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PERSPECTIVES IN ORNITHOLOGY

INFERRING THE ORIGINS OF LOWLAND NEOTROPICAL BIRDS

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Regional avian diversity reaches a zenith in the tropical rainforests of South America (Pearson 1977, Wilson 1992), the cumulative effects of biological, geological, climatological, hydrological, and other processes acting on the speciation, dispersal, and extinction of lineages, played out over millions of years at tropical latitudes (Haffer 1969, Duellman 1982, Colinvaux 1993, Bush 1994, Nores 1999, Moritz et al. 2000, Wiens and Donoghue 2004, Hoorn et al. 2010, Rull 2011a, Sandel et al. 2011). Birds are arguably the best-known Neotropical taxon in terms of scientific knowledge, yet the descriptions of new barbet and wren species that appear in this issue of *The Auk* (Lara et al. 2012, Seeholzer et al. 2012) remind us how rudimentary our knowledge is, not only of the distributions of species but of which species are in the landscape. It is the task of systematists to infer, from this patchy information, the evolutionary and ecological processes that produced it. Because the Neotropics cradle the world's most biologically rich regions, studies of Neotropical organisms, and birds in particular, have figured prominently in the development of models of historical diversification (Mayr 1963, Prance 1982).

Speciation results from the prolonged geographic isolation of populations. One has only to examine the current Neotropical landscape to find evidence of ongoing speciation via geographic isolation. Wallace (1852) first noted the geographic partitioning of primates on opposite banks of the Rio Negro and suggested that the river played some role in speciation, an observation that was eventually extended to birds and formalized as the "riverine barrier hypothesis" (Sick 1967, Capparella 1991). Similarly, Frank Chapman's seminal studies on the biogeography of birds in Colombia (Chapman 1917) and Ecuador (Chapman 1926) examined the effect of the Andes on lowland birds isolated on either side of the mountains (see Vuilleumier 2005). He proposed several hypotheses to explain these cross-Andes distributions, including vicariance associated with the Andean orogeny and dispersal around the northern end of the Andes.

The works of Chapman, Haffer, Sick, and others emphasize the simple fact that avian biogeographers have long known that heterogeneity in the Neotropical landscape facilitates speciation by isolating populations. It is not controversial to state that mountain building, climate change, and landscape heterogeneity are the primary physical drivers of avian speciation in the Neotropics (Hoorn et al. 2010). Although the effect of the contemporary landscape on the genetic differentiation of populations is evident, the specific effects of historical landscape changes on the diversification of lineages remain poorly understood (Rull 2008, Antonelli et al. 2010, Ribas et al. 2012). Here, I provide a brief overview of the challenges facing avian diversification studies focused on the lowland humid Neotropics, and highlight how recent studies of the family Furnariidae have provided new insights.

Avian Diversification in the Lowland Neotropics

Diversification studies of Neotropical birds have long focused their attention on attempting to disentangle the relative effects of various landscape features, both contemporary and historical, on the speciational history of birds (Chapman 1917, 1923; Capparella 1987). Some of this work used vicariance biogeography (Rosen 1978, Nelson and Platnick 1981) to test alternative diversification hypotheses based on predictions about area relationships produced from large-scale vicariant events (Prum 1988, Brumfield and Capparella 1996). Area relationships that are shared among some taxa have been identified (Cracraft and Prum 1988, Prum 1988, Brumfield and Capparella 1996, Stott et al. 1998, Eberhard and Bermingham 2005), such as basally branching trans-Andean

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or Atlantic forest clades, but for the most part there has been little consensus, so far, in terms of shared area relationships. That cladistic biogeography has shed few insights into Neotropical lowland biogeography is not an indictment of the method, but indicates the difficulty of identifying unique testable predictions from a set of competing vicariant hypotheses.

Implementation of vicariance biogeography or any method that uses contemporary patterns to infer historical processes is complicated by the fact that "birds fly" (Barker 2007). Although many Neotropical bird species appear to have limited dispersal ability (Moore et al. 2008), even flightless birds can disperse through a heterogeneous, semi-connected habitat matrix, given enough time (MacFadden et al. 2007). Post-vicariance movements of birds and extinction can erase or blur beyond recognition shared area relationships, or they may produce shared area relationships that are the product not of vicariance, but of the contemporary landscape (i.e., pseudocongruence; Hafner and Nadler 1990, Soltis et al. 2006). Even contact zones or hybrid zones between allotaxa that are situated at a physical barrier, such as a river, do not provide evidence either way concerning the barrier's potential historical role in their differentiation, because such zones are expected to migrate to population density troughs (Hewitt 1988). Comparisons between late Pleistocene and extant communities reveal many species in common, but also differences, including species that have gone extinct during this relatively short time frame (Steadman and Mead 2010, Oswald and Steadman 2011). The dispersal ability of birds makes it uncertain how far back in history one can extend results from contemporary phylogeographic patterns and genetic structuring.

From the perspective of hypothesis testing, dispersal explanations are problematic because dispersal can explain essentially any distribution (Donoghue 2011). This was one of the primary motivations for the historical shift away from dispersal explanations to testable vicariant hypotheses. However, as new empirical data have accumulated—primarily dates inferred from calibrated phylogenetic trees—it is clear that many of the divergence events once thought to be due to vicariance are either too young or too old to be consistent with the event. In addition, the breadth of divergence dates across vicariant barriers often cannot be explained by one, or even a few, vicariant events (Burney and Brumfield 2009, Naka et al. 2012). Historical biogeography may be in the midst of a paradigm shift from the vicariance approach back to one in which dispersal explanations predominate (Sanmartín et al. 2008). That long-distance "sweepstakes" dispersal plays some role in explaining the origin of the Neotropical flora and fauna has been known (Pennington and Dick 2004, Mayr et al. 2011), but new data suggest that dispersal ability within the Neotropics, landscape evolution, and time may be sufficient to explain most recent diversification (Salisbury et al. 2012).

Studies that have examined the population genetic and phylogeographic structuring of Neotropical birds have largely corroborated the phenotypic patterns described by Chapman and others in finding evidence of genetic differentiation across large-scale geographic barriers (Cheviron et al. 2005, Miller et al. 2008, Burney and Brumfield 2009, Naka et al. 2012, Ribas et al. 2012). These data confirm that landscape features are capable of structuring contemporary genetic variation, although detailed studies are needed to fully understand the role of these barriers in structuring variation. For example, Naka et al. (2012) found that the "river effect" of the Rio Negro is actually a synergistic effect of its wide lower reaches coupled with a number of nonriverine landscape features farther upstream, where the river is no longer a major barrier. Unfortunately, genetic data cannot conclusively resolve whether Neotropical barriers such as the Rio Negro represent the primary cause of differentiation, or are simply structuring genetic differentiation that arose elsewhere. The inability to distinguish primary from secondary differentiation is a major stumbling block to hypothesis testing in historical biogeography. Whether new genomic-level data of recently diverged species will be able to distinguish primary from secondary or higher-order differentiation needs to be explored (Nosil and Feder 2012).

Even though the primary physical drivers of diversification—mountain building, climate change, landscape evolution—are known, it is challenging to construct predictions from competing vicariance hypotheses that both capture the expected population genetic or phylogenetic effects and are falsifiable. Part of the problem is that knowledge of when vicariant events and landscape evolution occurred is inexact for much of the Neotropics. For example, the closing of the Isthmus of Panama and the subsequent Great American Biotic Interchange (GABI) are exemplars of historical biogeography and intercontinental dispersal (Dacosta and Klicka 2008, Burns and Racicot 2009). The GABI is often characterized as representing the largest and most rapid faunal interchange event between continents (Webb 1985) and has long been thought to have occurred 2.5 to 4 mya (Marshall et al. 1979, Stehli and Webb 1985, Coates et al. 1992, Kirby et al. 2008). Lessios (2008) noted that "no vicariant event is better dated than the isthmus." Yet new geochronological data suggest that the closing of the isthmus may have occurred as long as 15 mya (Farris et al. 2011, Montes et al. 2012).

Two recent avian studies of the GABI are emblematic of the challenges that avian biogeographers face (Weir et al. 2009, Smith and Klicka 2010). Using time-calibrated phylogenetic trees of multiple avian taxa, both studies reported increased diversification rates in many taxa soon after the isthmus's closing 2.5 to 4 mya, a presumed effect of the GABI. However, Smith and Klicka (2010) reported that 24% of the cross-isthmus taxa that they examined diverged prior to 4 mya, a result seemingly at odds with the geochronological date. This result now makes more sense, in light of the new closure date of 15 mya, but it raises the question: If the earlier geochronological isthmus-closure date is correct, why did the genetic studies detect a preponderance of diversification events coincident with the former, erroneous, closing date? It may be, in part, a consequence of the birth–death lineage-diversification process, which produces a preponderance of more recently derived lineages (Smith and Klicka 2010). The genetic results also suggest that phylogeographic and molecular phylogenetic data should be viewed as reciprocally informative with geological data when trying to age biogeographic events. Preclosure isthmus dates estimated from plant and bird genetic data were long ascribed to cross-isthmus dispersal (Rull 2011a) when they could have been interpreted alternatively as supporting an earlier isthmus closure date (Bermingham and Martin 1998). At this stage it is unclear which of the isthmus closure dates is accurate, but the example highlights the uncertainty shrouding a geological event whose age has long been thought to be well circumscribed (Lessios 2008).

Similar geochronological uncertainty obscures the age of all relevant vicariant barriers, climatic events, and landscape changes: each has its own set of error bars associated with both its "absolute age" when the event occurred and its "effective age" when it began

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to affect the genetic structuring of birds. There is debate about the age of the Amazon River system—10 to 12 mya versus a younger 2.5 to 6.0 mya (de Fátima Rossetti et al. 2005, Campbell et al. 2006, Figueiredo et al. 2009, Hoorn et al. 2010, Latrubesse et al. 2010, Gross et al. 2011). There is also uncertainty about when the Andes became a barrier to birds of humid lowland forest. In contrast to the relatively rapid formation of the Amazon River system (Hoorn et al. 2010), the Andean uplift was a long and complex process that extended from the initial orogeny in the late Cretaceous ~80 mya to the final uplift of the Cordillera Oriental in the late Pliocene approximately 2 to 5 mya (Case et al. 1990, Gregory-Wodzicki 2000, Garzione et al. 2008). Even assuming that the final uplift of the Cordillera Oriental at 2 to 5 mya provides an approximately correct "absolute age," the question then becomes at which point or time-slice during the uplift did the Andes become a dispersal barrier for a given species (Haffer and Prance 2001). To complicate matters, even after the Andean uplift was entirely complete, the Caribbean lowlands provided a periodic conduit for cross-Andes dispersal (Brumfield and Edwards 2007, Nyári 2007, Miller et al. 2008). All these factors contribute to the difficulty of defining testable predictions that are capable of falsifying hypotheses. Perhaps more importantly, the temporally and spatially dynamic nature of avian populations through time makes it unclear how well these contemporary patterns capture historical process. Studies that have identified avian dispersal centers and areas of endemism in the Neotropics noted that these patterns may or may not have anything to do with historical process (Müller 1973, Cracraft 1985).

Over the past few years, research in Neotropical biogeography has shifted toward statistical inference that is not dependent on specific phylogenetic or phylogeographic tree structure (e.g., statistical phylogeography; Knowles and Carstens 2007), and by reframing questions in a way that is more amenable to testing. For example, much recent debate has focused on whether the rich biological diversity of the Neotropics is primarily the outcome of Pleistocene or of pre-Pleistocene processes (Hoorn et al. 2010, Rull 2011b). This is a testable question, albeit a simple one, that is not linked to specific vicariant explanations (e.g., mountain building). A recent meta-analysis of a diversity of organisms, including birds, concluded that the bulk of contemporary Neotropical biological diversity is the outcome of pre-Quaternary processes (Hoorn et al. 2010). However, because Hoorn et al.'s (2010) analysis was restricted to genus-level avian diversity, it remains unclear to what extent Quaternary processes played a role in generating contemporary avian diversity. It is clear that much species-level Neotropical biodiversity has its origins in the Quaternary (Rull 2011b).

The Furnariidae

To address longstanding questions concerning the biogeography and tempo of speciation and phenotypic evolution in the Neotropics, Derryberry et al. (2011) reconstructed a species-level molecular phylogeny of the suboscine family Furnariidae (Marantz et al. 2003, Remsen 2003). The Furnariidae is one of the most species-rich Neotropical avian families, with >250 currently recognized species distributed among three subfamilies: the branch-climbing Dendrocolaptinae (woodcreepers), the ground-foraging Sclerurinae (miners and leaftossers), and the arboreal Furnariinae (ovenbirds) (Moyle et al. 2009). Morphological, behavioral, and nest-architecture diversity in the Furnariidae is extreme in relation to other suboscine families (Zyskowski and Prum 1999, Claramunt 2010), providing a unique forum in which to address the tempo and mode of phenotypic evolution (Terborgh 1985, Losos and Miles 2002). Henry Walter Bates's (1863) observations of a mixed-species understory flock in Brazil highlight the striking nature of this morphological diversity:

> There are scores, probably hundreds of birds, all moving about with the greatest activity—woodpeckers and Dendrocolaptidae (from species no larger than a sparrow to others the size of a crow) running up the tree trunks.

Indeed, the furnariid radiation encompasses a diversity of morphologies, behaviors, and nest architectures, many of which are convergent on those typical of other avian families.

Biogeographically, Furnariidae represents a large-scale evolutionary radiation that is confined almost entirely to South America. Approximately 97% of the currently recognized species-level diversity and 100% of the genus-level diversity occurs within South America (Remsen et al. 2012). Because Furnariidae is represented in essentially all terrestrial habitats in South America (Ridgely and Tudor 1994, Marantz et al. 2003, Remsen 2003), from the wettest Andean cloud forests to the driest deserts, they are a particularly well-suited taxon to use as a model system for investigating diversification patterns, processes, and timing at a continental scale (Haffer 1969, Remsen 1984, Braun and Parker 1985, García-Moreno et al. 1999, Zyskowski and Prum 1999, Aleixo 2002).

Publication of the furnariid phylogeny catalyzed a major taxonomic revision of the family, a process that is ongoing (Chesser et al. 2009; Claramunt et al. 2010; Derryberry et al. 2010a, b; Remsen et al. 2012). In general, most genera that included more than five species were polyphyletic (Derryberry et al. 2011). For example, the nine species of *Philydor* foliage-gleaners were found to occur in four distantly related clades in the tree, and the nine species of *Automolus* foliage-gleaners in two distant clades, one of which includes *Hyloctistes*. In general, the new phylogenetic results made biogeographic sense in that they conformed to Jordan's rule that geminate taxa should be allo-replacements (Jordan 1905). For example, *Hylocryptus rectirostris*, which occurs in semideciduous woodlands in the interior of southeastern Brazil, is both geographically and phylogenetically distant to *H. erythrocephalus* of the Tumbesian region of northwestern Peru. *Hylocryptus rectirostris* is instead sister to *Clibanornis dendrocolaptoides* of humid forest in montane and lowland regions of southeastern Brazil.

The Tempo of Furnariid Diversification in the Neotropics

Extant species diversity reflects the net effect of the birth and death of species over time, but the pace at which avian lineages have accumulated has long been uncertain. Ultrametric (clocklike) phylogenetic trees permit a retrospective analysis of the tempo of lineage accumulation through time. A lineages-through-time plot is calculated by tabulating the number of lineages occurring at each point along a continuous time scale, beginning with the most recent common ancestor of the clade under study and extending forward to the present. To extrapolate estimates of the underlying speciation and extinction rates that produced the plot requires the application of a series of lineage-diversification models that vary in the number of estimated parameters and

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assumptions about the tempo and mode of diversification (Ricklefs 2007). A number of excellent review papers summarize the challenges of analyzing and interpreting lineage-diversification plots (e.g., Ricklefs 2007), but one of the key issues is that the shape of any given plot can be produced by titrating the relative rates of speciation and extinction (Rabosky and Lovette 2008b, Wiens 2011). In particular, nonstationarity in birth and death rates across lineages and across time can dramatically affect the shape of plots, and it can be nearly impossible to disentangle the relative strengths of birth and extinction through time.

On the basis of the available, albeit limited, empirical data on diversification in New World bird clades, different patterns of diversification are apparent between the Nearctic and Neotropical regions. Lineages-through-time analyses of Nearctic clades of warblers, sparrows, buntings, thrushes, blackbirds, and longspurs show a pattern of rapid diversification early in history followed by a decline in the diversification rate (Zink et al. 2004, Rabosky and Lovette 2008a). This classic pattern of density-dependent diversification has also been observed in analyses of nonavian taxa (Harmon et al. 2003) and is commonly interpreted as reflecting the progressive filling of ecological niches over time (Weir 2006). It makes intuitive sense that as more niches in the landscape are filled, the opportunity for diversification decreases (Schluter 2000). Although this interpretation is ecologically plausible, a pattern of density-dependent diversification can arise through other processes, such as the geographic structuring of species produced by allopatric speciation (Pigot et al. 2010) or because of the protracted amount of time needed for speciation to occur (Etienne and Rosindell 2012). It can also arise as an artifact of incomplete taxon sampling (Nee et al. 1994).

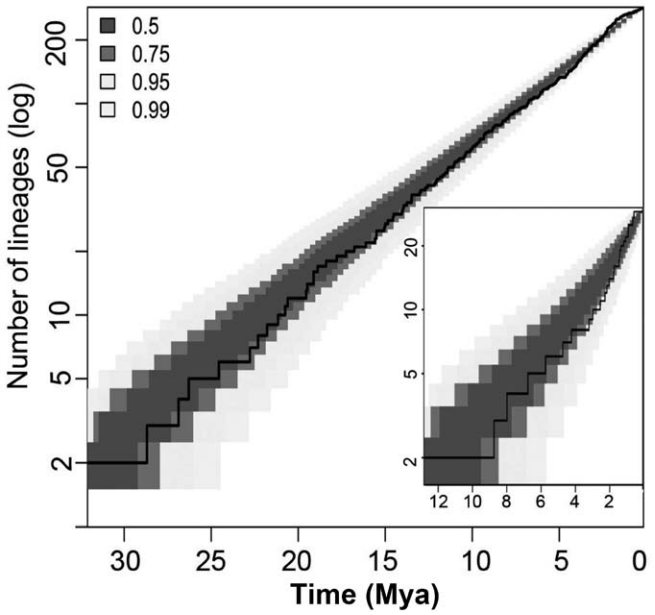


Fig. 1. Lineages-through-time (LTT) plot (black line) from species-level sampling of the Furnariidae, and illustrating near-constant lineage accumulation over time (Derryberry et al. 2011). Inset is the LTT plot from subspecies-level sampling of the furnariid genus *Sclerurus*, illustrating the "pull of the present" (d'Horta et al. 2012). Shading represents confidence limits of the number of lineages at any given time.

Using a phylogeny with nearly complete taxon sampling of currently recognized furnariid species, Derryberry et al. (2011) found that diversification through the 30-Ma history of the Furnariidae was essentially constant (Fig. 1). Genus ages in the furnariid tree were positively correlated with the amount of species richness stemming from the node, suggesting that species accumulation in the furnariid has not been limited by niche saturation or other factors that can limit clade size. Derryberry et al. (2011) found a significant negative relationship between node age and a morphological index of phylogenetically corrected morphological traits, which suggests that morphological space is being divided more finely over time in the Furnariidae.

This same pattern of constant diversification was uncovered in recent studies of toucanets in the genus *Pteroglossus* (Patel et al. 2011) and leaftossers in the genus *Sclerurus* (d'Horta et al. 2012), both of which had nearly complete intraspecific taxon sampling. Weir's (2006) comparative analysis of diversification in lowland avian taxa found that a model of constant diversification could not be rejected in 12 of the 17 taxa examined, although this analysis is not perfectly comparable to the others because taxa were selectively pruned so as to focus on diversification in the highlands versus the lowlands. Regardless, it is notable that, overall, analyses of 14 of the 19 taxa (Weir 2006, Patel et al. 2011, d'Horta et al. 2012) could not reject a model of constant diversification (one-tailed sign test; $P = 0.03$). If additional data corroborate constant diversification in the Neotropics versus density-dependent diversification in the Nearctic, the question will then become "why." Under an ecological-radiation interpretation, it is plausible that the carrying capacity for species is simply much greater in the Neotropical lowlands than in the Nearctic region.

It is worth noting that Derryberry et al. (2011) observed a small decrease in the diversification rate relatively recently in the history of the Furnariidae at ~1.7 mya (Fig. 1). This recent downturn most likely reflects an effect of incomplete sampling of intraspecific variation (Nee et al. 1994). Contemporary avian species diversity in the Neotropics is almost certainly underestimated, with many subspecies likely representing good biological and phylogenetic species (Tobias et al. 2008). A recent phylogenetic study of the furnariid genus *Sclerurus* illustrates how incomplete taxon sampling can affect lineages-through-time plots (d'Horta et al. 2012). Derryberry et al. (2011) included in their study only one exemplar individual from each of the six *Sclerurus* species, but d'Horta et al. (2012) included 119 samples representing 20 of the 26 *Sclerurus* subspecies. Lineages-through-time plots from both studies revealed an overall model of constant diversification, but the LTT plot in d'Horta et al. (2012) curves upward at ~2 mya. This upturn reflects the "pull of the present" expected in LTT plots with complete taxon sampling, because under a model of constant extinction (and birth) through time, the effects of extinction should be less pronounced as one moves toward the present.

The Timing of Furnariid Diversification in the Neotropics

As noted above, it remains unclear to what extent Neotropical diversity is the outcome of Pleistocene or of pre-Pleistocene processes (Hoorn et al. 2010, Rull 2011b). Because Furnariidae has its origins in the late Eocene, all of its extant diversity can be traced

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back to that point, but when did extant species-level diversity arise? A histogram of all branching events in the furnariid tree shows that diversification events peaked in the 1- to 4-Ma range, with a long tail extending into the past (Fig. 2A). When filtered to include divergence events only between congeneric sister species (i.e., the most recent diversification events across the furnariid tree, assuming that species-level taxa capture the most recent events), the histogram (Fig. 2B) illustrates that divergence events occurred more or less continuously from the late Pleistocene back to the middle Pliocene (4 Ma), with a peak in the 2- to 2.5-mya interval. In terms of the pre- versus post-Pleistocene debate, these data fail to detect a distinction. Derryberry et al.'s (2011) study included the more recent Panama Isthmus closure date as one of its calibration points, so it is plausible that a reanalysis using the new, older date would push furnariid divergence events farther into the past. Under this scenario the peak of divergence events between sister species would almost certainly occur in the late Pliocene.

Because current taxonomy likely underestimates species-level diversity (Tobias et al. 2008), it is important to consider how the timing of diversification would be viewed were many of the

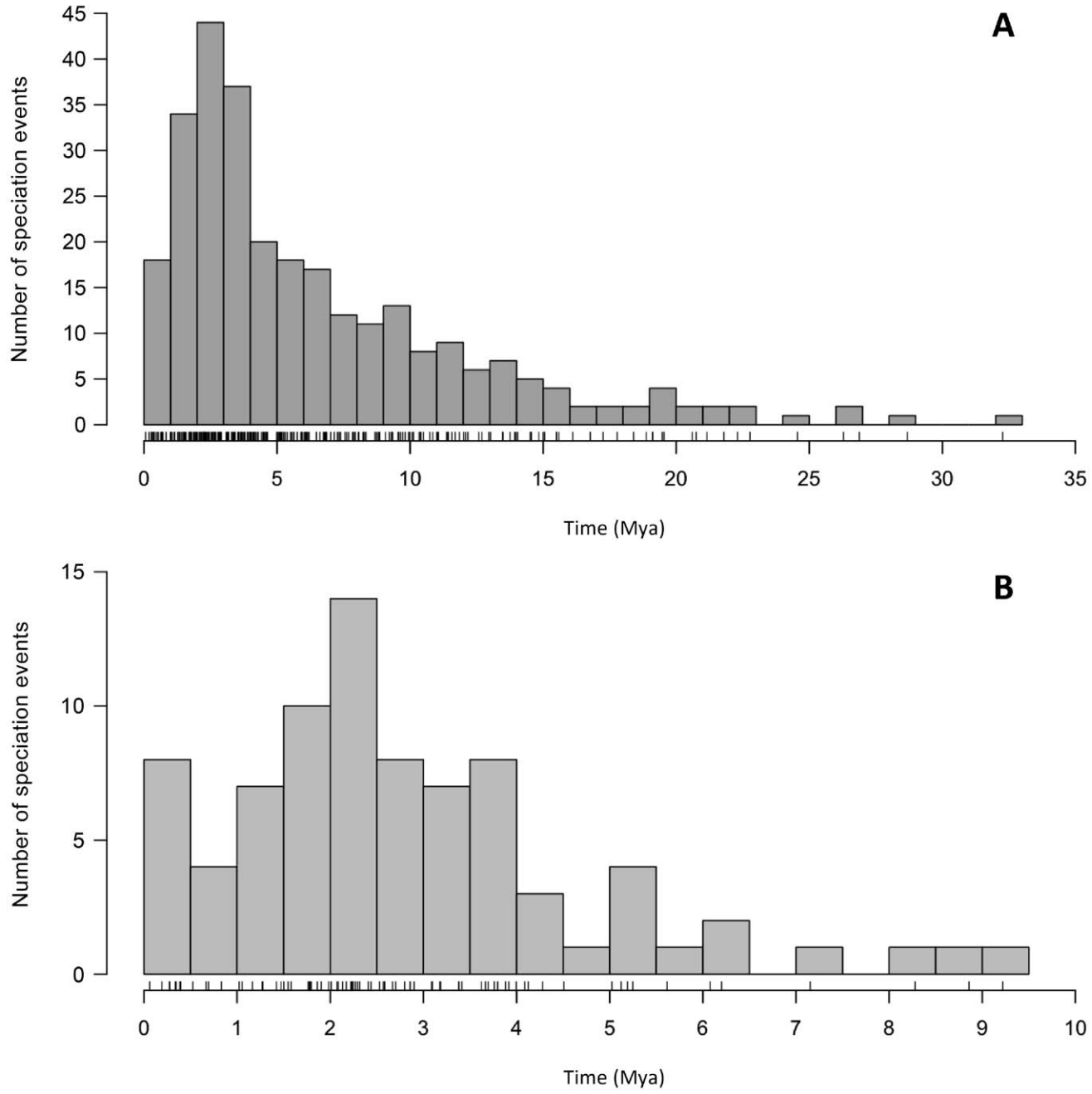


Fig. 2. Histograms of diversification events in the Furnariidae. (A) Panel depicts all events throughout the 30-mya history of the Furnariidae. (B) Panel depicts only those events between terminal sister species in the phylogeny (Derryberry et al. 2011).

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current subspecies elevated to species status. The effect of taxon sampling can be examined with the densely sampled *Sclerurus* study (d'Horta et al. 2012). Of the 10 terminal clades between sister subspecies, 8 of the 10 nodes are estimated to have occurred in the Pleistocene (see d'Horta et al. 2012: fig. 3, table 1). Coupled with the data from the species-level study of all furnariids (Derryberry et al. 2011), these results suggest that extant species-level diversity (assuming that many current subspecies should be elevated to biological species status) is the product of Pleistocene and Pliocene processes, with no clear demarcation between the two. Although it is true that dense sampling can reveal cryptic species-level diversity, it can also reveal that differentiated forms represent the ends of clines. For example, *Thamnophilus caerulescens aspersiventer*, *T. c. dinellii*, and *T. c. paraguayensis* exhibit striking differences in plumage, but dense geographic sampling revealed clines that unite the three (Brumfield 2005). In this case, their current taxonomic treatment as subspecies is valid. Many Amazonian subspecies are undoubtedly good biological species, but many of these will represent clinal variation.

A Role for Natural History in Furnariid Diversification

As part of the shift from vicariance biogeography back to explanations based on differential dispersal (Sanmartín et al. 2008), biogeographers have begun to focus on how natural-history characteristics of birds have influenced their speciational history. The dispersal ability of a species has a direct effect on the geographic structuring of its genetic variation, including the effective population size of its populations and their susceptibility to geographic isolation by intervening landscape barriers (Edwards 1997, Wakeley 2001). This provides a direct linkage between the natural history of birds and their propensity to be isolated by landscape features. From a genetic analysis of 40 taxonomically diverse avian species that have populations isolated in the lowlands on either side of the Andes, the Amazon River, and the Madeira River, Burney and Brumfield (2009) found that levels of genetic divergence were significantly lower in canopy than in understory species, in species that were more generalist in their habitat preferences, and in species with higher Kipp's indices—a proxy for wing aspect ratio that is correlated with dispersal ability. In a recent comparative analysis of 1,366 avian subspecies, Salisbury et al. (2012) found a negative association between dispersal ability and subspecies richness. They concluded that the relative preponderance of dispersal-limited species in the Neotropics compared with the Nearctic provides a partial and underappreciated explanation for the latitudinal gradient in species richness. These two studies of intraspecific variation indicate that dispersal ability has direct consequences on genetic structuring and diversification.

The furnariid tree was used recently to address whether the effects of dispersal ability are detectable at a phylogenetic scale (Claramunt et al. 2011). An organism must have sufficient dispersal ability to colonize the landscape, but the dispersal ability must be weak enough so that the landscape has an effect on the genetic structuring of populations. An "intermediate dispersal hypothesis" strikes a middle ground and predicts that lineage diversification will be highest in those lineages with intermediate dispersal ability. Claramunt et al. (2011) found a significant negative association between dispersal ability and diversification rate but could not distinguish statistically between a simple linear model and the nonlinear intermediate dispersal model. Regardless, the study detected a signature of dispersal ability on species richness over the 30-Ma history of the furnariid radiation. Further studies are needed to better understand the association between dispersal ability and diversification rates across the taxonomic breadth of avian diversity, particularly because some of the most species-rich families in the Neotropics, such as the Trochilidae, have high dispersal ability.

Conclusions

Studies of furnariids suggest that the bulk of extant species-level diversity is the product of landscape-level processes acting on the birth and extinction of lineages. The most recent diversification events occurred during the Pliocene and Pleistocene (Derryberry et al. 2011), with the distribution of divergence times extending to a greater degree into the Pleistocene with increased intraspecific sampling (d'Horta et al. 2012). Although large-scale geological (and possibly climatological) events are part of lowland Neotropical earth history during the Pliocene and Pleistocene, there appears to be no signature of their having had a pronounced effect on rates of diversification in the furnariids. The rate of lineage accumulation in the Furnariidae has been more or less constant since the origin of the family ~30 mya, with the skewed distribution of furnariid diversification events toward the Pliocene and Pleistocene a byproduct of a birth–death process that has not slowed down.

Speciation is ongoing in the contemporary landscape, and the observation that dispersal ability (or inability) influences rates of diversification suggests that diversification is the outcome of (1) a spatially and temporally dynamic landscape matrix, (2) the ability of organisms to traverse it, and (3) time. That these variables resulted in the diversification of lineages is evident in the contemporary landscape and comparative phylogeographic studies, but to what extent one can use contemporary patterns to make inferences about specific historical events is unclear. Dramatic changes in avian distributions can occur on the scale of a human lifetime, so any inferences to historical communities must be taken with a grain of salt in the absence of fossil data. None of the tumultuous events in lowland Neotropical earth history appear to have changed the rate of furnariid diversification. It may simply be that the ebb and flow of rates of landscape change are operating at a temporal scale that does not induce large-scale rates of change in the birth or extinction of furnariid lineages. Compared to the temperate region, the Neotropical lowlands have a had a relatively stable climatic history, and it may be that this relative stability has allowed furnariid lineages to diversify at a more or less constant click since the late Eocene.

Moving forward, it is vital that the effects of contemporary landscape features on the population differentiation and geographic structuring of genetic and phenotypic variation are well understood. As knowledge of earth history becomes more complete, this knowledge will help in understanding how landscape evolution would have influenced the birth and extinction of lineages, and how natural-history characteristics of the birds themselves—dispersal ability, diet, habitat preference—would have affected these rates. Analytically, the development of biogeographic methods that accommodate the nonstationarity of

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biological distributions is needed to better capture the temporal and spatial dynamics of speciation. Finally, additional vouchered sampling of avian diversity—both extant and extinct—should remain a high priority. The descriptions of two new species in this issue are dramatic examples of this need, but the development and testing of all models of diversification depend on a picture of diversity—down to allelic variation—that is as complete as it can be. The advent of next-generation DNA-sequencing methods is making the collection of genomic-scale data more affordable and more accessible to a greater number of ornithologists (Lerner and Fleischer 2010). The next generation of avian systematists will have all of the biotechnological horsepower they need to characterize the genetic and phenotypic variation of natural populations. It will be the availability of samples that is limiting.

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