 2 will likely have implications far beyond the scope imagined when the data was initially collected. Avian biometrics have been used in recent studies ranging from a test of Allen's rule (that larger bills are found in warmer climates to facilitate heat dissipation) (Danner and Greenberg 2015) to building trait-based models of biological invasions (Bitton and Graham 2015, Blackburn et al. 2009); data that I collected for Chapter 2 have already been used to validate models of trait structures under habitat fragmentation (Matthews et al. 2015), with several other collaborations currently underway.

One surprising use for this biometric data, specifically the dimensions of avian wings, has been in a global survey of avian egg shape. As part of a project led by Cassie Stoddard (Harvard University), I ran phylogenetic comparative models to test several hypotheses on the drivers of the egg shape evolution across 1,401 species of birds. Remarkably, the conventional egg wisdom does not hold across the entire clade – clutch size, nest shape (scrape, plate, or cup), nest location (ground, elevated, or cavity), and chick development mode (e.g., precocial versus altricial) have no relationship with egg asymmetry or eccentricity (Stoddard et al. in prep). Instead, the best explanation is a little-known alternative hypothesis, that the shape of the oviduct (the physiological origin of all egg shape variation) is determined by physiological adaptations for flight; it is the hand-wing index that best predicts egg shape, with more efficient fliers laying asymmetric, elliptical eggs. It is these sorts of analyses that will make a publically-available version of the data presented in Chapter 2 such an important contribution to the field.

Directions for future work: Evolution of female social signaling

Multimodal signals

Female song is not the only avian ornament. For example, Dale et al. (2015) recently published a survey of plumage dichromatism in 5,983 species of passerines, linking high levels of sexual selection to male-only ornamentation and cooperative breeding to female ornamentation. To what extent are plumage ornamentation and vocal ornamentation driven by similar selective pressures? Is there a trade-off between vocal and visual signals? Mason et al. (2014) found no relationship between song and plumage ornamentation in 321 species of tanagers (family *Thraupidae*), and Soma and Garamszegi (2015) surveyed song, plumage, and courtship dances in 85 species of estrildid finches (family *Estrildidae*) similarly found independent evolution of signals. On the other hand, Webb et al. (2016) found strong evidence for correlated evolution between female song and female plumage across 1314 species of oscine passerines, and Losin and Drury (2016) found a relationship between territorial displays and both plumage and song ornamentation in 49 species of wood warblers (*Parulidae*).

Most studies of animal ornamentation, including Chapters 4 and 5, consider signal modalities in isolation. As large global datasets become increasingly available, however, it will become important to test whether hypothesized functions of social and sexual signals hold true across all types of ornamentation.

An explicit measure of sexual selection

"Sexual selection" is a somewhat nebulous concept. Traditionally, the presence of elaborate secondary sexual characteristics has been used as a proxy for sexual selection (Andersson 1994, Darwin 1871, Panhuis et al. 2001); this is hardly a useful proposition when attempting to differentiate sexual and non-sexual social drivers of ornamentation. Other conventional indices of sexual selection include reproductive variance (Bateman 1948), parental investment (Trivers 1972, Clutton-Brock 1991), polygyny (Emlen and Oring 1977), testes size (Simmons and García-González 2008, Short 1979, Moller 1994), sperm length (Gage 1994), and mate guarding (Grafen and Ridley 1983), but the field has yet to agree on a single measure with parallels across many taxa, and precise definitions of "ornamentation" are similarly scarce. When studying the evolution of passerine plumage dichromatism, Dale et al (2015) measured sexual selection using a composite index of social mating system (a four-point scale, from strict social monogamy to obligate resource defense polygyny), sexual size dimorphism (differences in wing length), and paternal care (as a binary). This multi-composite system is a good model, and future comparative studies involving sexual selection would benefit from an explicit definition of what is meant by "sexual selection," using an index appropriate to the study system.

Sexual size dimorphism

An additional source of sexual dimorphism is body size, but the evolutionary drivers of sexual size dimorphism (SSD) remain largely unknown. SSD is widespread in birds, but the amount of dimorphism varies across taxa, and hypotheses abound to explain this variation. The two most popular explanations are that SSD lessens the overlap in ecological niches between males and females and thus minimizes intraspecific competition (Selander 1966), and/or that SSD is the result of traditional sexual selection wherein large body size is advantageous for intrasexual competition for mates (Darwin 1871, Andersson 1994). An alternatively hypothesis, however, is that differences in wing morphology could be an adaptation for sex-biased dispersal, a process which decreases the risk of inbreeding (Szulkin and Sheldon 2008). Finally, the *absence* of SSD could be explained by social selection, with sexual size monomorphism considered a mutual ornament (Tobias et al. 2012b, Lyon and Montgomerie 2012). That is, females may use increased body size as a signal for mutual mate choice, female-female competition over resources, or other intraspecific social interactions. The evidence for any of these four hypotheses, however, is generally restricted to studies of a single species or small groups of species (Székely, Reynolds and Figuerola 2000, Serrano-Meneses and Szekely 2006), and these studies typically use a single biometric trait as an index of dimorphism (Owens and Hartley 1998, Serrano-Meneses and Szekely 2006, Dale et al. 2007). There has not yet, to my knowledge, been a global survey of SSD.

In 2016, I co-supervised an MSc student, Anita Kristiansen (Imperial College London), who tested these four hypotheses using an index of SSD computed for 3890 species from the eight biometric measurements presented in Chapter 2. Using information on territory defense and pair bonding behavior as a proxy for social selection obtained from Tobias et al. (2016), migration and dispersal information (presented here in Chapter 6), diet specialization obtained from Wilman et al. (2014), and an index of sexual selection obtained from Dale et al. (2015), Kristiansen found that sexual selection was the only significant predictor of SSD (Kristiansen 2016).

These analyses are still preliminary, in large part because the biometric data I collected was typically limited to two males and two females per species, and thus it is difficult to tell if differences in biometric measurements reflect true SSD or just random chance. With additional data to verify the SSD index, however, and methodology designed to encompass intraspecific variation in biometric traits, a global investigation of the drivers of avian SSD would be an important contribution to the field of sexual and social signaling.

What are the females actually competing over?

One of the advantages of social selection theory is that it presents a generalized framework, one which encompasses all forms of social competition no matter what the resource in question is (West-Eberhard 1983, Tobias et al. 2012b, Lyon and Montgomerie

2012). There are many instances, however, in which a more specific understanding of the resources at stake could drive crucial research into the evolutionary origins of female aggression. When is it evolutionarily advantageous for females to compete for scarce resources, and when would the resources invested in competition detract from resources necessary to provision the offspring? In other words, when can increased female aggression be linked to increased fitness?

What little is known about the proximate causes of avian female aggression suggests that such behavior is largely mediated by testosterone, high levels of which also have a detrimental effect on offspring survival (Rosvall 2013). This trade-off between female aggression and reproduction remains largely unstudied (Clutton-Brock 2007, Stockley and Campbell 2013), but understanding the relationship between female ornamentation and resources necessary for reproduction would be a good place to start. The classic example of female ornamentation is in the parrot *Eclectus roratus*, where the males are bright green and use their plumage to compete for access to females while the females are red and blue and use their plumage to compete for access to cavity nesting sites (Heinsohn, Legge and Endler 2005). A recent set of experiments in tree swallows, *Tachycineta bicolor*, similarly demonstrated that females compete for nesting cavities (Rosvall 2008). To what extent do these examples hold true across all birds? An investigation of whether female ornamentation co-evolves with obligate cavity nesting behavior, for example, would provide insight into female aggression more explicitly than the analyses presented in this thesis. Comparative nest location data are already available on a broad scale (Stoddard et al. in prep, del Hoyo 1992-2011), as are other variables influencing female resource investment in offspring, such as egg mass (Stoddard et al. in prep), clutch size (del Hoyo 1992-2011, Jetz, Sekercioglu and

Böhning-Gaese 2008), rough estimates of dietary calcium composition (Wilman et al. 2014), and chick development mode (Starck 1993). To what extent do these reproductive costs either increase intrasexual competition (thus promoting ornamentation) or present costly physiological requirements (thus inhibiting ornamentation)?

Directions for future work: Limitations in the phylogenetic comparative methods

Phylogenetic comparative methods ("PCMs") are far from perfect (Cooper, Thomas and FitzJohn 2016a).

With the exception of the comparison of evolutionary rates presented in Chapter 3, methodology from Adams (2012), all PCMs in this thesis ignore intraspecific variation. This is a dangerous proposition. A recent paper by Cooper et al (2016b), for example, demonstrates that 5% measurement error in large phylogenies (> 500 species) is enough to favor an Ornstein Uhlenbeck model of trait evolution over a Brownian model 100% of the time, a phenomenon also found by Silvestro et al in a paper appropriately titled "Measurement errors should always be incorporated in phylogenetic comparative analysis" (Silvestro et al. 2015). Studies applying PCMs rarely check that the conclusions hold under simulated levels of measurement error (though see (Sandel et al. 2016) for a good exception), which almost certainly leads to a high rate of Type I error.

All of the phylogenies in this thesis use the avian phylogenies from (Jetz et al. 2012), which are based on mtDNA sequences from 6,670 birds. There are, however, more recently published avian phylogenies based on nuclear DNA which suggest different basal relationships between early clades. For example, a phylogeny of 198 species (Prum et al. 2015) reconstructs five major Neoaves clades: nightjars, swifts, and hummingbirds; turacos, bustards, cuckoos, and pigeons; *Gruiformes*; all shorebirds, diving birds, and wading birds; and all other landbirds. In contrast, an analysis of 48 species concludes that waterbirds and landbirds are largely paraphyletic groups, with the first major Neoaves split between the *Columbiformes* (doves and pigeons) and the *Passeriformes* (passerines). Such different tree topologies may have an effect on the PCMs presented here. For the phylogenetic analyses in the global survey of avian egg shape described earlier in this chapter (Stoddard et al. in prep), however, I combined the recent relationships modeled by Jetz et al. (2012) with the backbone presented by Prum et al. (2015) and ran all Bayesian phylogenetic mixed models on both the Jetz et al (2012) tree and this hybrid Jetz-Prum tree, with minimal differences in the results and no differences in the conclusions. Other methodologies, however, particularly ancestral state reconstruction and macroevolutionary models such as BiSSE and BAMM, might be more sensitive to such differences in crown clades.

Finally, the phylogenies used in this thesis are limited to 6,670 species, or about two-thirds of all avian diversity. As genetic sequencing becomes increasingly faster, cheaper, and more accessible, the phylogenetic relationships of the remaining third of avian species are likely to be soon resolved, but for now, this portion of the tree remains inaccessible. Furthermore, this missing third of avian diversity is not randomly sampled; species for which data is missing might show a geographic bias (i.e., be found in locations largely inaccessible to Western researchers), have small ranges, be more vulnerable to extinction, be more difficult to find within their ranges, etc. The effect of this non-random sampling on PCMs is currently unknown. As part of a recently-published paper on the evolution of communal signaling in birds (Tobias et al. 2016), I ran Bayesian taxonomic mixed models on the entire dataset of song behaviors (9230 species) with order, family, and genus as nested random effects as well as the phylogenetic mixed models on the species for which there are molecular-based phylogenies available. These models produced minimally different results, though it is entirely unclear whether these negligible differences are (A) due to a larger, more even sampling of avian evolutionary patterns, and thus more accurate, or (B) spurious, because of the failure to control for phylogenetic non-independence beyond the level of taxonomy. Similarly, analyses for Chapters 4 and 5 were run on the extended, 9993-species version of the tree presented in (Jetz et al. 2012) that is based on both genetic and taxonomic information; these results were largely the same and are excluded from this thesis due to space constraints. As genetic sequencing technology advances and our knowledge of the avian fossil record improves, it will be interesting to see how enhanced phylogenies increase our understanding of avian evolution.

Directions for future work: Macroevolutionary models

Methodological limitations

Linking the evolution of traits to shifts in speciation and extinction dynamics turns out to be a difficult problem. Chapters 5 and 6 rely on three different methodologies for detecting such links: the so-called "BiSSE-type" models, Binary-State Speciation and Extinction ("BiSSE") (Maddison et al. 2007), Multiple-State Speciation and Extinction ("MuSSE") (FitzJohn 2012), and Quantitative-State Speciation and Extinction ("QuaSSE") (FitzJohn 2010); Bayesian Analysis of Macroevolutionary Mixtures, or "BAMM" (Rabosky et al. 2014); and a cruder method, here called DR for "diversification rate," that presents a weighted average of branch levels (Jetz et al. 2012). BiSSE-type models, however, have known weaknesses, namely a substantial Type I error rate (Davis et al. 2013, Rabosky and Goldberg 2015), especially when there are "hidden" shifts in the data (substantial changes in speciation and extinction rate due to a character not in the analyses) (Beaulieu and O'Meara 2016). The BAMM methodology, however, has come under significant criticism as well, with posterior distributions being so strongly influenced by the priors as to render the methodology potentially invalid (Cadena 2016). These criticisms are unpublished as of the submission of this thesis, but were discussed publically at the Evolution 2016 meetings in Austin, TX, and are perhaps cause for concern.

Furthermore, the avian fossil record is notoriously poor (Gill 2006, Padian and Chiappe 1998). The phylogenies used in this thesis were produced by Jetz et al. (2012), relied upon mtDNA, and referred to only ten different fossil constraints in the construction of the final phylogeny; a more recent phylogeny of 198 avian species based on nuclear DNA similarly used 19 fossil records to date the phylogeny (Prum et al. 2015). When a fossil record is largely absent from a phylogeny, however, expected macroevolutionary patterns such as pull-of-the-present (Nee et al. 1994, Kubo and Iwasa 1995) are replaced by models of zero extinction (Weir and Hey 2006, Purvis 2008), which is hardly accurate or useful. The extent to which this affects macroevolutionary analyses apparently depends on the nature of the diversification dynamics (Etienne et al. 2012a), but careful consideration of the accuracy of extinction models is largely ignored in the literature (Quental and Marshall 2010).

Phylogenetics also suffers from the inverse problem: the underestimation of newly-formed species. Subspecies and newly-formed species are rarely considered in the construction of phylogenies and are thus excluded from phylogenetic comparative methods.

Furthermore, our subspecies knowledge gaps are hardly uniform; it is much more likely that we as a field have documented the subspecies of common birds, particularly in North America or Europe, than of rarer birds whose habitats are less accessible to Western researchers. Taxa for which the subspecies are distinguished by traits obvious to humans, such as stark non-UV plumage differences or a well-documented divergence in song, are also more likely to be known than subspecies distinguished by cryptic traits (Mayer and von Helversen 2001, Olsson et al. 2005). As such, macroevolutionary trends that are more important to younger, more ephemeral population splits will be largely overlooked by species-based methodology, with a strong geographic and taxonomic bias to what subspecies are studied. For example, a study of British birds found a negative relationship between dispersal and the number of subspecies, a pattern absent at the species level (Belliure et al. 2000). Would this pattern extend to tropical species? The data are not currently available to answer this question.

Dispersal and the accuracy of the hand-wing index

Ornithologists have largely accepted the hand-wing index (“HWI”, the ratio of Kipp’s distance to the unflattened wing chord) as an accurate proxy for avian dispersal (Weeks and Claramunt 2014, Claramunt et al. 2011, Pigot, Tobias and Jetz 2016a, Pigot and Tobias 2015, Trisos et al. 2014, Bitton and Graham 2015, Wright, Gregory and Witt 2014, White 2016, Burney and Brumfield 2009), but this relationship remains largely untested. The relationship between HWI and dispersal in *Furnariidae* presented in Claramunt et al. (2011), for example, is based on experimental releases in the Panama Canal of only 10 Neotropical birds (Moore et al. 2008), with the relationship between flight distance and HWI displaying an R^2 of only 0.68 ($p < 0.001$); another model, considering HWI as a predictor of migration distances in *Phylloscopus* warblers, is based on 13 species (Marchetti, Price and Richman 1995). An oft-cited paper on the dispersal abilities of 47 British and Irish passerine birds, based on ringing data, actually only considers Kipp's distance, rather than HWI – and Kipp's was a non-significant predictor of dispersal distance unless only Kipp's and bill depth were included in the model (Dawideit et al. 2009). Another frequent citation for the relationship between HWI and dispersal is anecdotal and purely descriptive (Savile 1957). Though there is certainly some relationship between flight ability and wing shape, and likely a strong one, HWI may not be a perfect measure of dispersal for all birds.

For example, as discussed in Chapter 6, migratory birds with high levels of philopatry (Weatherhead and Forbes 1994) might have high HWIs but would only rarely use those flight abilities to breed elsewhere, resulting in genetically discontinuous populations (Morris-Pocock, Anderson and Friesen 2016). It is also possible that HWI represents a physiological constraint on maximal dispersal levels, thus providing a ceiling on dispersal rather than a linear index (Marius Somveille, pers. comm.). It is generally unknown how quickly dispersal evolves (Ronce 2007, Wright et al. 2016), and thus HWIs may reflect a previous dispersal state rather than extant trait values. A study of the wings of European starlings (*Sturnus vulgaris*) before, during, and after the invasion of North America, for instance, found no differences in HWI that could be linked to the invasion (Bitton and Graham 2015), though another study of museum specimens did find that changes the HWI of North American forest songbirds reflected contemporaneous changes in available habitat (Desrochers 2010). Evolutionary changes in HWI may thus be driven by consequences of wing shape other than dispersal, such as maneuverability.

Therefore, an important step in future studies of dispersal and diversification dynamics would be to verify the accuracy of the HWI as a proxy for dispersal and explicitly consider the varying relationship between flight ability, range size, and inter-population gene flow. Natal dispersal data do not yet exist for many birds, particularly those outside of high-intensity ringing locations such as the UK. As technology improves and GPS trackers become smaller and cheaper, however, this is likely to change, and thus dispersal and/or migratory distance could be explicitly linked to HWI on a geographically and taxonomically broad scale. Furthermore, as the ecological contexts of dispersal become clearer, more explicit models of the relationship between dispersal and diversification can be made. The separate consideration of range size and dispersal ability in Chapter 6, for example, might provide a starting point for theoretical considerations of how the separate evolution of range size and dispersal might affect diversification.

Conclusion

Biodiversity can be measured both in terms of functional trait diversity and by species richness. In this thesis, I have combined novel datasets with modern phylogenetic comparative analyses to examine the roles of social and ecological processes in generating and maintaining diversity in birds across space and time. In particular, I have demonstrated that macroecological insights can inform macroevolutionary models and have established that social selection theory is a useful framework for understanding avian ornamentation. By presenting a survey of morphological measurements for 99% of all known bird species, I have also contributed to the field a dataset that can be used to test the generality of many ideas underpinning ecology, evolution, and conservation. Ultimately, such trait-based models will further our understanding of the variability of life on earth and of how biodiversity can best be preserved for future generations.

APPENDIX 1: SUPPLEMENTARY ANALYSES FOR CHAPTER 4.

Methods and Results

Though the bulk of this chapter has considered the evolution of male and female song as potential separate trajectories, a slightly different frame for these questions would be to consider the development and maintenance of female song as a subset of all singing behavior. There are 8284 species with have male song, of which 2928 also have female song. To separate the pressures driving singing behavior as a whole from the factors driving female song, I re-ran all of my female song models on just the species that sing. Within these models, when female song was consider a subset of all avian song, territoriality, body mass, migratory behavior, and annual temperature range remained significant predictors of female song. Species with year-round pair bonds still sung the most, but within singing species, species with seasonal bonds showed an intermediate amount of female song, with solitary species showing the least amount of female song ($p = 0.003$). Diet was no longer a significant predictor of female song, but mean annual temperature was, with species in warm climates more likely to have female song than those in cooler climes ($p = 0.045$). The co-evolutionary BayesTraits models showed little substantial difference in the relative evolutionary relationships within these datasets with the exception of the co-evolution of female song and social stability. Within this restricted dataset, there is a much higher transition rate between neither trait and the state of no song and pair bonding but a lower transition rate between neither trait and the state of female song and no pair bonding; the rates moving in and out of the state of female song but no pair bonding are commensurate with the other transition rates (that is, this is no longer a highly unstable state).

The 31 species with female song but with no male song can be considered special cases, instances of sex-role reversal subject to very different pressures than the other instances of female song. To be sure that these 31 “outliers” were not affecting the analyses, I ran models with these species excluded. Though the numerical results of the co-evolutionary models did change slightly, no result changed in order of magnitude or in value relative to the other rates. Similarly, there were very few differences in magnitude, direction, or significance in the linear models, though for both male and female, solitary lifestyle (a category of social stability, as opposed to season or permanent bonds) was a significant predictor of song, and mean annual temperate became a marginally significant rather than a marginally non-significant predictor of female song (average $p = 0.043$ versus $p = 0.062$).

Each model in BayesTraits was run twice to test for the effect of the randomized starting point. Only the first runs are reported in the main results; the results from both runs are reported below. Table S1.6, the results of the test for correlated evolution, shows only a slight difference in the likelihood of the independent female song – social stability model; the conclusion remains the same. The average transition rates (Table S1.7) between the two runs do differ more substantially, with nearly all (28 of 32) transition rates differing significantly between the two runs at three significant figures; over half (20 of 32) differing significantly at two significant figures; and almost one-quarter (7 of 32) differing at one significant figure. Finally, the nodal probabilities also vary between the two runs, with over half (10 of 16) varying at three significant figures, just under half (7 of 16) at two significant figures, and one at one significant figure. This indicates that whilst the overall and comparative conclusions within the BayesTraits models are robust, the exact values for the transition rates and nodal probabilities are influenced by stochasticity.

Since the 2012 publication of the Global Bird Tree (Jetz et al. 2012), many comparative analyses have used phylogenies containing some or all of the 3,323 species of birds within the tree that lack genetic data. As I have collected data on nearly all of these birds, to be consistent with the literature I ran the two main mixed models on a phylogeny containing 9,735 species of birds. Within the models testing all possible predictors, this expanded phylogenetic dataset indicates that diet might be a potential predictor of male song and that habitat may be a potential predictor of female song; within the best-fit models, the lowest level of sociality (solitary life) becomes a highly significant predictor on the full tree whereas its effect on female song on the genetic tree is only marginally significant (average p = 0.059). Otherwise, all other coefficients maintain their relative magnitude, direction, and significance.

Figures and Tables

Figure S1.1: Map showing the distribution of species with female song as a proportion of species with male song.

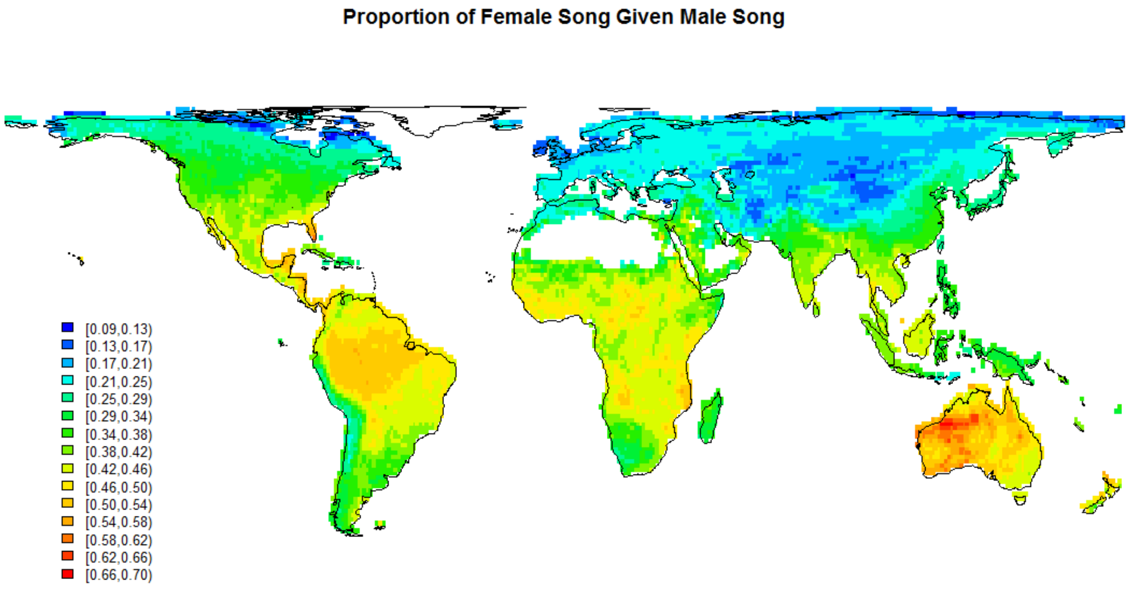


Table S1.1: Model likelihood values for BayesTraits runs on the entire tree (left, “All”) and on a dataset restricted to only species that sing (left, “Singing”).

		All				Singing			
		Mean Lh, Dep	SD, Dep	Mean Lh, Dep	SD, Ind	Mean Lh, Dep	SD, Dep	Mean Lh, Ind	SD, Ind
Female	Territory	-3539	2	-3668	2	-3095	4	-3173	1
	Stability	-2869	2	-2898	2	-2611	2	-2635	1

Table S1.2: Co-evolutionary transition rates for BayesTraits runs on the entire tree (right, “All”) and on a dataset restrict to only birds species that sing (right, “Singing”). Transition rates in the restricted model that differ in their relative relationships to the other rates compared with the relative relationships in the full model have been highlighted in grey.

		All		Singing	
		Mean	SD	Mean	SD
Territory	q12	0.530	0.063	0.902	0.476
	q13	0.116	0.022	0.315	0.125
	q21	0.520	0.054	0.403	0.098
	q24	1.791	0.122	1.856	0.134
	q31	0.955	0.596	0.264	0.201
	q34	0.217	0.182	0.235	0.147
	q42	1.792	0.123	1.708	0.204
	q43	0.115	0.020	0.080	0.030
Stability	q12	0.332	0.392	1.539	0.194
	q13	1.109	0.262	0.166	0.104
	q21	0.111	0.022	0.154	0.025
	q24	1.036	0.075	1.562	0.104
	q31	35.657	33.091	0.850	0.731
	q34	55.330	33.863	0.957	0.728
	q42	1.997	0.148	1.562	0.104
	q43	0.045	0.051	0.000	0.000

Table S1.3: Results of a generalized linear mixed model testing the effects of intrinsic and extrinsic predictors of female song across birds with song. Model used a Markov-chain Monte-Carlo algorithm (MCMCglmm) with phylogeny as a random effect averaged across 100 trees. Significant effects are highlighted in grey.

	COMMUNAL SONG					
	z	2.5% CL	97.5% CI	% Change	SD	p-value
Intercept	1.059	-0.661	2.826	-	-	0.284
Intrinsic Fixed Effect						
Migration (partially migratory)	**0.462**	**0.178**	**0.741**	**3.8**	**0.148**	**0.003**
Migration (fully migratory)	0.123	-0.265	0.515	1.1	0.214	0.549
Diet (fruit and nectar)	0.546	-0.221	1.317	3.8	0.413	0.176
Diet (invertebrates)	0.451	-0.274	1.174	3.2	0.396	0.235
Diet (omnivorous)	-0.106	-1.200	0.962	-1.6	0.587	0.846
Diet (plants)	0.448	-0.354	1.245	2.9	0.451	0.287
Dietary specialism (generalist)	0.415	-0.343	1.170	3.6	0.403	0.295
Dietary specialism (omnivore)	0.838	-0.296	1.998	7.0	0.604	0.154
Body mass	**0.479**	**0.291**	**0.667**	**3.7**	**0.100**	**0.001**
Territoriality (seasonal/weak)	**-2.222**	**-2.424**	**-2.021**	**-17.9**	**0.103**	**0.001**
Territoriality (none)	**-3.183**	**-3.589**	**-2.779**	**-25.8**	**0.224**	**0.001**
Mating system (cooperative breeding)	0.210	-0.050	0.470	1.8	0.136	0.122
Social stability (seasonal bonds)	**-0.973**	**-1.213**	**-0.736**	**-8.0**	**0.125**	**0.001**
Social stability (solitary)	**-1.222**	**-1.974**	**-0.481**	**-9.7**	**0.409**	**0.003**
Extrinsic Fixed Effect						
Mean annual temperature	**0.194**	**0.008**	**0.379**	**1.5**	**0.095**	**0.045**
Annual temperature range	**0.293**	**0.073**	**0.515**	**2.3**	**0.114**	**0.012**
Mean annual precipitation	-0.018	-0.164	0.131	-0.1	0.082	0.815
Annual precipitation range	0.032	-0.085	0.147	0.2	0.061	0.596
Median range latitude	-0.029	-0.149	0.090	-0.2	0.061	0.636
Habitat (semi-open)	0.184	0.000	0.370	1.4	0.097	0.055
Habitat (open)	-0.038	-0.320	0.243	-0.3	0.146	0.800
Random Effect				partial R^2		
Phylogeny (n = 8424)	6	6	6	0.746	-	-
Summary statistics						
DIC	2671	-	-	-	-	-
R2	0.860	-	-	-	-	-

Figure S1.2: Map showing the global distribution of the 31 bird species with only female song. Cells with fewer than 20 bird species are excluded.

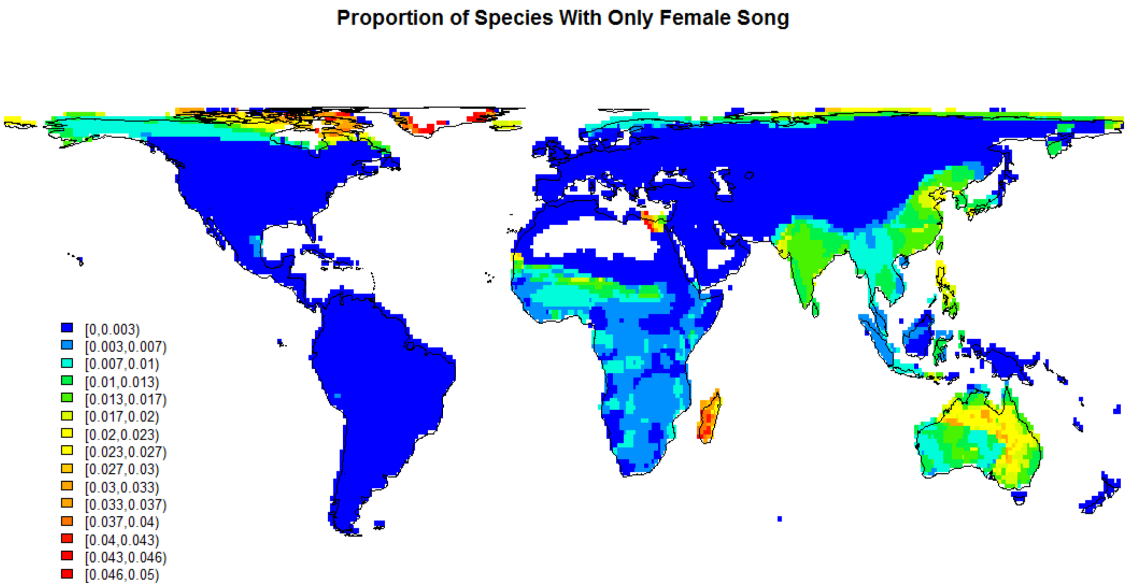


Table S1.4: Model likelihood values for BayesTraits runs on the entire dataset (left, "All") and on a dataset excluding the sex-role-reversed species (right, "Excluded"). Cf Table 4.5.

		All				Excluded			
		Mean Lh, Dep	SD, Dep	Mean Lh, Indep	SD, Ind	Mean Lh, Dep	SD, Dep	Mean, Indep	SD, Ind
Territory	Male	-2264	2	-2347	2	-2228	3	-2313	2
	Female	-3539	2	-3668	2	-3517	1	-3649	1
Stability	Male	-1578	4	-1581	2	-1548	4	-1552	2
	Female	-2869	2	-2898	2	-2850	4	-2883	1

Table S1.5: Co-evolutionary transition rates for BayesTraits runs on the entire dataset (left, “All”) and on a dataset excluding the sex-role-reversed species (right, “Excluded”). Cf Table 4.6.

		Male				Female			
		All		Excluded		All		Excluded	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Territory	q12	0.517	0.338	0.412	0.315	0.530	0.063	0.537	0.068
	q13	0.951	0.086	0.971	0.084	0.116	0.022	0.109	0.024
	q21	0.953	0.085	0.972	0.083	0.520	0.054	0.524	0.056
	q24	3.129	0.366	3.260	0.361	1.791	0.122	1.798	0.121
	q31	0.952	0.083	0.972	0.082	0.955	0.596	1.263	0.683
	q34	0.954	0.083	0.972	0.082	0.217	0.182	0.175	0.156
	q42	0.194	0.021	0.192	0.022	1.792	0.123	1.800	0.121
	q43	0.195	0.021	0.195	0.022	0.115	0.020	0.106	0.021
Stability	q12	0.591	0.605	0.691	0.682	0.332	0.392	0.534	0.447
	q13	1.299	0.618	1.492	0.637	1.109	0.262	1.011	0.246
	q21	0.077	0.013	0.078	0.014	0.111	0.022	0.104	0.023
	q24	1.770	0.219	1.902	0.217	1.036	0.075	1.018	0.070
	q31	0.929	0.432	0.781	0.400	35.657	33.091	26.131	14.324
	q34	1.118	0.442	1.129	0.493	55.330	33.863	27.813	13.258
	q42	0.237	0.028	0.221	0.032	1.997	0.148	2.032	0.144
	q43	0.077	0.012	0.078	0.013	0.045	0.051	0.045	0.045

Table S1.6: Model likelihood values for BayesTraits runs 1 and 2. Mean probabilities that differ significantly in the second run (two-sample t-test, α = 0.05) at are highlighted in light grey. Cf Table 4.5.

		Run 1				Run 2			
		Mean Lh, Dep	SD, Dep	Mean Lh, Ind	SD, Ind	Mean Lh, Dep	SD, Dep	Mean Lh, Ind	SD, Ind
Territory	Male	-2264	2	-2347	2	-2264	2	-2347	2
	Female	-3539	2	-3668	2	-3539	2	-3668	2
Stability	Male	-1578	4	-1581	2	-1578	4	-1581	2
	Female	-2869	2	-2898	2	-2869	2	-2897	1

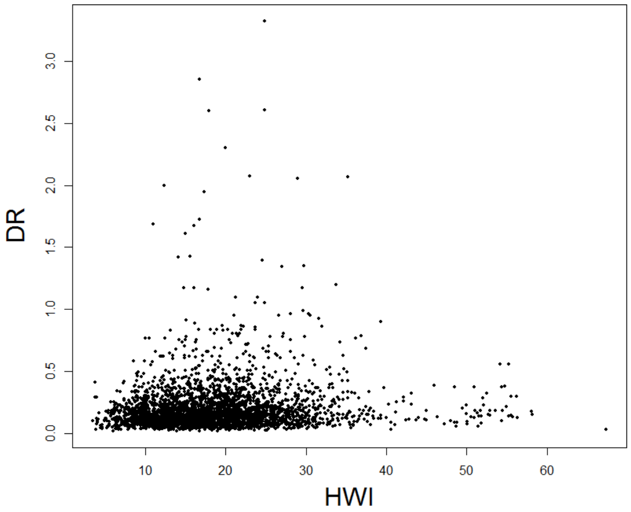
Table S1.7: Co-evolutionary transition rates for BayesTraits runs 1 and 2. Mean rates that differ significantly in the second run (two-sample t-test, α = 0.05) at one significant figure are highlighted in black, that differ at two significant figures are highlighted in dark grey, and that differ at three significant figures are highlighted in light grey. Cf Table 4.6.

		Male				Female			
		1		2		1		2	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Territory	q12	0.517	0.338	0.555	0.340	0.530	0.063	0.525	0.064
	q13	0.951	0.086	0.944	0.086	0.116	0.022	0.115	0.021
	q21	0.953	0.085	0.946	0.084	0.520	0.054	0.512	0.054
	q24	3.129	0.366	3.139	0.367	1.791	0.122	1.773	0.115
	q31	0.952	0.083	0.947	0.084	0.955	0.596	1.230	0.606
	q34	0.954	0.083	0.947	0.084	0.217	0.182	0.201	0.167
	q42	0.194	0.021	0.193	0.021	1.792	0.123	1.774	0.115
	q43	0.195	0.021	0.194	0.021	0.115	0.020	0.114	0.020
Stability	q12	0.591	0.605	0.582	0.609	0.332	0.392	0.307	0.371
	q13	1.299	0.618	1.300	0.625	1.109	0.262	1.072	0.221
	q21	0.077	0.013	0.077	0.013	0.111	0.022	0.112	0.022
	q24	1.770	0.219	1.776	0.213	1.036	0.075	1.023	0.078
	q31	0.929	0.432	0.851	0.456	35.657	33.091	17.599	11.673
	q34	1.118	0.442	1.178	0.478	55.330	33.863	21.247	9.565
	q42	0.237	0.028	0.239	0.028	1.997	0.148	1.978	0.154
	q43	0.077	0.012	0.077	0.012	0.045	0.051	0.023	0.039

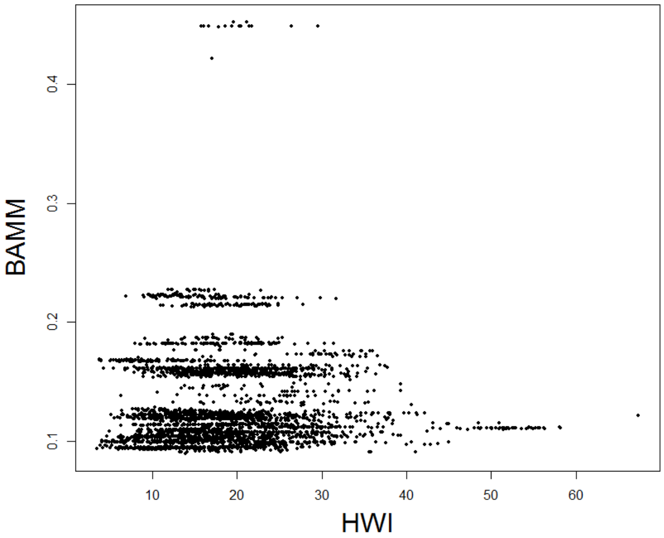
APPENDIX 2: SUPPLEMENTARY FIGURES FOR CHAPTER 6.

Figure S2.1: Diversification rates calculated by DR and BAMM. (a) HWI against diversification rate as calculated by the DR method. (b) HWI against diversification rate as calculated by BAMM. (c) The modeled Gaussian distribution of HWIs.

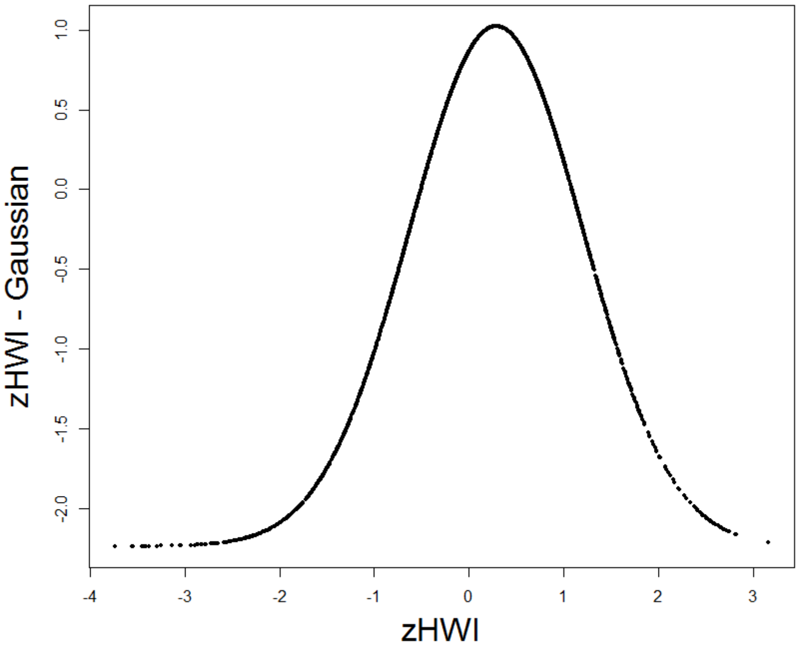
(d) Diversification rates as calculated by BAMM (y-axis) against those calculated by DR (x-axis). (e) Diversification rates calculated by DR as a function of the modeled Gaussian distribution of HWIs. (f) Diversification rates calculated by BAMM as a function of the modeled Gaussian distribution of HWIs.



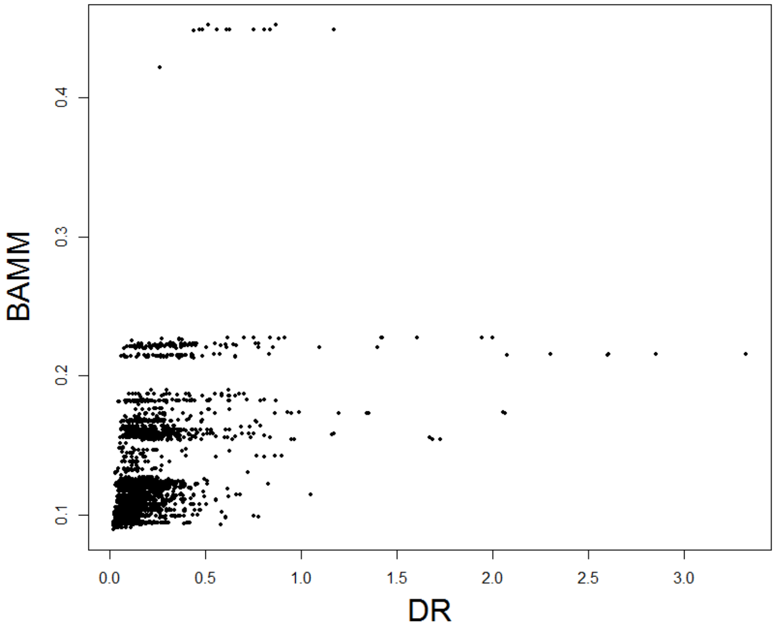
[A]



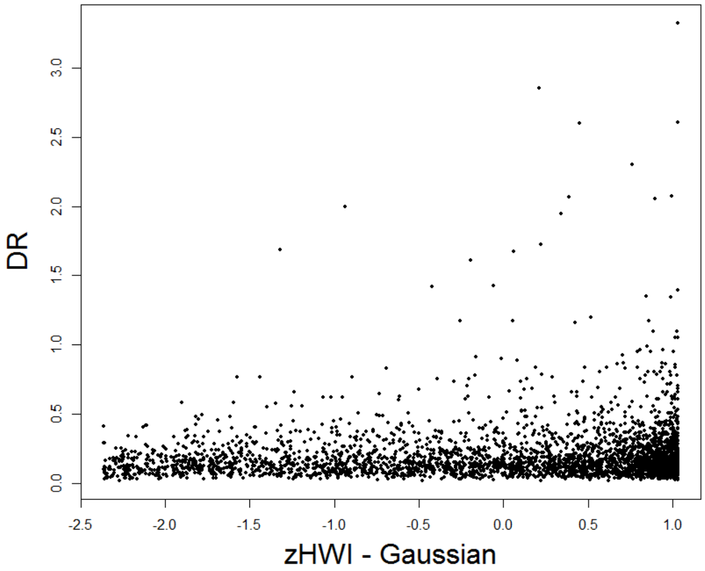
[B]


zHWI - Gaussian
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
-4
-3
-2
-1
0
1
2
3
zHWI

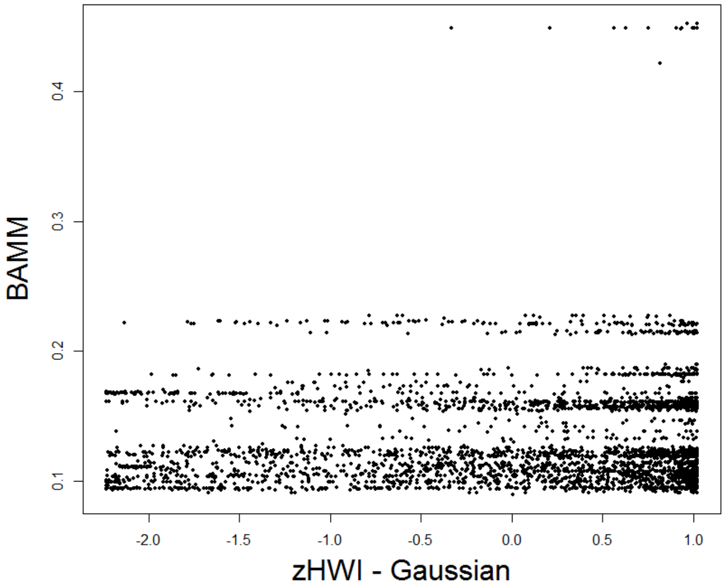
[C]


BAMM
0.4
0.3
0.2
0.1
0.0
0.5
1.0
1.5
2.0
2.5
3.0
DR

[D]


DR
0.0
0.5
1.0
1.5
2.0
2.5
3.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
zHWI - Gaussian

[E]


BAMM
0.1
0.2
0.3
0.4
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
zHWI - Gaussian

[F]

Table S2.1: The effect of dispersal on speciation along with other common predictors of avian speciation. The model shown estimates a hump-shaped relationship between dispersal diversification calculated by the “BAMM” method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.524	-1.323	0.136	-	-	0.132
HWI	0.031	-0.017	0.076	3.3	0.025	0.232
Song - none	-0.062	-0.272	0.173	-6.6	0.120	0.632
Song - male-only	0.001	-0.104	0.112	0.1	0.057	0.964
Latitude	-0.025	-0.066	0.026	-2.7	0.024	0.296
Range Size	0.001	-0.037	0.046	0.1	0.021	0.988
Mass	-0.045	-0.100	0.126	-4.8	0.030	0.124
Continental	-0.148	-0.425	0.094	-15.7	0.132	0.256
Island	-0.143	-0.654	0.327	-15.2	0.253	0.568
Territory (seasonal/weak)	0.038	-0.079	0.165	4.0	0.064	0.558
Territory (strong)	-0.062	-0.115	0.247	-6.6	0.095	0.518
Habitat (semi-open)	-0.059	-0.042	0.146	-6.2	0.047	0.224
Habitat (open)	0.088	-0.063	0.207	9.3	0.069	0.232
Feeding Specialization	0.023	-0.026	0.066	2.5	0.025	0.350
Passeri	-0.214	-0.978	0.615	-22.8	0.417	0.620
Random effects				σ^2 %		
Phylogeny (n = 3247)	0.391	0.214	0.458	16.8	-	-
Summary statistics						
DIC	6802	-	-	-	-	-
R^2	0.571	-	-	-	-	-

Table S2.2: The effect of dispersal on speciation along with other common predictors of avian speciation. The model shown estimates a monotonic relationship between dispersal diversification calculated by the "DR" method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.413	-1.254	0.515	-	-	0.378
HWI	0.079	0.016	0.143	6.5	0.032	0.014
Song (none)	-0.041	-0.312	0.191	-3.4	0.126	0.766
Song (male-only)	0.019	-0.101	0.136	1.5	0.061	0.796
Latitude	0.016	-0.033	0.067	1.3	0.026	0.570
Range Size	-0.056	-0.098	-0.015	-4.6	0.021	0.006
Mass	0.035	-0.101	0.029	2.9	0.034	0.318
Continental	-0.109	-0.394	0.159	-9.0	0.144	0.458
Island	-0.150	-0.666	0.380	-12.5	0.268	0.588
Territory (seasonal/weak)	-0.041	-0.164	0.090	-3.4	0.068	0.566
Territory (strong)	-0.085	-0.127	0.285	-7.1	0.106	0.426
Habitat (semi-open)	0.105	0.019	0.197	8.7	0.048	0.030
Habitat (open)	0.289	0.147	0.432	24.0	0.072	< 0.001
Feeding Specialization	-0.025	-0.072	0.028	-2.1	0.025	0.318
Passeri	-0.154	-1.226	1.014	-12.8	0.578	0.794
Random effects				σ^2 %		
Phylogeny (n = 3247)	0.689	0.526	0.842	23.8	-	-
Summary statistics						
DIC	8271	-	-	-	-	-
R^2	0.654	-	-	-	-	-

Table S2.3: The effect of dispersal on speciation along with other common predictors of avian speciation. The model shown estimates a monotonic relationship between dispersal diversification calculated by the "BAMM" method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.492	-1.223	0.180	-	-	0.186
HWI	0.047	-0.009	0.104	5.1	0.029	0.126
Song (none)	-0.071	-0.307	0.157	-7.7	0.120	0.550
Song (male-only)	0.000	-0.106	0.107	0.0	0.057	0.994
Latitude	-0.037	-0.088	0.010	-4.0	0.025	0.122
Range Size	-0.002	-0.042	0.036	-0.2	0.020	0.962
Mass	-0.049	-0.112	0.008	-5.3	0.030	0.110
Continental	-0.147	-0.412	0.125	-15.8	0.139	0.302
Island	-0.115	-0.578	0.442	-12.3	0.264	0.660
Territory (seasonal/weak)	0.033	-0.086	0.151	3.6	0.062	0.600
Territory (strong)	0.028	-0.162	0.219	3.0	0.096	0.764
Habitat (semi-open)	0.060	-0.020	0.154	6.5	0.044	0.174
Habitat (open)	0.079	-0.056	0.217	8.5	0.069	0.258
Feeding Specialization	0.025	-0.025	0.071	2.7	0.025	0.300
Passeri	-0.237	-1.075	0.599	-25.4	0.433	0.556
Random effects				σ^2 %		
Phylogeny (n = 3247)	0.392	0.325	0.470	16.9	-	-
Summary statistics						
DIC	6802	-	-	-	-	-
R^2	0.569	-	-	-	-	-

Table S2.4: The effect of dispersal on speciation along with the macroecological correlates of HWI, with the two least powerful predictors sequentially dropped. The model shown estimates a hump-shaped relationship between dispersal diversification calculated by the "DR" method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.607	-1.320	-0.044	-	-	0.064
HWI	0.055	-0.001	0.112	9.5	0.029	0.062
Range Size	-0.066	-0.108	-0.027	-11.5	0.021	0.004
Habitat (semi-open)	0.108	0.029	0.214	18.8	0.046	0.024
Habitat (open)	0.300	0.175	0.446	52.0	0.070	< 0.001
Migration	0.048	0.003	0.093	8.3	0.024	0.034
Random effects				σ^2 %		
Phylogeny (n = 3277)	0.683	0.540	0.843	30.2	-	-
Summary statistics						
DIC	8336	-	-	-	-	-
R^2	0.557	-	-	-	-	-

Table S2.5: The effect of dispersal on speciation along with the six macroecological correlates of HWI. The model shown estimates a hump-shaped relationship between dispersal diversification calculated by the “BAMM” method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.790	-1.307	-0.320	-	-	0.002
HWI	0.033	-0.017	0.078	3.3	0.024	0.184
Latitude	-0.030	-0.091	0.023	-3.0	0.028	0.258
Range Size	0.000	-0.035	0.042	0.0	0.020	0.976
Territory (seasonal/weak)	0.022	-0.082	0.125	2.2	0.055	0.734
Territory (strong)	0.030	-0.128	0.215	3.0	0.087	0.728
Habitat (semi-open)	0.063	-0.029	0.153	6.3	0.047	0.174
Habitat (open)	0.064	-0.061	0.191	6.4	0.067	0.344
Migration	0.011	-0.040	0.060	1.1	0.026	0.668
Diet (insectivores)	-0.006	-0.160	0.145	-0.6	0.080	0.948
Diet (nectarivores)	0.062	-0.264	0.426	6.2	0.175	0.716
Diet (omnivores)	0.443	0.203	0.682	44.1	0.128	0.002
Diet (granivores)	0.240	0.007	0.457	23.9	0.116	0.038
Random effects				σ^2 %		
Phylogeny (n = 3277)	0.359	0.291	0.426	15.2	-	-
Summary statistics						
DIC	6840	-	-	-	-	-
R^2	0.577	-	-	-	-	-

Table S2.6: The effect of dispersal on speciation along with the six macroecological correlates of HWI. The model shown estimates a monotonic relationship between dispersal diversification calculated by the “DR” method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.572	-1.169	0.130	-	-	0.080
HWI	0.062	0.001	0.127	5.11476	0.032	0.060
Latitude	-0.007	-0.057	0.052	-0.5626	0.029	0.844
Range Size	-0.070	-0.109	-0.025	-5.762	0.022	< 0.001
Territory (seasonal/weak)	-0.037	-0.158	0.094	-3.0	0.059	0.550
Territory (strong)	0.068	-0.121	0.262	5.6	0.097	0.490
Habitat (semi-open)	0.111	0.015	0.208	9.1	0.050	0.026
Habitat (open)	0.298	0.156	0.424	24.5	0.070	< 0.001
Migration	0.050	-0.006	0.102	4.1	0.028	0.084
Diet (insectivores)	-0.063	-0.220	0.107	-5.2	0.086	0.482
Diet (nectarivores)	0.252	-0.113	0.628	20.7	0.186	0.178
Diet (omnivores)	0.175	-0.099	0.406	14.4	0.128	0.162
Diet (granivores)	0.022	-0.208	0.278	1.8	0.125	0.846
Random effects				σ^2 %		
Phylogeny (n = 3277)	0.671	0.513	0.818	23.3	-	-
Summary statistics						
DIC	8340	-	-	-	-	-
R^2	0.653	-	-	-	-	-

Table S2.7: The effect of dispersal on speciation along with the macroecological correlates of HWI, with the two least powerful predictors sequentially dropped. The model shown estimates a hump-shaped relationship between dispersal diversification calculated by the "DR" method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.609	-1.222	0.039	-	-	0.056
HWI	0.070	0.013	0.128	12.2115	0.294	0.020
Range Size	-0.068	-0.113	-0.032	-11.862	0.021	0.002
Habitat (semi-open)	0.107	0.008	0.190	18.5	0.046	0.018
Habitat (open)	0.293	0.158	0.419	50.9	0.070	< 0.001
Migration	0.038	-0.009	0.090	6.6	0.025	0.114
Random effects				σ^2 %		
Phylogeny (n = 3277)	0.679	0.538	0.831		-	-
Summary statistics						
DIC	8334	-	-	-	-	-
R^2	0.557	-	-	-	-	-

Table S2.8: The effect of dispersal on speciation along with the six macroecological correlates of HWI. The model shown estimates a monotonic relationship between dispersal diversification calculated by the “BAMM” method.

	Bayesian phylogenetic mixed model (BPMM)					
	z	2.5% CL	97.5% CL			
Fixed effects (standardized)				% change	SD	p-value es
Intercept	-0.771	-1.265	-0.290	-	-	0.006
HWI	0.039	-0.021	0.094	4.0	0.030	0.208
Latitude	-0.036	-0.090	0.018	-3.6	0.028	0.206
Range Size	-0.009	-0.040	0.037	-0.9	0.019	0.976
Territory (seasonal/weak)	0.027	-0.079	0.126	2.7	0.053	0.602
Territory (strong)	0.011	-0.158	0.181	1.1	0.089	0.916
Habitat (semi-open)	0.059	-0.027	0.141	6.0	0.044	0.172
Habitat (open)	0.052	-0.081	0.183	5.2	0.067	0.424
Migration	0.002	-0.057	0.049	0.2	0.027	0.912
Diet (insectivores)	-0.001	-0.140	0.160	-0.1	0.078	0.976
Diet (nectarivores)	0.065	-0.275	0.399	6.6	0.175	0.700
Diet (omnivores)	0.445	0.212	0.682	44.9	0.123	< 0.001
Diet (granivores)	0.245	0.022	0.466	24.7	0.114	0.030
Random effects				σ^2 %		
Phylogeny (n = 3277)	0.361	0.291	0.431	15.4	-	-
Summary statistics						
DIC	6841	-	-	-	-	-
R^2	0.575	-	-	-	-	-

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