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Avian Diversity: Speciation, Macroevolution, and Ecological Function

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Abstract

The origin, distribution, and function of biological diversity are fundamental themes of ecology and evolutionary biology. Research on birds has played a major role in the history and development of these ideas, yet progress was for many decades limited by a focus on patterns of current diversity, often restricted to particular clades or regions. Deeper insight is now emerging from a recent wave of integrative studies combining comprehensive phylogenetic, environmental, and functional trait data at unprecedented scales. We review these empirical advances and describe how they are reshaping our understanding of global patterns of bird diversity and the processes by which it arises, with implications for avian biogeography and functional ecology. Further expansion and integration of data sets may help to resolve long-standing debates about the evolutionary origins of biodiversity and offer a framework for understanding and predicting the response of ecosystems to environmental change.

1. INTRODUCTION

For much of the last two centuries, the central goals of biodiversity science have been to understand the classification, diversification, and global distribution of species (von Humboldt & Bonpland 1807). Many core concepts in these fields were originally developed based on studies of birds, from adaptive radiation and ecological speciation in Galapagos finches (Darwin 1859) to the ecological niche in California thrashers (Grinnell 1917) and from species-level systematics (Mayr 1963) to the assembly of communities (Hutchinson 1959, Diamond 1975), regional biota (Wallace 1876), and large-scale biodiversity gradients (MacArthur 1972). These historical breakthroughs inspired decades of intensive research, yet progress toward a more general understanding of biodiversity has until recently been hampered by various shortfalls in information about geographical distributions, evolutionary relationships, interactions, traits, and functions (Hortal et al. 2015). These gaps in knowledge are the norm for most taxonomic groups and remain widespread even among vascular plants and vertebrate animals. Over the last decade, however, new technologies and the emergence of comprehensive global-scale data sets have catalyzed a new phase of research into avian diversification.

The history of early insights from birds, as well as their recent rise to prominence as one of the foremost study systems in macroevolution and macroecology, can be explained by the popularity of ornithology from the Victorian era onward. This has given rise to unusually detailed information about almost all birds—somewhere in the region of 10,000 species according to most taxonomic treatments—culminating in unparalleled global data sets of ecological (Wilman et al. 2014), morphological (Cooney et al. 2017a, Pigot et al. 2020), and behavioral traits (Tobias & Pigot 2019), as well as public repositories of acoustic signals (songs) for virtually all known bird species (see, e.g., Pearse et al. 2018) and vast citizen-science distribution data sets covering most of the globe (La Sorte & Somveille 2020). These resources are coupled with an expanding research toolkit, including the first global species-level phylogeny for a major clade (Jetz et al. 2012), whole-genome assemblies for use in comparative genomics (Jarvis et al. 2014), and state-of-the-art mapping of current and projected future geographical distributions (Biber et al. 2019).

The high profile and widespread availability of these novel techniques and data sets has triggered a surge in integrative studies exploring avian ecology and evolution. We review these empirical advances, focusing on findings that shed light on evolutionary processes and the ecological patterns that arise from them. Since several key advances are best understood in the context of geographical phases of speciation, we structure this review around the concept of speciation cycles in birds (Price et al. 2014, McEntee et al. 2018). We begin by addressing the general theme of lineage diversification, with particular reference to an initial phase of divergence in geographic isolation followed by secondary contact. We then examine the latter phases of the cycle, including the transition to species coexistence and the evolutionary implications of species interactions. Finally, we summarize how this accumulation of new insight and evidence is beginning to reshape ideas in a range of fields from community ecology to ecosystem science (**Figure 1**).

2. MECHANISMS OF DIVERSIFICATION IN GEOGRAPHICAL ISOLATION

Models of sister species distributions indicate that the proportion of extant avian diversity originating from sympatric speciation is likely to be less than 5% (Phillimore et al. 2008, Pigot & Tobias 2015), with most phylogenetic evidence suggesting that the true figure is substantially lower (Price 2008). Rare examples of sympatric speciation in birds, such as by host-switching in brood parasitic indigobirds (Viduidae) (Sorenson et al. 2003), serve only to prove the rule. Given the period of spatial isolation (allopatry) typically required for reproductive isolation to evolve (Price 2008), the
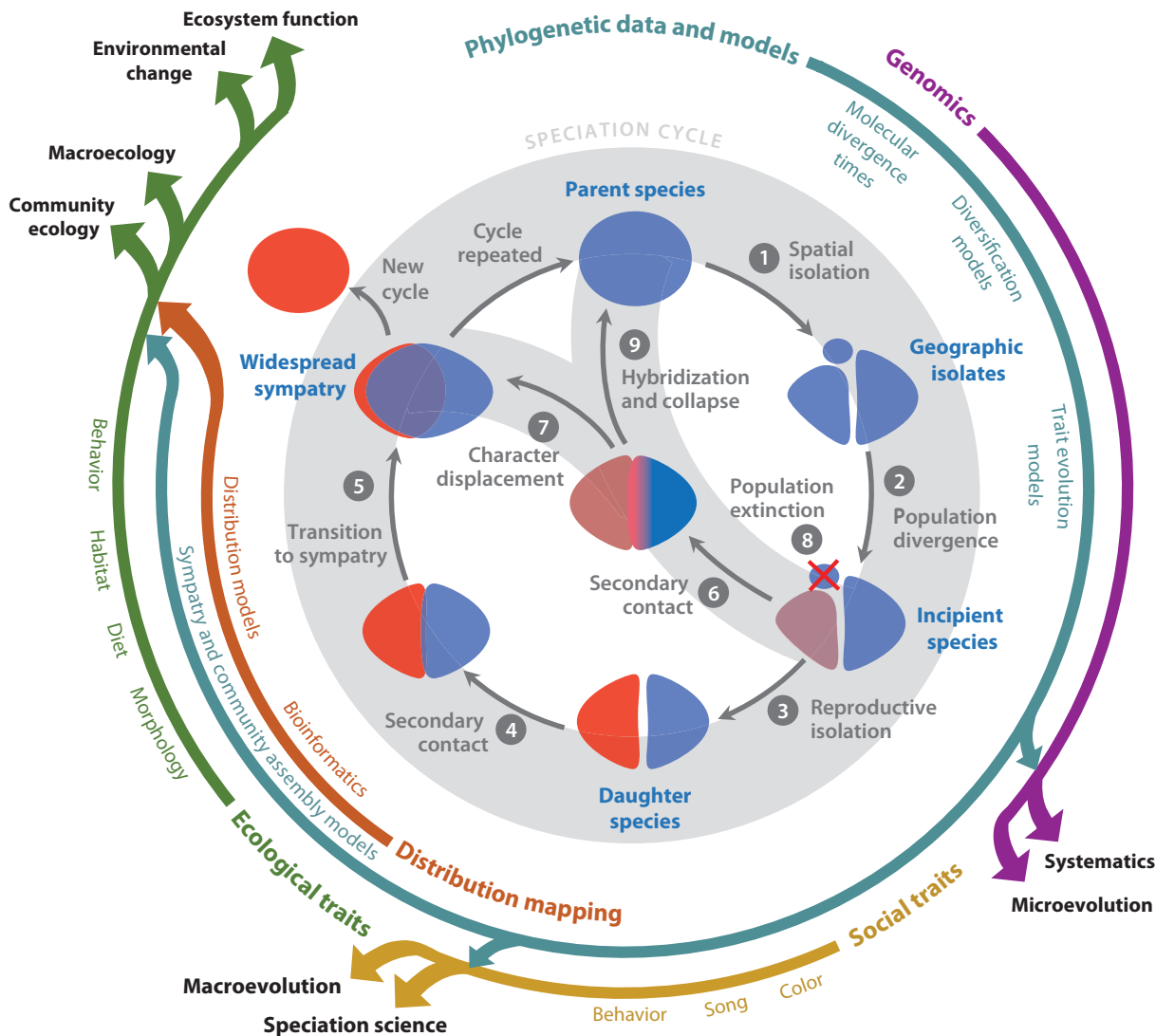
Figure 1

The speciation cycle in birds. Starting with a parent species (*top middle blue oval*), (①) populations become spatially separated by geographic barriers (vicariance) or dispersal (peripatry), then (②) geographic isolates form incipient species, after which the cycle can proceed along two alternative routes. In (③), lineages continue to diverge in allopatry until reproductively isolated. After range expansion, these species later achieve secondary contact (④), eventually followed by transition to widespread secondary sympatry (⑤). This final stage requires divergence in species ecological niches either prior to contact (ecological sorting) or upon contact (ecological character displacement). In the alternative route, incipient species disperse and come back into secondary contact before they are reproductively isolated (⑥). Incipient species may undergo reproductive character displacement (reinforcement) resulting in the transition to widespread sympatry (⑦). Once species attain widespread sympatry, the cycle is completed, initiating two new cycles of the process. Embedded within the full speciation cycle is a faster (ephemeral) speciation cycle (①→②→⑧ or ①→②→⑥→⑨) that does not lead to an increase in species richness. In this cycle, incipient species are rapidly formed but then aborted either because of stochastic extinction events (⑧, marked with a *red* ×) or high rates of gene flow (hybridization) upon secondary contact (⑨), causing them to merge back into a single population. Note that populations can stall at the secondary contact phase (⑥) if parapatry is maintained by hybridization. Also note that most steps in the cycle are reversible (bidirectional). The outer rings illustrate various types of research input and the stage of the cycle to which they are most relevant, highlighting new technologies, data sets, and potential applications.

classic model of avian speciation is intrinsically geographical. According to this framework, speciation is initiated by the fragmentation of an initially contiguous distribution into isolated populations, which then develop reproductive isolation (Mayr 1963). Subsequent geographic range expansion of these new lineages leads to a phase of secondary contact (parapatry) and ultimately to spatial coexistence in overlapping geographical ranges (sympatry) (McEntee et al. 2018). This overall sequence with three geographic phases helps to convey the cyclical nature of bird speciation, with the final stage of range expansion allowing the process to begin anew (Price et al. 2014, McEntee et al. 2018). It also bridges traditional research disciplines by connecting the processes generating avian diversity in the first instance (e.g., genomics and speciation biology) to the assembly of avian diversity in any particular location (e.g., community ecology) (Pigot & Tobias 2013, 2015; Price et al. 2014). We adopt this framework because it helps to structure ideas into a sequence of geographical contexts, each differing with respect to underlying theory and empirical implications (**Figure 1**).

In the first phase of the geographic speciation cycle, a single population is fragmented into isolated subpopulations. The traditional examples involve passive subdivision of the range by geographical barriers such as mountains (vicariance) or active colonization of new ranges such as islands (peripatry), with both processes likely to be widespread (Smith et al. 2014). Other less obvious routes to genetic isolation exist in birds, including breeding at different seasons (allochrony) (Friesen et al. 2007), extreme migratory divides (Withrow & Winker 2014), or migratory drop-offs (i.e., losses of migratory behavior) (Gómez-Bahamón et al. 2020). Once spatial or temporal isolation is established, much depends on the buildup of species differences, both in terms of phenotypic traits and genomic incompatibilities. In theory, and in the absence of gene flow between populations, this can occur simply by slow stochastic mutation leading to the chance occurrence and fixation of different alleles. The accumulation of differences can eventually lead to reproductive isolation despite similar selection pressure, a phenomenon known as mutation-order speciation (Schluter 2009). The main alternative hypothesis is that selective processes drive accelerated differentiation, promoting reproductive isolation through ecological speciation.

The idea that deterministic adaptation to divergent ecological niches can cause ecological speciation took many decades to verify, but this process is now accepted as a major driver of diversification across a wide range of taxonomic groups (Schluter 2009). However, the best examples of rapid ecological speciation are relatively species poor, causing some debate about whether the process often produces bursts of ephemeral species with little wider impact on diversity over time (e.g., Valente et al. 2015, Cutter & Gray 2016). Moreover, the extent to which ecological divergence takes place in geographical isolation or after secondary contact—for example, by character displacement—is often difficult to determine. Many authors from Darwin (1859) onward have suggested that interspecific competition is a primary mechanism explaining adaptive radiation because it drives divergent selection on niche-related traits (Pfennig & Pfennig 2010). This implies a major role for species interactions in sympatry, yet a growing body of evidence from avian macroecology suggests that most ecological trait divergence occurs prior to secondary contact, during the allopatric phase (Tobias et al. 2014a, McEntee et al. 2018, Quintero & Landis 2020).

The emphasis on species interactions has perhaps been exaggerated by the appeal of oceanic island radiations as study systems. In the context of species-poor archipelagos with high ecological opportunity (i.e., vacant ecological niche space) (Schluter 2016), the stage is set for rapid trait evolution, early secondary contact, and an increased likelihood of character displacement. Even under these favorable conditions, relatively few avian lineages undergo dramatic adaptive radiation on islands, with most groups producing either few species or little morphological diversity (e.g., Day et al. 2020). Cases of avian adaptive radiation may be limited to relatively few taxonomic groups,

such as Galapagos finches (Grant & Grant 2008) and Hawaiian honeycreepers (Lerner et al. 2011), perhaps with high preexisting evolvability of ecological traits related to foraging niches, including beak shape (Mallarino et al. 2011). It seems possible that a greater proportion of species, including much of continental biodiversity, is made up of nonadaptive radiations characterized by unremarkable divergence in ecological traits (Czekanski-Moir & Rundell 2019). In other words, standard ecological speciation may be less prevalent overall than either mutation-order speciation or some form of adaptive speciation mechanism mediated by divergence in signaling traits associated with species recognition (Price 2008).

In contrast with the deterministic process of ecological adaptation, this divergence of social signals depends on the less predictable effects of sexual selection and social competition (West-Eberhard 1983). Numerous examples of nonadaptive radiations, from bellbirds (*Procnias*) to trumpeters (*Psophia*), differ in their ornaments or social signals but hardly at all in ecological traits (Ribas et al. 2012, Hudson & Price 2014). In many of these cases, different populations are isolated in very similar habitats, suggesting that closely related lineages may experience similar environmental conditions yet still undergo mating signal divergence, potentially leading to mutation-order speciation (Mendelson et al. 2014). Since a pattern of signal divergence outpacing ecological divergence is most obvious in allopatric bird lineages (Drury et al. 2018), various forms of social selection may be viewed as a catalyst in the early stages of speciation cycles (Mendelson et al. 2014, Uy et al. 2018).

The extent to which allopatric divergence caused by sexual selection can also drive the completion of speciation cycles remains highly contentious. Indeed, theoretical models suggest that reproductive isolation maintained by sexual selection tends to break down after secondary contact (Servedio & Bürger 2014). Prezygotic mechanisms linked to sexual selection, such as assortative mating based on mating preferences alone, appear to be relatively ineffective in maintaining species boundaries unless other factors reduce hybrid fitness (Irwin 2020). These factors can include behavioral hybrid dysfunction, whereby mating success is reduced for hybrids with intermediate signals and preferences or with more intrinsic behavioral deficiencies (Servedio & Noor 2003). Whether underlying mechanisms are behavioral or developmental, reduced hybrid fitness can have powerful stabilizing effects on hybrid zones (Irwin 2020). Lineages on either side of the hybrid zone can be highly distinctive, warranting classification as species (Tobias et al. 2010b), yet they may be prevented from completing the final phase of the speciation cycle, particularly if introgression constrains ecological trait divergence (see Section 5.3).

Many questions remain about the extent to which either ecological selection or sexual selection can operate in isolation to drive allopatric bird speciation. Perhaps the most frequent pathway involves a combination of these factors, for example, when ecological selection on signal transmission properties (i.e., sensory drive) causes deterministic divergence in mating signals (Boughman 2002, Tobias et al. 2010a). Not only is speciation by sexual selection more likely when mediated by ecological selection on signals, the converse is also true when traits under direct ecological selection have indirect effects on mating signals through correlated evolution. Birds—and birdsong in particular—provide some of the best examples of these so-called magic traits (Servedio et al. 2011). Studies in both oscine (Podos 2001, Smith & Benkman 2007) and suboscine passerines (Derryberry et al. 2012, 2018) suggest that dietary niche divergence exerts ecological selection on body size and beak shape, which in turn generates divergent vocal signals, potentially leading to assortative mating on secondary contact. The exploration of allopatric bird speciation mechanisms should continue to evaluate the relative roles of ecological and sexual selection (Price 2008, Uy et al. 2018) with a particular focus on determining how these factors interact and govern the response of avian lineages to secondary contact.

3. SPECIATION MODELS: FROM GEOGRAPHY TO GENE FLOW

Many closely related bird species meet at hybrid zones of varying width, creating a pattern of abutting ranges (parapatry) traditionally ascribed to secondary contact after an allopatric phase (Mayr 1963). In theory, avian contact zones could also arise from parapatric speciation, whereby reproductive isolation builds up between adjoining populations connected by gene flow (Endler 1977). Although parapatric speciation is hard to demonstrate conclusively, phylogenetic studies suggest that contact between incipient species can occur very early in mobile animals, including birds (Pigot & Tobias 2015, McEntee et al. 2018). Since avian lineages often exchange genetic material during the speciation process (Fitzpatrick et al. 2009, Ottenburghs et al. 2017), a debate that once centered around the importance of allopatric versus sympatric speciation has shifted from a purely geographical context to a consideration of gene flow.

Parapatric speciation may occur along two pathways. First, gene flow may be reduced over large spatial distances, with the most distant populations diverging despite a chain of interconnected populations that continue to exchange genes. One version of this isolation-by-distance model concerns ring species, in which the chain of interconnected populations is distributed around the globe, or a major geographical barrier, with the terminal populations meeting and overlapping in range without interbreeding (Irwin et al. 2001). A major challenge to this idea is that historical disjunctions may have subdivided the ring into allopatric lineages sometime in the past. Over shorter distances, a single lineage may theoretically diverge into two separate species in response to deterministic adaptation, particularly on steep environmental gradients (Schluter 2009). In theory, reproductive isolation among different ecotypes can be driven or maintained by natural selection against maladapted immigrants (Nosil et al. 2005). This may occur when two forms are locally sympatric with divergent breeding habits (i.e., heteropatric speciation) (Winker et al. 2013). However, there is still no clear evidence that divergence across steep gradients in either elevation or vegetation can drive parapatric speciation in birds (Zhen et al. 2017).

Whether bird populations can speciate in the face of gene flow depends on the balance between genetic exchange and divergent selection. On the one hand, high gene flow can have a homogenizing effect that slows down or even reverses the speciation process. For example, genomic data revealed that two nonsister lineages of common ravens (*Corvus corax*) merged after approximately 1.5 million years of divergence (Kearns et al. 2018)—a case of speciation collapsing before completion (**Figure 1**). On the other hand, speciation can proceed despite the formation of a hybrid zone when gene flow is reduced by hybrid dysfunction so that ongoing mutation outside the hybrid zone results in the buildup of further genetic incompatibilities. For example, genomic evidence indicated that hybridization in contact zones among Amazonian woodcreepers (Dendrocolaptinae) can occur up to 2.5 million years after population divergence but that the proportion of the genome introgressing declines over time, presumably because avian genomes become less permeable to gene flow as reproductive isolation increases (Pulido-Santacruz et al. 2020). Once differentiation has reached a certain tipping point, speciation reversal becomes unlikely (Nosil et al. 2017).

Variation in avian genes and phenotypes across ecological gradients often reflects local adaptation to environmental conditions (Ribeiro et al. 2011, Zhen et al. 2017), yet reproductive isolation is unlikely to evolve unless gene flow is reduced to low levels by landscape, ecology, or behavior. In the case of Amazonian birds, for example, some populations are separated by wide rivers, with only narrow apertures for gene flow around headwater regions (Pulido-Santacruz et al. 2018). Similarly, gene flow is theoretically reduced when geographical ranges are distributed along linear topographical features, such as the Andean mountain range (Graves 1988). In all cases, ecological traits can play a major role, with gene flow particularly sensitive to variation in dispersal. Given that

the probability of speciation rests on this balance between divergent selection and gene flow, dispersal has moved to the center of speciation debates. Indeed, both taxonomic (e.g., Salisbury et al. 2012) and phylogenetic studies (e.g., Smith et al. 2014) suggest that variation in dispersal ability can help to explain large-scale patterns of bird speciation and species richness (see Section 5.1).

The critical importance of hybridization and gene flow in avian speciation has also revived interest in hybrid speciation. A hybrid origin has been proposed for several bird species (Ottenburghs 2018, Uy et al. 2018), although the overall proportion of species appearing by this route is probably quite small. The best studied example involves the Italian Sparrow (*Passer italiae*), which appears to be a hybrid between *Passer domesticus* and *Passer hispaniolensis*. This case study has provided important insights into the interplay between adaptation to local ecological conditions and the stabilization of hybrid genomes (Elgvin et al. 2017, Runemark et al. 2018) and also shows how mutations that arose in separate lineages can be brought together by hybridization, potentially leading to the rapid origin of new species (i.e., via combinatorial speciation) (Marques et al. 2019). Hybrid speciation is a special case of speciation with gene flow in that secondary contact does not lead to the merger of two related lineages but instead gives rise to a third form. It also highlights the key role of postzygotic factors linked to genomic synergies and incompatibilities (Ottenburghs 2018).

4. SPECIATION GENETICS

The development of molecular tools has allowed ornithologists to explore the genetic underpinnings of speciation. Initially motivated by the search for speciation genes involved in reproductive isolation (Edwards et al. 2005), most research has focused on genes contributing to postzygotic isolation mechanisms, namely hybrid sterility and unviability. These hybrid dysfunctions are often the outcome of negative epistatic interactions between two or more genes, in line with the Bateson-Dobzhansky-Muller model. One example involves conflicting mutations in nuclear and mitochondrial genes that potentially maintain species boundaries by disrupting cellular energy production in hybrid individuals (Hill 2017). However, most evidence points to sex chromosomes as key factors in avian speciation because meiotic drive and suppression readily build up incompatibilities at these loci, reducing hybrid fitness (Price 2008, Irwin 2018).

Hybrid sterility and unviability are common in birds (Price & Bouvier 2002), generally following the prediction of Haldane's rule that female hybrids are less fertile or viable compared to male hybrids, since females are the heterogametic sex (ZW). Loci on the Z chromosome routinely undergo reduced introgression between divergent bird populations compared to autosomal loci, suggesting that sex-linked loci contribute to reproductive isolation (Saetre et al. 2003, Price 2008, Taylor et al. 2014). One of the reasons could be that Z-linked genes show faster rates of evolution compared to autosomal genes, which may speed up the accumulation of genetic incompatibilities (Ellegren 2009, Zhang et al. 2014, Elgvin et al. 2017). Perhaps more importantly, Z-linked genes appear to regulate critical functions such as egg production in females (Carling & Brumfield 2008), territory-holding potential in males (Lamichhaney et al. 2020), and male plumage signals mediating species recognition (Saether et al. 2007, Toews et al. 2016). Indeed, it has been suggested that a speciation gene for male plumage traits and associated female preferences may be located on the Z chromosome in *Ficedula* flycatchers (Saether et al. 2007). Although it is often difficult to rule out the effects of imprinting on mate preferences, studies of Gouldian finches (*Erythrura gouldiae*) suggest that color morphs of both sexes are determined by a single locus on the Z chromosome and that preference for color in both sexes is also Z linked rather than learned (Pryke 2010). Genetic associations between signal and preference on the Z chromosome may contribute to speciation by preventing recombination and maintaining assortative mating (Pryke 2010).

Over the past decade, the increasing affordability of genomic research has shifted the focus from speciation genes to the whole genome (Campbell et al. 2018). In particular, genome scans calculating a genetic summary statistic (e.g., genetic differentiation, F_{ST}) across entire aligned genomes are providing important insights into the genetic basis of speciation. These scans have revealed highly heterogeneous landscapes of genetic differentiation across the genomes of closely related bird species, with genetic differentiation often concentrated in a few islands of differentiation (Ellegren et al. 2012, Poelstra et al. 2014, Ruegg et al. 2014, Delmore et al. 2015, Toews et al. 2016, Irwin et al. 2018, Mořkovský et al. 2018). These islands might contain loci involved in reproductive isolation (and hence were originally referred to as genomic islands of speciation), whereas the rest of the genome appears to be homogenized by interspecific gene flow (Wu 2001, Feder et al. 2012). However, other evolutionary processes can also give rise to islands of differentiation that have little effect on reproductive isolation (Cruickshank & Hahn 2014, Burri 2017, Wolf & Ellegren 2017). A major challenge now is to discriminate between islands of differentiation that directly contribute to reproductive isolation (so-called barrier loci) and those that do not (Ravinet et al. 2017, Battey 2019). Moreover, these barrier loci can have different effects on reproductive isolation and interact in various ways, generating a stronger combined barrier to gene flow (Butlin & Smadja 2018). Hence, the characterization of barrier loci and their combined effects on reproductive isolation are promising avenues toward a more integrated picture of the genomic drivers of speciation.

5. SPECIES COEXISTENCE

Regardless of whether speciation cycles begin with long-term spatial separation or genetic exchange at shared range boundaries, the resulting pattern is two (or more) species with nonoverlapping geographical ranges. Although speciation may often be completed long before secondary contact, the establishment of sympatry after range expansion is sometimes viewed as the only way to be certain that speciation is complete (Mayr 1963, Mallet 2008). Range expansions leading to sympatry are also essential both in renewing the speciation cycle—providing new opportunities for spatial isolation as well as reducing the likelihood of extinction—and as a prerequisite for the buildup of diversity in ecological communities (Diamond 1975, Price 2008). Without this critical step, any location on Earth would contain only a single bird species. In this purely allopatric world, speciation would grind to a halt and the diverse avian communities that we observe, with their complex webs of interactions, would never have formed. Despite this key role in the buildup and maintenance of diversity, the transition to sympatry remains a relatively poorly studied stage of the speciation cycle (Weir & Price 2011, Pigot & Tobias 2015).

Despite examples of young sympatric sister species, phylogenetic estimates of species divergence times along with current patterns of range overlap indicate that the attainment of sympatry in birds is often a highly protracted process spanning millions of years (Pigot & Tobias 2013, Pigot et al. 2016b). According to standard species limits, only approximately one in three avian sister-species pairs currently achieve more than marginal levels of sympatry (overlapping by >20% of their breeding ranges), and these are on average significantly older than allopatric pairs (Hudson & Price 2014, Tobias et al. 2014a), leading to estimates of the average waiting time to sympatry of approximately 5.5 million years (Pigot et al. 2016b). Such a slow rate of transition to sympatry may seem at odds with the large number of species coexisting in local communities, particularly in the tropics [e.g., >300 species in a single 100 ha plot in the Amazon basin (Terborgh et al. 1990)]. One possible explanation of this anomaly is that rates of range expansion were faster in the past but have since slowed as bird species filled ecological niche space (Price et al. 2014). Alternatively, given enough time and a large enough regional species pool, even very slow transitions to

sympatry may be sufficient to explain the high alpha diversity of tropical bird communities (Pigot & Etienne 2015).

While many bird species appear to be locked in spatial separation for millions of years following their initial divergence, genomic data implies that sympatry may occur among young lineages that have only recently started to diverge (i.e., <100 kya) (Tietze 2018). Cases of sympatry among young lineages appear to be distributed nonrandomly across the phylogeny, being particularly prevalent in some finch genera, which suggests that early sympatry is facilitated by certain aspects of ecology or developmental biology (Tietze 2018). For example, it is not surprising that the incidence of early sympatry is higher in *Vidua*, a genus uniquely characterized by sympatric speciation (Sorenson et al. 2003), and *Geospiza*, for which interisland colonization events are frequent (Zink & Vázquez-Miranda 2019) and intrinsic genetic mechanisms may facilitate the evolution of beak differences (Mallarino et al. 2011).

Another important aspect to consider is the potential inaccuracy of age estimates based on genetic divergence. This problem is particularly relevant to cases of apparent early sympatry because introgression can reduce genetic divergence between older species in secondary contact. For example, pine bunting (*Emberiza leucocephalos*) and yellowhammer (*Emberiza citrinella*) are distinctive species with almost nonexistent mtDNA (mitochondrial DNA) divergence, not because of recent speciation but presumably reflecting recent introgression of the mitogenome (Irwin et al. 2009). For any study using mtDNA to estimate the timing of evolutionary events, this type of introgression will simply reset the mtDNA clock to zero. Similarly, other species pairs connected by hybrid zones (e.g., golden-winged warbler and blue-winged warbler) retain divergent mtDNA but share near-identical nuclear genomes as a result of long-term introgression (Toews et al. 2016).

These insights may help to explain why the core radiation of Darwin's finches (*Geospiza*) appears to be very recent according to genetic divergence. While a simplistic interpretation is that lineages diversified suddenly in a rapid burst long after colonizing the Galapagos archipelago, it seems more likely that *Geospiza* diversified earlier in its history and that the young age of its constituent taxa is an illusion created by repeated introgression (Valente et al. 2015, Zink & Vázquez-Miranda 2019, Lamichhaney et al. 2020). A fundamental insight drawn from these studies is that avian genomes can be almost completely homogenized by introgression, and yet distinctive differences in plumage or beak traits can be maintained at a few genetic loci by hybrid disadvantage and partial assortative mating (Toews et al. 2016, Lamichhaney et al. 2020). As with many other hybridizing taxa, these distinctive populations of buntings, warblers, and finches are routinely classified as species, yet molecular divergence will not provide an accurate estimate of the time since they first split from a common ancestor. In other words, from the perspective of standard molecular-clock estimates of evolutionary time, they have discovered the secret of eternal youth inasmuch as time passes but they do not appear to age.

In these and many other cases, secondary contact or sympatry between genetically similar lineages may put the speciation process into reverse if environmental conditions change or extensive hybridization eventually leads to islands of differentiation being purged or destabilized (Kearns et al. 2018, Ottenburghs et al. 2020). If large numbers of incipient species eventually fuse in this way (**Figure 1**), it may help explain why macroevolutionary rates of speciation are typically much lower than expected given the rapid divergence often observed among young lineages (Harvey et al. 2019). Moreover, the fusion model may also clarify why rates of trait evolution and speciation are highest for oceanic islands (Valente et al. 2020), high latitudes (Weir & Schluter 2007), and high elevations (Quintero & Jetz 2018) yet diversity and species coexistence never seem to build up over longer timeframes in these environments. Most studies point to increased extinction as the likely explanation, but this may be too simplistic. Ecological opportunity and vicariance may

help drive rapid speciation events in insular, montane, temperate, and polar settings, with the resultant species often being short lived because they fuse after early secondary contact (see Martin et al. 2010, Valente et al. 2015, Cutter & Gray 2016, Ottenburghs et al. 2020).

The fusion of ephemeral populations may influence estimates of evolutionary rates and the timings of sympatry in younger lineages (Futuyma 1987, 2010; McEntee et al. 2018). In particular, if lineages that have undergone minor or slower trait divergence tend to fuse on contact (Kearns et al. 2018, Ottenburghs et al. 2020), leaving only a subset of lineages with larger trait differences, this will overestimate rates of trait divergence inferred from the current snapshot of phenotypic variation in extant species. Given these complex geographical and historical dynamics, phylogenetic evidence must be interpreted with caution and ideally integrated with genomic models to better resolve the dynamics of trait divergence and the timings of sympatry in avian speciation.

5.1. The Role of Dispersal in the Speciation Cycle

Although numerous factors influence the pace at which lineages progress through speciation cycles, dispersal is likely to play a pivotal role. The timing of secondary contact and the rate of geneflow thereafter are both influenced by dispersal, which in turn is shaped by a combination of species traits and landscape features, including the size of mountains or the remoteness of islands. This general concept is supported by accelerated rates of anagenetic speciation on remote islands, suggesting that the rate of dispersal or gene flow into a population is a key regulator of bird speciation (Valente et al. 2020). In addition, dispersal is of particular interest because it may have opposing effects at different stages of the cycle or in different geographic contexts (**Figure 2**). Earlier macroecological studies using qualitative descriptors of vagility concluded that more dispersive avian families were the most species rich (Phillimore et al. 2006). However, recent analyses suggest that the relationship is more complex. While there is little doubt that species with the weakest dispersal are unlikely to expand their ranges across geographic barriers, reducing opportunities for speciation (Price 2008), there is mounting evidence that species with the strongest dispersal may cross barriers so easily that high gene flow inhibits divergence (Claramunt et al. 2012, Weeks & Claramunt 2014). In these cases, even if isolated populations do begin to diverge, secondary contact may occur too early in the cycle, leading to the fusion of lineages before reproductive isolation can fully evolve (Mayr 1963, Kearns et al. 2018, Ottenburghs et al. 2020).

The prevalence of these different scenarios not only varies with intrinsic dispersal ability (Sheard et al. 2020) but is also tightly linked to both spatial scale (Kisel & Barraclough 2010) and landscape context. For example, high dispersal ability may increase rates of diversification for lineages able to colonize new continents or reach oceanic islands (Kennedy et al. 2018) but tends to impede speciation within continents (Claramunt et al. 2012). Avian lineages diversifying most readily on continents are those in which dispersal is sufficiently poor that gene flow is interrupted by mountain ranges, deep valleys, or wide rivers (Ribas et al. 2012), sometimes generating radiations of cryptic species with very poor dispersal (e.g., Cadena et al. 2020). Overall, the nonlinear effects of dispersal suggest a goldilocks zone for speciation where dispersal is neither too high nor too low, with speciation cycles completed more often and at faster rates in lineages with intermediate dispersal ability (White 2016) (**Figure 2**).

While it is notoriously difficult to quantify dispersal, the growing availability of ecomorphological proxies of dispersal ability has enabled broadscale tests of its influence on speciation cycles (Pigot & Tobias 2015). Studies of birds are leading the way in this regard, largely based on global data sets of the hand-wing index (HWI), a metric of avian wing shape that is correlated with
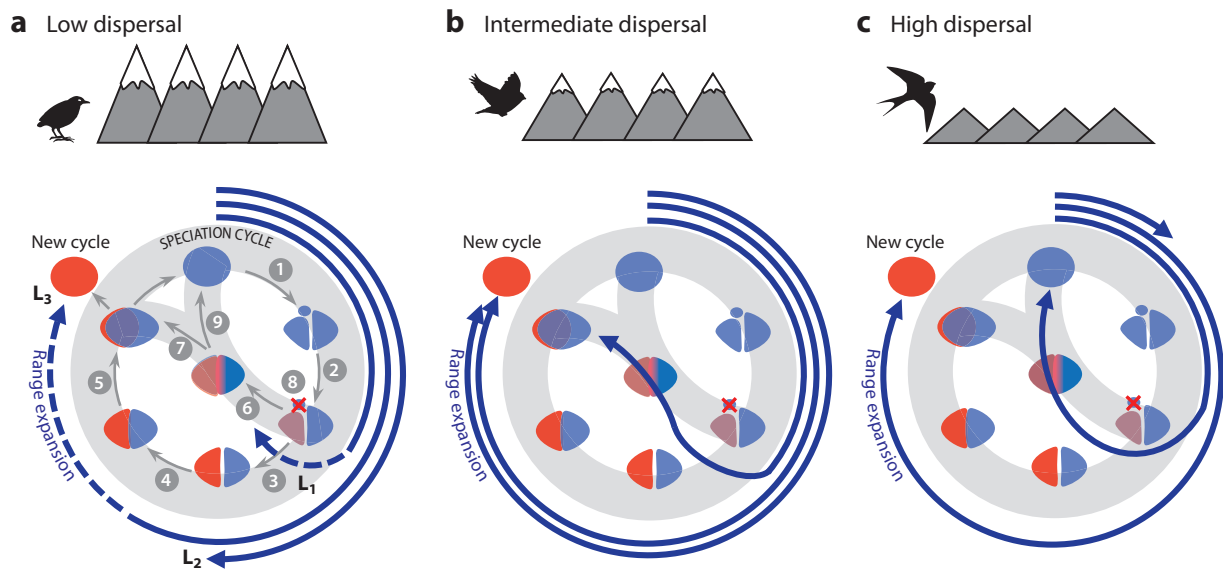
Figure 2

Three dispersal scenarios and their implications for avian speciation cycles: (*a*) low dispersal rate corresponding to poor flight ability and/or impermeable barriers, (*b*) intermediate dispersal rate, and (*c*) high dispersal rate corresponding to strong flight ability and/or weak barriers. We propose that dispersal does not merely change the geographic scale of speciation but that it does so by altering the probability of different pathways through the speciation cycle. Blue arrows indicate possible pathways for three exemplar lineages (L_{1-3}; *dashed lines* indicate slower progression). In panel *a*, low dispersal rates and limited gene flow facilitates the fragmentation of populations and thus the formation of incipient species. However, further progression through the cycle and initiation of new cycles often slows or stalls because of limited opportunities for range expansion or peripatric speciation (L_{1-2}). Only one lineage (L_3) produces a new species. In panel *b*, all three lineages produce new species because intermediate dispersal rates increase the likelihood of range expansion and peripatry without swamping gene flow, driving faster progression through the later stages of the cycle. In panel *c*, high rates of dispersal and gene flow typically prevent speciation from being initiated or lead to incipient species collapsing back into a single population (L_{1-2}). For a minority of lineages (L_3), high rates of dispersal may lead to a rapid completion of the cycle (e.g., via colonization of remote oceanic islands). Overall, a higher proportion of speciation cycles may be completed under intermediate dispersal because most lineages undergo relatively rapid progression through the cycle, leading to the initiation of new cycles.

flight efficiency and dispersal potential (Sheard et al. 2020). Bird species with high HWI have been shown to more rapidly surmount geographic barriers (White 2016), have larger geographic ranges (Kennedy et al. 2016, Sheard et al. 2020), and attain secondary contact sooner than species with low HWI (Pigot & Tobias 2015, McEntee et al. 2018, Pigot et al. 2018).

Strong dispersal ability—estimated by high HWI—appears to impede bird speciation in both continental (Claramunt et al. 2012) and insular systems (Weeks & Claramunt 2014), yet these studies provide only limited evidence for an intermediate peak in the curve relating speciation probability to dispersal. One possibility is that changes in wing morphology after speciation can blur the pattern, for example, if lineages with intermediate dispersal ability colonize islands then adapt to a more sedentary lifestyle (Hosner et al. 2017). Another possibility is that an intermediate peak may be more obvious when considering all organisms, whereas most bird species lie to the right of this optimum (Kisel & Barraclough 2010). Finally, it is also possible that while dispersal facilitates range expansions, it is insufficient to drive the completion of the speciation cycle, since HWI is only a weak predictor of whether lineages that have attained secondary contact can overlap more broadly in geographic distribution (McEntee et al. 2018, Pigot et al. 2018). Widespread sympatry may instead depend more on niche differentiation and ecological opportunity.

5.2. Ecological Constraints on the Speciation Cycle

The extent to which species diversity is regulated by ecological limits on the number of species that can coexist within a community or region remains contentious (Harmon & Harrison 2015, Rabosky & Hurlbert 2015). A central prediction of the ecological limits model is that rates of speciation will be most rapid early in a radiation when there is abundant ecological opportunity and will then slow down over time as ecological niches are filled (Rabosky 2013). Because the avian fossil record is patchy, tests for speciation slowdowns have focused on the branching times of molecular phylogenies of extant species. Evidence of speciation slowdowns have been reported across many avian clades, but the generality and causes of this pattern remain disputed. Most evidence of slowdowns comes from relatively shallow phylogenetic scales (i.e., at the genus level) (Phillimore & Price 2008) and clades restricted to small geographic areas, such as islands (Valente et al. 2015). Conversely, there is little evidence of an overall slowdown across the entire avian radiation (Jetz et al. 2012) or for highly diverse family-level clades, e.g., ovenbirds (Derryberry et al. 2011), hummingbirds (McGuire et al. 2014), and babblers (Cai et al. 2020). At these deeper temporal scales, high rates of speciation may be maintained by the occasional expansion of lineages into new regions of geographic or ecological-niche space, such as the colonization of high-elevation habitats by hummingbirds (McGuire et al. 2014) or of oceanic islands by *Zosterops* white-eyes and their relatives (Cai et al. 2020). Yet, the challenges of interpreting phylogenetic evidence for changes in speciation rates over deep time has prevented a consensus over the importance of ecological limits in regulating bird diversity.

Progress in understanding ecological constraints on diversity may come from examining how competition between species impinges on different stages of the speciation cycle. One possibility is that niche filling (i.e., the saturation of ecological niches) slows down the rate at which populations can evolve divergent ecological traits (Price et al. 2014). As a corollary, the high morphological disparity of some island radiations (e.g., Grant & Grant 2008, Lerner et al. 2011, Reddy et al. 2012) has supported the longstanding idea that ecological opportunity spurs adaptive evolution. The wider impacts of ecological opportunity are often hypothesized and increasingly revealed by ecomorphological trait data sets. At global scales, phylogenetic relatedness explains only part of avian phenotypic diversity, with strong evidence for repeated convergence between distantly related clades occupying similar niches (Pigot et al. 2020). Importantly, convergence is most apparent between clades isolated from each other on different continents and much rarer among potentially competing sympatric clades (Pigot et al. 2020). Yet, while niche filling appears to constrain the trajectories of phenotypic evolution, there is little evidence that high species diversity in continental radiations is suppressing the rate at which niches evolve (Cooney et al. 2017a) or indeed that rates of niche evolution limit rates of speciation (Crouch & Ricklefs 2019). Phylogenetic models indicate that sympatric coexistence has, if anything, accelerated rather than inhibited the differentiation of feeding-related traits in tanagers (Thraupidae) (Drury et al. 2018), but further studies are needed to test this in older clades.

Another way in which ecological niche filling may regulate the speciation cycle is by inhibiting geographic range expansions leading to sympatry, a key step in the initiation of new rounds of geographic isolation (**Figure 1**). Birds have provided some of the most compelling evidence that niche specialization and distributional limits on steep environmental gradients (e.g., elevation) are largely controlled by competition for space or ecological resources (Terborgh & Weske 1975, Price et al. 2014, Freeman et al. 2019). Yet, it is also widely claimed that, while competition may be relevant to understanding bird coexistence at the scale of survey plots or territories (Trisos et al. 2014), substantial environmental heterogeneity makes competitive exclusion unlikely at the larger spatial grains at which sympatry is often defined (Gotelli et al. 2010, Araújo & Rozenfeld 2014).

If ecological niche similarity limits geographic range overlap among species, then the incidence of sympatry should be positively associated with the extent of divergence in phenotypic traits associated with differences in resource or microhabitat use. Critically, this association should persist after accounting for the time elapsed since speciation was initiated, because both the extent of trait divergence and the likelihood of sympatry will tend to increase with species age (Pigot & Tobias 2013, Hudson & Price 2014). Evidence supporting this prediction has come from studies of ovenbirds (Furnariidae), a large Neotropical clade with remarkably complete sampling of species phylogenetic relationships and morphological traits (Tobias et al. 2014a). The estimated rate at which sister species transition to sympatry is higher in pairs that have undergone greater divergence in beak size and accelerates with time since speciation, presumably as these traits diverge (Pigot & Tobias 2013). This new generation of phylogenetic studies examining the dynamics of sympatry among closely related lineages is providing strengthened evidence for the role of ecological niche similarity in limiting species ranges across large spatial and temporal scales, rejecting neutral models of biodiversity (Hubbell 2001) and challenging the notion that competition affects community assembly only at fine spatial scales.

Given that both niche divergence and biogeographic processes are likely to be involved in structuring species assemblages, debate is moving beyond simply testing dispersal- or niche-based models of biodiversity and toward evaluating and understanding the relative contribution of these processes. Recent studies using global phylogenetic (Jetz et al. 2012) and trait data sets (Pigot et al. 2018) are now enabling more nuanced analyses of multiple predictors of sympatry across a much larger sample of species. These studies are showing that dispersal assembly models perform best at explaining the rate at which sister species come into secondary contact, whereas the subsequent step of transitioning to widespread sympatry is best predicted by metrics of competition, in particular divergence in beak and body size (McEntee et al. 2018, Pigot et al. 2018). By demonstrating how different processes dominate at different stages in the avian speciation cycle, these more integrative tests may yet help to reconcile the long-polarized debate over the role of niche and dispersal assembly processes in generating large-scale patterns of species coexistence.

5.3. Behavioral Interference and Reproductive Interference

Most macroecological approaches to species coexistence are framed in terms of exploitative competition, whereas the role of interference competition appears to be prominent in birds, placing a different set of constraints on range overlap (Grether et al. 2017). For example, niche-based assembly models are likely to be more relevant in avian communities than in many other taxonomic groups simply because many bird species are aggressively territorial, defending extensive home ranges both within and between species. It is perhaps no surprise that the strongest evidence for ecological niche divergence as a predictor of geographical range overlap comes from suboscine passerine birds (Pigot & Tobias 2013), a major clade characterized by widespread year-round and interspecific territoriality (Tobias et al. 2011, 2014a). Recent studies showing that year-round territoriality predicts patterns of species co-occurrence in forest fragments (Ulrich et al. 2017), elevational range overlaps on montane gradients (Freeman et al. 2019), and responses to heterospecifics in song playbacks (Weir & Price 2019) provide further evidence that interspecific aggression limits species coexistence in birds (Jankowski et al. 2010, Grether et al. 2017).

An even more potent force, in terms of potential constraints on range expansion at contact zones, is reproductive interference in the form of mating signal interference, hybridization, and genetic introgression (Gröning & Hochkirch 2008), all of which can extend the parapatric phase in speciation cycles, perhaps indefinitely (Grether et al. 2017). To overcome reproductive interference, the evolution of reproductive isolation is clearly an essential component in the transition to

sympatry, but whether it constitutes a rate-limiting step is an open question. Genetic evidence suggests that complete reproductive isolation evolves at highly variable rates, being relatively rapid in some groups, including *Zosterops* white-eyes (Cowles & Uy 2019), and slower in others, including suboscine passerines (Pulido-Santacruz et al. 2018, 2020). Moreover, it is unclear whether this variation owes more to premating mechanisms or differences in rates of genomic evolution (Cornetti et al. 2015).

Until recently, much of the literature on bird speciation and species limits focused on mating signals and associated preferences as indicators of premating isolation (e.g., Seddon & Tobias 2007, Tobias et al. 2010b). While these factors clearly play a role in maintaining species boundaries, recent research has highlighted the primary importance of postmating isolation via genomic incompatibilities or other forms of reduced hybrid fitness (Irwin 2020). Although rates of speciation in birds appear to be uncoupled from the rate at which intrinsic genetic incompatibilities evolve (Rabosky & Matute 2013), the existence of hybrid zones between even relatively old species pairs suggests it can be an important limit to sympatry (Weir & Price 2011; Pulido-Santacruz et al. 2018, 2020). If incipient species only partially isolated by premating mechanisms undergo secondary contact, species boundaries may be maintained by a few incompatible loci determining key traits, including egg production in females (e.g., Carling & Brumfield 2008), migration (Ruegg et al. 2014, Delmore et al. 2015), or mating signals (e.g., Toews et al. 2016), while introgression blends the rest of the genome, limiting the scope for ecological trait divergence. This differs from cases of hybridization that do not lead to gene flow, e.g., because hybrids of both sexes are infertile or otherwise dysfunctional, because evolutionary divergence in ecological traits can then proceed unhindered, ultimately promoting coexistence. From this perspective, hybridization leading to population-wide introgression over most of the genome is a form of reproductive interference that can lock two lineages into perpetual parapatry (Gröning & Hochkirch 2008).

The issue of reproductive interference brings into focus the importance of sexual selection as a driver of speciation and its limitations as a driver of species coexistence. Avian lineages with similar ecological traits and diagnostic plumage or song are widespread in *Phylloscopus* leaf warblers, *Poecile* tits, *Tangara* tanagers, *Myrmotherula* antwrens, and many other groups. It is tempting to interpret these cases as evidence that sexual selection can promote transitions to sympatry, for example, by driving rapid divergence of mating signals in hybridizing taxa and strengthening premating isolation through reinforcement and other forms of reproductive character displacement (RCD) (see Section 6), thereby facilitating coexistence (Servedio & Noor 2003, Pfennig & Pfennig 2010). However, there is little direct evidence that sexual selection can promote geographical range overlap in birds (see Section 2).

A recent comparative analysis revealed that avian sister species with higher levels of sexual selection (inferred from sexual dichromatism in plumage traits) undergo more rapid transitions to secondary contact and marginal range overlap but often fail to transition to wider sympatry (Cooney et al. 2017b). By promoting divergence in mating signals or other reproductive incompatibilities, sexual selection appears to decrease the likelihood that incipient species simply merge at secondary contact, but the subsequent transition to wider coexistence has a longer waiting time dependent on sufficient ecological divergence, which may be delayed indefinitely by genetic introgression (**Figure 3**). The positive effect on reproductive isolation coupled with the neutral or negative effect on coexistence may help to explain why sexual selection accelerates the early stages of speciation (Seddon et al. 2008, 2013) yet fails to explain overall patterns of speciation and species coexistence in birds (Morrow et al. 2003, Huang & Rabosky 2014, Cooney et al. 2017b). In particular, if sexual selection fails to drive the completion of speciation cycles, this will limit the range expansion phase required for such cycles to begin anew.
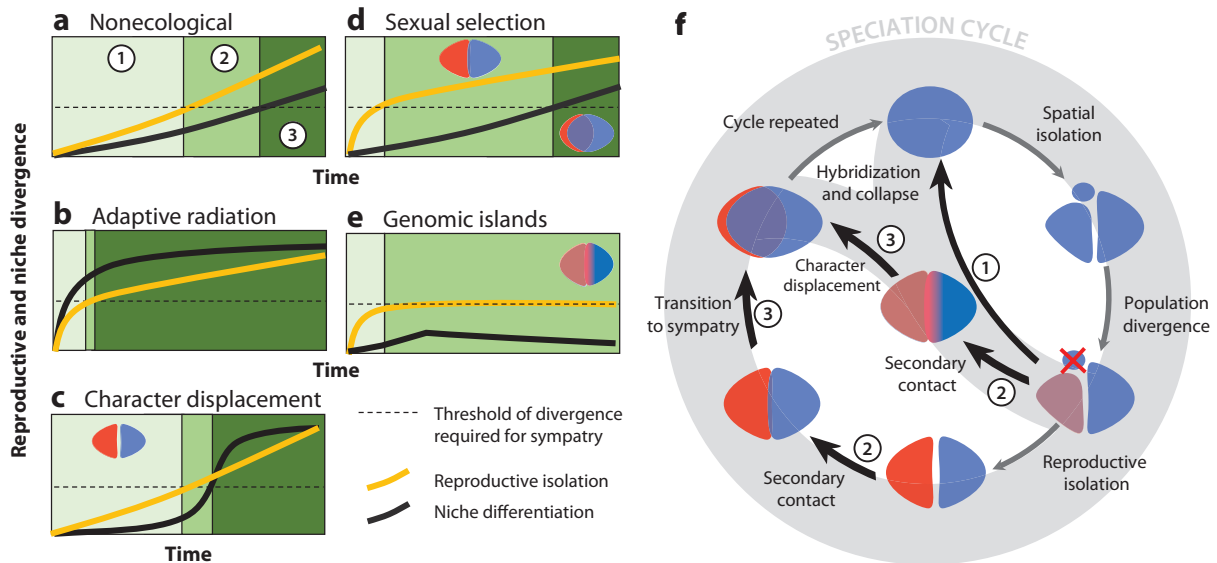
Figure 3

Progression through the avian speciation cycle depends on the timing of secondary contact and rates of divergence in sexual (*yellow line*) and niche-related (*black line*) traits under different speciation scenarios (*a–e*). Green blocks indicate periods during which secondary contact—which varies in timing according to stochastic dispersal and geographic events—would lead to alternative routes of progression through the speciation cycle. If (①) too early, the incipient lineages collapse back into a single species; (②) later contact leads to lineages maintaining largely abutting (parapatric) ranges; and finally, (③) contact at an even later stage leads to lineages becoming sufficiently divergent to expand their ranges into widespread sympatry. The dashed line indicates the threshold of ecological and reproductive divergence above which species can coexist in sympatry. Corresponding routes through the speciation cycle are highlighted in panel *f*. These are illustrated by five scenarios: (*a*) nonecological speciation involves mutation-order divergence characterized by slow ecological differentiation and delayed attainment of reproductive isolation; (*b*) classic adaptive radiation involves an early burst of trait divergence causing niche divergence and reproductive isolation, often preceding secondary contact, enabling earlier parapatry and accelerating the transition to sympatry; (*c*) slow allopatric divergence (either ecological or mutation-order) then drives rapid ecological divergence (character displacement) after secondary contact, facilitating the transition to sympatry; (*d*) sexual selection drives rapid evolution of reproductive isolation, facilitating parapatry, but slow ecological divergence delays the transition to sympatry; and (*e*) genomic islands of differentiation provide partial reproductive isolation on secondary contact, with species differences maintained by genomic islands of differentiation (barrier loci), while introgression homogenizes much of the genome, preventing further trait divergence and impeding the transition to sympatry.

6. SPECIES INTERACTIONS: FROM MICROEVOLUTION TO MACROECOLOGY

Darwin (1859, p. 111) proposed that competition among closely related lineages can drive "divergence of character," an idea that has evolved into the concept of character displacement. These claims are backed up by evidence from field studies of Darwin's finches indicating that competition for resources selects against intermediate forms, driving rapid ecological trait divergence in line with the predictions of character displacement theory (Grant & Grant 2008). The general impression from literature and textbooks is that ecological character displacement (ECD) and RCD are fundamental explanations for species differences in sympatry (Pfennig & Pfennig 2010). However, recent studies of avian macroecology and macroevolution appear to suggest otherwise.

Early explorations of character displacement tested whether phenotypic differences among pairs of species were greater in their region of overlap (sympatry) than where each species occurred alone (allopatry). However, while this spatial pattern of divergence is not uncommon, it

can be explained by habitat differences or chance and thus provides only weak support for the underlying process of character displacement (Stuart & Losos 2013). An alternative approach is to score large samples of species as either overlapping in range (sympatric) or not overlapping (allopatric) to test the more general prediction that ECD and RCD produce greater phenotypic disparity among sympatric species than among allopatric species. Research over many decades has repeatedly shown this pattern, but while it is tempting to conclude that it represents the signature of character displacement, it is hard to rule out more proximate explanations.

Phylogenetic analyses of trait divergence in larger bird radiations suggest that the pattern of increased trait divergence among sympatric species has little to do with character displacement because the same pattern is created by age disparities (Tobias et al. 2014a). The youngest sympatric relatives of any given species are older—and thus tend to be more phenotypically divergent—than their youngest relatives in allopatry, simply because of the time lag to sympatry associated with allopatric speciation (see Section 5). Even in cases when spatial and phylogenetic patterns provide evidence that sympatric species are more divergent than pairs of allopatric species of the same age (Drury et al. 2018), this pattern may reflect variation in trait divergence during the allopatric phase followed by differential rates of transition from secondary contact to sympatry, with sympatry occurring sooner among species that have diverged more rapidly. Unlike character displacement, this scenario is not an evolutionary process driven by species interactions but an ecological pattern or sorting mechanism whereby competitive exclusion and limiting similarity constrain range overlap until species differences have arisen in allopatry or parapatry (Tobias et al. 2014a, Drury et al. 2018). Most, if not all, published macroecological evidence for ECD and RCD fails to rule out this alternative pathway. The contribution of ecological sorting to macroevolutionary patterns remains unclear and critically depends on the timing and spatial context of trait divergence. Overall, large-scale analyses suggest that pulses in trait divergence during bird speciation typically precede the sympatric phase, suggesting that ecological sorting may explain the signature of divergence often ascribed to character displacement (Tobias et al. 2014a, McEntee et al. 2018, Quintero & Landis 2020).

Another issue complicating the interpretation of macroevolutionary patterns in birds is that character displacement can be either divergent or convergent (Grant 1972). In general, ECD and RCD are conceptualized as divergent processes (Pfennig & Pfennig 2010), with divergent ECD reducing the strength of resource competition and divergent RCD reducing maladaptive hybridization or reproductive interference. However, evolutionary mechanisms linked to interspecific dominance or territoriality—including competitive mimicry and agonistic character displacement (ACD)—may often lead to convergence in signals of status or aggression in birds (Grether et al. 2017). For example, smaller woodpecker species often share plumage features with larger sympatric woodpeckers, perhaps because this confers a competitive advantage (Miller et al. 2019). Even birdsong, so often considered a key arbiter of species recognition, can undergo convergence in sympatric congeners when interspecific competition is mediated by acoustic signals.

Studies of two sympatric species of *Hypocnemis* antbird with near-identical songs (Tobias & Seddon 2009) have shown them not to be sister species and to have separated approximately 3.4 Mya (Tobias et al. 2008). Males of both species use these convergent songs not only to defend interspecific territories but to attract conspecific mates (Tobias et al. 2011), raising the question of how species boundaries are maintained. Experimental studies reveal that although territory-holding males fail to discriminate between conspecific and heterospecific song in the context of territorial disputes (Tobias & Seddon 2009), females are perfectly able to discriminate between species and indeed individuals on the basis of male song (Seddon & Tobias 2010), thus maintaining complete reproductive isolation between lineages. These findings challenge the view that mating signal divergence is a universal prerequisite for (or outcome of) species coexistence in birds and

suggest instead that ACD may drive signal convergence in the context of intense ecological competition and low reproductive interference (Grether et al. 2017). How far these results generalize to explain trait differences across birds is not known, although studies suggest that convergent ACD can help to explain variation in birdsong both geographically (Kirschel et al. 2019), within interacting communities (Tobias et al. 2014b), and across entire radiations containing hundreds of species (Tobias et al. 2014a). In the latter case, species co-occurrence is not associated with convergence toward a particular song type, but co-occurring lineages are more similar than allopatric lineages of the same age, contradicting the predictions of RCD theory.

7. GRADIENTS OF AVIAN DIVERSITY

Explaining why lineage and trait diversity vary across major environmental and latitudinal gradients represents the ultimate test of our understanding of factors controlling biodiversity. Recent advances in modelling avian diversification coupled with the integration of genetic, phenotypic, and geographic data are providing novel insights into this long-standing question. A decade has passed since molecular analyses provided evidence that bird speciation cycles are completed faster at high latitudes (Weir & Schluter 2007, Martin et al. 2010), overturning some ideas about tropical speciation rates and the origins of latitudinal gradients in species richness (Mittelbach et al. 2007). Nonetheless, more recent analyses have shown that tropical species contain far greater phylogeographic diversity than high-latitude species of a similar age, suggesting that speciation is initiated at faster rates in the tropics (Smith et al. 2017). A separate point is that the sheer number of extant lineages in the tropics is far higher, so that even if average time to speciation is lower in the tropics, the number of lineages produced per unit of time is nonetheless higher (Cardillo et al. 2005). Thus, even if tropical speciation events are relatively slow, they are so numerous that bird diversity builds up more rapidly over time, contributing to the latitudinal gradient in richness through "tropical evolutionary momentum" (Schluter 2016).

One explanation for the vast number of tropical bird lineages that have completed the first or second phases of the speciation cycle is that tropical species are more prone to isolation by geographic barriers due to reduced gene flow linked to inherent dispersal constraints (Claramunt et al. 2012, Salisbury et al. 2012) (**Figure 2**). This ties in with emerging global patterns in avian dispersal ability, which is positively associated with seasonality and migratory tendency and thus increases toward the poles (Sheard et al. 2020). The dispersal gradient is further steepened because morphological adaptations to flight are reduced in species with year-round territoriality (Sheard et al. 2020) and in specialist understory insectivores (Moore et al. 2008, White 2016), two syndromes strongly associated with the tropics and tropical forests in particular (Salisbury et al. 2012). Another, nonmutually exclusive, explanation is that the greater environmental stability in the tropics makes incipient species less prone to extinction, increasing the chance that they become distinct species (Smith et al. 2017). According to both these models, progression through the early stages of tropical speciation cycles is promoted by environmental stability and reduced gene flow, producing large numbers of incipient allospecies (Czekanski-Moir & Rundell 2019).

While these analyses provide clues that the tropics may be a cradle for avian diversity, phylogenetic models of speciation rate applied to a global phylogeny of birds provide no support for the idea that the per lineage rates of recent speciation vary in a consistent way across latitude (Jetz et al. 2012, Rabosky et al. 2015). This decoupling between species diversity and speciation may be more general: Across mountain regions globally, rates of speciation tend to increase toward high elevations, where species diversity is lowest (Quintero & Jetz 2018). The standard interpretation of these patterns is that gradients in bird diversity are instead often controlled by differences in the rate of species extinction rather than formation, with the tropics being not so much a cradle

of diversity but a museum of surviving lineages (Mittelbach et al. 2007, Weir & Schluter 2007). A hidden component to this interpretation is the fusion of ephemeral species (**Figure 1**), which can be difficult to detect in studies based on current patterns of divergence and can potentially shape gradients of variation over space and time (Futuyma 1987, Cutter & Gray 2016).

Another possibility is that large-scale diversity gradients are controlled by differences in ecological limits to coexistence. Global data sets of ecomorphological traits may offer new insights into this question by clarifying how the volume and occupation of niche space varies across environmental gradients. For instance, a study of passerine assemblages at different elevations in the tropical Andes suggests that most of the extra species occurring in the diverse lowland community are accommodated through denser packing rather than expansion in the volume of occupied niche space (Pigot et al. 2016c). The coexistence of phenotypically similar species in productive tropical environments appears to have an ecological rather than a historical explanation. Across a global sample of avian sister species, the incidence of sympatry is increased in habitats with higher net primary productivity, a proxy for energy availability (Pigot et al. 2016b). These findings suggest that a relaxation of ecological limits likely contributes to the higher diversity of tropical bird communities, which cannot simply be explained by the greater time available for diversity to accumulate in the tropics.

8. FUNCTIONAL DIVERSITY

Studies of avian morphology provided classic examples of the close association between organism form and ecological function, such as how beak shape in *Geospiza* finches relates to the type of seeds or other resources on which they feed (Grant & Grant 2008). The way morphology maps on to ecological function is not always simple, not least because birds can diversify in their niche via different behaviors without diverging appreciably in morphological traits and because species can occupy similar functional roles through distinct phenotypic solutions (Bright et al. 2016, Miller et al. 2017). Nevertheless, recent phylogenetic studies have revealed that evolutionary convergence greatly strengthens the connection between form and function across all birds, at least once a sufficient number of traits are taken into account (Pigot et al. 2020). This repeated evolution of particular trait combinations associated with different trophic niches (see Section 5.2) not only provides strong evidence for evolutionary determinism (Blount et al. 2018) but also validates the use of morphological traits as a framework for understanding the structure and functioning of avian communities.

As bird-trait data sets have expanded, they have been used at ever larger scales to explore macroecological patterns, including gradients in avian diversity (Pigot et al. 2016c, Schumm et al. 2020) and biogeography (Sheard et al. 2020). They also provide a means to assess how functional diversity and associated ecological functions are affected by land-use change, including habitat fragmentation (Bregman et al. 2015), agricultural intensification (Cannon et al. 2019), and urbanization (Sol et al. 2020). For example, large-beaked frugivores supply an important seed dispersal service to large-seeded trees, such that clustered extinctions of key avian seed dispersers have implications for the survival, population dynamics, and commercial harvesting of large tree species (Bovo et al. 2018) (**Figure 4**). Similarly, shifts or contractions in the functional diversity of insectivorous bird communities can theoretically lead to the relaxation of predation pressure on insects and thus the proliferation of insect pests, including phytophagous insects and disease vectors, with implication for plant growth, productivity, and the spread of vector-borne diseases (Bregman et al. 2016). From this perspective, understanding how avian lineages and their traits diversify and assemble into regional biota or local communities is a critical step in understanding the structure and function of ecosystems.
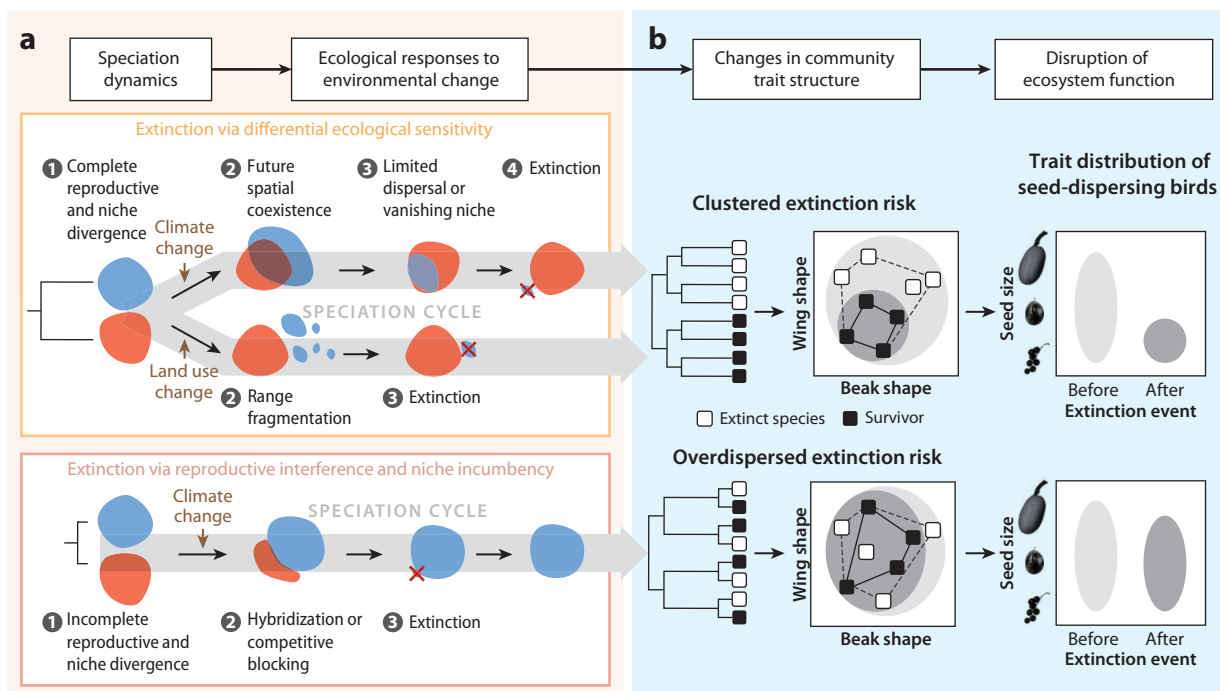
Figure 4

Using insights from avian diversity to understand and predict how ecosystems function and respond to change. For example, (*a*) climate change can have different impacts depending on the stage of lineages in the speciation cycle, with range shifts leading to some bird species transitioning directly into sympatry, while others are potentially blocked or even driven to extinction (marked by *red ×*) by ecological competition and/or reproductive interference. Equally, the effects of all anthropogenic threats (e.g., land-use change) may vary across the cycle if the recently formed and fragmented lineages are more prone to extinction than the widespread lineages at the end of the cycle. (*b*) Patterns of speciation, trait evolution, and the assembly of traits into communities collectively determine the functional structure of assemblages, providing a framework for understanding and predicting how ecosystem function responds to human activities or environmental change. Recent studies are exploring how species loss alters avian community structure in particular trophic groups, such as those delivering ecological services like seed dispersal, pollination, and insect predation. The examples illustrated show how clustered extinctions biased toward larger frugivores can theoretically impair seed dispersal for commercially valuable large-seeded trees, whereas functional diversity is better maintained when extinctions are overdispersed. The gray ovals show the predicted contraction in the distribution of traits of seed-dispersing birds after different patterns of extinction.

9. IMPLICATIONS AND FUTURE DIRECTIONS

A deeper understanding of drivers and constraints in avian speciation cycles may have numerous implications and potential applications. The importance of range expansion, for example, implies that insights can be drawn from invasion biology. A combination of environmental conditions and propagule pressure predicts the success of population establishment in avian invasions (Redding et al. 2019), suggesting that similar factors are key to initiating speciation cycles and driving transitions to sympatry. A recent focus on this latter phase of speciation cycles has produced little evidence of character displacement in birds (Tobias et al. 2014a) but plenty of support for ecological and behavioral sorting mechanisms (Pigot & Tobias 2013, Freeman et al. 2019, Quintero & Landis 2020), thus opening up new possibilities for predicting the response of bird communities to environmental change. In particular, the extent to which niche incumbency and reproductive interference constrain geographical range overlap is likely to be associated with

genetic or morphological divergence, suggesting that these factors offer a method for predicting the outcome of range shifts (Pigot & Tobias 2013, Grether et al. 2017). Further research is required to develop this method, and to explore alternative hypotheses explaining the maintenance of parapatric ranges or hybrid zones after secondary contact, including apparent competition mediated by pathogens and parasites (Ricklefs 2010a,b; Theodosopoulos et al. 2018).

An ongoing debate concerns the relative importance of intrinsic and extrinsic factors in driving bird speciation. For example, adaptive radiations on archipelagos are no doubt linked to elevated ecological opportunity in species-poor communities, but this still leaves open the possibility that preexisting features of some lineages confer an advantage in exploiting those opportunities. Further research is needed to evaluate the relative roles of intrinsic factors, such as niche plasticity (Cooney et al. 2016), brain size (Sayol et al. 2019), and specific developmental programs facilitating rapid evolution of beak shape (Mallarino et al. 2011) and acoustic mating signals (Mason et al. 2017).

Widespread hybridization and introgression associated with secondary contact leads to inevitable instability in species limits and taxonomic assessments, as well as high uncertainty when estimating evolutionary age from molecular distances (Hudson & Price 2014). For example, analyses showing a recent surge in speciation rate—as suggested by shallow mtDNA divergence in Darwin's finches and *Sporophila* seedeaters (Burns et al. 2014)—must consider the possibility that trait diversity is older than appearances suggest (see Section 4). Even in the remarkable allopatric radiation of *Zosterops* white-eyes (Cai et al. 2020), it seems plausible that relatively frequent and repeated colonization events from the same source populations may lead to ongoing hybridization and introgression, a drip-feed of gene flow occasionally topping up genetic similarities that potentially maintain short phylogenetic branch lengths among congeneric lineages. All spatial and temporal patterns in phylogenetic data must be interpreted cautiously in the context of these potential errors and biases in molecular divergence estimates.

The emergence of comprehensive global trait data sets means that avian trait variation at any spatial or taxonomic scale can now be quantified using a variety of functional diversity metrics (Bregman et al. 2016, Sol et al. 2020) or hypervolume methods (Blonder 2018, Schumm et al. 2020) and applied to a wide range of challenges, such as connecting microevolutionary processes to macroevolutionary patterns, formulating conservation strategies, and predicting the niche structure of future communities under climate and land-use change (**Figure 4**). In addition, bird-trait data sets can be used to explore ecological processes, for example, by integrating traits of avian frugivores with plant traits to understand the structure and functioning of seed dispersal networks (Pigot et al. 2016a, Bender et al. 2018). In all cases, a clear limitation of most broadscale trait data sets is that they are still averaged at the species level, so a key challenge involves further sampling to understand the implications of intraspecific trait variation.

Further research avenues are being opened by rapidly expanding molecular data sets, with efforts to sequence the genomes of all extant bird species now well underway (Jarvis 2016, Stiller & Zhang 2019). The vast influx of genomic data in birds and other taxonomic groups is driving the development of more sophisticated modelling approaches, such as phylogenetic networks (Ottenburghs et al. 2016, Blair & Ané 2019), machine learning algorithms (Schrider & Kern 2018), and techniques for exploring historical impacts of climate change over deep timescales (Nogues-Bravo et al. 2018). In combination, this wealth of new data and analytical methods will have numerous applications ranging from determining the genetic basis of particular functional traits to understanding the genomics of reproductive isolation (Stiller & Zhang 2019). Ultimately, the stage is set for the development of a multidimensional framework integrating traits, behaviors, and genes for exploring the evolution of global bird diversity and its links with ecosystem function.

10. CONCLUSIONS

The huge volume of research investigating the origin, structure, and functioning of biodiversity has for many decades been siloed into different fields, often with little communication between them. Using birds as a study system, we have attempted to integrate recent developments across disciplines—from molecular biology to macroevolution and functional ecology—based on the rationale that a holistic overview is required to understand and predict the properties of biological systems at large spatial and temporal scales. Recent findings suggest that macroscale patterns of avian biogeography, species richness, and trait diversity can be understood only in the light of microscale processes that operate at the level of individuals and their genomes. Conversely, genomic interactions and processes make sense only in the light of macroecological or biogeographical processes that regulate species interactions and gene flow. Using speciation cycles as a conceptual link, these insights can help us to understand and predict current patterns of bird diversity, as well as the diversity and functioning of future bird assemblages restructured by environmental change.

DISCLOSURE STATEMENT

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