SPECIAL PAPER

Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds

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ABSTRACT

Aim The aim of this study was to test a variant of the evolutionary time hypothesis for the bird latitudinal diversity gradient derived from the effects of niche conservatism in the face of global climate change over evolutionary time.

Location The Western Hemisphere.

Methods We used digitized range maps of breeding birds to estimate the species richness at two grain sizes, 756 and 12,100 km^2. We then used molecular phylogenies resolved to family to quantify the root distance (RD) of each species as a measure of its level of evolutionary development. Birds were classified as 'basal' or 'derived' based on the RD of their family, and richness patterns were contrasted for the most basal and most derived 30% of species. We also generated temperature estimates for the Palaeogene across the Western Hemisphere to examine how spatial covariation between past and present climates might make it difficult to distinguish between ecological and evolutionary hypotheses for the current richness gradient.

Results The warm, wet tropics support many species from basal bird clades, whereas the northern temperate zone and cool or dry tropics are dominated by species from more recent, evolutionarily derived clades. Furthermore, crucial to evaluating how niche conservatism among birds may drive the hemispherical richness gradient, the spatial structure of the richness gradient for basal groups is statistically indistinguishable from the overall gradient, whereas the richness gradient for derived groups is much shallower than the overall gradient. Finally, modern temperatures and the pattern of climate cooling since the Eocene are indistinguishable as predictors of bird species richness.

Main conclusions Differences in the richness gradients of basal vs. derived clades suggest that the hemispherical gradient has been strongly influenced by the differential extirpation of species in older, warm-adapted clades from parts of the world that have become cooler in the present. We propose that niche conservatism and global-scale climate change over evolutionary time provide a parsimonious explanation for the contemporary bird latitudinal diversity gradient in the New World, although dispersal limitation of some highly derived clades probably plays a secondary role.

Keywords

Climate change, evolutionary time, extinction, latitudinal gradient, mean root distance, New World birds, palaeoclimate, species diversity, species.

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INTRODUCTION

The latitudinal diversity gradient is one of the most important problems in ecology and biogeography, but there is little consensus on its causes. Broad-scale species richness gradients are usually correlated with contemporary climate, with the highest number of species in warm, wet areas (Wright *et al.*, 1993; Hawkins *et al.*, 2003a). Even so, such associations do not

address how species are added to or removed from the global pool over evolutionary time, a factor that clearly contributes to diversity patterns (Jablonski, 1991; McGlone, 1996; Ricklefs, 2004). Historically, tests of evolutionary mechanisms have been limited by a lack of phylogenetic data, but the increasing availability of phylogenetic trees now makes it possible to test explicit evolutionary hypotheses for diversity gradients (Cardillo, 1999; Ricklefs, 2005).

Recently, the intracontinental pattern of species richness of Australian birds was found to contain a spatial phylogenetic signal, with central and western deserts supporting relatively more birds from the most derived clades, and wetter areas dominated by birds that are on average from more basal clades (Hawkins *et al.*, 2005). This evolutionary pattern was hypothesized to be a result of the increase in aridity in central and western areas associated with continental-scale cooling and drying in the Oligocene and Miocene. The underlying mechanism is the conservation of morphological, biological and ecological traits of species within higher-level clades as they radiate (Wiens & Donoghue, 2004), a phenomenon well established for birds (Bennett & Owens, 2002). Consequently, Hawkins *et al.* (2005) proposed that species in clades that initially evolved in the warm, wet climates of the Cretaceous to Eocene have been differentially extirpated from areas that have undergone the most severe climate change, whereas clades that arose during the Miocene have radiated in areas where climates became drier. If true, this identifies niche conservatism in the face of climate change as the driver of large-extent diversity gradients, and represents a version of the evolutionary time hypothesis that argues that the tropics are richer in species because they have been climatically stable for longer (Fischer, 1960).

In this paper, we extend the hypothesis of Hawkins *et al.* (2005) to another part of the world, because the Eocene–Miocene climate shift was global in scope (Behrensmeyer *et al.*, 1992), and so the niche conservatism explanation should apply everywhere. Consistent with this hypothesis is the work of Gaston & Blackburn (1996), who analysed spatial patterns of the mean age of tribes for New World birds, based on Sibley & Ahlquist's (1990) DNA–DNA hybridization-based phylogeny, and showed that mean tribe age is greatest at the equator and declines towards the poles. However, Gaston & Blackburn (1996) interpreted this in a strictly latitudinal context, which can obscure more complex spatial patterns (see Hawkins & Diniz-Filho, 2004). More importantly, they did not examine the underlying processes, since spatial variation in the mean age of taxa can arise under a wide range of scenarios involving extinction, speciation and migration. Furthermore, because they estimated tribal ages from calibrations of a molecular clock, which can be biased by differences in generation times across clades, they also considered the possibility that spatial patterns in mean age are an artefact (although they concluded that this is unlikely). Here we revisit New World birds using a two-dimensional geographic perspective and a phylogenetic metric that is not sensitive to calibration procedures. Our primary goal is to test two predictions of the hypothesis that

the modern diversity gradient reflects a response of birds to the long-term history of global climate: (1) birds in the temperate zone and cool or dry tropics are younger and more evolutionarily derived than birds in the warm, wet tropics (a more refined version of the prediction made by Gaston & Blackburn, 1996), and (2) the gradient largely reflects the richness pattern of older clades as they have been extirpated from areas now with cool or dry climates. The second prediction is key for understanding the evolutionary processes underlying the latitudinal gradient.

Finally, whether it is past or present conditions that best explain diversity gradients has been strongly disputed (Currie & Paquin, 1987; Latham & Ricklefs, 1993; McGlone, 1996; Kerr & Currie, 1999; Francis & Currie, 2003; Currie & Francis, 2004; Qian & Ricklefs, 2004). We evaluate this by generating temperature estimates from the Palaeogene to compare the explanatory powers of contemporary climate vs. climate change as predictors of the current gradient. If diversity gradients are affected by both modern and past climates (Hawkins *et al.*, 2005), past conditions could explain current patterns as well as current conditions, and it may be difficult to extract their independent contributions because past and present climatic gradients covary spatially (it has always been cooler at the poles than at the equator, irrespective of the mean global temperature).

MATERIAL AND METHODS

Bird species richness

Digitized breeding ranges (Ridgley *et al.*, 2003) for 3839 native bird species were rasterized in ArcGIS 8.3 in grids of 27.5×27.5 km^2 (generating 49,100 cells for mapping) and 110×110 km^2 (with 3506 cells for statistical analysis). Islands were excluded from the grids (except for Tierra del Fuego), and island endemics and strictly feeding marine species were excluded from the analysis. Species richness was estimated directly from the rasters.

Mean root distance

The root distance (RD) for each species represents the number of nodes separating a species' family from the base of a phylogenetic tree, and the mean root distance (MRD) (Kerr & Currie, 1999) of all bird species resident in each cell of the New World was used as a measure of the level of evolutionary development of the local avifauna (Sibley & Ahlquist, 1990; Hawkins *et al.*, 2005). RD values were obtained from a combined phylogenetic tree resolved to family comprising the DNA–DNA hybridization analysis of Sibley & Ahlquist (1990) for non-passerines, and the DNA-sequence tree of Barker *et al.* (2004), based on the nuclear genes RAG-1 and -2, for passerines. We also combined Barker *et al.*'s (2004) phylogeny with an alternative phylogeny for non-passerines proposed by Fain & Houde (2004), based on intron 7 of the β-fibrinogen gene. Although 14 families in the New World are

absent from Fain & Houde's (2004) tree, which precludes its use in our biogeographical analyses, this combined tree was used to examine the robustness of RD estimates based on the Sibley-Ahlquist + Barker *et al.* combined tree.

The 3839 bird species were ranked from the most basal to the most derived clades (resolved to family), and the *c.* 30% and 70% percentiles were selected (1183 species from basal families and 1154 species from derived families; see Table 1). Species richness was then calculated separately for each of these groups. Basal richness reflects the net species diversification pattern of clades believed to have originated in the middle Cretaceous to middle Eocene, whereas the species richness of derived clades represents the net diversification of groups originating in the middle Eocene to early Miocene (Sibley & Ahlquist, 1990), although clade ages must be considered tentative owing to the problems of calibrating DNA–DNA hybridization data when generation times vary spatially or differ among clades.

Analysis

To determine if the pattern of evolutionary development could have arisen by chance, we tested the significance of each MRD (using data resolved to 110×110 km^2) with a randomization procedure that sampled without replacement the species in the overall species pool according to the observed species richness in each cell, repeated 10,000 times (Gaston & Blackburn, 1996; Hawkins *et al.*, 2005). This generated a statistical distribution of null MRDs for each cell, and a normalized Z-score for each cell was calculated by subtracting the observed and expected MRDs, divided by its standard error. Z-scores higher than 1.96 indicate that there is a 95% probability that the MRD in the cell is higher than would be expected if species found there were a random sample of the overall species pool.

Pearson correlation coefficients between basal, derived and total richness were used to quantify the similarity among spatial patterns in these multiple richness estimates. The strength of spatial structure in these richness estimates was measured using Moran's I autocorrelation coefficients, calculated for 15 geographic distance classes established at irregular distance intervals in order to keep the number of connections among cells similar in each class, so that errors of Moran's I are comparable (see Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003 for details). A restricted major-axis model II regression of the richness of basal against derived clades was conducted to evaluate differential patterns of species accumulation with increasing richness. Since species richness collected in a grid system usually displays strong spatial autocorrelation, reflecting redundant information owing to the proximity of grid cells, a bias in Type I errors of statistical tests resulting from overestimation of degrees of freedom occurs. Thus, all significance tests of correlations were performed using a conservative number of degrees of freedom ($v^{\star}$), based on the geographically effective sample size (Clifford *et al.*, 1989; Griffith, 2003), calculated using a modified version of MODTTEST (available from http://www.bio.umontreal.ca/

Table 1 Species richness of families used to compare richness gradients of basal and derived clades in North and South America. Also provided is the root distance of each family, based on a combined Sibley & Ahlquist (1990) + Barker *et al.* (2004) tree. Only species whose ranges extend north of the US–Mexican border are included in the sum for each family for North America, and island endemics have been excluded from both sets of lists. The average ages of the basal and derived clades were approximated by Sibley & Alquist's $\Delta T_{50}H$, calibrated using $1 \Delta T_{50}H = 4.7$ Myr for non-passerines and $1 \Delta T_{50}H = 2.3$ Myr for passerines. Basal clades average 75.7 Myr BP (range = 109–45), whereas derived clades average 29.3 Myr BP (range = 54–20)

Family	Root distance	Number of species	
		North America	South America
Basal			
Tinamidae	2	0	44
Anatidae	4	37	38
Anhimidae	4	0	3
Cracidae	4	1	42
Odontophoridae	4	5	14
Picidae	4	23	78
Rheidae	4	0	2
Bucconidae	5	0	33
Galbulidae	5	0	18
Phasianidae	5	11	0
Ramphastidae	5	0	40
Psittacidae	6	0	118
Trogonidae	6	1	14
Coccyzidae	7	2	8
Opisthocomidae	7	0	1
Crotophagidae	8	2	4
Neomorphidae	8	1	8
Columbidae	9	7	45
Momotidae	9	0	6
Trochilidae	9	14	240
Apodidae	10	5	19
Rallidae	11	9	42
Stringidae	11	18	32
Tytonidae	11	1	1
Number of species		137	850
Derived			
Anhingidae	17	0	1
Phoenicopteridae	18	0	4
Vireonidae	18	13	24
Threskiornithidae	19	4	11
Corvidae	20	15	15
Laniidae	20	2	0
Paridae	20	12	0
Alaudidae	21	1	1
Ciconiidae	21	3	8
Pelecanidae	21	1	1
Peucedramidae	21	1	0
Certhiidae	22	13	49
Regulidae	22	2	0
Sittidae	22	4	0
Bombycillidae	23	3	0
Fringillidae	23	143	407
Gaviidae	23	4	0

Table 1 *continued*

Family	Root distance	Number of species	
		North America	South America
Hirundinidae	23	7	17
Passeridae	23	5	7
Sturnidae	24	10	7
Sylviidae	25	16	33
Number of species		259	585

legendre) and implemented in SAM (Spatial Analysis in Macroecology) (Rangel *et al.*, 2005).

Palaeoclimate

We evaluated the hemispherical temperature gradient in the early Palaeogene (Palaeocene and Eocene) using mean annual temperature (MAT) estimates for 25 lowland sites ranging from Arctic Canada to western Antarctica. MAT data from the Palaeocene and Eocene were lumped together because they both represent a pronounced warming trend (Zachos *et al.*, 2001), much warmer than modern global MAT values. Locations of MAT zone boundaries were estimated using a polynomial regression of latitude vs. empirical MAT (24.93– 0.021Latitude $- 0.003$Latitude^2). MATs were based on leaf-margin analysis (Greenwood & Wing, 1995; Suárez *et al.*, 2000; Wilf, 2000; Wing *et al.*, 2000, 2004; Johnson & Ellis, 2002; Hinojosa, 2005; Wilf *et al.*, 2005), CLAMP (Climate-Leaf Analysis Multivariate Program) (Greenwood & Wing, 1995; Wolfe *et al.*, 1998; Francis *et al.*, 2004; Hinojosa, 2005), oxygen isotopes (Tripati & Zachos, 2002), wood (Francis & Poole, 2002), and pollen modern relatives (Graham, 1994). The average temperature at each site was used when multiple estimates were given. These were compared with contemporary mean annual temperatures obtained from http://www.ngdc.noaa.gov/paleo/ctl by taking the difference between modern temperature and estimated Palaeocene MAT at each site.

RESULTS

We first quantified the richness gradient across the New World, which was consistent with previous analyses based on range map data (Cook, 1969; Rahbek & Graves, 2001; Hawkins *et al.*, 2003b; Orme *et al.*, 2005; Fig. 1). Species richness is low everywhere in extra-tropical North America, with a relatively higher diversity from the Great Lakes westwards, and then increasing southwards in the mountainous west. Within the tropics, maximum richness occurs in the eastern Andes, but richness is also high in parts of Amazonia. Secondary centres of diversity occur in the Atlantic forest of southeastern Brazil and in the highlands of eastern Venezuela and Guyana. In South America, richness is lowest along the arid west coast, in the high Andes, and in central/southern Argentina and Chile.

Test of prediction 1

Consistent with our prediction and with Gaston & Blackburn (1996), the hemispherical diversity gradient contains a historical signal, as quantified by MRD, our measure of the evolutionary development of avifaunas (Fig. 2). Z-scores from the null model designed to test the significance of MRDs within each cell ranged from −4.92 to 7.69, and revealed that North American species are from more derived groups than expected by a random sample of the species pool, whereas species in South America are usually from more basal groups than expected by chance. The correlation between richness and the Z-scores was not significant ($r = -0.696$, $v^\star = 3.6$, $P = 0.135$). MRDs are highest in eastern and southwestern North America, and overall the Nearctic is characterized by a preponderance of species from more derived families. The lowest MRDs occur in lowland tropical forest, reflecting a dominance of birds from basal families. Within the Neotropics, the highest MRDs occur in mountains, the Atacama Desert, and the grasslands of Uruguay and southern Brazil. MRDs in Amazonia and the deciduous forests of the southeastern United States differ by more than five nodes (in a phylogenetic tree 25 nodes deep), representing a strong phylogenetic signal.

The hemispherical spatial pattern in MRD is robust to the combinations of trees used to construct the complete bird phylogeny, as RD values from the Sibley & Ahlquist (1990) + Barker *et al.* (2004) combined tree and from a Fain & Houde (2004) + Barker *et al.* (2004) combined tree, across the 3686 species common to both, are highly correlated ($r = 0.915$). Thus, spatial structure in the historical signal of diversity is evident even using a phylogenetic metric that makes no assumptions about the molecular clock and using phylogenies based on DNA sequences, so we can rule out the possibility that the pattern is an artefact arising from problems in calibrating the molecular clock based on DNA hybridization data.

Test of prediction 2

We examined the second prediction by comparing richness patterns of species in the most basal and derived clades (Table 1). The pattern for basal groups (Fig. 3a) strikingly parallels the pattern of all birds, being almost perfectly correlated with the overall diversity gradient (cf. Figs 1 and 3a; $r = 0.993$, $v^\star = 4.3$, $P < 0.01$). In contrast, the pattern for the most derived birds, albeit also correlated with the overall gradient ($r = 0.846$, $v^\star = 3.6$, $P < 0.01$), shows obvious spatial dissimilarities (Fig. 3b). However, because subsets of data and the complete data from which they are extracted are mathematically constrained to be positively correlated, we used autocorrelation analysis as an independent method to evaluate the similarities between the spatial gradients of basal, derived, and all clades. We found that the latitudinal gradient of derived groups is substantially weaker and shallower than the overall gradient (weaker autocorrelation coefficients than for
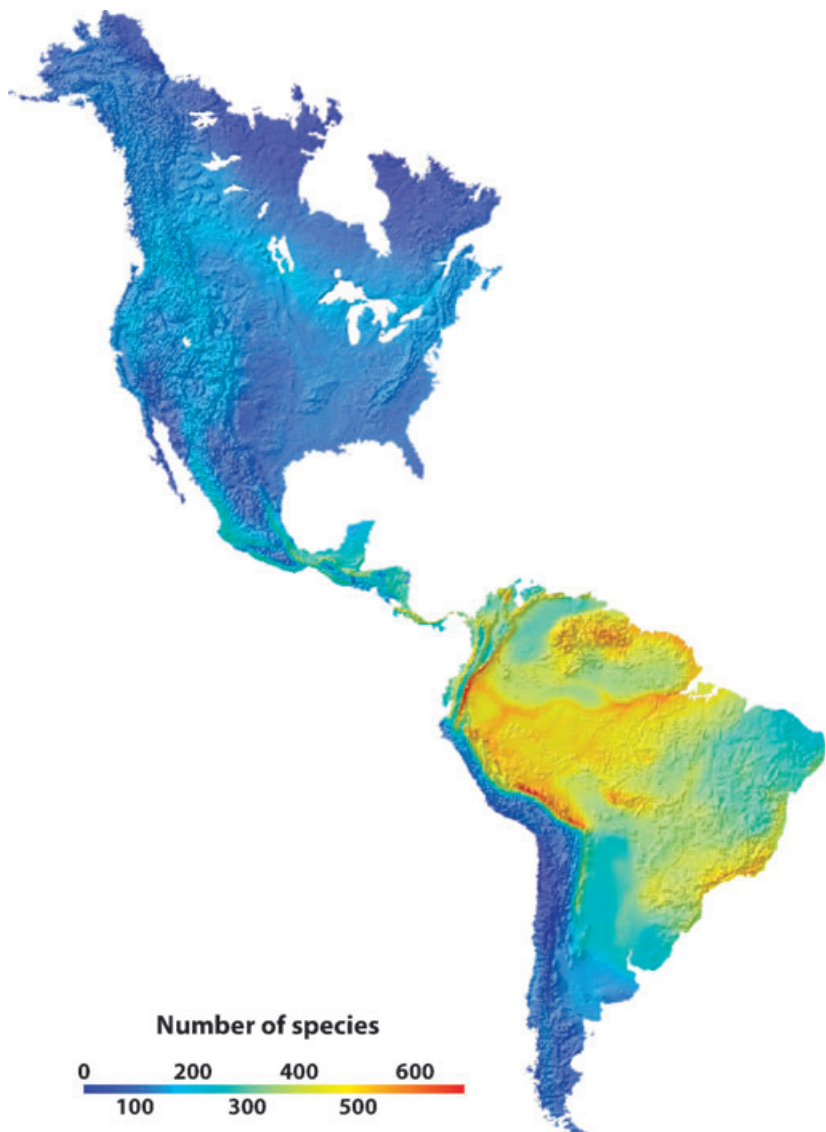
Figure 1 Geographical pattern of continental bird species richness in the Western Hemisphere, resolved at a 27.5×27.5 km^2 grain size.

the overall gradient in all 15 distance classes), whereas the gradient for basal clades is close to the overall gradient (Fig. 4). Notably, the spatial structure of basal clades is statistically indistinguishable from the pattern for all species (type II RMA regression of the Moran Is of total richness against the Moran Is of basal richness: $b = 0.984 \pm 0.014$, $P = 0.129$), whereas the slope of a regression of Is of total richness against Is of derived richness is substantially > 1.0 ($b = 2.504 \pm 0.175$, $P < 0.001$). Further, the slope of a model II RMA regression of basal against derived richness (Fig. 5) was > 1.0 ($b = 1.497 \pm 0.016$, $P < 0.001$), because the diversity of species from basal clades is low relative to that of derived clades in extra-tropical North America. Discrepancies between the overall gradient and that for derived groups are also apparent from the fact that southern Canada supports more species from derived families than eastern Brazil, and, although derived clades are richest within tropical latitudes, their centres of richness occur at higher altitudes rather than in lowlands (Fig. 3b).

Palaeoclimate vs. modern climate

The temperature estimates from the Palaeogene (Fig. 6), used to compare the explanatory powers of contemporary climate vs. climate change as predictors of the current gradient, revealed that correlations of richness against modern mean annual temperature and against the difference between current temperature and estimated Palaeogene temperature for the sites for which we have data are almost identical: $r = 0.857$ for current temperature, and $r = 0.850$ for the difference in temperature. This is because the temperature variables are themselves strongly correlated ($r = 0.889$).

DISCUSSION

First and foremost, both predictions derived from the niche conservatism hypothesis proposed by Hawkins *et al.* (2005) for Australian birds are supported in the western hemisphere [see also Latham & Ricklefs (1993) and Wiens & Donoghue (2004)
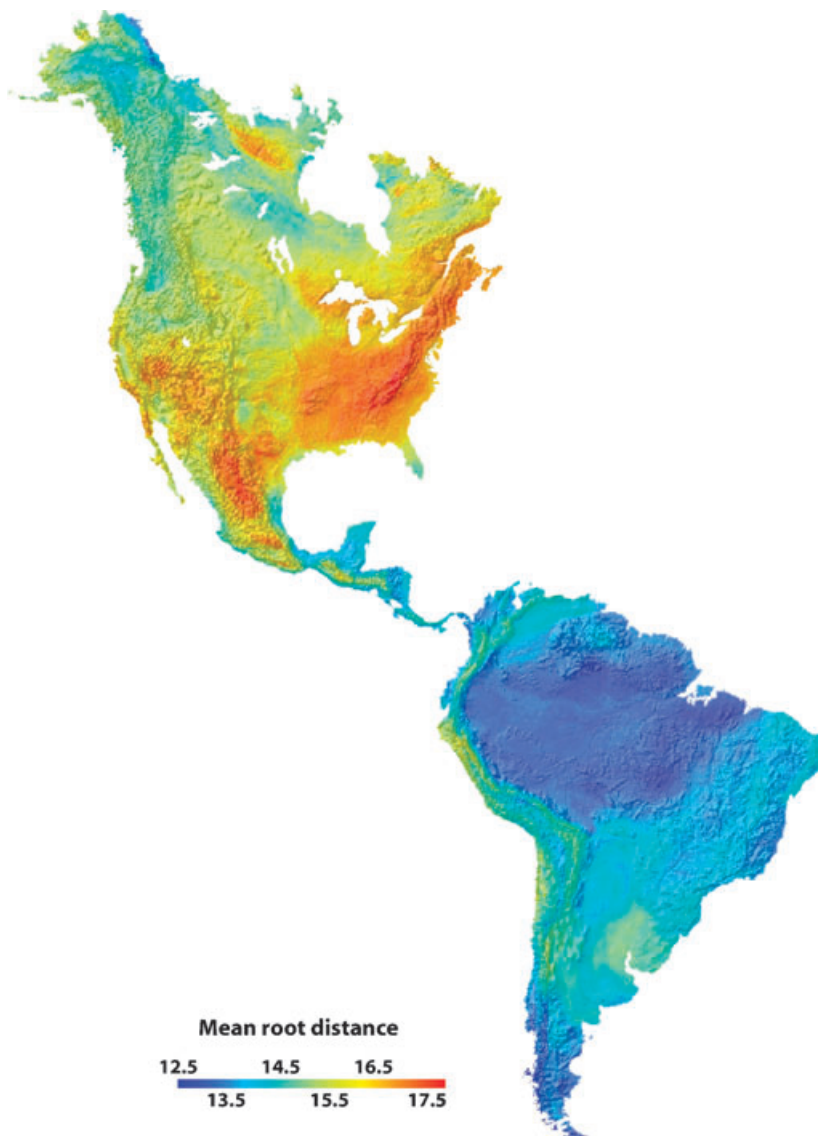
Figure 2 Geographical pattern of bird mean root distance (MRD), resolved to family and based on a combination of Sibley & Ahlquist's (1990) phylogeny for non-passerines and Barker *et al.*'s (2004) phylogeny for passerines. Grain size as in Fig. 1.

for discussions of similar hypotheses for other groups]. Specifically, the difference between richness patterns of basal and derived clades is consistent with an explanation for the contemporary diversity gradient based on responses of higher clades to climate change since the Eocene. It is well established that the world was much warmer in the Cretaceous and early Tertiary, with tropical rain forest extending into Colorado (Johnson & Ellis, 2002), subtropical forests in Canada and Patagonia, and temperate forests in the Arctic and Antarctic (Behrensmeyer *et al.*, 1992). Thus, the latitudinal temperature gradient was much narrower than at present (see Fig. 6), and all basal bird clades had probably appeared by this time (Sibley & Ahlquist, 1990, but see below). As the climate began to cool during the Oligocene, however, a temperature gradient similar to the current gradient developed, forcing a response by basal clades adapted to pre-existing warm climates. The period of global cooling was also concordant with the appearance of more derived clades that spread and radiated into newly created cooler and drier habitats.

Key to this interpretation of the phylogenetic structure of the bird fauna is that the ecological characteristics of basal clades are in fact linked to climatic conditions in the Cretaceous to Eocene, whereas derived clades indeed arose in the Oligocene and thus are adapted to these cooler conditions. Currently available age estimates for bird orders and families (Sibley & Ahlquist, 1990) are consistent with this, but the relatively poor fossil record coupled with the controversial nature of molecular clocks for birds (e.g. Barker *et al.*, 2004) make our interpretation necessarily tenuous. Even so, the empirical data indicate that basal bird clades are species-poor in the northern temperate zone relative to more derived clades, and this begs for an explanation.

The virtually identical spatial pattern of the overall richness gradient and that of the most basal 30% of species indicates that the contemporary gradient is strongly influenced by a paucity of basal clades in extra-tropical North America. This lack of 'tropical' clades in northern latitudes could have arisen by two processes. The clades may have
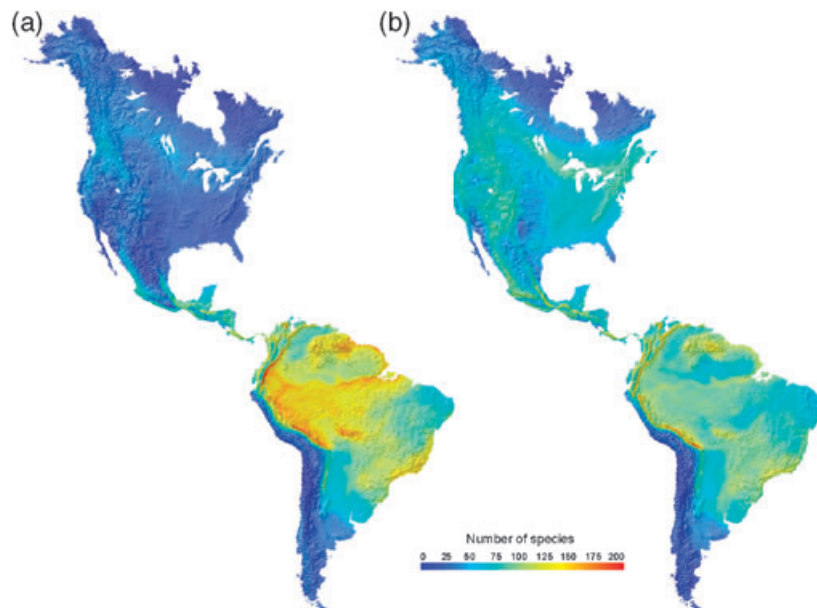
Figure 3 Species richness patterns for (a) the 24 most basal families and (b) the 21 most derived bird families in the New World. Spatial patterns in species richness for basal clades are stronger than those for derived clades (see Fig. 4 for details of the spatial analysis). Grain size as in Fig. 1.

originated in tropical latitudes and failed to disperse outwards (see Wiens & Donoghue, 2004). Alternatively, their current distributions could be relictual, reflecting the fact that ranges of old groups have contracted into regions where warm climates have persisted. We believe that both processes are occurring, but that the latter is probably more important for birds. Basal clades are oldest by definition, and most of these groups appear to have roots extending into the Eocene to Cretaceous (Sibley & Ahlquist, 1990). This presumably represents more than enough time for them to have radiated everywhere. Secondly, most basal clades are cosmopolitan in distribution, suggesting that a paucity of temperate species is not the result of a lack of opportunity to disperse into northern latitudes. Indeed, 61% (83 of 137) of North American species in basal clades are at least partially migratory, and the long-distance migratory groups are in clades now considered to be tropical (Böhning-Gaese & Oberrath, 2003). Thus, the richness of basal clades in the far north would be even lower if these species were unable to escape the winters, and the strength of the latitudinal gradient of basal clades is not caused by dispersal but is instead partially offset by it.

Hummingbirds represent an apparent exception to the supposition that current distributions of basal clades are relictual, as they are restricted to the New World and almost all species are Neotropical. However, 'modern-type' hummingbirds ranged into Europe in the Oligocene (Mayr, 2004), and fossils of stem lineages of hummingbirds dating from the Eocene have been found in the central Palaearctic (Mayr, 2005). So, the current distribution of even this signature

Neotropical clade is the result of biogeographical-scale range contractions following climate change rather than of dispersal limitation, although it leaves open the question of why hummingbirds did not also retreat into tropical Africa (Mayr, 2004). Finally, many bird (Fain & Houde, 2004) and mammal (Keast *et al.*, 1972) families now restricted to the southern hemisphere are known to have occurred in Europe and North America in the Palaeogene. The fossil record for angiosperms in general (Collinson, 2000) and trees in particular (Latham & Ricklefs, 1993) similarly indicates that tropical clades were more diverse in temperate latitudes in the Tertiary. Thus, although dispersal limitation out of the tropics almost certainly contributes to the latitudinal gradient of many groups, for volant birds this appears to play a weaker role than the loss of groups that were once much richer in temperate latitudes.

An additional way that dispersal could possibly influence the phylogenetic structure of the diversity gradient is if species in basal and derived clades differ in their innate dispersal rates and so have very different range size distributions. For example, Jetz & Rahbek (2002) argued that total richness patterns are driven by large-ranged species, so the correspondence between the spatial patterns of species in basal clades vs. total species could arise if the former have wider ranges than derived clades. However, we used range size estimates for all species (Hawkins & Diniz-Filho, in press) to evaluate if there is a phylogenetic signal in range sizes, and found no correlation between range sizes and the species' familial root distances ($r = 0.004$). Thus, the strong correspondence between spatial patterns in richness of basal
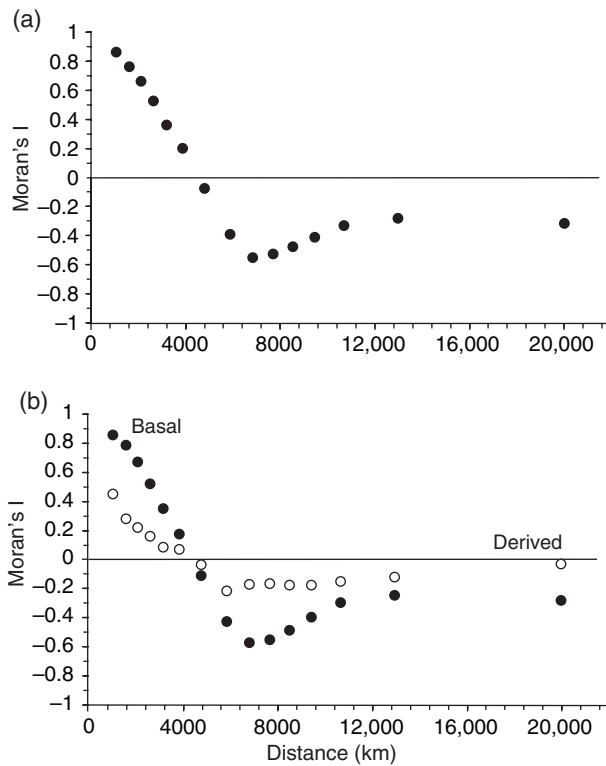
(a)

(b)

Figure 4 Correlograms for (a) total species richness and (b) richness of the basal 30% and most derived 30% of the avifauna, using data resolved at a $110 \times 110\ km^2$ grain size.
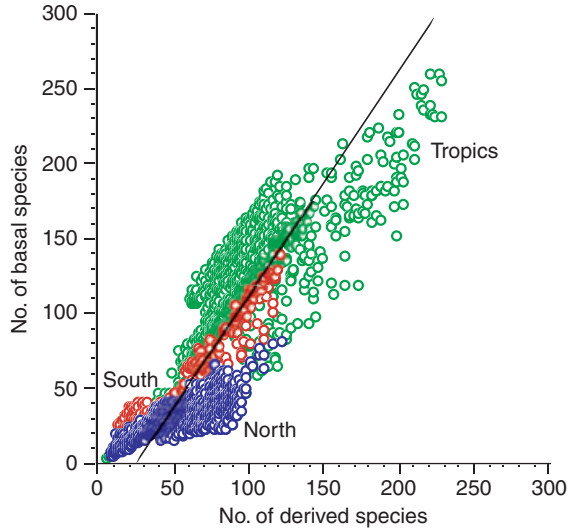

Figure 5 Relationship between species richness of derived families and species richness of basal families (data resolved to $110 \times 110\ km^2$). Extra-tropical North and South America and the Tropics are differentiated by colour. Note that the slope is strongly influenced by low numbers of species from basal clades in North America, although relatively low numbers of basal species also characterize the richest Neotropical cells, which are in the Andes.

clades and all birds cannot be the result of large ranges in basal groups, as we define them, and clearly requires an alternative interpretation.
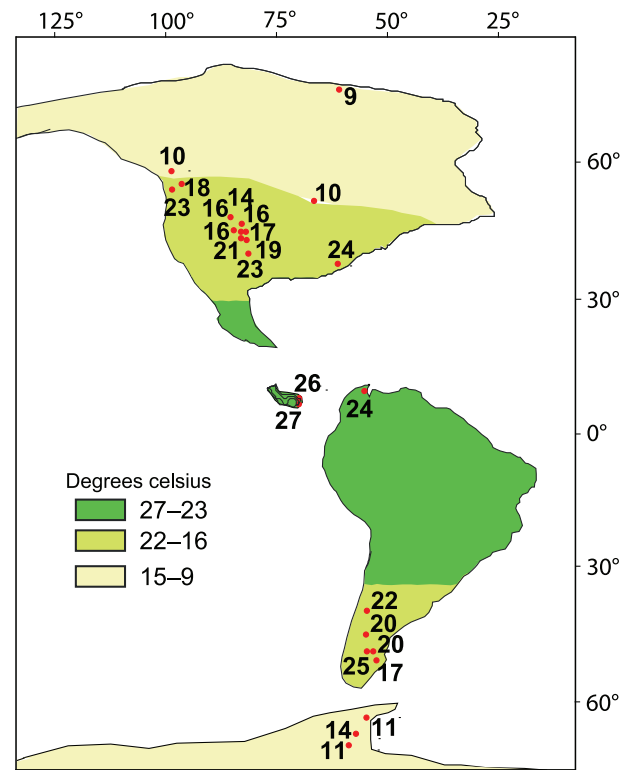

Figure 6 Terrestrial mean annual temperature (MAT) for the early Palaeogene. Dots and companion numbers represent an empirical estimate of MAT at specific sites. All sites are from lowland elevations. The Palaeogene coastline was derived from Scotese (2004).

A second issue is the contribution of decreased extinction rates vs. that of increased speciation rates in the tropics. Although difficult to evaluate in the absence of direct measures of extinction and speciation rates, the spatial pattern in richness of derived clades is suggestive. They are currently more diverse in southern Canada than in eastern Brazil and lowland Central America, so warm climates have not necessarily resulted in more diverse faunas for derived families. They are richest within tropical latitudes (see Fig. 2b), but their hotspots are at higher elevations (i.e. in cooler climates). The gradient of both basal and derived groups is further complicated by extinction episodes during the Pleistocene (Dynesius & Jansson, 2000), which could result in lower diversity levels in the north even if speciation rates were as high as in the tropics. Moreover, a time constraint exists for some Neotropical passerines. The more highly derived oscine passerines originated in the Old World (Barker *et al.*, 2004) and then spread into North America, perhaps not moving into South America until the rise of the Panamanian land bridge, initiated 12.8 Myr BP and completed 7.1 Myr BP (Coates *et al.*, 2004). The time these groups have had to colonize South America and diversify has thus been limited. Given the spatial variability in richness levels of the most derived families across northern South America, speciation rates probably vary substantially even within tropical latitudes, and their richness pattern suggests that tropical mountain ranges rather than tropical lowlands fuel the

engine of tropical diversity. Nevertheless, the relative weakness of the latitudinal gradient of derived clades compared with basal clades suggests that differential speciation plays a smaller role than differential extinction in setting up the diversity gradient within the New World, one of the various scenarios discussed by Gaston & Blackburn (1996). However, rates of evolution in the tropics vs. those in the extra-tropics require further evaluation (Bromham & Cardillo, 2003).

The pattern for derived clades also identifies influences on the diversity gradient operating independently of climate, especially in the southern Neotropics. If climate change were the only factor influencing the evolutionary development of avifaunas, MRDs in southern Argentina should be higher (see Fig. 2), since current climates there are cool. Given that the Old World oscines had to disperse into North America and then through the tropics to reach temperate South America, the latter's geographic isolation from centres of diversification has almost certainly affected bird diversity patterns in the south (Ricklefs, 2002). A similar isolation effect has also been identified for the birds of southwestern Australia (Hawkins et al., 2005).

Finally, it is not surprising that we find that modern temperatures are correlated with the extent to which temperatures have decreased since the Palaeogene, since the coldest parts of the planet are also where climate change has been most severe. On the other hand, it is perhaps more surprising that the contemporary richness gradient can be equally well explained statistically using either modern temperatures or a simple index of post-Eocene climate change. We believe that this explains why it is difficult to distinguish between historical and contemporary mechanisms for the latitudinal diversity gradient; spatial patterns of climate change and contemporary climatic gradients are so strongly collinear that their effects cannot be parcelled statistically. Thus, finding that a variable describing modern conditions explains more variance than a historical variable does not mean that the former is important whereas the latter is not, or *vice versa* (see also McGlone, 1996). Both past and present conditions drive broad-scale diversity patterns, and the contemporary bird richness gradient contains both ecological and evolutionary signals (e.g. Hawkins et al., 2005), so perhaps more progress can be made by integrating effects of the past and the present than by focusing on a single time-frame. Climate and climate change offer a framework for accomplishing this.

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