

Climate, Niche Conservatism, and the Global Bird Diversity Gradient

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ABSTRACT: We tested the proposition that there are more species in the tropics because basal clades adapted to warm paleoclimates have been lost in regions now experiencing cool climates. Molecular phylogenies were used to classify species as “basal” and “derived” based on their family, and their richness patterns were contrasted. Path models also evaluated environmental predictors of richness patterns. As predicted, basal clades are more diverse in the lowland tropics, whereas derived clades are more diverse in the extratropics and high-altitude tropics. Seventy-four percent of the variation in bird richness was explained by environmental variables, but models differed for basal and derived groups. The overall gradient is described by the spatial pattern of basal clades, although there are differences in the Old and New Worlds. We conclude that in ecological time, the global richness gradient reflects birds’ responses to climatic gradients, partially operating via plants. Over evolutionary time, the gradient primarily reflects the extirpation of species in older clades from parts of the world that have become cooler in the present. A strong secondary effect arises from dispersal of clades from centers of origin and subsequent radiations. Overall, the diversity gradient is well explained by niche conservatism and the “time-for-speciation” hypothesis.

Keywords: latitudinal gradient, species richness, niche conservatism, evolutionary time, extinction, time for speciation.

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Continental and intercontinental patterns of species richness of a wide range of plant and animal groups are known to be associated with measures of current climate, with the greatest number of species occurring in warm, wet areas (Wright et al. 1993; Hawkins et al. 2003a). For birds, a measure of water-energy balance, annual actual evapotranspiration (AET), has been shown to explain almost three-quarters of the variance in species richness measured in 220 × 220-km grid cells across most of the world (Hawkins et al. 2003b). Hawkins et al. (2005) subsequently found that in Australia, bird richness patterns were associated with both AET and annual plant production (measured by normalized difference vegetation index [NDVI]). Thus, the spatial distributions of currently existing bird species reflect a strong response to climate both directly and through its effect on plant biomass or vegetation structure. However, this association does not address the issue of how species are added to and removed from local and regional species pools, which is critical for understanding patterns of diversity over evolutionary timescales. Thus, linking ecological and evolutionary processes is a necessary step to generate a full understanding of richness gradients (Ricklefs 2004 and references therein).

Hawkins et al. (2005, 2006) proposed that the ecology and evolution of richness gradients of Australian and New World birds can be linked by an interaction between contemporary climate and the spatial pattern of change in paleoclimates since the Eocene. The underlying mechanism is niche conservatism in clades as they radiate (Wiens and Donoghue 2004; Wiens and Graham 2005). Developing a variant of the well-known evolutionary time hypothesis (Fischer 1960), Hawkins et al. (2005, 2006) argued that temperate zones contain fewer species primarily because many species of older, more basal bird clades originally adapted to the warmer, wetter climates of the early Tertiary have been excluded from the temperate zones in response to global-scale cooling in the Miocene and Oligocene, with the extratropics now occupied mainly by a subset of species from more derived clades that radiated

into cooler or drier climates in response to the change in climate. Consistent with this hypothesis, they found that Australian deserts support birds from more derived families (defined by their positions in molecular phylogenies) than do wetter areas (Hawkins et al. 2005). In the New World, basal clades are largely confined to the tropics and derived clades are relatively rich in the northern temperate zone and the Andes, where climates are cooler (Hawkins et al. 2006). However, they also identified probable secondary effects on the evolutionary structure of the bird faunas due to geographic isolation of both southwestern Australia and southern South America from centers of diversification for derived clades.

This article has two primary goals. First, we explore ecological correlates of diversity by developing a path model for the global bird richness gradient that includes actual evapotranspiration, a measure of plant productivity/biomass (the global vegetation index [GVI]), annual mean temperature, and a measure of mesoscale climatic gradients (the interaction between annual temperature and range in elevation). The first three variables are commonly used in richness analyses; the fourth is a new variable based on the fact that in warm climates, animals respond strongly to topography because orographic effects generate sharp climatic gradients over small spatial scales, and in cold climates, orographic effects are much weaker and have limited effects on animals (Janzen 1967). For example, Turner and Hawkins (2004) found that bird richness is associated with range in elevation much more strongly in the southern Nearctic and Palearctic than in the northern parts of both regions, and Hawkins and Diniz-Filho (2007) found that in the Neotropics and southern Nearctic, birds in the mountains have much smaller ranges than birds of the lowlands, whereas in the central and northern Nearctic, mean range sizes are similar in both mountains and lowlands. Rahbek and Graves (2001) also found that topographic effects on bird richness decreased in increasingly temperate climates in the Neotropics, quantified using the interaction between range in elevation and latitude.

Our second goal is to extend the hypothesis examined by Hawkins et al. (2005, 2006; see also Wiens and Donoghue 2004 for a related hypothesis) to the global bird richness gradient. Under the niche conservatism mechanism, few basal taxa should be found in extratropical regions, which instead should be largely confined to the Neotropical, Afrotropical, and Oriental regions where they first originated. Derived clades, in contrast, should be relatively rich in the temperate zones and at high elevations in the tropics. Further, if the most derived (i.e., oscine) passerines originated in eastern Australia, as argued by Barker et al. (2004) and Jönsson and Fjeldså (2006), we would expect a secondary gradient in their richness, based on the distance from Australia. Finally, if the latitudinal

richness gradient is defined by the distributions of basal taxa, there should be a strong spatial correspondence between basal richness patterns and the overall pattern for all birds. The reasoning behind the hypothesis also generates the prediction that the global diversity gradients of all birds and basal birds should be described by similar environmental models (because they have very similar diversity gradients), whereas the environmental model for derived clades should be different (because they are adapted to cooler climates and thus are richer across the temperate zones and in mountains in the tropics).

Material and Methods

Bird Species Richness

Range maps for Old World breeding birds were digitized from Cramp and Simmons (1977, 1980, 1983), Cramp (1985, 1988, 1992), Cramp and Perrins (1993, 1994a, 1994b), Keith et al. (1982, 1986, 1988, 1992, 1997), Fry et al. (2000), Fry and Keith (2004), Flint et al. (1984), Hollom et al. (1988), Simpson and Day (1984), Grimmett et al. (1999), MacKinnon and Phillips (2000), and Ding (2005). For the New World we used the digitized maps of Ridgely et al. (2003). Maps were rasterized in ArcGIS in grid systems of 27.5 km × 27.5 km and 110 km × 110 km using region-specific equal area projections. Islands were excluded from the grids (except for Tierra del Fuego and Great Britain), and island endemics and strictly feeding marine species were excluded from the database (the latter have complex range dynamics involving both terrestrial and marine habitats and utilize very different food sources than do terrestrial and freshwater birds). All continental areas are covered by the database except Afghanistan and Antarctica. Species richness was estimated directly from the rasters.

Environmental Predictors

Environmental path models of the contemporary richness gradient used four environmental variables known to be associated with species richness gradients and the newly derived interaction between mean annual temperature and range in elevation. All variables were processed in ArcGIS at the 110 × 110-km grain size for analysis.

1. Annual AET (Thorntwaite's; Tateishi and Ahn 1996; <http://www.grid.unep.ch/data/download/gnv183.zip>). The data are based on up to 60 years of weather data (1920–1980) and gridded at 0.5° resolution. We used the maximum value within each of our cells, assuming an “oasis effect” in which bird richness reflects the best conditions in an area rather than average conditions. The AET is strongly correlated with primary productivity at the global

extent (Rosenzweig 1968), but energy and water availability can have direct effects on birds (i.e., heat/cold and water stress) that operate independently of its influence on plants. Thus, it is not only a measure of productivity/biomass.

2. GVI (Kineman and Hastings 1992; <http://www2.ncdc.noaa.gov/docs/gviug/>). This index of “greenness” is derived from 1-km resolution NDVI. We averaged monthly data from January 1985 to December 1988 to generate an annual average. The average value in each cell was calculated, as the fine resolution of the data increases the chances that maximum values in our larger cells represent outliers. This variable examines the link between productivity/biomass and birds and thus provides a way to partition the direct effects (through bird physiology) and indirect effects (through plants) of AET on bird richness patterns. A problem with GVI, like NDVI, is that it saturates at high levels of plant greenness and consequently is unable to distinguish southern temperate and tropical forests in seasons of maximum plant growth. This prevents us from using seasonal measures of plant biomass, which might be expected to be more meaningful than annual measures (Hurlbert and Haskell 2003; Hawkins 2004). In addition, although an annual average does partially distinguish forests in the tropics (high GVI in all months) and temperate zones (high GVI in only some months), it remains that if bird richness responds more strongly to forests in the tropics than in the temperate zone due to either higher biomass or more complex vegetation structure in the former, GVI cannot capture that response fully, leading to an underestimation of the influence of vegetation on richness. However, no vegetation index that does not saturate (e.g., the enhanced vegetation index [EVI]) is currently usable at the global extent, so we use GVI despite its limitations.

3. Mean annual temperature (Leemans and Cramer 1991; <http://www.grid.unep.ch/data/data.php?category=atmosphere>). Annual average was generated from the mean monthly temperature data set (GNV15), which is based on weather records covering at least 5 years between 1930 and 1960 and gridded at 0.5° resolution. We calculated the average value in each of our 110 × 110-km cells.

4. Elevation range (<http://lpdaac.usgs.gov/gtopo30/gtopo30.asp>). The GTOPO30 digital elevation model (DEM) data with a horizontal grid spacing of 30" were used. A value representing the range between the minimum and the maximum elevation within each cell was calculated.

5. Temperature × range in elevation. The values of both variables in each cell were multiplied in the original units after adding 21 to the temperature data to generate all positive values (see also Hawkins and Diniz-Filho 2006). This interaction variable is necessarily collinear with its individual components, which was controlled by including direct paths

from both temperature and range in elevation to this variable in environmental path models (see “Path Models”).

Root Distance

Following Hawkins et al. (2005, 2006), each species was assigned a familial root distance (RD) based on a molecular phylogeny, and birds were assigned to families using the classification of Sibley and Monroe (1990). Root distance represents the number of nodes separating a species' family from the base of a phylogenetic tree (Kerr and Currie 1999). The tree used represented a combined tree resolved to family comprising the DNA-DNA hybridization analysis of Sibley and Ahlquist (1990) for nonpasserines and the DNA-sequence tree of Barker et al. (2004) for passerines. Previous analyses have indicated that distributions of root distances are robust to the specific combinations of trees used (Hawkins et al. 2005, 2006).

The 7,520 bird species were ranked from the most basal to the most derived (resolved to family), and the approximate 35% and 65% percentiles were selected: 2,700 species from 54 basal families (RD = 1–12) and 2,458 species from 16 derived families (RD = 23–25). Species richness was then calculated separately for each group. The percentiles were selected to balance insofar as possible the number of species in each group, but varying the percentiles used to separate out the most basal and derived sections of the bird phylogeny does not influence conclusions (Hawkins et al. 2005, 2006). It should also be noted that as the percentiles were selected at the species level rather than the family level, any future revision of the taxonomic ranks assigned to nodes in the phylogeny will have a very limited effect on the designation of groups of species as being basal or derived irrespective of whether the clade to which they belong is called a family or some higher or lower taxonomic unit. Finally, our use of “family” as the unit of phylogenetic analysis is primarily practical, as the tree we use is resolved to family, but the phylogenetic signal in life-history traits of birds is known to be strongest at higher taxonomic levels. For example, over 90% of the variation in clutch size is found among families and orders (Bennet and Owens 2002). Thus, we do not expect that defining clades at lower levels (tribal or generic) would provide much additional phylogenetic information or change the results, although this can be confirmed only when more a highly resolved tree for all birds becomes available.

Analysis

Spatial Autocorrelation Analysis. Pearson correlation coefficients between basal, derived, and total richness were used to quantify the similarity among richness patterns

among the groups. However, because subgroups of data are mathematically constrained to be correlated with the data set from which they are extracted, we further examined the strength of spatial structure in the three richness estimates using Moran's I autocorrelation coefficients, calculated for 40 geographic distance classes established at irregular distance intervals to keep the number of connections among cells similar in each class (see Diniz-Filho et al. 2003). Moran's I's for basal and derived clades were then correlated against the Moran's I's of all groups to evaluate the similarity of the spatial pattern for the subgroups with respect to the pattern for all birds (Hawkins et al. 2005).

We also calculated for basal, derived, and total richness the autoregressive parameter ρ using the model

$$\mathbf{y} = \rho \mathbf{W} \mathbf{y} + \boldsymbol{\varepsilon},$$

where \mathbf{y} is the vector of species richness, $\boldsymbol{\varepsilon}$ is the vector of residuals, and \mathbf{W} is a row-standardized matrix with a function of pairwise geographic distances D_{ij} among cells ($1/D_{ij}^2$). Because of the very large sample size (10,069 cells), we obtained ρ for samples of 500, 1,000, 2,000, 3,000, 4,000, and 5,000 cells, and we evaluated the change in the autocorrelation coefficient with increasing sample size. Values of ρ close to 1.0 indicate strong spatial association among neighbor cells, and thus it also estimates the amount of spatial autocorrelation in the data. We used the ρ values to obtain a conservative estimate of the number of degrees of freedom (v^*), based on the geographically effective sample size (n^* ; Griffith 2003). All significance tests and confidence intervals (CI) were based on geographically effective sample sizes.

Path Models. We initially conducted exploratory path analysis using EPA2 (Shipley 2002) to obtain alternative path models consistent with the data at $P > .05$. The program DGRAPH was then used to test each conditional independence statement in the defined path structure based on d-separation tests (Shipley 2002). Both EDA2 and DGRAPH were downloaded from <http://pages.usherbrooke.ca/jshipley/recherche/book.htm>.

After initial tests using EDA2 and DGRAPH, path coefficients were obtained iteratively using the maximum Wishart likelihood method based on the correlation matrix among variables, implemented in the RAMONA routine of SYSTAT 10.0 (Browne and Mels 2000) and tested using v^* degrees of freedom (see also Hawkins et al. 2005). Model fit was evaluated by χ^2 tests and the root mean square error of approximation (RMSEA), where values close to 0 indicate a perfect model fit. In practice, RMSEA values < 0.05 indicate a close model fit, and exceedance probabilities of achieving values of 0 and 0.05 can be obtained

based on their 95% CIs. Based on significance tests of individual path coefficients, some terms can then be deleted from the model.

Regional Effects on Diversity. Differences in the relationships between total richness and that of basal and derived clades at subglobal scales were documented by correlating the richness patterns for basal and derived groups against the pattern for all birds in the Old and New Worlds separately. If the global pattern of climate changes is the only factor driving bird diversity gradients, relationships between basal, derived, and total richness should be identical everywhere. In contrast, if major differences are found between regions, it indicates that one or more factors operating independently of global climate have influenced the evolutionary structure of the contemporary gradient.

Results

The Global Species Richness Gradient

The global species richness gradient (fig. 1) is consistent with previous presentations of continental and intercontinental patterns based on range-map data (e.g., Rahbek and Graves 2001; Jetz and Rahbek 2002; Hawkins et al. 2003b, 2006; Orme et al. 2005). Tropical South America is very rich, with the highest richness found anywhere in the world occurring in the eastern Andes. Richness is also high in the Afrotropics, especially in the Rift area, and it is moderately high in the eastern Himalayas and at the Chinese-Myanmar border. Richness is lowest at very high latitudes and in deserts.

The RMSEA of the optimal path model for all bird species was 0.031 (95% CI = 0, 0.111), confirming that the model provided an excellent fit to the data. The model (fig. 2) identified AET as having the strongest effect on richness (total path coefficient = 0.82), acting both directly (path coefficient = 0.69) and indirectly through its effect on plant productivity/biomass (indirect path coefficient via GVI = 0.13). The GVI-to-richness path is substantially weaker than the AET-to-richness path, but this could partially reflect that annual GVI is not an ideal measure of plant biomass and vegetation structure at the global extent (see "Environmental Predictors"). Our measure of mesoscale climatic gradients, the interaction between annual temperature and range in elevation, had a relatively weak but significant effect on richness. Neither temperature nor range in elevation had significant direct effects on richness at the global scale (fig. 2); rather, their effects were manifested indirectly through other variables in the model. The model explained 75% of the variance in global species richness.

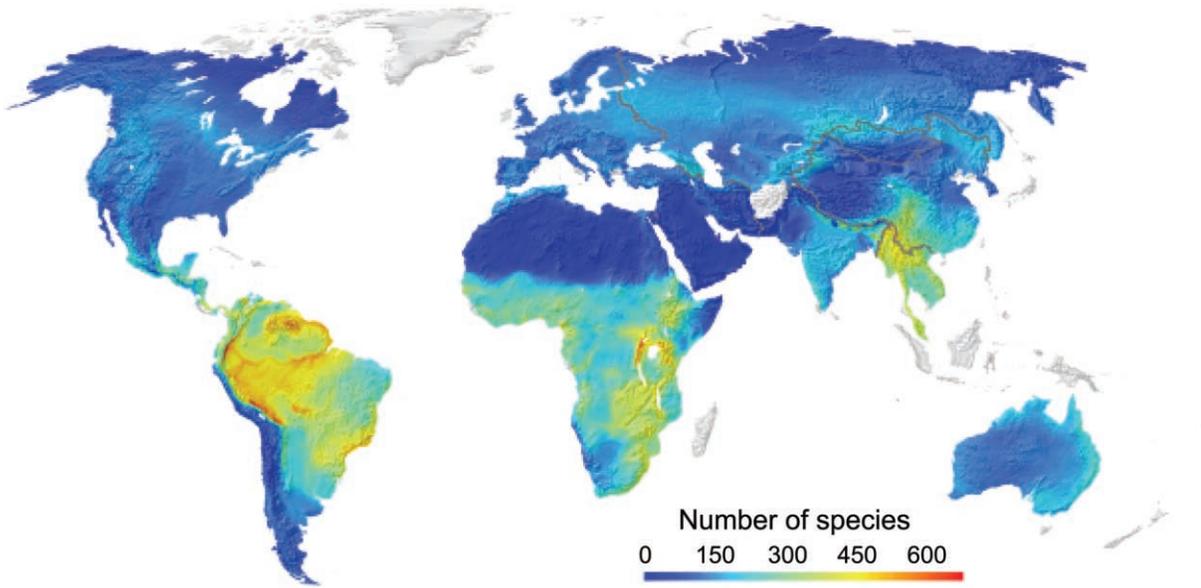


Figure 1: Geographical pattern of bird species richness resolved at a 27.5×27.5 -km grain size. The gray lines identify the regional limits of sets of sources of distribution maps.

Basal versus Derived Richness at the Global Scale

As expected, the richness of the bird species from the most basal clades is concentrated in the nonarid tropics, with few species in the temperate zones or deserts (fig. 3a). The overall pattern of richness of species in basal groups is also strongly correlated with the richness gradient for all birds ($r = 0.955$). It is notable that the richness of basal clades is highest in the Neotropics (fig. 3a), clearly contributing to the very high overall richness of cells in this region (fig. 1). The optimal path model for basal birds is similar to that of all birds, although not identical (fig. 4a). The AET and the temperature \times elevation interaction remain the strongest association with richness, but the path coefficient for AET is stronger for basal clades (basal groups are richest in the warmest and wettest climates), and the path from GVI to richness is no longer significant. The RMSEA of the model indicates a close fit with the data (0.050, 95% CI = 0, 0.118), and it explains 72% of the variance in richness.

The richness gradient of derived clades is weaker than that of basal clades, although their centers of diversity are found in high elevations of the Old World tropics and subtropics (fig. 3b). Despite this local congruence between derived and total richness in tropical mountains, the correlation between derived and total richness is substantially weaker than in the case of basal groups ($r = 0.793$). The path model for derived groups (fig. 4b) also differs substantially from that for all species, with temperature having

a significant negative path coefficient (richness decreases with increasing temperature), with a stronger effect of the temperature \times elevation interaction (richness is higher in tropical mountains), and with a weaker effect of AET. The

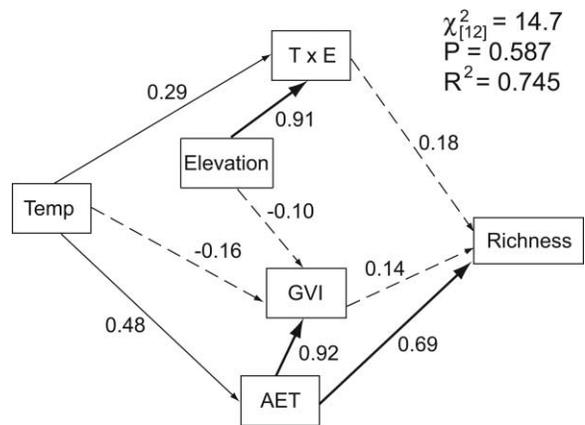
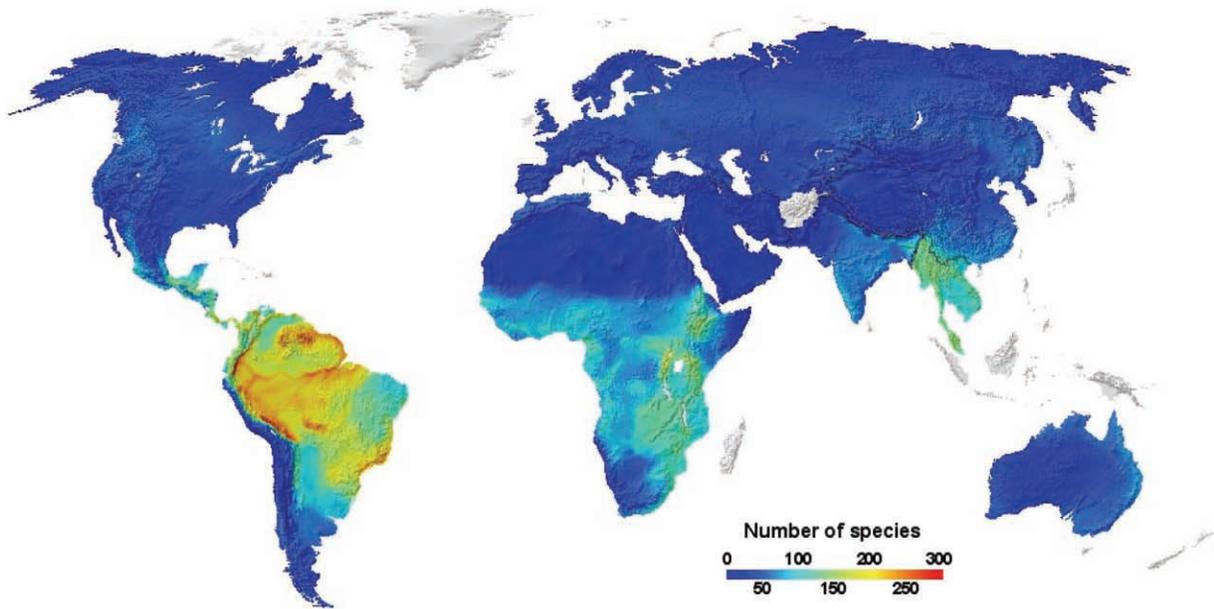


Figure 2: Path model for the global species richness pattern for data resolved at $110 \text{ km} \times 110 \text{ km}$. Types of lines (*dashed*, *normal*, and *bold*) identify low, moderate, and strong paths. Based on the series of autoregressive coefficients ρ calculated using subsamples of the total data set, ρ was ~ 0.95 for $n = 5,000$, and thus n^* is $\sim 2\%$ of the total sample size. Therefore, significance tests and confidence intervals were based on $\nu^* = 200$ degrees of freedom. The χ^2 tests the overall fit of the model to the data, based on the d-separation criterion (Shipley 2002). The R^2 is the proportion of the variance in richness explained by the model.

a) Basal clades



b) Derived clades

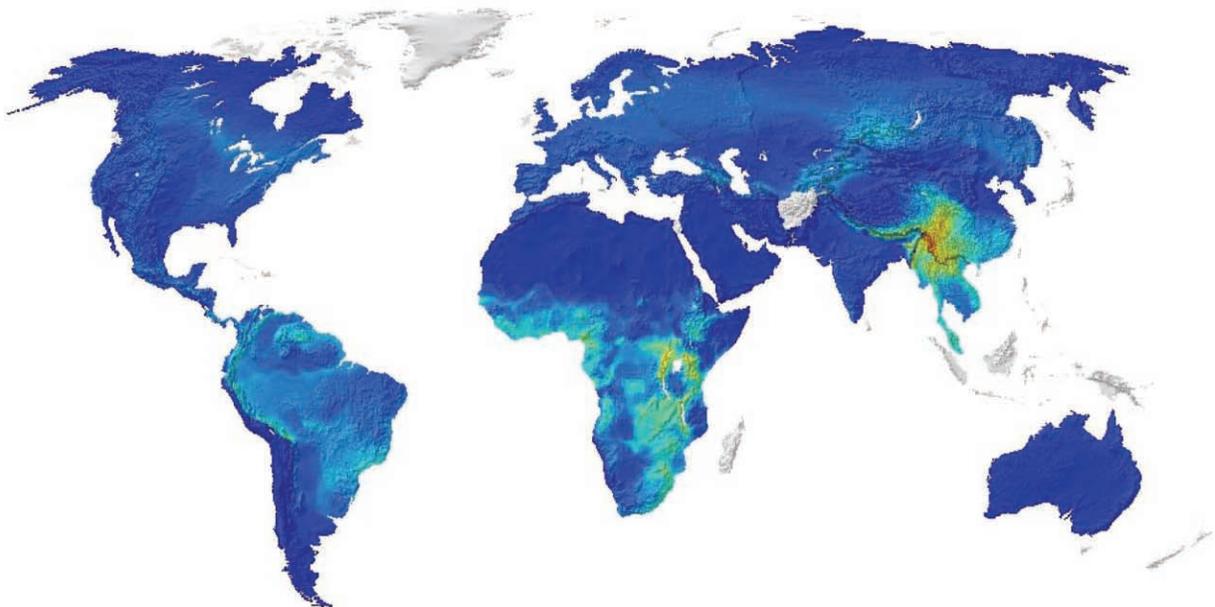


Figure 3: Geographical pattern of richness for the (a) 2,700 most basal species (in 54 families) and (b) 2,458 most derived species (in 16 families). Basal and derived families were classified using a family-level phylogenetic tree generated by combining the DNA-DNA hybridization tree of Sibley and Ahlquist (1990) for nonpasserines and the DNA-sequence-based tree of Barker et al. (2004) for passerines.

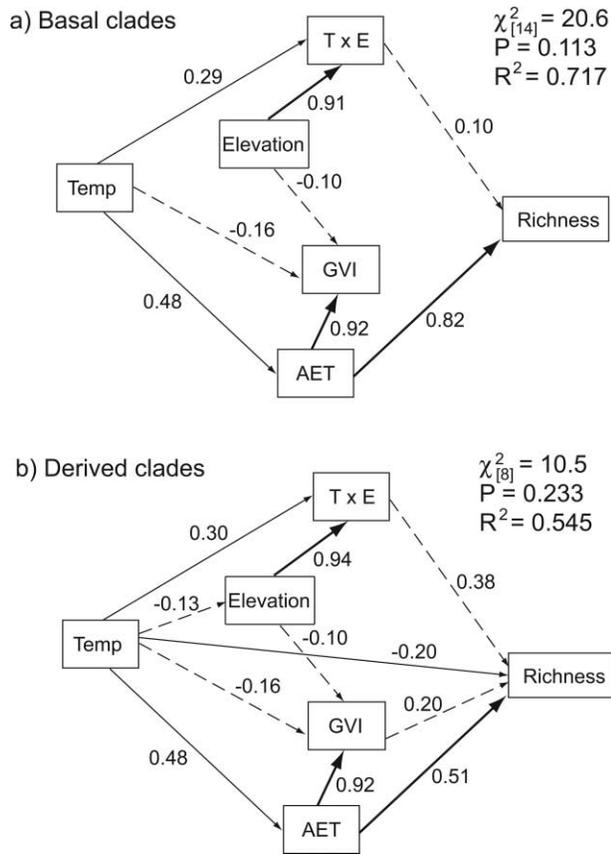


Figure 4: Path models for the species richness patterns of (a) basal and (b) derived bird families. Presentation as in figure 2. Because of strong similarity between spatial patterns of total and basal richness, n^* was set to 200 for basal richness. For derived richness, spatial patterns were not as strong, and $r = 0.896$ for $n = 5,000$, so we estimated n^* to be $\sim 4\%$ of the total sample size ($v^* = 400$).

RMSEA of the model indicates an excellent fit with the data (0.030, 95% CI = 0, 0.094), although the model explained substantially less of the variance in derived richness than did the models for both total and basal richness (fig. 4b).

The spatial correlogram for total richness (fig. 5a) shows a complex spatial structure, with strong positive autocorrelation at distances $< 5,000$ km and an inverted “hump” at larger scales. The pattern for basal groups (fig. 5b) is extremely similar to the overall pattern, and the Moran’s I ’s are strongly positively correlated with those of all birds, reflecting that the richness gradient for basal clades closely tracks the complete richness gradient (cf. figs. 1, 3a). In contrast, derived clades have a much weaker spatial gradient than do basal or all clades at most spatial scales, as indicated by lower values of Moran’s I ’s in most distance classes (fig. 5b). Consequently, the spatial pattern for de-

derived clades is more weakly correlated with that for all groups (fig. 5b). Even so, similar to basal groups, there is a longitudinal richness gradient for derived clades within the tropics, albeit in the opposite direction, with a center of diversity in the highlands of the Oriental region, moderate richness in the highlands of the Afrotropics, and very low richness in the Neotropics (fig. 3b).

The Old versus New World

Although the richness gradient of basal clades tracks the gradient for birds taken as a whole more strongly than does that of derived clades globally, the existence of longitudinal gradients of both basal and derived clades (fig. 3) suggests heterogeneity in the patterns at regional scales. This is confirmed by correlations of total richness against those of basal and derived clades in the Old and New Worlds separately (fig. 6). In both regions, basal richness tracks total richness very closely, although the slopes differ

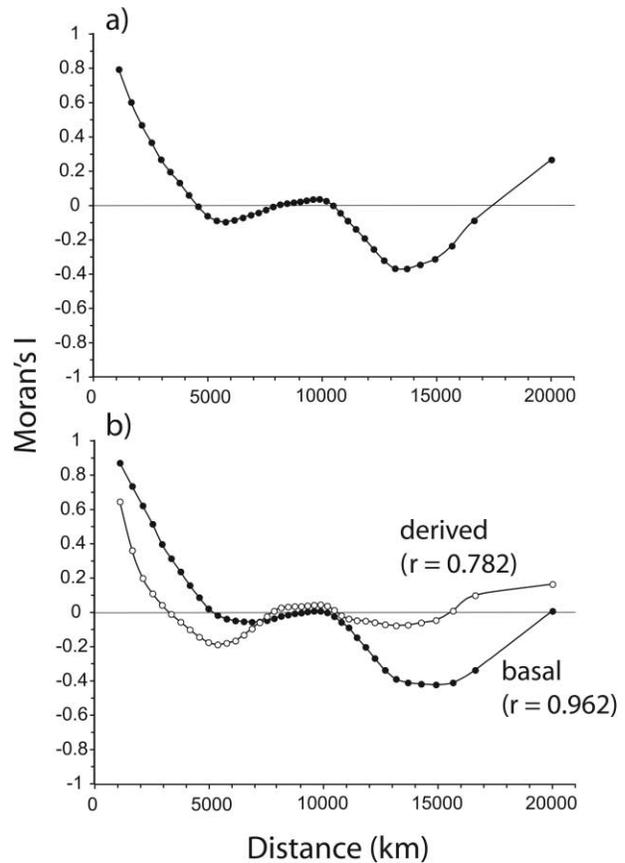


Figure 5: Spatial correlograms for (a) all species and (b) species from basal and derived families. Correlation coefficients (r) for Moran’s I ’s of basal and derived groups against Moran’s I ’s for all birds are also provided.

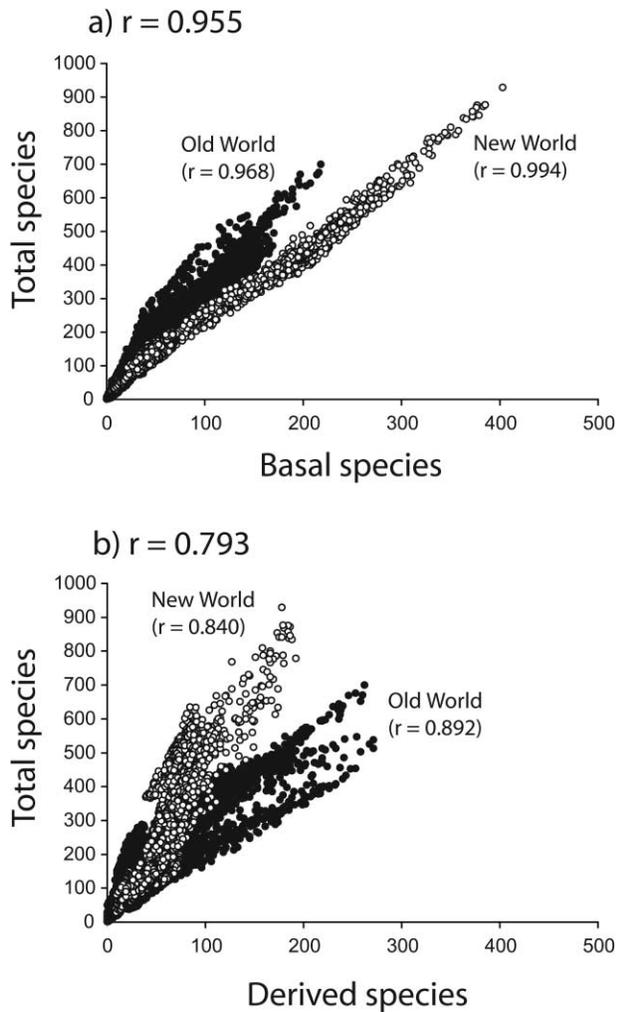


Figure 6: Relationships between total species richness and the richness of (a) basal and (b) derived birds for the Old and New Worlds. Correlation coefficients (r) above each figure are for both regions combined, and coefficients near data points are for each region separately.

(fig. 6a). However, there is an even stronger difference between the regions for derived clades (fig. 6b), such that in the Old World, the most derived clades represent a higher proportion of total richness in the tropics than in the New World. For example, in the richest 110×110 -km cell in the Neotropics (located in eastern Ecuador, $s = 914$), the derived clades compose 19.1% of the fauna, whereas in the richest cell in the Old World (located at the Zaire-Uganda border, $n = 700$), species from derived clades represent 37.4% of all species. Thus, although in both regions the total bird richness gradient primarily reflects the richness pattern for basal birds, as also indicated in the global analysis, additional factors have clearly in-

fluenced the evolutionary component of bird faunas in different parts of the world.

Discussion

The prediction that the bird latitudinal diversity gradient largely reflects a low number of species from basal bird clades in the extratropics is confirmed globally. This is consistent with the niche conservatism mechanism proposed to explain latitudinal diversity patterns. How niche conservatism in the face of climate change over evolutionary time can explain the contemporary bird richness gradient has been presented by Hawkins et al. (2005, 2006), but briefly, it is based on the fact that the world was much warmer and wetter in the late Cretaceous and early Tertiary, during which forests extended into Arctic Canada and Antarctica (Behrensmeyer et al. 1992). All basal Neoaves groups had appeared and began radiating by this time (Sibley and Ahlquist 1990; Ericson et al. 2006) and were presumably adapted to the prevailing climatic conditions. However, the climate began cooling (and drying) during the Oligocene, setting up a temperature gradient similar to the current gradient and forcing a response by basal clades, including the local extirpation of species in cooler climates and range shifts into the contracting “tropics.” This period of global cooling was also concordant with the spread and radiation of more derived clades into newly created cooler and drier habitats. For example, no eupasserines are known from Europe in the Eocene, appearing in the fossil record there only in the early Oligocene (Manegold et al. 2004; Mayr 2005). On the other hand, the dates of appearance of the major bird clades are controversial (Sibley and Ahlquist 1990; Ericson et al. 2003; Barker et al. 2004; Mayr 2005; Ericson et al. 2006), so it is not currently possible to confirm when specific groups arose. This represents the weakest link in our argument and requires additional work, but it does not alter the fact that “basal” and “derived” bird groups have distinct geographical richness patterns that are consistent with a climate-change scenario.

Our interpretation of the latitudinal richness patterns for basal and derived groups identifies a variant of the “evolutionary time” hypothesis as the primary explanation for the latitudinal gradient, as it argues that the warm, wet tropics are richer because they have been climatically stable longer than the temperate zones. The evolutionary time hypothesis is well known, and evidence is accumulating that one or more variants can explain the evolutionary structure of diversity gradients for a wide range of groups (e.g., Jablonski 1991; Latham and Ricklefs 1993; Stephens and Wiens 2003; Rex et al. 2005; Fine and Ree 2006). However, with respect to birds, the existence of longitudinal gradients in the richness of basal and derived groups

indicates that additional factors beyond the proposed climate change explanation have influenced the evolutionary structure underlying the contemporary species richness gradient at the global scale. The New World tropics support extremely rich basal clades, whereas the Old World tropics are relatively rich in derived groups, especially the Oriental region.

It is likely that both of these patterns reflect the effect of a second variant of the evolutionary time hypothesis. The richest basal family is the Tyrannidae (root distance = 12; 556 spp.), which is restricted to the New World and probably has a western Gondwana origin (Ericson et al. 2003). If so, the group has had a very long time to diversify in situ. The second richest basal family, the Trochilidae (root distance = 9; 323 spp.) is also restricted to the New World, although in this case, this reflects biogeographic-scale range contractions following global climate change, as modern-type hummingbirds occurred in central Europe in the Oligocene (Mayr 2004). But with these exceptions, most of the remaining 52 basal families have cosmopolitan or near cosmopolitan distributions, so their low diversity in the temperate zone cannot be exclusively due to their inability to reach areas currently supporting cool climates.

In contrast to the basal clades, the oscine passerines, including the most diverse family in the derived group, Fringillidae (root distance = 23; 936 spp.), are believed to have an eastern Gondwana origin, spreading into the rest of the world via Australia and southeast Asia (Ericson et al. 2003) with perhaps a second dispersal event from Australia directly into Africa (Jönsson and Fjeldså 2006). Indeed, we find that the richness of the most derived families is greatest near the presumed center of origin of oscines, in southeast Asia (although not in Australia itself). It is notable that these families are most depauperate in the Neotropics, almost certainly reflecting their relatively recent dispersal into South America soon before or after the emergence of the Isthmus of Panama (Ricklefs 2002). Thus, for the derived clades, the longitudinal gradient in their richness is related to how long they have been resident in each region (time for speciation; see Stephens and Wiens 2003; Stevens 2006), and this temporal component accounts for the differences in the relationships between basal, derived, and total richness in the Old and New Worlds. It can also account for the weaker path model for derived clades based on environmental predictors; the distance of a region from southeast Asia is independent of either past or current climates, and thus distance effects have not been included in the path model. When the biogeographic region in which cells are located (Nearctic, Neotropics, Palearctic, Afrotropics, Oriental, and Australasia) was added to a general linear model with AET, temperature, GVI, and the temperature \times elevation interac-

tion (the factors with significant path coefficients [see fig. 4b]), the R^2 increased from 0.548 to 0.686. Thus, physical location is a significant component of the longitudinal gradient that operates at least partially independently of climate.

The global richness gradient clearly contains a phylogenetic signal that can be associated with both how birds have responded to climate change over evolutionary time and how long different bird clades have been resident in specific biogeographic regions. Thus, it could be considered surprising that an environmental path model based on contemporary climate explains a high proportion of the variance in species richness (74.5%), which could be interpreted as indicating that there is no need to invoke "historical" differences in different parts of the world to account for the overall richness gradient. We confirmed the adequacy of our climate model as a first-order predictor of richness by first generating a GLM that included only the biogeographic region (as above), which serves as a general proxy for historical effects (see Hawkins et al. 2003b). We found that that region explained 53.8% of the global variance in richness. We then added region to a GLM containing AET, GVI, and the temperature \times elevation interaction ($R^2 = 0.735$) and found that it increased the coefficient of variation by only 4.6% ($R^2 = 0.781$, considerably less than for derived groups; see previous paragraph). Thus, most of the historical signal in the diversity gradient is masked by current climate (see also Francis and Currie 2003; Hawkins et al. 2003b), at least when all birds are considered.

The climate-change hypothesis, however, makes this prediction because it argues that the elements of climate that influence diversity now are the same that have influenced diversity over evolutionary time (Hawkins et al. 2005, 2006). In addition, because contemporary climatic gradients at very large scales are strongly correlated with the pattern of climate change since the Eocene (the poles have always been cooler than the equator irrespective of global mean temperature), we expect the explanatory power of measures of contemporary climate and measures of post-Eocene climate change to be similar, as has been found in the New World (Hawkins et al. 2006). Thus, the highest bird diversity is found in warm, wet climates both because birds have occupied these habitats longest and because this represents the climatic conditions permitting the continued survival of bird clades that arose when the world was much warmer than it is at present. Finally, forests provide a diverse array of potential food sources, nesting sites, shelter, and so forth, facilitating the persistence of more bird species than simpler, less productive habitats (see, e.g., MacArthur 1958, 1961). Thus, both contemporary and historical processes simultaneously contribute to the observed gradient, not just one or the other.

An explanation for diversity-climate relationships that integrates the temporal pattern of climate change rather than focusing solely on ecological processes can also explain why predictions of “species-energy theory” based only on contemporary patterns are often not supported by empirical data (Currie et al. 2004; Evans et al. 2005).

The structure of the path models for basal and derived groups also provides some insight into the complex nature of climate-diversity relationships and demonstrates the need to incorporate historical components into analyses of diversity gradients. The model for basal birds is dominated by AET for the reasons outlined above. Because the richness gradient for all birds is primarily driven by the pattern for basal groups, AET also explains overall bird richness patterns well. On the other hand, the model for derived richness has a more balanced relationship between broadscale climate gradients, as measured by AET, and mesoscale gradients, as captured by the elevation \times temperature interaction. This is not surprising given the concentration of derived groups in tropical mountains. More surprising is the negative path coefficient linking temperature and derived richness. The most derived clades are not most successful in the warm, wet climates of the lowland tropics but rather have radiated most in cooler climates of the temperate zones and at high elevations in the tropics. Thus, all birds are not equivalent, and theories that propose that temperature per se drives diversity gradients across all taxa (Brown et al. 2004) cannot be correct for birds. Further, we found that in no cases can temperature by itself explain diversity well when other variables are included in models; rather, warm temperatures must be coupled with high rainfall for most organisms to persist. This is true for the vast majority of groups (Hawkins et al. 2003a).

Under our version of the niche conservatism and climate change explanation, differential regional past extinction in the tropics and extratropics has been more important for driving the bird global diversity gradient than differential speciation rates. In our model, differential extinction driven by cooling created a geographical gradient in basal clades, after which new clades (primarily eupasserines) spread and radiated, being adapted to a variable set of environmental conditions in both tropical and temperate regions. Diniz-Filho et al. (2007) recently found that the occupation of temperate regions in New World birds has occurred under a balance between shifts in adaptive peaks of new clades and unique responses of species within (all) clades, and this balance explains why even derived clades show some geographic structure. Even so, the loss of basal clades in the temperate zone defines the gradient more than the accumulation of derived clades in the tropics. This is very similar to the “tropical conservatism” and “out of the tropics” hypotheses, which propose that the gradient develops as a consequence of the

differential appearance of new clades in the tropics that then are limited in their ability to spread poleward (Wiens and Donoghue 2004; Jablonski et al. 2006; Wiens et al. 2006). The difference is that we emphasize range contractions into low latitudes and differential regional extinction during cooling periods, whereas the alternatives focus on range expansions out of the tropics. We expect both processes are operating, and whether “out of the tropics” or “into the tropics” dominates depends on history of the group, specifically, the global climatic conditions when clades appear and begin to spread and radiate.

That regional past extinctions appear to be a more important driver of the global gradient for birds does not mean that speciation rates are not higher in the tropics (Cardillo 1999; Cardillo et al. 2005; but see Bromham and Cardillo 2003; Wiens et al. 2006). However, even if true, it is not necessary to invoke differential speciation to explain the main features of the contemporary gradient. For birds, most groups are in fact more diverse at tropical latitudes, but this may reflect only that the clades have had more time to diversify there (e.g., Tyrannidae in the New World and Fringillidae in the Old). We also believe it is important that derived clades in the tropics are most diverse in mountainous areas but not in lowlands, suggesting that speciation is associated with climatic gradients that vary strongly over small spatial scales rather than with macroclimatic conditions per se (Hawkins and Diniz-Filho 2006). Warm climates may be necessary for rapid speciation, but they are not sufficient.

In sum, we propose that climate and climate change operating over evolutionary time offers a parsimonious explanation for the global diversity gradient for birds, with secondary influences of centers of origin of specific clades. We also join others in arguing that explanations that integrate effects operating in both ecological and evolutionary time provide more explanatory power than hypotheses that treat the past and present as separate processes (see also Ricklefs 2004). It remains to be seen if gradients for other taxonomic groups can be similarly explained, but given the congruence of diversity patterns for most taxonomic groups at the global scale, at least in terrestrial ecosystems, we consider it likely that niche conservatism will be shown to influence many groups. Thus, we agree with Wiens and Graham (2005) and Wiens et al. (2006) that niche conservatism is a fruitful approach to link ecological and evolutionary phenomena.

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