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Minimal effects of latitude on present-day speciation rates in New World birds

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The tropics contain far greater numbers of species than temperate regions, suggesting that rates of species formation might differ systematically between tropical and non-tropical areas. We tested this hypothesis by reconstructing the history of speciation in New World (NW) land birds using BAMM, a Bayesian framework for modelling complex evolutionary dynamics on phylogenetic trees. We estimated marginal distributions of present-day speciation rates for each of 2571 species of birds. The present-day rate of speciation varies approximately 30-fold across NW birds, but there is no difference in the rate distributions for tropical and temperate taxa. Using macroevolutionary cohort analysis, we demonstrate that clades with high tropical membership do not produce species more rapidly than temperate clades. For nearly any value of present-day speciation rate, there are far more species in the tropics than the temperate zone. Any effects of latitude on speciation rate are marginal in comparison to the dramatic variation in rates among clades.

1. Introduction

Many groups of organisms are characterized by a striking latitudinal gradient in species diversity, with many more species occurring in tropical regions than in temperate regions [1–4]. Despite decades of study, the causes of this latitudinal diversity gradient (LDG) remain poorly understood. Many hypotheses for the LDG have been proposed that ultimately involve differential rates of species formation and/or extinction in the tropics relative to temperate regions [5,6]. Hence, the presence or the absence of a latitudinal gradient in diversification rates can support or reject a number of specific models for the LDG, even if the precise mechanisms underlying rate variation remain unknown.

Some recent studies have suggested that rates of species diversification vary systematically between tropical and temperate regions, although these studies have reached contrasting conclusions [7–10]. Others have found little evidence for latitudinal variation in diversification rates [11,12]. At least in part, these discrepancies may reflect taxon-specific differences in the relationship between latitude and diversification. However, it is also true that we face many challenges in the reconstruction of historical diversification rates using phylogenetic and distributional data from extant species. One challenge involves the inference of extinction rates. Even when all assumptions of the inference model used for reconstructing extinction rates are satisfied, confidence intervals on extinction rates are large [13,14]. When assumptions of the inference model are violated, extinction rate estimates can range from biased to nonsensical [15]. Another challenge involves the accuracy of historical biogeographic reconstructions: it is difficult to study the history of diversification rates with respect to geographical region, because—in the absence of a detailed fossil record—the only biogeographic information to which we have direct access consists of present-day distributions of species. Recent studies have demonstrated the challenges in reconstructing historical geographical distributions, even at the coarse scales of ‘tropical’ and ‘temperate’ [16].

In this study, we describe the latitudinal gradient in present-day speciation rates across all New World (NW) land birds. The LDG in species richness for

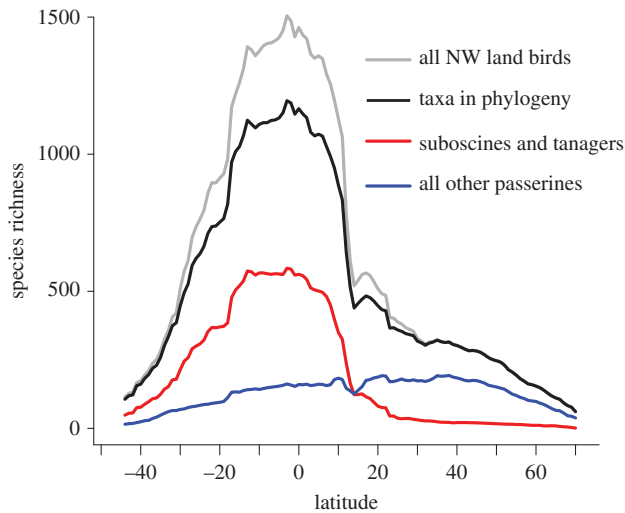


Figure 1. Latitudinal gradient in the land birds of the NW (breeding range). The true latitudinal gradient in species richness (grey curve) is very similar to the latitudinal gradient across the set of taxa present in the phylogenetic dataset (black curve). The latitudinal diversity in passerine birds ($n = 2260$ species in total) is driven almost entirely by two large clades: the suboscine passerines and the tanagers. These clades are largely restricted to the NW tropics yet highly diverse. When we consider the gradient in passerines after removing these two clades (blue), the tropics no longer contain more species than the temperate zone. (Online version in colour.)

NW birds is extreme [17–19], with many more species occurring in tropical South and Central America relative to southern South America and North America (figure 1). We focus explicitly on ‘recent’, or ‘present-day’ rates of speciation for several reasons. First, speciation rates can be estimated with much greater confidence than extinction rates, even when extinction rates vary among lineages [13,20]. The reason for this is simple, if not widely appreciated. Extinction events are unobserved quantities, and any pattern on a time-calibrated phylogeny is consistent, in principle, with high extinction as well as zero extinction. This is not true for speciation rates, because the density of nodes near the tips of a reconstructed phylogenetic tree is an absolute count of the minimum number of speciation events that could have occurred: to observe a node, a speciation event must have occurred. The minimum number of speciation events that could have occurred across any portion of a phylogenetic tree must always be greater than or equal to the corresponding minimum number of extinction events (typically zero). Narrower bounds on plausible numbers of speciation events mean that speciation rates will always be inferred with greater accuracy than extinction rates in the absence of fossils.

A more important reason for focusing on present-day speciation rates is that it enables robust tests of alternative hypotheses for the LDG without requiring the use of assumption-laden methods for reconstructing the historical geography of specific lineages [16,21]. Many candidate explanations for the LDG predict that present-day speciation rates should be higher in species from the tropics relative to those that inhabit the temperate zone. Mittlebach *et al.* [5] reviewed evolutionary causes of the LDG, identifying at least seven distinct hypotheses that predict faster present-day rates of speciation in the tropics. For example, several hypotheses invoke relationships between evolutionary speed and temperature [6] and its kinetic effects on speciation rate [22]. Others have proposed that the strength of biotic interactions in the tropics might drive faster speciation

[23]. Another class of explanations holds that biogeographic processes in tropical regions have led to faster speciation rates [24,25]. The general hypothesis of ‘speciation rate’ is thus an omnibus class of explanations that includes many potential mechanisms, all of which predict faster present-day rates of speciation in the tropics relative to temperate regions [5]. We addressed these hypotheses by focusing on a simple question: what are the distributions of present-day speciation rates for tropical and temperate land birds of the NW?

2. Material and methods

(a) Phylogenetic and latitudinal data

We used the phylogenetic framework from [11] to study the relationship between speciation rates and latitude. The Jetz *et al.* dataset (JEA) consists of two distributions of phylogenetic trees: one constructed with the higher level Hackett backbone topology [26], and a second distribution constructed using the Ericson backbone topology [27]. The phylogenetic positions of 33% of all species in the original JEA study were imputed subject to taxonomic constraints; we eliminated these species from the Hackett and Ericson distributions of phylogenies, as no genetic data were available to guide the placement of these taxa. We then computed the maximum clade credibility (MCC) tree for the distributions of both the Hackett and Ericson phylogenies, where each phylogeny included the 6670 taxa whose placement used at least some genetic data. These two trees—the MCC Hackett and Ericson phylogenies—form the core of all analyses described below. Hereafter, we refer to these MCC trees as the ‘Hackett’ and ‘Ericson’ phylogenies. Species distributional data were acquired for over 10 000 species from BirdLife International as GIS shapefiles [28]. Minimum, maximum and centroid latitude were measured from these distributions using the *sp* [29] and *rgeos* [30] packages in R. Each species distribution was tested for its intersection with major continents using the *rgeos* package.

(b) Analyses with BAMM

We used BAMM to study patterns of speciation rate variation across the avian phylogenies. BAMM is a software program that uses reversible jump Markov chain Monte Carlo (RJMCMC) to quantify complex patterns of diversification rate variation on phylogenetic trees [20,31,32]. BAMM can estimate posterior distributions of evolutionary rates at any point in time along the branches of phylogenetic trees. BAMM does not estimate a single ‘best’ set of evolutionary rate shifts, but simulates a posterior distribution of evolutionary rate shift configurations, where each shift configuration is sampled in proportion to its posterior probability. Each evolutionary rate shift in BAMM creates a ‘cohort’ of taxa that share common evolutionary parameters of speciation and extinction; by definition, all species in a cohort have identical diversification rates at any point in time. At the end of a BAMM run, posterior distributions of present-day speciation rates can be estimated for each individual taxon, by taking the marginal density of rates at the tips of the trees across all sampled rate shift configurations [33]. Because we are averaging speciation rates across multiple rate shift configurations, all taxa can potentially have a unique rate of speciation.

Tip rates computed in this fashion are essentially a predictive estimate of the present-day rate of speciation for every species in the tree. Marginal rates computed for individual species can potentially track rate variation that would be overlooked if we focused solely on rates inferred under the overall best shift configuration [31]. Consider a scenario where a ‘background’ speciation rate increases to a ‘fast’ speciation rate, but where the rate increase is mediated by a nested sequence of minor evolutionary innovations

that occur along a set of adjacent ancestor-descendant branches in a phylogenetic tree. The effect of any single innovation on speciation rate might be relatively small, but a clade that inherits all the innovations together might have a greatly increased rate of speciation. However, an early diverging lineage might only share one or several such innovations and would thus have a lower speciation rate. BAMM can track such variation with a single rate shift, if the posterior shift density along branches is proportional to the cumulative number of minor innovations that have occurred. The marginal rates for individual species would reflect this variation and allow early diverging lineages to have rates that are intermediate between the background and fast rates.

Because incomplete taxon sampling can bias diversification analyses [34,35], we addressed incomplete sampling by including family-specific sampling fractions directly into our diversification analysis. To correct for sampling at the family level, we used a taxonomic classification for all birds to estimate the percentage of taxa from each family-level clade that were not included in the analysis; this approach has been described previously in an analysis of fish diversification [32]. Species were assigned to families using the modified Birdlife taxonomy as described in Jetz *et al.* [11].

We analysed the 6670 taxon Hackett and Ericson phylogenies with BAMM, performing two separate runs of 250 million generations of RJMCMC sampling on each phylogeny. We placed exponential priors with mean values of 1.0 on all rate parameters, and an exponential hyperprior with rate 0.02 on the rate parameter of the Poisson distribution governing the number of diversification shifts across the phylogeny. We placed a normal prior with a mean of 0.0 and standard deviation of 0.05 on the exponential change parameter for the speciation rate with respect to time. We discarded the first 10% of each run as 'burn-in' and tested the distribution for convergence by computing the effective sample size in the number of evolutionary rate regimes in the dataset.

All BAMM analyses were performed on the avian phylogeny of 6670 species (both Hackett and Ericson topologies), with the analytical family-level correction for incomplete taxon sampling. For all subsequent analyses with BAMM output, we pruned the trees to include only NW land birds (2571 species). This included only those taxa with breeding ranges in continental North or South America, and we also excluded all taxa from the following aquatic or semi-aquatic orders: Anseriformes, Charadriiformes, Gaviiformes, Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Podicipediformes, Procellariiformes, Sphenisciformes and Suliformes.

(c) Analysis of the relationship between speciation rate and latitude

We estimated the marginal distribution of present-day speciation rates for each taxon for both Hackett and Ericson phylogenies. We then merged these distributions by computing the overall mean speciation rate across both topologies, yielding a single average rate of speciation. We compared distributions of species-level rates for taxa with centroid midpoints in the tropics and temperate zone. If speciation rates are faster in the tropics relative to the temperate zone, the distribution of species-level speciation rates should be right-shifted relative to the corresponding temperate zone rate distribution.

We also tested the relationship between latitude and speciation rate using statistically independent cohorts of lineages from BAMM analyses, where each cohort represents a set of lineages that are assigned to the same dynamic rate class [31]. Rates for any given cohort are, by definition, statistically independent of those for all other cohorts. The macroevolutionary cohort matrix [31] describes the pairwise matrix of correlations in evolutionary rates that are attributable to the BAMM model itself. Cohorts are not merely a simple grouping of lineages with similar rate dynamics: they are lineages that are inferred

to share an unobserved organismal trait or geographical state that results in identical diversification dynamics for all lineages possessing the feature. Lineages can only belong to the same cohort by virtue of common ancestry: clades that have converged on similar diversification rate dynamics cannot be part of the same cohort. For each sample in the posterior set of macroevolutionary rate shift configurations simulated using BAMM, we computed: (i) the fraction of taxa in the cohort that are from the tropics, and (ii) the latitudinal midpoint of all taxa in the cohort. We tested whether the speciation rate of each cohort was associated with either of these metrics of 'tropical-ness'. If latitude has a consistent effect on speciation rate, then more tropical cohorts should have faster rates of speciation than temperate cohorts.

(d) Analyses with time-constant rate of speciation

In a seminal paper, Weir & Schluter [7] found that present-day speciation and extinction rates were faster in the temperate zone relative to the tropics for NW birds and mammals. In the full BAMM model, each macroevolutionary rate regime includes a time-varying speciation process, where the rate of speciation varies through time using an exponential change function [20]. We repeated the analyses above but constrained speciation rates to be constant through time within rate regimes, in order to compare our results more directly with those of Weir & Schluter [7]. To constrain rates through time, we fixed the value of the exponential change parameter for speciation rate variation to zero during the MCMC simulation. After constraining the exponential change parameter, the BAMM model is similar to the MEDUSA model [36], because both approaches assume that phylogenies include a mixture of distinct constant-rate diversification partitions.

3. Results

(a) BAMM results

All BAMM runs had effective sample sizes in excess of 900 for the number of rate shifts. Independent runs had nearly identical distributions of log-likelihoods: we computed the 0.05, 0.10, 0.15 ... 0.85, 0.90 and 0.95 quantiles of the distribution of log-likelihoods for the Ericson and Hackett runs; the slope of the relationship between quantiles from the two Hackett runs was 0.992, and the slope of the relationship between quantiles for the two Ericson runs was 0.990. Median log-likelihoods were nearly identical for the Hackett runs (−20 314 and −20 317) as well as for the Ericson runs (−20 579 and −20 581). Log-likelihoods from the Hackett and Ericson phylogenies cannot be compared, as the trees are not identical.

Within the two Hackett runs, speciation rate estimates at the tips of the trees were highly correlated with each other (Pearson $r = 0.996$), and the same was true of the two Ericson runs ($r = 0.998$). The correlation between branch-specific marginal shift probabilities was 0.986 for the two Hackett runs, and 0.976 for the two Ericson runs. These results imply that the Ericson and Hackett runs converged on the similar posterior distributions of macroevolutionary rate shift configurations. Finally, tip-specific rates for the Hackett runs were highly correlated with those of the Ericson runs ($r = 0.90$; electronic supplementary material, figure S1). This indicates that, despite the overall structural differences between these phylogenies, the overall taxon-specific rate estimates are relatively robust to uncertainty about phylogenetic tree topology.

Comparisons of posterior and prior distributions on the number of rate shifts provide strong support for highly heterogeneous diversification dynamics across birds (electronic

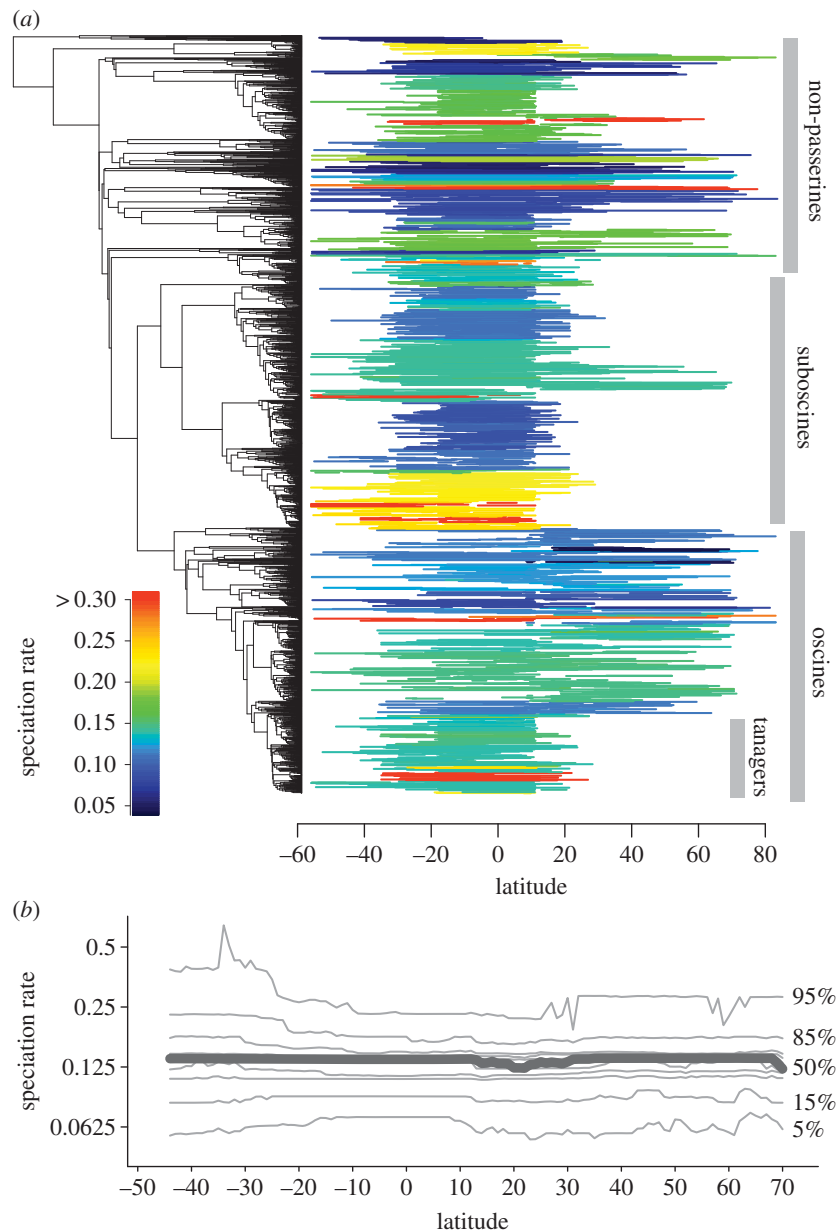


Figure 2. Latitudinal range and present-day speciation rate for NW land birds. (a) Latitudinal extent of breeding range for each of 2571 NW land birds (horizontal lines); the phylogenetic tree from [11] is shown for reference. Line colour indicates present-day speciation rate for each taxon. Tropical niche conservatism is clearly visible as blocks of related taxa that generally fail to extend northwards out of the tropics. Speciation rates vary widely among clades, but tropical groups (e.g. the suboscine passerines and tanagers) do not have faster rates of speciation than clades with high temperate zone representation. (b) Quantiles (grey) and median (black) of the distribution of speciation rates with respect to latitude.

supplementary material, figure S2). Posterior distributions of the number of macroevolutionary rate regimes across the full Hackett and Ericson trees were nearly identical: the maximum *a posteriori* probability estimate of the number of rate shifts for the Hackett tree was 68, versus 69 for the Ericson tree. The 95% CI on the number of rate shifts were nearly identical for these two datasets: 58–79 for the Hackett dataset, and 59–79 for the Ericson dataset. Because the prior distribution is identical for both sets of analyses, statistical support for complex rate variation is nearly identical for Hackett and Ericson trees; hence, we summarize only the results for the Hackett tree here. There is no measurable overlap between prior and posterior distributions for these data (electronic supplementary material, figure S2): the observed posterior distribution of the number of shifts is substantially right-shifted relative to the prior distribution. All observed rate shift counts in the posterior have prior

probabilities that are effectively equal to zero, indicating that the data contain very strong evidence for heterogeneous speciation dynamics.

(b) Rate distributions for tropical and temperate taxa

We estimated marginal distributions of present-day rates of species formation for all 2571 species of NW land birds in the phylogenetic dataset (figure 2a); these per-taxon rates range from 0.04 to 1.11 new species per million years (Myr). There is no trend in the distribution of speciation rates with respect to latitude, but all latitudes include a mixture of lineages with relatively fast and slow rates of speciation (figure 2b). Latitude is structured phylogenetically: some large clades, such as the suboscine passerines (flycatchers, ovenbirds, antbirds, cotingas, manakins) are largely restricted to the NW tropics. However, the suboscines comprise a mixture of

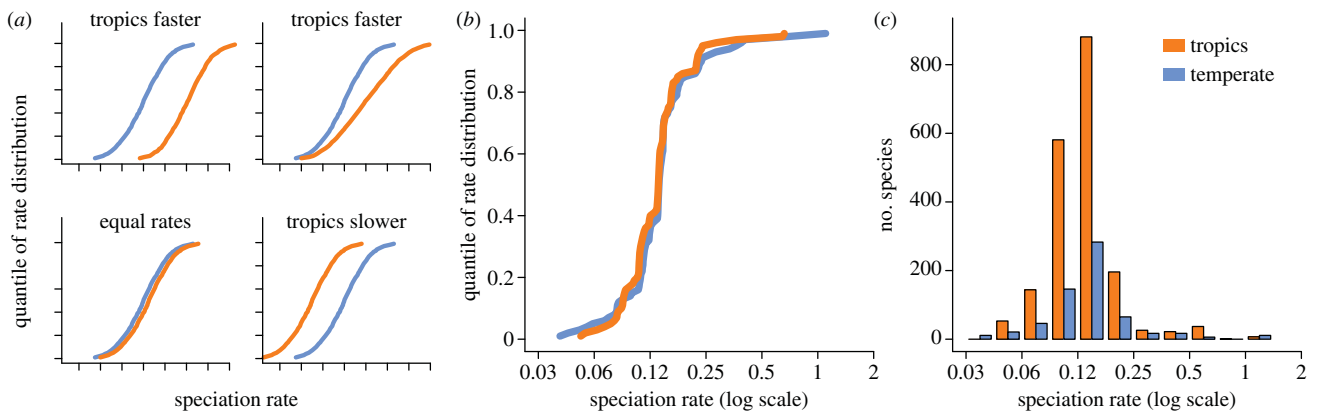


Figure 3. Speciation rate distributions for tropical and temperate taxa are nearly identical. (a) Predicted rank-ordered plots of speciation rates for tropical (orange) and temperate (blue) taxa under several hypotheses for the LDG. If speciation is faster in the tropics, rate distributions for tropical taxa should be right-shifted or slope-shifted relative to those of temperate taxa. If speciation rates are faster at high latitudes, as predicted by the faster turnover hypothesis, tropical rates should be left-shifted. (b) Observed rate distributions for tropical ($n = 1948$) and temperate ($n = 643$) taxa. (c) Frequency distribution of speciation rates for tropical and temperate taxa. For most values of speciation rate, there are more tropical than temperate species, indicating that the large number of tropical species is not driven by an excess of fast-speciating lineages.

lineages with slow, intermediate and fast speciation rates (figure 2a). To a first approximation, the latitudinal gradient in species richness for NW passerine birds is driven by just two clades with many species and few temperate representatives: the suboscines and the oscine tanagers (figures 1 and 2a).

Overall, there is a weak correlation between the absolute centroid midpoint of each species' breeding range and the corresponding rate of speciation (Pearson $r = 0.046$, $p = 0.02$; electronic supplementary material, figure S3). Median values of speciation rate across all temperate and tropical lineages are nearly identical (tropical: 0.139; temperate 0.140), although the means are slightly higher for temperate lineages (0.169 versus 0.154; t -test: $p = 0.024$).

If faster speciation rates in the tropics generate the LDG, the overall individual-level speciation rate distribution for the tropics should be right-shifted relative to the corresponding temperate zone distribution when visualized using a speciation-percentile plot (figure 3a). This would indicate that tropical species have faster rates than temperate regions for a given distributional percentile. If speciation rates are faster in the temperate region, as predicted by the 'faster turnover' hypothesis [7], we should find the tropical distribution left-shifted relative to the temperate distribution (figure 3a). We found that the distributions of speciation rates for tropical ($n = 1948$) and non-tropical ($n = 623$) taxa were virtually identical (figure 3b), a result that holds across both Ericson and Hackett phylogenies (electronic supplementary material, figure S4). Both distributions include many lineages with fast and slow rates of speciation, but there is a remarkable overall correspondence between these rate distributions.

We tabulated the frequency distribution of speciation rates for tropical and non-tropical taxa (figure 3c). For any given value of speciation rate, there are many more species in the tropics relative to the temperate zone. For example, if we consider only those species with speciation rates between 0.09 and 0.13 lineages Myr^{-1} , we find 146 non-tropical species and 581 tropical species. For the median value of speciation observed in non-tropical lineages (0.140), we estimate that there are approximately 3.60 times more species in the tropics with this same speciation rate. This number accords surprisingly well with the overall ratio of tropical to temperate

land birds in the NW ($N_{\text{tropics}}/N_{\text{temperate}} = 4.01$). These results are robust across both passerine and non-passerine lineages (electronic supplementary material, figures S3 and S5).

(c) Macroevolutionary cohort analysis

Each rate shift in a BAMM analysis defines a cohort of lineages that share a common set of macroevolutionary rate parameters. An illustrative example of cohorts identified through BAMM analysis is shown in the electronic supplementary material, figure S6. We computed the fraction of taxa from each cohort that were centered in the tropics; if speciation rates are faster in tropical regions, cohorts with greater percentages of tropical taxa should have faster rates of speciation. We also tested the relationship between the mean latitude for all taxa assigned to a cohort and the present-day rate of speciation for the cohort.

Individual cohorts vary widely in their fraction of tropical taxa: some cohorts are nearly equal mixtures of tropical and temperate species, but many large cohorts—such as the neotropical tanagers (figure 2)—are almost exclusively tropical. Despite this variation, there is no overall relationship between the fraction of tropical taxa and cohort speciation rate (figure 4a; 95% CI on distribution of correlations: -0.19 to 0.31 ; median $r = 0.06$). Likewise, the latitudinal midpoint of each cohort is not associated with speciation rate (figure 4b; 95% CI on distribution of correlations: -0.25 to 0.25 ; median $r = -0.01$). The electronic supplementary material, figure S7 shows the distribution of correlations between speciation rate, latitude and the fraction of tropical species for all samples from the posterior distribution simulated with BAMM. Electronic supplementary material, figure S8 demonstrates that the independence assumption that underlies our cohort analyses is reasonable for these data. Our observation that some major clades (e.g. suboscines; figure 2) and macroevolutionary cohorts (figure 4) are largely tropical yet show no evidence for accelerated speciation provides strong evidence against the hypothesis that the LDG is caused by latitudinal variation in speciation rates.

(d) Constant speciation through time

When we constrain our analyses such that speciation rates do not vary through time, we find statistical support for the faster turnover hypothesis [7]. The median speciation rate for

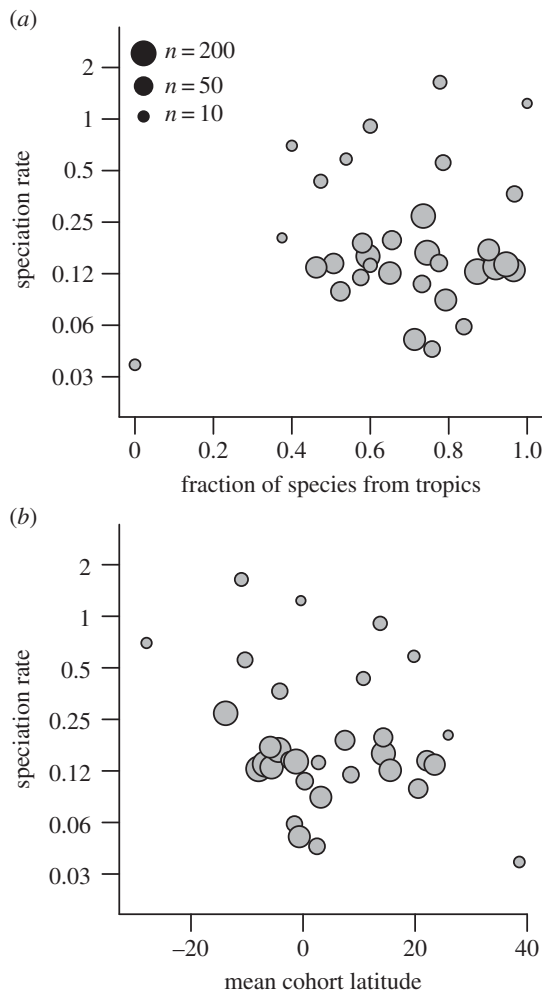


Figure 4. Speciation rates for macroevolutionary cohorts as a function of the percentage of tropical species (a) and the mean latitude (b) of all species in each cohort. Macroevolutionary cohorts are statistically independent clades (potentially paraphyletic) that are inferred to share common evolutionary rate dynamics. Speciation rate is uncorrelated with both metrics of ‘tropicalness’. Results are shown for the best macroevolutionary shift configuration identified with BAMM; results for the full posterior are shown in the electronic supplementary material, figure S7. Point size is proportional to the number of taxa in each cohort.

temperate taxa was 0.21 lineages Myr^{-1} , versus 0.17 lineages Myr^{-1} for temperate taxa. Clearly, both tropical and temperate taxa comprise a mixture of fast- and slow-speciating lineages, even with the constant-rate constraint. However, there is a shift in the rate distributions under the constant rate model (figure 5): proportionately more temperate taxa have faster rates of speciation, accounting for the overall difference in median rates. When we relax the assumption of constant rates through time, the rate distributions for tropical and temperate taxa are effectively identical (figures 3 and 5; electronic supplementary material, figure S9).

4. Discussion

Despite great variation in the rate of speciation across the land birds of the NW, we find a striking similarity in the speciation rate distributions for taxa from tropical and temperate regions (figure 3b,c). Even if we ultimately find a slight excess of fast-speciating lineages in either tropical or temperate regions, our reconstructed rate distributions (figure 3) indicate that

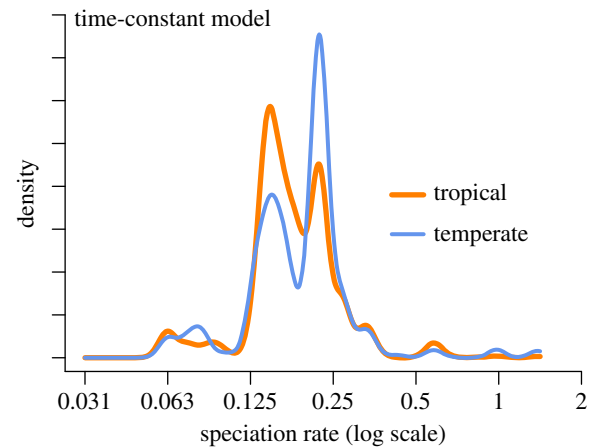


Figure 5. Speciation rates are faster in the temperate zone when speciation rates are constrained to be constant in time. Frequency distributions are kernel density estimates for tropical and temperate taxa, inferred with the constraint that speciation rates do not vary through time. There is a clear increase in the proportion of ‘fast-speciation’ temperate taxa relative to the tropics. Results presented in figures 2, 3 and 4 are based on the more general model that allows speciation rates to vary through time. See the electronic supplementary material, figure S9 for explicit comparison with the time-variable model.

the distribution of speciation rates is largely identical for most taxa. For any given value of speciation rate, there are more species in the tropics than in the temperate zone, and this result is not expected under any hypothesis that links speciation rates to high tropical diversity. Using macroevolutionary cohort analysis, we showed that clades with proportionately more tropical taxa do not speciate at faster rates than clades with lower tropical representation.

Our results imply that diversity-independent variation in speciation rate is unlikely to be a primary cause of the latitudinal gradient in species richness for this group of organisms. As such, our results—at least for NW birds—reject a broad class of evolutionary mechanisms for the LDG that involve variation in speciation rates [5], including the effects of temperature on speciation rates [6,37], greater capacity for allopatric speciation in tropical organisms [5] and the effects of biotic specialization on reproductive isolation [38]. The results here are based on a parametric model of speciation and extinction [20] but are nonetheless similar in broad outline to those reported using the ‘DR’ statistic, a weighted path measure of node density along the branches of a phylogenetic tree [11,39].

It is possible that tropical and temperate regions differ in levels of cryptic diversity, but this cannot drive the results presented here: downward biases in speciation estimates owing to yet-undescribed tropical diversity can only apply to yet-undescribed features of the latitudinal diversity curve, and our dataset already encompasses a substantial LDG for birds (figure 1). Thus, even if there is proportionately more undescribed taxonomic diversity in the tropics, our results remain valid as an explanation for the known LDG (figure 1).

It is also possible that revisions to the phylogenetic framework we have used here will influence the rate distributions presented here. In particular, there is emerging evidence that the Passeriformes are substantially younger than suggested by the JEA phylogenies. In our analyses, passerines—which account for approximately 55% of avian diversity—have crown ages of 66.8 and 73.3 Myr for the Hackett and Ericson backbones, respectively. Using complete genomes for 48 bird species, Jarvis *et al.* [40] estimated a crown age for Passeriformes

that was approximately 30 Myr younger. This age discrepancy would affect our estimates of speciation rates. If the dates reported in [40] are reasonably correct, speciation rates for passerine birds are almost certainly faster than those reported here. However, we presently have no reason to expect these biases to act directionally with respect to latitude.

All latitudinal regions contain mixtures of taxa from fast- and slow-speciation clades (figure 2). This rate heterogeneity has important implications for the study of geographical variation in speciation rates, because it is clear that there is no single ‘tropical’ or ‘temperate’ rate of speciation. Several models for studying the effects of traits or geography on diversification assume that rates are identical for all lineages possessing a particular character state or inhabiting a similar region [7,14,21], but it is clear that speciation rates vary widely among lineages within a given geographical region. State-dependent models of diversification are known to be sensitive to violations of this assumption. We do not fully understand the consequences of violating these assumptions, but unaccommodated rate heterogeneity can result in inflated Type I error rates [41,42] and severely biased ancestral state estimates [43].

A previous study suggested that rates of species turnover in NW birds were faster in the temperate zone [7], mediated by faster rates of both speciation and extinction at high latitudes. The statistical model used in their analyses assumed that evolutionary rates varied with respect to latitude but did not address the possibility that rates vary predictably through time. Our BAMM analyses recover the same general pattern they reported, but only after we constrained speciation rates to be constant in time (figure 5).

Relaxing this assumption yields latitudinal invariance in the rate of speciation (figure 3), consistent with the suggestion that tropical and temperate clades might vary predictably in the rate at which speciation changes through time, even if present-day rates do not differ among regions [39]. If rates are constrained to be time-constant, the present-day estimate of speciation rate should be more of a time-averaged rate, rather than a true estimate of the present-day rate. Hence, we expect that the difference between these analyses (figure 5) may reflect the possibility that some temperate clades underwent faster episodes of speciation in the past but that these rates have decelerated towards the present. This is consistent with the observation that some predominantly temperate zone clades, such as *Dendroica/Setophaga* wood-warblers (Parulidae), have undergone explosive bursts of speciation followed by pronounced temporal decelerations towards the present [44,45].

It is also possible that, at least in part, the general lack of relationship between speciation rate and latitude reflects relatively low power to identify clades or cohorts with shifts to lower diversification rates. In addition, the power of BAMM and other methods to identify diversification rate

heterogeneity on large phylogenetic trees remains poorly known. Thus, it is possible that our analyses have failed to detect a number of temperate lineages that have undergone diversification rate declines. However, macroevolutionary cohort analyses (figure 4) argue against low power as an explanation for these results.

Because we analysed present-day rates of speciation, it remains possible that ecological modulation of the rate of speciation through time, through diversity-dependent feedback mechanisms, is the primary cause of the LDG [39,46]. However, our results do not enable us to distinguish between diversity-dependence and other potential causes of the LDG. We did not assess the relationship between extinction and latitude, and it is possible that net diversification rates are faster in the tropics. Studies comparing species richness of tropical and temperate avian clades have yielded mixed results [10,12], though we find it interesting that the tropical suboscine clade has approximately the same diversity as the oscines (figure 2b). If systematic differences in net diversification rates underlie the LDG in passerines, we would expect the suboscines, which are largely restricted to the neotropics, to have greater species richness than the oscines.

It is also possible that the LDG reflects greater ‘evolutionary time’ for diversity to accumulate in tropical regions [47–49]. However, at least two observations argue against this, at least for the passerines. First, the suboscines have been present in the NW for at least 10 Myr longer than oscine lineages [39,50,51], but—in spite of this age difference—the clades are roughly equal in species richness. Second, the LDG within the oscine passerines is not consistent with a greater age for tropical clades. It is true that oscines on the whole are characterized by higher tropical diversity [39], but this is almost entirely driven by the tanagers, a single tropical clade, nested within a set of largely temperate oscine lineages [16,39,52].

As noted by other researchers [11,52–54], the radiation of modern birds is characterized by considerable variation in diversification rates. We are only beginning to understand the complex relationships between biotic and abiotic factors that lead to clade-specific differences in diversification, but our results suggest that such factors have profoundly shaped the diversity of living birds independent of their relationship with latitude.

Authors’ Contributions. D.R. conceived of the study, conducted diversification analyses and drafted the manuscript. P.T. and H.H. collected and analysed geographical range data. All authors helped draft the manuscript and gave final approval for publication.

Competing Interests. We have no competing interests.

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