GLOBAL PATTERNS AND PROCESSES IN AVIAN DIVERSIFICATION

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ABSTRACT

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The natural world consists of a vast array of forms, some more plentiful than others, yet our understanding of the processes responsible the production of biological diversity remains surprisingly limited. Here I combine novel datasets with powerful phylogenetic modeling techniques and computer simulations to test the effects of both biotic and abiotic factors on the dynamics of species radiations and the evolution of organism traits in birds.

In the first part of this thesis, I develop our understanding of the importance of abiotic factors for diversification by showing that in the early stages of lineage diversification at least, rapid adaptation to novel climatic conditions is likely to represent a prominent driver of avian diversification. In the second part I concentrate on the role of biotic factors, in particular that of sexual selection. I show that not only is sexual selection associated with accelerated rates of speciation and secondary sympatry—as well as faster rates of net diversification across the entire avian tree of life—but also that across-species variation in rates of phenotypic evolution is best understood with reference to the focus and intensity of sexual selection. Finally, given that the relative importance of such processes appears to vary predictably across latitudes, in the final part of the thesis I argue that latitudinal differences in the speciation process offers a potentially powerful explanation for conflicting viewpoints regarding the contribution of speciation to high tropical diversity. Overall, this work provides fresh insight into the processes governing broad-scale patterns in biodiversity.

DECLARATION

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

Avian ecological trait data relating to species' habitat occupation and migratory behaviour used in Chapters 2, 3 and 4 were provided by my supervisors Dr. Nathalie Seddon and Dr. Joseph Tobias (both University of Oxford). My supervisors also provided considerable structural and editorial input on all chapters.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 WHAT EXPLAINS VARITION IN SPECIES DIVERSITY?

Variation in species diversity is a characteristic feature of life on Earth, and explaining why some taxonomic groups or geographical regions are more diverse than others remains one of the greatest challenges in evolutionary biology (Gaston 2000; Currie *et al*. 2004; Mittelbach *et al*. 2007; Rabosky *et al*. 2012; Ricklefs & Renner 2012; Rabosky 2013). For instance, why are there so many kinds of passerine birds and an 'inordinate' number of beetles (Hutchinson 1959; Raikow 1986), whereas by contrast other groups contain so few? Likewise, what explains the ubiquitous increase in species diversity towards the equator—perhaps the most prominent and widespread spatial biodiversity pattern on Earth (Hillebrand 2004; Krug *et al*. 2009)? Questions such as these have intrigued biologists for centuries (Von Humboldt 1850; Darwin 1859; Darwin 1871; Wallace 1878), and over recent decades the boom in molecular phylogenetics has allowed researchers to tackle these longstanding problems from a new angle. Yet, despite significant progress (e.g. Nee *et al*. 1992; Barraclough *et al*. 1995; Owens *et al*. 1999; Isaac *et al*. 2005; Phillimore *et al*. 2006; Ricklefs 2006; Weir & Schluter 2007; Pyron & Wiens 2013; Baker *et al*. 2014), our knowledge of the processes involved in generating large-scale variation in species diversity remains surprisingly limited (Mittelbach *et al*. 2007; Butlin *et al*. 2012; Rabosky 2013).

One possible explanation is that much of this variation in species diversity could simply be due to chance. For instance, even if all lineages are equally likely to speciate or to go extinct, the stochastic nature of these events means that by chance, some lineages will end up diversifying more than others (Raup *et al*. 1973; Gould *et al*. 1977). Prominent spatial diversity patterns could also potentially be the product of neutral process related to historical contingency and geographic constraints on the distribution of species richness across landmasses (e.g. Colwell & Lees 2000; Wiens *et al*. 2011). However, it now seems apparent that neutral processes cannot account for the great disparity in species diversity we observe: some clades are simply far too diverse and others too species-poor to be explained by chance alone (Dial & Marzluff 1989; Slowinski & Guyer 1993; Mooers & Heard 1997; Owens *et al*. 1999; Alfaro *et al*. 2009; Rabosky *et al*. 2012). Furthermore, the fact that the same lineages tend to be highly diverse wherever in the world they are found (Ricklefs 2009; Ricklefs & Renner 2012) hints at the existence of clade-specific properties capable of driving or constraining diversification. In other words, it now appears clear that gradients in species diversity are to a large extent the product of deterministic not stochastic processes.

In order for such diversity to accumulate, lineages must repeatedly cycle through the three stages of speciation. As the vast majority of speciation events are initiated in allopatry (Coyne & Orr 2004), this process begins when (i) an ancestral species becomes sub-divided into isolated populations, continues as (ii) populations diverge and become reproductively isolated, and is completed when (iii) incipient species expand their ranges, permitting further range sub-division (Mayr 1942; Grant & Grant 1997; Mayr & Diamond 2001). While this basic model of speciation is well known, it is now more widely appreciated that deterministic processes acting at any of these stages could ultimately control the rate at which new species form (Price 2008; Weir & Price 2011;

Price *et al*. 2014). Understanding how and why some lineages progress through the speciation cycle but others do not is therefore essential to explaining why some groups and regions are so much more diverse than others.

A wide variety of factors have been suggested to influence progression through the stages of speciation and the subsequent build up of diversity, but a fundamental distinction exists between the role of abiotic and biotic drivers (Van Valen 1973; Barnosky 2001; Benton 2009; Venditti *et al*. 2010; Ezard *et al*. 2011). On the one hand, diversification may primarily be controlled by aspects of the physical environment, which act to influence speciation and extinction rates extrinsically. On the other hand, diversification may happen largely as a result of biotic pressures, and large-scale gradients in diversity may be best understood in terms of biotic processes intrinsic to regions or organisms. Although logically distinct, abiotic and biotic factors rarely act exclusively, and the interplay between extrinsic and intrinsic drivers has long been recognised as fundamental for generating and maintaining diversity (Valentine 1980; Jablonski 2008). However, despite having been at the center of discussions for decades, our understanding of the roles of abiotic and biotic factors in diversification remains highly incomplete (Mittelbach *et al*. 2007; Benton 2009). In the following two sections, I briefly review mechanisms thought to link abiotic and biotic factors to diversification, highlighting their potential importance for understanding large-scale gradients in species diversity.

1.2 THE ROLE OF ABIOTIC FACTORS

The idea that variation in species diversity can be best understood with reference to abiotic conditions is an old one (Von Humboldt 1850; Darwin 1859; Wallace 1876;

Wallace 1878), and most hypotheses resolve into one of two categories. In one set of explanations, abiotic environmental conditions are treated as extrinsic factors that primarily shape patterns of diversity indirectly. For instance, high temperature may drive faster molecular evolution, potentially increasing rates of speciation by elevating evolutionary speed (Rohde 1992; Allen *et al*. 2002; Allen 2006). Alternatively, stabile climatic conditions typical of tropical environments may promote the specialisation of biotic interactions (e.g. mutualisms and antagonisms), thereby driving rapid speciation indirectly via co-evolutionary mechanisms (Schemske *et al*. 2009). Abiotic conditions could also indirectly affect diversification patterns by regulating levels of species diversity. For example, one well-known set of hypotheses is that highly productive environments give rise to habitats of greater structural complexity, which in turn provides more niches and permits the build up of greater numbers of species through niche packing (MacArthur 1964; Hawkins *et al*. 2003). Under each of these scenarios, diversification gradients arise as a result of the indirect effects of abiotic conditions on ecological and evolutionary processes related to speciation.

An alternative view is that environmental variation can itself act as a strong barrier to gene flow, such that abiotic factors influence patterns of species diversification directly through intrinsic processes related to climate (Janzen 1967; Moritz *et al*. 2000; Sobel *et al*. 2010). Under this set of ideas, abiotic factors play an important role in promoting diversification not through the diversifying effects of specific climatic conditions (e.g. high temperatures), but by directly influencing the dynamics of colonisation and gene flow between populations distributed across climatic gradients. Thus, how lineages evolve with respect to variation in abiotic conditions such as temperate and precipitation may have important consequences for explaining

variation in species diversification (Evans *et al*. 2009; Kozak & Wiens 2010; Schnitzler *et al*. 2012).

It is also possible that the role of abiotic factors in shaping diversity gradients varies deterministically with latitude. Latitude correlates strongly with many aspects of climatic variation, with increased thermal stability and zonation towards the equator. Faced with greater thermal stability, it is possible that tropical species have evolved narrower thermal tolerances, becoming increasingly specialised to a particular set of climatic conditions (Janzen 1967). In contrast, high levels of climatic specialisation may be unfeasible for many temperate-zone species, given the harsh and unpredictable climates characteristic of high latitudes (Dynesius & Jansson 2000). Higher sensitivity to and reduced dispersal across climatic gradients in tropical environments may therefore deterministically alter species' interactions with variation in abiotic conditions in tropical vs. temperate lineages, modifying the likelihood of population sub-division with respect to latitude with the potential to help explain spatial gradients in diversity (Salisbury *et al*. 2012).

1.3 THE ROLE OF BIOTIC FACTORS

In contrast to abiotic mechanisms, biotic explanations for species diversification are generally focused on how aspects of species' intrinsic biology influence diversification rates and the build up of species diversity. Traditionally, these explanations have focused on the importance of natural selection and ecological factors in driving speciation rates. For instance, species' dispersal ability (Wright 1940; Mayr 1963; Slatkin 1987) and the availability of unoccupied niche space (MacArthur 1972; Diamond 1975; Schluter 2000) represent two well-established ecological explanations

for variation in levels of species diversification. Indeed, ecological factors such as these have been at the center of discussions about speciation mechanisms since the inception of the field (Sobel *et al*. 2010), and there now exists a compelling framework for understanding variation in species diversity amongst groups and across regions primarily in terms of ecological processes (Schluter 2000; Schluter 2001; Rundle & Nosil 2005; Price 2008; Nosil & Harmon 2009; Rabosky 2009a; Schluter 2009; Nosil 2012; Rabosky 2013).

However, an alternative set of ideas emphasises the importance of sexual selection rather than natural selection in driving rates of speciation. Social competition among conspecifics over mates often involves the use of conspicuous phenotypic signals, and Darwin (1871) was the first to highlight the spectacular diversity in sexually selected traits across the animal kingdom. In particular he noted that such traits tended to be both highly variable yet species or population specific (Darwin 1871). Since then, observations such as these and similar have cemented the now well-established hypothesis that sexual selection represents a powerful driver of species diversification across animal groups (West-Eberhard 1983; Price 1998; Panhuis *et al*. 2001; Ritchie 2007; Kraaijeveld *et al*. 2011).

The effect of sexual selection on diversification is thought to derive primarily from its ability to catalyse the divergence of sexual signals among allopatric populations. For instance, under a runaway process, sexual selection is expected to trigger episodes of unpredictable male-female co-evolution driven by the attractiveness of novel signals combined with the absence of optimum trait values (Fisher 1930; Lande 1981; Iwasa & Pomiankowski 1995). If male-female co-evolution occurs independently in geographically isolated populations, continuous yet arbitrary divergence in sexually selected traits and preferences could lead to the rapid pre-mating

isolation between populations (Lande 1981; Iwasa & Pomiankowski 1995). Moreover, even if sexual trait and preference divergence is driven by ecological adaption to new environments, as predicted by the 'sensory drive' hypothesis (Endler 1992; Endler 1993), rather than by purely stochastic male-female co-evolution, sexual selection for locally adapted signals should also be an important intrinsic barrier to gene flow between populations (Boughman 2002).

Whilst it is widely appreciated that variation in levels of sexual selection among lineages may explain differential diversification across taxonomic groups (reviewed in Kraaijeveld *et al*. 2011), spatial gradients in the intensity of sexual selection may also play an important role in shaping other large-scale patterns of diversification. For instance, there are strong theoretical reasons to expect an increase in the relative importance of sexual selection with distance from the equator, as environmental and ecological conditions at high latitudes increase the chances of social competition between males for access to females (Stutchbury & Morton 1995; Irwin 2000; Macedo *et al*. 2008). As a result, it is possible that latitudinal clines in the intensity of sexual selection may also play an important role in shaping spatial patterns of species diversification with respect to latitude.

1.4 OUTSTANDING QUESTIONS

Whilst their fundamental importance has long been appreciated, our understanding of the processes linking abiotic and biotic factors to species diversification remains highly incomplete (Mittelbach *et al*. 2007; Ritchie 2007; Price 2008; Benton 2009; Wiens *et al*. 2010; Kraaijeveld *et al*. 2011; Wiens 2011; Butlin *et al*. 2012). Here I highlight some

important gaps in our knowledge and identify key questions that I address in this thesis in order to clarify the mechanisms underlying species diversification.

How does climatic niche evolvability influence species diversification?

If variation in abiotic conditions represent important barriers to gene flow, the extent to which species evolve climatic tolerances should influence lineage diversification (Kozak & Wiens 2010). On the one hand, if conspecific populations readily adapt to divergent climatic conditions, to the extent that neither could persist in the climatic niche now occupied by the other, climatic niche evolvability could represent an important determinant of species diversification (Kozak & Wiens 2007; Cadena *et al*. 2012). On the other hand, theory predicts that a tendency to retain rather than evolve climatic niche characteristics over evolutionary time could also lead to increased opportunities for diversification, if conspecific populations frequently become separated by areas of unsuitable environmental conditions (Wiens & Graham 2005). Thus, under this alternative scenario, increased species diversification should be associated with evolutionary conservatism of climatic niches, rather than high levels of evolvability.

However, whether climatic niche evolvability or conservatism influences species diversification, and the extent to which one process dominates, remains largely unknown. This is primarily because previous tests have been either taxonomically or geographically restricted (e.g. Evans *et al*. 2009; Kozak & Wiens 2010; Schnitzler *et al*. 2012), but also because there are strong theoretical reasons to expect that the relative importance of each mechanism may vary deterministically across latitude. To fully understand the role of abiotic factors in promoting diversification, we need to conduct tests of hypotheses linking climatic niche evolution to variation in species diversification over much broader phylogenetic and spatial scales.

Does sexual selection drive speciation?

Despite strong theoretical predictions and decades of empirical research, the question of whether sexual selection drives speciation remains highly contentious (Price 1998; Panhuis *et al*. 2001; Ritchie 2007; Price 2008; Kraaijeveld *et al*. 2011; Butlin *et al*. 2012). Much of this controversy stems from the conflicting results emerging from comparative studies (Kraaijeveld *et al*. 2011). For instance, a number of studies have found significant correlations between species diversity and proxies of sexual selection, including mating system (Mitra *et al*. 1996), sexual dimorphism (Barraclough *et al*. 1995; Owens *et al*. 1999) and song characteristics (Seddon *et al*. 2008). Other studies, however, have found no such effects (Morrow *et al*. 2003; Phillimore *et al*. 2006). Moreover, the effect of sexual selection on diversification—if any exists—is believed to weaken over evolutionary time (Kraaijeveld *et al*. 2011), again casting doubt on the importance of sexual selection for explaining large-scale gradients in diversity. However, it is possible that much of the current ambiguity over whether sexual selection drives species diversification stems from methodological issues associated with the traditional comparative approach (Kraaijeveld *et al*. 2011). As a result, until conceptual developments and methodological advantages can be synthesised, the importance of sexual selection as a biotic engine of speciation remains an open question.

There is also increasing recognition that sexual selection may play an important yet underappreciated role in speciation by allowing newly formed species expand their ranges and co-exist in sympatry. By driving sexual trait divergence and the development of reproductive isolation, sexual selection should theoretically ease the difficulty of achieving sympatry with close relatives by reducing the likelihood that incipient species suffer reproductive interference upon secondary contact (Hochkirch *et al*. 2007;

Gröning & Hochkirch 2008). By generating rapid reproductive isolation between species, sexual selection should also increase rates of species diversification by fostering rapid progression of lineages through the latter stages of the speciation cycle. Indeed, the general idea that sexual selection could play a key role in facilitating species co-existence is gaining momentum, especially given that assortative mating alone may be sufficient to maintain stable co-existence without the need for species to be ecologically differentiated (van Doorn *et al*. 2009; M'Gonigle *et al*. 2012). It has become clear that a thorough reappraisal of the role of sexual selection in driving speciation is now necessary and timely.

What drives latitudinal gradients in rates of phenotypic evolution?

Given that divergence in traits important for pre-mating reproductive isolation can lead to rapid species diversification, it is perhaps surprising that rates of phenotypic evolution appear to be fastest not in the species-rich tropical regions but in the comparatively depauperate temperate zones (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012). Several explanations for this counter-intuitive pattern have been proposed, chief among them being an underlying latitudinal cline in the intensity of sexual selection (Irwin 2000; Irwin *et al*. 2001). Under this hypothesis, latitudinal gradients in rates of phenotypic evolution are generated by the strong diversifying effect of sexual selection at high latitudes.

Yet, whether latitudinal variation in the strength of sexual selection represents a viable explanation for elevated rates of phenotypic evolution at high latitudes is unclear. First and foremost, although theoretically plausible, robust empirical evidence for the underlying assumption that temperate zone lineages experience greater levels of sexual selection is scarce. In addition, latitude co-varies with numerous other ecological and

environmental variables, many of which could also account for faster rates of phenotypic divergence at high latitudes. As a result, whether or not sexual selection plays a role in driving latitudinal gradients in phenotypic evolution is largely unknown.

Is it possible to resolve the controversy over whether speciation rates are faster in the tropics or the temperate zones?

Regardless of the underlying cause, accelerated rates of evolution at high latitudes in traits important for speciation adds to the growing controversy over whether speciation rates are faster in the tropics or in temperate regions. On the one hand, whole-clade analyses strongly suggest that rates of net diversification are greater at lower latitudes than high (e.g. Cardillo 1999; Cardillo *et al*. 2005; Ricklefs 2006), potentially reflecting a latitudinal cline in speciation rates, with rates of speciation being fastest in equatorial regions and slower in the temperate zones (Mittelbach *et al*. 2007). On the other hand, analyses of recent speciation events (i.e. sister species) suggest that rates of speciation are in fact faster in the species-poor temperate zone (Weir & Schluter 2007; Weir & Price 2011) elevating the importance of extinction in shaping the latitudinal cline in net diversification.

However, there is increasing awareness that speciation mechanisms may be fundamentally different with regards to temperate and tropical systems, driven by the effects of changing biotic and abiotic conditions across latitudes (Tobias *et al*. 2008; Jocque *et al*. 2010; Salisbury *et al*. 2012). It is therefore possible that the conflicting conclusions regarding latitudinal gradients in speciation rates may simply arise from alternative methodological approaches and ambiguity over what we mean by rates of speciation (Tobias *et al*. 2008).

1.5 BIRDS AS A MODEL SYSTEM

Birds represent the best group in which to tackle these outstanding questions for many key reasons. First and foremost, as one of the most intensively studied groups, there is an abundance of morphological, ecological, behavioural and distributional data for the vast majority of the world's bird species. Importantly, they are a large ecologically-diverse group and have evolved to exploit the vast majority of environmental conditions. Moreover, most birds are highly social and therefore an excellent group in which to study the role of behaviour in speciation, especially regarding social factors related to mate choice and sexual selection (Price 2008). As a result, birds represent an ideal study system in which to concurrently examine the importance of both ecological and non-ecological biotic drivers of diversification (e.g. Phillimore *et al*. 2006; Phillimore *et al*. 2007). Also, in recent years the explosion of molecular data has exponentially increased our understanding of the phylogenetic history of birds (Barker *et al*. 2004; Hackett *et al*. 2008; Jetz *et al*. 2012) and genetic information is available for a vast proportion of the world's bird species. In addition to—or perhaps because of—such in-depth survey, many classic theoretical advances in our understanding of the speciation process and mechanisms regulating diversity have come from the study of birds (e.g. Darwin 1859; Darwin 1871; Mayr 1942; Lack 1947; MacArthur 1958; Mayr 1963; Lack 1976; Mayr & Diamond 2001). As a consequence, it is possible to place tests of new and existing hypotheses in a clear, well-defined conceptual framework (reviewed in Price 2008). Birds also represent a prominent component of global fauna and show taxonomic (Owens *et al*. 1999; Ricklefs 2003; Ricklefs 2006) and spatial (Rahbek 2001; Ricklefs 2006; Hawkins *et al*. 2007; Jetz *et al*. 2012) patterns of diversity characteristic of many other taxa. Therefore, advances drawn from the study of

birds are likely to represent general features of evolution, applicable to many other groups where such investigation is currently out of reach.

1.6 THESIS OUTLINE

In this thesis I address several unresolved questions regarding the processes responsible for species diversification and the build up of large-scale patterns in biological diversity. To do this, I use a range of phylogenetic comparative and simulation approaches combined with geographic, ecological and phenotypic data from the majority of the world's birds. In Chapter 2, I use global climate layers, species' range maps and phylogenetic models of trait evolution to conduct a large-scale test the role of climatic niche evolution in shaping taxonomic patterns of diversity. In Chapter 3, I examine the role of biotic factors in diversification by testing whether sexual selection accelerates the cycle of speciation in birds, and if so, whether this leaves a detectable signature in broad-scale patterns of diversification. To do this, I conduct two independent sets of analyses based on novel datasets describing the degree of plumage dichromatism across birds. In Chapters 4 and 5, I shift focus to examine how both and abiotic and biotic factors can be used to explain spatial rather than taxonomic variation in diversification. Chapter 4 sheds light on the mechanisms underlying speciation rate variation across latitudes by testing the significance of several ecological and non-ecological hypotheses for apparent latitudinal clines in the rate of phenotypic evolution. In Chapter 5, I develop a simulation model of phylogenetic tree growth to explore whether latitudinal gradients in the tempo and mode of speciation could resolve the recent controversy over whether speciation rates are faster in the tropics or in the

temperate zones. Finally, in Chapter 6, I synthesise the principal findings of the thesis and offer some thoughts on their wider implications.

1.7 General concepts and caveats

The work presented in this thesis is subject to many of the general caveats associated with the use of comparative approaches to study diversification, including but not limited to the accuracy of the phylogenetic hypotheses analysed, the power and limitations of the statistical models employed to analyse them, and the quality of the datasets used to investigate the factors influencing diversification. These and other issues relating to the comparative approaches employed in this thesis are discussed in more depth in the relevant sections. When explicitly studying patterns of species diversification, however, it is important to acknowledge the fact that much of this work depends on the way in which a 'species' is defined. Various definitions exist but the concept most commonly applied—and the one followed throughout this thesis—is the biological species concept (BSC), which defines a species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). I favour the BSC over other species concepts as the emphasis placed on achieving reproductive isolation stresses the central importance of evolutionary independence from other such lineages following alternative evolutionary trajectories. Furthermore, adhering to the BSC also provides additional practical benefits in that it is most often the species concept employed by the vast number of taxonomists and phylogeneticists whose work underpins our current understanding of avian diversity.

Another general theme running throughout this thesis is the role of sexual selection in driving species diversification and the evolution of phenotypic traits. Sexual selection can be defined as the selection pressures on traits arising from differences in reproductive success caused by competition for access to mates or fertilisation opportunities (Andersson 1994; Jones & Ratterman 2009). This definition acknowledges the fact that sexual selection can take multiple forms, with 'access to mates' primarily referencing pre-copulatory aspects of sexual selection (e.g. mate choice) and 'fertilisation opportunities' acknowledging the existence of post-copulatory mechanisms (e.g. sperm competition). In order to quantify the intensity of sexual selection experienced by a given species, throughout this thesis I employ one commonly used index of sexual selection in birds: that is, sexual dichromatism. Plumage dichromatism represents a robust and well-established index of sexual selection in birds, as large-scale analyses reveal that it correlates strongly with other independent measures of sexual selection (Owens & Hartley 1998; Dunn *et al*. 2001).

It must be noted, however, that there are limitations associated with using dichromatism as a proxy for the intensity of sexual selection. First, plumage dichromatism is likely to provide a more direct measure of the strength of pre-copulatory forms of sexual selection, such as female mate choice and/or male-male competition, rather than post-copulatory mechanisms, which are likely to be more accurately represented by other traits such as testes mass (Owens & Hartley 1998; Dunn *et al*. 2001). Second, the use of dichromatism as a class-wide index of sexual selection assumes that all species experience similar pattern of selection (with regards to selection for crypsis, for example), and that all species possess similar levels of evolvability in plumage traits used to signal in social contexts. These assumptions are unlikely to be met in some cases, however, adding noise to the relationship between dichromatism

estimates and the true intensity of sexual selection Third, it is also likely that this approach may underestimate sexual selection in species where both sexes are mutually ornamented (Badyaev & Hill 2003). Whilst this is undoubtedly also a concern, attempts have been made in certain sections of the thesis to address the confounding impact of mutual ornamentation (see Chapter 3), and the results of these analyses indicate that the main conclusions of the thesis should be robust to this issue.

CHAPTER 2

CLIMATIC NICHE EVOLUTION PREDICTS GLOBAL PATTERNS OF DIVERSIFICATION IN BIRDS

2.1 ABSTRACT

The adaptability of species' climatic niches theoretically influences the dynamics of colonisation and gene flow across climatic gradients. However, the extent to which increased rates of niche evolution act to promote or inhibit diversification remains contentious, particularly as previous studies are geographically or taxonomically restricted, yielding mixed results. Here I conduct the largest-scale test of associations between climatic niche evolution and diversification by analysing global data for 7780 bird species. My analyses reveal that, across avian genera, species richness is strongly predicted by rates of evolution in key climatic variables, regardless of variation in latitudinal distribution or key ecological traits. I conclude that rapid adaptation to unoccupied areas of climatic niche space is a prominent driver of avian diversification in the early stages of adaptive radiation, irrespective of the geographical and ecological context of speciation. However, I detected no evidence of a similar relationship across family-level clades, suggesting that the impact of labile climatic niche traits on diversification may weaken over longer time-frames, when speciation is perhaps more tightly constrained by mechanisms of species coexistence than the rate at which niches

evolve. These findings highlight the direct influence of recent evolutionary processes in regulating the link between climate and biodiversity at broad geographical scales.

2.2 INTRODUCTION

Environmental conditions (e.g. temperature and precipitation) have long been viewed as key predictors of biological diversity across spatial and temporal scales (Wallace 1876). These conditions are often considered to be extrinsic factors that primarily shape patterns of diversification indirectly, for instance through their effects on productivity and habitat complexity, both of which correlate with species richness (MacArthur 1964; Hawkins *et al*. 2003). In recent years, however, the focus of research has shifted away from examining the importance of specific environmental conditions in driving diversification, and towards understanding the role of intrinsic processes linked to climate, in particular the role of climatic niche evolution in regulating diversification (e.g. Kozak & Wiens 2007; Kozak & Wiens 2010; Cadena *et al*. 2012). This idea is intuitively appealing because it suggests that abiotic environmental factors such as temperature and rainfall influence patterns of diversity directly via deterministic evolutionary processes. However, the role of climatic niches in diversification remains highly unclear, not least because two strikingly different hypotheses linking niche evolution and diversification have been proposed.

The first hypothesis, focusing on niche lability, predicts that species' diversification should be greatest among lineages in which climatic niches evolve most rapidly (Moritz *et al*. 2000; Kozak & Wiens 2007; 2010). This is based on the logic that lability of climatic niches allows populations to successfully colonise novel environments, and that this in turn will lead to local adaptation in ecological or sexual

traits, reducing gene flow and promoting reproductive isolation (Sobel *et al*. 2010). Similarly, lineages with wide environmental tolerances may have large geographic ranges that are more susceptible to vicariance events leading to speciation (Rosenzweig 1995) or be better able to resist extinction in periods of environmental change (Holt 1990). In contrast, a second hypothesis predicts that diversification may be greatest when climatic niches are conserved over evolutionary time. This could occur when constraints on the evolution of climatic tolerances limit dispersal across unsuitable habitats or climatic gradients, for example in lineages specialised to a particular climatic regime (Janzen 1967; Wiens 2004; Kozak & Wiens 2006; Cadena *et al*. 2012). If gene flow is consequently interrupted between populations, then diversification may be greatest in those groups where climatic niche evolution is slowest, provided the diversifying influence of this mechanism outweighs the potential impact of increased extinction in specialised species (Kozak & Wiens 2010). The central tenet of both these hypotheses is that the dynamics of climatic niche evolution within lineages has the potential to impact species diversification, but they make opposite predictions as to how diversification should be associated with rates of climatic niche evolution.

Most previous studies have tested these predictions indirectly by assessing whether specific speciation events are associated with shifts in climatic niche. This approach has produced conflicting results. For instance, amphibian sister species can inhabit either similar (Kozak & Wiens 2006) or dissimilar (Graham *et al*. 2004; Kozak & Wiens 2007) climatic conditions. Likewise, speciation events in other taxa, such as birds, insects, and mammals, variously occur both with (e.g. Rice *et al*. 2003; Eaton *et al*. 2008) and without (e.g. Peterson *et al*. 1999; Peterson & Nyári 2007) significant divergence in climatic niches. There have been few direct tests of the link between rates of climatic niche evolution and diversification in a broader context, with one study

(Schnitzler *et al*. 2012) finding no significant association in a single genus of plants (*Babiana*; n = 89 species restricted to Southern Africa), and another study (Kozak & Wiens 2010) showing that more diverse clades of lungless salamanders (Plethodontidae; n = 250 species restricted to the New World) have faster rates of climatic evolution than less diverse clades. Thus, although climatic niche lability may facilitate diversification among one family of salamanders, the idiosyncratic results emerging from other taxonomic groups make it difficult to infer which, if any, of the proposed mechanisms offer a general explanation for patterns of diversification at larger spatial and taxonomic scales.

A possible reason for inconsistency in previous results is that climate influences diversification in ways that vary with latitude or ecology. Latitude correlates strongly with many aspects of climatic variation, with increased thermal stability and zonation towards the equator potentially leading to narrower thermal tolerance, and hence reduced dispersal across climatic gradients, in tropical organisms (Janzen 1967). Thus, allopatric speciation among subdivided populations with conserved climatic niches may be more prevalent in tropical than temperate systems, modifying the relationship between climatic niche evolution and rates of diversification (Kozak & Wiens 2007; Cadena *et al*. 2012). Similarly, the association between niche evolution and diversification could be influenced by variation among species in ecological factors, such as habitat or dispersal ability (Gavrilets 2004; Cadena *et al*. 2012). The effect of climatic niche evolution on diversification may therefore differ consistently across latitudinal and ecological gradients. However, the extent and direction of these effects has not explicitly been considered in previous studies, partly because doing so requires data on phylogenetic history, climatic niche, latitudinal range and ecological traits for extensive samples of species at large geographic and taxonomic scales.

Here I compile distributional, climatic, ecological and phylogenetic data for a global dataset of 7780 bird species—almost 80% of the world's bird diversity—to assess the importance of climatic niche evolution in explaining large-scale patterns of diversification. To achieve this, I first quantified species' climatic niches as described by a suite of environmental variables, then tested for an association between lineage diversification and rates of niche evolution across a broad sample of genera and families. By incorporating latitudinal position and ecological traits into these models, I further considered whether the effect of rapid niche evolution is mediated by major biogeographical or ecological factors. Birds provide an ideal system for these approaches for two main reasons. First, comprehensive data are available on geographical ranges and ecological traits for all avian species, with a vast majority also included in phylogenetic analyses (Orme *et al*. 2005; Jetz *et al*. 2012). Second, since birds occur across an almost full spectrum of latitudes, climatic conditions and habitats, it is possible to explore the role of these secondary factors in unprecedented detail and with much improved sample size.

2.3 METHODS

2.3.1 Phylogenetic data and clade selection

As a phylogenetic framework for this study I used a set of virtually complete species-level molecular phylogenies compiled by Jetz *et al*. (2012). These trees were constructed in a Bayesian framework, combining multi-gene phylogenetic inference (6670 species) with a taxonomic placement approach (3323 species). To account for phylogenetic uncertainty, I sampled 100 trees from the posterior distribution of complete trees analysed by Jetz *et al*. (2012) based on the Hackett *et al*. (2008) family-level backbone. Each tree in this sample then formed the basis for an independent run of all subsequent analyses (see below). By incorporating this phylogenetic sampling into my analyses, I was able to simultaneously maximise the coverage of species within clades, and clades across the entire avian radiation, while assessing the impact of phylogenetic uncertainty on each stage of our analysis.

In the Jetz *et al*. (2012) phylogenies, both genus and family-level clades are frequently reconstructed as para- or polyphyletic, so to select clades I used an approach designed to identify monophyletic groups of species largely corresponding to traditional taxonomic classifications of genera and families, without excluding major clades made up of representatives from multiple genera/families simply due to taxonomic misclassification (see Appendix 1 for details). Briefly, I used the taxonomy provided by Jetz *et al*. (2012) to search through each phylogeny, identifying all genera/families that were monophyletic when (i) the species of each clade were considered separately, or (ii) when the species of each clade were considered together with those of one other clade. I then restricted this sample to clades containing at least four species with climatic data, to avoid estimating rates of evolution in very small clades (Kozak & Wiens 2010;

Rabosky *et al*. 2013). Applying this procedure across the distribution of trees provided 100 'pseudoreplicate' samples of clades containing a median of 95 (range: 93–99) family-level clades and 507 (500–513) genus-level clades, representing a total of 7780 species.

2.3.2 Metric of clade diversification

Before examining the factors influencing species richness and diversification rates within clades, it is important to test the validity of alternative diversification metrics (Rabosky & Adams 2012). One commonly used metric is clade diversification rate, which can be defined as the rate at which species accumulate over time, or the rate of speciation minus the rate of extinction. However, a simple constant-rate estimate may bear little relationship to the underlying diversification rate if diversification within clades is bounded over time by some constraint such as density dependence (Rabosky 2009a; Rabosky 2009b). In such cases, clade age will be unrelated to species richness and uninformative for estimating underlying diversification rates (Rabosky 2009a; Rabosky 2009b). Preliminary analyses using phylogenetic generalized least squares (PGLS) revealed that, despite being statistically correlated, clade crown age explained little of the variation in (log) species richness across both family ($\beta = 0.015$, $R^2 = 0.04$, $p = 0.048$, $f = 0.51$) and genus ($\beta = 0.009$, $R^2 = 0.02$, $p = 0.001$, $f = 0.93$) level clades. In addition, estimated diversification rates [log(species richness)/crown age] were strongly negatively related to crown age (families: $\beta = –0.022$, $R^2 = 0.31$, $p < 0.001$, $f = 1.00$; genera: $\beta = –0.054$, $R^2 = 0.47$, $p < 0.001$, $f = 1.00$), indicating non-constant rates of diversification through time and thus suggesting that diversification rate estimates are strongly confounded with clade age. To overcome this problem, I did not infer rates of net diversification for each clade, and instead used log-transformed species richness

(i.e., total time-integrated diversification experienced by a clade; Rabosky 2009a; Rabosky 2009b; Rabosky & Adams 2012).

2.3.3 Evolutionary rates of climatic niche evolution

To characterise species' climatic niches, I combined geographic range maps from an equal-area dataset of species' breeding distributions at a resolution comparable to a 1º (96.49 x 96.49 km) grid (Orme *et al*. 2005), with information on six climatic variables present in the WorldClim database (Hijmans *et al*. 2005): (i) annual mean temperature (BIO1), (ii) maximum temperature of the warmest month (BIO5), (iii) minimum temperature of the coldest month (BIO6), (iv) annual precipitation (BIO12), (v) precipitation in the wettest quarter (BIO16), and (vi) precipitation in the driest quarter (BIO17). This combination of variables is frequently used (e.g. Cooper *et al*. 2011; Quintero & Wiens 2013) to characterise species' broad-scale climatic niches, as it reflects the fact that both average and extreme environmental conditions are important in determining geographical range boundaries (Grinnell 1914; Soberón 2007; Pigot *et al*. 2010a). For each grid cell occupied by a species in my analysis, I extracted the relevant climatic information at a spatial resolution of 30s (0.93 x 0.93 km), and then matched the resolutions by taking the average of all the values falling within a given grid cell. All climatic variables were log-transformed and standardised (Cooper *et al*. 2011) before being subjected to a principal components analysis (PCA). This procedure identified two dominant PCs (Appendix 1 Fig. S1) that explained more variation in climatic variables than expected under a neutral broken stick model (Jackson 1993). These PCs were used in all subsequent analyses. To characterise both inter- and intraspecific variation in each climatic axis, I calculated species' mean PC scores as well as the standard error around each mean. For the 58 species in the dataset that were

restricted to a single grid cell, I assumed their intraspecific variation was equivalent to the minimum standard error value estimated across all other species (Claramunt *et al*. 2011). In total, I characterized the climatic niches for 7267 (93%) species in the dataset.

To infer rates of climatic niche evolution, I estimated the Brownian rate parameter (σ^2) using phylogenetic models of trait evolution (Kozak & Wiens 2010; Cooper *et al*. 2011; Olalla-Tárraga *et al*. 2011; Machac *et al*. 2013). This parameter measures the rate at which trait values of related species diverge from one another, and in phylogenetic studies of species' climatic niches is commonly estimated using a Brownian motion (BM) model of trait change (e.g. Cooper *et al*. 2010; Boucher *et al*. 2014). The BM model assumes that ancestral trait values are inherited by daughter lineages and then evolve randomly over time and without bounds. However, these assumptions are likely to be inappropriate for climatic niche traits (Boucher *et al*. 2014). For instance, if speciation predominantly occurs in allopatry, daughter lineages may occur in divergent climatic environments to that of their immediate ancestor. Furthermore, the range of climatic conditions in which lineages are able to diversify may frequently be restricted by a combination of large-scale biogeographic factors (e.g. continental boundaries) and dispersal limitation (Boucher *et al*. 2014). Thus, climatic niche evolution may best be characterised by models that specifically incorporate punctuated trait evolution, bounded trait evolution, or both (Boucher *et al*. 2014).

Here, I explicitly incorporate this uncertainty over model selection into my analyses by estimating σ^2 under both BM and non-BM scenarios. Specifically, in addition to the BM model I tested three models observed to outperform the BM model in describing neutral patterns of climatic niche evolution in simulated data (Boucher *et al*. 2014); these were: (i) an Ornstein-Uhlenbeck (OU) model of constrained evolution (Hansen 1997), (ii) the kappa (KA) model of variable punctuated change (Pagel 1999),

and (iii) an OU model with strict punctuated change (OUp), in which trait change is both constrained and only occurs at speciation (Boucher *et al*. 2014). Using the *R* package *geiger* (Harmon *et al*. 2008), I estimated rates of niche evolution for every clade in the dataset under each of the four models (BM, OU, KA, and OUp). Models were fitted separately using species' mean scores for each PC, while accounting for intraspecific variation. I then assessed relative model fit by calculating the Akaike weight attributed to each model based on AIC scores (Burnham & Anderson 2002), which describes the proportion of support received by a particular model in relation to the support for all other models considered. Using these weightings, I then calculated a model-averaged estimate of σ^2 for each PC within each clade using the weighted sum of σ^2 estimates derived from each of the four models (Burnham & Anderson 2002). This type of model-averaging approach, whereby strongly supported models contribute more to averaged parameter estimates than weakly supported models, is commonly used in phylogenetic comparative studies (e.g. Price *et al*. 2013).

I note that the evolutionary rate estimates described above are independent of the number of species sampled from each clade (unless rates themselves influence clade richness), as well as the amount of time available for diversification in each clade (Rabosky & Adams 2012). I assessed the validity of the latter suggestion for our dataset using preliminary PGLS analyses, which confirmed that niche rate estimates were not confounded with clade age either among families (PC1: $\beta = -0.002$, $R^2 < 0.01$, $p = 0.583$, $f = 0.00$; PC2: $\beta = -0.014$, $R^2 = 0.023$, $p = 0.142$, $f = 0.23$) or among genera (PC1: $\beta = -0.004$, $R^2 < 0.01$, $p = 0.544$, $f = 0.01$; PC2: $\beta = -0.006$, $R^2 < 0.01$, $p = 0.386$, $f = 0.12$).

2.3.4. Latitude and ecological traits

To investigate the influence of geographical distribution and ecological traits on the relationship between climatic niche evolution and diversification, I quantified clade latitude and ecological traits for all species in my analysis. For clade latitude, I used range maps to calculate latitudinal centroid values for each species, and then generated mean (absolute) values as a crude but informative estimate of the dominant latitudinal position of each clade. To capture ecological variation among these clades, I quantified three key ecological attributes—habitat, territorial system, and migratory behaviour—using information provided by del Hoyo *et al*. (1992–2011). Species were assigned to the following (ordinal) classifications in each ecological axis: (i) habitat: dense (e.g. evergreen forest, deciduous forest), semi-open (e.g. thorn forest, shrubland), or open habitats (e.g. grassland, desert); (ii) territorial system: permanent year-round territoriality, seasonal/weak territoriality, or non-territorial; (iii) migration: sedentary, local movements (e.g. nomadism, altitudinal migration), or long-distance migration (e.g. intercontinental movements). In each case, dispersal ability is proposed to be most limited in the first category, and to increase progressively in the second and third categories (Salisbury *et al*. 2012). To provide clade-level indices, I used the mean value for each ecological trait averaged across all species in the clade. In total, I collated data on latitude and ecological traits for 7724 (99%) species in our dataset. Methods for classifying species and an expanded justification for the use and classification of ecological variables are available in Appendix 1.

2.3.5 Comparative analyses

I used PGLS models to assess the ability of climatic niche evolution to predict variation in diversification across bird clades. By estimating Pagel's (1997) lambda parameter,

these models correct for the level of phylogenetic dependence in the residuals of fitted models. Using this approach, I conducted two sets of analyses. In the first set, I tested whether rates of niche evolution in each climatic axis predicted variation in log-transformed species richness. As niche rates were positively correlated across clades (families: $\beta = 0.369$, $R^2 = 0.15$, $p < 0.001$, $f = 1.00$; genera: $\beta = 0.413$, $R^2 = 0.21$, $p < 0.001$, $f = 1.00$), I also ran models containing both niche rate variables to assess their relative importance. In addition, I examined whether clades exhibiting fast rates of niche evolution in both climatic axes are disproportionately diverse, or species poor, by including an interaction term between niche rate variables. Finally, I tested the prediction that, if rates of niche evolution reflect the rate at which lineages adapt to novel areas of niche space through time, then climatic disparity (measured as the sum of the squared Euclidean distances between species' mean scores in both PC axes) should increase significantly with the age of a clade (Rabosky & Adams 2012). Each of these analyses was performed across both family- and genus-level clades.

In the second set of analyses, I examined the impact of latitude and ecology on the link between climatic niche evolution and diversification. I did this by fitting a multi-predictor model containing both niche rate variables, as well as latitude and all three ecological variables. I then conducted a more nuanced test of the link between rates of diversification and climatic niche evolution by examining whether the relationship between these variables varied systematically with latitude, or with ecological traits. This was achieved by running separate models in which diversification was predicted by the interaction between climatic niche rate and each latitudinal/ecological variable. Although it would be useful to assess the importance of all variables and their interactions with climatic niche evolution simultaneously, single models with such a large number of variables and interaction terms are difficult to

interpret and require greater statistical power than permitted by the available sample sizes. For clarity, therefore, I tested the effects of latitude and each ecological variable separately. This second set of analyses focused specifically on genera because geographic and ecological variables are likely to provide a more accurate index of species' traits within genera than families, simply because data are averaged across fewer species.

In all cases, I assessed the impact of phylogenetic uncertainty on model estimates by running each model set over the entire range of pseudoreplicate datasets. I inferred the overall significance of predictors using the median *P* value across these datasets, and also by counting the frequency of models (*f*) in which the predictor was statistically significant ($p < 0.05$). I also estimated model fit by computing median R^2 values for each model set. Rate variables were log-transformed prior to analysis, and PGLS models were run using the *R* package *caper* (Orme *et al*. 2011).

2.4 RESULTS

2.4.1 Rates of climatic niche evolution

PCA analysis revealed two major axes characterising the variation in climatic niches of bird species. The first component (PC1) accounted for 57% of the variation and loaded negatively with all six climatic variables (Appendix 1 Table S1), capturing differences in species' exposure to warm/wet and cold/dry conditions (Fig. 2.1). The second component (PC2) accounted for an additional 30% of the variation and loaded positively with precipitation, but negatively with temperature (Appendix 1 Table S1), capturing differences in exposure to warm/dry and cold/wet conditions (Fig. 2.1).

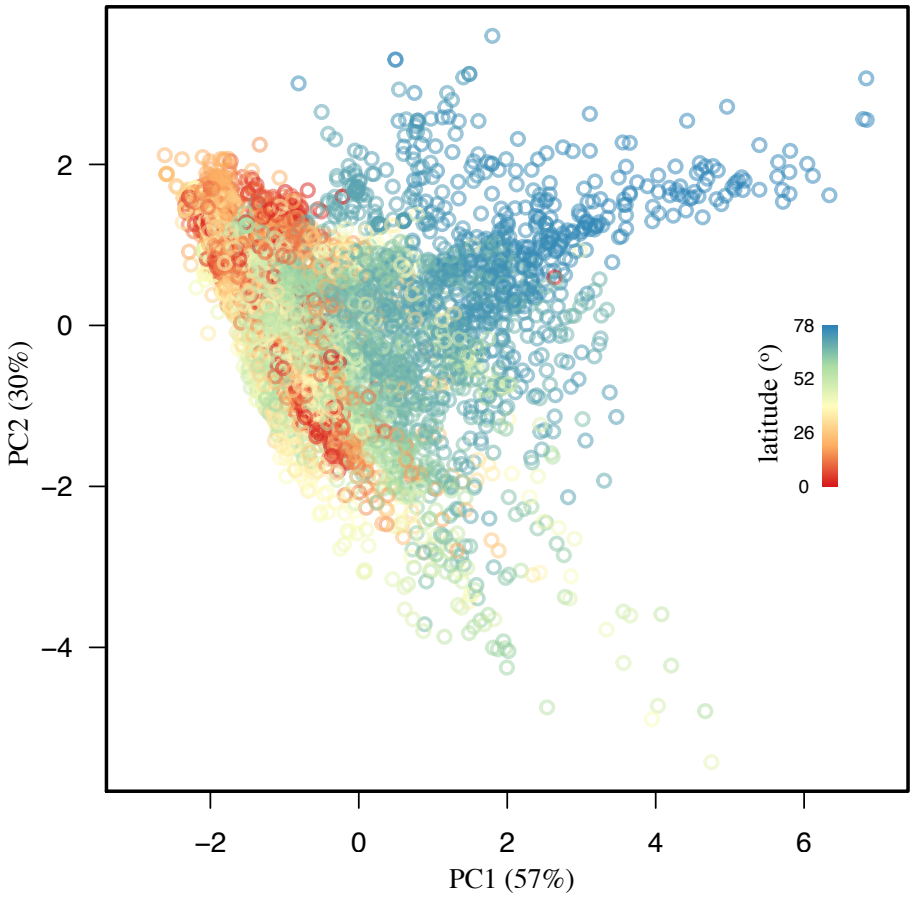

Figure 2.1 Climatic niche variation across 7780 species of birds, plotted as the relationship between two principal components (PCs) derived from six climatic variables (see table S1 for primary trait loadings). PC1 captures differences in species' exposure to warm/wet (low values) and cold/dry conditions (high values), whereas PC2 captures differences in species' exposure to warm/dry (low values) and cold/wet conditions (high values). Each point represents the mean position of a species in bivariate climatic niche space, coloured according to species (absolute) mean latitudes.

By fitting a range of phylogenetic models of trait evolution to species' scores in each PC, I was able to estimate model-averaged rates of climate niche evolution for each clade in my analysis. In a small number of cases (~1% of >60000 clades tested), reliable estimates of niche rates could not be obtained as models of trait evolution failed to converge. These clades were excluded from all subsequent analyses. In general, across both family and genus-level clades, climatic niche evolution in both PC axes was best characterised by bounded models of trait evolution (OU and OUp; Fig. 2.2). Of these, models in which climatic niches evolve randomly within bounds (OU) received similar levels of support to those where niche evolution occurs at speciation (i.e. punctuated trait change; OUp; Fig. 2.2). An unbounded BM model received slightly higher levels of support among genera than family-level clades (Fig. 2.2), suggesting that this model provided a moderately better characterisation of climatic niche evolution than across family-level clades. In accordance with the idea of less bounded climatic niche evolution in genus-level clades, I found that (log-transformed) climatic disparity increased significantly with clade age among genera ($\beta = 0.037$, $R^2 = 0.03$, $p < 0.001$, $f = 1.00$), but that this relationship was absent when comparing family-level clades ($\beta = 0.028$, $R^2 = 0.03$, $p = 0.092$, $f = 0.29$).

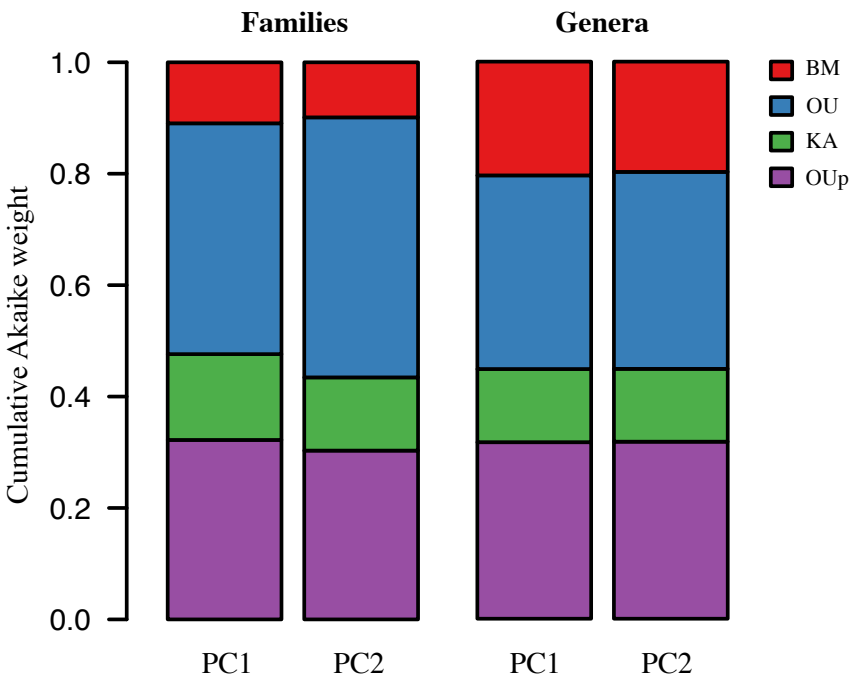

Figure 2.2. Relative support for four models of trait evolution (BM, Brownian motion; OU, Ornstein-Uhlenbeck; KA, kappa; OUp, Ornstein-Uhlenbeck with punctuated evolution) across 95 (range: 93–99) family-level clades and 507 (500–513) genus-level clades. The strength of support is represented by average Akaike weights for each model. Models were fitted separately to each clade based on species' mean scores and interspecific variation in each principal component (PC).

2.4.2 Climatic niche evolution and diversification

Relating rates of climatic niche evolution to species richness differences across families, I found no evidence that clades with faster evolutionary rates in PC1 tended to be more diverse than those with slower rates ($\beta = 0.065$, $R^2 = 0.01$, $p = 0.422$, $f = 0.4$; Fig. 2.3a). This result was similar when considering niche rates derived from PC2 ($\beta = 0.100$, $R^2 = 0.01$, $p = 0.255$, $f = 0.13$; Fig. 2.3b), and also when considering variation in both niche rates together (Appendix 1 Table S2). In contrast, when viewed across genera, I found a striking positive relationship between diversification and rate of niche evolution for both PC1 ($\beta = 0.069$, $R^2 = 0.04$, $p < 0.001$, $f = 1.00$; Fig. 2.3c) and PC2 ($\beta = 0.101$, $R^2 = 0.08$, $p < 0.001$, $f = 1.00$; Fig. 2.3d). Moreover, when considered together, both variables remained significant (Appendix 1 Table S2). Across both genus and family-level clades, however, I found no evidence of a significant interaction between niche rate variables in predicting diversification (Appendix 1 Table S2).

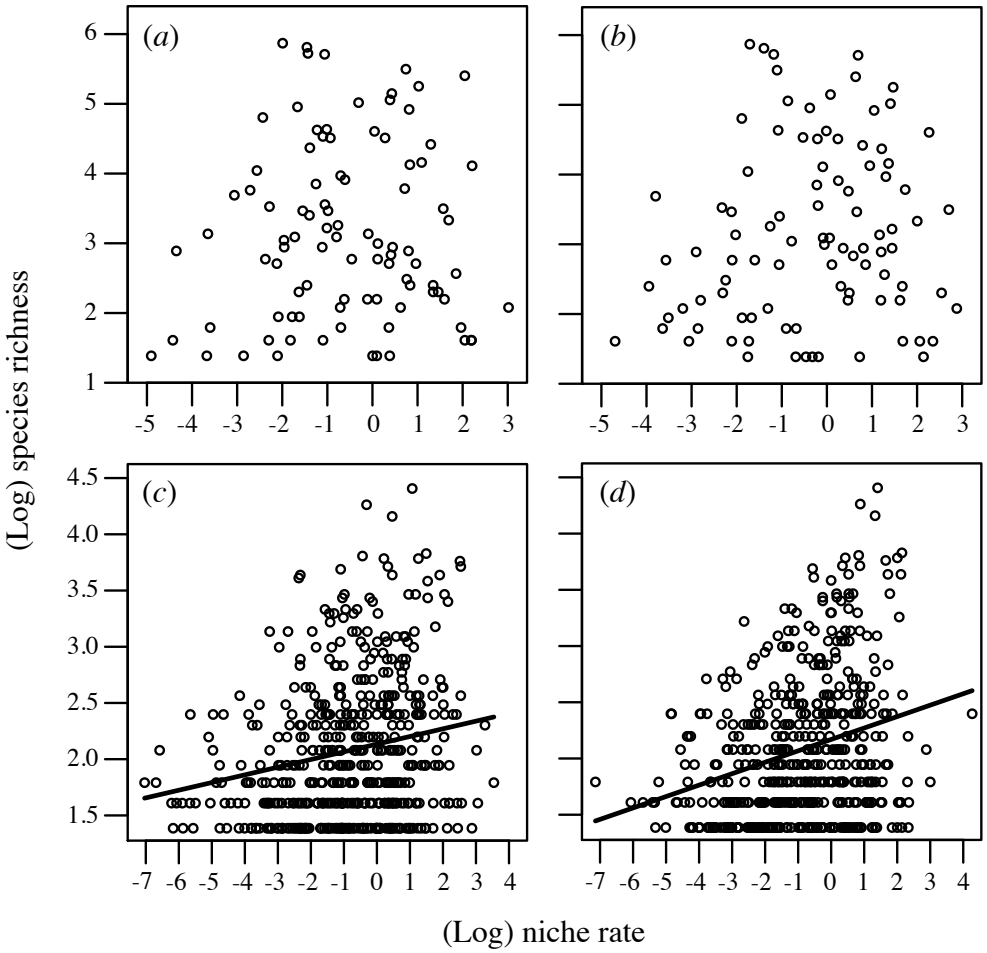

Figure 2.3. The relationship of (log-transformed) family (a, b) and genus (c, d) species richness with rates of climatic niche evolution derived from species' scores in PC1 (a, c) and PC2 (b, d). For clarity, plotted points are from one pseudoreplicate dataset, whereas regression lines are plotted using median parameter values estimated from PGLS models fitted to 100 pseudoreplicate datasets. Regression lines indicate a significant association between two variables.

2.4.3 The role of latitude and ecology

Focusing exclusively on genera, I found that the significant effect of climatic niche rates on diversification could not be explained as a by-product of underlying correlations with gradients in latitude or ecology. Specifically, using a multi-predictor model I found that genera were more diverse at tropical than temperate latitudes, but that this had little effect on the strong positive relationship between rates of niche evolution and diversification (Appendix 1 Table S3). Habitat, territoriality and migration were uncorrelated with genus diversity, and thus do not predict the effect of niche evolution on diversification (Appendix 1 Table S3). Moreover, when I fitted separate models with interaction terms to explore these associations in more detail, I found no evidence that the slope of the relationship between climatic niche evolution and diversification varied deterministically with variation in either latitude or any of the three ecological axes considered (Table 2.1). In all cases, models containing an interaction term between niche rate variables and clade latitude or ecology provided no significant increase in explanatory power (interaction terms $p >> 0.05$; Table 2.1), implying that the effect of rapid niche evolution on genus-level diversification is largely equivalent across broad-scale differences in species' geography and ecology.

	PC1				PC2			
Term	**β**	***p***	***f***	***R²***	**β**	***p***	***f***	***R²***
(Intercept)	2.338	<0.001	1.00	0.08	2.312	<0.001	1.00	0.09
Niche rate	0.102	<0.001	1.00		0.127	<0.001	1.00	
Latitude	–0.010	<0.001	1.00		–0.008	0.003	0.99	
Niche rate * latitude	–0.001	0.637	0.00		–0.001	0.379	0.01	
(Intercept)	2.308	<0.001	1.00	0.05	2.310	<0.001	1.00	0.08
Niche rate	0.103	0.009	0.96		0.115	0.006	0.93	
Habitat	–0.085	0.053	0.46		–0.070	0.117	0.27	
Niche rate * habitat	–0.014	0.529	0.01		–0.002	0.714	0.00	
(Intercept)	2.223	<0.001	1.00	0.05	2.211	<0.001	1.00	0.08
Niche rate	0.093	0.027	0.61		0.094	0.045	0.53	
Territoriality	–0.041	0.327	0.01		–0.016	0.669	0.00	
Niche rate * territoriality	–0.012	0.520	0.01		0.004	0.705	0.00	
(Intercept)	2.413	<0.001	1.00	0.07	2.396	<0.001	1.00	0.09
Niche rate	0.122	0.002	1.00		0.154	<0.001	0.99	
Migration	–0.194	0.001	1.00		–0.170	0.007	0.93	
Niche rate * migration	–0.029	0.296	0.01		–0.035	0.247	0.02	

Table 2.1. Summary of results of multi-predictor PGLS models of log(species richness) across avian genera. Shown are median values for models fitted to 100 pseudoreplicate datasets, and the frequency of models (*f*) in which the predictor was statistically significant ($p < 0.05$).

2.5 DISCUSSION

In this study I have shown that avian genera with more labile climatic niches are, on average, more diverse than those exhibiting slower rates of niche evolution. Furthermore, the positive association between climatic niche evolution on diversification was remarkably consistent across clades despite profound differences in latitudinal distributions and ecological traits. Although these patterns were prominent in genus-level clades, I found that rates of climatic niche evolution were unable to predict the extent of diversification across family-level clades. Taken together, these results indicate a pervasive role for rapid adaptation to novel climatic regimes as a driver of speciation in the early stages of lineage diversification, but suggest that the coupling between fast rates of niche evolution and diversification weakens over time.

The link between rapid shifts in climatic regimes and the build up of species richness is opposite to the pattern predicted by the niche conservatism hypothesis, and instead supports the niche lability hypothesis. The only previous comparative support for this idea was found in a much smaller and more geographically restricted sample of 250 New World salamanders (Kozak & Wiens 2010). My study adds considerable weight to this initial finding, confirming that the pattern exists at larger spatial and taxonomic scales, even when controlling for differences in latitude, ecology, and variation in the mode of niche evolution across clades. As I do not test for underlying mechanisms, it is not possible to identify the precise drivers of such patterns, but it seems likely that they arise through the effects of climatic niche evolution on speciation and extinction. One possible mechanism is that populations inhabiting contrasting environments speciate as a result of reduced gene flow (Kozak & Wiens 2007; Sobel *et al*. 2010). In the most commonly postulated form of this scenario, speciation is

accelerated in geographically isolated populations subjected to different environmental conditions, which in turn drive divergence in ecological traits and mating signals (Schluter 2001). This may even apply to contiguous populations under the gradient model of speciation (Moritz *et al*. 2000), in which reproductive isolation evolves as a result of local adaptation across steep environmental gradients (Rice *et al*. 2003; Eaton *et al*. 2008). Both these ideas are supported by the finding that contact zones between sister species often occur in transition zones between regions that differ markedly in climate and habitat, for instance, across the wet/dry environmental gradient of the Great Plains of North America (Moore & Price 1993). In either scenario, adaptability to divergent climatic conditions directly promotes speciation, potentially explaining the positive relationship we detect between rates of climatic niche evolution and diversification across avian clades.

I note that a similar pattern could also arise as a consequence of indirect processes. For example, if speciation occurs within a climatically uniform environment through vicariance, daughter lineages may be forced to disperse into novel environmental conditions owing to range expansion and competition after geographic barriers break down. Under this scenario, fast rates of climatic niche evolution are an effect, rather than a cause, of species diversification. Although this process may contribute to the patterns I detect, I emphasise that this would make little difference to our conclusions. Whether the mechanism is direct or indirect, evolutionary lability of the climatic niche remains a fundamental pre-requisite for the build up of diversity because range expansion to novel environments is necessary for repeated rounds of speciation (Rosenzweig 1995; Weir & Price 2011). Thus, tolerance of divergent climatic conditions may promote range expansion directly by allowing the colonisation of novel environments, or indirectly by allowing species to survive when forced to shift

into new areas of climatic niche space because of competition with a close relative. Diversity is likely to accumulate under this latter scenario not only because evolutionary niche lability promotes speciation, but also because it theoretically relaxes spatial competition and thereby reduces rates of extinction.

My analyses also reveal that the link between climatic niche evolution and diversification across a large sample of the world's birds is consistent across clades regardless of their latitudinal and ecological context. Thus, I found no evidence to support the idea that speciation by niche conservatism occurs more frequently towards the equator, contrary to the prediction that increased climatic stability and zonation in the tropics will facilitate greater specialisation to climatic conditions, thereby reducing gene flow across environmental gradients (Janzen 1967) and driving speciation in populations with conserved climatic niches (Cadena *et al*. 2012). While this process may be more prevalent in the tropics, my findings suggest that rapid niche shifts nonetheless lead to higher diversity in both climatically stable (Kozak & Wiens 2010) and unstable (Holt 1990) environments.

In addition, the niche evolution–diversification relationship does not appear to be moderated by key ecological traits (habitat, territorial system, migration) generally indicative of species' differences in dispersal ability (Moore *et al*. 2008; Salisbury *et al*. 2012). This is in spite of the fact that speciation occurs over a smaller geographic scale in non-dispersive organisms (Kisel & Barraclough 2010), and frequently involves vicariance events or rare dispersal events across barriers in what appear to be essentially climatically uniform environments (Kozak & Wiens 2006; Cadena *et al*. 2012). Thus, even among those groups predicted to show the greatest effect of niche conservatism, my results provide little evidence to support the idea that conserved climatic niches play an important role as a catalyst of diversification.

My results suggest that climatic niche lability represents an important determinant of avian diversification in the early stages of lineage diversification. Over longer timescales, however, fast rates of climatic evolution appear to exert little influence on family-level diversification. One explanation for this discrepancy is that rapid climatic niche evolution promotes speciation most strongly in the initial stages of diversification by allowing lineages to diverge into unoccupied areas of climatic niche space, and thereafter the effect of niche lability on diversification is reduced as lineages have already filled all accessible niche space. In other words, if the number of species in a clade is determined to some extent by the size of its adaptive zone (Simpson 1953), then in the initial stages of diversification (i.e. that captured by genus-level clades) an increase in the 'evolvability' of niche traits should permit lineages to accumulate more species as they expand their adaptive zone by exploring novel areas of niche space (Vermeij 1973; Rabosky & Adams 2012; Rabosky *et al*. 2013). In contrast, over longer time-scales, diversifying lineages may reach the limits of accessible climatic niche space set by impermeable biogeographic barriers (e.g. oceans), thus placing constraints on the continued accumulation of new species in different climatic regimes.

A shift in the importance of climatic niche lability over time would not only explain the observation that clade age is associated with an increase in climatic disparity among genus- but not family-level clades, but also that unbounded (BM) models of niche evolution received a higher proportion of support among genera than among families. The suggestion that niche evolution is more bounded over deeper timescales makes sense because, once a clade has reached the limits of available climatic niche space, incipient species are likely to arise in areas of niche space already exploited by existing members of the clade. After this stage, continued lineage diversification may be more strongly influenced by mechanisms facilitating species coexistence through

ecological (MacArthur 1972; Diamond 1975) or reproductive isolation (Hochkirch *et al*. 2007; Gröning & Hochkirch 2008) under equivalent climatic conditions.

These conclusions, however, are subject to a several important caveats. The first is that my results may to some extent be influenced by the disrupting effect of intraspecific variation when estimating evolutionary rates. When unaccounted for, the presence of considerable intraspecific variation and/or measurement error in trait estimates can lead to overestimated evolutionary rates and underestimated levels of phylogenetic signal (Ives *et al*. 2007; Revell *et al*. 2008), compromising the fit of the simpler BM model in favour of more complex models (Silvestro *et al*. 2015). Furthermore, these biases may be more severe as intraspecific variation or measurement error becomes large relative to the branch lengths connecting species. As a result, finding that OU models generally provide a better fit than BM models across clades could simply reflect an artefact due to the effect of intraspecific variation. Moreover, combined with the fact that more diverse clades have necessarily shorter branches, it is possible that the observation that high rates of change occur in more diverse groups may be explained by variation in branch length alone, and not by any causal relationship between niche evolution and diversification. Although recent work indicates that incorporating measurement error (i.e. intraspecific variation) in phylogenetic analyses considerably improves the accuracy of model selection (Silvestro *et al*. 2015), these problems may not be entirely mitigated by estimating the standard error around species' climatic mean values, as these values themselves are likely to reflect variation in species' distributional ranges.

Another issue is that these results are undoubtedly contingent to some extent on the range-wide approach I use to characterise species' climatic tolerances. This method assumes that each species' geographic range reflects its fundamental climatic niche—

the range of combinations of climatic variables in which a species could exist (Soberón 2007). However, species' distributions may be shaped by other factors, including dispersal limitation (Pigot & Tobias 2015) or competitive exclusion by ecological counterparts (Pigot & Tobias 2013), and therefore more accurately represents its realised niche. Also, by averaging climatic conditions over whole grid cells, I make the implicit assumption that species occupy the full range of environmental conditions present within a cell, whereas organisms often only occupy a subset of the total area captured by a grid cell (Hurlbert & White 2005). These assumptions are common to large-scale comparative studies of climatic niche evolution (e.g. Kozak & Wiens 2010; Cooper *et al*. 2011; Quintero & Wiens 2013) mainly because detailed physiological information and fine-scale occurrence data is generally not available for most species. However, it is generally appreciated that environmental limiting factors are regarded as the major determinant of species' range boundaries (Holt *et al*. 2005; Pigot *et al*. 2010a) and it is therefore practical to assume that species' distribution in space approximately characterises the maximum geographical extent of a species' environmental niche (Brown *et al*. 1996; Tingley *et al*. 2009; Price *et al*. 2011).

Overall, my analyses suggest that the diversifying effect of rapid adaptation to novel climatic niches is pervasive under a range of contexts, being consistent across both tropical and temperate latitudes, and across contrasting ecological settings. I conclude that the dominant evolutionary process linking species' climatic niches to diversification is one of divergence rather than conservatism, and that climatic niche lability is an important predictor of non-random variation in species richness among taxonomic groups, much of which remains to be explained (e.g. Phillimore *et al*. 2006; Ricklefs & Renner 2012). Although the generality of this pattern provides fresh insight into the importance of evolutionary processes in regulating the link between climate and

biodiversity at broader scales, we find that the importance of climatic niche lability for diversification appears to decline over time, and may ultimately be limited by the ability of mature radiations to colonise further unoccupied areas of climatic niche space.

CHAPTER 3

SEXUAL SELECTION ACCELERATES THE INITIATION AND COMPLETION OF SPECIATION CYCLES IN BIRDS

3.1 ABSTRACT

Whether sexual selection accelerates the rates at which new species form or their transition from geographic isolation (allopatry) to coexistence (sympatry) has not yet been resolved. Thus the extent to which sexual selection generates broad-scale patterns of animal diversity remains uncertain. By applying phylogenetic modeling approaches to 144 recent speciation events in birds, I find that sexual selection—as indicated by the degree of sexual dichromatism—increases both per-lineage speciation rate and also the rate at which lineages then become sympatric after periods of isolation. Furthermore, an alternative phylogenetic method applied across an independent dataset encompassing 6670 species appears to corroborate these findings, revealing that dichromatic lineages diversify 2–3 times more rapidly than monochromatic lineages. Taken together, these results suggest that sexual selection not only drives diversification, but also facilitates species co-existence, thus accelerating both key stages in the build up of avian diversity.

3.2 INTRODUCTION

Animal speciation has long been viewed as a cyclical process beginning with the divergence of population traits in allopatry and ending with co-existence in sympatry once the evolution of reproductive isolation permits the overlap of geographic ranges (Dobzhansky 1937; Mayr 1942). The concept of a 'speciation cycle' (Grant & Grant 1997; Price *et al*. 2014) provides a unifying framework for understanding how lineage diversification gives rise to pervasive patterns of species richness over space and time, first by determining spatial turnover among non-overlapping species ranges (β-diversity), and second by regulating the build-up of species assemblages at single points in space (α-diversity). The rate at which these two stages of the cycle are completed is therefore fundamental, and potentially influenced by a combination of ecology and sexual selection—i.e. selection within and between the sexes, driven by competition for matings (Darwin 1871; West-Eberhard 1983). However, although the role of ecology in driving or constraining speciation cycles is well established (Sobel *et al*. 2010; Pigot & Tobias 2013; Price *et al*. 2014), the extent to which sexual selection contributes to diversification remains highly contentious (Price 1998; Panhuis *et al*. 2001; Ritchie 2007; Kraaijeveld *et al*. 2011; Butlin *et al*. 2012).

Mating signals are key to maintaining species boundaries and evolve more rapidly under sexual selection (Darwin 1871; Mayr 1942; Seddon *et al*. 2013). Thus, by driving evolutionary divergence in sexual traits, sexual selection may promote diversification both by generating reproductive isolation among lineages in allopatry (West-Eberhard 1983), and also by facilitating co-existence between closely related species when geographic ranges expand into sympatry (Gröning & Hochkirch 2008; Weir & Price 2011; M'Gonigle *et al*. 2012). However, a contrasting view is that the

effect of sexual selection on diversification is limited, as sexual selection delays the build up of α-diversity either by producing species that are ecologically equivalent and thus prevented from occurring in sympatry (Price 1998; Panhuis *et al*. 2001; Price *et al*. 2014), or by causing divergent lineages to collapse back into single species through high rates of hybridization (Mayr 1942; Sibley 1957).

Yet, despite their importance for our understanding of large-scale biodiversity patterns, progress in resolving these conflicting perspectives has been slow primarily because they are difficult to test experimentally (Rice & Hostert 1993). Whereas the impact of sexual selection on co-existence has been addressed solely by theoretical work (van Doorn *et al*. 2009; M'Gonigle *et al*. 2012), most empirical studies of the role of sexual selection on diversification (reviewed in Ritchie 2007; Kraaijeveld *et al*. 2011) have instead used comparative methods to search across higher order clades (genera and families) for associations between average sexual dimorphism (a surrogate for sexual selection) and species richness (a surrogate for speciation). This approach has produced mixed results (Kraaijeveld *et al*. 2011), but has three main drawbacks. First, it is difficult to make inferences about speciation rates, because the assumption that rates are constant over time is rarely met (Rabosky 2009b), and also because the confounding effect of extinction is unknown and potentially large at these broader taxonomic scales (Kraaijeveld *et al*. 2011). Second, sexual dimorphism varies widely within clades, suggesting that averaging dimorphism across clade members produces a weak index of sexual selection. Third, the intensity of sexual selection can change over evolutionary time (Wiens 2001; Badyaev & Hill 2003; Price & Eaton 2014) and thus dimorphism in contemporary lineages may not reflect levels of sexual selection during speciation.

Thus, the aim of this study was to overcome these issues by applying a set of recently developed phylogenetic models (Weir & Schluter 2007; FitzJohn *et al*. 2009;

Pigot & Tobias 2013) to two novel independent datasets on birds in order to provide a thorough test of the hypotheses linking sexual selection to diversification. First, using a large sample of passerine sister species pairs, I compare the effects of sexual selection on rates of speciation and extinction separately, and assess the relationship between sexual selection and rates of transition from allopatry to sympatry. By focusing on recent speciation events, the sister species approach minimises the difficulties associated with inferring the geographic, phenotypic, and evolutionary history of taxa descended from deeper phylogenetic nodes (Losos 2011), and maximises the power to detect an accurate signal of sexual selection on speciation (Kraaijeveld *et al*. 2011). In addition, this approach allows me to distinguish the effect of sexual selection from the potentially confounding influence of latitude and migratory behaviour on rates of speciation and species co-existence (Weir & Schluter 2007; Weir & Price 2011; Rolland *et al*. 2014b), as well as the problem of taxonomic bias (Ritchie 2007). I then corroborate these insights with an independent broad-scale analysis across 6670 species which is able to account for the well-established fact that sexually selected traits are frequently lost over evolutionary time (Price & Birch 1996; Wiens 2001; Badyaev & Hill 2003). Birds provide an ideal system in which to conduct these tests as they are a well studied group with the most comprehensive data on phylogeny, ecology and biogeography, and because avian plumage dichromatism—the difference in coloration of males and females of the same species—is a robust and widely used index of sexual selection (Owens & Hartley 1998; Dunn *et al*. 2001; Calhim & Birkhead 2006).

3.3 METHODS

3.3.1 Sister species analyses

3.3.1.1 Sister species dataset

Focusing on passerine birds (Aves: Passeriformes), published molecular phylogenies were used to compile a broad sample of sister species pairs, defined as two species that together represent each other's closest extant relative. Sister species were identified from published phylogenetic trees of families or genera generated using protein coding mtDNA in which (i) more than 70% of taxa had been sampled, and (ii) node support was high (either posterior probability > 95% or ML bootstrap support > 70%). More recent phylogenetic studies were preferred over earlier studies, except in a small number of cases where older studies included more taxa and had a better resolution of sister-species relationships. When several phylogenetic trees were presented in a paper, only sister species pairs that were resolved in all trees were selected. In situations where nodal support varied with the method of phylogenetic reconstruction used, ML bootstrap values took precedence. It was assumed that consensus trees and trees based on concatenated molecular datasets provided the most reliable source of phylogenetic information and thus, whenever possible, nodal support was judged based on the values given in these trees. The resulting dataset contained 144 sister species from 36 families distributed evenly throughout the passerine radiation (Appendix 2 Fig. S1 and Table S1).

3.3.1.2 Sexual dichromatism as an index of sexual selection

Avian plumage dichromatism—typically characterised by males possessing a brighter, more distinctive, or more colorful phenotype than females—has long been thought to arise primarily from female choice or male-male competition (Andersson 1994). A key assumption underlying my analyses is that this form of sexual dimorphism is a valid proxy for the intensity of sexual selection in birds. This is supported by a number of studies revealing strong positive relationships between dichromatism and other indices of sexual selection such as testes size, the degree of polygyny and the frequency of extra-pair paternity (Owens & Hartley 1998; Dunn *et al*. 2001). As a consequence, dichromatism has been used as a standard proxy for sexual selection in many studies, including those examining the effects of sexual selection on speciation in birds (Barraclough *et al*. 1995; Owens *et al*. 1999; Morrow *et al*. 2003; Sol *et al*. 2005; Phillimore *et al*. 2006; Krüger 2008; Seddon *et al*. 2008), lizards (Stuart-Fox & Owens 2003), insects (Misof 2002) and fish (Wagner *et al*. 2012), as well as in comparative studies of the effects of sexual selection on extinction (McLain *et al*. 1995; Sorci *et al*. 1998; Morrow & Pitcher 2003), mortality (Promislow *et al*. 1992), immune defense (Møller 1997), signal evolution (Garamszegi *et al*. 2007), molecular evolution (Nadeau *et al*. 2007) and even response to climate change (Spottiswoode *et al*. 2006).

I note, however, that the use of sexual dichromatism as a proxy for the intensity of sexual selection is subject to a number of important caveats. The first is that correlation between sexual dichromatism and sexual selection is unlikely to be perfect, not least because other mechanisms can influence patterns of sex-differences in plumage coloration, such as natural selection for female crypsis in species with female-only incubation (Badyaev & Hill 2003) or social selection on females to signal quality in the context of male mate choice or female-female competition (see Section 3.3.1.4).

In addition, sexual dichromatism may only provide a lower bound estimate of the overall intensity of sexual selection. This is because of potential trade-offs between signaling modalities (Darwin 1871), where investment in one signaling modality (e.g. visual signals) constrains elaboration in another (e.g. acoustic signals). Indeed, pairs of avian sister species with low levels of plumage divergence tend to have more elaborate songs (Tobias *et al*. 2010b), weakening the association between dichromatism and sexual selection. Whilst it would therefore be preferable to compare direct measures of sexual selection from detailed studies of behavior or reproduction, these estimates are lacking for large numbers of species. Thus, dichromatism represents the best proxy currently available for the purposes of broad-scale comparative analyses. I note, however, that the disrupting effect of these issues mean that my analyses may tend to underestimate the effects of sexual selection on diversification rates and the transition to sympatry, rather than exaggerate them.

3.3.1.3 Quantifying sexual dichromatism

To quantify avian sexual dichromatism, I calculated sex-differences in colour directly from spectrophotometric analyses of plumage. I estimated plumage reflectance (320–700 nm) with a spectrophotometer to avoid problems with human misrepresentation of avian colour, including the inability of humans to see in the ultraviolet spectrum (Cuthill *et al*. 1999). All spectrophotometer measurements were collected using an Ocean Optics (Dunedin, Florida) USB2000 spectrophotometer and a PX-2-pulsed Xenon light source with the spectrophotometer probe at 90º to the feather's surface. Measurements were standardized to a WS-1 white standard, considered to reflect more than 98% of light with 250–1500 nm wavelength.

To capture plumage colouration, I took five replicate spectrophotometric measurements at six body regions (crown, throat, belly, wing coverts, back and tail) from three male and three female adult specimens (where possible) in full breeding plumage for all 288 species in the sample. For each reflectance reading, I averaged the reflectance data into bins covering 20 nm of the spectrum between 320 and 700 nm, the approximate visible spectrum of most avian species (Hart 2001). I then quantified colour using standard descriptors of reflectance spectra: brightness (or intensity) and hue/chroma (Endler 1990). Following previous work (Cuthill *et al*. 1999; Seddon *et al*. 2013), I calculated brightness by summing reflectance scores across 20 nm bins. By dividing the binned reflectance values by the corresponding brightness value of the whole spectrum, it was possible to standardise all reflectance spectra according to brightness, such that subsequent indices of chroma and hue were independent of brightness (Seddon *et al*. 2013).

Spectra analysed from each study individual consisted of 19 reflectance scores (based on 20 nm bins) that were highly correlated at similar wavelengths. I therefore used principal components analysis (PCA) to collapse standardised reflectance values into fewer independent axes of variation capable of summarising spectrum shape (Endler 1990; Cuthill *et al*. 1999). I used a PCA approach rather than modeling the spectral sensitivity of the avian eye (Stoddard & Prum 2008) to avoid making assumptions about colour perception in numerous species for which data on spectral sensitivity are lacking. I note that PCA analysis is a widely-used procedure for handling spectral data (Endler & Théry 1996; Bennett *et al*. 1997; Hunt *et al*. 1999; Macedonia 2001; Stein & Uy 2006; Seddon *et al*. 2013), and previous analyses comparing the outputs with those of visual models have yielded qualitatively similar estimates of colour (Stoddard & Prum 2008) and dichromatism (Armenta *et al*. 2008). In my dataset,

the first three PCs together explained over 97% of the variation in spectrum shape (component loadings and weights given in Appendix 2 Table S2), and so were used in all subsequent analyses.

To calculate dichromatism scores for each body region, I calculated the mean Euclidean distance between scores of PC1–PC3 for males and females separately. I then summed the distances between male and female scores for each PC across all six body regions to produce an overall dichromatism score for a species. A dichromatism score of zero indicates identical colouration in both sexes (monochromatism) with higher positive values indicating greater degree of dichromatism. The distribution of raw dichromatism scores was highly right-skewed, so scores were log transformed prior to analysis. To calculate pair-level scores, I used the average score of both species in each pair (Seddon *et al*. 2013).

3.3.1.4 Identifying species with mutual ornamentation

Mutual mate-choice and intrasexual aggression in both sexes can result in males and females sharing equally bright plumage or elaborate ornaments (Tobias *et al*. 2012). In such cases of 'mutual ornamentation', low dichromatism scores may provide poor proxy for the strength of sexual selection, if mutual ornamentation is a consequence of high levels of inter- and/or intrasexual selection. To assess the impact of including pairs containing such species in my sister species analyses, I re-ran models whilst excluding sister pairs containing mutually ornamented species. Following Seddon *et al*. (2013), I examined illustrations in the Handbook of the Birds of the World series and, using a conservative definition of mutual ornamentation, classified species as 'mutually ornamented' if both males and females had bold patterning such as stripes or spots in any region of the body, or if both sexes had a similar extent of highly colourful or

iridescent plumage patches. Pairs containing at least one species identified as being mutually ornamented (n = 48) were then excluded from re-run analyses. However, I did not exclude pairs containing species exhibiting dull monomorphic plumages, in which both males and females share similar plumage features but lack conspicuous colours or ornamentation.

3.3.1.5 Lag time to species description

In this study I use variation in the ages of sister species pairs across a gradient of sexual dichromatism to make inferences about how the strength of sexual selection influences the dynamics of speciation and extinction. This approach assumes that the most recent speciation events within a lineage have been accurately identified. However, taxonomists may fail to describe reproductively isolated lineages as separate species if they are morphologically cryptic, thereby influencing what we consider to be sister species pairs. If such cryptic species are overlooked (i.e. treated as intraspecific lineages), then estimates of the average age of sister species in a given sample are likely to be skewed towards older values. This issue represents a particular problem, however, when the length of time necessary to recognise lineages as separate species after population splitting—in other words, the 'lag time' to species description—varies across the gradient of interest. In the case of sexual selection, it is well known that taxonomists tend to overlook cryptic diversity in species lacking conspicuous sexual ornamentation (West-Eberhard 1983; Panhuis *et al*. 2001; Ritchie 2007; Tobias *et al*. 2010b). If so, this could lead to longer lag times to species description in monochromatic taxa than in dichromatic taxa and exaggerated differences in observed sister species ages across the dichromatism gradient.

To address this issue, I estimated the lag time to species description across the dichromatism gradient by compiling a dataset on the ages of intraspecific phylogroup splits; that is, monophyletic groups of mitochondrial haplotypes that correspond to geographically segregated populations within each species (Avise & Walker 1998; Avise *et al*. 1998). This approach builds on the idea that separated phylogroups have begun the process of speciation, but are not yet recognised as separate species. Thus, by estimating the age of differentiated lineages currently recognised as the same species, it is possible to put a lower bound on an estimate of the time necessary for divergent lineages to be recognised as separate species (Weir & Schluter 2007), and ask how this varies with levels of sexual dichromatism. The presence and age of phylogroups within species were inferred at the tree-building stage (see below).

3.3.1.6 Evolutionary ages of sister species and intraspecific phylogroups

I generated estimates of time since divergence between sister species and intraspecific phylogroups simultaneously by building a dated phylogenetic tree, based on mitochondrial cytochrome (cyt) *b* sequences with backbone constraints. To compile this data set, I began by searching GenBank to assemble a list of all available cyt-*b* sequences for each species. To maximise quality from the outset, I excluded all sequences <400 bp in length, and all sequences that were excessively divergent from other conspecific sequences, which are likely to represent nuclear copies of the cyt-*b* gene (i.e. 'numts'). Using this refined dataset, and focusing only on the species for which multiple cyt-*b* sequences were available, I inferred the presence of phylogroups within species by establishing the geographic location and/or subspecies from which a particular cyt-*b* sequence originated. I only included intraspecific sequences if they were sampled from widely spaced geographic locations within a species' range to

maximise the likelihood that only those sequences corresponding to geographically segregated phylogroups were included (Avise & Walker 1998; Avise *et al*. 1998; Weir & Schluter 2007). In the final tree, species possessing phylogroups were represented by several sequences corresponding to haplotype variants present within phylogroups, thereby allowing simultaneous estimation of sister species ages and phylogroup split ages. To reduce computational load at the tree-building stage, I pruned out multiple sequences originating from similar localities/subspecies that had identical (or extremely similar) sequence identity. For the remaining species in the dataset that lacked sequence data or did not appear to possess phylogroups, I included a single representative cyt *b* sequence in order to infer the time since divergence between sister species. In all cases, where a choice of sequences was available for a given species, I chose the longest. In summary, the resulting dataset contained 556 cyt-*b* sequences, with 86/288 species represented by more than one sequence, corresponding to phylogroup variation.

To build a time-calibrated phylogeny, all chosen cyt-*b* sequences were downloaded from GenBank, aligned using MAFFT (Katoh *et al*. 2002), and checked by visual inspection. The phylogenetic tree was built using BEAST v1.7.4 (Drummond *et al*. 2012), by implementing an uncorrelated lognormal relaxed-clock model with a Yule prior on branch lengths, in combination with a GTR-gamma model of sequence evolution. To date the tree, I set the mean rate of molecular evolution to be 1.05% per lineage per million years, a rate strongly supported by an extensive avian-clock calibration dataset also based on cyt *b* (Weir & Schluter 2008). This clock is consistent over the past 12 million years, and across most avian orders, supporting its use for estimating evolutionary age over the timescales relevant to this study. However, beyond this timeframe, cyt-*b* is inappropriate for inferring evolutionary relationships, so I used backbone constraints to define *a priori* all the known species pairs and genera in our

sample. I conducted four runs, each of 20 million generations sampled every 5000 generations. Using TRACER (Rambaut & Drummond 2007), I found that all runs converged on a similar posterior distribution, so I combined the samples from each run after removing the first 25% of each run as burn in. To produce a dated phylogeny, I generated a maximum sum of clade credibilities (MSCC) tree, with node ages equal to the mean age across trees in the combined posterior sample, on which estimates of sister species ages and intraspecific split ages are based.

3.3.1.7 Geographic and migration data

Two key factors with the potential to confound my analysis testing the effect of sexual selection on rates of speciation, extinction and transitions to sympatry are latitude and migration. Both high latitudes (Weir & Schluter 2007) and migratory behavior (Rolland *et al*. 2014b) have been linked to elevated rates of diversification, and sexual selection is also thought to be more intense towards the poles and among migratory species (Badyaev & Hill 2003), as breeding seasons are short, population densities high and mate-competition intense (Irwin 2000; Macedo *et al*. 2008). Likewise, both variables are likely to be key predictors of range overlap amongst sister species, presumably because rapid climatic shifts at high latitudes and the increased vagility of migratory species reduce the strength of geographic barriers to range expansion (Weir & Price 2011). Thus, in addition to assessing the extent of range overlap of sister species, I also quantified the latitudinal distribution and level of migratory behaviour in each pair.

Latitudinal distribution. I based my analyses of latitudinal patterns and range overlap on species' current breeding range distributions, using range polygons provided by Birdlife International and NatureServe (http://www.birdlife.org/datazone/home) with a small number of modifications (n = 3) to reflect recent taxonomic revisions.

Geographical range maps were available for 141 of the 144 sister pairs in our sample. I estimated species' latitudinal centroids in the R package PBSmapping, and then used the average (absolute) latitude of sister species' centroid values to approximate the latitudinal position of a sister species pair (Weir & Schluter 2007).

Range overlap. To assess range overlap, I first quantified the degree of overlap (sympatry) between sister species, calculated as the proportion of the smaller range that occurred within the larger range. Following previous studies (Weir & Price 2011; Pigot & Tobias 2013) I then converted range overlap to a binary variable in which species pairs are categorised as allopatric or sympatric. In studies of reproductive isolation, cases of minimal range overlap (e.g. 5%) may be appropriately classified as sympatry because even low levels of sympatry indicate the ability of both species to maintain their identity despite coexisting (Weir & Price 2011). Thus, I defined allopatric sister species as those with non-overlapping breeding ranges (0% overlap) and sympatric sister species as those in which breeding ranges overlapped (>0% overlap), and the majority of my analyses of rates of transition to sympatry are based on this classification (see below). However, it is possible that under marginal levels of overlap (i.e. <10%) the costs associated with reproductive interference between sister species may be negligible as interactions at the population level occur relatively infrequently (Pfennig & Pfennig 2009). I therefore conducted a more conservative test of whether sexual selection facilitates species coexistence by exploring alternative thresholds of range overlap, in which species were only considered sympatric if they exhibit either moderate (>10%) or substantial (>20%) levels of range overlap. This has the benefit of allowing me to rule out the influence of erroneous overlap estimates caused by the fact that digital range polygons tend to overestimate the extent of species occurrence (Hurlbert & Jetz 2007). I note that, even under stringent overlap thresholds, the

inference of sympatry may be spurious if species range polygons overlap due the presence of extensive hybrid zones, or if species occur in areas of complex topography (Weir & Price 2011; Pigot & Tobias 2013). To address this, I examined the range maps of sympatric pairs (inferred using the >0% overlap threshold) to identify possible cases where the inference of sympatry was in doubt and then searched the literature to confirm or refute the inferred cases of sympatry. This process resulted in eight cases where sympatry [overlap range (%) = 0.003–0.182] was potentially spurious due to mapping inaccuracies or the presence of extensive hybrid zones, rather than stable coexistence. However, sympatry analyses (see below) run excluding these pairs resulted in qualitatively identical results, so for brevity I present only the results of analyses including all pairs.

Migratory behaviour. Following previous methods (Rolland *et al*. 2014b), I used descriptions in the Handbook of the Birds of the World series (del Hoyo et al. 1992–2011) to score species as (i) sedentary, (ii) partially migratory (i.e. minority of population migrates long distances, or most of population undergoes short-distance migration, nomadic movements, distinct altitudinal migration), or (iii) migratory (i.e. majority of population undertakes long-distance migration). I then used the mean of sister species' scores to create a simple index of the relative level of migratory behavior in a sister species pair.

3.3.1.8 Sister species age and phylogroup age analyses

To allow a preliminary assessment of the factors explaining sister species ages and lag times to species description, I used single and multi-predictor regression models (Weir & Schluter 2007): sister species ages were assessed in relation to sexual dichromatism, latitude and migration; lag times were assessed in relation to sexual dichromatism alone.

3.3.1.9 Estimating rates of speciation and extinction

To assess whether sexual selection influences rates of speciation and extinction, I fit a set of birth-death models (Weir & Schluter 2007) to the data set of 144 sister species pair ages. In these models, rates of speciation and extinction were allowed to vary linearly with increasing extent of sexual dichromatism, and the approach estimated the rates of speciation and extinction most likely to yield the distribution of species' ages observed in our sample. Probability distributions of sister-species ages (see below) were simulated under a birth-death model with speciation rate λ, extinction rate μ, and lag-time to species recognition ϕ. The lag time correction prunes out nodes from phylogenetic trees if they are younger than a focal lag time drawn at random from an exponential distribution with mean age ϕ. This corrects for the fact that empirical species trees lack nodes representing intraspecific splits between taxa currently recognised as subspecies. This approach not only allows direct comparison between sister species' ages from simulated and empirical trees, but also makes it possible to correct estimates of speciation and extinction rate for the existence of a coincidental gradient in lag time to species description (Weir & Schluter 2007). I fit models separately under two different scenarios: (i) lag time invariant across the dichromatism gradient and equal to the mean phylogroup age observed in the data set, and (ii) a declining lag time across the gradient, equal to the line of best fit describing the

negative relationship between phylogroup age and dichromatism. To assess the significance of estimated slopes in rates of speciation and extinction, I compared the maximum likelihood model to models in which all sister species had a single rate of speciation and a single rate of extinction using likelihood ratio tests (LRT; df = 1).

Birth-death trees with the lag time correction were simulated using the R package Phylogen (Weir & Schluter 2007). λ values were simulated ranging from 0 to 0.15 in 0.01 intervals, and from 0.15 to 0.90 in 0.05 intervals. For $\lambda \leq 0.4$, μ ranged from 0λ, 0.05λ, 0.1λ, 0.2λ, 0.3λ, 0.4λ, 0.5λ, 0.6λ, 0.7λ, 0.8λ, 0.9λ, 0.95λ, 0.99λ. For $\lambda > 0.4$, the same rates of μ were used provided $\lambda-\mu < 0.45$. This restriction was necessary for computational reasons given the excessively large tree sizes when $\lambda-\mu > 0.45$, but should not bias our likelihood search because such trees are unrealistically large. For each set of λ and μ, 21 values of ϕ (0, 0.1, 0.2…1.9, 2) were used. For each set of sister species age distributions, the probability density function was obtained using the LOCFIT package in R, and the probability of given sister species age equals the probability density at the corresponding point in the simulated distribution. For a given set of slope and intercept parameters describing the change in speciation and extinction rates with increasing dichromatism, the likelihood was obtained by multiplying the probabilities of each sister species age, derived from the appropriate simulated distribution. The combination of slope and intercept parameters that result in the highest likelihood are the maximum likelihood estimates. The likelihood support intervals (equivalent to the 95% confidence interval) included all parameter combinations within 1.92 log-likelihood units of the maximum likelihood estimate. Full details of the simulation approach can be found in Weir and Schluter (2007).

3.3.1.10 Estimating rates of transition from allopatry to sympatry

To examine the impact of sexual selection on the rates of transition from allopatry to sympatry, I followed Pigot and Tobias (2013) by modeling the process using continuous time multi-state Markov models. Under this approach, each sister pair contributes two observations: the geographic state at the time of population divergence and that of the present day. In these models, I assumed that sister pairs originated in allopatry (i.e., first observation). This is based on substantial evidence that the predominant mode of speciation in birds is allopatric (Coyne & Orr 2004; Phillimore *et al*. 2008), while cases of unequivocal sympatric speciation are very rare (Price 2008). I considered a general model with two possible states for secondary distributions, allopatry and sympatry, and used maximum likelihood to estimate the rate at which species pairs transition from allopatry to sympatry per million years (Myr). For simplicity, I made the assumption that the transition to sympatry is irreversible. A detailed description of the modeling approach can be found in (Pigot & Tobias 2013)

In my analysis, I compared two types of model. (1) Constant rate (CR): the transition rate from allopatry to sympatry is constant with time and equal across species pairs, providing an estimate of the general transition rate to sympatry in the sample. (2) Trait dependent (TD): the transition rate from allopatry to sympatry is no longer constrained to be equal across species, but is allowed to vary in accordance with one or more variables. To compare model fit, I used AIC scores corrected for small sample size (AICc) and inferred the significance of individual covariates using LRTs (df = 1) by comparing the model including the covariate to the nested model in which the focal covariate was excluded. All models were implemented in R using the msm library (Jackson 2011).

3.3.2 Clade-wide analyses

3.3.2.1 Phylogenetic framework and species sample

As a framework for clade-wide analyses, I used a recent set of species-level phylogenies for the world's birds (Jetz *et al*. 2012). These trees were constructed in a Bayesian framework, combining multi-gene phylogenetic inference (6670 species) with a taxonomic placement approach (3323 species). Here, I restrict my analysis to species placed using genetic data, which are evenly sampled from across the entire avian clade (Jetz *et al*. 2012). To address the problem of phylogenetic uncertainty, I randomly selected 100 trees from the Bayesian posterior probability distribution of phylogenies produced using the 'Hackett' family-level backbone (Hackett *et al*. 2008).

3.3.2.2 Human scores of sexual dichromatism

Sexual dichromatism was scored on a scale from 0 (monochromatic) to 10 (maximum dichromatism) following standard methodology (Owens & Bennett 1994; Owens & Hartley 1998). For each species, I scored the difference in plumage coloration between the sexes over five body regions (head, nape-rump-back, throat-belly, tail, and wings). Each region was scored separately using three scores: 0, no difference between the sexes; 1, difference between the sexes only in shade or intensity of color; 2, difference in color or pattern between the sexes. The dichromatism scores for all five body regions were then summed to give species-specific scores of plumage dichromatism. To assess observer error in visual estimates of dichromatism, a random subset of species (n = 2698) were scored independently by a naive observer with no knowledge of the study's predictions. Scores were highly correlated between observers (Spearman's r = 0.97), indicating that observer subjectivity is minimal. Human observers may underestimate

the extent of sexual dichromatism in birds because of an inability to perceive signals in ultraviolet wavelengths (Cuthill *et al*. 1999). Nevertheless, among the species common to both datasets (n = 287), spectrophotometric and human-derived estimates of dichromatism where highly correlated (Spearman's r = 0.76), as demonstrated in previous studies (Armenta *et al*. 2008; Seddon *et al*. 2010), suggesting that human scores can provide a reliable estimate of sexual dichromatism for the purposes of comparative analyses (Seddon *et al*. 2010).

3.3.2.3 Binary-state speciation and extinction (BiSSE) analyses

Justification of the BiSSE approach. When traits hypothesised to impact rates of speciation and extinction undergo frequent evolutionary transitions, it may be difficult to detect correlations using comparisons of higher taxa because we cannot assume that the current value of a phenotypic trait such as dichromatism was the same at the point of speciation (Goldberg *et al*. 2010). To assess the impact of sexual selection on diversification, I therefore employed a BiSSE method (Maddison *et al*. 2007; FitzJohn *et al*. 2009) using a birth-death model of diversification to estimate character-dependent speciation and extinction rates. By explicitly modeling transitions between states, BiSSE models have the crucial benefit of accounting for frequent evolutionary changes between monochromatic and sexually dichromatic states (Badyaev & Hill 2003; Johnson *et al*. 2013; Price & Eaton 2014) in a clade-wide test of the importance of sexual selection on diversification rates. However, there are also limitations to the BiSSE method, one of which is the use of a birth-death model (FitzJohn *et al*. 2009; FitzJohn 2010), which assumes that diversification rates are constant through time and across lineages. When these assumptions are violated, as they frequently are across many clades of appreciable age and size (Rabosky 2009b), the accurate detection of

extinction rates—and therefore speciation rates—becomes notoriously difficult (Rabosky 2010). Given that a simple birth-death process is unlikely to represent the most appropriate characterisation of avian diversification (Jetz *et al*. 2012), I focused on the inferred differences between monochromatic and sexually dichromatic lineages in rates of net diversification alone. These are reliably estimated under the BiSSE approach, even with increasing uncertainty in extinction rates (FitzJohn *et al*. 2009).

Categorising species as monochromatic and dichromatic. As BiSSE considers the difference between two states of a binary character, I classified species as monochromatic or dichromatic. Although it is possible to model sexual dichromatism as a quantitative trait (see FitzJohn 2010), the form of binary classification we adopt is used extensively in large-scale comparative analyses of sexual dichromatism (e.g. Price & Birch 1996; Omland 1997; Owens *et al*. 1999; Phillimore *et al*. 2006), providing a transparent way of testing the association between sexual dichromatism and diversification that is directly comparable to most previous analyses. However, this approach is susceptible to the threshold used to categorise species as either monochromatic or dichromatic based on their dichromatism score. The majority of species in the dataset (63.6 %) were scored as entirely monochromatic (dichromatism score = 0), indicating that a score of >0 represents a natural threshold above which to classify species as dichromatic (Appendix 2 Fig. S2). However, I also explored two increasingly conservative thresholds (score >1 or >2) under which to assign species as dichromatic. The numbers of species classified as monochromatic or dichromatic were 4245 vs. 2425, 4492 vs. 2178 and 5057 vs. 1613 under threshold scores of >0, >1 and >2, respectively. I note that the relatively low tip ratio bias of monochromatic to dichromatic character states (1:1.8, 1:2.1 and 1:3.1, respectively), combined with the

large (+300 tips) phylogeny size, satisfy the recommendations outlined by Davis *et al*. (2013) for the accurate estimation of rate asymmetries using the BiSSE approach.

Model fitting. I used maximum likelihood (ML) to fit models estimating rates of speciation and extinction associated with monochromatic and dichromatic states, as well as rates of transition between states. I fit ML models to each phylogeny in the 100-tree sample, retaining all of the 6670 species represented in the phylogenies generated using molecular data. This accounts for 66.7% of the total diversity recognized by Jetz *et al*. (2012), and all models were corrected for this level of sampling incompleteness (FitzJohn *et al*. 2009). I considered all eight possible model permutations in these analyses, ranging from the simplest (equal rates of speciation and extinction associated with each state, as well as transitions between states) to the most complex (all rates free to vary). For each model, I estimated parameters individually for each tree, and identified the best fitting model by comparing AIC scores across the posterior distribution of trees, and by checking that the chosen model was a significantly better fit than all those models nested within it using likelihood ratio tests with the appropriate degrees of freedom. All models were fit using the R package *diversitree* (FitzJohn 2012).

3.4 RESULTS

3.4.1 Sister species analyses

3.4.1.1 Sister species and phylogroup ages

By comparing the ages of sister species pairs to levels of sexual dichromatism, I found that the average age of sister species decreased markedly with increasing sexual dichromatism (Fig. 3.1), declining from 5.14 Myr (95% CI: 4.28, 5.77) at the monochromatic end of the gradient to 2.67 Myr (95% CI: 1.64, 3.69) at the dichromatic end. This decline in sister species age with increasing sexual dichromatism was highly significant (slope ± SE = –0.639 ± 0.219, t = –2.92, P = 0.004) and remained even after the exclusion of 48 pairs containing species in which both sexes have mutually bright ornamentation (n = 96, slope ± SE = –0.646 ± 0.242, t = –2.67, df = 94, P = 0.009). Furthermore, the relationship remained strong even after accounting for the potentially confounding effects of variation in pair latitude and level of migratory behaviour (Table 3.1).

In contrast, the average age of the oldest phylogroup splits within species was not strongly related to dichromatism (Fig. 3.1). Phylogroups tended to be younger in highly dichromatic species (1.10 Myr; 95% CI: 0.42, 1.78) than in more monochromatic species (1.99 Myr; 95% CI: 1.53, 2.44), but this decline was not statistically significant (slope ± SE = –0.264 ± 0.152, t = –1.731, P = 0.087). Furthermore, this trend disappeared when the 34 mutually ornamented species in this sample were excluded (n = 52, slope ± SE = –0.183 ± 0.153, t = –1.197, df = 50, P = 0.237).

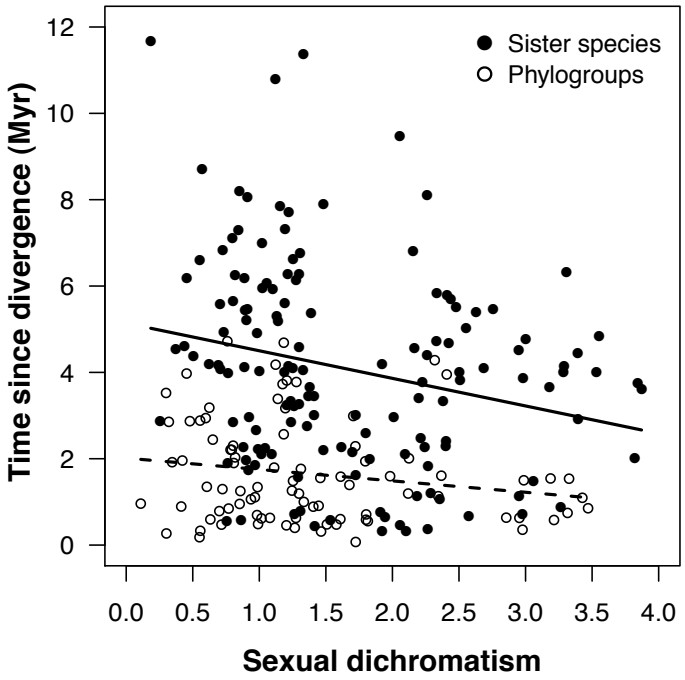

Figure. 3.1. Relationship between time since divergence and sexual dichromatism in birds. Best fit models are shown for pairs of avian sister species (n = 144, P = 0.004) and oldest intraspecific splits within species, where these represent geographically distinct phylogroups (n = 86, P = 0.087). Sexual dichromatism is quantified as the (log) total Euclidean distance in colour space between male and female plumage.

Fixed effects	**Estimate**	**SE**	***t***	***P***
(Intercept)	5.872	0.532	11.033	<0.001
Dichromatism	–0.571	0.222	–2.578	0.011
Latitude	0.001	0.017	0.056	0.955
Migration	–0.531	0.355	–1.496	0.137

Table 3.1. Parameter estimates from a linear model predicting variation in avian sister species pair ages (n = 141 sister pairs). SE = standard error.

3.4.1.2 Rates of speciation and extinction

Using the observed age distribution of sister species across the dichromatism gradient, the maximum likelihood model estimated a positive slope for the relationship between speciation rate and dichromatism (Fig. 3.2). This model received much stronger support than one in which speciation rate was constrained to be equal across pairs (Table 3.2). In contrast, extinction rate appeared to be unrelated to dichromatism (Fig. 3.2) and a model with equal rates of extinction across the dichromatism gradient could not be rejected (Table 3.2). Overall, the difference in estimated rates of speciation and extinction caused inferred net diversification rates (speciation minus extinction) to double across the gradient of sexual dichromatism [start = 0.08 lineages per Myr (95% CI: 0.01, 0.09), end = 0.20 lineages per Myr (95% CI: 0.15, 0.30)]. These results correspond to models fit assuming a constant lag time to species description, with the average time taken set equal to the mean age of phylogroup splits in the dataset (1.65 Myr). However, models fit assuming a declining lag time to species description with increasing dichromatism produced similar results (Appendix 2 Table S3).

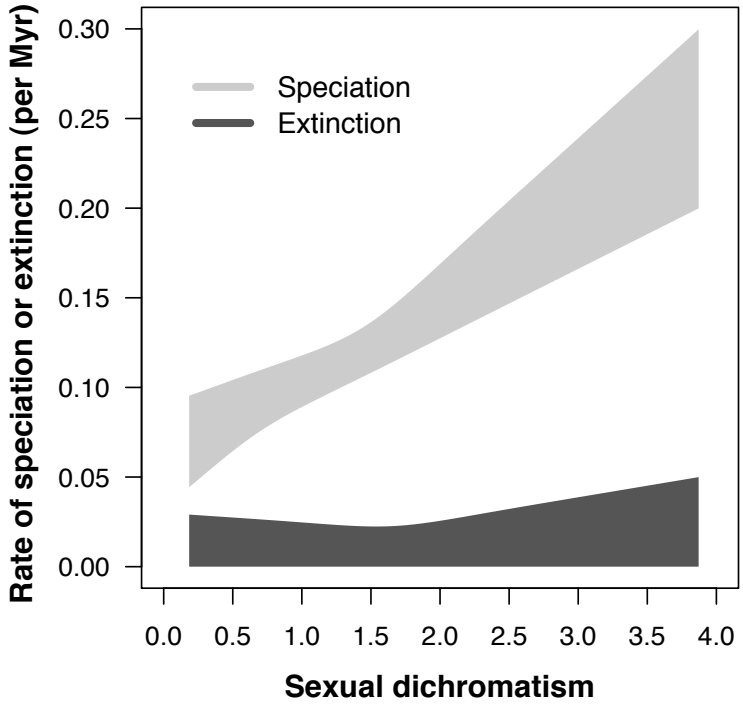

Figure 3.2. The relationship between sexual selection and rates of speciation and extinction in birds. Speciation and extinction rates across a gradient of sexual dichromatism, with estimates shown in units of lineages per millions of years (Myr). Shaded regions encompass all slopes within 1.92 log-likelihood units (95% confidence interval) of the maximum likelihood estimate.

Parameter	Estimate	95% CI	*P*
λ_0	0.090	0.030, 0.090	–
λ_{slope}	0.028	0.028, 0.070	0.001
μ_0	0.010	0.000, 0.030	–
μ_{slope}	–0.003	–0.008, 0.013	0.506

Table 3.2. Maximum likelihood parameter estimates (and 95% CI) describing the linear change in speciation and extinction rates with increasing dichromatism, corrected for a constant lag time to species description across this gradient (n = 144 sister pairs).

3.4.1.3 Rates of transition into sympatry

By comparing constant rate models to models in which the rate of transition from allopatry to sympatry across sisters varied along a gradient of increasing dichromatism, I found that dichromatism has a strong positive effect on the rate at which sister species achieve sympatry (Fig. 3.3). This striking effect was detected even under increasingly conservative range overlap thresholds used to assign sympatry (Table 3.3), and also after excluding pairs containing mutually ornamented species (Appendix 2 Table S4). Overall, these analyses revealed that, on average, highly dichromatic sister species become sympatric approximately 2-3 times more rapidly than monochromatic sister species (Table 3.3).

Furthermore, the positive association between dichromatism and the achievement of sympatry was independent of the effects of latitude and migration (Table 3.4). Comparing the fit of models covering all (additive) combinations of the three variables, I found that both latitude and migratory behavior influenced rate of transitions into sympatry, with significantly faster rates in migratory species, as well as those occurring at high latitude (Appendix 2 Table S5). Nonetheless, controlling for these variables, the effect of dichromatism remained strong (Table 3.4). Indeed, in all models dichromatism remained a significant predictor of rates of transition into sympatry, and I recovered the strongest support for a model in which the rate of transition to sympatry was influenced by the additive effect of dichromatism and level of migratory behaviour in a pair (Table 3.4).

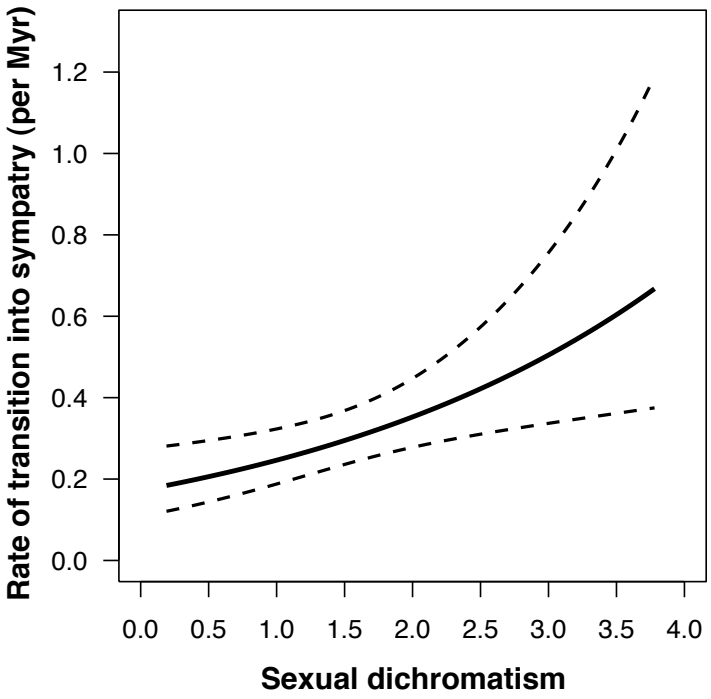

Figure 3.3. The relationship between sexual selection and rates of transition into sympatry in birds. The rate at which lineages transition into sympatry (and 95% confidence intervals) shown as the probability of becoming sympatric per Myr. Sexual dichromatism is quantified as the (log) total Euclidean distance in colour space between male and female plumages.

Threshold	$Rate_{(Dichro\ not\ in\ model)}$	$Rate_{(Dichro\ min)}$	$Rate_{(Dichro\ max)}$	P^a
>0%	0.301 (0.243, 0.374)	–	–	–
	–	0.184 (0.120, 0.281)	0.690 (0.379, 1.255)	0.005
>10%	0.218 (0.173, 0.275)	–	–	–
	–	0.139 (0.089, 0.218)	0.447 (0.246, 0.813)	0.016
>20%	0.155 (0.120, 0.199)	–	–	–
	–	0.107 (0.066, 0.174)	0.277 (0.145, 0.528)	0.073

Table 3.3. Maximum likelihood estimates of sympatry rates (and 95% CI) under alternative range overlap thresholds used to define sympatry across sister species pairs (n = 141).

Covariate(s)	*P*	AICc
–	–	198.0
Latitude	0.067	196.7
Migration	0.005	192.3
Dichromatism	0.005	192.3
Latitude + Migration	0.922; 0.034	194.3
Latitude + Dichromatism	0.084; 0.006	191.4
Migration + Dichromatism	**0.028; 0.028**	**189.5**
Latitude + Migration + Dichromatism	0.806; 0.168; 0.027	191.6

Table 3.4. Comparison of support for models predicting the rate of transition to sympatry (per Myr) across sister species pairs (n = 141). Bold denotes the model with the lowest AICc score in the model set. Maximum likelihood parameter estimates shown separately in Appendix 2 Table S5.

3.4.2 Clade-wide analyses

3.4.2.1 BiSSE models

The distribution of monochromatic and dichromatic character states across the avian radiation is illustrated in Fig. 3.4a. Under a threshold score of >0 to assign species as dichromatic, the best-supported model across all trees (Table 3.5) inferred asymmetric rates of transition between states (LRTs: $P < 0.001$ in all trees), with sexual dichromatism being lost from lineages 3.8–8.2 times more rapidly than it is gained (Fig. 3.4b). Focusing on lineage diversification, under the best-supported model speciation rates for monochromatic and dichromatic lineages were constrained to be equal, whereas parameter estimates indicated that extinction rates were considerably lower in dichromatic lineages (Table 3.5). Translating this into rates of net diversification—which are more reliably estimated than speciation or extinction rates alone on large trees using the BiSSE approach—these differences meant that dichromatic lineages were characterised by significantly faster rates of net diversification (LRTs: $P < 0.001$ in all cases; Table 3.5): across the 100 trees tested, net diversification rates were 1.4–2.1 times faster in sexually dichromatic lineages than in monochromatic lineages (Fig. 3.4b). These effects were detected irrespective of the threshold used to assign dichromatism (Appendix 2 Table S6).

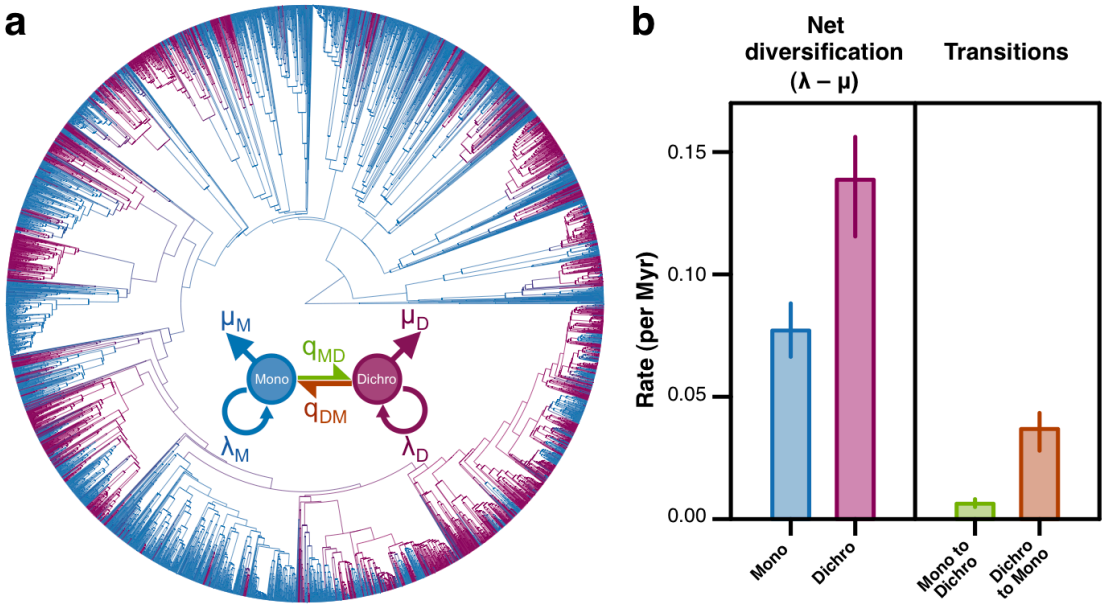

Figure 3.4. Sexual dichromatism, diversification, and character evolution in birds. (a) Maximum clade credibility phylogenetic tree illustrating the distribution of monochromatism (blue) and dichromatism (purple) across 6670 species, based on visual scores of dichromatism and using a threshold score of >0 (out of 10) to assign species as dichromatic. Inset shows a schematic summary of the BiSSE modeling approach, which simultaneously estimates speciation (λ) and extinction (μ) rates for monochromatic (Mono) and dichromatic (Dichro) states, accounting for unequal transition rates (q) from Mono to Dichro (MD; green) and vice versa (DM; orange). (b) Maximum likelihood BiSSE estimates under the best-supported model (Table 5) showing net diversification rate associated with Mono and Dichro states (left panel) calculated as state-specific speciation rate minus extinction rate, and the rates of transition between states (MD and DM; right panel). Parameter means and ranges are calculated from 100 randomly sampled trees.

Threshold	λ	μ	q	Best	K	DeltaAIC	λM	λD	μM	μD	NetM	NetD	qMD	qDM
> 0	=	=	=	0	3	188.96 (28.12)	0.158 (0.010)	0.158 (0.010)	0.063 (0.010)	0.063 (0.010)	0.095 (0.004)	0.095 (0.004)	0.015 (0.001)	0.015 (0.001)
	=	=	≠	0	4	72.63 (18.22)	0.158 (0.010)	0.158 (0.010)	0.063 (0.010)	0.063 (0.010)	0.095 (0.004)	0.095 (0.004)	0.010 (0.001)	0.026 (0.001)
	=	≠	=	0	4	187.73 (28.99)	0.158 (0.010)	0.158 (0.010)	0.060 (0.010)	0.070 (0.012)	0.099 (0.005)	0.088 (0.005)	0.015 (0.001)	0.015 (0.001)
	≠	=	=	0	4	179.86 (23.90)	0.152 (0.010)	0.165 (0.010)	0.06 0(0.010)	0.060 (0.010)	0.092 (0.004)	0.105 (0.005)	0.014 (0.001)	0.014 (0.001)
	=	**≠**	**≠**	**83**	**5**	**0.30 (0.93)**	**0.155 (0.010)**	**0.155 (0.010)**	**0.078 (0.010)**	**0.016 (0.010)**	**0.077 (0.004)**	**0.139 (0.008)**	**0.006 (0.001)**	**0.037 (0.003)**
	≠	=	≠	0	5	22.40 (6.57)	0.147 (0.009)	0.177 (0.012)	0.062 (0.010)	0.062 (0.010)	0.085 (0.004)	0.115 (0.005)	0.008 (0.001)	0.029 (0.002)
	≠	≠	=	0	5	132.27 (18.28)	0.141 (0.009)	0.193 (0.013)	0.040 (0.009)	0.107 (0.014)	0.101 (0.005)	0.086 (0.004)	0.016 (0.001)	0.016 (0.001)
	≠	≠	≠	17	6	1.22 (0.77)	0.156 (0.010)	0.152 (0.010)	0.079 (0.010)	0.012 (0.011)	0.077 (0.004)	0.140 (0.008)	0.006 (0.001)	0.037 (0.003)

Table 3.5. Comparison of model support and mean (sd) maximum likelihood parameters from BiSSE models fit to 100 trees using a threshold score of >0 to assign species as dichromatic. λ = speciation rate; μ = extinction rate; q = transition rate; Net = net diversification rate (λ – μ); M = monochromatic; D = dichromatic. Bold denotes best model in the model set.

3.5 DISCUSSION

By focusing on the evolutionary age of recent avian speciation events and quantifying sex differences using spectrophotometric measurements of plumage colouration, I have tested the role of sexual selection in driving rates of diversification in birds. My key finding is that sexually dichromatic sister pairs have speciated more recently on average than more monochromatic sister pairs. This decline in species pair age alone is consistent with the hypothesis that lineages under intense sexual selection experience faster rates of net diversification than lineages in which sexual selection is less intense. An alternative explanation for this pattern however is that it is a by-product of underlying correlations with latitude or migratory behavior. Specifically, species tend to be younger towards the poles (Weir & Schluter 2007) where migratory species predominate, along with short breeding seasons, high population densities, intense mate-competition, and thus more intense sexual selection (Irwin 2000; Badyaev & Hill 2003). Yet, when I accounted for the effects of latitude and migration, the association between species age and sexual dichromatism remained strong, indicating that my results are not confounded by variation in latitude and behavior.

Another possible explanation for younger species age with increasing dichromatism is that taxonomists tend to overlook cryptic diversity in unadorned species (West-Eberhard 1983; Ritchie 2007). If this is the case, my results could simply reflect a longer average time required to recognise new species in monochromatic lineages. However, by relating the age of the deepest split between intraspecific phylogroups to levels of dichromatism, I found that the average lag time to species description was not significantly shorter in dichromatic lineages. Thus, although the sample size for this analysis (n = 82 species) was limited by the availability of

intraspecific genetic data, the absence of a strong signal suggests that taxonomic bias cannot explain the key finding of a pronounced decline in species age with increasing sexual dichromatism. More generally, however, this result also suggests that despite considerable concern in the literature (Panhuis *et al*. 2001; Ritchie 2007), the results of studies comparing levels of species richness (e.g. Barraclough *et al*. 1995; Owens *et al*. 1999; Seddon *et al*. 2008) in largely monochromatic and dichromatic taxa are unlikely to be confounded by the issue of taxonomic bias.

Having ruled out the effect of important confounding variables, a key finding emerging from this study is that models fit to the distribution of sister species ages estimated a strong positive relationship between speciation rate and the degree of dichromatism. Indeed, finding that sexual dichromatism and speciation rates are linked across avian species pairs provides strong support for the notion that sexual selection increases the rate at which new species form (Darwin 1871; West-Eberhard 1983), most likely by accelerating signal evolution and the evolution of pre-mating reproductive isolation in allopatry (Seddon *et al*. 2013). This is in contrast to rates of lineage extinction, which showed no significant association with dichromatism in these analyses, in line with the results of previous studies that suggest extinction risk is largely unrelated to the intensity of pre-mating sexual selection (Morrow & Pitcher 2003; Morrow & Fricke 2004). Thus, overall, these results suggests that the net effect of sexual selection is to increase—rather than decrease (Tanaka 1996; Kokko & Brooks 2003)—the rate at which new lineages diversify.

Yet, these findings alone shed little light on the persistence of lineages over longer timescales, and it is possible that species produced by sexual selection frequently dwindle to extinction in the face of strong ecological competition or high rates of hybridisation when they eventually occur in sympatry with closely related species

(Mayr 1942; Sibley 1957; Price 1998; Panhuis *et al*. 2001). However, in stark contrast to these expectations, my analyses revealed that highly dichromatic sister species achieve sympatry faster than do more monochromatic pairs. Moreover, I found that rates of transition into sympatry were also significantly faster in migratory species and those occurring at high latitude. This agrees with the general idea that both latitude and migratory behaviour can affect the age at which sister species become sympatric, presumably because rapid climatic shifts at high latitudes and increased vagility reduce the strength of geographic barriers to range expansion (Dynesius & Jansson 2000; Weir & Price 2011). Nonetheless, even after controlling for these effects, the positive relationship between rates of sympatry and dichromatism remained strong. This result is striking as it suggests that sexual selection is associated with faster rates of transition into sympatry—a pattern that is opposite to the relationship expected if ecological competition or hybridisation plays a key role in preventing species co-existence. Instead, if reproductive isolation evolves more rapidly in species experiencing intense sexual selection (Seddon *et al*. 2013), my results are consistent with theoretical models suggesting that species boundaries among related lineages will be strengthened (van Doorn *et al*. 2009; M'Gonigle *et al*. 2012) rather than weakened (Servedio & Bürger 2014) by sexual selection.

Range expansion is a necessary step for repeated rounds of speciation, and the large amount of time required to establish sympatry among close relatives places a severe limit on the rate of on-going speciation (Weir & Price 2011; Price *et al*. 2014). Thus, although rapid establishment of sympatry in highly sexually selected lineages complements my initial finding of elevated rates of speciation in sexually dichromatic taxa, together these results are seemingly difficult to reconcile with the overwhelmingly weak signature arising from previous comparative studies of sexual selection on rates of

net diversification across higher taxa in birds (Price 1998; Morrow *et al*. 2003; Phillimore *et al*. 2006; Kraaijeveld *et al*. 2011).

In this study, however, using species-level diversification models I detected a conspicuous positive effect of sexual selection on net diversification across an extensive sample of the world's birds, providing strong corroborative support for the results of my sister-species analyses. It must be noted, however, that in contrast to the sister species results, clade-wide analyses indicated that the main driver of this pattern was reduced extinction rates rather increased speciation rates in dichromatic taxa. Whilst some theory exists to suggest that intense sexual selection could lead to a decrease in extinction risk—possibly by accelerating the rate of adaptive evolution (Proulx 1999; Kokko & Brooks 2003; Lorch *et al*. 2003)—this result should be interpreted with caution. This is due to the problems associated with accurately disentangling rates of speciation and extinction using tree-wide birth-death approaches when there is a signal of significant diversification rate heterogeneity among groups (Rabosky 2010), as there is in birds (Jetz *et al*. 2012). Indeed, the only large-scale comparative analysis to date examining the link between pre-mating sexual selection and extinction risk in birds detected so such effect (Morrow & Pitcher 2003). Thus, if comparisons between the results of the sister species and clade-wise approaches are limited to net diversification rates, rather than rates of speciation or extinction separately, these two independent analyses yielded remarkably similar results, both suggesting that rates of diversification are approximately twice as fast in highly dichromatic lineages compared to monochromatic lineages.

An important additional insight emerging from these analyses is that the signature of sexual selection is only readily detectable when the frequent evolutionary loss of sexual dichromatism is accounted for (Table 3.5). Indeed, in line with previous

estimates (Price & Birch 1996; Omland 1997; Burns 1998b), these models inferred that sexual dichromatism has been lost from avian lineages approximately 4-8 times more frequently than it is has been gained. Thus, this insight may help to reconcile the results of previous studies comparing diversification rates among higher taxa. Most studies have shown a diminishing effect of sexual selection on diversification over time (Kraaijeveld *et al*. 2011), from which it has been inferred that sexual selection plays a role in the generation of new bird species but is unimportant in their persistence, which instead is thought to depend on ecological factors (Phillimore *et al*. 2006; Price 2008). In contrast, my findings suggest that the fading signature of sexual selection on diversification over time simply reflects the difficulty of inferring the historical intensity of sexual selection in older lineages given the high frequency of transitions between monochromatism and dichromatism.

Taken together, my results indicate that sexual selection accelerates rates of diversification and shortens the lag time to species co-existence in birds, thus shaping patterns of diversity at broad temporal and spatial scales. The idea that biotic interactions limit geographic range expansion and species co-existence is well established (MacArthur 1972; Diamond 1975), with previous studies finding evidence that this effect is mediated by competition over ecological resources (Sobel *et al*. 2010; Pigot & Tobias 2013; Price *et al*. 2014). My study adds a further dimension to this view by providing the first comparative evidence that co-existence is constrained by fitness costs associated with sexual, rather than ecological, interactions between species (Gröning & Hochkirch 2008). Moreover, my analyses suggest that the complex evolutionary history of sexual traits can obscure the impact of sexual selection on diversification and biogeography, potentially helping to explain the inconsistent, and largely negative, results of previous studies. I conclude that sexual selection is a

powerful diversifying force in nature through its ability to influence both the initiation of the speciation cycle in allopatry and its completion in sympatry, and that the evolution of premating reproductive isolation among incipient species represents a critical rate-limiting step in the build up of α-diversity (West-Eberhard 1983; Gröning & Hochkirch 2008). Although this study focuses on birds—a group in which visual signals play a central role in mate-choice, species recognition, and reproductive isolation (Price 2008)—there are numerous examples in other taxa where species boundaries appear to be generated in allopatry or maintained in sympatry by the evolutionary divergence of sexually selected traits (Darwin 1871; West-Eberhard 1983). These conclusions are therefore likely to be of general consequence for understanding patterns of diversification in animals.

CHAPTER 4

SEXUAL SELECTION AND THE LATITUDINAL GRADIENT IN RATES OF PHENOTYPIC EVOLUTION

4.1 ABSTRACT

Latitudinal gradients in rates of phenotypic evolution are common, but the underlying mechanisms are poorly understood. One key hypothesis is that the pattern is driven by sexual selection, which is thought to be elevated at high latitudes, but the existing evidence is ambiguous because previous studies have failed to rule out the influence of a variety of correlated factors. By studying song and plumage evolution in a globally-distributed sample of 233 avian species pairs from 34 passerine families, I show that rates of overall song divergence increase away from the tropics, but only in pairs lacking sex-differences in plumage colouration. On the other hand, sexually dichromatic pairs were characterised by much greater levels of male plumage colour divergence, providing evidence of a trade off between signalling modalities. In tandem, I show that the intensity of SS, as indexed by relative testes size, increases with latitude. Taken together these findings strongly support a key role for sexual selection in shaping patterns of phenotypic evolution. The overarching importance of sexual selection is independent of latitudinal differences in acoustic signalling environments, the strength of interspecific competition and the prevalence of cultural evolution, all of which

contribute to rapid rates of song divergence at high latitudes. As phenotypic divergence in sexual signals is central to the build up of pre-mating reproductive isolation, these findings suggest a key role for sexual selection in driving diversification at high latitudes.

4.2 INTRODUCTION

In many animal species, individuals recognise conspecifics on the basis of unique phenotypic signals, and the rate at which such signals diverge likely represents an important contributory factor in the origin of new species (West-Eberhard 1983; Coyne & Orr 2004; Ritchie 2007; Price 2008). Indeed, one explanation for the conspicuous latitudinal gradient in species richness is that rates of change in traits important for speciation are faster at low latitudes (Mittelbach *et al*. 2007; Schemske *et al*. 2009). Several recent studies challenge this view finding that phenotypic traits involved in pre-mating reproductive isolation diverge more rapidly at high, not low, latitudes (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012). Such an observation supports the idea that recent rates of speciation have been fastest not where species diversity is currently highest, but rather in the relatively depauperate temperate regions (Weir & Schluter 2007; Botero *et al*. 2014). Despite having important implications for our understanding of large-scale patterns of diversity, our knowledge of the mechanisms responsible for generating latitudinal gradients in rates of phenotypic evolution are limited (Price 2008; Weir *et al*. 2012; Wilkins *et al*. 2013).

One prominent hypothesis is that these patterns are driven by underlying latitudinal differences in the relative intensity of sexual selection (Irwin 2000; Irwin *et al*. 2001). Sexual selection has long been viewed as a potent diversifying force (Darwin

1871; West-Eberhard 1983; Price 1998), as female preferences for novel signals and the absence of well-defined trait optima can theoretically drive continuous and often arbitrary divergence in sexually selected traits between populations (Fisher 1930; Lande 1981; West-Eberhard 1983; Iwasa & Pomiankowski 1995). Furthermore, the strength of sexual selection should in theory be greatest at high latitudes, where unpredictable climates, short breeding seasons, and high population densities increase both the strength of female choice and the severity of male-male competition (Stutchbury & Morton 1995; Irwin 2000; Macedo *et al*. 2008; Botero *et al*. 2009). Thus, according to this view, latitudinal clines in rates of phenotypic evolution are the macroevolutionary outcome of stronger sexual selection at high latitudes. There are also strong theoretical reasons to predict that if multiple sexual signals are costly for males to produce and for females to choose between, then within a given species, sexual selection should focus exclusively on a single sexually selected trait, rather than multiple traits (Darwin 1871; Iwasa & Pomiankowski 1994; Shutler 2010). Thus, if a macroevolutionary trade-off exists between the elaboration of different sexual signals, then a key prediction of the sexual selection hypothesis is that rates of phenotypic evolution in alternative signaling modalities such as song and plumage will show contrasting patterns, according to whether sexual selection targets acoustic traits or visual traits, respectively.

However, a number of alternative hypotheses have also been proposed to explain rapid phenotypic evolution at high latitudes. For instance, the acoustic adaptation (Morton 1975) and more broad sensory drive (Endler 1992; Endler 1993) hypotheses predict that species' signals should be adapted to the signal transmission properties of the environment. Thus, increased phenotypic divergence at high latitudes could reflect habitat-mediated differences in the availability of signaling space, leading to greater constraints on phenotypic divergence in dense closed forests, where

transmission optima are more narrowly defined, than in open habitats more characteristic of high latitudes, where there are fewer constraints on signal transmission (Morton 1975; Ryan & Brenowitz 1985). Alternatively, interspecific interactions in sympatry could play an important role, if the high number of species competing for signaling space in tropical environments constrains divergence in song traits (Nelson & Marler 1990; Luther 2009), or if rapid sympatry with close relatives at high latitudes drives divergence through character displacement (Martin *et al*. 2010). Finally, characteristic morphological and behavioural differences between oscine and suboscine passerines could also contribute to latitudinal gradients in rates of phenotypic evolution in birds, especially if cultural evolution elevates rates of song divergence through the rapid accumulation of copying errors between generations (Lachlan & Servedio 2004). If so, then latitudinal clines in rates of song divergence could also be explained by the preponderance of oscine passerines at high latitudes, especially in the New World (Kennedy *et al*. 2014), among which song transmission has a strong cultural component (Baptista 1996; Kroodsma 2004).

Distinguishing among possible causes of latitudinal gradients in rates of phenotypic evolution has proven difficult for a number of reasons. First, the primary focus of existing studies has been to describe patterns of rapid phenotypic evolution at high latitudes (e.g. Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012), rather than directly examining the underlying mechanisms. Second, previous studies have been either taxonomically (Martin *et al*. 2010) or geographically (Weir & Wheatcroft 2011; Weir *et al*. 2012) restricted, limiting the extent to which generalities can be inferred. Third, sexual signals are often complex and composed of discrete phenotypic traits, each potentially subject to distinct selection pressures (Wilkins *et al*. 2013). Therefore, although single-trait studies are informative (e.g. Weir & Wheatcroft

2011; Weir *et al*. 2012), they provide an incomplete picture of the factors shaping patterns of phenotypic divergence, and may over-emphasise the importance of one selective process over another. Moreover, it is generally unknown whether divergence in sub-components of phenotypic signals are likely to result in reproductive isolation (Wilkins *et al*. 2013). Thus, studies aiming to explore the implications of phenotypic evolution for speciation may benefit from a more holistic approach, in which the significance of potential drivers are assessed with respect to overall phenotypic divergence, as well as divergence in distinct signalling traits.

To address these issues, I conducted a comprehensive broad-scale test of the key mechanisms hypothesised to underlie latitudinal gradients in rates of phenotypic divergence between closely related taxa. I compiled phenotypic, ecological and distributional data for a large global dataset of 233 avian species pairs sampled from 37 passerine families, and examined rates of song and plumage evolution with respect to latitude and a suite of correlated variables. I focused on birds because of the general availability of phylogenetic and natural history data, and because both song and plumage colouration are key species recognition traits in birds (Darwin 1871; West-Eberhard 1983; Andersson 1994; Catchpole & Slater 1995; Collins 2004; Slabbekoorn 2004; Beecher & Brenowitz 2005), and are straightforward to quantify in a repeatable way using standard spectrographic and spectrophotometric techniques. Thus, in this study, I first establish whether rates of phenotypic evolution show latitudinal gradients using my expanded dataset and then go on to examine whether latitudinal clines in the relative intensity of sexual selection represents a feasible explanation for increased rates of phenotypic divergence at high latitudes. In this context, I test whether phenotypic divergence between pairs of closely related species could be explained by variables capturing the target and intensity of sexual selection. Although the main aim of this

study is to test the predictions of (1) the sexual selection hypothesis, I also assessed whether latitudinal variation in rates of song evolution could be explained by (2) acoustic adaptation, (3) interspecific interactions, and (4) cultural evolution.

If rapid phenotypic divergence at high latitudes is driven principally by sexual selection, then this leads to three specific predictions. The first is that an independent measure of sexual selection—i.e., one that is unrelated to phenotypic signaling traits (e.g. testes size; Dunn *et al*. 2001)—should indicate an increase in the intensity of sexual selection with latitude (prediction 1). Furthermore, if sexual selection tends to drive phenotypic evolution in either acoustic signals or visual signals, but not both simultaneously, then this should lead to faster rates of song divergence in monochromatic taxa (prediction 2) in contrast to faster rates of male plumage colour divergence in sexually dichromatic taxa (prediction 3), assuming that plumage dichromatism is indicative of sexual selection acting predominately on male visual traits (Darwin 1871; Andersson 1994). Conversely, if latitudinal gradients in phenotypic divergence are primarily influenced alternative mechanisms related to sensory adaptation, interspecific interactions or cultural evolution, then rates of phenotypic divergence should be more closely associated with habitat structure, number of competitors and sympatry with close relatives, and differences between oscines and suboscines, respectively.

4.3 METHODS

4.3.1 Species pairs and evolutionary ages

A globally distributed sample of 233 passerine species pairs were identified from published molecular phylogenies (using the criteria outlined in Chapter 3, section 3.3.1). This sample was comprised primarily of sister species pairs (i.e. each other's closest extant relative; $n = 216$), with the addition of a small number of pairs ($n = 17$) containing congeneric species that are closely related but not true sisters (Appendix 2 Table S1). Pairs belonging to the latter group were included to bolster sample size under the assumption that phenotypic divergence between closely related congeners is informative about rates of phenotypic divergence during recent evolutionary history, even when lineages are not each other's closest relative (Seddon *et al*. 2013). Congeneric pairs were generated by pairing a focal species with a member of a sister clade for which phenotypic data were available. Where more than one clade member had data allowing multiple possible pairings, I included only the youngest pair. I note that no species pairing was nested within that of another (i.e. no species was represented twice in the sample), thereby providing a set of phylogenetically independent species pair comparisons (Weir & Wheatcroft 2011; Weir *et al*. 2012).

In order to assess estimates of trait divergence in the context of evolutionary time, I generated robust estimates of the evolutionary age of each pair (i.e. the time since initial divergence) by calculating the mean age of the node connecting sister species from 1000 randomly sampled trees from the posterior distribution of time-calibrated molecular phylogenies produced by Jetz *et al*. (2012).

4.3.2 Measuring song divergence

High-quality song recordings were available for 223 species pairs of the 233 pairs present in the dataset (Appendix 2 Table S1). Songs were obtained primarily from the Macaulay Library of Natural Sounds (http://macaulaylibrary.org) or the online database Xeno Canto (http://www.xeno-canto.org). For each species, at least three high-quality recordings were measured (mean = 4.8 recordings per species; range = 3 to 34; 242 species had three recordings, 74 had four, 45 had 5, and 115 had six or more), resulting in a data set totaling 2139 songs. Sound files were digitised in Raven Pro v1.4 using standard settings, from which seven key temporal and spectral traits were measured that together capture important interspecific differences in overall signal design (Tobias *et al*. 2010a; Tobias *et al*. 2014b). These traits were: (i) maximum frequency (kHz), (ii) minimum frequency (kHz), (iii) peak frequency (kHz; frequency in the signal with the greatest amplitude), (iv) bandwidth (kHz; maximum frequency minus minimum frequency), (v) signal duration (s), (vi) number of notes, and (vii) pace (number of notes s^{-1}). To quantify overall song structure, I conduced a principal component (PC) analysis on the correlation matrix of individual (log-transformed) song measurements. Three uncorrelated PCs were extracted using Varimax rotation and Kaiser normalisation, one of which reflected song pitch (PC1), one of which reflected song duration and note number (PC2), and one of which reflected song pace (PC3). Together, these three variables accounted for over 75% of the variance in the original acoustic dataset (Table 4.1).

Trait	PC1	PC2	PC3
Max freq	**0.946**	0.023	0.108
Min freq	0.067	-0.060	0.023
Peak	**0.679**	-0.045	0.103
Bandwidth	**0.976**	0.021	0.092
Note number	0.079	**0.902**	0.402
Duration	-0.049	**0.911**	-0.383
Pace	0.140	-0.003	**0.989**
Eigenvalue	2.826	1.703	1.194
Cumulative variation	0.335	0.570	0.759

Table 4.1. Component loadings and weights from a rotated principal component analysis of song variables**.** Standardised loadings of the main contributors to each component shown in bold.

To measure within-pair evolutionary divergence, I calculated the Euclidean distance between species' PC scores. I did this in two ways. First, I calculated the distance between species' values in PCs 1 to 3 separately to generate measures of divergence in song pitch, length and pace, respectively. Second, to produce an estimate of overall divergence in signal design, as opposed to divergence in specific song traits, I calculated the multivariate distance between species' values from all three PCs, weighted by the proportion of variation explained by each. One issue to consider when estimating the Euclidean distance between species scores, however, is that the distance between mean trait values tend to be inflated by sampling and measurement error within species, especially when few individuals are measured and intraspecific variation is high. Therefore, following Weir and Wheatcroft (2011) and Weir *et al*. (2012), I account for this bias by calculating corrected Euclidean distances using an approach

based on ANOVA in which the variation between species is calculated relative to the variation within species, weighted by the number of individuals measured (equations given in Weir *et al*. 2012). This correction results in some estimated Euclidean distances becoming negative; these distances were set to zero.

4.3.3 Measuring plumage colour divergence

Male plumage colouration data was available for 124 of the 233 pairs present in the dataset (data from Chapter 3). Of these 124 pairs, 114 were common to the song dataset, whereas 10 were unique to analyses involving plumage (Appendix 2 Table S1). Briefly, for each species I took five replicate spectrophotometric measurements to estimate plumage reflectance (320-700 nm) at six body regions (crown, throat, belly, wing coverts, back and tail) from three adult male specimens (where possible; 12 species had two males measured, 236 had three) in full breeding plumage. For each reflectance reading, I averaged the reflectance data into bins covering 20 nm of the spectrum. I then standardised all reflectance spectra according to brightness by dividing the binned reflectance values by the total reflectance summed across all bins (Cuthill *et al*. 1999; Seddon *et al*. 2013). The resulting reflectance scores are therefore indices of colour (chroma and hue), independent of brightness (Endler 1990). Full details regarding the collection and processing of reflectance data can be found in Chapter 3.

To quantify overall plumage colour, I used PCA with Varimax rotation and Kaiser normalisation to collapse individual standardised reflectance values into fewer independent axes of variation capable of summarising spectrum shape (Endler 1990; Cuthill *et al*. 1999). I used a PCA approach rather than modeling the spectral sensitivity of the avian eye (Stoddard & Prum 2008) to avoid making assumptions about color perception in numerous species for which data on spectral sensitivity are lacking. This

approach identified three dominant PCs, which together explained over 96% of the variation in spectrum shape (Appendix 3 Table S2).

To measure divergence in male plumage colouration, I followed the same approach used to estimate song divergence by calculating the multivariate distance between species' values using all three PCs, weighted by the proportion of variation explained by each and corrected for measurement error. Unlike song traits, for plumage colouration multiple wavelength bins contributed heavily to each extracted PCs (Appendix 3 Table S2), making interpretation of individual PCs problematic. Therefore for plumage colouration, rather than analysing divergence in each colour PC separately, I restricted my analyses to overall colour divergence (PC1-3) only. Thus, corrected distance values were estimated separately for each of the six plumage patches, and then summed across all patches to give an overall estimate of within-pair divergence in male plumage colouration.

4.3.4 Testing for latitudinal gradients in phenotypic evolution

To test whether rates of phenotypic evolution varied with latitude, I calculated the latitudinal midpoint of the pair, defined as the mean of the two absolute midpoint latitudes for each member of the sister pair (Weir & Schluter 2007; Weir & Wheatcroft 2011; Weir *et al*. 2012). While there are some concerns about condensing the range of latitudes and variety of ecological conditions occupied by a species into a single midpoint latitude (e.g. Botero *et al*. 2014), I use this approach here for consistency with previous studies examining rates of phenotypic evolution across latitude (Weir & Wheatcroft 2011; Weir *et al*. 2012). Latitudes were measured from an equal-area dataset describing the geographic breeding distribution of bird species, at a resolution comparable to a 1° grid (Orme *et al*. 2005).

4.3.5 Testing the sexual selection hypothesis

First, I explored whether a latitudinal cline in the intensity of sexual selection represents a viable hypothesis for explaining increased rates of phenotypic evolution at high latitudes. To do this, I used a global dataset of avian testes size estimates (n = 1010 species) collated by Dunn *et al*. (2001). Testes size is correlated with population-level estimates of extrapair paternity in birds (Møller & Briskie 1995) and is a reliable indicator of the severity of sperm competition across a variety of taxa (e.g. Stockley *et al*. 1997; Hosken & Ward 2001; Byrne *et al*. 2002). As a result, interspecific variation in relative testes size (corrected for total body mass) is used to signal of differences in levels of extrapair mating (e.g. Dunn *et al*. 2001; Pitcher *et al*. 2005), and therefore provides a useful independent measure of variation in the intensity of sexual selection across species. To test whether relative testes size showed a significant latitudinal cline (prediction 1), I calculated (absolute) midpoint latitudes for 1001 species in the Dunn *et al*. (2001) represented in the Jetz *et al*. (2012) phylogenies, and conducted a phylogenetic generalised least-squares (PGLS) regression using a randomly-selected phylogeny from the Jetz *et al*. (2012) distribution.

Second, I tested whether patterns of phenotypic evolution differed according to whether sexual selection seemingly involved acoustic or visual signals (prediction 2). Darwin (1871) was the first to suggest that plumage sexual dimorphism—i.e. sexual dichromatism: the difference in coloration of males and females of the same species—was mainly result of strong sexual selection for visual signals of male condition, and since then it has been well established by population-level studies that in dichromatic species, male plumage patterns are subject to sexual selection (e.g. Price 1984; Hill 1990; Møller & Birkhead 1994). Thus, to give an indication of whether plumage

signals, rather than song traits, were likely to be involved in sexual signaling, I scored each species for the presence of sexual dichromatism.

Sexual dichromatism was initially scored on a scale from 0 (monochromatic) to 10 (maximum dichromatism) following standard methodology (Owens & Bennett 1994; Owens & Hartley 1998). For each species I scored the difference in plumage coloration between the sexes over five body regions (head, nape-rump-back, throat-belly, tail, and wings) using three scores: 0, no difference between the sexes; 1, difference between the sexes only in shade or intensity of colour; 2, difference in colour or pattern between the sexes. Dichromatism scores for all five body-regions were then summed to give species-specific scores of plumage dichromatism ranging from 0 (complete monochromatism) to 10 (sexes entirely dichromatic). Although human observers may generally underestimate the extent of sexual dichromatism in birds because of an inability to perceive signals in ultraviolet wavelengths (e.g. Eaton 2005), the typically high congruence between spectrophotometric and human estimates of dichromatism [e.g. Spearman's $r = 0.76$, $P < 0.001$ across the 248 species included in this analysis possessing spectrophotometric measurements (reflectance data from Chapter 3)] provides support for the view that visual scores can provide a reliable estimate of avian sexual dichromatism (Armenta *et al*. 2008; Seddon *et al*. 2010). As the aim of this analyses was to examine whether sexually monochromatic and dichromatic taxa showed distinct evolutionary trajectories in rates of song evolution, these scores were then converted into a binary pair-level variable by firstly categorising species as either monochromatic (dichromatism score of 0) or dichromatic (score > 0), and then classifying pairs as dichromatic only if both constituent species were considered dichromatic. The practice of scoring dichromatism as a binary character is likely to provide a relatively conservative test of the predictive power of dichromatism, as much

of the variation in sexual dichromatism across taxa is ignored, but I note that this approach has been employed successfully in a number of other large-scale comparative studies of birds (e.g. Barraclough *et al*. 1995; Price & Birch 1996; Owens *et al*. 1999; Phillimore *et al*. 2006).

4.3.6 Testing alternative hypotheses

I explored the role of three alternative drivers of latitudinal gradients in rates of phenotypic evolution: sensory adaptation to different signaling environments, interspecific competition and cultural evolution.

Sensory adaptation. To test the role of divergent signaling environments in determining patterns of phenotypic divergence, I collected data on species' habitat use based on descriptions available in the Handbook of the Birds of the World series (del Hoyo *et al*. 1992–2011). Following previous studies (Weir *et al*. 2012; Mason *et al*. 2014; Tobias *et al*. 2014a), species were scored as occurring in either (i) dense habitats (e.g. lower or middle storey forest), (ii) semi-open habitats (e.g. shrubland or dry forest), or (iii) open habitats (e.g. desert or grassland). Using these scores, pairs were then categorised as closed habitat specialists if both species occupied dense habitats; otherwise, pairs were classed as occupying open habitats.

Interspecific interactions. To estimate the intensity of interspecific competition for signaling space, I quantified the number of sympatric species in each species range. For each species in the dataset I quantified the maximum number of co-occurring species using the range map dataset (Orme *et al*. 2005), from which a pair-level average was calculated. I focused on the maximum number of co-occurring species, rather than the

mean or median number, as the severity of acoustic competition is likely to vary across species' ranges and peak in areas of the highest diversity. Thus, using the maximum number of overlapping species is likely to represent the strongest test of the importance of species interactions on rates of song divergence.

To specifically explore the role of interspecific interactions with close relatives, I followed previous studies (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012) and categorised species pairs as either allopatric or sympatric. To do this, I first calculated the proportion of the smaller species' range that overlapped with that of the larger-ranged species, then converted this to a binary variable by classifying species as sympatric if species' ranges overlapped by >10%, or allopatric if ranges overlapped by <10%. The 10% threshold to assign sympatry was used to minimise the risk that species' were erroneously classified as sympatric due to the fact that digital range polygons tend to overestimate areas of species occurrence (Hurlbert & Jetz 2007; Jetz *et al*. 2008).

Oscines/suboscines. In suboscine passerines, songs develop without learning (Touchton *et al*. 2014), whereas in oscines the development of full adult songs is dependent on the presence of a conspecific tutor (Kroodsma 2004). If copying errors occur during the song acquisition stage very early in development, then cultural (i.e. non-genetic) mutations may rapidly accumulate, leading to rapid song divergence and the formation of population-specific song dialects (Lachlan & Servedio 2004). Thus, to explore the impact of cultural evolution on song divergence, whilst accounting for other potentially important ecological and behavioural differences between the two groups, pairs were categorised as belonging to either the suboscine or oscine passerine suborders following the taxonomy of Jetz *et al*. (2012).

4.3.7 Estimating rates of phenotypic evolution

I estimate evolutionary rates of song divergence under two widely used models of trait evolution (Weir & Wheatcroft 2011; Weir *et al*. 2012; Seddon *et al*. 2013). Under a Brownian motion (BM) model, sister species trait values are assumed to diverge according to a particular rate of trait evolution (β), which is estimated from the data using the observed within-pair phenotypic distance between species, relative to their age. In the case of an Ornstein-Uhlenbeck (OU) model, however, this approach is extended to include a constraint parameter (α) that estimates the extent to which trait divergence becomes more difficult as distance from an initial starting value increases (i.e. as species become more divergent). Under this model, sister species trait values may initially diverge rapidly according to rate β, but divergence slows over time (if $\alpha > 0$) as divergence reaches an asymptote set by α (Weir & Wheatcroft 2011; Weir *et al*. 2012).

Using this approach, the first step was to establish whether phenotypic evolution showed a strong latitudinal gradient in my expanded dataset. To do this, I compared the fit of models in which β and α were allowed to vary in line with latitude, to models in which β and α were forced to be similar with respect to pair latitude (equations given in Weir *et al*. 2012). The next step was to test the importance of variables related to underlying mechanisms. To do this, I followed previous studies (Weir & Wheatcroft 2011; Weir *et al*. 2012; Seddon *et al*. 2013) by fitting models that allowed for evolutionary rates and constraints to be constant or change linearly with species richness or latitude, and/or to vary for alternative subsets of taxa within the dataset. These subsets were (i) monochromatic/dichromatic, (ii) closed/open habitat, (iii) allopatric/sympatric, and (iv) oscine/suboscine. This approach meant that I compared the fit of 36 different models to explain levels of song divergence, providing an

integrative framework within which to distinguish the relative importance of multiple factors influencing phenotypic divergence. This modeling approach was used to explain levels of divergence in overall song structure (song PC1-3), sub-components of song structure [namely, song pitch (PC1), song length (PC2) and song pace (PC3)], as well as divergence in male plumage colouration (plumage PC1-3). To assess model fit, I computed second order Akaike Information Criterion (AICc) scores and Akaike weights (Burnham & Anderson 2002) based on maximum likelihood (ML) fits of each model, using equations given in Weir *et al*. (2012). In cases where models were fit separately to alternative subsets of the data, joint AIC values were computed by summing the likelihood values of subset models and adjusting the number of parameters accordingly. The best-fitting model for each song trait was identified using ΔAICc values (model AICc – AICc for the best-fit model), where the best model has a ΔAICc value of 0. To give an indication of relative support, I also calculated the AICc weight of each model, which measure the proportion of support attributed to a given model, relative to support for all other models. All models were fit using functions provided in the R package 'EvoRAG' v. 2.0 (http://cran.r-project.org/web/packages/EvoRAG/index.html).

4.4 RESULTS

4.4.1 Latitudinal gradients in phenotypic evolution

By comparing models incorporating latitude to those without, I found weak support for the existence of simple latitudinal effects on rates of divergence in both song and plumage traits (Table 4.2). Overall, OU models were favoured over BM models, and for all traits the estimated effect of latitude on divergence rate ("β slope") was positive (Table 4.2), indicative of faster rates of phenotypic divergence at high latitudes. However, for all traits, AICc values indicated that models with variable rates provided a less parsimonious explanation for levels of divergence than models in which rates and constraints were assumed to be invariant across latitude (Table 4.2).

			β		α				
Trait	**Model**	**Gradient**	**Intercept**	**Slope**	**Intercept**	**Slope**	**AICc**	**ΔAICc**	**Weight**
Song	BM	-	0.071	-	-	-	409.93	45.64	0.00
	BM	Latitude	0.065	0.000	-	-	411.44	47.15	0.00
	OU	-	0.296	-	0.907	-	364.29	0.00	0.73
	OU	Latitude	0.121	0.010	0.273	0.037	366.25	1.96	0.27
Pitch	BM	-	0.053	-	-	-	345.65	26.64	0.00
	BM	Latitude	0.053	0.000	-	-	347.69	28.68	0.00
	OU	-	0.130	-	0.413	-	319.01	0.00	0.68
	OU	Latitude	0.042	0.007	0.033	0.031	320.56	1.55	0.32
Duration	BM	-	0.082	-	-	-	442.03	10.94	0.00
	BM	Latitude	0.076	0.000	-	-	443.64	12.55	0.00
	OU	-	0.139	-	0.201	-	431.09	0.00	0.70
	OU	Latitude	0.092	0.003	0.071	0.007	432.82	1.73	0.29
Pace	BM	-	0.185	-	-	-	623.25	104.30	0.00
	BM	Latitude	0.174	0.001	-	-	624.98	106.03	0.00
	OU	-	2.997	-	5.066	-	518.95	0.00	0.85
	OU	Latitude	1.444	0.082	2.056	0.166	522.37	3.42	0.15
Plumage	BM	-	12.922	-	-	-	885.07	39.12	0.00
	BM	Latitude	10.800	0.085	-	-	886.19	40.24	0.00
	OU	-	208.318	-	3.995	-	845.95	0.00	0.62
	OU	Latitude	0.001	7.728	0.000	0.145	846.92	0.97	0.38

Table 4.2. Comparison of support for models assessing the effect of latitude on phenotypic trait evolution across pairs of avian sister species (*n* pairs = 223 and 124 for song and plumage models, respectively). β, rate of divergence; α constraint parameter.

4.4.2 Testing the role of sexual selection

In support of prediction 1, I found a highly significant positive correlation between species' relative testes size and their latitudinal range midpoints (PGLS: $\beta = 0.004$, $R^2 = 0.02$, $p < 0.001$): on average, relative testes size increased with distance away from the equator (Fig. 4.1).

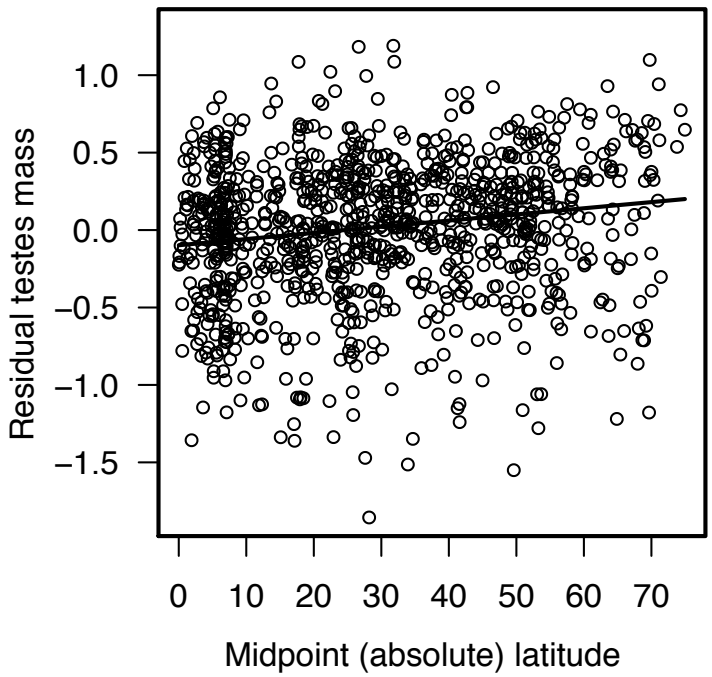

Figure 4.1. The relationship between midpoint latitude and residual testes mass in birds ($n = 1001$ species). Line indicates a significant relationship ($p < 0.001$) inferred using PGLS regression.

By comparing the fit of alternative models to explain across-pair variation in the extent of phenotypic divergence, I found significant differences in the evolutionary rates of song divergence in monochromatic versus dichromatic taxa (Fig. 4.2; Table 4.3). In support of prediction 2, the best-supported model (Table 4.3) estimated a positive latitudinal gradient in rates of overall song evolution across monochromatic species pairs, but a negative latitudinal gradient in dichromatic pairs (Fig. 4.2A; Appendix 3 Table S1). In other words, although divergence rates are approximately similar for monochromatic and dichromatic pairs in the tropics (Fig. 4.2B), at high latitudes monochromatic species diverge rapidly in overall song structure whereas dichromatic species show the opposite trend (Fig. 4.2C).

I also found significant differences between monochromatic and dichromatic pairs in rates of divergence in song length (PC2). Again, the best-fitting model—which here received >90% of model support (Table 4.3)—inferred faster rates of song length divergence at high latitudes across monochromatic pairs, but a latitudinal decline in rates of song length divergence across dichromatic pairs (Fig. 4.3D; Appendix 3 Table S1). Thus, these results reveal that, on average, within-pair divergence in song length appears to proceed more rapidly amongst dichromatic species than monochromatic species at low latitudes (Fig. 4.3E), but that this situation is reversed at high latitudes, where song length evolves more rapidly—and is more divergent—within monochromatic species pairs than dichromatic pairs (Fig. 4.3F).

In terms of male plumage colour divergence, I also found that the best-supported model identified distinct differences between monochromatic and dichromatic pairs (Table 4.3). Yet, this model did not include latitudinal effects on parameter estimates and also suggested that divergence rates were faster within monochromatic pairs than dichromatic pairs (Fig. 4.4A, Appendix 3 Table S1). However, this unexpected effect

was counterbalanced by the inference of much stronger constraints on plumage divergence in monochromatic taxa (Fig. 4.4A, Appendix 3 Table S1), such that, overall, predicted levels of plumage divergence through time are much greater in dichromatic pairs than monochromatic pairs (Fig. 4.4B). This result reflected the fact that the males of sexually dichromatic pairs tended to be much more divergent in plumage colouration than males of monochromatic pairs (Fig. 4.4B), providing partial support for prediction 3.

4.4.3 Alternative hypotheses

Sensory adaptation and interspecific interactions. I found that the best-fitting model explaining within-pair divergence in song pitch (PC1) estimated separate parameters for forest and nonforest pairs that varied with the number of competing species (Table S1). This model was strongly favoured over all other models tested (Table 3), revealing that in closed habitat (forest) taxa, divergence in song pitch is generally highly constrained and only weakly influenced by the number of competing species (Fig. 3A). In contrast, in open habitat, evolutionary constraints on pitch divergence increase and rates of divergence decrease with the number of co-occurring species (Fig. 3A). In other words, in open habitats such as woodland and grassland (but not in closed forested habitats), interspecific competition for acoustic space appears to constrain rates of divergence in song pitch (Fig. 3B and C). In contrast, I found little evidence that habitat type or the number of co-occurring species influences male plumage colour divergence (Table 3). Moreover, I found little support for the idea that interspecific interactions with close relatives play an important role in shaping rates of either song or plumage evolution (Table 3).

Oscines/suboscines. The best-fitting model explaining divergence in song pace (PC3) estimated model parameters separately for oscines and sub-oscines (Tables 3 and S1). The inferred differences corresponded to faster rates of song pace evolution within oscine species pairs than sub-oscines pairs, but also stronger constraints to continued divergence in oscines rather than sub-oscines (Fig. 3G and H). In contrast, I found little evidence to suggest that male plumage colour divergence was best explained by differences between oscines and suboscines.

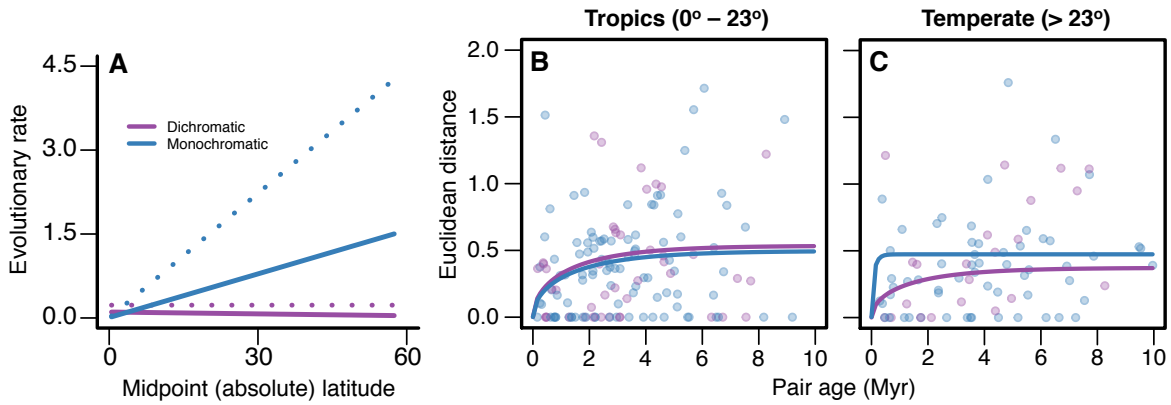

Figure 4.2. Evolutionary rates of divergence in overall song structure (PC1-3) for monochromatic and dichromatic species pairs (n = 223) across latitude under the best supported model. Shown are (A) maximum likelihood (ML) estimates of rate (β; solid lines) and constraint (α; dashed lines) parameters, and observed divergence between sister species (points), as well as expected divergence over time (lines) based on parameter estimates at midpoint latitudes representing the 10% quartile (B) or 90% quartile (C) of each plotted subset of pairs.

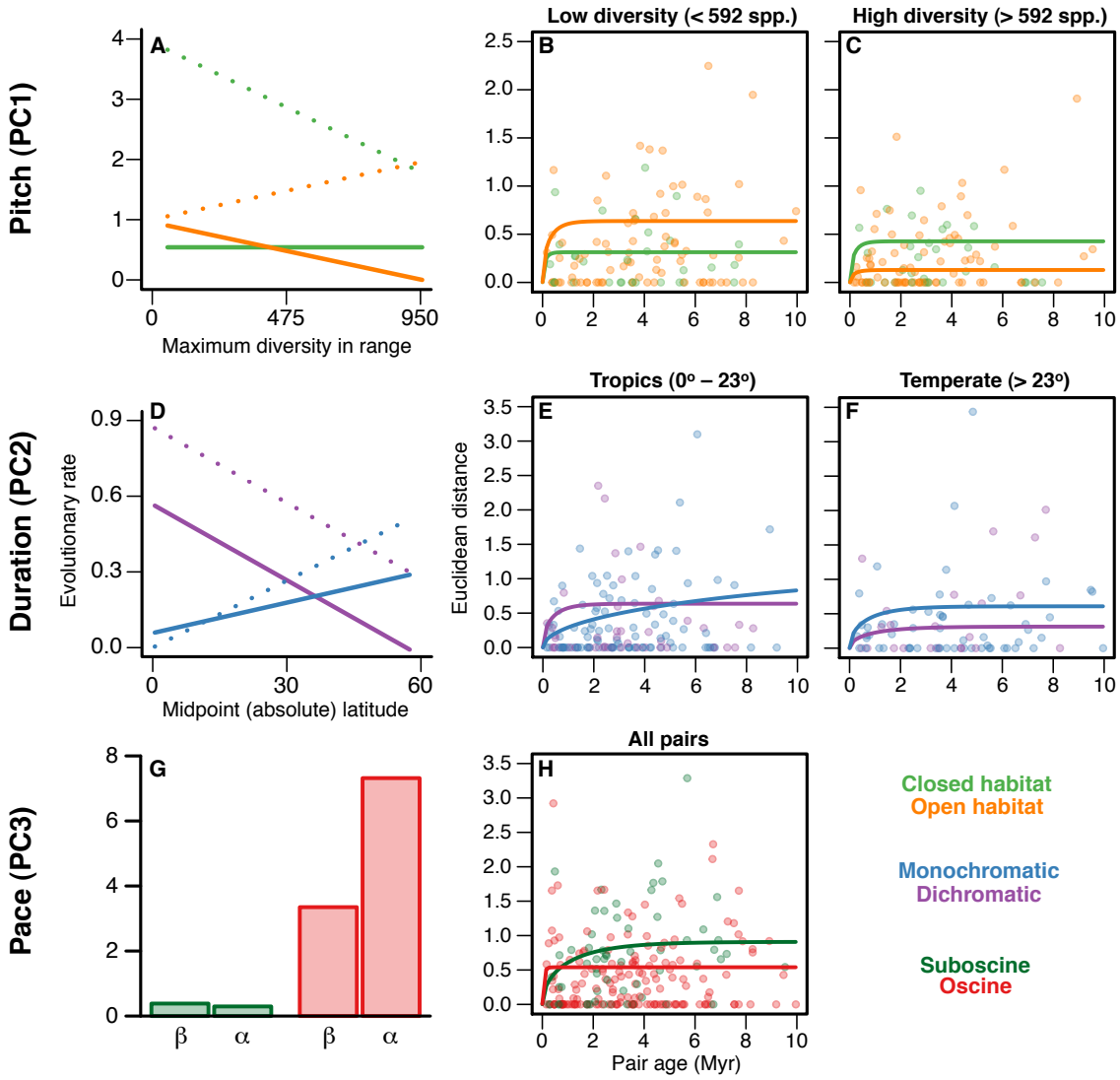

Figure 4.3. Evolutionary rates of individual song trait divergence across avian species pairs (n = 223). Shown are (A, D, G) maximum likelihood (ML) estimates of rate (β; solid lines) and constraint (α; dashed line) parameters under the best supported model for each song trait, and (B, C, E, F, H) observed divergence in song traits between sister species (points) as well as expected divergence over time (lines). For PC1 and PC2 expected divergence is based on parameter estimates at gradient values representing the 10% quartile (B, E) or 90% quartile (C, F) of each plotted subset of pairs.

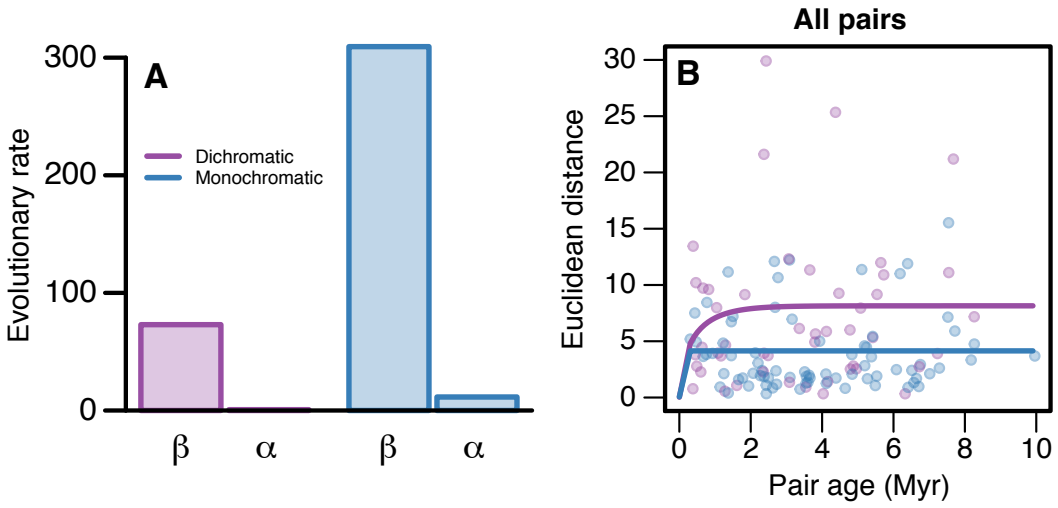

Figure 4.4. Evolutionary rates of divergence in overall plumage colouration (PC1-3) for monochromatic and dichromatic species pairs (*n* = 124) across latitude under the best supported model. Shown are (A) maximum likelihood (ML) estimates of rate (β) and constraint (α) parameters, and observed divergence between sister species (points), as well as expected divergence over time (lines) based on ML parameter estimates.

Table 4.3. Following page. Comparison of support for different models of phenotypic trait evolution among pairs of avian sister species (*n* pairs = 223 and 124 for song and plumage models, respectively). The best-fitting model for each phenotypic trait is highlighted and underlined in bold.

		Brownian motion models						Ornstein-Uhlenbeck models					
		No gradient		Latitude		Diversity		No gradient		Latitude		Diversity	
Trait	**Subset**	**ΔAICc**	**Weight**	**ΔAICc**	**Weight**	**ΔAICc**	**Weight**	**ΔAICc**	**Weight**	**ΔAICc**	**Weight**	**ΔAICc**	**Weight**
Song	All	48.69	0.000	50.20	0.000	50.73	0.000	3.05	0.065	5.01	0.024	3.55	0.050
	Monochromatic/Dichromatic	46.53	0.000	46.20	0.000	50.64	0.000	0.43	0.240	**0.00**	**0.298**	6.84	0.010
	Forest/Nonforest	48.41	0.000	44.33	0.000	50.97	0.000	6.53	0.011	4.97	0.025	7.39	0.007
	Allopatric/Sympatric	49.09	0.000	48.59	0.000	53.22	0.000	2.88	0.071	2.70	0.077	2.34	0.092
	Oscine/Suboscine	50.70	0.000	48.12	0.000	49.35	0.000	5.44	0.020	7.59	0.007	9.73	0.002
Pitch	All	76.00	0.000	78.04	0.000	78.04	0.000	49.36	0.000	50.91	0.000	48.38	0.000
	Monochromatic/Dichromatic	71.02	0.000	67.20	0.000	73.98	0.000	45.56	0.000	41.75	0.000	18.57	0.000
	Forest/Nonforest	77.78	0.000	79.12	0.000	81.91	0.000	46.19	0.000	46.06	0.000	**0.00**	**1.000**
	Allopatric/Sympatric	68.74	0.000	70.42	0.000	66.71	0.000	43.36	0.000	37.04	0.000	38.15	0.000
	Oscine/Suboscine	77.89	0.000	73.57	0.000	82.00	0.000	49.98	0.000	54.66	0.000	52.02	0.000
Duration	All	21.04	0.000	22.65	0.000	22.96	0.000	10.10	0.006	11.83	0.003	12.70	0.002
	Monochromatic/Dichromatic	23.08	0.000	23.45	0.000	21.61	0.000	13.03	0.001	**0.00**	**0.936**	10.75	0.004
	Forest/Nonforest	21.51	0.000	18.47	0.000	22.78	0.000	12.60	0.002	11.47	0.003	18.84	0.000
	Allopatric/Sympatric	23.06	0.000	26.77	0.000	27.05	0.000	11.41	0.003	9.45	0.008	7.31	0.024
	Oscine/Suboscine	22.90	0.000	22.83	0.000	22.25	0.000	13.91	0.001	10.54	0.005	13.09	0.001
Pace	All	116.48	0.000	118.21	0.000	114.26	0.000	12.18	0.001	15.60	0.000	15.66	0.000
	Monochromatic/Dichromatic	112.68	0.000	102.78	0.000	111.89	0.000	12.46	0.001	10.43	0.003	16.96	0.000
	Forest/Nonforest	110.32	0.000	104.19	0.000	110.75	0.000	14.25	0.000	14.55	0.000	17.02	0.000
	Allopatric/Sympatric	117.29	0.000	110.42	0.000	115.16	0.000	14.94	0.000	20.67	0.000	18.54	0.000
	Oscine/Suboscine	118.41	0.000	115.98	0.000	122.54	0.000	**0.00**	**0.584**	3.14	0.122	1.42	0.287
Plumage	All	58.84	0.000	59.96	0.000	60.51	0.000	19.73	0.000	20.70	0.000	22.89	0.000
	Monochromatic/Dichromatic	35.99	0.000	35.12	0.000	33.52	0.000	**0.00**	**0.679**	6.49	0.026	6.37	0.028
	Forest/Nonforest	57.75	0.000	57.85	0.000	51.71	0.000	20.51	0.000	25.14	0.000	24.74	0.000
	Allopatric/Sympatric	58.44	0.000	54.04	0.000	52.30	0.000	14.92	0.000	20.34	0.000	20.97	0.000
	Oscine/Suboscine	51.56	0.000	52.64	0.000	52.66	0.000	2.20	0.226	7.17	0.019	6.97	0.021

4.5 DISCUSSION

Evidence that phenotypic traits involved in mate choice and species recognition evolve more rapidly at high latitudes is growing (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012) and the apparent generality of this pattern demands a common explanation. Here I tested the importance of latitude in determining rates of interspecific phenotypic divergence across a globally distributed sample of avian species pairs. My analyses showed that although there is a tendency for more rapid phenotypic evolution at high latitudes, simple latitudinal gradients in rates of phenotypic evolution operating equally across all taxa appear to be either weak or absent. This is consistent with the view that latitudinal variation plays a role in promoting rapid phenotypic evolution, but that the overall pattern is shaped by a more complex set of underlying processes (Weir & Wheatcroft 2011; Weir *et al*. 2012). Based on distributional, ecological and phenotypic variation among species pairs I show that, overall levels of divergence in sexually selected traits are best explained by variation in the intensity of sexual selection and the signaling modality it targets, and only weakly influenced by sensory adaption, interspecific interactions and oscine/suboscine differences. These results suggest that strong sexual selection may be an important driver of rapid divergence in traits important for pre-mating isolation at high latitudes.

4.5.1 Evidence for sexual selection driving phenotypic evolution

Previous studies describing latitudinal gradients in phenotypic rates have suggested that increased sexual selection may play a role in promoting rapid divergence at high latitudes (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012), but were unable to test its importance. Whilst there are strong theoretical reasons to believe that

the intensity of sexual selection increases markedly with latitude (Stutchbury & Morton 1995; Irwin 2000; Macedo *et al*. 2008; Botero *et al*. 2009), this hypothesis has rarely been directly tested, especially across large numbers of species. Finding that relative testes size—a measure of sperm competition and frequency of extrapair mating—exhibits a significant albeit noisy positive relationship with latitude therefore provides the first empirical support for the idea that the intensity of sexual selection increases with latitude. With regard to the mechanisms underlying gradients in phenotypic evolution, this result also suggests that a latitudinal cline in the intensity of sexual selection a viable hypothesis for faster rates of phenotypic evolution at high latitudes.

Against this backdrop, finding that rates of divergence across monochromatic taxa in both overall song structure and song length increase strongly with latitude—independently of the number of competing species or variation in habitat structure—is consistent with the idea of an underlying latitudinal gradient in sexual selection. In terms of song length, a latitudinal increase in divergence rates makes sense, given that song length is targeted by both female choice and male-male competition (e.g. Irwin 2000; Badyaev *et al*. 2002; Botero *et al*. 2009; Ornelas *et al*. 2009; Weir & Wheatcroft 2011; Mason *et al*. 2014). Empirical studies have shown that strong intersexual selection (i.e. female choice) generally favours the evolution of longer, more complex song types as condition-dependent indictors of male quality (Catchpole 1982), and that song length increases with increasing latitude suggesting a cline in the strength of female choice from the tropics to the temperate zone (Irwin 2000; Botero *et al*. 2009). Thus, if strong selection for song elaboration leads to population-level differences in song length, more intense female choice at high latitudes may account for latitudinal increases in levels of song length divergence. On the other hand, male-male competition, which tends to favour the development of shorter, more stereotyped songs

(Catchpole 1982; Collins 2004), also theoretically increases with latitude. Thus, a latitudinal cline in the rate of song length evolution may also reflect greater within-pair differences in the balance of female choice vs. male-male competition at high latitudes, which causes divergent selection on song length (Irwin 2000).

Moreover, my results suggest that the diversifying effect of sexual selection is not limited to particular elements of song structure. Overall levels of structural divergence were only weakly related to variation in the signaling or competitive environment, or the potential for cultural evolution. Instead, rates of song structure evolution followed the pattern predicted by the sexual selection hypothesis of more rapid divergence at high latitudes amongst monochromatic taxa. There are several potential explanations for this result. It is possible that this pattern simply reflects the overwhelming effect of sexual selection on divergence in one sub-component of overall song structure, namely song length. However, this seems unlikely given that my index of overall structural divergence was weighted according to the variance explained by each sub-component, with divergence in song length accounting for less than a third of the total inferred divergence. A more likely explanation is that, to some extent, sexual selection shapes many if not all aspects of song evolution, thus explaining the link between sexual selection and rates of overall song evolution inferred here. For instance, in addition to song length, sexual selection may also generate arbitrary divergence in song pitch or pace, if signaling over wider bandwidths or using novel combinations of song syntax elicits beneficial responses in receivers (Irwin *et al*. 2008; Weir & Wheatcroft 2011). Furthermore, even under adaptive—rather than stochastic—scenarios of divergence, sexual selection could increase rates of song divergence through mechanisms related to sensory drive (Endler 1992; Boughman 2002), if female choice for locally adapted signals enhances selection for divergence. Thus, increased sexual

selection operating on multiple song traits to favour either arbitrary or adaptive divergence may explain more rapid divergence of overall song structure in monochromatic taxa.

Furthermore, finding that divergence patterns in monochromatic and dichromatic taxa are reversed when focusing on male plumage colouration rather than song provides strong evidence for the importance of sexual selection in driving phenotypic evolution in sexual traits. Specifically, my results revealed that levels of divergence in male plumage colouration are greatest not in monochromatic taxa but in dichromatic taxa. However, there appeared to be little support for latitudinal gradients in rates of plumage colour evolution across dichromatic pairs in my plumage dataset, which may simply reflect lower statistical power caused by smaller sample size (*n* dichromatic pairs = 48). Nonetheless, the sharp contrast between monochromatic and dichromatic taxa in rates of song and plumage evolution is consistent with the suggestion of an interspecific trade off between signaling modalities (Darwin 1871; Schluter & Price 1993; Iwasa & Pomiankowski 1994; Shutler 2010). Currently, evidence for the existence of trade offs in sexually selected signals is mixed (Badyaev *et al*. 2002; Ornelas *et al*. 2009; Tobias *et al*. 2010b; Gonzalez-Voyer *et al*. 2013; Mason *et al*. 2014), but most studies have approached this question by searching for negative associations between trait elaboration in one signaling modality (e.g. long songs) and trait elaboration in another (e.g. bright plumage). My results, on the other hand, provide evidence of an alternative macroevolutionary consequence of a trade-off in sexual signaling, in which divergence rates are negatively related across species, rather than trait elaboration per se. Although it remains to be seen whether trade offs between divergence rates in alternative signaling modalities represents a general feature of sexual trait evolution in other groups, my results provide considerable support for the

idea that sexual selection—targeted at either acoustic or visual signals, but not both simultaneously—is a key determinant of phenotypic divergence in birds.

4.5.2 Alternative explanations for phenotypic evolution

Despite the overarching importance of sexual selection on overall levels of divergence in both song and plumage colouration, I found clear evidence that additional selective processes shape patterns of divergence in specific sub-components of song. The identity and direction of these effects are, to a large extent, explicable based on the nature of the song traits involved. For instance, finding that constraints on song pitch divergence vary according to habitat type supports the predictions of the acoustic adaptation hypothesis (Morton 1975), and is consistent with the view of signal pitch as a finite resource, the breadth of which is ultimately set by the acoustic properties of the environment (reviewed in Wilkins *et al*. 2013). This is in contrast to other elements of signaling traits, such as song syntax or plumage colouration, which are can seemingly diverge in an almost limitless number of ways (Weir *et al*. 2012). In closed forested habitats, the available acoustic window within which species are able to signal effectively is severely limited by insect din and rapid signal attenuation. In open habitat types, however, these restrictions on signal frequency are absent (e.g. Morton 1975; Ryan & Brenowitz 1985), meaning effective signal transmission is theoretically possible over a much wider range of frequencies. Thus, estimates of lower constraints on pitch divergence among open-habitat species as found here are compatible with this idea. Nonetheless, despite habitat-mediated variation in constraints, a previous study inferred latitudinal clines in rates of song pitch divergence irrespective of whether species occupy open or closed habitat types (Weir *et al*. 2012); however, the mechanism underlying this effect is unknown.

My results also reveal that faster rates of song pitch divergence at high latitudes can be primarily explained by latitudinal variation in the number of competing species. Specifically, I show that rapid divergence in song pitch at high latitudes can be explained by the lower density of species competing for signaling space in temperate regions than in tropical regions, providing strong support for the importance of interspecific interactions in shaping latitudinal gradients in song evolution. In a similar manner to competition over ecological resources (Slatkin 1980), competition over acoustic signal space may act to constrain song divergence if species partition out distinct regions of signal space (Nelson & Marler 1990; Seddon 2005; Luther 2009). In species rich (i.e. tropical) environments, therefore, signal divergence may be difficult as the available signaling space is comparatively small and already saturated with a large number of co-existing species, limiting the opportunity for species to diverge into unoccupied areas of acoustic space. In relatively species poor (i.e. temperate) environments, however, signal divergence may be relatively unconstrained as acoustic space rarely becomes saturated by the small number of competing species. However, the effect of competitor richness on frequency evolution was detected exclusively across open habitat pairs, whereas competitor richness had comparatively little effect on divergence rates across closed habitat species. This suggests therefore that the constraining effect of competition on levels of frequency divergence are most pronounced in habitats possessing a large acoustic window (i.e. open habitats), within which species would otherwise be able to diversify. In contrast, in habitats with a much narrower acoustic window (i.e. closed habitats), competition may have a comparatively small effect on frequency divergence that is difficult to detect using the broad approach employed here, as frequency evolution is generally highly constrained by the restrictions imposed by the width of the acoustic window.

In addition to acoustic adaptation and interspecific competition, cultural evolution also may also play a role in explaining latitudinal gradients in rates of song evolution. My analyses revealed that oscines, in which song development relies on learning from conspecific tutors (Beecher & Brenowitz 2005), have significantly higher rates of song pace divergence than suboscines, in which song transmission is primarily genetic. This result is consistent with elevated rates of song syllable divergence in oscines compared to sub-oscines (Weir & Wheatcroft 2011), and together these studies support a role for cultural song transmission as an important driver of song divergence (Lachlan & Servedio 2004). Indeed, contrasting this effect with the lack of a similar oscine/suboscine difference in rates of plumage evolution supports the idea that cultural evolution specifically—and not other more fundamental ecological or behavioural differences between oscines and suboscines—explains elevates rates of song pace evolution. Thus, the effect of cultural evolution in driving rapid divergence in oscine songs may also contribute to the pattern of latitudinal clines in phenotypic rates, as oscines dominate the avifauna at high latitudes, especially in the New World (Kennedy *et al*. 2014), whereas suboscines are largely restricted to tropical South America.

Yet, whether cultural song transmission in oscines promotes long-term evolutionary divergence in song is unclear, as song learning may act to retard divergence if individuals from divergent populations learn each other's songs upon secondary contact (Price 2008). My results suggest that this is a possibility, as pace divergence in oscines—although rapid—was subject to much higher evolutionary constraints than in suboscines. It is possible, however, that this finding may be a consequence of intraspecific variation in pace, brought about by rapid rates of cultural divergence. Indeed, a simple *post hoc* test reveals that oscine species in the dataset were characterised by much higher levels of within-species variance in pace than suboscines

(t test: $t = –4.03$, $p < 0.001$), which reduces estimates of interspecific divergence once intraspecific variation is taken into account. Either way, increased cultural evolution at high latitudes may contribute to fast temperate rates of song evolution, but whether or not this leads to long-term evolutionary divergence in song traits is unknown.

4.5.3. Caveats

These conclusions, however, depend on the extent to which the approaches used provide accurate and unbiased estimates of evolutionary rates. One potentially important issue is related to sample size. In this study, as in others (Weir & Wheatcroft 2011; Weir *et al*. 2012; Lawson & Weir 2014), most estimates of song divergence were derived from song measurements taken from a minimum of three individuals of each species. In some cases, however, the sample size for each species was much larger. As larger sample size within pairs is likely to increase the power to detect divergence—especially as divergence estimates were down-weighted when considerable intraspecific variation in song traits was present—this could upwardly bias divergence estimates in pairs possessing larger sample sizes. This issue is likely to apply more to song traits than plumage colouration, for which the sampling of individuals was more even.

In my dataset, however, post-hoc tests revealed that evidence for this effect was weak, with only one song trait exhibiting a (marginally) significant positive association between estimated divergence and the mean sample size within a pair (PC1-3: $t = 2.01$, $p = 0.046$; PC1: $t = –0.17$, $p = 0.862$; PC2: $t = 1.85$, $p = 0.065$; PC3: $t = 1.56$, $p = 0.119$). Furthermore, average pair sample size did not differ across the categories analysed (monochromatic/dichromatic: $t = 0.56$, $p = 0.576$; allopatric/sympatric: $t = –1.54$, $p = 0.124$; forest/nonforest: $t = 0.17$, $p = 0.868$; oscine/suboscine: $t = –1.33$, $p = 0.189$), suggesting that variation in sample size is unlikely to bias estimates of

evolutionary rates among categories. Sample intensity also did not covary with range-based diversity estimates ($t < 0.01$, $p = 0.858$), but there was some evidence that sample sizes were larger for high latitude pairs than low latitude pairs ($t = 2.141$, $p = 0.033$), as would be expected given the general bias towards temperate-zone research. Thus, whilst variation in sample size across latitudes may play a role, the overall weak signature for an effect on divergence estimates in my dataset suggests that sample size variation cannot fully account for the patterns I report here.

A more general issue, however, concerns the limitations of the evolutionary models used. These models rely on the accurate measurement of both trait divergence and time-since-speciation within sister pairs in order to accurately estimate evolutionary parameters relating to the way in which phenotypic traits diverge over evolutionary time. However, as with almost any biological variable, it is likely that these measurements are subject to error. In the case of the models employed here, measurement error in both trait values and species age estimates could erode the temporal signal of trait divergence, upwardly biasing parameter estimates towards fast rates combined with strong evolutionary constraints, thereby affecting model selection (Thomas *et al*. 2014). It is possible therefore that the general finding reported here and elsewhere (e.g. Weir *et al*. 2012; Lawson & Weir 2014) that OU models tend to be more heavily favoured than BM models has little to do with strong evolutionary constraints on phenotypic divergence among sister pairs, and more to do with limitations of the modeling approach exacerbated by measurement error. On the other hand, the available evidence suggests that the OU model applied to sister pairs (as opposed to whole-tree implementations) exhibits no appreciable signal of bias (Lawson & Weir 2014), suggesting that whilst more needs to be done to address these problems, the patterns reported here may be relatively robust with respect to these issues.

4.5.4. Linking sexual selection, speciation, and latitude

These issues aside, by conducting a global comparative analysis of patterns and rates of phenotypic evolution in birds, I have shown that the intensity of sexual selection increases with latitude, and that this may drive latitudinal gradients in rates of phenotypic divergence. While latitudinal differences in the signaling environment, the strength of interspecific competition and the prevalence of cultural evolution contribute to elevated rates of song (but not plumage) divergence at high latitudes, my findings support the general view that female choice and male-male competition are overall much more important determinants of phenotypic evolution in signaling traits (Darwin 1871; West-Eberhard 1983; Seddon *et al*. 2013). Thus, if the effect of sexual selection on rates of phenotypic divergence translates to the rapid build up of pre-mating isolation, as seems likely (Seddon *et al*. 2013), these results suggest a key role for sexual selection in driving rapid recent speciation at high latitudes.

CHAPTER 5

RESOLVING THE EVOLUTIONARY ORIGINS OF THE LATITUDINAL DIVERSITY GRADIENT

5.1 ABSTRACT

The extent to which spatial patterns in biodiversity are generated and maintained by evolutionary mechanisms remains contentious. Recent debate has centred on whether rates of lineage diversification increase towards the tropics or the poles, with previous studies finding evidence supporting both views. Here I argue that such results are not contradictory but may instead arise because the two most widespread analytical techniques quantify diversification in different ways. Specifically, clade-based analyses consider the total frequency of lineage splitting ('speciation volume'), whereas analyses focusing on sister species ages consider the speed at which lineages complete the speciation process ('speciation rate'). Here, I use a simple simulation model to illustrate that when both volume and rate influence total diversification, the age of sister species become largely decoupled from clade-level estimates of diversification. Applying this insight to previous findings suggests that speciation volume peaks in the tropics, accelerating the build up of tropical diversity regardless of whether speciation rate is higher towards the poles. This perspective offers a resolution to conflicting viewpoints regarding the contribution of speciation to global gradients in biodiversity.

5.2 INTRODUCTION

The latitudinal diversity gradient (LDG) of increasing species richness towards the equator is perhaps the most ubiquitous biodiversity pattern on Earth (Hillebrand 2004; Krug *et al*. 2009), yet the underlying mechanisms remain poorly understood and highly controversial despite many decades of study (Mittelbach *et al*. 2007). Most hypotheses emphasise the importance of either ecological, historical or evolutionary factors in generating the LDG (Mittelbach *et al*. 2007), with a complete explanation likely to involve elements from all three types of mechanism (Jablonski *et al*. 2006; Pyron & Wiens 2013; Rolland *et al*. 2014a). However, while support for the role of ecology and history is widespread and robust, the influence of evolutionary factors is less clear (e.g. Cardillo 1999; Cardillo *et al*. 2005; Ricklefs 2006; Weir & Wheatcroft 2011; Jetz *et al*. 2012; Soria-Carrasco & Castresana 2012; Pyron & Wiens 2013; Rolland *et al*. 2014a).

One of the key obstacles to progress in recent years is that different analytical approaches appear to produce contradictory results. Studies using clade-based techniques to estimate net diversification rates (speciation – extinction) in relation to latitude tend to conclude that speciation occurs more rapidly in the tropics (e.g. Cardillo *et al*. 2005; Ricklefs 2006; Pyron & Wiens 2013; Rolland *et al*. 2014a), providing support for the widespread view that the build up of tropical diversity is primarily driven by rapid speciation rates at low latitudes (Dobzhansky 1950; Fischer 1960; Janzen 1967; Haffer 1969; Rosenzweig 1995; Schemske 2002; Schemske *et al*. 2009). However, several studies primarily focused on the distribution of species ages along a latitudinal gradient have revealed that species tend to be younger towards the poles than at low latitudes (Weir & Schluter 2007; Jetz *et al*. 2012). Indeed, this pattern is especially pronounced in New World, where tropical regions appear to contain much

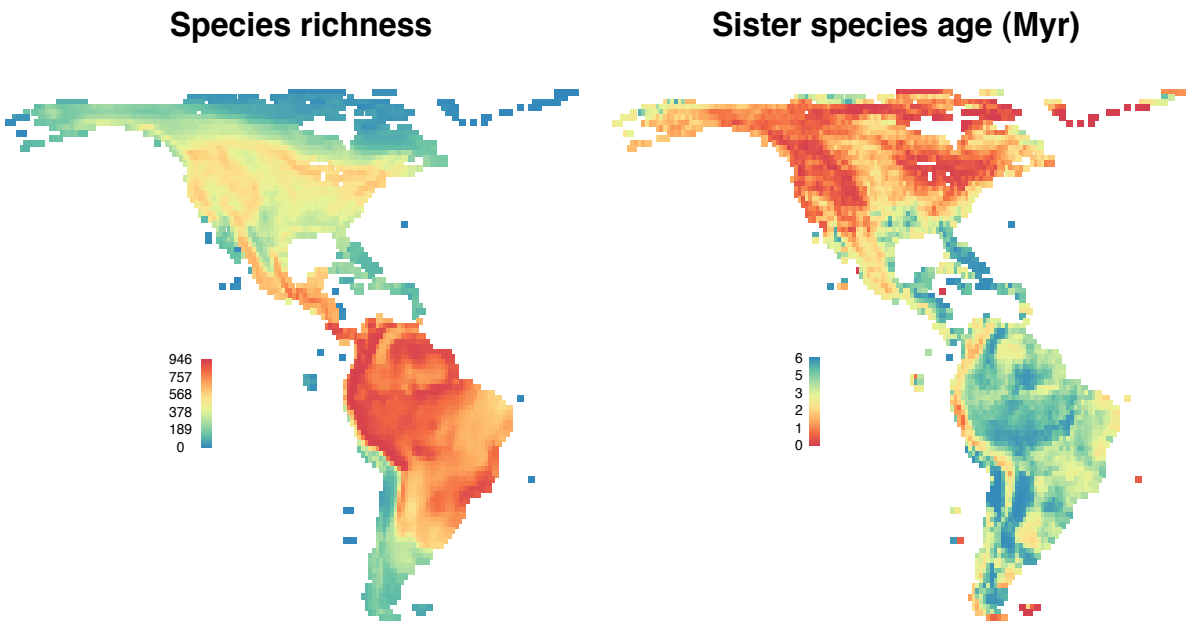

Figure 5.1. Contrasting patterns in the distribution of avian species richness and sister species ages across the New World latitudinal gradient. Mean cell sister species ages were generated from 100 randomly sampled global time-calibrated molecular phylogenies generated by Jetz *et al*. (2012).

older species than the north temperate zone (Fig. 5.1). Furthermore, when constant rate birth–death models were fitted to the age distributions of sister species of New World birds and mammals across latitudes, rates of speciation were estimated to increase rather than decrease towards the poles, leading to the contrasting conclusion that speciation rates are actually slower in tropics than in the temperate zones (Weir & Schluter 2007).

Logical explanations have been forwarded for both of these findings. Higher rates of speciation in the tropics may be explained by a range of environmentally mediated variables, such as higher solar energy driving more rapid rates of molecular evolution (Rohde 1992), greater habitat heterogeneity providing greater ecological

opportunity (MacArthur 1964) or latitudinal gradients in dispersal constraints (Jocque *et al*. 2010). Conversely, it is possible that speciation occurs more rapidly towards the poles because of vicariance events caused by ice sheets (Weir & Schluter 2004), ecological opportunity due to low species diversity (Weir & Price 2011) or faster divergence of traits involved in mate choice and species recognition (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012).

It is possible, however, that these conflicting confusions simply arise from different methodological approaches, and ambiguity about what is meant by rates of speciation. For instance, consider the shape of phylogenetic trees produced under two different scenarios. Under the first scenario (Fig. 5.2, top) diversity is accumulated through the process of sequential splitting. In this scenario, speciation events complete rapidly as indicated by short branch lengths between speciation events, but diversity may build up relatively slowly because the number of independently evolving lineages is low because ancestral species tend to produce only two daughter lineages at the point of speciation. In an alternative scenario, however, several ancestral populations are isolated more or less concurrently, giving rise to multiple independently evolving lineages connected by a polytomy (Fig. 5.2, bottom). In this case, the rate at which speciation is completed may be slow, as indicated by relatively long branch lengths subtending the species, but similar overall levels of diversity accumulate by way of the large number of independent lineages produced at any given speciation event. Thus, in these two scenarios, diversity accrues primarily through distinct mechanisms. In the first, diversity accumulates primarily because speciation is completed relatively rapidly, whereas in the second, diversity accumulates even though rate of speciation completion is slow because concurrent lineage splitting commonly occurs.

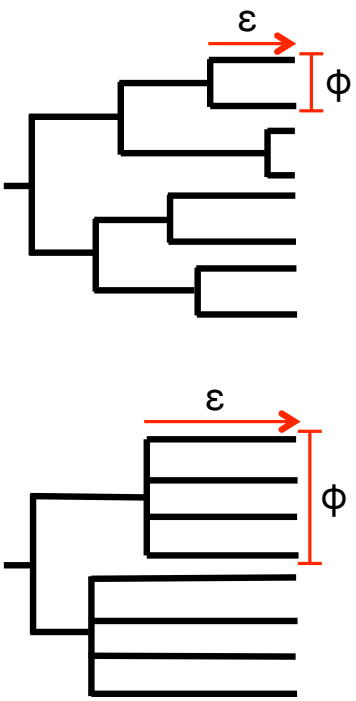

Figure 5.2. Hypothetical phylogenetic trees illustrating the difference between rate of speciation (ε) and speciation volume (ϕ). In the first (top) lineages complete the speciation process rapidly but the volume of lineages produced is low. In the second, however, lineages complete the speciation process slowly, but a large number of lineages are produced at any given speciation event.

The former scenario—fast rates of completion but low volume of speciation—could reflect the situation in the temperate regions, where speciation often involves the isolation of a large-ranged dispersive species into two daughter species separated by ice sheets (Weir & Schluter 2004), followed by rapid ecological and phenotypic divergence (Weir & Price 2011; Weir & Wheatcroft 2011). In contrast, the latter scenario may occur more frequently in the tropics, where a higher volume of polytomous speciation could occur under certain conditions due to the predominance of low dispersal species

and complex vicariance events (Tobias *et al*. 2008; Burney & Brumfield 2009; Salisbury *et al*. 2012), but the rate at which reproductive isolation evolves may be slow because of less ecological opportunity or greater constraints on sexual signal divergence (Weir *et al*. 2012). Thus, whilst polytomous speciation is unlikely to represent a general process, it may be relevant under certain conditions (e.g. during refugia formation or sea-level change), and therefore the distinction between speciation rate and the volume of lineage splitting events—and how these two mechanisms of speciation vary deterministically with latitude—could have important implications for resolving the apparent inconsistencies emerging from empirical studies focused on distinct components of phylogenetic information, as well as our general understanding of the processes underlying the LDG.

Here, I explore these issues in two ways. First, I use a simple model of phylogenetic tree growth, which incorporates both concurrent lineage splitting and variable waiting times to speciation completion, to illustrate that each mechanism leaves a distinct signature in the shape of phylogenetic trees. Moreover, I use this model to show that variation in the frequency of concurrent speciation events can lead to a breakdown between the average age of sister species and overall levels of clade diversification. With these insights in mind, I then go on to discuss the evidence supporting the existence of latitudinal differences in the tempo and mode of speciation, and the potential for these processes to resolve conflicting viewpoints regarding the contribution of speciation to the LDG.

5.3 METHODS

5.3.1 Model outline

To illustrate the effects of variation in speciation rate and speciation volume on the shape of phylogenetic trees, I constructed a simple simulation model based on the widely-used stochastic pure birth model of tree growth (Yule 1925). As the primary goal of this work was to generate a model for purely illustrative purposes, the decision to build on a pure birth rather than birth-death model of tree growth (Kendall 1948; Nee *et al*. 1992) was taken to maximise clarity. Nonetheless, it does mean that my simulations ignore the effect of extinction on tree shape, the implications of which I discuss fully below (see *Discussion*). In a standard pure birth model, every lineage has an equal probability of undergoing a speciation event at a per-lineage rate of λ. Here I refer to λ as the rate at which speciation events are initiated (i.e. the rate of speciation initiation; Etienne & Rosindell 2012). In addition to this, my model adds two parameters that distinguish it from a simple pure birth process. First, rather than assuming speciation events simply involve individual lineages splitting into two daughter lineages (i.e. bifurcating), here I allow multifurcation events where a random number of additional lineages is drawn from a Poisson distribution with mean ϕ. For instance, if the number of additional lineages drawn is one, the speciation event becomes a trifurcation, whereas if no additional lineages are added then the speciation event remains a standard bifurcation.

Second, unlike standard pure birth and birth-death models in which speciation occurs instantaneously and all lineages (including those that have recently divided) have equal probability of speciating at any given time, here I follow previous modeling

approaches (Etienne & Rosindell 2012) and assume that speciation takes time to be completed. The rate at which lineages complete the speciation processes after being initially split is determined by the parameter ε, which controls the length of time lineages are treated as "incipient species" before being recognised as "good species" (Etienne & Rosindell 2012). Under this model, the time needed to complete speciation is therefore exponentially distributed with a mean of 1/ε. This approach is similar to the protracted model of speciation outlined by Etienne and Rosindell (2012) except that here I effectively do not allow incipient species to speciate again before becoming good species (the probability that an incipient lineage divides again before becoming a good species is fixed to a low value equal to 1% of the speciation initiation rate λ). This decision has the benefit of reducing the number of free parameters, but was primarily taken to reflect the fact that incipient lineages are unlikely to speciate soon after becoming isolated, as they are often geographically restricted (Pigot *et al*. 2010b) and face competition from closely related lineages that are ecologically similar (Pigot & Tobias 2013).

5.3.2 Simulations

I used the multifurcation model to simulate trees under a variety of conditions. Each simulation was initiated with two lineages at time $T = 0$. For each lineage present in a simulation, the waiting time to a speciation initiation event was sampled from an exponential distribution with rate λ for good species and rate (λ*0.01) for incipient species. To decide which event occurred (i.e. initiation of a speciation event involving a good species or an incipient species), I applied Gillespie's (1976) algorithm and selected the event with the shortest waiting time. When a speciation initiation event

occurred, I assumed that at least two daughter lineages were produced, but also sampled a random number of additional lineages from a Poisson distribution with mean ϕ. For instance, if the number of additional lineages drawn was one, the speciation involved a trifurcation, whereas if no additional lineages were added then the speciation event remained a standard bifurcation. Initially, new lineages formed at time T_1 are treated as incipient species until they complete the speciation process and transition into good species at time T_2. The waiting time from time T_1 to time T_2 was sampled from an exponential distribution with rate ε; for simplicity, I gave all incipient species arising from a single speciation initiation event the same waiting time to completion. All simulations were run for a length of 10 time units (i.e. until $T = 10$).

To explore the impact of speciation rate and speciation volume on phylogenetic tree shape, I used the multifurcation model to simulate trees under a range of parameter combinations. For speciation volume, I explored 21 values of ϕ ranging from 0 to 2 in increments of 0.1. This range covered situations where lineages where only able to bifurcate ($\phi = 0$) to a scenario where the mean number of incipient lineages produced was four ($\phi = 2$). For rate of speciation, I also explored 21 values of ε ranging from 0.2 to 10, equivalent to mean per-lineage waiting times to speciation completion of 5, 4.75, 4.5…0.5, 0.25, 0.1 time units. In all simulations, the rate of speciation initiation was λ set equal to 0.2.

For each of the 441 combinations of parameter values, I performed 1000 simulations, recording the resulting phylogenetic tree in each case. At the end of many simulations, trees often contained a mix of good and incipient species. This is because at the end of a simulation (i.e. "the present"), some lineages have completed the speciation process (good species) whereas for incipient species, the point at which they would have completed the speciation process occurs at some point after the simulation

ended (i.e. "the future"). This is analogous to the situation found in nature where lineages currently recognised as species may be undergoing speciation events, or contain intraspecific lineages, that have not yet been recognised as species-level units by taxonomists (Weir & Schluter 2007; Purvis *et al*. 2009). At the end of a simulation, I therefore collapsed all terminal branches leading to incipient lineages into a single branch representing a good species, to reflect the fact that taxonomists may miss incipient or recently isolated lineages. By "pruning back" intraspecific lineages in this way, inferences made using simulated trees are more directly comparable to the patterns we would observe amongst empirical phylogenies (Weir & Schluter 2007). Thus, from each of the pruned phylogenetic trees, I noted the observed number of species and the ages of all sister species pairs present in the tree. Speciation events involving multifurcation events were randomly resolved prior to recording sister species ages. All simulations were performed in R v.3.0.2, using code customised from functions provided in the package *geiger* (Harmon *et al*. 2008).

5.4 RESULTS

I used the multifurcation model to explore the effect of speciation rate and speciation volume on patterns emerging from phylogenetic trees. Fig. 5.3 illustrates the distinct patterns typically found in simulations performed under contrasting parameter combinations. For instance, under a scenario of low speciation volume but fast speciation rate ($\varepsilon = 10$, $\phi = 0$; Fig. 5.3a), speciation involves bifurcation events and diversity builds up steadily as a result of small internode intervals (Fig. 5.3c). In contrast, under a different scenario of high speciation volume but slow speciation rate ($\varepsilon = 0.1$, $\phi = 2$; Fig. 5.3b), diversity predominately accumulates through the concurrent formation of multiple independent lineages followed by relatively long periods of stasis before being split again (Fig. 5.3c). However, the sister species age distribution curves (Fig. 5.3d) resulting from each tree illustrate that it is possible for similar or even greater levels of diversity to accumulate under the slow rate/high volume scenario, despite the fact that sister species pairs appear older than those produced under the fast rate/low volume scenario.

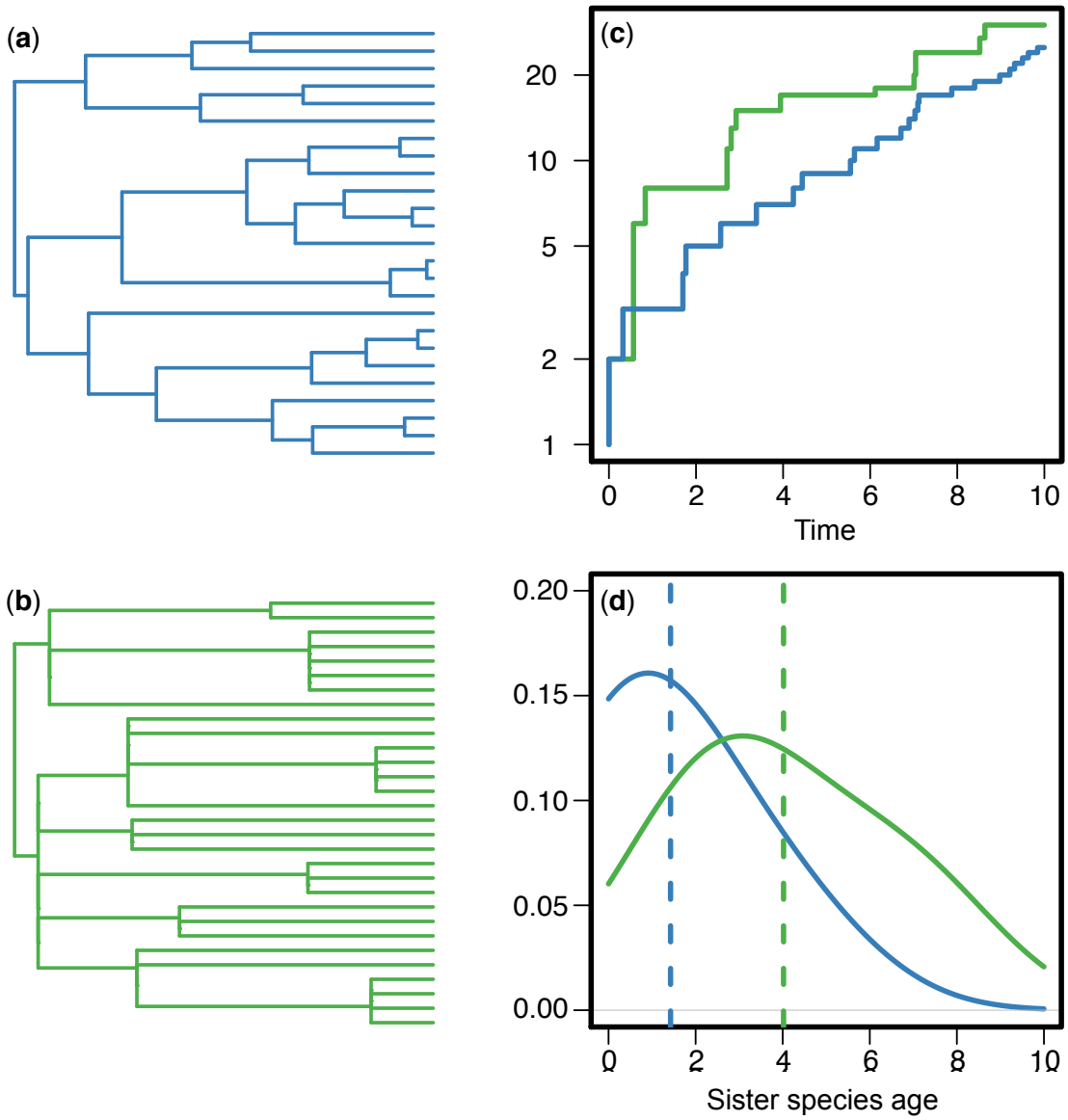

Figure 5.3. Representative phylogenetic trees simulated under contrasting parameters of speciation rate (ε) and volume (ϕ). The tree shown in (a) was produced under a scenario of fast completion rate and low volume ($\varepsilon = 10, \phi = 0$), whereas (b) was simulated under a scenario of slow rate and high volume ($\varepsilon = 0.1, \phi = 2$). The resulting lineages-through-time plots (c) and sister species age distribution curves (d) are also shown.

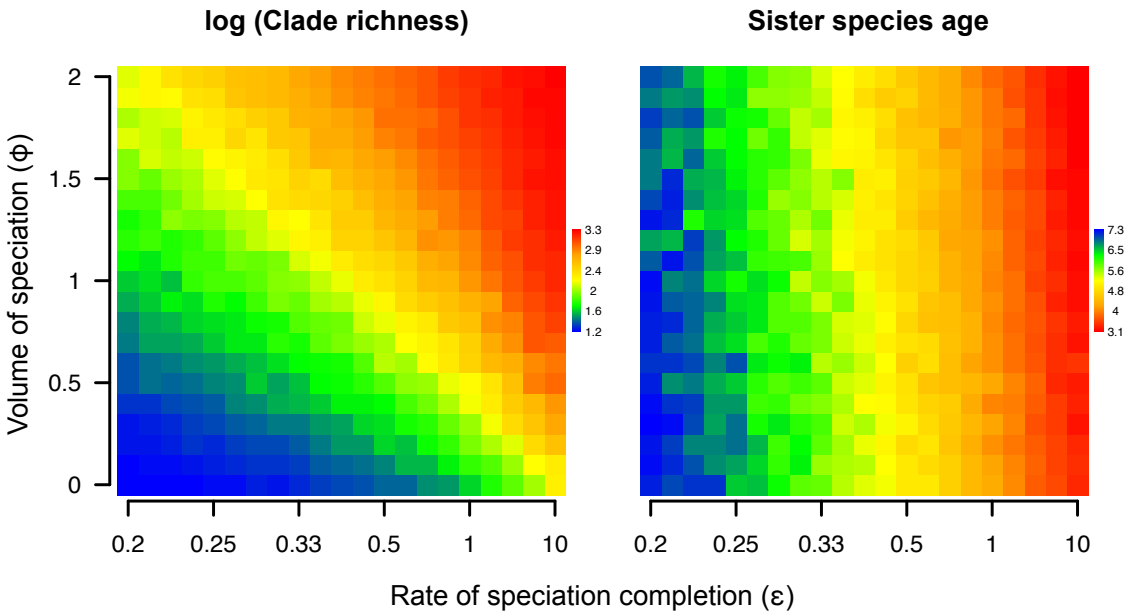

Figure 5.4. The effect of speciation rate (ε) and volume of speciation (ϕ) on (a) ln-transformed clade richness and (b) sister species age. Colours corresponded to mean values calculated from 1000 phylogenetic trees simulated under each parameter combination. These plots show that whereas clade richness is independently influenced by speciation rate and volume, sister species age largely varies as a function of the speciation rate alone.

Exploring these patterns over a wide area of parameter space using a large number of simulated trees revealed the extent to which speciation rate and volume impact phylogenetic patterns of diversification (Fig. 5.4). The model demonstrated that both speciation rate and speciation volume both independently influence clade diversity: intuitively, clades become increasingly diverse if many lineages are produced at a single speciation event or if lineages complete the speciation process rapidly, and especially diverse if speciation involves both fast rates of completion and high volume of lineages

(Fig. 5.4a). In contrast, Fig. 5.4b shows that the mean age of sister species extracted from simulated phylogenetic trees primarily varies as a function of speciation rate, but not variation in the volume of lineages produced at speciation events.

Viewed another way, as in Fig. 5.5, the effect of frequent multifurcations is clear. For a given multifurcation probability (e.g. $\phi = 0$), the average age of sister species correlates strongly with the overall diversity of a clade, which both vary as a result of the rate of speciation (ε). However, if the propensity to multifurcate differs across clades, then similar levels of diversity may be associated with young and old species ages (Fig. 5.5, dashed lines), even when rates of speciation are faster in bifurcating lineages ($\phi = 0$) than in mulitfurcating lineages ($\phi = 2$). Moreover, Fig. 5.5 also illustrates that, over the range of parameter values examined, speciation volume appears to exert a greater influence over the accumulation of diversity than does the rate of speciation. Evidence for this comes from the fact that modest increases in the mean number of lineages produced during speciation (i.e. $\phi = 1$ vs. $\phi = 0$) produces similar levels of diversity even if speciation rate is ~50 times slower (Fig. 5.5; blue squares vs. red circles). Overall, these results indicate that species ages may provide a relatively poor index of overall clade diversification if the propensity for multiple lineage splitting varies across clades.

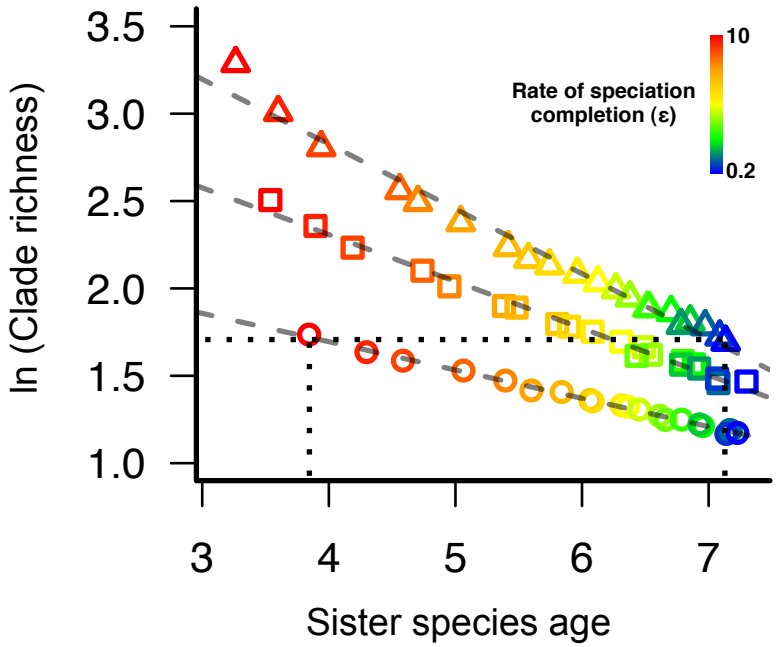

Figure 5.5. The relationships between sister species age and ln-transformed clade richness under varying speciation rates (colours) and volumes (shapes). Plotted points are mean values calculated from 1000 phylogenetic trees simulated under each parameter combination. The plot illustrates that sister species ages may provide a relatively poor index of overall diversification if the volume of speciation differs across regions: both young and old species ages may be associated with similar levels of diversification (dashed lines) depending on whether multifurcations are common ($\phi = 2$; triangles) or if species tend to bifurcate ($\phi = 0$; circles).

5.5 DISCUSSION

My simulations illustrate that when the propensity for concurrent lineage splitting varies across clades, the average age of sister species sampled from phylogenetic trees can be largely uninformative of clade diversification. Specifically, I show that whilst both speciation rate and speciation volume contribute to the number of lineages in a clade, the ages of sister species almost exclusively reflect the rate of speciation completion, and not the extent to which diversity is added through the appearance of multiple independent lineages. Thus, my simulations help to illustrate the point that although sister species analyses may indicate that speciation appears to be faster in the temperate regions, greater overall diversity may be achieved in the tropics because of the contribution of multiple-splitting events. However, the extent to which this represents a viable explanation for the conflicting results emerging from clade and tip-based approaches to the LDG relies on the fact that speciation mechanisms vary deterministically across latitudes.

In support of this idea, fundamental differences between tropical and temperate taxa suggest that the potential for concurrent lineage splitting is far greater at low latitudes. Under relatively stable conditions, many tropical species have evolved to become highly sedentary (Levey & Stiles 1992; Stratford & Robinson 2005; Moore *et al*. 2008) and it has long been appreciated that dispersal limitation is a strong promoter of population sub-division (e.g. Wright 1940). Thus, it is likely that the low vagility of many low-latitude lineages explains in part why tropical species tend to exhibit increased levels of genetic structuring and intraspecific differentiation compared to temperate species (Martin & McKay 2004; Phillimore *et al*. 2007; Martin & Tewksbury 2008; Tobias *et al*. 2008). Indeed, support for the idea that greater dispersal constraints

in the tropics act to isolate considerable numbers of intraspecific lineages is bolstered by the fact that taxa occupying common low-dispersal tropical niches (e.g. forest understory specialists) tend to have higher levels of intraspecific genetic divergence and contain greater numbers of species (Burney & Brumfield 2009; Claramunt *et al*. 2011; Ikeda *et al*. 2012; Salisbury *et al*. 2012). Thus, it seems clear that high dispersal limitation, combined with an abundance of persistent geographic barriers (Rosenzweig 1995), should increase the likelihood that tropical speciation events often involve complex multiple splitting events, whereby several intraspecific lineages become isolated more or less simultaneously and then slowly diverge in parallel (Tobias *et al*. 2008; Salisbury *et al*. 2012).

In contrast, temperate species are much less likely to be dispersal limited due to the impact of climatic fluctuations increasing selection for vagility at high latitudes (Dynesius & Jansson 2000; Jocque *et al*. 2010). Indeed, complex parallel splitting may be relatively rare within temperate species, as volatile range dynamics and high levels of gene flow between populations reduce the likelihood that populations remain isolated for long enough for reproductive barriers to evolve (Dynesius & Jansson 2000). Thus, if temperate species are not dispersal limited, biogeographic barriers may often provide weak barriers to gene flow at high latitudes, heavily reducing the likelihood of parallel population splitting often observed in tropical lineages (Tobias *et al*. 2008). In fact, population isolation amongst highly dispersive temperate species may often require the intervention of large-scale geographic barriers such as ice sheets (Weir & Schluter 2004), which tend to bifurcate lineages rather than isolating multiple intraspecific populations.

In contrast to the frequency of lineage splitting, it is apparent that isolated lineages often complete the speciation process most rapidly at temperate rather than

tropical latitudes. A number of studies indicate that signaling traits involved in species recognition diverge fastest among high latitude species than low latitude species (Martin *et al*. 2010; Weir & Wheatcroft 2011; Weir *et al*. 2012), possibly driven by more intense sexual selection at high latitudes (Irwin 2000; Botero *et al*. 2009). Moreover, because temperate habitats are comparatively species poor, the potential for rapid ecological divergence is also theoretically greater at high latitudes owing to a larger amount of unoccupied niche space (Weir & Price 2011). This is contrast to highly diverse tropical regions in which phenotypic divergence between incipient species is likely to be limited by strong interspecifc competition (Weir & Price 2011; Weir *et al*. 2012). The net result of such latitudinal gradients in rates of phenotypic divergence is that by becoming reproductively and ecologically divergent, isolated lineages at temperate latitudes may rapidly progress through the speciation cycle, quickly expanding their ranges following speciation and increasing the probability of further speciation (Weir & Price 2011). In contrast, isolated tropical lineages are likely to complete the speciation cycle at a much slower rate if reproductive and ecological divergence is difficult in the face of strong interspecific competition (Pigot & Tobias 2013). Thus, overall it seems clear that high volumes of lineage splitting accompanied by slow rates of phenotypic divergence in tropical systems, combined with rapid but infrequent speciation events in the temperate zone, offers a plausible explanation for the conspicuous mismatch in sister species ages versus species richness.

Furthermore, it is unlikely that gradients in extinction would reduce the importance of these mechanisms. To maximise clarity my simulations were built around a pure birth model of species diversification, rather than a birth-death model incorporating lineage extinction (Kendall 1948; Nee *et al*. 1992). However, if extinction had been included, such that extinction occurred at a standard rate across all scenarios,

then this would have little impact on the observed breakdown between sister species age and clade diversification, as its impact would be to simply reduce the average age of sister species and total richness similarly across all scenarios. Furthermore, even if extinction were to occur disproportionately frequently within 'high latitude' scenarios (Darwin 1859; Wallace 1878; Weir & Schluter 2007), a bias towards increased extinction in these simulations would simply serve to lower the average sister species age by tending to removing older sisters (Weir & Schluter 2007), whilst also reducing the overall diversity of clades produced under this scenario. Thus, if an extinction gradient does exist across latitudes, it is likely to accentuate—rather than diminish—the patterns I illustrate here.

A compelling alternative explanation for the pattern of older species ages in tropical regions, however, is that tropical environments are older and closer to their species carrying capacity than relatively young temperate regions (Weir & Schluter 2007; Weir & Price 2011). Within this explanation, older species ages in the tropics are the product of density-dependent speciation rates that have slowed over time as tropical diversity has accumulated and approached saturation point (Weir & Schluter 2007). In the younger, less diverse temperate regions, however, density-dependent effects on speciation rates are believed to be less severe, meaning that young species ages at high latitudes are a signal that current rates of speciation are faster in the temperate regions than in the tropics (Weir & Schluter 2007). This is in contrast to the explanation put forward here, which ignores density-dependent effects on diversification rates, and instead argues that overall rates of speciation in the tropics remain high due to the greater prevalence of parallel lineage splitting, but that older tropical species are a signal of longer waiting time to speciation completion.

Unambiguous evidence for the idea that tropical clades are closer to saturation than temperate clades is currently weak (see Pyron & Wiens 2013), but if diversity dependence was incorporated into the framework described here, its effects would most likely depend on the relative extent to which extant diversity depresses speciation rate, speciation volume, or both. For instance, if the presence of competitors constrains only speciation rate (i.e. the rate at which lineages complete the speciation cycle and are thus able to speciate again), but has little impact on the extent to which lineages tend to be split multiply, then the addition of diversity dependence within 'tropical' scenarios may have little impact on the patterns illustrated, as the tropic clades may still attain higher diversity than temperate clades as the contribution of high speciation volume to total diversification tended to outweigh negative effects of slower rates of speciation completion (Fig. 5.5). However, until more is known regarding the precise population-level processes responsible for generating macroevolutionary patterns consistent with diversity dependence, it remains unclear precisely how diversity dependent effects would alter the patterns described here.

Irrespective of how concurrent lineage splitting and diversity-dependent diversification interact, distinguishing between these competing hypotheses using empirical phylogenies however is likely to prove difficult. This is because both explanations make similar predictions about the shape of phylogenetic trees derived from different latitudes. In particular, both models predict that tropical clades should show evidence of stronger slowdowns in lineage accumulation towards the present than temperate clades. In the case of the model presented here, strong slowdowns in rates of lineage accumulation towards the present occur under "tropical" scenarios primarily as a result of long waiting times to speciation completion coupled with high speciation volume (e.g. Fig. 5.3b, c), as many lineages in the recent past have not yet completed

the speciation process, or speciated again following recent completion (Etienne & Rosindell 2012). One distinguishing feature of my model, however, is the existence of lineage-specific "bursts" of speciation corresponding to multiple-splitting events, which leave a characteristic sharp upturn in LTT plots (e.g. Fig. 5.3c; green curve). Yet, although analytical approaches capable of detecting significant clustering of speciation events within a single lineage do exist (Ford *et al*. 2009), the ability to detect multiple simultaneous splitting events in phylogenies may be hampered by a more general issue of how polytomous nodes (i.e. nodes involving multifurcations rather than bifurcations) are handled in phylogenetic analyses. Often, if polytomies are recovered in phylogenetic analyses, they are considered to represent a lack of phylogenetic resolution (i.e. 'soft' polytomies) rather than a signal of parallel splitting events (i.e. 'hard' polytomies). Moreover, the likelihood of inferring polytomous nodes where they do exist is potentially low, given that most current phylogenetic analysis tools (e.g. BEAST; Drummond & Rambaut 2007) employ pure birth or birth-death priors on branch lengths, which bias against the inference of multiple simultaneous splitting events at the tree construction stage. Thus, although there is strong evidence to predict that the prevalence of multiple splitting events should be greater in tropical systems than in temperate systems, whether the phylogenetic information currently available is appropriate to assess this possibility remains unclear.

In summary, the idea that mechanisms of speciation might differ with latitude has received relatively limited attention in the recent past (Mittelbach *et al*. 2007), but there is increasing evidence that underlying latitudinal gradients in climate and ecology might generate differences in the speciation process between tropical and temperate systems (Kozak & Wiens 2007; Cadena *et al*. 2012; Salisbury *et al*. 2012). Here I argue that a tropical bias towards a propensity for lineages to experience concurrent splitting

events offers a potential explanation as to why clade-based approaches (e.g. Cardillo *et al*. 2005; Ricklefs 2006) and sister species approaches (e.g. Weir & Schluter 2007) to the LDG have come to different conclusions about the rate at which species are produced in tropical and temperate regions. Whether these patterns are currently detectable in empirical phylogenies remains to been, but my results suggest that exploring the impact of variation in tempo and mode of speciation, and relating this to latitude provides a potentially fruitful approach to understanding the evolutionary dynamics shaping the latitudinal gradient in species richness.

CHAPTER 6

GENERAL DISCUSSION

6.1 THE ROLE OF ABIOTIC AND BIOTIC DRIVERS OF AVIAN DIVERSIFICATION

A central goal of evolutionary biology is to explain how and why species diversify (Butlin *et al*. 2012). While the diverse mechanisms that generate and maintain diversity have been grouped in many ways, a fundamental distinction exists between abiotic and biotic drivers (Benton 2009; Ezard *et al*. 2011). In this thesis I examined the extent to which these factors, and the interplay between them, can explain variation in species diversity in birds among lineages and regions. In the General Introduction (Chapter 1) I identified four key unresolved questions. First, how does climatic niche evolvability influence species diversification? Second, does sexual selection drive speciation and species coexistence? Third, what explains latitudinal gradients in rates of phenotypic divergence? And finally, is it possible to resolve the controversy over whether speciation rates are faster in the tropics or the temperate zone? Here, I summarise and discuss the main findings relating to each question and suggest directions for future research.

6.2 CLIMATIC NICHE EVOLUTION AND SPECIES DIVERSIFICATION

In Chapter 2, I tested the hypothesis that the rate at which species' climatic niches evolve has important implications for lineage diversification. In support of a key prediction of this hypothesis, I showed that avian genera with more labile climatic niches are, on average, more diverse than those exhibiting slower rates of niche evolution. However, no such pattern was found at the level of family. An important implication of the results for genera is that evolutionary lability in abiotic tolerances appears to be an important determinant of speciation in the early stages of lineage diversification. I also found that the positive effect of climatic niche evolution on diversification was consistent across clades despite profound differences in latitudinal distributions and ecological traits. However, whether this pattern may be largely explained by methodological issues remains to be seen, and disentangling signal from bias may require a detailed assessment of the null relationship between clade richness and estimates of evolutionary rate using simulation approaches. These issues aside, the overall implication of my results is that divergence into novel abiotic conditions may represent a general feature of divergence in radiating clades. The role of evolvability of biotic factors such as species' ecology (Rabosky & Adams 2012; Rabosky *et al*. 2013) or mating signals (Chapters 3 and 4) in driving species diversification is well established. The results of Chapter 2 suggest that evolvability in terms of extrinsic abiotic conditions can also play an important role in driving diversification, in addition to that of intrinsic biotic components.

The finding that rates of climatic niche evolution had no effect on diversification across avian families implies that climatic niche evolvability is of limited importance in explaining variation in diversification over larger spatial and temporal scales. Instead,

my results suggested that climatic niche evolution is more bounded across family-level clades, such that the diversifying influence of climatic lability is reduced when lineages have expanded to fill all climatic niche space. Viewed in this way, the effect of climatic niche lability on diversification over broader phylogenetic scales may be highly contingent on the historical and geographical opportunities for radiations to continually access novel areas of niche space. If such unoccupied regions are not available, then the continued accumulation of species diversity may more strongly depend on the rate at which related species are able to co-exist (Chapter 3) in areas of niche space already exploited by other members of the clade.

6.3 SEXUAL SELECTION AND THE CYCLE OF SPECIATION

In Chapter 3, I demonstrated that sexual selection plays a key role in driving speciation rates and shaping patterns of co-existence in birds. Using a well-supported proxy for the intensity of sexual selection—that is, sexual dichromatism—I showed that species experiencing high levels of sexual selection are typically younger than those experiencing lower levels of sexual selection. This pattern was best explained by the existence of faster rates of speciation in highly dichromatic species, a result that on its own provides strong support for the longstanding yet contentious view that sexual selection represents a powerful agent of diversification (Darwin 1871; Lande 1981; West-Eberhard 1983; Iwasa & Pomiankowski 1995; Price 1998; Panhuis *et al*. 2001; Ritchie 2007; Kraaijeveld *et al*. 2011).

However, in Chapter 3 I also demonstrated that highly sexually selected sister species are able to achieve co-existence more rapidly following speciation in allopatry. This finding is important because it suggests that sexual selection plays a hitherto

underappreciated role in driving diversification by accelerating the rate at which species are able to overcome barriers to range expansion imposed by the presence of closely related species. Range expansions are critical to repeated rounds of diversification (Rosenzweig 1995; Pigot *et al*. 2010b), and it is becoming increasingly recognised that, along with dispersal ability and the permeability of geographic barriers, competition from recently diverged taxa may impose strong limits on the likelihood of post-speciational range expansion (e.g. Weir & Price 2011). The idea that biotic interactions can limit geographic range expansion and species co-existence is well established (MacArthur 1972; Diamond 1975), but most studies have searched for evidence that this effect is mediated by competition over shared ecological resources (Pigot & Tobias 2013; Price *et al*. 2014). My findings, however, support the alternative idea that interspecific competition over sexual resources represents a key biotic barrier to range expansion (Gröning & Hochkirch 2008), and add weight to the emerging view that co-existence may strongly depend on the development of reproductive isolation between lineages, rather than ecological differentiation (van Doorn *et al*. 2009; M'Gonigle *et al*. 2012).

Previous comparative studies have failed to establish a consistent link between sexual selection and speciation (Kraaijeveld *et al*. 2011). A crucial element of the work presented in Chapter 3 therefore was to show that by fitting species-level diversification models that incorporate trait evolution, it is possible to demonstrate a strong association between sexual selection and elevated rates of net diversification across the entire avian tree of life, once the fluctuating history of sexual selection over time is taken into account. While more needs to be done to assess the relative contributions of speciation and extinction in driving this pattern, this finding offers a powerful explanation for the seemingly inconsistent results of previous studies assessing the impact of sexual

selection on diversification, as it illustrates how traits that affect rates of species diversification may go undetected when such traits themselves undergo frequent transitions between states (Goldberg *et al*. 2010). As sexual trait evolution generally outpaces ecological divergence (e.g. Arnegard *et al*. 2010; Seddon *et al*. 2013), the difficultly of detecting the diversifying effect of rapidly evolving traits may also explain why ecological factors are commonly found to be better predictors of diversification patterns across higher taxa than indices of sexual selection (e.g. Isaac *et al*. 2005; Phillimore *et al*. 2006). It is therefore possible that the general importance of sexual selection relative to ecological factors in explaining patterns species diversification may prove to be much greater than current evidence suggests.

6.4 LATITUDE, SEXUAL SELECTION AND RATES OF PHENOTYPIC EVOLUTION

While my work suggests that sexual selection can play a major role in driving speciation and species co-existence, the importance of sexual selection on these processes is assumed to derive from its ability to accelerate rates of mating signal evolution. However, the basic assumption that stronger sexual selection should be associated with more rapid phenotypic divergence is rarely directly tested (Seddon *et al*. 2013). In Chapter 4, I found evidence to suggest that latitudinal clines in rates of mating signal evolution are best explained by elevated levels of sexual selection at high latitudes. Given that divergence in such traits is important for the development of reproductive isolation, these findings supports the longstanding view that sexual selection is a powerful engine of diversification. Provided these conclusions are robust to issues related to variation in sample size and measurement error, they suggest that

latitudinal differences in the intensity of sexual selection may have a central role in explaining the finding that rates of recent speciation are fastest at high, not low, latitudes (Weir & Schluter 2007; Chapter 5). However, a latitudinal cline in the intensity of sexual selection is ultimately caused by increases in seasonality and climatic harshness at high latitudes (Irwin 2000; Botero *et al*. 2009; Botero *et al*. 2014). Taken together, my findings demonstrate the importance of the interplay between biotic and abiotic factors in explaining broad-scale patterns in species diversification.

Also in Chapter 4, I uncover evidence of a macroevolutionary trade off between signaling modalities. Theoretical support for the idea that sexual selection should favour the use of only a single sexual trait rather than multiple traits is strong (Darwin 1871; Schluter & Price 1993; Iwasa & Pomiankowski 1994; Shutler 2010), and most studies seek to test these ideas by searching for negative correlations between indices of trait elaboration in alternative signaling modalities. However, as sexual selection appears to accelerate the evolution of traits in one signaling modality or another—but not both simultaneously—one important insight emerging from my work is that a trade-off in sexual signaling may also influence the rates at which traits in alternative signaling modalities diverge. Trade-offs between rates of divergence in one signaling modality (e.g. song) versus another (e.g. plumage) have important implications for understanding the impact of sexual selection on diversification. In particular, studies focusing on the effects of sexual selection on only one element of sexual signaling (i.e. plumage dichromatism) may underestimate the effect of sexual selection on speciation if reproductive isolation is also being triggered by sexually-selected trait evolution in other signaling modalities. Given that most analyses quantify the intensity of sexual selection using information from a single signaling modality (e.g. Chapter 3), the

implication is that the effect of sexual selection on diversification may frequently be stronger than most existing studies imply.

6.5 LATITUDINAL VARIATION IN THE TEMPO AND MODE OF SPECIATION

Higher rates of sexual signal divergence at high latitudes (Chapter 4) suggest that speciation rate increases towards the poles. This view is contentious given the abundance of theoretical and empirical evidence arguing that the build up of tropical diversity is primarily driven by rapid speciation rates at low latitudes (reviewed in Mittelbach *et al*. 2007). In Chapter 5, I used a simple model of cladogenesis to illustrate that such perspectives need not be contradictory and can instead arise through contrasting mechanisms. In particular, I emphasised the distinction between the frequency with which speciation events are initiated (speciation volume) and the rate at which such lineages subsequently progress through the speciation cycle (speciation rate), arguing that multiple biotic and abiotic factors co-vary with latitude to mean that speciation volume peaks in the tropics, accelerating the build up of tropical diversity regardless of whether speciation rate is faster towards the poles. Although polytomous speciation is unlikely to represent a general process, it remains to been seen whether evidence of these processes can be detected from empirical phylogenies or elsewhere. At the very least, these ideas offer fresh perspective on how speciation mechanisms could vary with latitude, and may ultimately provide insight into the processes underlying the accumulation of diversity in both tropical and temperate systems.

More generally, acknowledging the pivotal distinction between speciation rate and volume may provide a useful framework within which to study diversification patterns in other groups and systems. For instance, when attempting to infer trait-

dependent diversification, it may be advantageous to predict *a priori* whether a given trait influences speciation rate, speciation volume, or both, as the phylogenetic signature—and the most appropriate method to detect such a signature—is likely to vary as a result. It is therefore possible that the implications of the fundamental distinction between speciation rate and volume may extend beyond the study of diversification patterns in a latitudinal context.

6.6 FUTURE DIRECTIONS

My research has lead to several advances in our understanding of the causes of species diversification in birds, and there are clear avenues for further research that I am keen to explore further. In particular, my work suggests that sexual selection plays a major role in shaping diversification patterns through its effects on rates of speciation and species co-existence. However, the precise mechanisms underpinning these relationships remain unclear. Given that my work also supports the suggestion that sexual selection can drive rapid divergence in traits important for reproductive isolation, progress in this area is likely to require a deeper understanding of the role of mating signal evolution in the origin and maintenance of diversity.

In particular, the mode and tempo of mating signal evolution is rarely directly quantified, especially across large radiations, and how such variation in evolutionary rates links to the origination and persistence of new species is poorly understood. An important next step would therefore be to more broadly assess the abiotic and biotic factors driving mating signal evolution among species, before directly testing the link between rates of mating signal evolution and speciation rates. Moreover, the importance of mating signal evolution for the build up of sympatric diversity over longer time-

scales remains an open question, and further work is required to assess the importance of reproductive isolation alone for stable species co-existence and continued species diversification.

Moreover, the relationship between mating signal evolution and ecological trait evolution and the relative importance of each for the origin and maintenance of diversity is largely unknown. For instance, the relative frequency with which speciation events and species co-existence involve divergence in ecological traits, signalling traits, neither, or both, is largely unknown, but is critical to our understanding of the processes responsible for generating and maintaining diversity. Theory predicts that diversification rates should be most rapid when species diverge along both ecological and signalling trait axes, but there are also strong reasons to expect that evolutionary rates may be traded off against one another, especially if intense sexual selection constrains ecological adaptation. Existing work has focused on the importance of ecological factors, but my work suggests the importance of signal divergence may have been overlooked. Thus, a clear avenue for further work would be to assess the extent to which speciation events involve the divergence of mating signals and ecological traits, examine the relationship between rates of mating signal evolution and ecological trait evolution, and assess their relative importance in determining rates of speciation/extinction, and the build up of local diversity.

6.7 CONCLUSIONS

In this thesis I have examined the causes of evolutionary radiations in birds across broad phylogenetic and spatial scales. By combining novel datasets with state-of-the-art phylogenetic modeling techniques and computer simulations I have shown that both

abiotic and biotic factors can have a profound effect on the dynamics of species radiations and the evolution of organismal traits. In particular, my work sheds light on the importance of climate-related mechanisms for species diversification, as well as highlighting the critical role of sexual selection for speciation and the build up of biodiversity. Whilst much remains to be discovered regarding the biotic and abiotic forces driving evolutionary diversification, ultimately these insights help to further our understanding of why species diversity is so strikingly variable among groups of organisms and across geographical space.

APPENDIX 1

Expanded methods

Clade selection. To select clades, I used an approach designed to identify monophyletic groups of species largely corresponding to traditional taxonomic classifications of genera and families, without excluding major clades made up of representatives from multiple families/genera simply due to taxonomic misclassification (Supporting Information). To do this at the family level, I used the taxonomy provided by Jetz et al. (2012) to search through each phylogeny, identifying all those families forming a monophyletic group when (i) the species of each family were considered separately, or (ii) when the species of each family were considered together with those of one other family. I restricted the search to include clades containing a maximum of two paraphyletic/polyphyletic families to ensure that the chosen groups remained comparable with traditional groups of the same taxonomic level. In other words, I used the taxonomy and phylogenies to identify three different 'types' of clade: (i) clades containing all species (and only those species) belonging to a single family ('monophyletic' clades); (ii) clades in which the species of one family were nested within species of another ('paraphyletic' clades); and (iii) clades in which the species of two families were mixed amongst one another ('polyphyletic' clades). As this procedure resulted in some groups of species appearing in two clades within the same sample (i.e. a monophyletic family could also occur within a paraphyletic clade when considered together with the species of another family), I randomly excluded either the monophyletic or paraphyletic incarnation of the species group. I also excluded clades that contained less than four species with climatic data to avoid problems associated

with model fitting and estimating rates of evolution for small clades (Adams et al. 2009; Kozak & Wiens 2010; Rabosky & Adams 2012). The same procedure was used to provide a sample of genus-level clades. The result of applying this approach across the distribution of trees was 100 'pseudoreplicate' samples of clades, containing a median of 95 (range 93-99) family-level clades and 507 (range 500-513) genus-level clades covering 7780 species in total—approximately 78% of the world's bird diversity.

Ecological trait data. I quantified three ecological traits for each species: habitat, territoriality, and migration. The justification for the link between these ecological variables and dispersal propensity is outlined below.

Habitat: species restricted to dense habitats (e.g. tropical forest, dense thickets or dense shrubland) are less likely to disperse across areas of alternative habitat than species that inhabit more open habitats, and forest specialisation has previously been used an index of dispersal tendency in birds (Weir *et al*. 2009).

Territoriality: I assumed that species with year-round territoriality are less mobile within and between seasons than species in which territorial behaviour is weak or absent. This is based on the generality that individuals defending year-round territories have relatively small and spatially fixed home ranges over many years (Greenberg & Gradwohl 1997; Gill & Stutchbury 2006; Tobias *et al*. 2011), whereas species with weaker forms of territoriality have larger home ranges, and are often adapted for relatively long-distance dispersal (Boyle 2008; Lees & Peres 2009).

Migratory behaviour: I assume that sedentary species have a lower propensity or capability to disperse than those species that migrate locally, which in turn have lower dispersal tendency than species undertaking long-distance migrations (Dawideit *et al*. 2009).

Appendix 1

Information regarding species' habitat, territorial system and migratory behaviour was based on the descriptions provided in *The Handbook of the Birds of the World* series (del Hoyo *et al*. 1992–2011), and species were categorised according to the following criteria. I assigned species to one of three habitat categories: (1) occurring in dense forested habitats (species primarily lives in the lower or middle storey of forest, or in dense thickets, dense shrubland, including canopy dwellers of tall forests); (2) occurring in semi-open habitats (species primarily lives in open shrubland, scattered bushes, parkland, low dry or deciduous forest or thorn forest); (3) occurring in open habitats (species primarily lives in desert, grassland, open water, low shrubs, rocky habitats, seashores or cities). To quantify territorial system I assigned species to one of three categories: (1) permanent year-round territoriality, or territorial for much of the year (for example, migrants that are territorial on both the breeding and non-breeding quarters); (2) seasonal or weak territoriality (including species with home ranges which broadly overlap, and species which habitually join mixed flocks with poorly defined spatial ranges, even those that may defend their position in such flocks); (3) never territorial (including species that may defend very small areas around nest sites, including seabirds, and species where males defend singing posts, such as honeyguides and tyrant-manakins). To quantify migratory behaviour I assigned species to one of three categories: (1) sedentary; (2) local movements (i.e. part of range undertakes short-distance migrations, nomadism, distinct altitudinal migration); (3) long-distance migration (most of population undertakes long-distance migration).

Supplementary figures and tables

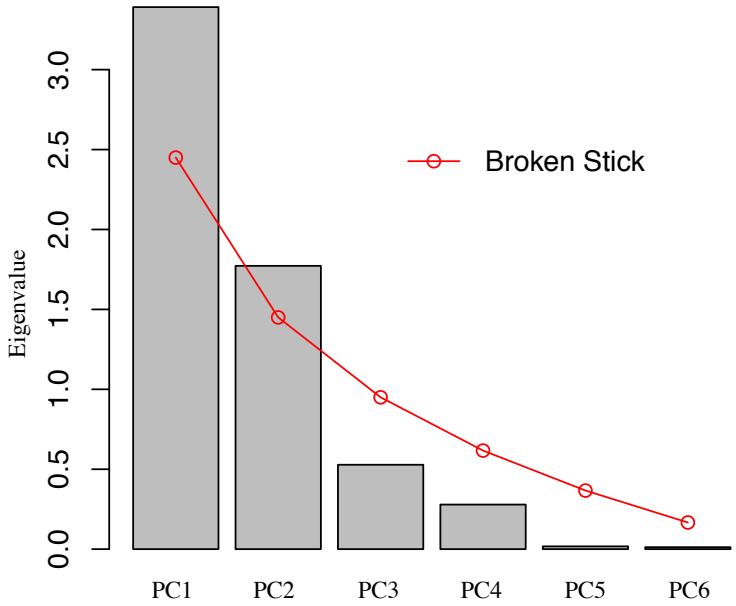

Figure S1. Comparison between the eigenvalues of each principal component (PC) and those expected under a neutral broken stick model.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
BIO1	-0.487	-0.303	0.171	-0.162	-0.732	-0.282
BIO5	-0.366	-0.464	0.088	0.755	0.258	0.082
BIO6	-0.480	-0.219	0.239	-0.594	0.509	0.228
BIO12	-0.427	0.437	-0.257	0.067	0.292	-0.686
BIO16	-0.437	0.327	-0.543	0.060	-0.215	0.598
BIO17	-0.158	0.589	0.738	0.207	-0.082	0.182
Eigenvalue	3.391	1.772	0.528	0.279	0.017	0.012
Proportion of variance	0.565	0.295	0.088	0.046	0.003	0.002

Table S1. Variable loadings for principal components (PCs) of species' climatic niches.

Term	β	*p*	*f*	R^2
Families				
(Intercept)	3.301	<0.001	1.00	0.02
Niche rate (PC1)	0.044	0.592	0.00	
Niche rate (PC2)	0.074	0.418	0.03	
(Intercept)	3.313	<0.001	1.00	0.02
Niche rate (PC1)	0.042	0.646	0.01	
Niche rate (PC2)	0.074	0.425	0.03	
Niche rate (PC1) * Niche rate (PC2)	-0.004	0.696	0.00	
Genera				
(Intercept)	2.178	<0.001	1.00	0.08
Niche rate (PC1)	0.034	0.032	0.65	
Niche rate (PC2)	0.086	<0.001	1.00	
(Intercept)	2.177	<0.001	1.00	0.08
Niche rate (PC1)	0.038	0.046	0.51	
Niche rate (PC2)	0.087	<0.001	1.00	
Niche rate (PC1) * Niche rate (PC2)	0.003	0.621	0.01	

Table S2. Summary of results of PGLS models of log(species richness) across avian families and genera. Shown are median values for models fitted to 100 pseudoreplicate datasets, and the frequency of models (*f*) in which the predictor was statistically significant ($p < 0.05$).

Term	**β**	***p***	***f***	R^2
(Intercept)	2.432	<0.001	1.00	0.12
Niche rate (PC1)	0.065	<0.001	1.00	
Niche rate (PC2)	0.084	<0.001	1.00	
Latitude	-0.008	0.021	0.77	
Habitat	-0.032	0.524	0.02	
Territoriality	0.019	0.623	0.00	
Migration	-0.064	0.425	0.00	

Table S3. Summary of results of multi-predictor PGLS models of log(species richness) across avian genera. Shown are median values for models fitted to 100 pseudoreplicate datasets, and the frequency of models (*f*) in which the predictor was statistically significant ($p < 0.05$).

APPENDIX 2

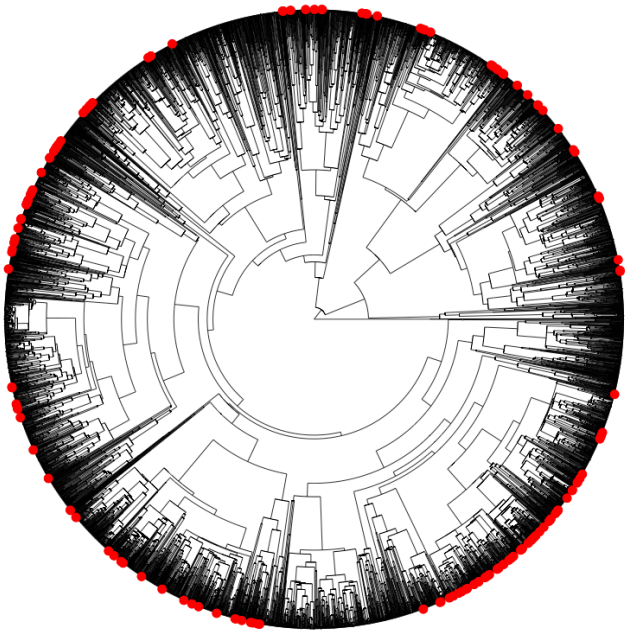

Figure S1 Sampling of sister species in this study. Sister species (n = 288; red circles) are distributed evenly throughout the passerine radiation (n = 5966 species). The phylogeny shown here is a single representative passerine tree from the 'complete' species trees compiled by (Jetz *et al*. 2012).

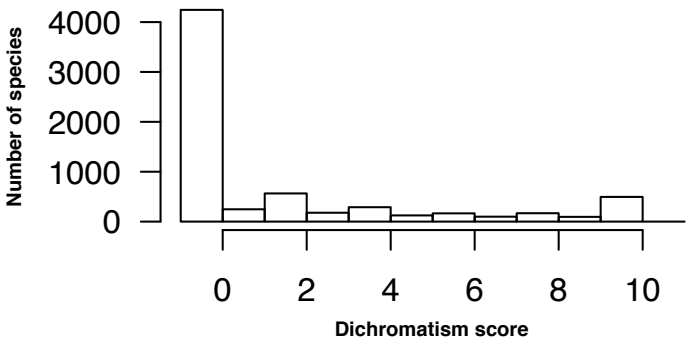

Figure S2. Histogram of dichromatism scores generated by human observers for 6670 bird species. Dichromatism was assessed visually from colour plate illustrations.

Appendix 2

Table S1. Species pairs analysed in this thesis with supporting references.

Species 1	Species 2	Chp. 3	Chp. 4 Song	Chp. 4 Plumage	Reference
Acanthiza katherina	Acanthiza pusilla		1		Gardner *et al*. (2010)
Acanthiza lineata	Acanthiza nana	1			Seddon *et al*. (2013)
Acrocephalus baeticatus	Acrocephalus scirpaceus	1	1	1	Fregin *et al*. (2009)
Acrocephalus gracilirostris	Acrocephalus rufescens		1		Fregin *et al*. (2009)
Agelaius phoeniceus	Agelaius tricolor		1		Price *et al*. (2009)
Agelasticus cyanopus	Agelasticus xanthophthalmus		1		Lanyon and Omland (1999)
Aimophila aestivalis	Aimophila cassinii	1	1	1	DaCosta *et al*. (2009)
Aimophila carpalis	Aimophila sumichrasti		1		DaCosta *et al*. (2009)
Aimophila notosticta	Aimophila ruficeps		1		DaCosta *et al*. (2009)
Aimophila stolzmanni	Aimophila strigiceps		1		DaCosta *et al*. (2009)
Ammodramus caudacutus	Ammodramus nelsoni	1			Klicka and Spellman (2007)
Anairetes nigrocristatus	Anairetes reguloides	1	1	1	Roy *et al*. (1999)
Anisognathus igniventris	Anisognathus lacrymosus	1	1	1	Sedano and Burns (2010)
Anisognathus notabilis	Anisognathus somptuosus	1	1	1	Sedano and Burns (2010)
Anthochaera carunculata	Anthochaera paradoxa	1		1	Seddon *et al*. (2013)
Anumbius annumbi	Coryphistera alaudina	1	1	1	Moyle *et al*. (2009)
Arremonops chloronotus	Arremonops rufivirgatus	1	1	1	DaCosta *et al*. (2009)
Asthenes sclateri	Asthenes wyatti		1		Derryberry *et al*. (2011)
Atticora fasciata	Neochelidon tibialis		1		Sheldon *et al*. (2005)
Automolus rubiginosus	Hylocryptus erythrocephalus		1		Derryberry *et al*. (2011)
Baeolophus bicolor	Baeolophus inornatus	1	1	1	Gill *et al*. (2005)
Bangsia aureocincta	Bangsia edwardsi		1		Sedano and Burns (2010)
Basileuterus belli	Basileuterus melanogenys	1		1	Seddon *et al*. (2013)
Basileuterus cinereicollis	Basileuterus conspicillatus		1		Lovette *et al*. (2010)
Basileuterus coronatus	Basileuterus fraseri		1		Lovette *et al*. (2010)
Basileuterus culicivorus	Basileuterus hypoleucus		1		Lovette *et al*. (2010)
Basileuterus flaveolus	Basileuterus leucoblepharus	1	1	1	Lovette *et al*. (2010)
Basileuterus trifasciatus	Basileuterus tristriatus		1		Lovette *et al*. (2010)
Batara cinerea	Hypoedaleus guttatus		1		Gómez *et al*. (2010)
Bradypterus cinnamomeus	Bradypterus lopezi		1		Alström *et al*. (2011)
Buthraupis eximia	Chlorornis riefferii		1		Sedano and Burns (2010)
Cacicus chrysopterus	Cacicus sclateri		1		Price and Whalen (2009)
Calamospiza melanocorys	Chondestes grammacus	1	1	1	Carson and Spicer (2003)
Calcarius ornatus	Calcarius pictus	1	1	1	Klicka *et al*. (2003)
Camarhynchus pallidus	Camarhynchus psittacula	1	1	1	Sato *et al*. (1999)
Camarhynchus parvulus	Camarhynchus pauper		1		Sato *et al*. (1999)
Campylorhamphus procurvoides	Campylorhamphus trochilirostris		1		Claramunt *et al*. (2010)
Campylorhynchus albobrunneus	Campylorhynchus fasciatus		1		Barker (2007)
Campylorhynchus chiapensis	Campylorhynchus griseus		1		Barker (2007)
Campylorhynchus megalopterus	Campylorhynchus zonatus	1	1	1	Barker (2007)

Cantorchilus leucopogon	Cantorchilus thoracicus		1		Mann *et al*. (2006)
Cantorchilus nigricapillus	Cantorchilus semibadius	1	1	1	Mann *et al*. (2006)
Cardellina rubrifrons	Ergaticus ruber		1		Lovette *et al*. (2010)
Cardinalis phoeniceus	Cardinalis sinuatus		1		Klicka *et al*. (2007)
Carduelis cannabina	Carduelis flavirostris	1	1	1	Arnaiz-Villena *et al*. (2009)
Carduelis flammea	Carduelis hornemanni	1		1	Seddon *et al*. (2013)
Carduelis magellanica	Carduelis yarrellii		1		Arnaiz-Villena *et al*. (2009)
Carduelis psaltria	Carduelis tristis	1	1	1	Arnaiz-Villena *et al*. (2009)
Caryothraustes canadensis	Caryothraustes poliogaster	1	1	1	Klicka *et al*. (2007)
Catharus guttatus	Catharus occidentalis	1	1	1	Winker and Pruett (2006)
Catherpes mexicanus	Hylorchilus sumichrasti		1		Mann *et al*. (2006)
Cercomacra melanaria	Cercomacra nigricans		1		Gómez *et al*. (2010)
Cercomacra serva	Cercomacra tyrannina		1		Gómez *et al*. (2010)
Certhia americana	Certhia brachydactyla	1	1	1	Tietze *et al*. (2006)
Chlamydera cerviniventri	Chlamydera nuchalis	1		1	Seddon *et al*. (2013)
Chlorothraupis carmioli	Chlorothraupis olivacea		1		Klicka *et al*. (2007)
Chrysomus icterocephalus	Chrysomus ruficapillus	1	1	1	Price *et al*. (2009)
Cincloramphus mathewsi	Megalurus timoriensis	1			Seddon *et al*. (2013)
Copsychus malabaricus	Copsychus stricklandii	1	1	1	Lim *et al*. (2010)
Cranioleuca albiceps	Cranioleuca marcapatae		1		Derryberry *et al*. (2011)
Cranioleuca antisiensis	Cranioleuca curtata		1		Derryberry *et al*. (2011)
Cranioleuca sulphurifera	Limnoctites rectirostris		1		Derryberry *et al*. (2011)
Culicicapa ceylonensis	Culicicapa helianthea	1	1	1	Fuchs *et al*. (2009)
Cyanistes caeruleus	Cyanistes cyanus	1	1	1	Päckert *et al*. (2007)
Cyanocitta cristata	Cyanocitta stelleri	1	1	1	Bonaccorso and Peterson (2007)
Cyanocompsa brissonii	Cyanoloxia glaucocaerulea	1	1	1	Klicka *et al*. (2007)
Cyanocorax chrysops	Cyanocorax cyanopogon		1		Bonaccorso *et al*. (2010)
Cyanocorax cristatellus	Cyanocorax cyanomelas	1	1	1	Bonaccorso *et al*. (2010)
Deconychura longicauda	Sittasomus griseicapillus	1	1	1	Derryberry *et al*. (2011)
Delothraupis castaneoventris	Dubusia taeniata		1		Sedano and Burns (2010)
Dendrexetastes rufigula	Nasica longirostris		1		Irestedt *et al*. (2009a)
Dendrocincla anabatina	Dendrocincla fuliginosa	1	1	1	Derryberry *et al*. (2011)
Dendrocincla merula	Dendrocincla tyrannina		1		Derryberry *et al*. (2011)
Dendrocolaptes certhia	Dendrocolaptes sanctithomae	1			Derryberry *et al*. (2011)
Dendroica castanea	Dendroica fusca	1	1	1	Lovette *et al*. (2010)
Dendroica graciae	Dendroica nigrescens	1	1	1	Lovette *et al*. (2010)
Dendroica occidentalis	Dendroica townsendi	1	1	1	Lovette *et al*. (2010)
Dendroica pensylvanica	Dendroica striata	1	1	1	Lovette *et al*. (2010)
Dicrurus adsimilis	Dicrurus macrocercus	1	1	1	Pasquet *et al*. (2007)
Dicrurus balicassius	Dicrurus hottentottus	1	1	1	Pasquet *et al*. (2007)
Diglossa baritula	Diglossa plumbea		1		Mauck and Burns (2009)
Diglossa carbonaria	Diglossa humeralis		1		Mauck and Burns (2009)
Diglossa gloriosissima	Diglossa lafresnayii		1		Mauck and Burns (2009)

Diphyllodes magnificus	Diphyllodes respublica	1	1	1	Irestedt *et al*. (2009b)
Emberiza bruniceps	Emberiza melanocephala	1	1	1	Alström *et al*. (2008)
Emberiza caesia	Emberiza hortulana	1	1	1	Alström *et al*. (2008)
Emberiza citrinella	Emberiza leucocephalos	1	1	1	Alström *et al*. (2008)
Emberiza elegans	Emberiza siemsseni		1		Alström *et al*. (2008)
Emberiza pallasi	Emberiza schoeniclus	1	1	1	Alström *et al*. (2008)
Eminia lepida	Hypergerus atriceps	1	1	1	Cibois *et al*. (1999)
Empidonax alnorum	Empidonax traillii	1	1	1	Johnson and Cicero (2002)
Empidonax atriceps	Empidonax fulvifrons	1	1	1	Johnson and Cicero (2002)
Empidonax difficilis	Empidonax occidentalis		1		Johnson and Cicero (2002)
Empidonax hammondii	Empidonax oberholseri		1		Johnson and Cicero (2002)
Entomodestes coracinus	Entomodestes leucotis		1		Klicka *et al*. (2005)
Epimachus fastuosus	Epimachus meyeri	1	1	1	Irestedt *et al*. (2009b)
Epinecrophylla haematonota	Epinecrophylla spodionota		1		Gómez *et al*. (2010)
Epthianura albifrons	Epthianura aurifrons	1		1	Seddon *et al*. (2013)
Epthianura crocea	Epthianura tricolor	1		1	Seddon *et al*. (2013)
Eucometis penicillata	Trichothraupis melanops	1	1	1	Burns and Racicot (2009)
Euphagus carolinus	Euphagus cyanocephalus	1	1	1	Price *et al*. (2009)
Eurillas latirostris	Eurillas virens	1			Johansson *et al*. (2007b)
Ficedula albicollis	Ficedula hypoleuca	1	1	1	Outlaw and Voelker (2006)
Ficedula dumetoria	Ficedula platenae		1		Outlaw and Voelker (2006)
Ficedula superciliaris	Ficedula westermanni		1		Outlaw and Voelker (2006)
Frederickena unduligera	Frederickena viridis		1		Gómez *et al*. (2010)
Furnarius cristatus	Furnarius leucopus		1		Derryberry *et al*. (2011)
Geositta crassirostris	Geositta rufipennis		1		Derryberry *et al*. (2011)
Geositta isabellina	Geositta saxicolina		1		Derryberry *et al*. (2011)
Geothlypis nelsoni	Geothlypis trichas		1		Lovette *et al*. (2010)
Granatellus sallaei	Granatellus venustus		1		Joseph *et al*. (2004)
Gymnopithys leucaspis	Gymnopithys rufigula	1	1	1	Gómez *et al*. (2010)
Gymnopithys lunulatus	Gymnopithys salvini		1		Gómez *et al*. (2010)
Habia fuscicauda	Habia gutturalis		1		Klicka *et al*. (2007)
Hartertula flavoviridis	Thamnornis chloropetoides	1			Johansson *et al*. (2008)
Herpsilochmus axillaris	Herpsilochmus longirostris		1		Gómez *et al*. (2010)
Herpsilochmus dorsimaculatus	Herpsilochmus stictocephalus		1		Gómez *et al*. (2010)
Herpsilochmus motacilloides	Herpsilochmus parkeri		1		Gómez *et al*. (2010)
Hippolais icterina	Hippolais polyglotta	1	1	1	Fregin *et al*. (2009)
Hirundo neoxena	Hirundo tahitica	1		1	Seddon *et al*. (2013)
Hylophylax naevioides	Hylophylax naevius	1	1	1	Gómez *et al*. (2010)
Icterus chrysater	Icterus graduacauda	1	1	1	Jacobsen *et al*. (2010)
Icterus graceannae	Icterus pectoralis		1		Jacobsen *et al*. (2010)
Icterus gularis	Icterus nigrogularis	1	1	1	Omland *et al*. (1999)
Iduna caligata	Iduna rama	1			Fregin *et al*. (2009)
Illadopsis albipectus	Illadopsis cleaveri	1	1	1	Nguembock *et al*. (2008)

Illadopsis puveli	Illadopsis rufescens	1	1	1	Nguembock *et al*. (2008)
Iridosornis analis	Iridosornis porphyrocephalus		1		Sedano and Burns (2010)
Lanio aurantius	Lanio leucothorax	1	1	1	Burns and Racicot (2009)
Lepidocolaptes affinis	Lepidocolaptes leucogaster	1	1	1	Derryberry *et al*. (2011)
Lepidocolaptes albolineatus	Lepidocolaptes angustirostris		1		Derryberry *et al*. (2011)
Leptasthenura yanacensis	Sylvorthorhynchus desmursii		1		Derryberry *et al*. (2011)
Limnornis curvirostris	Phleocryptes melanops		1		Derryberry *et al*. (2011)
Limnothlypis swainsonii	Protonotaria citrea	1	1	1	Lovette *et al*. (2010)
Locustella fluviatilis	Locustella luscinioides	1	1	1	Alström *et al*. (2011)
Luscinia calliope	Luscinia pectoralis	1	1	1	Sangster *et al*. (2010)
Luscinia luscinia	Luscinia megarhynchos	1	1	1	Sangster *et al*. (2010)
Mackenziaena leachii	Mackenziaena severa	1	1	1	Gómez *et al*. (2010)
Malurus amabilis	Malurus lamberti	1		1	Seddon *et al*. (2013)
Malurus cyaneus	Malurus splendens	1		1	Seddon *et al*. (2013)
Manorina flavigula	Manorina melanocephala	1		1	Seddon *et al*. (2013)
Melanochlora sultanea	Sylviparus modestus	1			Gill *et al*. (2005)
Melospiza georgiana	Melospiza lincolnii	1	1	1	Klicka and Spellman (2007)
Mionectes macconnelli	Mionectes oleagineus	1	1	1	Miller *et al*. (2008)
Mionectes olivaceus	Mionectes striaticollis	1	1	1	Miller *et al*. (2008)
Molothrus ater	Molothrus bonariensis	1	1	1	Price *et al*. (2009)
Myrmeciza berlepschi	Myrmeciza nigricauda		1		Gómez *et al*. (2010)
Myrmeciza fortis	Myrmeciza immaculata		1		Gómez *et al*. (2010)
Myrmeciza goeldii	Myrmeciza melanoceps		1		Gómez *et al*. (2010)
Myrmeciza loricata	Myrmeciza squamosa		1		Gómez *et al*. (2010)
Myrmothera campanisona	Myrmothera simplex		1		Rice (2005)
Neomixis striatigula	Neomixis tenella	1	1	1	Moyle *et al*. (2009)
Ochetorhynchus phoenicurus	Ochetorhynchus ruficaudus	1	1	1	Irestedt *et al*. (2009a)
Oenanthe isabellina	Oenanthe oenanthe		1		Outlaw *et al*. (2010)
Oporornis philadelphia	Oporornis tolmiei	1	1	1	Lovette *et al*. (2010)
Oreothlypis gutturalis	Oreothlypis superciliosa	1	1	1	Lovette *et al*. (2010)
Oreothlypis luciae	Oreothlypis virginiae		1		Lovette *et al*. (2010)
Paradisaea apoda	Paradisaea raggiana	1	1	1	Irestedt *et al*. (2009b)
Pardalotus punctatus	Pardalotus striatus	1	1	1	Gardner *et al*. (2010)
Parkesia motacilla	Parkesia noveboracensis	1	1	1	Lovette *et al*. (2010)
Paroaria capitata	Paroaria gularis	1	1	1	Sedano and Burns (2010)
Paroaria coronata	Paroaria dominicana		1		Sedano and Burns (2010)
Parula americana	Parula pitiayumi	1	1	1	Lovette *et al*. (2010)
Passerina amoena	Passerina caerulea	1	1	1	Klicka *et al*. (2007)
Passerina ciris	Passerina versicolor	1	1	1	Klicka *et al*. (2007)
Periparus amabilis	Periparus elegans	1	1	1	Päckert *et al*. (2007)
Periporphyrus erythromelas	Rhodothraupis celaeno	1	1	1	Klicka *et al*. (2007)
Phaeothlypis fulvicauda	Phaeothlypis rivularis		1		Lovette *et al*. (2010)
Pheugopedius coraya	Pheugopedius genibarbis	1	1	1	Mann *et al*. (2006)

Pheugopedius fasciatoventris	Pheugopedius mystacalis		1		Mann *et al*. (2006)
Pheugopedius maculipectus	Pheugopedius rutilus		1		Mann *et al*. (2006)
Phlegopsis borbae	Phlegopsis nigromaculata		1		Aleixo *et al*. (2009)
Phylloscopus affinis	Phylloscopus griseolus	1	1	1	Johansson *et al*. (2007a)
Phylloscopus armandii	Phylloscopus schwarzi	1	1	1	Johansson *et al*. (2007a)
Phylloscopus claudiae	Phylloscopus reguloides	1			Johansson *et al*. (2007a)
Phylloscopus collybita	Phylloscopus sindianus	1			Johansson *et al*. (2007a)
Phylloscopus davisoni	Phylloscopus trivirgatus		1		Johansson *et al*. (2007a)
Phylloscopus humei	Phylloscopus inornatus	1			Johansson *et al*. (2007a)
Phylloscopus maculipennis	Phylloscopus pulcher	1	1	1	Johansson *et al*. (2007a)
Phylloscopus plumbeitarsus	Phylloscopus trochiloides	1			Johansson *et al*. (2007a)
Pipilo aberti	Pipilo crissalis	1	1	1	DaCosta *et al*. (2009)
Pipilo erythrophthalmus	Pipilo maculatus	1			DaCosta *et al*. (2009)
Piranga bidentata	Piranga ludoviciana	1	1	1	Burns (1998a)
Piranga leucoptera	Piranga rubriceps	1	1	1	Burns (1998a)
Pithys albifrons	Pithys castaneus		1		Gómez *et al*. (2010)
Pitohui dichrous	Pitohui kirhocephalus	1	1	1	Dumbacher *et al*. (2008)
Poecile atricapillus	Poecile gambeli	1	1	1	Gill *et al*. (2005)
Poecile carolinensis	Poecile sclateri	1	1	1	Gill *et al*. (2005)
Poecile hudsonicus	Poecile rufescens	1	1	1	Gill *et al*. (2005)
Poecile montanus	Poecile palustris	1			Gill *et al*. (2005)
Pomatorhinus erythrocnemis	Pomatorhinus erythrogenys	1	1	1	Dong *et al*. (2010)
Pomatorhinus ferruginosus	Pomatorhinus ochraceiceps	1	1	1	Dong *et al*. (2010)
Pomatorhinus ruficollis	Pomatorhinus schisticeps	1	1	1	Dong *et al*. (2010)
Pomatostomus halli	Pomatostomus temporalis	1			Seddon *et al*. (2013)
Pomatostomus ruficeps	Pomatostomus superciliosus	1			Seddon *et al*. (2013)
Premnoplex brunnescens	Premnoplex tatei		1		Derryberry *et al*. (2011)
Psarocolius angustifrons	Psarocolius atrovirens	1	1	1	Price *et al*. (2009)
Pseudocolaptes boissonneautii	Pseudocolaptes lawrencii		1		Derryberry *et al*. (2011)
Pseudoleistes guirahuro	Pseudoleistes virescens	1	1	1	Lanyon and Omland (1999)
Ptiloris intercedens	Ptiloris magnificus	1	1	1	Irestedt *et al*. (2009b)
Pygiptila stellaris	Thamnistes anabatinus	1			Gómez *et al*. (2010)
Quiscalus major	Quiscalus niger	1	1	1	Price *et al*. (2009)
Ramphocelus dimidiatus	Ramphocelus nigrogularis	1	1	1	Burns and Racicot (2009)
Ramphocelus flammigerus	Ramphocelus passerinii		1		Burns and Racicot (2009)
Regulus goodfellowi	Regulus regulus	1			Päckert *et al*. (2009)
Sakesphorus canadensis	Sakesphorus luctuosus		1		Brumfield and Edwards (2007)
Saltator atricollis	Saltatricula multicolor		1		Joseph *et al*. (2004)
Saxicola ferreus	Saxicola jerdoni	1	1	1	Illera *et al*. (2008)
Schistochlamys melanopis	Schistochlamys ruficapillus		1		Sedano and Burns (2010)
Seicercus affinis	Seicercus poliogenys	1	1	1	Johansson *et al*. (2007a)
Seicercus burkii	Seicercus tephrocephalus	1			Johansson *et al*. (2007a)
Seicercus castaniceps	Seicercus montis	1	1	1	Johansson *et al*. (2007a)

Sialia currucoides	Sialia sialis	1	1	1	Klicka *et al*. (2005)
Spizella breweri	Spizella passerina	1	1	1	Carson and Spicer (2003)
Sylvia deserticola	Sylvia undata		1		Böhning-Gaese *et al*. (2006)
Synallaxis candei	Synallaxis erythrothorax		1		Derryberry *et al*. (2011)
Tachycineta leucorrhoa	Tachycineta meyeni		1		Sheldon *et al*. (2005)
Tachyphonus coronatus	Tachyphonus rufus	1	1	1	Burns and Racicot (2009)
Tangara cayana	Tangara vitriolina		1		Sedano and Burns (2010)
Tangara cyanicollis	Tangara nigrocincta	1	1	1	Sedano and Burns (2010)
Tangara nigroviridis	Tangara vassorii		1		Sedano and Burns (2010)
Tarphonomus certhioides	Tarphonomus harterti		1		Chesser *et al*. (2007)
Thamnomanes caesius	Thamnomanes schistogynus		1		Gómez *et al*. (2010)
Thamnophilus aethiops	Thamnophilus aroyae		1		Gómez *et al*. (2010)
Thamnophilus atrinucha	Thamnophilus bridgesi	1			Gómez *et al*. (2010)
Thamnophilus cryptoleucus	Thamnophilus nigrocinereus		1		Gómez *et al*. (2010)
Thamnophilus murinus	Thamnophilus schistaceus	1	1	1	Gómez *et al*. (2010)
Thamnophilus nigriceps	Thamnophilus praecox		1		Gómez *et al*. (2010)
Thamnophilus ruficapillus	Thamnophilus torquatus		1		Gómez *et al*. (2010)
Thraupis episcopus	Thraupis sayaca	1	1	1	Sedano and Burns (2010)
Thraupis ornata	Thraupis palmarum		1		Sedano and Burns (2010)
Thryomanes bewickii	Thryothorus ludovicianus	1	1	1	Mann *et al*. (2006)
Thryophilus pleurostictus	Thryophilus sinaloa	1	1	1	Mann *et al*. (2006)
Toxostoma bendirei	Toxostoma cinereum		1		Zink *et al*. (1999)
Toxostoma crissale	Toxostoma lecontei		1		Zink *et al*. (1999)
Toxostoma longirostre	Toxostoma rufum	1	1	1	Zink *et al*. (1999)
Turdus albicollis	Turdus assimilis		1		Nylander *et al*. (2008)
Turdus aurantius	Turdus plumbeus		1		Nylander *et al*. (2008)
Turdus dissimilis	Turdus unicolor	1	1	1	Nylander *et al*. (2008)
Turdus fumigatus	Turdus hauxwelli	1	1	1	Nylander *et al*. (2008)
Turdus grayi	Turdus nudigenis		1		Nylander *et al*. (2008)
Turdus ignobilis	Turdus maranonicus		1		Nylander *et al*. (2008)
Turdus iliacus	Turdus plebejus		1		Nylander *et al*. (2008)
Turdus infuscatus	Turdus nigrescens		1		Nylander *et al*. (2008)
Turdus migratorius	Turdus rufitorques	1	1	1	Nylander *et al*. (2008)
Turdus nigriceps	Turdus serranus		1		Nylander *et al*. (2008)
Upucerthia jelskii	Upucerthia validirostris		1		Derryberry *et al*. (2011)
Xiphocolaptes major	Xiphocolaptes promeropirhynchus	1	1	1	Derryberry *et al*. (2011)
Xiphorhynchus elegans	Xiphorhynchus spixii		1		Derryberry *et al*. (2011)
Xiphorhynchus erythropygius	Xiphorhynchus triangularis	1	1	1	Derryberry *et al*. (2011)
Xiphorhynchus flavigaster	Xiphorhynchus lachrymosus	1	1	1	Derryberry *et al*. (2011)
Xiphorhynchus ocellatus	Xiphorhynchus pardalotus		1		Derryberry *et al*. (2011)
Zonotrichia atricapilla	Zonotrichia leucophrys		1		Carson and Spicer (2003)

Wavelength bin (nm)	PC1	PC2	PC3
320-340	0.197	-0.312	0.264
340-360	0.212	-0.267	0.315
360-380	0.233	-0.196	0.278
380-400	0.256	-0.095	0.122
400-420	0.263	0.007	-0.053
420-440	0.256	0.088	-0.171
440-460	0.242	0.162	-0.248
460-480	0.222	0.248	-0.278
480-500	0.198	0.316	-0.283
500-520	0.046	0.529	0.131
520-540	-0.143	0.384	0.408
540-560	-0.206	0.266	0.337
560-580	-0.245	0.147	0.199
580-600	-0.262	0.035	0.048
600-620	-0.263	-0.045	-0.066
620-640	-0.259	-0.090	-0.137
640-660	-0.255	-0.118	-0.179
660-680	-0.249	-0.139	-0.205
680-700	-0.242	-0.155	-0.225
Eigenvalue	13.94	3.09	1.47
Variation (%)	73.37	16.28	7.75

Table S2. Component loadings and weights from a principal components analysis of reflectance spectra.

Parameter	Estimate	95% CI	*P*
λ_0	0.090	0.040, 0.120	–
λ_{slope}	0.028	0.003, 0.054	0.046
μ_0	0.000	0.000, 0.070	–
μ_{slope}	0.013	–0.018, 0.018	0.330

Table S3. Maximum likelihood parameter estimates (and 95% CI) describing the linear change in speciation and extinction rates with increasing dichromatism, corrected for a declining lag time to species description across this gradient (n = 144 sister pairs).

Threshold	$Rate_{(Dichro\ not\ in\ model)}$	$Rate_{(Dichro\ min)}$	$Rate_{(Dichro\ max)}$	P^a
>0%	0.331 (0.255, 0.429)	–	–	–
	–	0.197 (0.119, 0.326)	0.703 (0.375, 1.316)	0.013
>10%	0.229 (0.174, 0.303)	–	–	–
	–	0.139 (0.081, 0.238)	0.456 (0.245, 0.806)	0.024
>20%	0.156 (0.115, 0.212)	–	–	–
	–	0.103 (0.057, 0.187)	0.273 (0.138, 0.539)	0.093

Table S4. Maximum likelihood estimates of sympatry rates (and 95% CI) under alternative range overlap thresholds used to define sympatry across sister species pairs (n = 94), after excluding 47 pairs containing mutually ornamented species.

Model	Covariate	$Rate_{(No\ covariate\ in\ model)}$	$Rate_{(Covariate\ min)}$	$Rate_{(Covariate\ max)}$
1	–	0.301 (0.243, 0.374)	–	–
2	Latitude	–	0.218 (0.143, 0.332)	0.466 (0.282, 0.770)
3	Migration	–	0.242 (0.183, 0.319)	0.556 (0.350, 0.881)
4	Dichromatism	–	0.184 (0.120, 0.281)	0.690 (0.379, 1.255)
5	Latitude	–	0.317 (0.184, 0.545)	0.300 (0.154, 0.585)
	Migration	–	0.240 (0.174, 0.331)	0.567 (0.308, 1.041)
6	Latitude	–	0.228 (0.149, 0.351)	0.473 (0.285, 0.787)
	Dichromatism	–	0.187 (0.122, 0.286)	0.681 (0.374, 1.238)
7	**Migration**	**–**	**0.259 (0.194, 0.344)**	**0.506 (0.317, 0.808)**
	Dichromatism	**–**	**0.205 (0.133, 0.318)**	**0.600 (0.326, 1.107)**
8	Latitude	–	0.296 (0.169, 0.518)	0.344 (0.171, 0.690)
	Migration	–	0.265 (0.190, 0.371)	0.478 (0.254, 0.902)
	Dichromatism	–	0.204 (0.131, 0.317)	0.609 (0.328, 1.131)

Table S5. Parameter estimates from the full set of models estimating rates of transition to sympatry (per Myr) across sister species pairs (n = 141). In models with multiple covariates, focal rate expressed with other covariate(s) set to mean value(s). Bold denotes the best-supported model (see Chapter 3 Table 4).

Threshold	λ	μ	q	Best	K	DeltaAIC	λM	λD	μM	μD	NetM	NetD	qMD	qDM
> 1	=	=	=	0	3	395.84 (34.87)	0.158 (0.010)	0.158 (0.010)	0.063 (0.010)	0.063 (0.010)	0.095 (0.004)	0.095 (0.004)	0.015 (0.001)	0.015 (0.001)
	=	=	≠	0	4	134.37 (20.79)	0.158 (0.010)	0.158 (0.010)	0.063 (0.010)	0.063 (0.010)	0.095 (0.004)	0.095 (0.004)	0.008 (0.000)	0.033 (0.002)
	=	≠	=	0	4	388.19 (35.46)	0.159 (0.010)	0.159 (0.010)	0.057 (0.011)	0.078 (0.012)	0.101 (0.006)	0.081 (0.006)	0.016 (0.001)	0.016 (0.001)
	≠	=	=	0	4	378.54 (30.21)	0.150 (0.010)	0.168 (0.010)	0.057 (0.010)	0.057 (0.010)	0.093 (0.004)	0.111 (0.005)	0.014 (0.001)	0.014 (0.001)
	=	**≠**	**≠**	**82**	**5**	**0.30 (1.10)**	**0.155 (0.009)**	**0.155 (0.009)**	**0.081 (0.009)**	**0.002 (0.004)**	**0.075 (0.004)**	**0.153 (0.007)**	**0.005 (0.000)**	**0.047 (0.003)**
	≠	=	≠	0	5	35.69 (7.37)	0.144 (0.009)	0.185 (0.012)	0.061 (0.010)	0.061 (0.010)	0.083 (0.004)	0.124 (0.005)	0.007 (0.000)	0.037 (0.002)
	≠	≠	=	0	5	269.91 (20.68)	0.135 (0.009)	0.217 (0.015)	0.030 (0.009)	0.138 (0.015)	0.105 (0.005)	0.079 (0.005)	0.017 (0.001)	0.017 (0.001)
	≠	≠	≠	18	6	1.26 (0.74)	0.154 (0.010)	0.155 (0.009)	0.079 (0.010)	0.001 (0.004)	0.075 (0.004)	0.154 (0.008)	0.005 (0.000)	0.047 (0.003)
> 2	=	=	=	0	3	755.59 (45.18)	0.158 (0.010)	0.158 (0.010)	0.063 (0.010)	0.063 (0.010)	0.095 (0.004)	0.095 (0.004)	0.014 (0.001)	0.014 (0.001)
	=	=	≠	0	4	239.11 (28.64)	0.158 (0.010)	0.158 (0.010)	0.063 (0.010)	0.063 (0.010)	0.095 (0.004)	0.095 (0.004)	0.007 (0.000)	0.049 (0.002)
	=	≠	=	0	4	668.51 (44.17)	0.155 (0.010)	0.155 (0.010)	0.041 (0.010)	0.102 (0.011)	0.114 (0.005)	0.053 (0.003)	0.019 (0.001)	0.019 (0.001)
	≠	=	=	0	4	753.62 (43.97)	0.155 (0.011)	0.164 (0.009)	0.060 (0.011)	0.060 (0.011)	0.095 (0.004)	0.104 (0.007)	0.014 (0.001)	0.014 (0.001)
	=	≠	≠	1	5	11.88 (6.94)	0.165 (0.009)	0.165 (0.009)	0.095 (0.009)	0.000 (0.000)	0.070 (0.003)	0.165 (0.009)	0.003 (0.000)	0.076 (0.005)
	≠	=	≠	0	5	52.69 (6.32)	0.142 (0.009)	0.205 (0.014)	0.063 (0.009)	0.063 (0.009)	0.079 (0.004)	0.143 (0.007)	0.005 (0.000)	0.061 (0.004)
	≠	≠	=	0	5	495.01 (27.07)	0.134 (0.009)	0.264 (0.020)	0.022 (0.009)	0.206 (0.020)	0.112 (0.005)	0.058 (0.003)	0.020 (0.001)	0.020 (0.001)
	≠	**≠**	**≠**	**99**	**6**	**0.01 (0.09)**	**0.152 (0.009)**	**0.173 (0.009)**	**0.080 (0.010)**	**0.000 (0.000)**	**0.072 (0.004)**	**0.173 (0.009)**	**0.004 (0.000)**	**0.076 (0.005)**

Table S6. Comparison of model support and mean (sd) maximum likelihood parameters from BiSSE models fit to 100 trees using alternate threshold scores to assign species as dichromatic. λ = speciation rate; μ = extinction rate; q = transition rate; Net = net diversification rate (λ – μ); M = monochromatic; D = dichromatic. Bold denotes best model in the model set.

APPENDIX 3

				Subset 1				Subset 2			
				β		α		β		α	
Trait	**Subset 1**	**Subset2**	**Gradient**	**Inter**	**Slope**	**Inter**	**Slope**	**Inter**	**Slope**	**Inter**	**Slope**
Song	Mono	Dichro	Latitude	0.020	0.024	0.000	0.071	0.149	-0.002	0.368	-0.004
Pitch	Forest	Nonforest	Diversity	0.541	0.000	3.945	-0.002	0.956	-0.001	1.003	0.001
Duration	Mono	Dichro	Latitude	0.059	0.004	0.000	0.009	0.567	-0.010	0.874	-0.010
Pace	Oscine	Suboscine	-	3.349	-	7.318	-	0.384	-	0.295	-
Plumage	Mono	Dichro	-	309.359	-	11.468	-	72.980	-	0.700	-

Table S1. Maximum likelihood parameter estimates for the best-fitting models for each phenotypic trait (see Table 2). β, rate of divergence; α constraint parameter.

Wavelength bin (nm)	PC1	PC2	PC3
320-340	0.071	-0.884	-0.409
340-360	0.129	-0.934	-0.330
360-380	0.264	-0.905	-0.299
380-400	0.492	-0.768	-0.324
400-420	0.696	-0.584	-0.338
420-440	0.826	-0.429	-0.319
440-460	0.912	-0.295	-0.268
460-480	0.968	-0.182	-0.164
480-500	0.981	-0.089	-0.060
500-520	0.626	0.050	0.680
520-540	-0.120	0.215	0.967
540-560	-0.364	0.368	0.842
560-580	-0.534	0.516	0.625
580-600	-0.650	0.622	0.374
600-620	-0.698	0.671	0.182
620-640	-0.713	0.690	0.069
640-660	-0.717	0.693	0.003
660-680	-0.714	0.685	-0.042
680-700	-0.705	0.673	-0.078
Eigenvalue	13.960	3.067	1.464
Cumulative variation	0.421	0.783	0.965

Table S2. Component loadings and weights from a rotated principal component analysis of plumage reflectance variables**.**

BIBLIOGRAPHY

Adams, D.C., Berns, C.M., Kozak, K.H. & Wiens, J.J. (2009). Are rates of species diversification correlated with rates of morphological evolution? *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2729-2738.

Aleixo, A., Burlamaqui, T.C.T., Schneider, M.P.C. & Gonçalves, E.C. (2009). Molecular systematics and plumage evolution in the monotypic obligate army-ant-following genus *Skutchia* (Thamnophilidae). *Condor*, **111**, 382-387.

Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L. *et al.* (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences*, **106**, 13410-13414.

Allen, A.P. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences*, **103**, 9130-9135.

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545-1548.

Alström, P., Fregin, S., Norman, J.A., Ericson, P.G.P., Christidis, L. & Olsson, U. (2011). Multilocus analysis of a taxonomically densely sampled dataset reveal extensive non-monophyly in the avian family Locustellidae. *Molecular Phylogenetics and Evolution*, **58**, 513-526.

Alström, P., Olsson, U., Lei, F., Wang, H.T., Gao, W. & Sundberg, P. (2008). Phylogeny and classification of the Old World Emberizini (Aves, Passeriformes). *Molecular Phylogenetics and Evolution*, **47**, 960-973.

Andersson, M. (1994). *Sexual selection*. Princeton University Press, Princeton.

Armenta, J.K., Dunn, P.O. & Whittingham, L.A. (2008). Quantifying avian sexual dichromatism: a comparison of methods. *Journal of Experimental Biology*, **211**, 2423-2430.

Arnaiz-Villena, A., Gomez-Priet, P. & Ruiz-del-Valle, V. (2009). Phylogeography of finches and sparrows. In: *Phylogeography: concepts, intraspecific patterns and speciation processes* (ed. Rutgers, DS). Nova Science Publishers Hauppauge, NY.

Arnegard, M.E., McIntyre, P.B., Harmon, L.J., Zelditch, M.L., Crampton, W.G., Davis, J.K. *et al.* (2010). Sexual signal evolution outpaces ecological divergence during electric fish species radiation. *American Naturalist*, **176**, 335-356.

Avise, J.C. & Walker, D. (1998). Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 457-463.

Avise, J.C., Walker, D. & Johns, G.C. (1998). Speciation durations and Pleistocene effects on vertebrate phylogeogrpahy. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 1707-1712.

Badyaev, A.V. & Hill, G.E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 27-49.

Badyaev, A.V., Hill, G.E. & Weckworth, B.V. (2002). Species divergence in sexually selected traits: increase in song elaboration is related to decrease in plumage ornamentation in finches. *Evolution*, **56**, 412-419.

Baker, T.R., Pennington, R.T., Magallon, S., Gloor, E., Laurance, W.F., Alexiades, M. *et al.* (2014). Fast demographic traits promote high diversification rates of Amazonian trees. *Ecology Letters*, **17**, 527-536.

Baptista, L.F. (1996). Nature and its nurturing in vocal development. In: *Ecology and evolution of acoustic communication in birds* (eds. Kroodsma, DE & Miller, EH). Cornell University Press Ithaca, NY.

Barker, F.K. (2007). Avifaunal interchange across the Panamanian isthmus: insights from *Campylorhynchus* wrens. *Biological Journal of the Linnean Society*, **90**, 687-702.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. (2004). Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences*, **101**, 11040-11045.

Barnosky, A.D. (2001). Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *Journal of Vertebrate Paleontology*, **21**, 172-187.

Barraclough, T.G., Harvey, P.H. & Nee, S. (1995). Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **259**, 211-215.

Beecher, M.D. & Brenowitz, E.A. (2005). Functional aspects of song learning in songbirds. *Trends in Ecology & Evolution*, **20**, 143-149.

Bennett, A.T., Cuthill, I.C., Partridge, J.C. & Lunau, K. (1997). Ultraviolet plumage colors predict mate preferences in starlings. *Proceedings of the National Academy of Sciences*, **94**, 8618-8621.

Benton, M.J. (2009). The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science*, **323**, 728-732.

Böhning-Gaese, K., Caprano, T., van Ewijk, K. & Veith, M. (2006). Range size: disentangling current traits and phylogenetic and biogeographic factors. *American Naturalist*, **167**, 555-567.

Bonaccorso, E. & Peterson, A.T. (2007). A multilocus phylogeny of New World jay genera. *Molecular Phylogenetics and Evolution*, **42**, 467-476.

Bonaccorso, E., Peterson, A.T., Navarro-Sigüenza, A.G. & Fleischer, R.C. (2010). Molecular systematics and evolution of the *Cyanocorax* jays. *Molecular Phylogenetics and Evolution*, **54**, 897-909.

Botero, C.A., Boogert, N.J., Vehrencamp, S.L. & Lovette, I.J. (2009). Climatic patterns predict the elaboration of song displays in mockingbirds. *Current Biology*, **19**, 1151-1155.

Botero, C.A., Dor, R., McCain, C.M. & Safran, R.J. (2014). Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Molecular Ecology*, **23**, 259-268.

Boucher, F.C., Thuiller, W., Davies, T.J. & Lavergne, S. (2014). Neutral biogeography and the evolution of climatic niches. *American Naturalist*, **183**, 573-584.

Boughman, J.W. (2002). How sensory drive can promote speciation. *Trends in Ecology & Evolution*, **17**, 571-577.

Boyle, W.A. (2008). Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology*, **77**, 1122-1128.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597-623.

Brumfield, R.T. & Edwards, S.V. (2007). Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. *Evolution*, **61**, 346-367.

Burney, C.W. & Brumfield, R.T. (2009). Ecology predicts levels of genetic differentiation in Neotropical birds. *American Naturalist*, **174**, 358-368.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.

Burns, K.J. (1998a). Molecular phylogenetics of the genus *Piranga*: implications for biogeography and the evolution of morphology and behavior. *Auk*, **115**, 621-634.

Burns, K.J. (1998b). A phylogenetic perspective on the evolution of sexual dichromatism in tanagers (Thraupidae): The role of female versus male plumage. *Evolution*, **52**, 1219-1224.

Burns, K.J. & Racicot, R.A. (2009). Molecular phylogenetics of a clade of lowland tanagers: implications for avian participation in the Great American Interchange. *Auk*, **126**, 635-648.

Butlin, R., Debelle, A., Kerth, C., Snook, R.R., Beukeboom, L.W., Castillo Cajas, R.F. *et al.* (2012). What do we need to know about speciation? *Trends in Ecology & Evolution*, **27**, 27-39.

Byrne, P.G., Roberts, J.D. & Simmons, L.W. (2002). Sperm competition selects for increased testes mass in Australian frogs. *Journal of Evolutionary Biology*, **15**, 347-355.

Cadena, C.D., Kozak, K.H., Gómez, J.P., Parra, J.L., McCain, C.M., Bowie, R.C.K. *et al.* (2012). Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 194-201.

Calhim, S. & Birkhead, T.R. (2006). Testes size in birds: quality versus quantity—assumptions, errors, and estimates. *Behavioral Ecology*, **18**, 271-275.

Cardillo, M. (1999). Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1221-1225.

Cardillo, M., Orme, C.D.L. & Owens, I.P.F. (2005). Testing for latitudinal bias in diversification rates: An example using new world birds. *Ecology*, **86**, 2278-2287.

Carson, R.J. & Spicer, G.S. (2003). A phylogenetic analysis of the emberizid sparrows based on three mitochondrial genes. *Molecular Phylogenetics and Evolution*, **29**, 43-57.

Catchpole, C.K. (1982). The evolution of bird sounds in relation to mating and spacing behavior. In: *Acoustic communication in birds, Vol. 1* (eds. Kroodsma, DE & Miller, EH). Academic Press New York, NY, pp. 297-319.

Catchpole, C.K. & Slater, P.J.B. (1995). *Birdsong: biological themes and variations*. Cambridge University Press, Cambridge UK.

Chesser, R.T., Barker, F.K. & Brumfield, R.T. (2007). Fourfold polyphyly of the genus formerly known as Upucerthia, with notes on the systematics and evolution of the avian subfamily Furnariinae. *Molecular Phylogenetics and Evolution*, **44**, 1320-1332.

Cibois, A., Pasquet, E. & Schulenberg, T.S. (1999). Molecular systematics of the Malagasy babblers (Passeriformes: Timalidae) and warblers (Passeriformes: Sylviidae), based on cytochrome *b* and 16S rRNA sequences. *Molecular Phylogenetics and Evolution*, **13**, 581-595.

Claramunt, S., Derryberry, E.P., Chesser, R.T., Alexio, A. & Brumfield, R.T. (2010). Polyphyly of *Campylorhamphus*, and description of a new genus for *C. pucherani* (Dendrocolaptinae). *Auk*, **127**, 430-439.

Claramunt, S., Derryberry, E.P., Remsen, J.V. & Brumfield, R.T. (2011). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1567-1574.

Collins, S.A. (2004). Vocal flirting and fighting: the functions of birdsong. In: *Nature's music: the science of birdsong* (eds. Marler, P & Slabbekoorn, H). Elsevier Academic Press San Diego, CA, pp. 39-79.

Colwell, R.K. & Lees, D.C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, **15**, 70-76.

Cooper, N., Freckleton, R.P. & Jetz, W. (2011). Phylogenetic conservatism of environmental niches in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2384-2391.

Cooper, N., Jetz, W. & Freckleton, R.P. (2010). Phylogenetic comparative approaches for studying niche conservatism. *Journal of Evolutionary Biology*, **23**, 2529-2539.

Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinauer, Sunderland, MA.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.-F., Hawkins, B.A. *et al.* (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121-1134.

Cuthill, I.C., Bennett, A.T.D., Partridge, J.C. & Maier, E.J. (1999). Plumage reflectance and the objective assessment of avian sexual dichromatism. *American Naturalist*, **153**, 183-200.

DaCosta, J.M., Spellman, G.M., Escalante, P. & Klicka, J. (2009). A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*. *Journal of Avian Biology*, **40**, 206-216.

Darwin, C.R. (1859). *On the origin of species, or the preservation of favoured races in the struggle for life*. John Murray, London, UK.

Darwin, C.R. (1871). *The descent of man, and selection in relation to sex*. John Murray, London.

Davis, M.P., Midford, P.E. & Maddison, W.P. (2013). Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evolutionary Biology*, **13**, 38.

Dawideit, B.A., Phillimore, A.B., Laube, I., Leisler, B. & Böhning-Gaese, K. (2009). Ecomorphological predictors of natal dispersal distances in birds. *Journal of Animal Ecology*, **78**, 388-395.

del Hoyo, J., Elliott, A., Sargatal, J. & Christe, D.A. (1992–2011). *The Handbook of the Birds of the World*. Lynx Edicions, Barcelona.

Derryberry, E.P., Claramunt, S., Derryberry, G., Chesser, R.T., Cracraft, J., Aleixo, A. *et al.* (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: the Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, **65**, 2973-2986.

Dial, K.P. & Marzluff, J.M. (1989). Nonrandom diversification within taxonomic assemblages. *Systematic Zoology*, **38**, 26-37.
Diamond, J.M. (1975). Assembly of species communities. In: *Ecology and Evolution of Communities* (eds. Cody, ML & Diamond, JM). Harvard University Press Cambridge, MA.
Dobzhansky, T. (1937). *Genetics and the origin of species*. Columbia University Press, New York.
Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist*, **38**, 209-221.
Dong, F., Li, S.-H. & Yang, X.-j. (2010). Molecular systematics and diversification of the Asian scimitar babblers (Timaliidae, Aves) based on mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution*, **57**, 1268-1275.
Drummond, A.J. & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.
Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969-1973.
Dumbacher, J.P., Deiner, K., Thompson, L. & Fleischer, R.C. (2008). Phylogeny of the avian genus *Pitohui* and the evolution of toxicity in birds. *Molecular Phylogenetics and Evolution*, **49**, 774-781.
Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, **55**, 161-175.
Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences*, **97**, 9115-9120.
Eaton, M.D. (2005). Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds. *Proceedings of the National Academy of Sciences*, **102**, 10942-10946.
Eaton, M.D., Soberón, J. & Peterson, A.T. (2008). Phylogenetic perspective on ecological niche evolution in american blackbirds (Family Icteridae). *Biological Journal of the Linnean Society*, **94**, 869-878.
Endler, J.A. (1990). On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society*, **41**, 315-352.
Endler, J.A. (1992). Signals, signal conditions, and the direction of evolution. *American Naturalist*, **139**, S125-S153.
Endler, J.A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **340**, 215-225.
Endler, J.A. & Théry, M. (1996). Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. *American Naturalist*, **148**, 421-452.
Etienne, R.S. & Rosindell, J. (2012). Prolonging the past counteracts the pull of the present: protracted speciation can explain observed slowdowns in diversification. *Systematic Biology*, **61**, 204-213.
Evans, M.E.K., Smith, S.A., Flynn, R.S. & Donoghue, M.J. (2009). Climate, niche evolution, and diversification of the "bird‐cage" evening primroses

(*Oenothera*, sections *Anogra* and *Kleinia*). *American Naturalist*, **173**, 225-240.
Ezard, T.H.G., Aze, T., Pearson, P.N. & Purvis, A. (2011). Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, **332**, 349-351.
Fischer, A.G. (1960). Latitudinal variations in organic diversity. *American Scientist*, **49**, 50-74.
Fisher, R.A. (1930). *The genetical theory of natural selection*. Clarendon Press, Oxford, UK.
FitzJohn, R.G. (2010). Quantitative traits and diversification. *Systematic Biology*, **59**, 619-633.
FitzJohn, R.G. (2012). Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution*, **3**, 1084-1092.
FitzJohn, R.G., Maddison, W.P. & Otto, S.P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology*, **58**, 595-611.
Ford, D., Matsen, F.A. & Stadler, T. (2009). A method for investigating relative timing information on phylogenetic trees. *Systematic Biology*, **58**, 167-183.
Fregin, S., Haase, M., Olsson, U. & Alström, P. (2009). Multi-locus phylogeny of the family Acrocephalidae (Aves: Passeriformes) – the traditional taxonomy overthrown. *Molecular Phylogenetics and Evolution*, **52**, 866-878.
Fuchs, J., Pasquet, E., Couloux, A., Fjeldså, J. & Bowie, R.C. (2009). A new Indo-Malayan member of the Stenostiridae (Aves: Passeriformes) revealed by multilocus sequence data: biogeographical implications for a morphologically diverse clade of flycatchers. *Molecular Phylogenetics and Evolution*, **53**, 384-393.
Garamszegi, L.Z., Pavlova, D.Z., Eens, M. & Møller, A.P. (2007). The evolution of song in female birds in Europe. *Behavioral Ecology*, **18**, 86-96.
Gardner, J.L., Trueman, J.W.H., Ebert, D., Joseph, L. & Magrath, R.D. (2010). Phylogeny and evolution of the Meliphagoidea, the largest radiation of Australasian songbirds. *Molecular Phylogenetics and Evolution*, **55**, 1087-1102.
Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*, **405**, 220-227.
Gavrilets, S. (2004). *Fitness landscapes and the origin of species*. Princeton University Press, Princeton.
Gill, F.B., Slikas, B. & Sheldon, F.H. (2005). Phylogeny of titmice (Paridae): II. species relationships based on sequences of the mitochondrial cytochrome-*B* gene. *Auk*, **122**, 121-143.
Gill, S.A. & Stutchbury, B.J.M. (2006). Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). *Behavioral Ecology and Sociobiology*, **61**, 245-253.
Gillespie, D.T. (1976). A general method for numerically simulating the stochastic time evolution of coupled reactions. *Journal of Computational Physics*, **22**, 403-434.
Goldberg, E.E., Kohn, J.R., Lande, R., Robertson, K.A., Smith, S.A. & Igić, B. (2010). Species selection maintains self-incompatibility. *Science*, **330**, 493-495.
Gómez, J.P., Bravo, G.A., Brumfield, R.T., Tello, J.G. & Cadena, C.D. (2010). A phylogenetic approach to disentangling the role of competition and habitat

filtering in community assembly of Neotropical forest birds. *Journal of Animal Ecology*, **79**, 1181-1192.
Gonzalez-Voyer, A., den Tex, R.J., Castelló, A. & Leonard, J.A. (2013). Evolution of acoustic and visual signals in Asian barbets. *Journal of Evolutionary Biology*, **26**, 647-659.
Gould, S.J., Raup, D.M., Sepkoski, J.J., Schopf, T.J.M. & Simberloff, D.S. (1977). The shape of evolution: a comparison of real and random clades. *Paleobiology*, **3**, 23-40.
Graham, C.H., Ron, S.R., Santos, J.C., Schneider, C.J. & Moritz, C. (2004). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*, **58**, 1781-1793.
Grant, P.R. & Grant, B.R. (1997). Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences*, **94**, 7769-7775.
Greenberg, R. & Gradwohl, J. (1997). Territoriality, adult survival, and dispersal in the Checker-throated Antwren in Panama. *Journal of Avian Biology*, **28**, 103-110.
Grinnell, J. (1914). Barriers to distribution as regards birds and mammals. *American Naturalist*, **48**, 248-254.
Gröning, J. & Hochkirch, A. (2008). Reproductive interference between animal species. *Quarterly Review of Biology*, **83**, 257-282.
Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J. *et al.* (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, **320**, 1763-1768.
Haffer, J. (1969). Speciation in Amazonian forest birds. *Science*, **165**, 131-137.
Hansen, T.F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, **51**, 1341-1351.
Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008). GEIGER: investigating evolutionary radiations. *Bioinformatics*, **24**, 129-131.
Hart, N.S. (2001). The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research*, **20**, 675-703.
Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007). Climate, niche conservatism, and the global bird diversity gradient. *American Naturalist*, **170**, S16-S27.
Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003). Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, **84**, 1608-1623.
Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.
Hill, G.E. (1990). Female house finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behaviour*, **40**.
Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 192-211.
Hochkirch, A., Gröning, J. & Bücker, A. (2007). Sympatry with the devil: reproductive interference could hamper species coexistence. *Journal of Animal Ecology*, **76**, 633-642.
Holt, R.D. (1990). The microevolutionary consequences of climate change. *Trends in Ecology & Evolution*, **5**, 311-315.

Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A. & Taper, M.L. (2005). Theoretical models of species' borders: single species approaches. *Oikos*, **108**, 18-27.
Hosken, D. & Ward, P.I. (2001). Experimental evidence for testis size evolution via sperm competition. *Ecology Letters*, **4**, 10-13.
Hunt, S., Cuthill, I.C., Bennett, A.T. & Griffiths, R. (1999). Preferences for ultraviolet partners in the blue tit. *Animal Behaviour*, **58**, 809-815.
Hurlbert, A.H. & Jetz, W. (2007). Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences*, **104**, 13384-13389.
Hurlbert, A.H. & White, E.P. (2005). Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters*, **8**, 319-327.
Hutchinson, G.E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, **93**, 145-159.
Ikeda, H., Nishikawa, M. & Sota, T. (2012). Loss of flight promotes beetle diversification. *Nat Commun*, **3**, 648.
Illera, J.C., Richardson, D.S., Helm, B., Atienza, J.C. & Emerson, B.C. (2008). Phylogenetic relationships, biogeography and speciation in the avian genus *Saxicola*. *Molecular Phylogenetics and Evolution*, **48**, 1145-1154.
Irestedt, M., Fjeldså, J., Dalén, L. & Ericson, P.G.P. (2009a). Convergent evolution, habitat shifts and variable diversification rates in the ovenbird-woodcreeper family (Furnariidae). *BMC Evolutionary Biology*, **9**, 268.
Irestedt, M., Jønsson, K.A., Fjeldså, J., Christidis, L. & Ericson, P.G.P. (2009b). An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evolutionary Biology*, **9**, 235.
Irwin, D.E. (2000). Song variation in an avian ring species. *Evolution*, **54**, 998-1010.
Irwin, D.E., Bensch, S. & Price, T.D. (2001). Speciation in a ring. *Nature*, **409**, 333-337.
Irwin, D.E., Thimgan, M.P. & Irwin, J.H. (2008). Call divergence is correlated with geographic and genetic distance in greenish warblers (*Phylloscopus trochiloides*): a strong role for stochasticity in signal evolution? *Journal of Evolutionary Biology*, **21**, 435-448.
Isaac, N.J.B., Jones, K.E., Gittleman, J.L. & Purvis, A. (2005). Correlates of species richness in mammals: body size, life history, and ecology. *American Naturalist*, **165**, 600-607.
Ives, A.R., Midford, P.E. & Garland, T., Jr. (2007). Within-species variation and measurement error in phylogenetic comparative methods. *Systematic Biology*, **56**, 252-270.
Iwasa, Y. & Pomiankowski, A. (1994). The evolution of mate preferences for multiple sexual ornaments. *Evolution*, **48**, 853-867.
Iwasa, Y. & Pomiankowski, A. (1995). Continual change in mate preferences. *Nature*, **377**, 420-422.
Jablonski, D. (2008). Species selection: theory and data. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 501-524.
Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102-106.
Jackson, C.H. (2011). Multi-state models for panel data: the msm package for R. *Journal of Statistical Software*, **38**, 1-28.

Jackson, D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology*, **74**, 2204-2214.
Jacobsen, F., Friedman, N.R. & Omland, K.E. (2010). Congruence between nuclear and mitochondrial DNA: combination of multiple nuclear introns resolves a well-supported phylogeny of New World orioles (*Icterus*). *Molecular Phylogenetics and Evolution*, **56**, 419-427.
Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *American Naturalist*, **101**, 233-249.
Jetz, W., Sekercioglu, C.H. & Watson, J.E.M. (2008). Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology*, **22**, 110-119.
Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, **491**, 444-448.
Jocque, M., Field, R., Brendonck, L. & De Meester, L. (2010). Climatic control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, **19**, 244-252.
Johansson, U.S., Alström, P., Olsson, U., Ericson, P.G., Sundberg, P. & Price, T.D. (2007a). Build-up of the Himalayan avifauna through immigration: a biogeographical analysis of the *Phylloscopus* and *Seicercus* warblers. *Evolution*, **61**, 324-333.
Johansson, U.S., Fjeldså, J. & Bowie, R.C. (2008). Phylogenetic relationships within Passerida (Aves: Passeriformes): a review and a new molecular phylogeny based on three nuclear intron markers. *Molecular Phylogenetics and Evolution*, **48**, 858-876.
Johansson, U.S., Fjeldså, J., Lokugalappatti, L.G.S. & Bowie, R.C.K. (2007b). A nuclear DNA phylogeny and proposed taxonomic revision of African greenbuls (Aves, Passeriformes, Pycnonotidae). *Zoologica Scripta*, **36**, 417-427.
Johnson, A.E., Price, J.J. & Pruett-Jones, S. (2013). Different modes of evolution in males and females generate dichromatism in fairy-wrens (Maluridae). *Ecology and Evolution*, **3**, 3030-3046.
Johnson, N.K. & Cicero, C. (2002). The role of ecological diversification in sibling speciation of *Empidonax* flycatchers (Tyrannidae): multigene evidence from mtDNA. *Molecular Ecology*, **11**, 2065-2081.
Jones, A.G. & Ratterman, N.L. (2009). Mate choice and sexual selection: what have we learned since Darwin? *Proceedings of the National Academy of Sciences*, **106**, 10001-10008.
Joseph, L., Wilke, T., Bermingham, E., Alpers, D. & Ricklefs, R.E. (2004). Towards a phylogenetic framework for the evolution of shakes, rattles, and rolls in *Myiarchus* tyrant-flycatchers (Aves: Passeriformes: Tyrannidae). *Molecular Phylogenetics and Evolution*, **21**, 139-152.
Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, **30**, 3059-3066.
Kendall, D.G. (1948). On the generalized "birth-and-death" process. *Annals of Mathematical Statistics*, **19**, 1-15.
Kennedy, J.D., Wang, Z., Weir, J.T., Rahbek, C., Fjeldså, J. & Price, T.D. (2014). Into and out of the tropics: the generation of the latitudinal gradient among New World passerine birds. *Journal of Biogeography*, **41**, 1746-1754.

Kisel, Y. & Barraclough, T.G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *American Naturalist*, **175**, 316-334.
Klicka, J., Burns, K. & Spellman, G.M. (2007). Defining a monophyletic Cardinalini: a molecular perspective. *Molecular Phylogenetics and Evolution*, **45**, 1014-1032.
Klicka, J. & Spellman, G.M. (2007). A molecular evaluation of the North American "grassland" sparrow clade. *Auk*, **124**, 537-551.
Klicka, J., Voelker, G. & Spellman, G.M. (2005). A molecular phylogenetic analysis of the "true thrushes" (Aves: Turdinae). *Molecular Phylogenetics and Evolution*, **34**, 486-500.
Klicka, J., Zink, R.M. & Winker, K. (2003). Longspurs and snow buntings: phylogeny and biogeography of a high-latitude clade (*Calcarius*). *Molecular Phylogenetics and Evolution*, **26**, 165-175.
Kokko, H. & Brooks, R. (2003). Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici Fennici*, **40**, 207-219.
Kozak, K.H. & Wiens, J.J. (2006). Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution*, **60**, 2604-2621.
Kozak, K.H. & Wiens, J.J. (2007). Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2995-3003.
Kozak, K.H. & Wiens, J.J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378-1389.
Kraaijeveld, K., Kraaijeveld-Smit, F.J.L. & Maan, M.E. (2011). Sexual selection and speciation: the comparative evidence revisited. *Biological Reviews of the Cambridge Philosophical Society*, **86**, 367-377.
Kroodsma, D.E. (2004). The diversity and plasticity of birdsong. In: *Nature's music: the science of bird song* (eds. Marler, P & Slabbekoorn, H). Academic Press London, UK.
Krug, A.Z., Jablonski, D., Valentine, J.W. & Roy, K. (2009). Generation of Earth's first-order biodiversity pattern. *Astrobiology*, **9**, 113-124.
Krüger, O. (2008). Engines of speciation: a comparative study in birds of prey. *Journal of Evolutionary Biology*, **21**, 861-872.
Lachlan, R.F. & Servedio, M.R. (2004). Song learning accelerates allopatric speciation. *Evolution*, **58**, 2049-2063.
Lack, D. (1947). *Darwin's finches*. Cambridge University Press, Cambridge, UK.
Lack, D. (1976). *Island biology, illustrated by the land birds of Jamaica*. University of California Press, Berkley, CA.
Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences*, **78**, 3721-3725.
Lanyon, S.M. & Omland, K.E. (1999). A molecular phylogeny of the blackbirds (Icteridae): five lineages revealed by cytochrome-*b* sequence data. *Auk*, **116**, 629-639.
Lawson, A.M. & Weir, J.T. (2014). Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters*, **17**, 1427-1436.
Lees, A.C. & Peres, C.A. (2009). Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos*, **118**, 280-290.
Levey, D.J. & Stiles, F.G. (1992). Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *American Naturalist*, **140**, 447-476.

Lim, H.C., Zou, F., Taylor, S.S., Marks, B.D., Moyle, R.G., Voelker, G. *et al.* (2010). Phylogeny of magpie-robins and shamas (Aves: Turdidae: *Copsychus* and *Trichixos*): implications for island biogeography in Southeast Asia. *Journal of Biogeography*, **37**, 1894-1906.

Lorch, P.D., Proulx, S., Rowe, L. & Day, T. (2003). Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research*, **5**, 867-881.

Losos, J.B. (2011). Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *American Naturalist*, **177**, 709-727.

Lovette, I.J., Pérez-Emán, J.L., Sullivan, J.P., Banks, R.C., Fiorentino, I., Córdoba-Córdoba, S. *et al.* (2010). A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). *Molecular Phylogenetics and Evolution*, **57**, 753-770.

Luther, D. (2009). The influence of the acoustic community on songs of birds in a neotropical rain forest. *Behavioral Ecology*, **20**, 864-871.

M'Gonigle, L.K., Mazzucco, R., Otto, S.P. & Dieckmann, U. (2012). Sexual selection enables long-term coexistence despite ecological equivalence. *Nature*, **484**, 506-509.

MacArthur, R.H. (1958). Population ecology of some warblers of northeastern coniferous forest. *Ecology*, **39**, 599-619.

MacArthur, R.H. (1964). Environmental factors affecting bird species diversity. *American Naturalist*, **98**, 387-397.

MacArthur, R.H. (1972). *Geographical ecology: patterns in the distributions of species*. Harper and Row, New York.

Macedo, R.H., Karubian, J. & Webster, M.S. (2008). Extrapair paternity and sexual selection in socially monogamous birds: are tropical birds different? *Journal of Ornithology*, **125**, 769-777.

Macedonia, J.M. (2001). Habitat light, colour variation, and ultraviolet reflectance in the Grand Cayman anole, *Anolis conspersus*. *Biological Journal of the Linnean Society*, **73**, 299-320.

Machac, A., Storch, D. & Wiens, J.J. (2013). Ecological causes of decelerating diversification in carnivoran mammals. *Evolution*, **67**, 2423-2433.

Maddison, W.P., Midford, P.E. & Otto, S.P. (2007). Estimating a binary character's effect on speciation and extinction. *Systematic Biology*, **56**, 701-710.

Mann, N.I., Barker, F.K., Graves, J.A., Dingess-Mann, K.A. & Slater, P.J.B. (2006). Molecular data delineate four genera of "*Thryothorus*" wrens. *Molecular Phylogenetics and Evolution*, **40**, 750-759.

Martin, P.R. & McKay, J.K. (2004). Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution*, **58**, 938-945.

Martin, P.R., Montgomerie, R. & Lougheed, S.C. (2010). Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution*, **64**, 336-347.

Martin, P.R. & Tewksbury, J.J. (2008). Latitudinal variation in subspecific diversification of birds. *Evolution*, **62**, 2775-2788.

Mason, N.A., Shultz, A.J. & Burns, K.J. (2014). Elaborate visual and acoustic signals evolve independently in a large, phenotypically diverse radiation of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140967.

Mauck, W.M., III & Burns, K.J. (2009). Phylogeny, biogeography, and recurrent evolution of divergent bill types in the nectar-stealing flowerpiercers (Thraupini: *Diglossa* and *Diglossopis*). *Biological Journal of the Linnean Society*, **98**, 14-28.

Mayr, E. (1942). *Systematics and the origin of species*. Cambridge University Press, New York.

Mayr, E. (1963). *Animal species and evolution*. Harvard University Press, Cambridge, MA.

Mayr, E. & Diamond, J.M. (2001). *The birds of northern Melanesia: speciation, ecology, and biogeography*. Oxford University Press, New York, NY.

McLain, D.K., Moulton, M.P. & Redfearn, T.P. (1995). Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos*, **74**, 27-34.

Miller, M.J., Bermingham, E., Klicka, J., Escalante, P., do Amaral, F.S.R., Weir, J.T. *et al.* (2008). Out of Amazonia again and again: episodic crossing of the Andes promotes diversification in a lowland forest flycatcher. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1133-1142.

Misof, B. (2002). Diversity of Anisoptera (Odonata): infering speciation processes from patterns of morphological diversity. *Zoology*, **105**, 355-365.

Mitra, S., Landel, H. & Pruett-Jones, S. (1996). Species richness covaries with mating system in birds. *Auk*, **113**, 544-551.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B. *et al.* (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315-331.

Møller, A.P. (1997). Immune defence, extra-pair paternity, and sexual selection in birds. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 561-566.

Møller, A.P. & Birkhead, T.R. (1994). The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution*, **48**, 1089-1100.

Møller, A.P. & Briskie, J.V. (1995). Extra-pair paternity, sperm competition and the evolution of testis size in birds. *Behavioral Ecology and Sociobiology*, **36**, 357-365.

Mooers, A.Ø. & Heard, S.B. (1997). Inferring evolutionary process from phylogenetic tree shape. *Quarterly Review of Biology*, **72**, 31-54.

Moore, R.P., Robinson, W.D., Lovette, I.J. & Robinson, T.R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, **11**, 960-968.

Moore, W.S. & Price, J.T. (1993). Nature of selection in the norther flicker hybrid zone and its implications for speciation theory. In: *Hybrid Zones and the Evolutionary Process* (ed. Harrison, RG). Oxford University Press Oxford, pp. 196-225.

Moritz, C., Patton, J.L., Schneider, C.J. & Smith, T.B. (2000). Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics*, **31**, 533-563.

Morrow, E.H. & Fricke, C. (2004). Sexual selection and the risk of extinction in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 2395-2401.

Morrow, E.H. & Pitcher, T.E. (2003). Sexual selection and the risk of extinction in birds. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1793-1799.

Morrow, E.H., Pitcher, T.E. & Arnqvist, G. (2003). No evidence that sexual selection is an 'engine of speciation' in birds. *Ecology Letters*, **6**, 228-234.

Morton, E.S. (1975). Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17-24.

Moyle, R.G., Chesser, R.T., Brumfield, R.T., Tello, J.G., Marchese, D.J. & Cracraft, J. (2009). Phylogeny and phylogenetic classification of the antbirds, ovenbirds, woodcreepers, and allies (Aves: Passeriformes: Infraorder Furnariides). *Cladistics*, **25**, 386-405.

Nadeau, N.J., Burke, T. & Mundy, N.I. (2007). Evolution of an avian pigmentation gene correlates with a measure of sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1807-1813.

Nee, S., Mooers, A.Ø. & Harvey, P.H. (1992). Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences*, **89**, 8322-8326.

Nelson, D.A. & Marler, P. (1990). The perception of bird song and an ecological concept of signal space. In: *Comparative perception: complex signals* (eds. Stebbins, WC & Berkley, MA). Wiley New York.

Nguembock, B., Fjeldså, J., Couloux, A. & Pasquet, E. (2008). Phylogeny of *Laniarius*: Molecular data reveal *L. liberatus* synonymous with *L. erlangeri* and "plumage coloration" as unreliable morphological characters for defining species and species groups. *Molecular Phylogenetics and Evolution*, **48**, 396-407.

Nosil, P. (2012). *Ecological specation*. Oxford University Press, Oxford, UK.

Nosil, P. & Harmon, L.J. (2009). Niche dimensionality and ecological speciation. In: *Speciation and Patterns of Diversity* (eds. Butlin, RK, Bridle, JR & Schluter, D). Cambridge University Press Cambridge, UK.

Nylander, J.A.A., Olsson, U., Alström, P. & Sanmartín, I. (2008). Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, **57**, 257-268.

Olalla-Tárraga, M.Á., McInnes, L., Bini, L.M., Diniz-Filho, J.A.F., Fritz, S.A., Hawkins, B.A. *et al.* (2011). Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. *Journal of Biogeography*, **38**, 2237-2247.

Omland, K.E. (1997). Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution*, **51**, 1636-1646.

Omland, K.E., Lanyon, S.M. & Fritz, S.J. (1999). A molecular phylogeny of the New World orioles (*Icterus*): the importance of dense taxon sampling. *Molecular Phylogenetics and Evolution*, **12**, 224-239.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A. *et al.* (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436**, 1016-1019.

Orme, C.D.L., Freckleton, R.P., Thomas, G.H., Petzoldt, T. & Fritz, S.A. (2011). Caper: comparative analyses of phylogenetics and evolution in R.

Ornelas, J.F., Gonzalez, C. & Espinosa de los Monteros, A. (2009). Uncorrelated evolution between vocal and plumage coloration traits in the trogons: a comparative study. *Journal of Evolutionary Biology*, **22**, 471-484.

Outlaw, D.C. & Voelker, G. (2006). Systematics of *Ficedula* flycatchers (Muscicapidae): a molecular reassessment of a taxonomic enigma. *Molecular Phylogenetics and Evolution*, **41**, 118-126.

Outlaw, R.K., Voelker, G. & Bowie, R.C. (2010). Shall we chat? Evolutionary relationships in the genus *Cercomela* (Muscicapidae) and its relation to *Oenanthe* reveals extensive polyphyly among chats distributed in Africa, India and the Palearctic. *Molecular Phylogenetics and Evolution*, **55**, 284-292.

Owens, I.P.F. & Bennett, P.M. (1994). Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society B: Biological Sciences*, **257**, 1-8.

Owens, I.P.F., Bennett, P.M. & Harvey, P.H. (1999). Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society B: Biological Sciences*, **266**, 933-939.

Owens, I.P.F. & Hartley, I.R. (1998). Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society B: Biological Sciences*, **265**, 397-407.

Päckert, M., Martens, J. & Severinghaus, L.L. (2009). The Taiwan Firecrest (*Regulus goodfellowi*) belongs to the Goldcrest assemblage (*Regulus regulus* s. l.): evidence from mitochondrial DNA and the territorial song of the Regulidae. *Journal of Ornithology*, **150**, 205-220.

Päckert, M., Martens, J., Tietze, D.T., Dietzen, C., Wink, M. & Kvist, L. (2007). Calibration of a molecular clock in tits (Paridae)—do nucleotide substitution rates of mitochondrial genes deviate from the 2% rule? *Molecular Phylogenetics and Evolution*, **44**, 1-14.

Pagel, M. (1997). Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, **26**, 331-348.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, **401**, 877-884.

Panhuis, T.M., Butlin, R., Zuk, M. & Tregenza, T. (2001). Sexual selection and speciation. *Trends in Ecology & Evolution*, **16**, 364-371.

Pasquet, E., Pons, J.M., Fuchs, J., Cruaud, C. & Bretagnolle, V. (2007). Evolutionary history and biogeography of the drongos (Dicruridae), a tropical Old World clade of corvoid passerines. *Molecular Phylogenetics and Evolution*, **45**, 158-167.

Peterson, A.T. & Nyári, Á.S. (2007). Ecological niche conservatism and Pleistocene refugia in the Thrush-like Mourner, *Schiffornis* sp., in the neotropics. *Evolution*, **62**, 173-183.

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, **285**, 1265-1267.

Pfennig, K.S. & Pfennig, D.W. (2009). Character displacement: ecological and reproductive responses to a common evolutionary problem. *Quarterly Review of Biology*, **84**, 253-276.

Phillimore, A.B., Freckleton, R.P., Orme, C.D.L. & Owens, I.P.F. (2006). Ecology predicts large-scale patterns of phylogenetic diversification in birds. *American Naturalist*, **168**, 220-229.

Phillimore, A.B., Orme, C.D.L., Davies, R.G., Hadfield, J.D., Reed, W.J., Gaston, K.J. *et al.* (2007). Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. *Evolution*, **61**, 942-957.

Phillimore, A.B., Orme, C.D.L., Thomas, G.H., Blackburn, T.M., Bennett, P.M., Gaston, K.J. *et al.* (2008). Sympatric speciation in birds is rare: insights from range data and simulations. *American Naturalist*, **171**, 646-657.

Pigot, A.L., Owens, I.P.F. & Orme, C.D.L. (2010a). The environmental limits to geographic range expansion in birds. *Ecology Letters*, **13**, 705-715.

Pigot, A.L., Phillimore, A.B., Owens, I.P.F. & Orme, C.D.L. (2010b). The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Systematic Biology*, **59**, 660-673.

Pigot, A.L. & Tobias, J.A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, **16**, 330-338.

Pigot, A.L. & Tobias, J.A. (2015). Dispersal and the transition to sympatry in vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20141929.

Pitcher, T.E., Dunn, P.O. & Whittingham, L.A. (2005). Sperm competition and the evolution of testes size in birds. *Journal of Evolutionary Biology*, **18**, 557-567.

Price, J.J. & Eaton, M.D. (2014). Reconstructing the evolution of sexual dichromatism: current color diversity does not reflect past rates of male and female change. *Evolution*, **68**, 2026-2037.

Price, J.J., Lanyon, S.M. & Omland, K.E. (2009). Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1971-1980.

Price, J.J. & Whalen, L.M. (2009). Plumage evolution in the oropendolas and caciques: different divergence rates in polygynous and monogamous taxa. *Evolution*, **63**, 2985-2998.

Price, S.A., Tavera, J.J., Near, T.J. & Wainwright, P.C. (2013). Elevated rates of morphological and functional diversification in reef-dwelling fishes. *Evolution*, **67**, 417-428.

Price, T. (1998). Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353**, 251-260.

Price, T.D. (1984). Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. *Evolution*, **38**, 327-341.

Price, T.D. (2008). *Speciation in birds*. Roberts and Co., Greenwood Village, CO.

Price, T.D. & Birch, G.L. (1996). Repeated evolution of sexual color dimorphism in passerine birds. *Auk*, **113**, 842-848.

Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P. *et al.* (2014). Niche filling slows the diversification of Himalayan songbirds. *Nature*, **509**, 222-225.

Price, T.D., Mohan, D., Tietze, D.T., Hooper, D.M., Orme, C.D.L. & Rasmussen, P.C. (2011). Determinants of northerly range limits along the Himalayan bird diversity gradient. *American Naturalist*, **178**, S97-S108.

Promislow, D.E.L., Montgomerie, R. & Martin, T.E. (1992). Mortality costs of sexual dimorphism in birds. *Proceedings of the Royal Society B: Biological Sciences*, **250**, 143-150.

Proulx, S.R. (1999). Mating systems and the evolution of niche breadth. *American Naturalist*, **154**, 89-98.

Purvis, A., Orme, C.D.L., Toomey, N.H. & Pearson, P.N. (2009). Temporal patterns in diversification rates. In: *Speciation and Patterns of Diversity* (eds. Butlin, R,

Bridle, J & Schluter, D). Cambridge University Press Cambridge, pp. 278-300.
Pyron, R.A. & Wiens, J.J. (2013). Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131622.
Quintero, I. & Wiens, J.J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecology Letters*, **16**, 1095-1103.
Rabosky, D.L. (2009a). Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, **12**, 735-743.
Rabosky, D.L. (2009b). Ecological limits on clade diversification in higher taxa. *American Naturalist*, **173**, 662-674.
Rabosky, D.L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution*, **64**, 1816-1824.
Rabosky, D.L. (2013). Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 481-502.
Rabosky, D.L. & Adams, D.C. (2012). Rates of morphological evolution are correlated with species richness in salamanders. *Evolution*, **66**, 1807-1818.
Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J. *et al.* (2013). Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat Commun*, **4**, 1958.
Rabosky, D.L., Slater, G.J. & Alfaro, M.E. (2012). Clade age and species richness are decoupled across the eukaryotic tree of life. *PLoS Biology*, **10**, e1001381.
Rahbek, C. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, **98**, 4534-4539.
Raikow, R.J. (1986). Why are there so many kinds of passerine birds? *Systematic Zoology*, **35**, 255-259.
Rambaut, A. & Drummond, A.J. (2007). Tracer v1.4.
Raup, D.M., Gould, S.J., Schopf, T.J.M. & Simberloff, D.S. (1973). Stochastic models of phylogeny and the evolution of diversity. *Journal of Geology*, **81**, 525-542.
Revell, L.J., Harmon, L.J. & Collar, D.C. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, **57**, 591-601.
Rice, N.H. (2005). Phylogenetic relationships of antpitta genera (Passeriformes: Formicariidae). *Auk*, **122**, 673-683.
Rice, N.H., Martínez-Meyer, E. & Peterson, A.T. (2003). Ecological niche differentiation in the *Aphelocoma* jays: a phylogenetic perspective. *Biological Journal of the Linnean Society*, **80**, 369-383.
Rice, W.R. & Hostert, E.E. (1993). Laboratory experiments on speciation: what have we learned in 40 years? *Evolution*, **47**, 1637-1653.
Ricklefs, R.E. (2003). Global diversification rates of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2285-2291.
Ricklefs, R.E. (2006). Global variation in the diversification rate of passerine birds. *Ecology*, **87**, 2468-2478.
Ricklefs, R.E. (2009). Speciation, extinction, and diversity. In: *Speciation and Patterns of Diversity* (eds. Butlin, R, Bridle, J & Schluter, D). Cambridge University Press Cambridge.

Ricklefs, R.E. & Renner, S.S. (2012). Global correlations in tropical tree species richness and abundance reject neutrality. *Science*, **335**, 464-467.
Ritchie, M.G. (2007). Sexual selection and speciation. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 79-102.
Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514-527.
Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014a). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology*, **12**, e1001775.
Rolland, J., Jiguet, F., Jønsson, K.A., Condamine, F.L. & Morlon, H. (2014b). Settling down of seasonal migrants promotes bird diversification. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140473.
Rosenzweig, M.L. (1995). *Species diversity in space and time*. Cambridge University Press, New York, NY.
Roy, M.S., Torres-Mura, J.C. & Hertel, F. (1999). Molecular phylogeny and evolutionary history of the tit-tyrants (Aves: Tyrannidae). *Molecular Phylogenetics and Evolution*, **11**, 67-76.
Rundle, H.D. & Nosil, P. (2005). Ecological speciation. *Ecology Letters*, **8**, 336-352.
Ryan, M.J. & Brenowitz, E.A. (1985). The role of body size, phylogeny, and ambient noise profiles in the evolution of bird song. *American Naturalist*, **126**, 87-100.
Salisbury, C.L., Seddon, N., Cooney, C.R. & Tobias, J.A. (2012). The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters*, **15**, 847-855.
Sangster, G., Alström, P., Forsmark, E. & Olsson, U. (2010). Multi-locus phylogenetic analysis of Old World chats and flycatchers reveals extensive paraphyly at family, subfamily and genus level (Aves: Muscicapidae). *Molecular Phylogenetics and Evolution*, **57**, 380-392.
Sato, A., O'hUigin, C., Figueroa, F., Grant, P.R., Grant, B.R., Tichy, H. *et al.* (1999). Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proceedings of the National Academy of Sciences*, **96**, 5101-5106.
Schemske, D. (2002). Tropical diversity: patterns and processes. In: *Ecological and evolutionary perspectives on the origins of tropical diversity: key papers and commentaries* (eds. Chazdon, R & Whitmore, T). University of Chicago Press Chicago, IL, pp. 163-173.
Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, **40**, 245-269.
Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford University Press, Oxford, UK.
Schluter, D. (2001). Ecology and the origin of species. *Trends in Ecology & Evolution*, **16**, 372-380.
Schluter, D. (2009). Evidence for ecological speciation and its alternative. *Science*, **323**, 737-741.
Schluter, D. & Price, T. (1993). Honest, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society B: Biological Sciences*, **253**, 117-122.

Schnitzler, J., Graham, C.H., Dormann, C.F., Schiffers, K., Linder, H.P. & Higgins, S. (2012). Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography*, **39**, 2201-2211.

Sedano, R.E. & Burns, K.J. (2010). Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). *Journal of Biogeography*, **37**, 325-343.

Seddon, N. (2005). Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. *Evolution*, **59**, 200-215.

Seddon, N., Botero, C.A., Tobias, J.A., Dunn, P.O., Macgregor, H.E., Rubenstein, D.R. *et al.* (2013). Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131065.

Seddon, N., Merrill, R.M. & Tobias, J.A. (2008). Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *American Naturalist*, **171**, 620-631.

Seddon, N., Tobias, J.A., Eaton, M. & Ödeen, A. (2010). Human vision can provide a valid proxy for avian perception of sexual dichromatism. *Auk*, **127**, 283-292.

Servedio, M.R. & Bürger, R. (2014). The counterintuitive role of sexual selection in species maintenance and speciation. *Proceedings of the National Academy of Sciences*, **111**, 8113-8118.

Sheldon, F.H., Whittingham, L.A., Moyle, R.G., Slikas, B. & Winkler, D.W. (2005). Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **35**, 254-270.

Shutler, D. (2010). Sexual selection: when to expect trade-offs. *Biology Letters*, **7**, 101-104.

Sibley, C.G. (1957). The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor*, **59**, 166-191.

Silvestro, D., Kostikova, A., Litsios, G., Pearman, P.B. & Salamin, N. (2015). Measurement errors should always be incorporated in phylogenetic comparative analysis. *Methods in Ecology and Evolution*, In press.

Simpson, G.G. (1953). *The major features of evolution*. Columbia University Press, New York, NY.

Slabbekoorn, H.W. (2004). Singing in the wild: the ecology of birdsong. In: *Nature's music: the science of birdsong* (eds. Marler, P & Slabbekoorn, HW). Elsevier Academic Press San Diego, CA, pp. 178-205.

Slatkin, M. (1980). Ecological character displacement. *Ecology*, **61**, 163-177.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, **236**, 787-792.

Slowinski, J.B. & Guyer, C. (1993). Testing whether certain traits have caused amplified diversification: an improved method based on a model of random speciation and extinction. *American Naturalist*, **142**, 1019-1024.

Sobel, J.M., Chen, G.F., Watt, L.R. & Schemske, D.W. (2010). The biology of speciation. *Evolution*, **64**, 295-315.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115-1123.

Sol, D., Stirling, D.G. & Lefebvre, L. (2005). Behavioural drive or behavioural inhibition in evolution: subspecific diversification in Holarctic passerines. *Evolution*, **59**, 2669-2677.

Sorci, G., Møller, A.P. & Clobert, J. (1998). Plumage dichromatism of birds predicts introduction success in New Zealand. *Journal of Animal Ecology*, **67**, 263-269.

Soria-Carrasco, V. & Castresana, J. (2012). Diversification rates and the latitudinal gradient of diversity in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4148-4155.

Spottiswoode, C.N., Tøttrup, A.P. & Coppack, T. (2006). Sexual selection predicts advancement of avian spring migration in response to climate change. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 3023-3029.

Stein, A.C. & Uy, J.A.C. (2006). Plumage brightness predicts male mating success in the lekking golden-collared manakin, Manacus vitellinus. *Behavioral Ecology*, **17**, 41-47.

Stockley, P., Gage, M.J.G., Parker, G.A. & Møller, A.P. (1997). Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. *American Naturalist*, **149**, 933-954.

Stoddard, M.C. & Prum, R.O. (2008). Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of New World buntings. *American Naturalist*, **171**, 755-776.

Stratford, J.A. & Robinson, W.D. (2005). Gullier travels to the fragmented tropics: geographic variation in the mechanisms of avian extinction. *Frontiers in Ecology and the Environment*, **3**, 91-98.

Stuart-Fox, D. & Owens, I.P.F. (2003). Species richness in agamid lizards: chance, body size, sexual selection or ecology? *Journal of Evolutionary Biology*, **16**, 659-669.

Stutchbury, B.J. & Morton, E.S. (1995). The effect of breeding synchrony on extra-pairmating systems in songbirds. *Behaviour*, **132**, 675-690.

Tanaka, Y. (1996). Sexual selection enhances population extinction in a changing environment. *Journal of Theoretical Biology*, **180**, 197-206.

Thomas, G.H., Cooper, N., Venditti, C., Meade, A. & Freckleton, R.P. (2014). Bias and measurement error in comparative analyses: a case study with the Ornstein Uhlenbeck model. *bioRxiv*, doi:10.1101/004036.

Tietze, D.T., Martens, J. & Sun, Y.H. (2006). Molecular phylogeny of treecreepers (*Certhia*) detects hidden diversity. *Ibis*, **148**, 477-488.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences*, **106**, 19637-19643.

Tobias, J.A., Aben, J., Brumfield, R.T., Derryberry, E.P., Halfwerk, W., Slabbekoorn, H. *et al.* (2010a). Song divergence by sensory drive in Amazonian birds. *Evolution*, **64**, 2820-2839.

Tobias, J.A., Bates, J.M., Hackett, S.J. & Seddon, N. (2008). Comment on "The latitudinal gradient in recent speciation and extinction rates of birds and mammals". *Science*, **319**, 901c.

Tobias, J.A., Cornwallis, C.K., Derryberry, E.P., Claramunt, S., Brumfield, R.T. & Seddon, N. (2014a). Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, **506**, 359-363.

Tobias, J.A., Gamarra-Toledo, V., García-Olaechea, D., Pulgaría, P.C. & Seddon, N. (2011). Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. *Journal of Evolutionary Biology*, **24**, 2118-2138.

Tobias, J.A., Montgomerie, R. & Lyon, B.E. (2012). The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2274-2293.

Tobias, J.A., Planqué, R., Cram, D.L. & Seddon, N. (2014b). Species interactions and the structure of complex communication networks. *Proceedings of the National Academy of Sciences*, **111**, 1020-1025.

Tobias, J.A., Seddon, N., Spottiswoode, C.N., Pilgrim, J.D., Fishpool, L.D.C. & Collar, N.J. (2010b). Quantitative criteria for species delimitation. *Ibis*, **152**, 724-746.

Touchton, J.M., Seddon, N. & Tobias, J.A. (2014). Captive rearing experiments confirm song development without learning in a tracheophone suboscine bird. *PLoS One*, **9**, e95746.

Valentine, J.W. (1980). Determinants of diversity in higher taxonomic categories. *Paleobiology*, **6**, 444-450.

van Doorn, G.S., Edelaar, P. & Weissing, F.J. (2009). On the origin of species by natural and sexual selection. *Science*, **326**, 1704-1707.

Van Valen, L.M. (1973). A new evolutionary law. *Evolutionary Theory*, **1**, 1-30.

Venditti, C., Meade, A. & Pagel, M. (2010). Phylogenies reveal new interpretation of speciation and the Red Queen. *Nature*, **463**, 349-352.

Vermeij, G.J. (1973). Adaptation, versatility, and evolution. *Systematic Zoology*, **22**, 466-477.

Von Humboldt, A. (1850). *Aspects of nature, in different lands and in different climates; with scientific elucidations*. Lea and Blanchard, Philadelphia, PA.

Wagner, C.E., Harmon, L.J. & Seehausen, O. (2012). Ecological opportunity and sexual selection together predict adaptive radiation. *Nature*, **487**, 366-370.

Wallace, A.R. (1876). *The geographic distribution of animals*. Macmillan, London.

Wallace, A.R. (1878). *Tropical nature and other essays*. Macmillan, New York, NY.

Weir, J.T., Bermingham, E. & Schluter, D. (2009). The Great American Biotic Interchange in birds. *Proceedings of the National Academy of Sciences*, **106**, 21737-21742.

Weir, J.T. & Price, T.D. (2011). Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *American Naturalist*, **177**, 462-469.

Weir, J.T. & Schluter, D. (2004). Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1881-1887.

Weir, J.T. & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **315**, 1574-1576.

Weir, J.T. & Schluter, D. (2008). Calibrating the avian molecular clock. *Molecular Ecology*, **17**, 2321-2328.

Weir, J.T. & Wheatcroft, D. (2011). A latitudinal gradient in rates of evolution of avian syllable diversity and song length. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1713-1720.

Weir, J.T., Wheatcroft, D.J. & Price, T.D. (2012). The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evolution*, **66**, 2773-2783.

West-Eberhard, M.J. (1983). Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, **58**, 155-183.

Wiens, J.J. (2001). Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology & Evolution*, **16**, 517-523.

Wiens, J.J. (2004). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, **58**, 193-197.

Wiens, J.J. (2011). The causes of species richness patterns across space, time, and clades and the role of "ecological limits". *Quarterly Review of Biology*, **86**, 75-96.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V. *et al.* (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310-1324.

Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519-539.

Wiens, J.J., Pyron, R.A. & Moen, D.S. (2011). Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecology Letters*, **14**, 643-652.

Wilkins, M.R., Seddon, N. & Safran, R.J. (2013). Evolutionary divergence in acoustic signals: causes and consequences. *Trends in Ecology & Evolution*, **28**, 156-166.

Winker, K. & Pruett, C.L. (2006). Seasonal migration, speciation, and morphological convergence in the genus *Catharus* (Turdidae). *Auk*, **123**, 1052-1068.

Wright, S. (1940). Breeding structure of populations in relation to speciation. *American Naturalist*, **74**, 232-248.

Yule, G.U. (1925). A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, F.R.S. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **213**, 21-87.

Zink, R.M., Dittmann, D.L., Klicka, J. & Blackwell-Rago, R.C. (1999). Evolutionary patters of morphometrics, allozymes, and mitochrondrial DNA in thrashers (genus *Toxostoma*). *Auk*, **116**, 1021-1038.