



Extinction as a driver of avian latitudinal diversity gradients

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The role of historical factors in driving latitudinal diversity gradients is poorly understood. Here, we used an updated global phylogeny of terrestrial birds to test the role of three key historical factors—speciation, extinction, and dispersal rates—in generating latitudinal diversity gradients for eight major clades. We fit a model that allows speciation, extinction, and dispersal rates to differ, both with latitude and between the New and Old World. Our results consistently support extinction (all clades had lowest extinction where species richness was highest) as a key driver of species richness gradients across each of eight major clades. In contrast, speciation and dispersal rates showed no consistent latitudinal patterns across replicate bird clades, and thus are unlikely to represent general underlying drivers of latitudinal diversity gradients.

KEY WORDS: Birds, extinction rate, historical factors, latitudinal diversity gradients, speciation rate, species richness.

Species richness varies geographically for many taxonomic groups. For example, species richness often varies with latitude, elevation, or between geographic regions that vary in precipitation, temperature, or other factors. Two major schools of thought have emerged as to the underlying causes of these patterns. The first emphasizes the role of history in driving these patterns (historical hypothesis). Namely, different geographic regions differ in the timespans over which they have been accumulating species richness, or vary in their rates of speciation, extinction, or immigration (e.g., dispersal), all of which should result in geographic variation in species richness (Fischer 1960; Pianka 1966; Latham and Ricklefs 1993; Ricklefs 2004; Hawkins et al. 2006; McPeck and Brown 2007; Mittelbach et al. 2007; Rabosky et al. 2007; Schluter 2016; Harmon and Harrison 2015). The second school of thought suggests that limited resources (e.g., net primary productivity) place a constraint on species richness (ecological limits hypothesis), with geographic differences in these limits leading to geographic variation in species richness. Under the ecological limits hypothesis, history may initially contribute, but once

species richness approaches saturation by local ecological conditions, further accumulation of species richness is limited, and history ceases to play an important role (Mittelbach et al. 2007; Rabosky 2009; Losos 2010; Rabosky et al. 2012; Price et al. 2014; Rabosky and Hurlbert 2015c).

Trying to disentangle support for these two schools of thought is difficult. The key evidence supporting the ecological limits hypothesis comes from strong correlations between ecological factors such as net primary productivity and species richness (Mittelbach et al. 2001; Francis and Currie 2003; Hawkins et al. 2003; Jetz and Fine 2012; Rabosky and Hurlbert 2015c). However, it remains unknown whether these correlations indicate a causal effect of productivity on species richness, or if both productivity and richness may be governed by an underlying historical factor (e.g., Hawkins et al. 2007; Jansson and Davies 2007; Harmon and Harrison 2015). Without a detailed fossil record for most groups, the historical hypothesis has been difficult to test. However, the recent availability of large phylogenetic trees (e.g., birds: Jetz et al. 2012; mammals: Rolland et al. 2014; squamates: Pyron et al.

2013; amphibians: Pyron and Wiens 2013) for major taxonomic groups now make it possible to test the role of history in driving geographic patterns in species richness.

Phylogenetic data can be used to test the role of a variety of potential historical factors as drivers of species richness patterns. These factors include geographic differences in the time available for species accumulation and in rates of speciation, extinction (including local extirpation), and dispersal. Most historical explanations for patterns of species richness emphasize one or several of these factors. Here, we discuss how speciation, extinction, and dispersal could each individually drive geographic patterns of species richness.

First, speciation rates may differ among different geographic regions and a number of factors have been proposed to explain these differences (see Schluter 2016). These include the geographical area available for speciation, with larger areas providing more opportunities for range fragmentation and allopatric speciation (Coleman et al. 1982; Rosenzweig 1995; Chown and Gaston 2000; Jansson and Davies 2007). Others have stressed the role of environmental factors, such as warmer ambient temperatures in more tropical regions that could increase rates of mutation (at least in ectotherms) and consequently lead to faster rates of evolution (Rohde 1992; Gillman and Wright 2014). In addition, greater biotic interactions in species rich regions—including competition, parasitism, predation, mutualism, etc.—may accelerate evolutionary divergence leading to speciation (Dyer et al. 2007; Schemske et al. 2009). Estimates of trait evolution across latitudinal gradients, however, generally support faster divergence in traits relevant to species discrimination (coloration, Martin et al. 2010; mating vocalizations, Weir et al. 2012) and ecology (climatic niche: Cadena et al. 2012; Lawson and Weir 2014; but see Pyron and Wiens 2013; body mass: Lawson and Weir 2014) at high latitudinal regions with poor species richness.

Second, geographic patterns of species richness may result from differences in extinction rates. For example, the area (species with larger range sizes being less prone to extinction; Gaston 1996) and climatic stability (regions experiencing intense climatic fluctuations should have increased rates of extinction; Dynesius and Jansson 2000 and see also Claramunt and Cracraft 2015) of a geographic region may play key roles in setting levels of extinction. Third, dispersal rates into different geographic regions may vary, leading to patterns of species richness. Dispersal asymmetry could be driven by the difficulty tropical species face in adapting to freezing conditions when expanding their ranges polewards (Wiens and Donoghue 2004; Smith et al. 2012). Likewise, many vertebrate clades that evolved in South America appear reluctant to expand into temperate North America, while many families with northern ancestral origins are able to inhabit both Nearctic and Neotropical regions (Weir et al. 2009;

Smith et al. 2012). For example, the formation of the Central American Land bridge allowed for a recent wave of immigration between tropical regions of North and South America that had long been separated. This had the potential to rapidly increase species richness in the tropics, but less so at high latitudes (Weir et al. 2009).

Estimating the contribution of these historical factors in promoting species richness patterns from phylogenetic data is challenging. A recent study failed to find differences in net diversification rates (speciation minus extinction) across latitudinal gradients using a complete phylogeny of modern birds (Jetz et al. 2012), but the methods used to estimate these rates did not account for differences in extinction with latitude and assumed that latitudinal distributions have remained constant through time. What are needed are models that simultaneously allow rates of speciation, extinction, and dispersal to change with latitude across a phylogeny. Here we make use of the recently developed Geographic State Speciation and Extinction modeling framework (GeoSSE, Goldberg et al. 2011) that estimates speciation, extinction, and dispersal rates associated with specific geographic regions. We apply this modelling framework to the global bird phylogeny to test the contribution of speciation, extinction, and dispersal in driving latitudinal diversity gradients. Analyses were performed on the entire bird phylogeny (excluding pelagic and oceanic island clades), as well as separately on eight of the largest avian clades. Six of these clades possess typical latitudinal diversity gradients whereby species richness increases toward the equator, while two show the opposite patterns with increased species richness at high latitudes. Strong support for the role of history in driving latitudinal diversity gradients would be obtained if the same historical factors (either speciation, extinction, or immigration) were repeatedly associated with species richness across avian clades independent of whether or not they follow the typical latitudinal diversity gradient of increased richness near the equator. In contrast, support for different historical factors across different clades would undermine the role of a universal historical explanation for latitudinal diversity gradients (see Krug et al. 2007) as expected if ecological limits ultimately drive latitudinal diversity gradients.

Methods

DATA

We used 1000 time-calibrated Bayesian posterior phylogenies of all birds evenly sampled from the Bayesian posterior distribution of trees provided by Jetz et al. (2012). A multigene dataset for the large Neotropical family Furnariidae (Derryberry et al. 2011) was not included in the Jetz et al., phylogeny. We used the same methods as Jetz et al., to include this dataset (see Appendix S1 in Supporting Online Materials). We excluded all pelagic and island species, resulting in a total of 8334 recognized terrestrial species, 71% of which had molecular data. The maximum clade credibility

tree (MCC) from these 1000 trees was calculated in TreeAnnotator v 2.1.3 (implemented in BEAST; Heled and Bouckaert 2013) using median node ages. Except as indicated, all analyses were performed using trees with genetic data only (5850 species; see below).

Latitudes were obtained from digitized range maps from BirdLife International and Nature Serve (Ridgely et al. 2005; BirdLife International 2013), using the maximum and minimum latitudinal geographic range for each species in its breeding distribution. We used the breeding range because recent reconstructions have generally supported the origin of long-distance migrants from sedentary high latitude ancestors (Winger et al. 2014). Thus, in most cases, we expected the latitude of the breeding range to be representative. Moreover, the breeding range in birds is directly responsible for allopatric fragmentation leading to speciation, which is not generally true for the wintering range.

MODEL

To test for a relationship between latitude and diversification rates we used the Geographic State Speciation and Extinction modeling framework (GeoSSE; Goldberg et al. 2011) to simultaneously estimate speciation, extinction, and rate of character state transition (i.e., dispersal) for different geographic characters. We considered two GeoSSE type models. First, we developed a model that allows for three geographic character states: low latitude, high latitude, and a mixed state for species that span both (G-3 hereafter). This model has seven parameters and is almost identical to the model published by Goldberg et al. (2011). The model includes three rates of speciation (λ), two rates of extinction (μ), and two rates of dispersal (e.g., range expansion) (d) (Fig. 1A). This model differs from the Goldberg et al. (2011) model only in that it does not allow species in the mixed character state to vicariantly speciate into discrete low and high latitude sister species. This is important given the lack of geographic barriers distinctly separating tropical and temperate regions that could promote such speciation. Instead, we allow species in the mixed character state to speciate without character state change (i.e., a mixed species producing two daughter species, both of which are mixed).

The G-3 model assumes that diversification dynamics are the same in the New and Old World. A previous analysis uncovered strong differences in net diversification rates between Old World (OW) and New World (NW) (Jetz et al. 2012). Therefore, we built a second model (G-7 model hereafter) that allows diversification dynamics to differ between both hemispheres while simultaneously estimating the effect of latitude (Fig. 1B). Our new model includes seven character states: NW low latitude, NW high latitude, OW low latitude, OW high latitude, NW mixed (species that span NW tropical and temperate latitudes), OW mixed, and a H-mixed category for species that span high latitude regions of the NW and OW (mostly Holarctic species; Fig. 1B). To reduce

the number of potential parameters in our models, we do not allow mixed character states between more than two distinct geographic regions. For the entire bird dataset, only 42 species occurred in more than two geographic regions. These were randomly assigned to one of the three mixed categories. The model has a total of 17 parameters: seven speciation (λ), four extinction (μ), and six dispersal (d) rates. G-7 includes a parameter $\lambda_{\text{H MIXED}}$ that represents the rate at which widespread Holarctic species (i.e., found at high latitudes in both OW and NW) subsequently evolve to become distinct species in the NW and OW. This parameter is justified given that OW and NW regions have been repeatedly connected by the Bering Land Bridge, during which time interhemispheric dispersal may have been promoted, followed by episodes when the OW and NW were separated by oceanic barriers, and Holarctic species could then differentiate in each hemisphere. We do not allow dispersal directly between tropical regions of the NW and OW because in terrestrial species of birds, such dispersal events are likely to be rare (see also Claramunt and Cracraft 2015), and when we included these dispersal connections in our modeling framework, the model estimated these rates to be very small. Both the G-3 and G-7 models were implemented using the flexible ClaSSE modeling framework (Goldberg and Igić 2012) in the *diversitree* 3.01 R-package (FitzJohn 2012).

We used 23° (north and south) latitude to define the transition between tropical and temperate latitudes, but note that there is no biogeographic barrier at this latitude that clearly demarks tropical and temperate regions as discrete geographic units. Other studies have classified all species that span their tropical to temperate breakpoint as occurring in the “mixed” state (e.g., Rolland et al. 2014). We see little point in classifying a species as “mixed” if its geographic range just marginally overlaps 23°. Instead, we classified species as “mixed” only when at least 15% of the latitudinal range occurs in tropical and at least 15% in temperate regions. Using threshold values other than 15% (e.g., 5%, 10%, or 20%) gave similar results, and we report results only for the 15% threshold.

DIVERSIFICATION ANALYSES

The GeoSSE modeling framework incorporates information for missing species for each character state in its calculations (FitzJohn et al. 2009). Jetz et al. (2012) added species with missing genetic data to their phylogeny using a best guess of placement based on taxonomy, and used a constant rate pure birth model (which assumes no extinction) to approximate the ages at which these species join the tree. Here we pruned species on the avian phylogeny that were not represented with genetic data, and accounted for them as missing in our modeling framework (i.e., we set “sampling.f” to designate the proportion of species missing.)”

The proportion of species on the avian phylogeny with missing genetic data was highest in the tropics. This is especially true

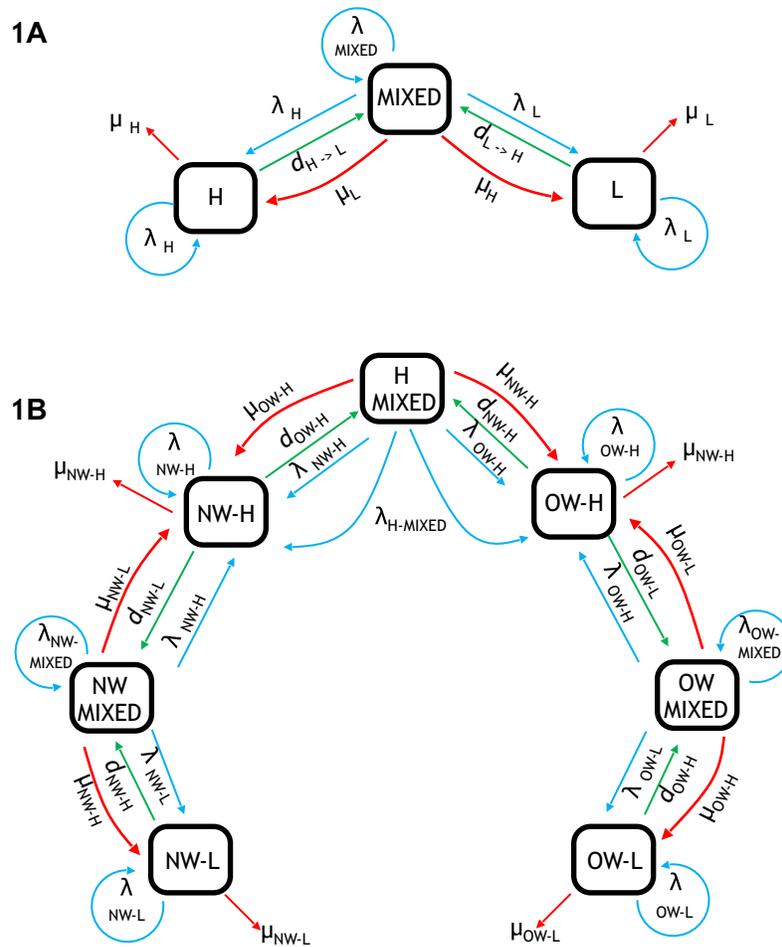


Figure 1. Schematic implementation of the two GeoSSE models. (A) The 3-state GeoSSE model (G-3 model) with seven parameters for species occurring at low (L) or high latitude regions (H) or both (MIXED). (B) the 7-state GeoSSE model (G-7 model) with 17 parameters that allow diversification dynamics to differ between the New World (NW) and Old World (OW). The G-7 model extends the G-3 model to allow separate character states in low, high, or mixed latitudes of the NW and OW, and also assigns a state for Holarctic species distributed at high latitude regions of both the NW and OW (H-MIXED). In both models, rates of speciation (λ), extinction within a region (which can lead to global extinction) (μ), and range expansion (dispersal) (d) are shown by blue, red, and green arrows, respectively.

for the New World where 32% of species are missing from the tropics and only 7% from high latitudes. To test whether the “sampling.f” correction for missing taxa might generate a latitudinal bias in model parameter estimates we randomly pruned species from the phylogeny of all terrestrial birds so that all geographic character states in the New World (Holarctic and high, mixed and tropical states) had the same level of missing species. We then used the “sampling.f” function to correct for missing species in our reestimate of diversification rates using the G-7 model across 1000 posterior trees.

Support for the G-3 and G-7 models cannot be directly compared (e.g., using information criteria or likelihood ratio tests etc.) because the underlying datasets differ (definition of geographic character states). We therefore used the posterior distribution of parameter values under the G-7 model to determine if param-

eter values differed significantly between the NW and OW as previously suggested (Jetz et al. 2012). In a Bayesian context, significant differences between parameters are often tested by comparing Bayes Factors for a model in which two parameters being compared are allowed to vary, versus a model in which the parameters are constrained to be equal. Calculating robust Bayes Factors (e.g., using stepping stone sampling or path sampling to estimate the marginal likelihoods) requires computationally intensive methods (Baele et al. 2013) that were not feasible for the complexity of our G-7 model and the size of our dataset, and thus we do not compare Bayes factors as a means of model choice. Instead, we used the following approach to determine if parameter values between the OW and NW differed significantly. At each Bayesian iteration, the value of an OW parameter in low or high latitudes was subtracted from the corresponding value in

Table 1. Total number of species used in the Jetz et al. (2012) phylogeny and the percentage of species with genetic data included in our analyses. In addition to the entire phylogeny of all terrestrial species we also analyzed taxonomic orders (or groups of orders in some cases) separately, for which a minimum of 60% of species were included with genetic data.

Clade	Total number of species	Species with genetic data	Percentage of species with genetic data
All terrestrial birds	8272	5850	71%
Accipitriformes ¹	198	160	80%
Caprimulgiformes ²	502	325	64%
Coraciiformes ³	508	304	60%
Galliformes	274	189	68%
Passeriformes	5067	3668	72%
Psittaciformes	263	197	74%
Anseriformes	143	131	91%
Charadriiformes	301	229	76%

¹Accipitriformes excludes Cathartidae.

²Caprimulgiformes includes Apodiformes.

³Coraciiformes includes Piciformes.

the NW. Positive values corresponded to faster rates in the OW and negative values to faster rates in the NW. Latitudinal effects were considered significant if greater than 97.5% of the posterior distribution of these differences occurred either above or below zero for a two-tailed test. Significant differences between parameter values for the OW and NW would support the use of the G-7 model.

Bayesian methods were used to fit the G-3 and G-7 models to both the MCC tree and to a subsample of 1000 posterior trees for all terrestrial birds, and for eight clades with the most complete genetic sampling (see Table 1). These clades represent reciprocally monophyletic assemblages with high posterior probability (as defined on the Hackett et al. 2008 phylogeny) and in most cases represent taxonomic orders as follows: Accipitriformes (excluding Cathartidae), Anseriformes, Caprimulgiformes (including Apodiformes), Charadriiformes, Coraciiformes (including Piciformes), Galliformes, Psittaciformes, Passeriformes. The Bayesian analyses were subjected to 7200 postburn-in iterations of Markov chain Monte Carlo (MCMC) with all parameters receiving an exponential prior with rate 0.5. We checked for both convergence and effective sample size (> 250 per parameter) using the program TRACER v1.5 (Rambaut et al. 2014). To determine if parameter rates varied significantly with latitude, we performed a similar test as for when comparing rates in the OW and NW. At each Bayesian iteration, the value of a parameter at high latitudes was subtracted from the value in the tropics. This was done separately for the NW and OW for the G-7 model. Positive values corresponded to faster rates at low latitudes, and negative values to faster rates at

high latitudes. Latitudinal effects were considered significant if greater than 97.5% of the posterior distribution of these differences occurred either above or below zero for a two-tailed test.

MODEL PERFORMANCE

We used simulations to explore whether our G-7 model was capable of providing realistic parameter estimates for our dataset. The models' ability to estimate parameters was considered robust if it was capable of estimating similar parameter values from simulated datasets as the values under which data were simulated. Strong departures between simulated values and parameter reestimates would indicate biases in the model. We simulated 300 phylogenies and associated geographic category data using the median of the posterior distribution of each parameter obtained from our Bayesian analysis applied to all terrestrial birds on the MCC tree. Trees were simulated with ancestor state at the root node occurring in the OW (states 5, 6, and 7) and NW (states 1, 2, and 3) with equal frequency (ancestor states were set to low, high, or mixed latitudes with equal frequency in both hemispheres). Each phylogeny was simulated to 8334 species. To correct for species with missing genetic data, we pruned a total of 30% of species from each simulated tree using the same proportions of missing species for each geographic character state as present in our actual dataset. The same Bayesian methods as detailed above were used to reestimate model parameters from each simulated tree. For each of the 300 simulations the median value for each parameter was tabulated and compared to our actual estimates.

A recent critique of SSE models demonstrated that, when applied to real phylogenies (as opposed to phylogenies simulated under the given model), these models often overestimate support for models in which alternative character states are associated with different diversification rates (Rabosky and Goldberg 2015a). While character associated differences in speciation or extinction rates may be overestimated along a single phylogeny, they should not consistently be overestimated in the same direction across replicate phylogenies, so as to generate a bias. We verified this using simulations along the phylogeny of all terrestrial birds and found no differences in the estimated speciation and extinction rates for different character states (see Appendix S2 for details).

Results

MODEL FITS

For all terrestrial birds, both the G-3 and G-7 models estimated net diversification rates to be significantly higher at low versus high latitudes (Fig. 2 and Fig. S1 in Supporting Online Materials). However, in the G-3 model, higher net diversification rates were due primarily to a significantly faster speciation rate in the tropics. For the G-7 model, both speciation and extinction

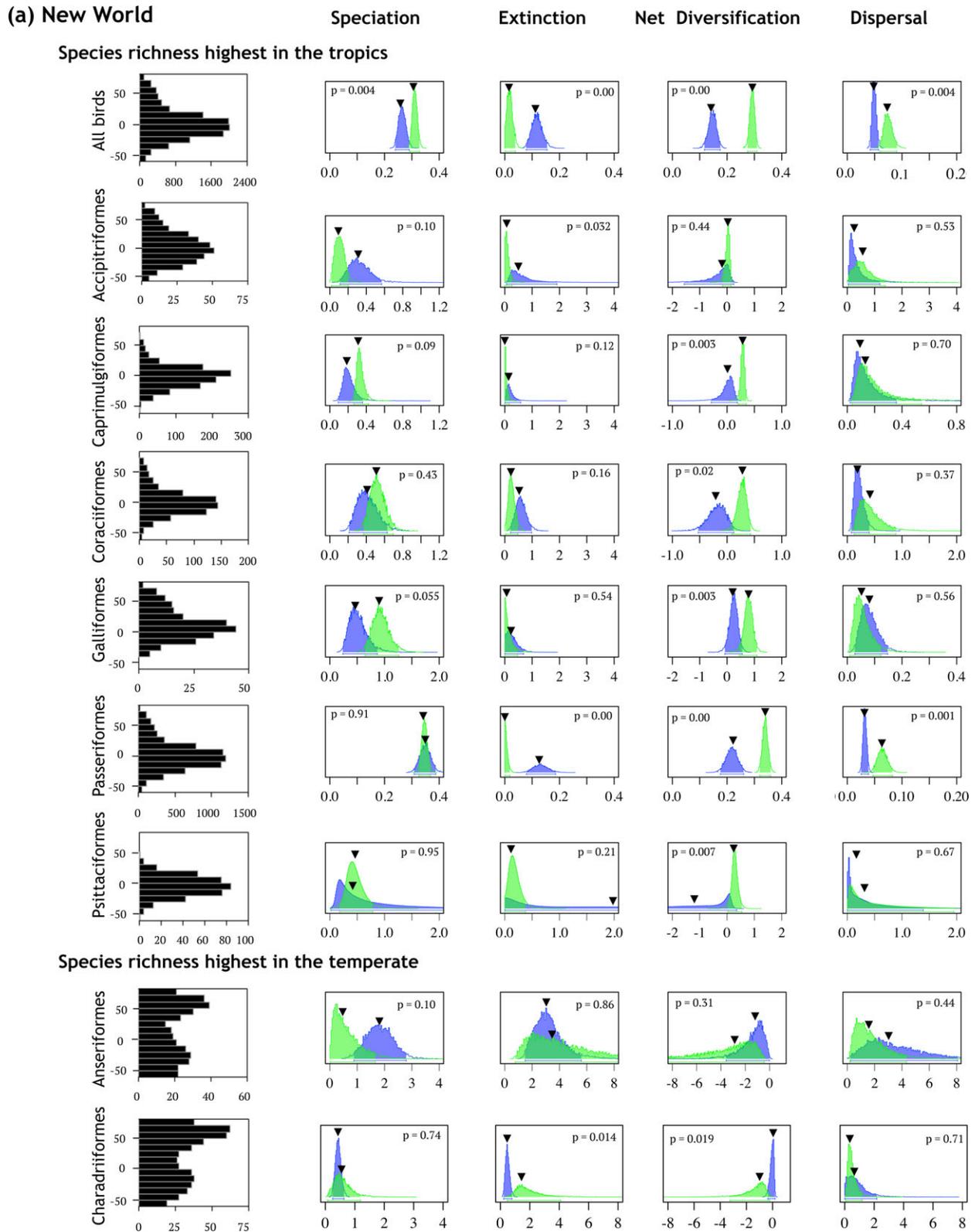


Figure 2. Bayesian posterior distributions of diversification parameters (speciation, extinction, net diversification, and dispersal) estimated for all terrestrial birds and for eight clades (See Table 1) using the 7-state GeoSSE model (G-7 model) across a subsample of 1000 trees. In each parameter, we report the posterior distribution at high latitudes (in blue) and low latitudes (in green) for both the New and Old World. Bars below each distribution correspond to the shaded area and represent the 95% confidence interval of each estimated parameter. The latitudinal diversity gradient for each respective hemisphere (New vs. Old World) is presented in the left column.

(b) Old World

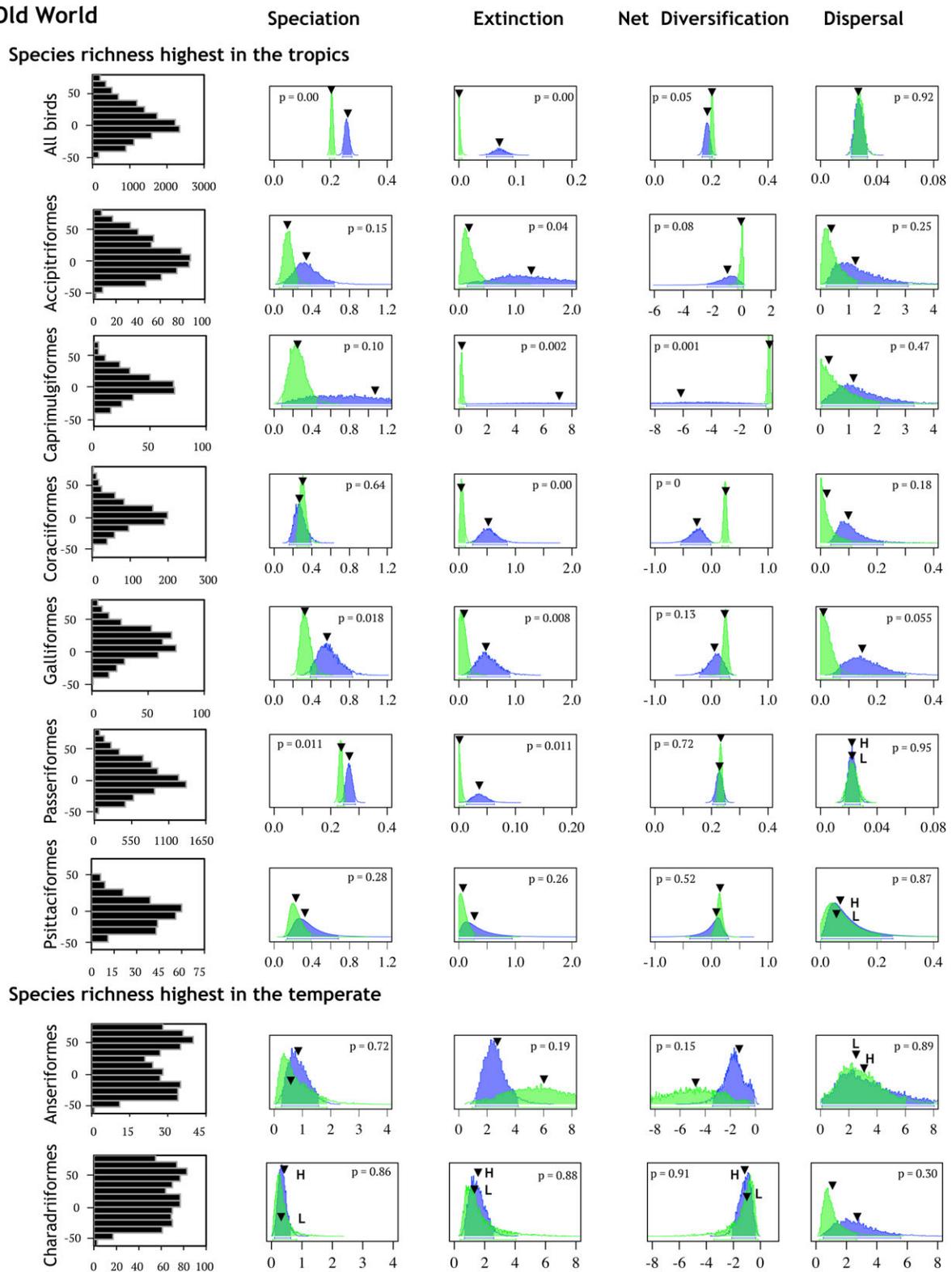


Figure 2. Continued.

differed significantly with latitude and together contributed to faster tropical net diversification rates. These results remained true regardless of whether species with missing genetic data were included or excluded (and accounted for using the “sampling.f” function) in model fits (Fig. S2 in Supporting Online Materials).

The avian phylogeny had the highest proportion of missing species in the tropics. To test whether this might have generated a latitudinal bias in parameter estimates we randomly pruned tips from the phylogeny of all terrestrial birds so that Holarctic, New World high latitude, and New World mixed character states had the same proportion of species sampling as in the New World tropics. The resulting parameter estimates obtained from the G-7 model fit to the pruned tree were qualitatively identical to those obtained without pruning (see Fig. S3), indicating that a latitudinal bias in parameter estimates was not generated due to the proportion of missing species on the phylogeny at each latitude.

To determine if the additional complexity of the G-7 model was justified, we tested for differences in diversification rate dynamics between the NW and OW across the phylogeny of all birds (See Table S1). Model parameters differed significantly between the NW and OW for all model parameters at tropical latitudes and for net diversification and dispersal at high latitudes. All parameters exhibiting significant differences between the OW and NW possessed higher rates in the NW. Given support for differences in parameter values between the OW and NW under the G-7 model, analysis of the eight replicate avian clades were performed only with the G-7 model.

For each of the eight avian clades, median net diversification rates were highest and extinction rates were lowest at the latitudinal region with highest species richness for the G-7 model (Fig. 2). This was true for both the NW and OW with one exception: OW Charadriiformes, had marginally higher net diversification and lower extinction rates at low latitudes, despite having marginally lower species richness there, but the latitudinal diversity gradient is almost flat in the OW for this clade. In many cases, these latitudinal differences in net diversification and extinction rate were significant (Fig. 2). In contrast, an association between speciation or dispersal rates with species richness was not consistently found across replicate bird clades. Median speciation rate estimates were highest where species diversity was highest in only half of the clade comparisons, only one of which was significant (all NW birds; Fig. 2). Speciation rates were significantly highest where diversity was lowest in three clade comparisons (all OW birds, OW Galliformes, and OW Passeriformes; Fig. 2). For dispersal, only two orders showed significant latitudinal differences (all NW birds and NW Passeriformes), with dispersal greater into the tropics than in the reverse.

MODEL PERFORMANCE

Datasets (trees and associated geographic character data) were simulated under our G-7 model using the median parameter values obtained from 1000 actual phylogenies of all birds. The G-7 model was then fit to each simulated dataset and the median values were calculated. If the model works well for our actual dataset, then reestimated parameter values should be similar to the values under which trees were simulated (See Table S2). When the ancestor state of the root node was set to be in the OW (states 5, 6, or 7), the model performed well, estimating model parameters (and latitudinal gradients in these parameters) to be very similar to those values under which they were simulated. However, when the root nodes' ancestor state was set to be in the NW (states 1, 2, or 3), the model correctly estimated model parameters only for the NW and performed poorly for the OW. This latter result arises because dispersal rates between the NW and OW are an order of magnitude lower than in the reverse direction (0.0035 vs. 0.034). The low probability of dispersal from the NW to OW results in few lineages having colonized the OW in our simulations. The resulting parameter estimates for the OW are then based on very small numbers of species in each character state. These results indicate that the G-7 model performs well at reestimating parameter values on the tree of all birds, provided datasets are simulated using an OW ancestor character state.

Discussion

Species richness patterns along latitudinal gradients are a well-documented phenomenon, yet it is still debated to what extent historical factors (e.g., time, rates of speciation, extinction, dispersal) influence these patterns, with proponents of the ecological limits hypothesis favoring the role of limited resources in constraining species richness (e.g., Fisher 1960; Pianka 1966; Mittelbach et al. 2007; Rabosky 2009; Losos 2010; Price et al. 2014; Rabosky and Hurlbert 2015c). While our results do not reject the ecological limits hypothesis, they do suggest a strong and consistent role of net diversification in driving latitudinal species richness gradients across each of the replicate avian clades tested. Under the ecological limits hypothesis, we probably would not expect such a consistent result for each replicate group, but rather would expect that net diversification, dispersal, or time would each contribute to diversity gradients in different replicate clades, with ecological limits ultimately placing a cap on diversity. The consistent role of net diversification across replicate clades thus suggests that latitudinal diversity gradients may be driven by an underlying historical cause (see Krug et al. 2007). The faster net diversification at high latitudes in the two clades with contrarian latitudinal diversity gradients (see also Krug et al. 2007) further argues for the strong role of history.

With only one exception (OW Charadriiformes), median net diversification rates were highest (and often significantly so) at the latitudinal region with highest species richness, suggesting that net diversification differences may be a key driver of gradients in species richness. These results agree with many other studies that net diversification is generally highest in the tropics (birds, Cardillo 1999; Cardillo et al. 2005; Weir and Schluter 2007; primates, Böhm and Mayhew 2005; mammals, Rolland et al. 2014; squamates, Pyron 2014; amphibians, Pyron and Wiens 2013; marine bivalves, Crame 2002; foraminifera, Buzas et al. 2002; butterflies, Cardillo 1999; plants Jansson and Davies 2007), but conflict with a recent global analysis of net diversification rates for birds (e.g., using a similar dataset to our study) that failed to uncover latitudinal differences (Jetz et al. 2012). Our rates are estimated across the entire history of the bird phylogeny, whereas the Jetz et al. approach weights their estimates toward the tips of the phylogeny so that earlier history plays little role. Given the differences in time scale, these studies are not directly comparable.

Net diversification rates are the outcome of both speciation and extinction—with net rates representing the difference between these. Many authors have presumed that accelerated speciation in the tropics is the key factor driving high tropical net diversification rates (see review in Schluter 2016). For the phylogeny of all terrestrial birds we find higher tropical speciation rates only for the New World, while the Old World had significantly greater speciation at high latitudes, despite the fact that species richness is highest near the equator for both the Old and New World. Likewise, speciation rates were highest when net diversification was highest in only five of eight clades in the New World and in two of eight clades in the Old World, suggesting that a consistent association between high net diversification and speciation rates is lacking in our data. Similarly, Rabosky et al. (2015b) failed to find latitudinal differences in speciation rate for terrestrial birds using a very different modeling approach, while other taxonomic groups have produced mixed results for speciation as a potential driver of net diversification (e.g., mammals, Rolland et al. 2014; squamates, Pyron 2014; amphibians, Pyron and Wiens 2013).

Here, we find that extinction is consistently lowest where net diversification rates and diversity are highest across each of the replicate bird clades, despite the fact that these clades differ widely in terms of life histories, ecology, and species diversity. The consistency of the association between low extinction rate and high species richness suggests that extinction may play a more important role than speciation in driving differences in net diversification rates along latitudinal gradients, though we caution that extinction rates can be difficult to estimate from phylogenetic trees (see below; Rabosky 2010; Rabosky and McCune 2010). GeoSSE type analyses for squamates, amphibians, and

mammals also support lower extinction rates in the tropics, and extinction rates in these studies contributed more to net diversification than speciation (Rolland et al. 2014, when estimated for all mammals; Pyron 2014, for squamates; Pyron and Wiens 2013 for amphibians). Likewise, avian and mammalian sister species support reduced extinction rates in the tropics (Weir and Schluter 2007). This latter study sampled only the most recent time slice of evolutionary history encompassing the past several million years. Together, these studies suggest that extinction may play a key role, both near the recent and over the much longer time frames encompassed by the GeoSSE-type studies.

The key factors driving higher extinction rates at high latitudes are not definitively known, but it would seem plausible that climate plays an important role (see also Claramunt and Cracraft 2015). During the Eocene Optimum global temperatures were warmer than today, and resulted in less of a temperature gradient between the poles and equator (Clyde and LeCain 2012). Fossil records likewise demonstrate that the latitudinal diversity gradient seen today was less pronounced, or even flat at this time with many warm-adapted clades of plants, mammals, and insects occurring at high latitudes (Wing et al. 2005; Jaramillo et al. 2006; Yan et al. 2006; Beard 2008; Jaramillo et al. 2010; Archibald et al. 2010; Harrington et al. 2012). Global temperatures gradually cooled following the end of the Eocene Optimum at ~49 Ma, resulting in a progressively larger temperature difference between the poles and equator. Here, we propose that the terrestrial latitudinal diversity gradient we see today is largely the effect of a post-Eocene increase in extinction rates at high latitudes resulting from this cooling trend (see also Hawkins et al. 2006). Several major extinction events at high latitudes are tied directly to major drops in temperature since the Eocene Optimum. For example, the Eocene-Oligocene extinction event is associated with a major drop in global temperature that resulted in the establishment of the Antarctic ice cap at 34 Ma (Berggren and Prothero 1992; Zachos et al. 2001). This global cooling is believed to have caused extinction of 60% of endemic European taxa, making it one of the most severe mammalian extinctions (Berggren and Prothero 1992). More recently, Milankovitch cycles, which have occurred throughout Earth's history, but are especially known as the drivers of the Plio-Pleistocene ice ages, have resulted in greater variance in temperature fluctuations at high versus low latitudes. Paleo-temperature records support temperature changes on the order to 10–12°C at 55° latitude between the most recent glacial maximum and the present, but only a few degrees near the equator (Thompson et al. 2000; Zachos 2001). Such climatic fluctuations forced species at high latitudes to adapt to new thermal regimes or shift their geographic ranges (Dynesius and Jansson 2000; Jansson and Davies 2007), with extinction being the end result for species unable to do either.

A by-product of higher extinction rates at high latitudes is that the amount of time available for diversification toward the poles is repeatedly being reset. Severe episodes of extinction may reset the clock for entire clades at high latitudes, with recolonization from the tropics ensuing and generating an “out-of-the-tropics” signature whereby high latitude clades are younger and are phylogenetically nested within tropical clades as expected if they had been colonized from the tropics (Hawkins et al. 2006). Such signatures could be driven by two historical factors—the older age of the tropics, or elevated high latitude extinction. A common interpretation is that tropical biomes are older than high latitude ones, and have therefore had more time for species richness to accumulate (the Time hypothesis). While this may be true to some degree, elevated high latitude extinction could also drive this signature (see Fisher 1960; Hawkins et al. 2006), even if low and high latitude biomes were of the same age, or if clades have diversified in temperate and tropical regions over the same time frames.

Caution in interpreting the support for extinction is warranted given the difficulties in estimating extinction from phylogenies (Rabosky 2010; Rabosky and McCune 2010; Morlon 2014; Rabosky 2016; though see Beaulieu and O’Meara 2015). Our modeling approach assumes rate constancy through time and across lineages within each of the seven geographic character states. Violations of rate constancy through time for extinction have been shown to result in imprecise extinction rate estimates from phylogenetic trees (Rabosky 2010). Similar tests have not been performed for speciation, but we expect the same would be true for it as well. While models have been developed that allow for a monotonic decline in extinction and speciation rates through time (e.g., currently available for 3-state GeoSSE models, but would require too many additional parameters to be feasibly incorporated into our 7-state model), these models still do not reflect the diversification dynamics of real clades where rates of speciation, extinction, and dispersal are likely to fluctuate through time in ways not easily captured by a simple monotonic decline. Despite these uncertainties, our analyses consistently provide support for extinction as a driving factor across all but one replicate bird clade. Either latitudinal estimates of extinction are repeatedly biased under the GeoSSE framework—and our various tests of bias argue against this—or extinction may play a genuine role in driving latitudinal gradients.

A recent analysis (not using the GeoSSE model) of a global phylogeny of all birds suggested that diversification rate dynamics differ significantly between the OW and NW (Jetz et al. 2012), with rates higher in the NW. Here we expanded the already available GeoSSE model from three (G-3 model) to seven geographic character states (G-7 model) so as to incorporate diversification rate differences between the OW and NW. Our simulation analysis demonstrates that, despite its complexity, the G-7 model performs

well at providing unbiased parameter estimates from large phylogenies. Like the Jetz et al. (2012) analysis, the G-7 model showed significant differences in net diversification as well as speciation and extinction rates between the OW and NW, with rates in all three parameters higher in the NW. The key result of this paper, that extinction is the primary driver of latitudinal diversity gradients, was not consistently recovered across avian clades when using the simpler 3-state (G-3) GeoSSE model (see Fig. S1) that ignored differences in diversification dynamics between the OW and NW. The apparent failure on the part of the 3-state model suggests that merging different geographic regions with different rates may result in parameter estimates with little meaning. While our 7-state model (G-7) may be an improvement over previous studies of global phylogenies using the more simplistic 3-state GeoSSE model, our G7-GeoSSE model may still fail to capture the geographic complexity of how diversification and dispersal rates vary globally. For example, our model did not allow for potential differences in parameter values between high latitude regions of the Northern and Southern Hemispheres. Likewise, the Old World possesses a number of isolated tropical regions (e.g., Africa, Asia and Australasia) which we combined together here in a single geographic character state. While greater model realism may be desirable, the increase in number of parameters would make such models impractical within the GeoSSE modeling framework.

Also, our approach (like other GeoSSE and related models) assumes that parameter values are constant across all lineages within each character state. Here, we performed separate model fits on eight major clades of birds, some of which had very different diversification dynamics. These results demonstrate variability in speciation, extinction, and dispersal rates between different bird clades. We expect model parameters to potentially vary across lineages within each of these clades as well (Kennedy et al. 2014), and thus to violate this assumption of the model. Such a violation may have the greatest consequences when only a few character state transitions have occurred within the dataset (e.g., a single subclade may drive a result for reasons unrelated to its occurrence in a given geographic character state; Maddison and FitzJohn 2014) while many such transitions are likely to occur within most of the avian clades used here.

We also acknowledge that the Jetz et al. (2012) phylogenetic dataset, along with other large “supertrees” constructed using available sequence data in Genbank (e.g., mammals: Rolland et al. 2014; amphibians: Pyron and Wiens 2013), are on the low end of data quality. We suspect that the Jetz et al. phylogenetic datasets will possess numerous topological errors. Therefore, we performed our analyses on 1000 posterior trees from the Jetz et al. (2012) dataset to account for topological uncertainty. Likewise, some of the fossil calibrations applied by Jetz et al. (2012) have been criticized (Barker et al. 2015; Burleigh et al. 2015). Imprecise

or faulty calibration may alter the root node age on the Jetz et al. (2012) phylogeny, but is unlikely to have had a major effect on the relative node ages and thus on the general latitudinal patterns we uncovered. Most of the replicate avian clades we analyzed are not represented by fossil calibrations on the phylogeny and when they are so represented, it is usually just by one or a small number of such calibrations. Our analyses of these clades are likely robust to imprecise or faulty calibrations that may occur in other parts of the tree. Importantly, it is very difficult to see how topological errors or miscalibration on the phylogeny would result in the consistent latitudinal patterns we detect in net diversification and extinction rates across avian orders.

Despite the limitations of GeoSSE type models and uncertainties in the dating and topology of the Jetz et al. phylogeny that we use, this study contributes to a deeper understanding of the differences in global patterns of species richness. Like many other studies, our results strongly support increased net diversification rates as a driver of latitudinal gradients in species richness. However, while many studies have assumed that speciation is the primary factor driving net diversification, our results find a consistent role of extinction rather than speciation as the key driver. We consistently find reduced extinction where diversity is highest for all eight bird clades tested, including two clades that show contrarian latitudinal diversity gradients in which species richness increased toward high latitudes. Higher extinction rates at high latitudes suggest that bird clades may often go extinct there, allowing for recolonization from tropical source faunas, and generating an “out-of-the-tropics” signature. Given the difficulty of estimating extinction, our extinction results should be viewed with caution and we encourage additional phylogenetic and fossil-based estimates of extinction across latitudinal gradients.

DATA ARCHIVING

The doi for our data is 10.5061/dryad.2v462.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1

Appendix S2

Figure S1. Posterior distributions of diversification parameters (Speciation, Extinction, Net diversification and Dispersal) estimated for all terrestrial birds and for eight clades using the G-3 GeoSSE model.

Figure S2. Posterior distributions of diversification parameters (Speciation, Extinction, Net diversification and Dispersal) estimated for all terrestrial birds—including species without genetic data—using the G-7 GeoSSE model.

Figure S3. Posterior distributions of diversification parameters (Speciation, Extinction, Net diversification and Dispersal) obtained from G-7 model fit, where we randomly pruned tips from our phylogeny of all terrestrial birds so that Holarctic, New World high latitude, and New World mixed character states had the same proportion of species sampling as in the New World tropics.

Table S1. Comparisons of parameter estimates between the NW and OW for the G-7 model fit to all terrestrial birds.

Table S2. Simulation based performance of the G-7 model.