



Phylogenetic patterns in the geographic distributions of birds support the tropical conservatism hypothesis

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ABSTRACT

Aim Recent research suggests that the latitudinal diversity gradient (LDG) in birds is unlikely to result from faster diversification in the tropics. This puts the focus on other mechanisms, such as dispersal, as the primary drivers for the LDG. We aim to distinguish two prominent models, tropical conservatism (TCH) and out of the tropics (OTM), which make distinct predictions about dispersal across latitudes and the phylogenetic clustering of assemblages in temperate regions.

Location Global.

Methods We used geographic and phylogenetic data for more than 9000 bird species to reconstruct the ancestral latitudinal zone for each node in each of 100 bird phylogenetic estimates. We used methods that consider discrete latitudinal zones, as well as those that consider latitudinal position as a continuous variable. We then estimated the frequency of ancestor–descendant dispersal within and across latitudinal zones. We also quantified phylogenetic clustering in latitudinal zones separately for bird assemblages within the Old World and the New World.

Results Latitudinal distributions are relatively conserved: 60–96% of nodes had the same inferred latitude as their immediate ancestral node. We find that dispersal events out of the tropics were less frequent (4–5%) than dispersal events into the tropics (15–21%), the opposite of what would be expected under the OTM. Nodes with inferred temperate distributions are generally younger than the Eocene–Oligocene Climate Transition, as expected under the TCH. Phylogenetic clustering shows no regular patterns of association with latitude, and is likely to be largely driven by radiations within a few large forested biomes.

Main conclusions Our results provide support for the expectations of the TCH, but are less consistent with those of the OTM. Both the deeper origins of tropical clades and the comparatively recent but infrequent dispersal events into temperate regions appear to play a role in generating the strong disparity in tropical and temperate species richness in birds.

Keywords

Ancestral dispersal, biogeography of birds, diversification of birds, latitudinal diversity gradient, out of the tropics hypothesis, tropical conservatism.

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INTRODUCTION

The latitudinal diversity gradient (LDG) – the decrease in species richness from the equator to the poles – is one of the largest geographic patterns of biodiversity, yet there is limited consensus about the processes that could explain it. Although geographic variation in species richness can be predicted from

current environmental conditions, such as geographic area, primary productivity, topography and energy availability (Currie, 1991; Jetz & Rahbek, 2002; Blackburn & Gaston, 2006; Evans *et al.*, 2006; Storch *et al.*, 2006; Davies *et al.*, 2007; Jetz & Fine, 2012), an understanding of the mechanisms underlying variation in diversity must be based on evolutionary and biogeographic processes: speciation, extinction and dispersal. The

growing amount of phylogenetic and geographic data available for large groups of organisms provides an opportunity to investigate how the processes leading to present-day species richness vary with latitude. Here, we use a near-complete fossil-calibrated phylogenetic estimate for the birds, together with geographic distribution data, to investigate whether patterns of dispersal across latitudes and phylogenetic clustering of species within latitudes are consistent with the expectations of two prominent hypotheses for the LDG.

Ultimately, the LDG must be shaped by the three processes that can change species richness, namely speciation, extinction and dispersal (Mittelbach *et al.*, 2007), but the relative importance of these processes is poorly understood. Furthermore, the processes of diversification and dispersal have not received equal attention; numerous studies have investigated how rates of speciation and extinction might vary across latitudes (Jablonski, 1993; Cardillo, 1999; Buzas *et al.*, 2002; Davies *et al.*, 2004; Cardillo *et al.*, 2005; Hawkins *et al.*, 2006; Ricklefs, 2006; Weir & Schluter, 2007; Wiens, 2007; Jetz & Fine, 2012; Jetz *et al.*, 2012; Soria-Carrasco & Castresana, 2012; Jansson *et al.*, 2013; Pyron & Wiens, 2013; Rolland *et al.*, 2014; Rabosky *et al.*, 2015), but relatively few studies have explicitly investigated the patterns of dispersal events across latitudes (Jablonski *et al.*, 2006; Jansson *et al.*, 2013; Pyron & Wiens, 2013; Kerkhoff *et al.*, 2014). Nonetheless, describing patterns of dispersal across latitudes could help distinguish two prominent hypotheses for explaining the LDG. Under the 'out of the tropics' model (OTM), rates of origination (speciation) are highest in tropical regions and there is a net movement of species from tropical to extra-tropical regions, as tropical clades continually produce descendant lineages that adapt to temperate conditions (Jablonski *et al.*, 2006). Most of the support for this model comes from palaeontology of marine organisms, but the OTM has been suggested to apply generally (Jansson *et al.*, 2013). Support for higher tropical origination as suggested by the OTM has been mixed, with some studies providing support (Jablonski *et al.*, 2006, 2013; Jansson *et al.*, 2013) but others failing to do so (Smith *et al.*, 2012; Pyron & Wiens, 2013; Kerkhoff *et al.*, 2014). Under the tropical niche conservatism hypothesis (TCH), high tropical diversity has arisen as a consequence of the tropical origins of most major groups of organisms (Wiens & Donoghue, 2004). Wiens & Donoghue (2004) argued that many major taxa originated and began diversifying in tropical environments, which occurred primarily because the climatic conditions that are currently within the tropics extended far into temperate zones until the mid-Tertiary (Behrensmeyer, 1992). Phylogenetic conservatism in adaptations to tropical environments means that dispersal events into temperate zones are rare. Under this scenario, the comparatively high diversity of the tropics is the result of the longer time available for tropical assemblages to diversify.

Hence, the OTM and TCH make distinct predictions regarding the patterns of evolutionary dispersal across latitudes. Under the OTM, dispersal is frequent and asymmetric – tropical to temperate dispersal is frequent, and temperate to tropical dispersal is rare. On the other hand, under the TCH dispersal is generally rare, and there is no expectation of asymmetry in the

direction of dispersal. The two models also differ in the expected phylogenetic structure of temperate assemblages (Kerkhoff *et al.*, 2014). The OTM proposes that taxa from across the phylogeny can readily disperse out of the tropics, so that temperate assemblages are either phylogenetically overdispersed compared with a null model (i.e. species are less closely related to one another than expected), or that phylogenetic structure is indistinguishable from a null model. Under the TCH, dispersal events into temperate zones are rare and can give rise to endemic and phylogenetically clustered temperate radiations (i.e. temperate species are more closely related to each other than expected). Such a pattern of phylogenetic clustering was recently found by Kerkhoff *et al.* (2014) in New World angiosperms, and has been interpreted as evidence in support of the TCH.

Although evidence consistent with the TCH is accumulating (Wiens & Donoghue, 2004; Hawkins *et al.*, 2006; Hawkins *et al.*, 2007; Hawkins & DeVries, 2009; Wiens *et al.*, 2009; Buckley *et al.*, 2010; Condamine *et al.*, 2012; Smith *et al.*, 2012; Kerkhoff *et al.*, 2014) there has to our knowledge been no reconstruction of dispersal events across latitudes for the global bird fauna or explicit comparison of the expectations under OTM and TCH. In this study, we make use of a phylogenetic estimate for birds and a database of geographic distributions. We use these data to reconstruct ancestral latitudinal zones and infer the frequency of dispersal events into and out of the tropics. As an additional means of distinguishing the OTM and TCH, we follow the approach by Kerkhoff *et al.* (2014) for analysing the phylogenetic structure of bird assemblages across latitudes.

METHODS

Phylogenetic and geographic data

We downloaded the geographic ranges of 9118 bird species (approximately 90% of known species) including both breeding and winter distributions from BirdLife International (BirdLife International and NatureServe, 2012). As the phylogenetic estimate, we used 100 randomly selected trees sampled from the stage 2 posterior distribution of phylogenies presented by Jetz & Fine (2012) and Jetz *et al.* (2012).

From the geographic range maps we calculated the latitudinal centroid of each bird species. In a recent study, Kerkhoff *et al.* (2014) used the maximum and minimum latitudes of species distributions to calculate an index of 'tropicality'. We applied a modified form of their index that maintains the distinction between northern and southern temperate zones, allowing us to recover the patterns associated with the historical biogeography of bird clades rather than simply their association with tropical environments. We refer to this measure as the 'latitude index' (LI). It is calculated as the proportion of the latitudinal range that falls north of the tropics minus the proportion of the latitudinal range that falls south of the tropics. The result is a continuous variable ranging from -1 for entirely southern species, through 0 for entirely tropical species, to 1 for entirely northern species. We used 23.5° N and 23.5° S as boundaries for the tropics.

To categorize species into latitudinal zones, we refer to the species with a proportion of 25%/75% of their latitudinal range either south or north of the tropics as southern subtropical (SST) or northern subtropical (NST), respectively ($-0.75 \leq LI \leq -0.25$ and $0.25 \leq LI \leq 0.75$), species with > 75% of their range outside the tropics as either southern temperate (ST) or northern temperate (NT) ($-0.75 \geq LI \geq 0.75$), and species with < 25% of their range outside the tropics as 'tropical' ($-0.25 \leq LI \leq 0.25$). Of course, geographic summary measures based solely on latitude will not fully capture the environmental affinities of some species, for example high-elevation tropical species. At a global scale, however, we believe that latitude is correlated strongly enough with major climatic variables that latitudinal range should be a reasonable proxy of environmental affinity.

Inferring ancestral latitudes

To infer dispersal events across latitudes, we reconstructed ancestral latitudinal zones for each of the internal nodes in the phylogenies. We then produced a matrix of dispersal events between each of the latitudinal zones. We combined the matrices for the 100 phylogenies by calculating mean values for the frequencies of dispersal events. Under the OTM we expect an excess of tropical to temperate events, whereas the expectation under the TCH is that there is no asymmetry in the direction of dispersal. To test whether dispersal has occurred with similar frequency across latitudinal zones, we used a χ^2 test of matrix homogeneity on the combined matrix of dispersal events. Another expectation under the two models is that dispersal events are common under the OTM but uncommon under TCH. There is no simple objective way to define 'common' and 'uncommon' in order to test these predictions statistically, but in general we expect that if a great majority of phylogenetic branches show no latitudinal shift, it would more strongly support the TCH.

We used two methods to estimate ancestral latitudinal zones. The first treated latitudinal zones as a categorical variable, using models of geographic range evolution implemented in the R package BioGeoBEARS (Matzke, 2013). To account for the uncertainty in the best model of geographic range evolution we used the results based on the best-fitting model for each of the 100 trees sampled from the posterior. We chose to test two models describing the processes that are likely to have occurred during the radiation of birds. The simplest model was the DEC model (Ree *et al.*, 2005; Ree & Smith, 2008), which includes parameters for dispersal, extinction and changes in geographic range during cladogenesis. We tested this model against the more complex DEC + J model, which includes an additional parameter for founder-speciation events (Matzke, 2014). We used the reconstructed nodal values of LI with the highest estimated probabilities to infer latitudinal transition frequencies.

The second method for estimating ancestral latitudinal zones was based on LI as a continuous trait. We first tested four alternative models for the temporal pattern of evolution of LI using

the R package GEIGER v2.0 (Harmon *et al.*, 2008). The models we selected to test included: (1) the Ornstein–Uhlenbeck model, which is plausible if dispersal away from the ancestral range is penalized by decreased fitness; (2) Pagel's λ -transformed random walk, which is plausible if northern and southern limits of species distributions drift randomly and non-directionally through time; (3) the trend model, in which evolution occurs under a Brownian motion process with a trend through time; and (4) the early burst model, which also describes a process in which the rate of evolution varies through time and is plausible if rapid geographic expansion occurs early in a clade's history, as expected under an adaptive radiation scenario. For each of the 100 phylogenies, the model with the lowest Akaike information criterion (corrected for small sample sizes; AICc) score was selected (see Table S1). To reflect the pattern of LI evolution on the phylogeny, we transformed the branch lengths according to the best-fitting model and estimated parameters. This allowed us to calculate the maximum likelihood ancestral estimate of LI for each node in the tree using the sequential re-rooting method (Garland *et al.*, 1999; Garland & Ives, 2000) implemented in the R package PHYTOOLS v0.4 (Revell, 2012). This method re-roots the phylogeny at every node and calculates the phylogenetically independent contrast for the root node (Felsenstein, 1985), taking advantage of the fact that this value is the maximum likelihood estimate for that node.

A potential issue with estimating ancestral latitudes is that the great excess of tropical compared with temperate species may bias the reconstructed latitudes towards the tropics. For this reason, we carried out an additional analysis in which we randomly subsampled each of the 100 phylogenies such that each of the five LI categories contained the same number of species as the least species-rich category. The least species-rich category was ST with 458 species, so the subsampled phylogenies from the posterior had 2290 species. We repeated the analyses using BioGeoBEARS and PHYTOOLS for each of the subsampled phylogenies, and present these results in the both Figures S1 and S2.

Quantifying phylogenetic clustering within latitudinal zones

To quantify the degree of phylogenetic clustering of bird assemblages within latitudinal bands of 10° width, we used the net relatedness index (NRI; Webb & Ackerly, 2002), a standardized measure of the mean patristic distance among pairs of species. We assigned each species to the latitudinal band that contained its centroid latitude, so that each species was only included in the analysis once. We performed this analysis separately for species belonging to the New World ($n = 3730$) and the Old World ($n = 5205$), excluding species that occurred in both regions and entirely marine species. NRI is standardized with respect to a null assemblage, which we generated by randomizing species identities 999 times among all latitudinal zones using the independent swap algorithm, maintaining the observed number of species per zone (Gotelli, 2000). In this way we obtained values of NRI that indicate the degree of phylogenetic clustering or

dispersion in the context of the entire fauna of the New World and Old World, respectively. NRI values were calculated using functions in the R package PICANTE v1.6 (Kembel *et al.*, 2010).

RESULTS

The reconstructed latitudinal zones for the deepest nodes in the phylogeny of birds, including the crown node for all birds, are inferred to have a distribution in the southern part of the tropical zone (Fig. 1). Hence, all the internal and tip nodes reconstructed with temperate distributions are nested within older tropical clades. There is a strong asymmetry in the distribution of node ages between the Northern and Southern Hemispheres. Diversification into southern temperate regions began around 70–80 Ma, while widespread diversification into northern temperate regions did not begin until around 50 Ma. The spread into far northern regions is likely to have accelerated during the first half of the Miocene, less than 20 Ma (Fig. 1b). Results based on phylogenies subsampled to an equal number of species per zone show similar results (see Figure S2).

The matrix of the frequency of evolutionary transitions across latitudes is not homogeneous. This result was consistent when reconstructed ancestral latitudes were based on categorical range evolution models ($\chi^2 = 26,933.75$, d.f. = 16, $P < 0.001$) or on a continuous measure of latitude ($\chi^2 = 24,011.25$, d.f. = 16, $P < 0.001$). Overall, a disproportionately high number of nodes descended from nodes found in the same latitudinal zone (a mean of 67% for analyses based on categorical range models, Fig. 2a; a mean of 79% for analyses based on continuous trait models, Fig. 2b). Latitudinal conservatism is particularly high in the northern and southern temperate zones, with more than 90% of nodes from that zone remaining in the same zone in the continuous trait models (Fig. 2b). There is also a net movement of species into the tropics from the subtropical

regions, which can be observed in the low rates of transition out of the tropics ($\leq 5\%$). These results were similar when the data were subsampled to contain an equal number of species in each latitudinal category. In subsampled data, however, transitions across latitudes were more frequent, with average conservatism of 47% and 76% in analyses using models of discrete geographic and continuous-trait evolution, respectively (see Figure S1).

Analyses of phylogenetic structure show that none of the mean values of NRI indicate significant clustering or significant overdispersion (Fig. 3) with respect to the entire terrestrial avifauna of the New World (Fig. 3c) or the Old World (Fig. 3d). Nonetheless, the degree of phylogenetic clustering varies considerably among latitudinal zones, with some zones showing a far greater degree of clustering than others. The pattern of phylogenetic clustering among zones does not vary systematically with species richness or latitude. Instead, some of the regions with the highest clustering are in latitudes corresponding to tropical and temperate forests that have produced large avian radiations, including the Amazon rain forests (latitudes 20° S to 0° of the New World; Fig. 3c), North American temperate forests (latitudes 35–40° N of the New World; Fig. 3c), sub-Saharan Africa and Indonesia/Papua-New Guinea (latitudes 5° S to 5° N of the Old World; Fig. 3d) and Southeast Asia (latitudes 25–30° N of the Old World; Fig. 3d).

DISCUSSION

Both the TCH and the OTM rest on the assumption that the major bird clades originated in tropical environments, and that temperate clades are derived from older tropical clades. The TCH explicitly links the timing of tropical–temperate transitions with the Eocene–Oligocene Climate Transition around 34 Ma. During this period, average temperatures in high lati-

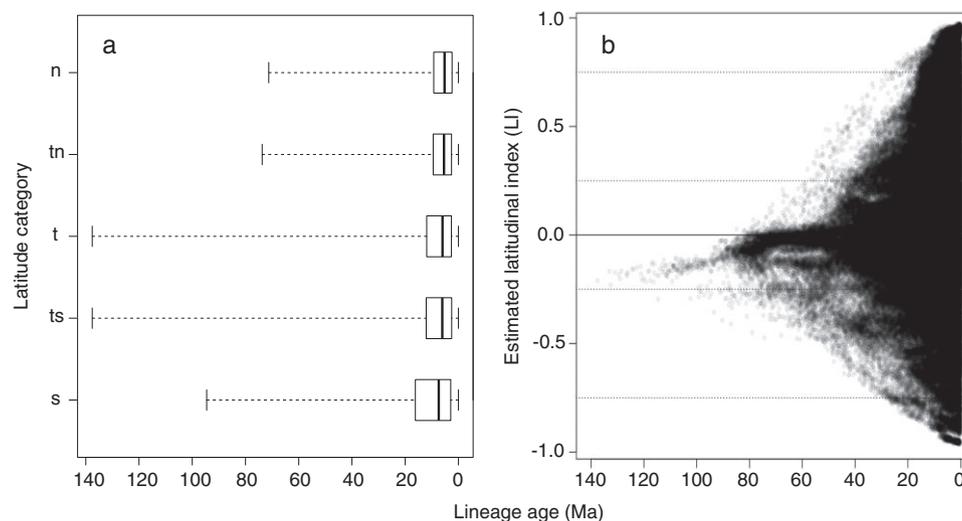


Figure 1 Ancestral estimates of the latitude index (LI) for nodes across node age estimates (Ma) of the nodes of 100 posterior trees, made using (a) geographic models of range evolution and (b) models of continuous trait evolution. The dotted vertical bands indicate the onset of global cooling and drying at the start of the Oligocene (*c.* 34 Ma).

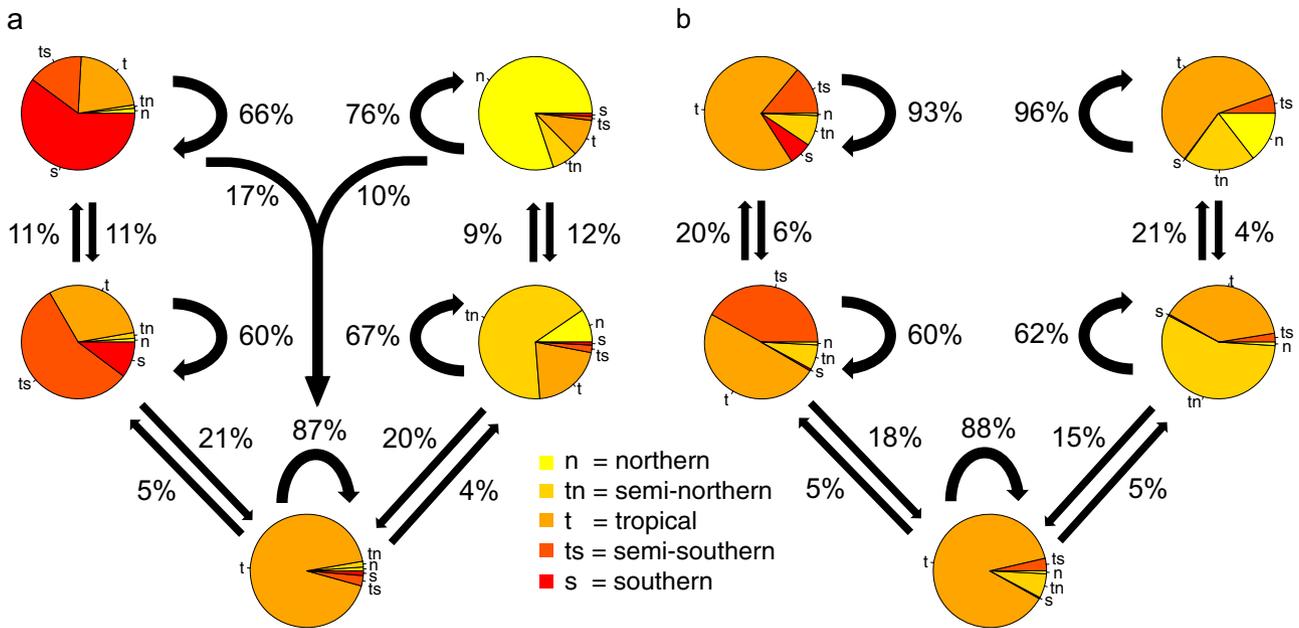


Figure 2 Proportion of transitions into each category (i.e. ancestry) represented as circle sections from 100 posterior trees. Arrows show the mean frequencies of evolutionary transitions between latitudinal zones. Values were inferred from reconstructed nodal values of the latitude index using (a) geographic models of range evolution and (b) models of continuous-trait evolution. Transitions percentages below 1% are not shown.

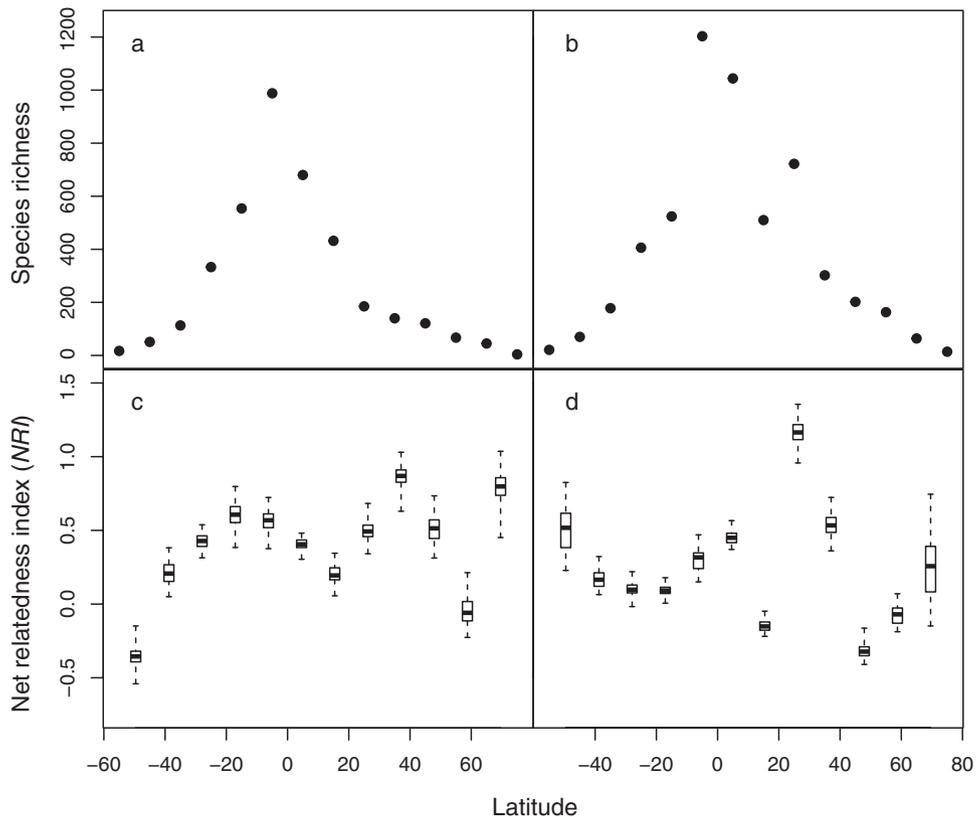


Figure 3 Species richness (upper panels) and standardized net relatedness index (NRI) (lower panels) across latitudes for avifauna of the (a, c) New World and (b, d) the Old World, excluding marine species. The uncertainty in NRI at each latitudinal band is derived from the results of 100 posterior trees.

tudes dropped by around 5 °C (Liu *et al.*, 2009), leading to the emergence of new large areas with a temperate climate regime. In contrast, the OTM suggests continuous dispersal of lineages into temperate latitudes, and is less explicit about the timing of tropical–temperate transitions (Jablonski *et al.*, 2006, 2013). Our results from inferred latitudinal zones for nodes of the avian phylogeny support the nestedness of temperate within tropical clades. We also find that the bird clades from temperate zones originated almost entirely after the Eocene–Oligocene Climate Transition. This is consistent with evidence from the fossil record that the appearance of high-latitude bird clades occurred almost exclusively after the Oligocene (Manegold *et al.*, 2004; Mayr, 2004). Because this pattern is explicit about the timing of diversification, it is consistent with the expectations of the TCH; a similar pattern was found recently in New World angiosperms (Kerkhoff *et al.*, 2014).

Further support for the TCH is provided by the patterns of evolutionary transitions across latitudes. While the TCH predicts a generally low rate of transition across latitudes, making no explicit predictions about the relative frequency of transitions into and out of the tropics, the OTM suggests that transitions are both frequent and asymmetric, with a higher rate of dispersal out of the tropics. Although it is difficult to define a transition rate that would distinguish the OTM and TCH models objectively, our results indicate that the majority of nodes (>60%) occupy the same latitudinal zone as their immediate ancestral node, supporting the TCH prediction of widespread latitudinal conservatism. Furthermore, the asymmetry in the transitions into and out of the tropical zone is biased in favour of dispersal into the tropics, the opposite of what would be expected under the OTM. This provides support for the TCH and mirrors the pattern for New World plants (Kerkhoff *et al.*, 2014).

Our results for the phylogenetic structure of bird assemblages do not support one model over the other. We find no evidence for significant phylogenetic clustering of assemblages at high latitudes, in contrast with the findings in New World angiosperms (Kerkhoff *et al.*, 2014). This result might be caused by limited power in our tests to reject null models in the direction of phylogenetic clustering. This is because we standardized empirical values of NRI by drawing random samples of species from all latitudinal zones, and calculating their mean pairwise distance (MPD). These samples of the null distribution will typically include close relatives from large tropical radiations (such as the New World suboscines), leading to high MPD values for random samples. Even endemic temperate radiations derived from only a few lineages are unlikely to be sufficiently closely related to be significantly clustered. On the other hand, the metric for quantifying phylogenetic clustering used by Kerkhoff *et al.* (2014), the standardized effect size of phylogenetic diversity (PD_z), probably suffers from the opposite problem. The phylogenetic diversity of an assemblage is the sum of the branch lengths connecting the species in the assemblage. A random sample of species is likely to traverse the root of the tree, while small, non-random subsets of the fauna are not likely to traverse the root. In this way, PD_z will frequently indicate

significant phylogenetic clustering. NRI is less sensitive to traverses through the root of the tree because it is based on mean pairwise branch lengths compared with total branch lengths. For this reason, we believe NRI provides a more reasonable metric for phylogenetic clustering than PD_z. Although our NRI estimates do not reject the null models, they indicate substantial variation in the degree of phylogenetic clustering among latitudinal zones. We find that NRI does not vary in a monotonic fashion with latitude, suggesting that clustering is more likely to be related to the patterns of avian radiations in different biomes. This is consistent with evidence that the history of bird diversification is closely linked with the emergence and expansion of global floristic regions (Hawkins *et al.*, 2005, 2007).

We conclude that our findings broadly support the expectations of the TCH, but are less consistent with the expectations of the OTM. At the same time, our results do not contradict the third major model for the high diversity of the tropics, namely faster diversification rates in the tropics. Although some previous analyses based on smaller subsets of bird fauna have supported faster diversification at lower latitudes (e.g. Cardillo, 1999; Cardillo *et al.*, 2005), two recent analyses of the global bird fauna have failed to do so (Jetz & Fine, 2012; Jetz *et al.*, 2012; Rabosky *et al.*, 2015). Instead, these studies found that diversification rates vary idiosyncratically among clades, with some of the highest diversification rates associated with radiations in temperate regions or on islands (Jetz & Fine, 2012; Jetz *et al.*, 2012). This places the time available for diversification and latitudinal conservatism as the mechanisms at the forefront of explanations for the latitudinal diversity gradient in birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Proportion of transitions into each category (i.e. ancestry) represented as circle sections from 100 posterior trees, using subsampled phylogenies to contain an equal number of species at each category.

Figure S2 Ancestral estimates of LI for nodes across node age estimates (Ma) of 100 posterior trees, made using subsampled phylogenies to contain an equal number of species at each category.

Table S1 Mean support for each of the models tested for 100 posterior trees, expressed in terms of likelihood and AICc.

BIOSKETCH

David Duchene is interested in the processes that drive macroevolution and molecular evolution as seen under the framework of phylogenetics. He is also interested in how patterns of diversification and molecular evolution influence our ability to make phylogenetic estimates and inferences.

Marcel Cardillo works on a range of questions in community ecology, macroecology, macroevolution and conservation biology, mostly using a comparative or modelling approach.

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