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ORIGINAL ARTICLE

Different evolutionary histories underlie congruent species richness gradients of birds and mammals

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ABSTRACT

Aim The global species richness patterns of birds and mammals are strongly congruent. This could reflect similar evolutionary responses to the Earth's history, shared responses to current climatic conditions, or both. We compare the geographical and phylogenetic structures of both richness gradients to evaluate these possibilities.

Location Global.

Methods Gridded bird and mammal distribution databases were used to compare their species richness gradients with the current environment. Phylogenetic trees (resolved to family for birds and to species for mammals) were used to examine underlying phylogenetic structures. Our first prediction is that both groups have responded to the same climatic gradients. Our phylogenetic predictions include: (1) that both groups have similar geographical patterns of mean root distance, a measure of the level of the evolutionary development of faunas, and, more directly, (2) that richness patterns of basal and derived clades will differ, with richness peaking in the tropics for basal clades and in the extra-tropics for derived clades, and that this difference will hold for both birds and mammals. We also explore whether alternative taxonomic treatments for mammals can generate patterns matching those of birds.

Results Both richness gradients are associated with the same current environmental gradients. In contrast, neither of our evolutionary predictions is met: the gradients have different phylogenetic structures, and the richness of birds in the lowland tropics is dominated by many basal species from many basal groups, whereas mammal richness is attributable to many species from both few basal groups and many derived groups. Phylogenetic incongruence is robust to taxonomic delineations for mammals.

Main conclusions Contemporary climate can force multiple groups into similar diversity patterns even when evolutionary trajectories differ. Thus, as widely appreciated, our understanding of biodiversity must consider responses to both past and present climates, and our results are consistent with predictions that future climate change will cause major, correlated changes in patterns of diversity across multiple groups irrespective of their evolutionary histories.

Keywords
Bird diversity, climate change, diversity gradients, global biodiversity, mammal diversity, niche conservatism, species richness, tropical niche conservatism.

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INTRODUCTION

The decrease in the number of species from the tropics to the poles is a ubiquitous feature of life on Earth (Hillebrand, 2004 and references therein). Even so, not all taxa have identical patterns, nor must there be a single explanation for all groups. Global-scale diversity gradients are complex and can arise from combinations of, among other things, organisms' responses to contemporary and past climates (Hawkins *et al.*, 2003, 2007; Araújo *et al.*, 2008), geographical variation in the timing of the origin and spread of clades (Wiens & Donoghue, 2004; Jablonski *et al.*, 2006; Wiens *et al.*, 2006, 2009; Krug *et al.*, 2009) and variable diversification rates (Hawkins *et al.*, 2006, 2007; Mittelbach *et al.*, 2007; Weir & Schluter, 2007; Wiens, 2007; Jansson & Davies, 2008). This complexity has resulted in a plethora of explanations and proposed mechanisms for broad-scale species richness gradients over the past 200 years (Whittaker *et al.*, 2001; Willig *et al.*, 2003), and a current challenge is to identify similarities and differences among taxa.

Among terrestrial organisms, the species richness gradients of birds and mammals have received by far the most attention, and their charismatic nature has led to the availability of distributional data across the whole planet. Global-scale distributional databases have been generated for birds (Orme *et al.*, 2005; Hawkins *et al.*, 2007; Jetz *et al.*, 2007) and mammals (Grenyer *et al.*, 2006), and, although it has long been realized that both groups have many species in the tropics and few at the poles, the availability of gridded data across multiple continents has revealed a close congruence of their diversity gradients. Grenyer *et al.* (2006), using a global grid of 9310 km^2 cells, reported a correlation of 0.90 between mammal and bird species richness, with even stronger correlations at coarser grains. Commonalities between the groups, including homeothermy and extensive post-Cretaceous radiations, generate some expectation of congruence in geographical patterns. However, important behavioural differences between them might also be expected to generate different gradients. For example, the extreme migratory habits found in many bird clades allow the use of seasonally suitable conditions and the avoidance of stressful periods, and the burrowing behaviour widespread in small mammals allows manipulation of the microclimates to which they are exposed and may permit persistence in otherwise harsh conditions. But understanding how the highly similar global richness patterns of these two groups as a whole have been formed, despite their differences, may have important implications for understanding biodiversity in general.

It has been argued that both birds and mammals responded to the global climate change that occurred during the mid-Tertiary (35–15 Ma), and that the richness patterns observed today are at least partially driven by phylogenetic niche conservatism, which is defined as the retention of ecological traits over time among related species (Wiens *et al.*, 2010). Hawkins *et al.* (2005, 2006, 2007) concluded that bird species richness patterns derive from a combination of current climate, operating both directly via physiological stresses and indirectly via vegetation (which provides nesting sites, protection from predators, amelioration of climatic extremes, food, structural heterogeneity, etc.), tropical niche conservatism (TNC) at higher taxonomic levels [see Wiens & Donoghue (2004) for detailed discussion of TNC], and time for speciation. These inferences rested on three observations. First, there was a strong correspondence between current richness patterns and environmental gradients. Second, species in basal families accounted for a high proportion of richness in the lowland tropics, suggesting early radiations in the relatively warm Late Cretaceous (100–65 Ma) and early Eocene (55–49 Ma) versus a dominance of species in families that radiated in the colder post-Eocene (34 Ma onwards) at temperate latitudes and in high-altitude tropics. Third, longitudinal gradients reflected high richness for specific groups depending on whether they originated in western or eastern Gondwana (e.g. suboscine passerines in the west and oscine passerines in the east).

Buckley *et al.* (2010) recently analysed the global species richness gradient of mammals using a phylogenetic perspective to evaluate four evolutionary scenarios, three of which were variations on niche conservatism models. They concluded that the richness gradient reflects 'strict phylogenetic niche conservatism' in which positive richness–climate correlations are driven by older mammal groups with tropical origins in the early Tertiary, whereas younger groups arising after the late Eocene tend to have negative richness–climate relationships (they are richer in the extra-tropics). Thus, although the methods employed by Hawkins *et al.* (2007) for birds and by Buckley *et al.* (2010) for mammals were very different, they arrived at similar conclusions: tropical niche conservatism in both groups generates species richness gradients that arise from the tropical origin of older groups, but with younger groups that have evolved traits that permit the colonization of cold post-Eocene climates and that are relatively richer outside the tropics. If true, the similarity of bird and mammal species richness gradients largely reflects similar evolutionary responses via a shared mechanism.

Commonality of an evolutionary mechanism is not the only possible reason why birds and mammals have highly concordant species richness gradients. Evidence for tropical niche conservatism does not rule out the possibility that both birds and mammals are also responding to current patterns of climate and vegetation independently of their evolutionary histories. If climate and vegetation structures, the latter itself strongly affected by climate, influence richness gradients, either because species have inherited particular environmental preferences (phylogenetic niche conservatism) or because climate limits diversity via resources or interactions with the physiological tolerances of species, contemporary processes are critical for the maintenance of richness patterns. This is consistent with concerns about the impact of future global climate change on diversity. Nonetheless, we are left with the following question. How much does the current species richness gradient of endotherms reflect the outcome of long-term evolutionary processes as opposed to limits to richness influenced by current environmental conditions? Opinions about their relative importance divide the literature (see, e.g. Latham & Ricklefs, 1993; McGlone, 1996; Francis & Currie, 1998, 2003; Currie & Francis, 2004; Qian & Ricklefs, 2004; Algar *et al.*, 2009; Wiens *et al.*, 2011), and it is not straightforward to disentangle their influences. Although analyses of single taxonomic groups are informative, comparisons among groups clearly represent a stronger test.

In this paper we examine the extent to which the global richness gradients of birds and mammals reflect similar evolutionary histories. It is well established that species richness is correlated with climate, most often with measures of energy and water availability (Wright *et al.*, 1993; Hawkins *et al.*, 2003). Perhaps unsurprisingly, therefore, richness gradients themselves may be strongly correlated. This covariation is most conspicuous in the 'latitudinal diversity gradient', but it is also a fundamental tenet underlying attempts to identify global conservation priorities, such as Conservation International's Biodiversity Hotspots (http://www.biodiversityhotspots.org). More recently, as information on phylogenetic affinities across species has become available, the evolutionary history of groups has also been mapped, and the relationship between evolutionary history and current richness gradients explored (e.g. Sechrest *et al.*, 2002; Hawkins *et al.*, 2007; Davies *et al.*, 2008; Wiens *et al.*, 2011). These studies suggest that phylogenetic niche conservatism has been an important factor in structuring the geographical distribution of species richness (also see a recent review by Wiens *et al.*, 2010). However, whether taxa display congruent evolutionary histories as well as congruent richness gradients has not been assessed; here we aim to fill this gap.

Our analysis focuses on three predictions, one arising from the supposition that contemporary climate/vegetation has a strong influence on patterns, and two based on evolutionary responses by both groups to post-Eocene climate change. If diversity gradients for both birds and mammals are a product of the same underlying mechanism(s) we predict that: (1) overall mammal diversity should be strongly associated with the contemporary environmental factors known to influence birds; (2) the phylogenetic structure of the mammal gradient should reflect the relative dominance of more basal clades in the tropics and Southern Hemisphere, with more derived faunas in the northern temperate zone; and (3) clades originating in the Cretaceous to Eocene should be rich in the lowland tropics but depauparate in high-altitude tropics and the extra-tropics, whereas clades originating in the Miocene or Pliocene should be relatively rich in cooler climates. If tropical niche conservatism is the dominant influence on both bird and mammal diversity, the third prediction should hold true irrespective of how clades are defined and across multiple taxonomic levels. Our goal is to explore the extent to which bird and mammal richnesses reflect similarity in their evolutionary responses to long-term climate change, or if current climate can account for their convergence of pattern independently of the evolutionary histories of these two large taxonomic groups.

MATERIALS AND METHODS

Richness data

The bird database comprises almost all continental areas in which non-marine birds breed, as well as Great Britain and Tierra del Fuego. All other islands and Afghanistan were excluded, the former to minimize potential area effects, and the latter owing to a failure to locate range maps. The data were gridded in a 9310 km^2 equal-area global grid based on a Behrmann projection (see also Grenyer *et al.*, 2006). The mammal database includes all land areas except Antarctica and was binned in the same grid. Global trends in species richness were compared statistically with correlation and regression. In all statistical comparisons, only cells with both mammal and bird data were included.

Phylogenetic metrics

We used the mean root distance resolved to family ($\mathrm{MRD_F}$) as our phylogenetic metric for birds. The root distance ($\mathrm{RD_F}$) of each species represents the number of nodes separating a species' family from the base of a phylogenetic tree [see also Prinzing *et al.* (2004), who refer to this metric as 'clade rank'], and the $\mathrm{MRD_F}$ of all birds found in each grid cell was used as a measure of the level of evolutionary development of the local fauna (Kerr & Currie, 1999; Hawkins *et al.*, 2005, 2006, 2007; Algar *et al.*, 2009). For operational purposes, we define 'basal clades' as those with few nodes separating them from the base of the tree, and 'derived clades' as those with many nodes separating them from the tree base (Prinzing *et al.*, 2004), although more formally the latter will generally comprise groups of species having larger numbers of synapomorphies or shared genetic rearrangements relative to clades nearer the root of the tree.

We analysed a phylogenetic tree for birds generated using several available phylogenies. The family-level classification system of Sibley & Monroe (1990) was placed into the phylogeny provided by Hackett *et al.* (2008) for clades they included. Missing families were then inserted based on fully resolved sister-group relationships provided by Sibley & Ahlquist (1990), Barker *et al.* (2004), Fain & Houde (2004) or Davis (2008). A few families were placed based on information about those families in the general avian literature. We also used the tree to partition the species richness patterns into basal and derived components based on $\mathrm{RD_F}$ [2259 species from 64 basal families ($\mathrm{RD_F}$ = 1–12) and 2681 species from 20 derived families ($\mathrm{RD_F}$ = 20–28)] (see Appendix S1 in Supporting Information for the families, their species richnesses and their root distances). These $\mathrm{RD_F}$ ranges were selected to balance the numbers of species in each group as much as possible and to compare patterns for clades at opposite extremes of the bird phylogeny, which makes the analysis less sensitive to future changes in the structure of the tree. The $\mathrm{RD_F}$ cut-offs were also guided by estimates of crown-group ages using the differences in the 50% dissociation temperatures between DNA homoduplexes and heteroduplexes (ΔT_{50}Hs) reported by Sibley & Ahlquist (1990). Splitting the birds at these root distances, and excluding the middle section of the tree described by root distances between 13 and 19, allowed us to compare the species richness gradients of clades whose initial radiations pre-dated the Eocene–Oligocene climate shift with the youngest clades that radiated in concert with the episodic global cooling and drying that has characterized the Earth's climate over the past 34 Myr (Behrensmeyer *et al.*, 1992), although ages defined by ΔT_{50}H are by no means exact and were not analysed explicitly.

The availability of a supertree for mammals (Bininda-Emonds *et al.*, 2007) allowed us to generate a broader range of phylogenetic metrics and to estimate clade ages more precisely. For the direct comparison with birds we first calculated mammal MRD_F as per birds. Because the mammal tree includes branch lengths, we also calculated time-calibrated MRD_F by replacing the node count with how far from the base of the tree each crown group arose, measured in millions of years with the base assumed to be 166 Ma (Bininda-Emonds *et al.*, 2007). This metric cannot be directly compared with birds, but it provides an alternative metric of mammalian phylogenetic structure. Third, we generated mean root distance at the species level (MRD_S) by counting the number of nodes from the base of the tree to each species. This allows us to examine the phylogenetic structure of the mammal gradient at a finer taxonomic level and captures the phylogenetic pattern arising from all extant radiations spanning the Late Cretaceous to the Pleistocene. Finally, we used crown-group ages to partition mammal families into older groups (534 species from 16 families older than 49 Ma) and younger groups (533 species in 46 families younger than 23 Ma), from which families of intermediate ages were excluded (see Appendix S1 for the families, their richnesses and their ages). Similar to the case for birds, the numbers of species in the two groups were as balanced as possible, and their radiations were initiated either well before or after the Oligocene climate shift. The extremely diverse rodent superfamily Muroidea (Musser & Carleton, 2005), estimated to have arisen 48.1 Ma, was examined separately to enable comparison of their richness gradient with the other early and mid-Eocene radiations.

A potential criticism of RD_F as a comparative phylogenetic metric stems from the assumption of equivalency among families both within birds and mammals and between the groups, which is undoubtedly not the case (Avise & Johns, 1999). For birds, the taxonomic (but not phylogenetic) treatment follows from DNA–DNA hybridization studies dating from the late 1970s and 1980s that used thresholds in melting profiles of the hybridized DNA to delineate taxonomic ranks (Sibley & Ahlquist, 1990). Therefore, bird families represent discrete evolutionary units exceeding some minimum threshold in genetic distance, which might translate into minimum divergence times, assuming a monotonic decay in similarity over time (Fitch, 1976). This is fundamentally different from how mammal families are currently defined (McKenna & Bell, 1997; Wilson & Reeder, 2005). Basically, taxonomic families are artificial constructs, and the exact nature of these constructs differs for birds and mammals. To explore how the designation of families might influence our comparison, we used a time-based method to generate alternative classifications of mammals. The phylogeny was 'sliced' at 10-Myr intervals (ranging from 20 to 80 Ma), and family ranks were assigned to each clade descending from nodes at this time interval or from the next oldest node. Thus, we generated root distances for each species based on seven arbitrary family classifications, with families assigned using various minimum divergence times. These RD_Fs were used to generate new MRD_Fs, which were then compared with the pattern of bird MRD_F. Although the use of familial root distances will always leave room for doubt about how patterns compare across different taxonomic groups, by exploring alternative taxonomic classification schemes we can evaluate how early (suprafamily) radiations determine MRD_F versus vagaries of taxonomic nomenclature.

Finally, because the lack of a species-level supertree for birds effectively makes 'family' rather than species the basic unit of comparison across birds and mammals from a phylogenetic perspective, we compare the richness patterns of families of the oldest (Cretaceous/Eocene) and most recent (Miocene/Pliocene) birds and mammals. This allows us to ascertain if differences in species richness reflect differences in the early differentiation of lineages (above the family level) or arise from exceptional radiations within a few families (young or old). It is important to bear in mind that the absence of a bird phylogeny at the species level strongly constrains our analysis and makes it essentially impossible to address all of the possible issues related to comparing the phylogenetic structure of two large, independently evolving groups. Given this, our strategy is to utilize a 'weight of evidence' approach: we attempt a wide range of comparisons, and, although none of the approaches is perfect, if all results lead to similar conclusions it suggests that they are reasonably robust [see McGill (2003) for discussion of the use of multiple tests in macroecology].

Environmental data and analysis

The relationships between current environment and bird and mammal species richness were tested with a path model derived from the one presented by Hawkins *et al.* (2007) for birds. Selection of the optimal model for birds used the program EPA2 (Shipley, 2002) followed by d-separation tests of paths using the program DGRAPH (Shipley, 2002). Path coefficients were then obtained iteratively using the maximum Wishart likelihood method implemented in the RAMONA routine of SYSTAT 10.0 (Browne & Mels, 2000) and tested for significance using a geographically effective degrees of freedom of 200 to control for residual spatial autocorrelation (as in Hawkins *et al.*, 2007). The predictors included annual actual evapotranspiration (AET, a measure of water–energy balance, available at http://www.grid.unep.ch/data/data.php?category=atmosphere), Global Vegetation Index (GVI, available at http://www.osdpd.noaa.gov/ml/

land/gvi.html), range in elevation (Relev) from the gtopo30 digital elevation model (available at http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info) and mean annual temperature (available at http://www.worldclim.org/). To capture mesoscale interactions between topography and macroclimate, we also calculated the interaction between annual temperature (+21 °C to make all values positive) and range in elevation in each cell (T × Relev). The five variables in the model are known to have explanatory power for birds via direct and indirect paths (Hawkins *et al.*, 2007), and may similarly influence mammals. Model fits were evaluated by the root mean square error of approximation (RMESA) and tested against the null model of a perfect fit (H_0: RMESA = 0).

RESULTS

As found by Grenyer *et al.* (2006), bird and mammal species richness are strongly correlated (Fig. 1), although absolute numbers of bird species in cells are generally greater than those of mammals. Patterns within biogeographical regions are also correlated, although some differences within and among regions exist (r = 0.74–0.90; cf. Figs 2a & 3a). The most noticeable difference at the global extent is the extremely high richness of birds in the tropical Andes, whereas mammals, albeit also being rich in the Andes, are richest in the eastern Africa Rift zone and are relatively more diverse in most of tropical Africa.

Contemporary environment and richness

Given the similarity in richness patterns, we expected both bird and mammal gradients to be associated with similar environmental gradients. This was confirmed by the path models (Fig. 4). There were small differences in the standardized path coefficients leading to the richness of each group, but the model designed to explain bird richness explained as much variance in mammal richness. Mammals also had a slightly stronger association with water–energy balance (AET) than birds, and a weaker direct association with vegetation, but the rankings of the direct coefficients were identical in both models. The RMESAs of the two models were not significantly different from a perfect fit (Fig. 4). Thus, the model optimized for birds had similar explanatory power for mammals, and we conclude that both groups respond to broad-scale and mesoscale climatic gradients and vegetation. That is, the shared pattern between climate and richness for birds and mammals suggests that these clades have similar responses to contemporary environmental structure, meeting our first prediction.

Phylogenetic structure of the richness gradients

The familial mean root distance (MRD_F) of birds has high variance and shows strong but complex spatial structure (Fig. 5a). The fauna with the largest proportion of species

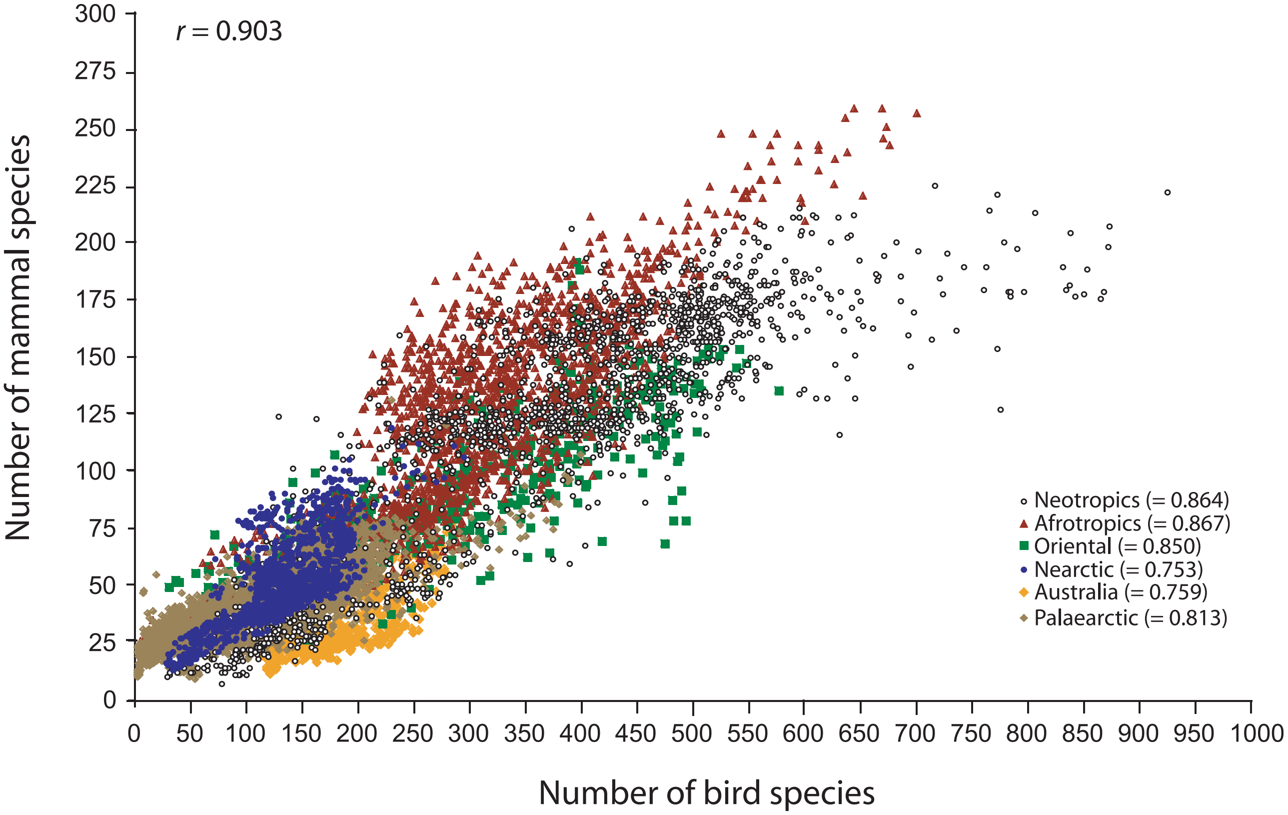
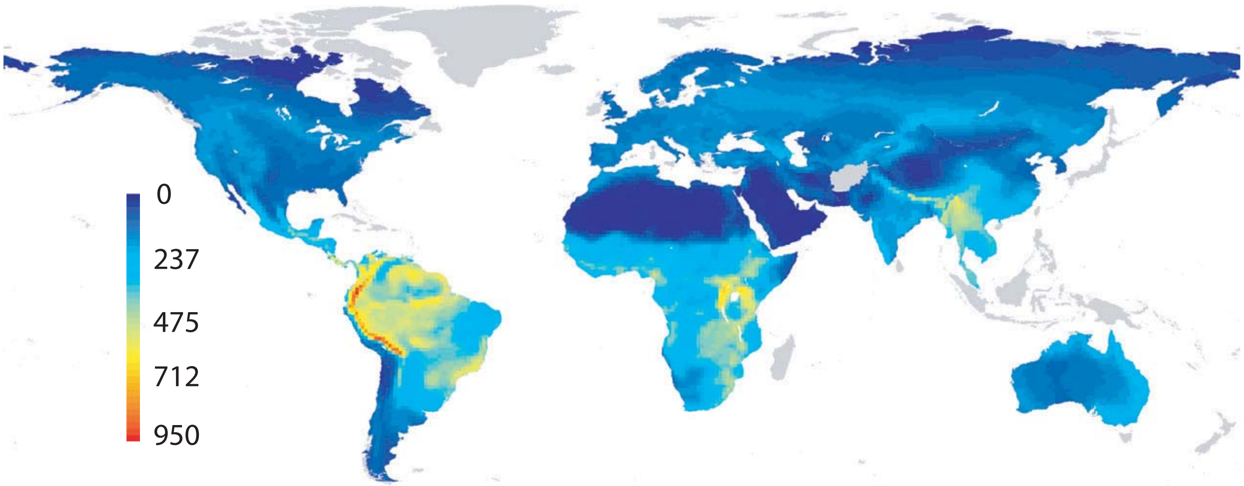
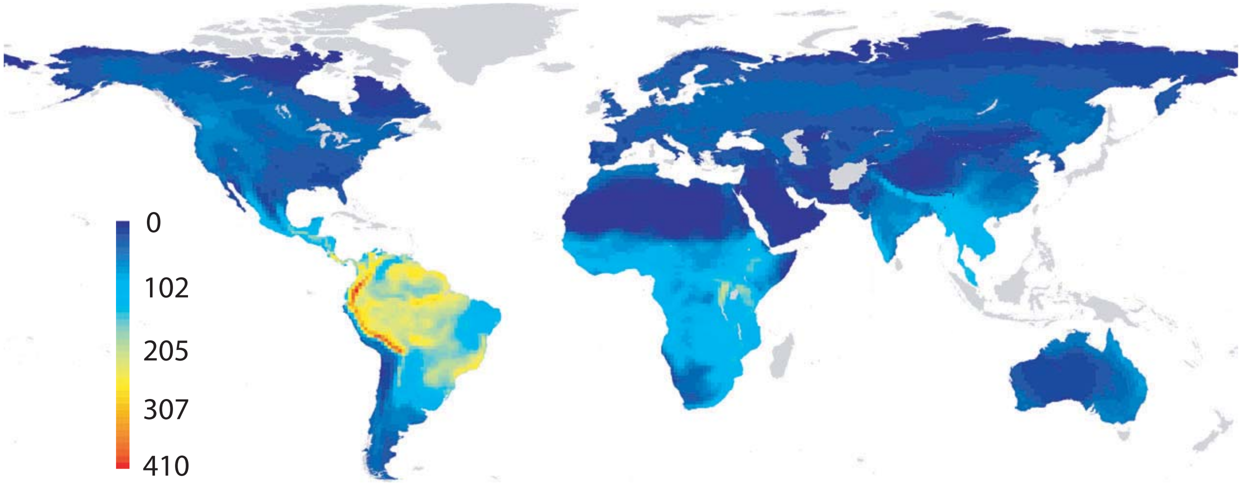


Figure 1 Relationship between the species richness of birds and mammals in a global 9310 km^2 grid. Biogeographical regions are also distinguished. Correlations in richness patterns are presented across all data and within each region.

(a) All birds



(b) Basal groups ($r = 0.955$)



(c) Derived groups ($r = 0.793$)

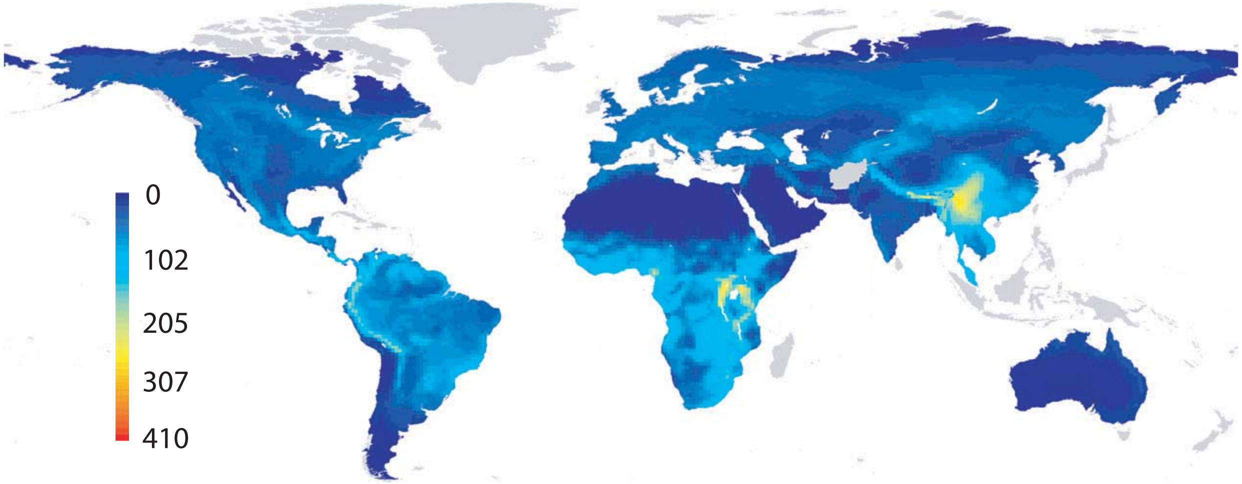
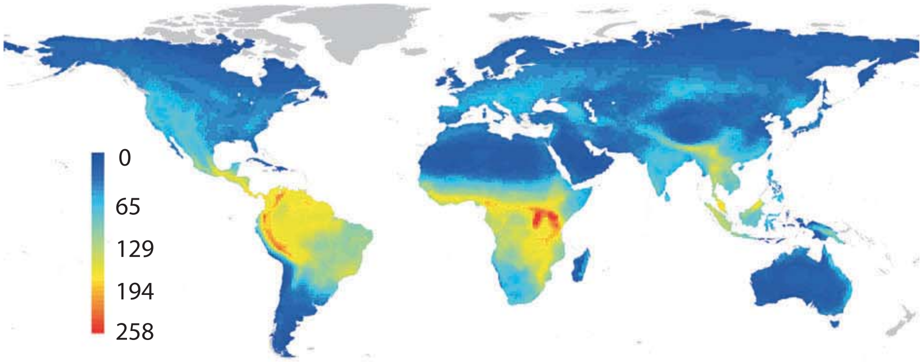
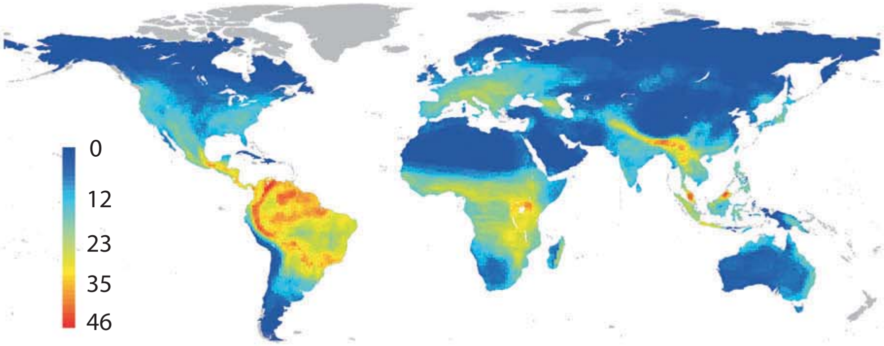


Figure 2 Species richness patterns of birds in a 9310 km^2 grid. (a) All species, (b) species belonging to families with a root distance of 1–12, and (c) species belonging to families with a root distance of 20–28. Correlation coefficients in (b) and (c) are for the associations between the richness of each subgroup and all birds.

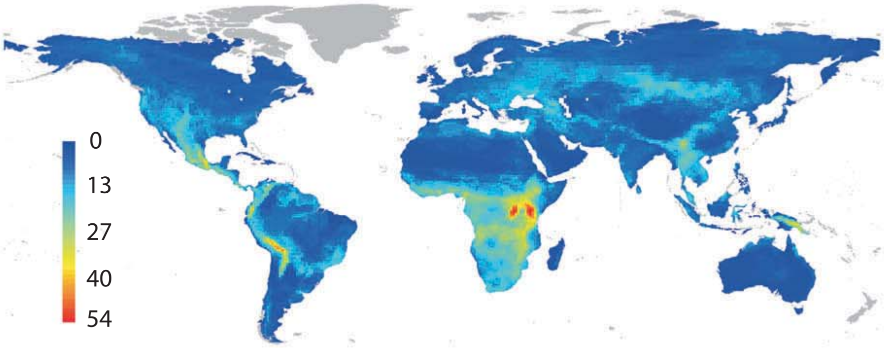
(a) All mammals



(b) Cretaceous/Eocene groups ($r = 0.915$)



(c) Muroidea ($r = 0.743$)



(d) Miocene/Pliocene groups ($r = 0.920$)

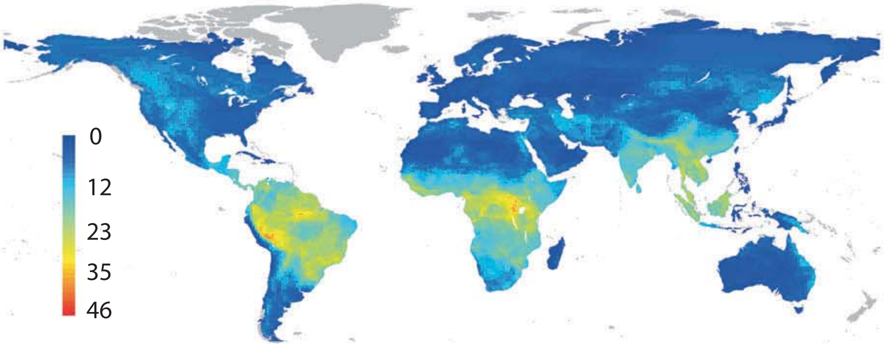


Figure 3 Species richness patterns of mammals in a 9310 km^2 grid. (a) All species, (b) species belonging to families with crown groups arising prior to 48 Ma, (c) Old and New World rats and mice, which arose 48.1 Ma but are distinguished from other Eocene groups, and (d) species belonging to families with crown groups younger than 23 Ma. Correlation coefficients in (b), (c) and (d) are for the associations between the richness of each subgroup and all mammals.

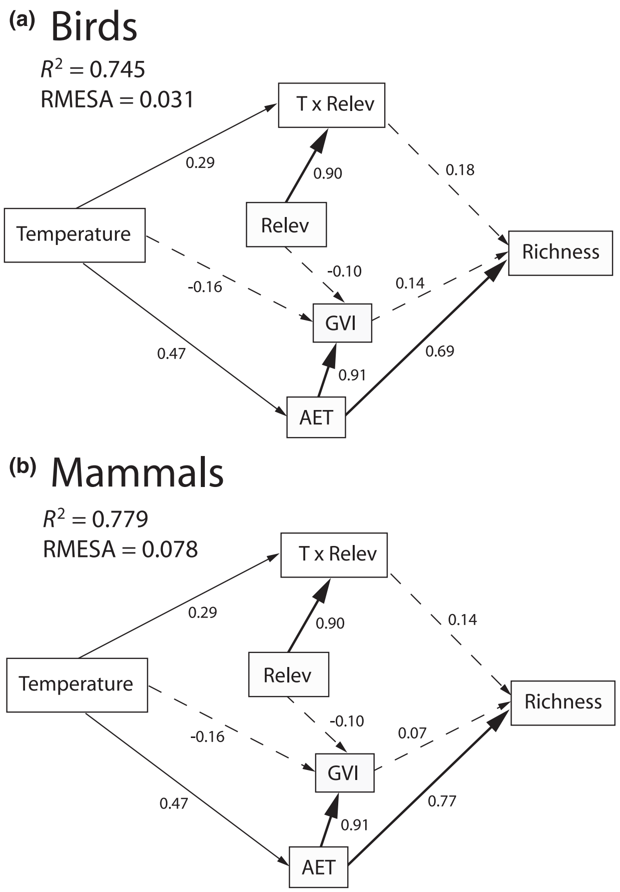


Figure 4 Environmental path models for (a) birds and (b) mammals. Standard path coefficients are provided for each link, as is the model coefficient of determination (R^2) and the model root mean square error of approximation (RMESA). Types of lines (dashed, normal and bold) identify low, moderate and high coefficients, respectively. H_0 refers to the null hypothesis that the model fits the data perfectly (RMESA = 0), which in neither case can be rejected. Variable abbreviations: AET, annual actual evapotranspiration; GVI, Global Vegetation Index; Relev, range in elevation; T × Relev, the interaction between annual temperature (+21 °C) and range in elevation in each cell (see text for further details of variables).

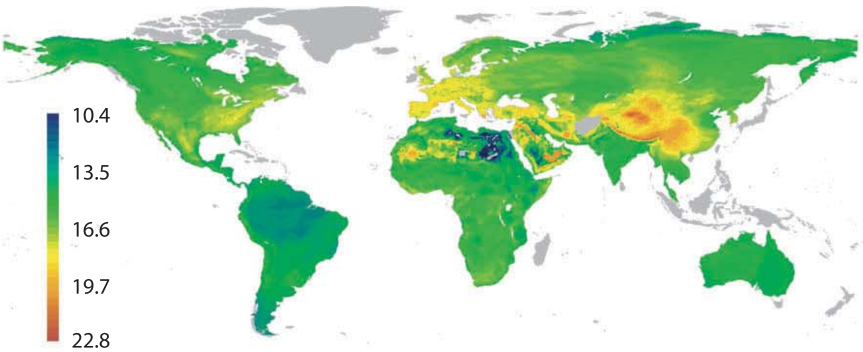
descending from early diverging families is found in the eastern Sahara, but fewer than 10 bird species occur there. In areas with more diverse faunas, the highest richness of species descending from basal families is found in Amazonia, partially reflecting the extensive radiations of Trochilidae and Psittacidae, but also attributable to a paucity of species from derived families in Neotropical lowland forest. Generally, bird assemblages are from more derived families in deciduous forests in the Holarctic, Himalayas and mountains of the south-central Palaearctic (Fig. 5a), reflecting extensive mid-latitude radiations among the most highly derived oscine passerines.

Mammalian $\mathrm{MRD_F}$ based on accepted families has a global pattern strikingly different from that of birds (Fig. 5b). The mammals of Australia (with its rich marsupial fauna) and extra-tropical central South America are composed largely of species from basal families. Across the rest of the world, species in basal families are over-represented across the conterminous USA and western Eurasia (as well as on some southern islands). The details of the $\mathrm{MRD_F}$ pattern for mammals change dramatically when calculated using time-based family ranks (see Appendix S2). At most times, Australia is identified as supporting the most basal faunas, but with changing patterns over the rest of the world, most noticeably moving from low relative $\mathrm{MRD_F}$ in Africa when families are defined as 60 Ma or older, to low relative $\mathrm{MRD_F}$ in the Neotropics when the threshold for families is 40 Ma. Patterns in the Northern Hemisphere resemble trends for Africa when families are constrained to be old, but there is no clear pattern for younger family thresholds. Irrespective of the complexity of the $\mathrm{MRD_F}$ patterns for mammals using a range of temporally defined higher-level classifications, none shows strong relationships with bird $\mathrm{MRD_F}$ patterns (Table 1). In fact, classifications assigning family rank to clades that arose post-Eocene (e.g. after 33.9 Ma, which is broadly consistent with the actual mammal classification system, with average family ages of 29.3 ± 16.2 Ma) have virtually no association with bird phylogenetic structure, and to achieve the highest, albeit still low, level of association in $\mathrm{MRD_F}$ it is necessary to assume that all mammal families arose in the early Eocene (Table 1), which is far too old for either the mammal or the bird classification schemes (Sibley & Monroe, 1990; Monroe & Sibley, 1993).

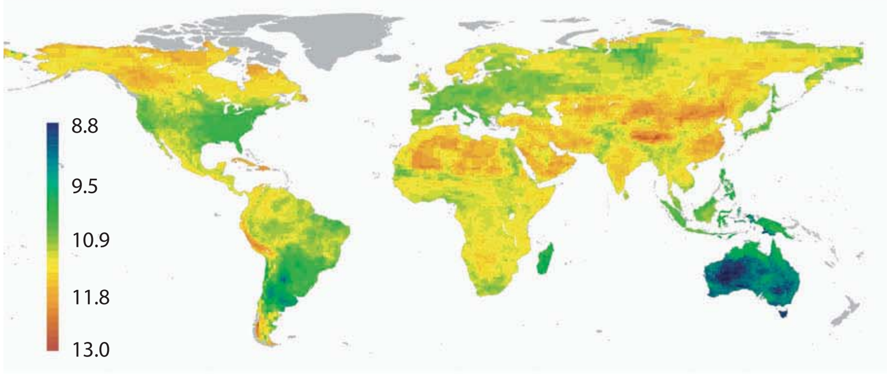
A direct comparison of cell $\mathrm{MRD_F}$ of birds and mammals based on accepted families also reveals covariation within biogeographical regions to be variable, ranging from a moderate negative covariance in the Nearctic, to weak negative covariance in the Afrotropics, and to near independence in the rest of the world (Fig. 6). Adding family ages to the mammalian $\mathrm{MRD_F}$ again changes the details of their phylogenetic structure, but the pattern remains inconsistent with our evolutionary prediction (Fig. 5c). Australia no longer stands out (cf. Fig. 5b), but Europe, the south-eastern USA, extra-tropical South America and Madagascar support faunas derived from older families on average. The weak association between bird $\mathrm{MRD_F}$ and mammal time-calibrated $\mathrm{MRD_F}$ ($r = 0.336$) further reinforces the difference between the spatial phylogenetic patterns of birds and mammals, however measured.

Mean root distance at the species level for mammals revealed spatial phylogenetic structure not apparent at the family level (Fig. 5d), irrespective of how families are defined. There is a strong south-to-north gradient, with species in assemblages of the Southern Hemisphere branching 13–15 nodes from the base of the phylogeny on average, and far northern assemblages branching 19–22 nodes from the tree base on average, suggesting that species currently in the north have descended from lineages with higher net diversification rates (more phylogenetic branching). However, $\mathrm{MRD_S}$ explains little of the variance in mammal species richness globally ($r^2 = 0.071$), and if it cannot explain the mammal pattern, logically it cannot explain why mammals and birds have similar patterns.

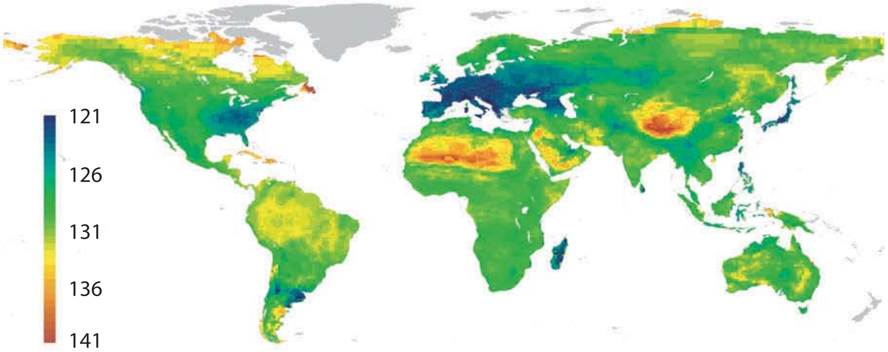
(a) Birds (family MRD)



(b) Mammals (family MRD)



(c) Mammals (time calibrated family MRD)



(d) Mammals (species MRD)

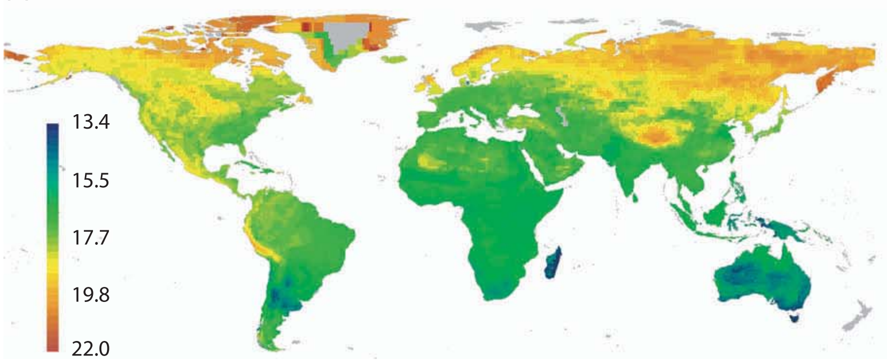


Figure 5 Geographical pattern of mean root distance at the family level for (a) birds and (b) mammals in a 9310 km^2 grid. (c) Time-calibrated mean root distance at the family level for mammals and (d) mean root distance at the species level for mammals. Units in (c) are 1×10^6 years from the base of the phylogeny.

Table 1 Correlation matrix (r) for cell mean root distance (MRD_F) using actual bird families (Birds), actual mammal families (Mammals) and seven arbitrary classification systems for mammals derived from the designation of families based on the slicing of the mammal phylogeny at 10-Myr intervals (20–80 Ma). The final column provides the correlations between the MRD_F of birds and those using each mammal classification.

Time (Ma)	30	40	50	60	70	80	Mammals	Birds
20	0.664	0.552	0.165	0.067	0.360	0.221	0.352	0.054
30	1	0.711	0.184	−0.179	0.093	0.121	0.249	0.040
40		1	0.507	0.108	0.138	0.196	0.455	0.119
50			1	0.453	0.045	0.048	0.444	0.332
60				1	0.753	0.779	0.769	0.161
70					1	0.905	0.667	0.146
80						1	0.696	0.174
Mammals							1	0.116

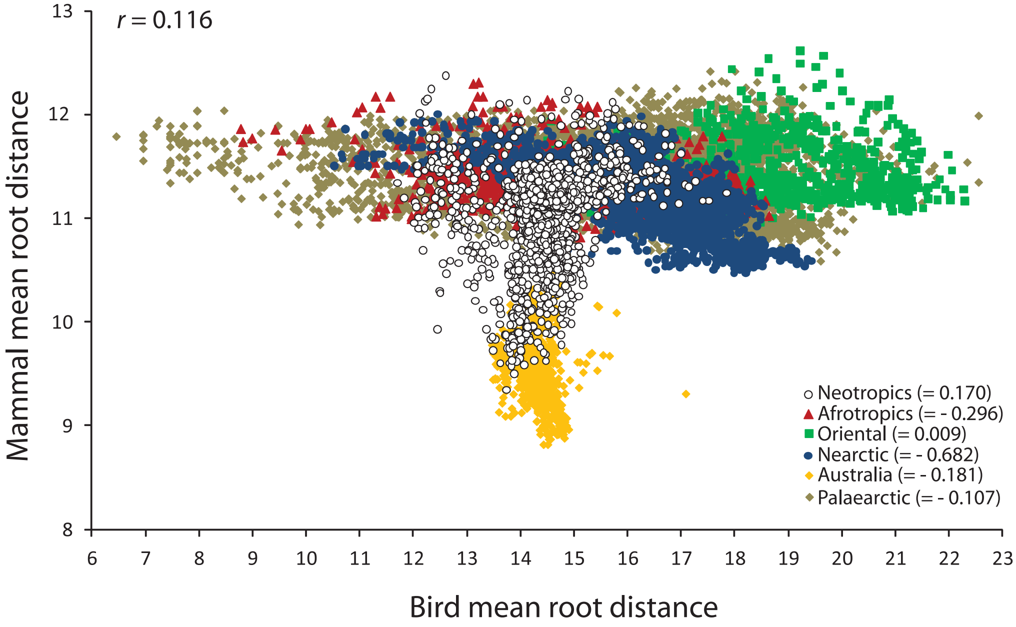


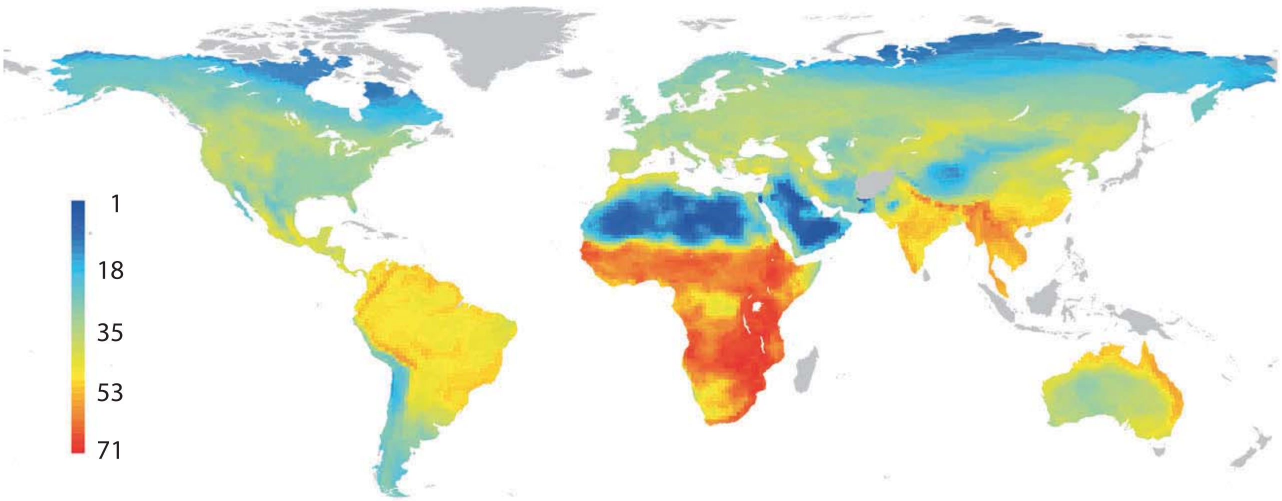
Figure 6 Relationship between mean root distances (MRD_F) of birds and mammals. Presentation as in Fig. 1.

Clade ages and patterns of species and family richness

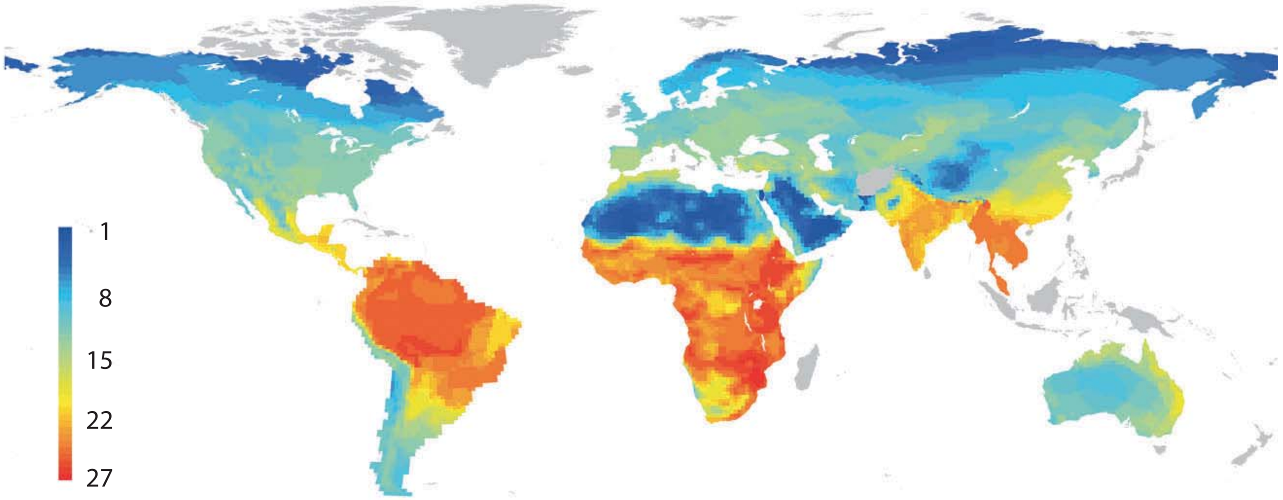
The richness gradient of bird species in old (basal) families is strongly correlated with the overall bird gradient, with most species concentrated in the tropics (Fig. 2b) (see Hawkins *et al.*, 2007 for a similar result with basal families delineated using a different phylogeny). Within the tropics themselves, most species are concentrated in the Neotropics and Afrotropics. The species in the youngest families, in contrast, have a much weaker global gradient and are most diverse in the montane tropics and sub-tropics, especially the eastern Himalayas (Fig. 2c). Consequently, the correlation between the species richness of younger families and total richness is also weaker. Although it is not possible to determine whether the high richness of older clades is a product of ancient or recent diversification, the high richness of younger clades must reflect recent speciation; hence these results suggest that the history of recent speciation may have been highest in low-latitude mountains for birds.

In contrast to birds, species in mammal families older than 49 Ma (Cretaceous and early Eocene) and younger than 23 Ma (Miocene and Pliocene) have similar richness gradients (r = 0.806), and both are strongly correlated with the overall gradient (Fig. 3b,d). Old groups are also moderately rich in North America and Europe (Fig. 3b), indicating that they have not been excluded from the cool climates found at mid-latitudes as were most species in old bird families (Fig. 2b). Species from young families are concentrated in the tropics (Fig. 3d), despite the fact that these families began radiating after the Earth's climate began cooling. Finally, the Muroidea (New and Old World rats and mice), although a relatively old group, are diverse in some areas with cold climates and are especially diverse in parts of the montane tropics (Fig. 3c). Thus, the evolutionary predictions derived from the bird gradient are not met for mammals. In mammals, combined clades of different ages do not have distinct diversity gradients, and the overall gradient reflects a combination of species in

(a) All families



(b) Basal families



(c) Derived families

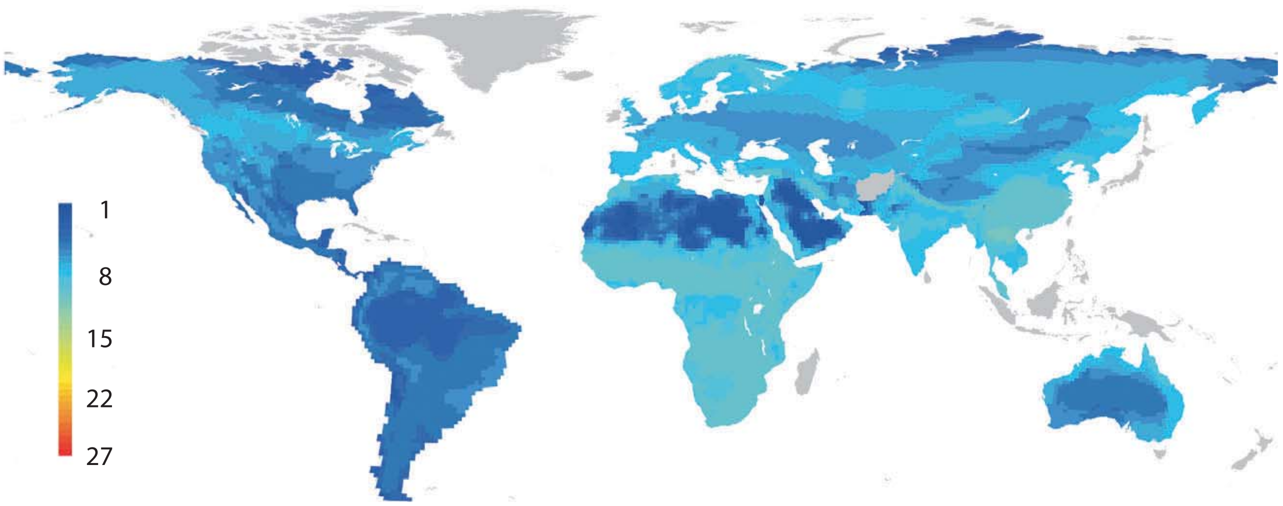
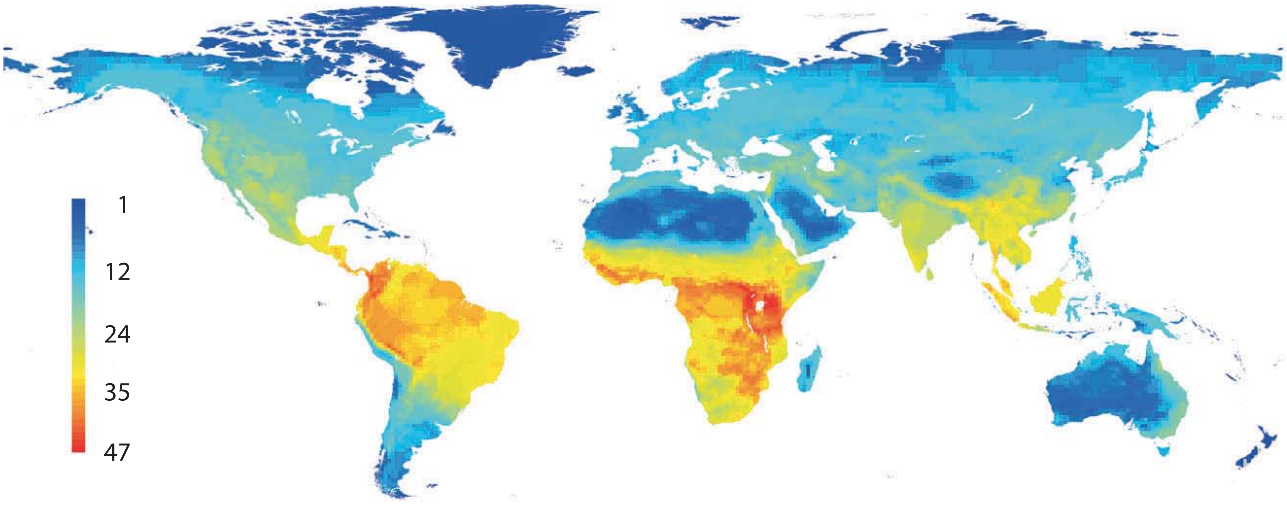
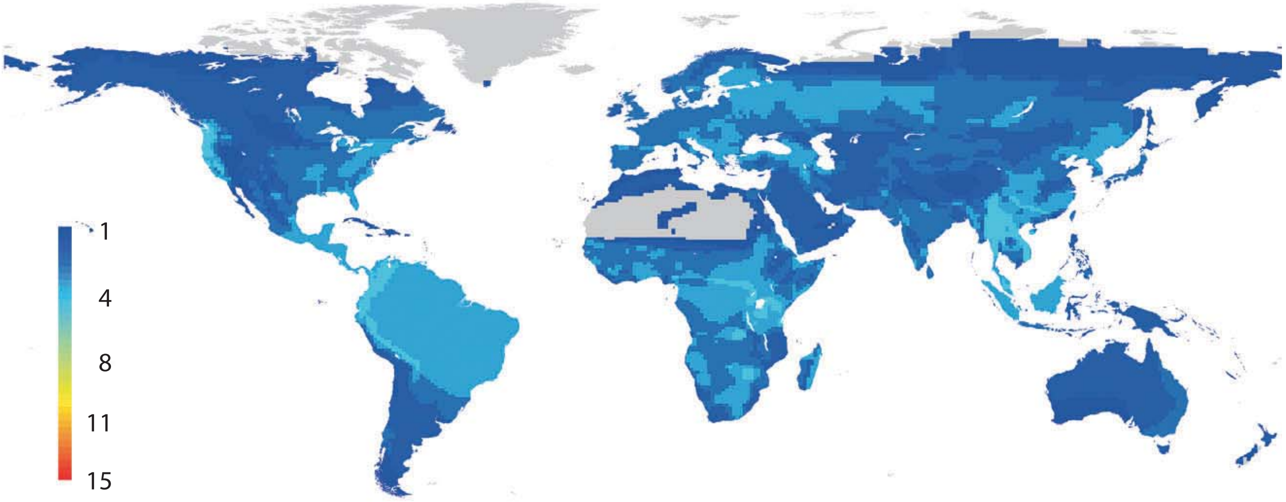


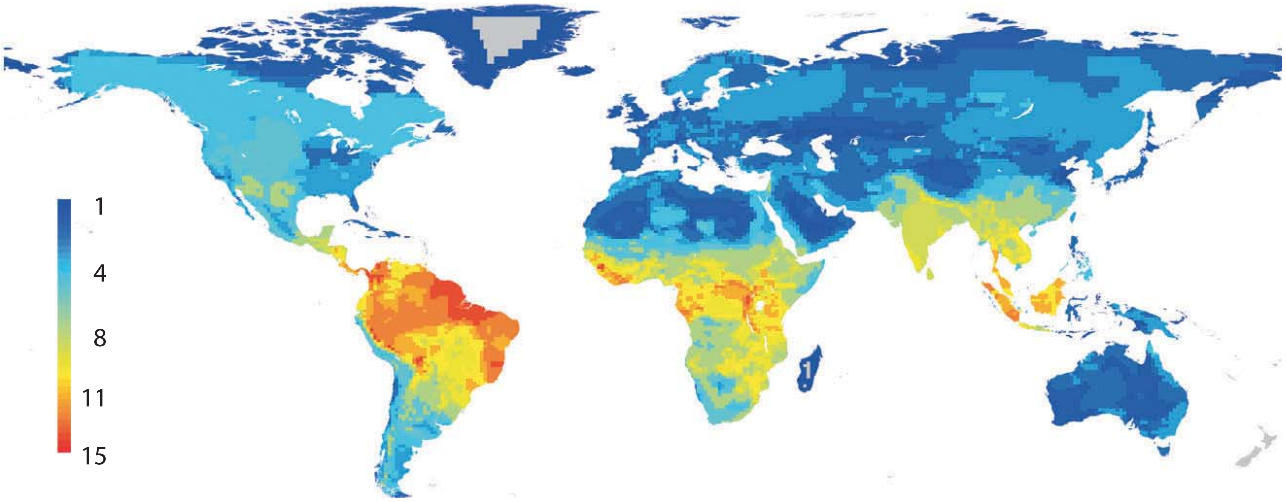
Figure 7 Family richness patterns of birds in a 9310 km^2 grid. (a) All families, (b) families with a root distance of 1–12, and (c) families with a root distance of 20–28.



(a) All families



(b) Cretaceous/Eocene families



(c) Miocene/Pliocene families

Figure 8 Family richness patterns of mammals in a 9310 km^2 grid. (a) All families, (b) families with crown groups arising prior to 48 Ma, and (c) families with crown groups younger than 23 Ma.

families that originated in a world much warmer than present and species in families that originated during periods of severe climate change.

A comparison of family richness gradients for old and young groups also provides a stark contrast between birds and mammals (Figs 7 & 8). Bird family richness (which is correlated with species richness, $r = 0.829$) is much more strongly characterized by the distributions of the oldest families than by those of the youngest (Fig. 7), suggesting that the early diversification of bird lineages was key to shaping present-day gradients of bird species richness. The reverse is the case for mammals: high family richness (which is even more strongly correlated with species richness, $r = 0.942$) in the tropics is associated with large numbers of young families, whereas there is little spatial variation in the few old families (Fig. 8). The tropical diversity gradient for mammals must have arisen, therefore, after the initial diversification of lineages defining basal families with origins in the Cretaceous to early Eocene. In summary, lowland tropical bird faunas contain many species arising from many basal families, whereas mammal faunas contain both many species arising from a few basal families and many species from a large number of more recent families.

DISCUSSION

Of the predictions for the geographical structure of bird and mammal species richness, the one based on contemporary climate is met whereas the evolutionary predictions are not. If both groups are responding similarly to current climate gradients we would expect congruent diversity gradients and close similarity of environmental models for richness, and this is what we find. This aspect of our results is not surprising, because the similarity of patterns virtually guarantees that they will be associated with similar environmental gradients. Our analysis used only a single grain, but this must remain true across alternative grain sizes at which the analysis could be conducted because the correlation between bird and mammal diversity remained very strong at every grain examined by Grenyer *et al.* (2006). It is perhaps more surprising that the phylogenetic structures of the diversity patterns are essentially independent, and in some cases even in opposite directions, leading to the conclusion that the evolutionary and biogeographical pathways by which birds and mammals have arrived at their current gradients must have been quite different. This is not evidence that history or evolution do not influence contemporary diversity patterns; indeed, the two diversity gradients are not identical, with a high richness of birds in the Neotropics and of mammals in the Afrotropics. Higher tropical richness might still be explained by phylogenetic conservatism of tropical niches in both groups, but the phylogenetic structures we observe indicate either that the evolutionary pathways to tropical conservatism were different or that the biogeographical pathways to the tropics were different. We suspect that the richness gradients of other groups that are similar in structure will show equally incongruent evolutionary histories, perhaps divergent from both birds and mammals, although we have no data to evaluate this at present.

Broad-scale richness patterns of most plant and animal groups are correlated with climate (Wright *et al.*, 1993; Hawkins *et al.*, 2003), an association so obvious that it formed the basis of early explanations for richness gradients (Forster, 1778; von Humboldt, 1808). Even after the influence of evolution became apparent in the mid-19th century, climate was still invoked to explain 'latitudinal' diversity gradients, with the major distinction being the claim that past climates also mattered (Wallace, 1876). Despite this history, associations between climate and richness are sometimes dismissed as 'mere correlations' lacking explanatory power (see, e.g. McGlone, 1996; Ricklefs, 2004). There are a number of possible explanations for these associations (reviewed by Evans *et al.*, 2005), but initial empirical tests of the predictions of some proposed mechanisms have not been supportive (Currie *et al.*, 2004). On the other hand, a thought experiment illustrates how contemporary climate shapes geographical patterns of species richness. Africa currently has a very uneven distribution of richness, at least partially owing to the complex geophysical and climatic history of the continent. But if climate change over the next century were to cause the Sahara Desert to cover the entire continent, the richness patterns of all plant and animal groups would be drastically modified. Clearly, a 'contemporary' climate-based process would be responsible for the resulting spatial pattern of richness, and we would also predict that African diversity patterns would again change if we were able to reverse this climate change and generate significant rainfall over at least part of the continent. A relatively rapid and broad-scale change in climate as envisaged in our thought experiment is analogous to what happened in Canada *c.* 24 times during the Pleistocene glacial cycles, so the line between what is considered historical or contemporary climate is actually very blurred. Climate change is obviously a continuous process, and the claim that richness patterns must depend entirely on either the past or the present is almost certainly based on a false dichotomy.

The bird richness gradient has a phylogenetic structure consistent with tropical niche conservatism: the richness of older, more basal families as well as the number of basal families have a strong tropical bias, whereas younger, more derived families are relatively richer (in terms of both number of families and number of species) in the extra-tropics and cool tropics (see also Hawkins *et al.*, 2006, 2007). This results in a complex spatial pattern of root distances, with high variance in $\mathrm{MRD_F}$ within and among continents. It also generates a strong correlation between the richness of species from basal families and overall bird richness. In contrast, the richness gradients of species of basal versus derived mammal families are more similar, generating a weak $\mathrm{MRD_F}$ gradient across all continents except Australia. Although the $\mathrm{MRD_F}$ pattern for mammals using a range of possible family classification systems varied considerably, none approached patterns observed for birds, and when families were delineated using node ages that might best approximate minimum ages for many bird families (20–30 Ma;

Sibley & Ahlquist, 1990), correlations of MRD_F were especially weak. For mammals, the richness patterns of species belonging to basal versus derived families provide no evidence that the richness of tropical mammal faunas can be explained by differential radiation of lineages prior to the Oligocene climate shift, but rather reflect patterns of more recent diversification within both basal and derived families.

Because there are no objective criteria for recognizing higher taxa, it remains possible that the distribution of basal versus derived family richness reflects a geographical bias in the circumscription of families. For example, basal families might simply represent more inclusive clades when compared with derived families (Scotland & Sanderson, 2004). If this were the case, however, we would expect basal families also to be more species-rich than derived families, but the reverse is true for birds ($P < 0.002$, data in Appendix S1), and there is no significant difference for mammals ($P > 0.05$; data in Appendix S1). Hence, the dominance of tropical lowland bird faunas by species in basal clades does not result from more inclusive definitions of basal families in the tropics, and there is no discernible bias in mammals.

It is perhaps informative that, although the global gradient of old mammal families is weak (see Fig. 8b), the species richness gradient within these groups is strong (see Fig. 3b). If these families arose in areas with tropical climates in the Cretaceous and early Palaeogene, this suggests that time for speciation may be contributing to their diversity gradient (Buckley *et al.*, 2010), as also indicated for birds (Hawkins *et al.*, 2007). Unlike the case for birds, however, lowland tropical mammal richness also is comprised of large numbers of species from the most recent families, of which there are many (cf. Figs 3c & 8c). Although we lack direct evidence, differential diversification rates across latitudes may play a larger role in mammal diversity (Davies *et al.*, 2008) than in the case of birds, because young bird families are not especially rich in tropical lowlands. On the other hand, tropical mountains may represent species pumps for both birds and mammals, as younger families of both are species-rich there.

Why might the evolutionary underpinnings of the richness gradient for mammals appear to differ fundamentally from that for birds, especially when both Hawkins *et al.* (2007) and Buckley *et al.* (2010) have argued that tropical niche conservatism is important for both? If we assume that one or both of the previous papers are not in error, several scenarios for the evolution of mammalian diversity are plausible. One possibility is that the mammalian basal form was cold-adapted, and global spread resulted from an easier adaptation from cold tolerance to warm tolerance. Evidence consistent with this scenario includes: (1) the selection for the hair, homeothermy and extreme energetic efficiency that characterize mammalian evolution (Kielan-Jaworowska *et al.*, 2004); (2) the persistence and subsequent radiation of lineages in regions that would have been temperate in the Late Jurassic and Early Cretaceous (Australia, South America), which were then contiguous with Antarctica; (3) the extensive geographical distribution of fossils from the major early lineages of mammals (prototherians, metatherians and eutherians) in the Late Jurassic and Cretaceous (Kielan-Jaworowska *et al.*, 2004); and (4) the many northern clades able to colonize and radiate in tropical South America during the Great American Biotic Interchange (Vaughan, 1986; Webb, 2006).

Another possibility is that the basal mammalian niche may result less from climatic conditions and more from their evolving during a period of dinosaur domination. A dinosaur-dominated fauna might have restricted the available niche space for early mammal diversification. The basal mammalian form was small, insectivorous, nocturnal and sneaky (Kielan-Jaworowska *et al.*, 2004), relying on tunnels, burrows, and nests underground or under vegetation. These traits may have also shielded many mammals from the full impact of extra-tropical climatic conditions, thus opening up this habitat for later occupation and diversification, whereas birds are able to avoid extreme climates (i.e. freezing temperatures) only through torpor or migration. If so, this only reinforces the biological differences between birds and mammals and makes their similarity in contemporary diversity patterns even more surprising. It is also possible that a model of explosive mammal radiation following the extinction of dinosaurs (Alroy, 1999) explains why much of mammal diversity, even in the tropics, belongs to relatively young clades, although phylogenetic evidence suggests the diversification of modern mammals was more closely linked to climatic shifts around the Cenozoic and the Early Eocene Climatic Optimum (Bininda-Emonds *et al.*, 2007). Modern birds, in contrast, may have been less constrained by the presence of dinosaurs and have begun their radiation in the Late Cretaceous (Clarke *et al.*, 2005; Zhou, 2007), but, again, this is not universally accepted (Chiappe & Dyke, 2002). If these scenarios are true, it would provide a partial explanation for why the bird richness gradient largely reflects the spatial distribution of lineages that diverged in the Cretaceous to early Eocene, whereas the mammal gradient is derived more from later radiations within lineages arising in the Miocene and Pliocene. Unfortunately, the fossil record is currently too incomplete to provide unambiguous answers.

In sum, although spatial patterns of speciation and extinction must ultimately dictate the number of species on the planet, contemporary diversity gradients may not all derive from a single evolutionary process or from a uniform response of all major taxonomic groups to the Earth's history. Contemporary patterns of bird and mammal species richness reflect different phylogeographical histories, yet display remarkable geographical congruence at the global scale. Current climate almost certainly has a role to play in this congruence, although underlying mechanisms remain elusive. We conclude that richness patterns reflect complex integrated influences of past and present climates over evolutionary and ecological timescales. Logically, future climate will also have a major impact, which virtually all ecologists and biogeographers realize.

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REFERENCES

Algar, A.C., Kerr, J.T. & Currie, D.J. (2009) Evolutionary constraints on regional faunas: whom, but not how many. *Ecology Letters*, **12,** 57–65.

Alroy, J. (1999) The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. *Systematic Biology*, **48,** 107–118.

Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31,** 8–15.

Avise, J.C. & Johns, G.C. (1999) Proposal for a standardized temporal scheme of biological classification for extant species. *Proceedings of the National Academy of Sciences USA*, **96,** 7358–7363.

Barker, F.K., Cibois, A., Schilker, P., Feinstein, J. & Cracraft, J. (2004) Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences USA*, **101,** 11040–11045.

Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.D., Potts, R., Sues, H.-D. & Wing, S.L. (eds) (1992) *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. University of Chicago Press, Chicago, IL.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007) The delayed rise of present-day mammals. *Nature*, **446,** 507–512.

Browne, M. & Mels, G. (2000) *SYSTAT 10: statistics II*. SPSS, Chicago, IL.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.-A., Hawkins, B.A., McCain, C.M., Stephens, P.R. & Wiens, J.J. (2010) Phylogeny, niche conservatism, and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277,** 2131–2138.

Chiappe, L.M. & Dyke, G.J. (2002) The Mesozoic radiation of birds. *Annual Review of Ecology and Systematics*, **33,** 91–124.

Clarke, J.A., Tambussi, C.P., Noriega, J.I., Erickson, G.M. & Ketcham, R.A. (2005) First definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature*, **433,** 305–308.

Currie, D.J. & Francis, A.P. (2004) Regional versus climatic effect on taxon richness in angiosperms: reply to Qian and Ricklefs. *The American Naturalist*, **163,** 780–785.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7,** 1121–1134.

Davies, T.J., Fritz, S.A., Grenyer, R., Orme, C.D.L., Bielby, J., Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., Gittleman, J.L., Mace, G.M. & Purvis, A. (2008) Phylogenetic trees and the future of mammalian biodiversity. *Proceedings of the National Academy of Sciences USA*, **105**(Suppl. 1)**,** 11556–11563.

Davis, K.E. (2008) *Reweaving the tapestry: a supertree of birds*. PhD Thesis, University of Glasgow, UK.

Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80,** 1–25.

Fain, M.G. & Houde, P. (2004) Parallel radiations in the primary clades of birds. *Evolution*, **58,** 2558–2573.

Fitch, W.M. (1976) Molecular evolutionary clocks. *Molecular evolution* (ed. by F.J. Ayala), pp. 160–178. Sinauer, Sunderland, MA.

Forster, J.R. (1778) *Observations made during a voyage round the world, on physical geography, natural history, and ethnic philosophy*. G. Robinson, London.

Francis, A.P. & Currie, D.J. (1998) Global patterns of tree species richness in moist forests: another look. *Oikos*, **81,** 598–602.

Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, **161,** 523–536.

Grenyer, R., Orme, C.D.L., Jackson, S.E., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.-S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature*, **444,** 93–96.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C. & Yuri, T. (2008) A phylogenetic study of birds reveals their evolutionary history. *Science*, **320,** 1763–1768.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84,** 3105–3117.

Hawkins, B.A., Diniz-Filho, J.A.F. & Soeller, S.A. (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. *Journal of Biogeography*, **32,** 1035–1042.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, **33,** 770–780.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007) Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, **170,** S16–S27.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163,** 192–211.

von Humboldt, A. (1808) *Ansichten der Natur mit wissenschaftlichen Erläuterungen*. J.G. Cotta, Tübingen.

Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314,** 102–106.

Jansson, R. & Davies, T.J. (2008) Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecology Letters*, **11,** 173–183.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5,** e157.

Kerr, J.T. & Currie, D.J. (1999) The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience*, **6,** 329–337.

Kielan-Jaworowska, Z., Cifelli, R.L. & Luo, Z.-X. (2004) *Mammals from the age of dinosaurs: origins, evolution, and structure*. Columbia University Press, New York.

Krug, A.Z., Jablonski, D., Valentine, J.W. & Roy, K. (2009) Generation of Earth's first-order biodiversity pattern. *Astrobiology*, **9,** 113–124.

Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67,** 325–333.

McGill, B. (2003) Strong and weak tests of macroecological theory. *Oikos*, **102,** 679–685.

McGlone, M.S. (1996) When history matters: scale, time, climate and tree diversity. *Global Ecology and Biogeography Letters*, **5,** 309–319.

McKenna, M.C. & Bell, S.K. (1997) *Classification of mammals above the species level*. Columbia University Press, New York.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10,** 315–331.

Monroe, B.L., Jr & Sibley, C.G. (1993) *A world checklist of birds*. Yale University Press, New Haven, CT.

Musser, G.G. & Carleton, M.D. (2005) Superfamily Muroidea. *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn (ed. by D.E. Wilson and D.M. Reeder), pp. 894–1531. Johns Hopkins University Press, Baltimore, MD.

Orme, C.D.L., Davies, R.G., Burgess, M., Eogembrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature*, **436,** 1016–1019.

Prinzing, A., Ozinga, W.A. & Durka, W. (2004) The relationship between global and regional distribution diminishes among phylogenetically basal species. *Evolution*, **58,** 2622–2633.

Qian, H. & Ricklefs, R.E. (2004) Taxon richness and climate in angiosperms: is there a globally consistent relationship that precludes region effects? *The American Naturalist*, **163,** 773–779.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7,** 1–15.

Scotland, R.W. & Sanderson, M.J. (2004) The significance of few versus many in the tree of life. *Science*, **303,** 643.

Sechrest, W., Brooks, T.M., de Fonseca, G.A.B., Konstant, W.R., Mittermeier, R.A., Purvis, A., Rylands, A.B. & Gittleman, J.L. (2002) Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences USA*, **99,** 2067–2071.

Shipley, B. (2002) *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge.

Sibley, C.G. & Ahlquist, J.E. (1990) *Phylogeny and classification of birds: a study in molecular evolution*. Yale University Press, New Haven, CT.

Sibley, C.G. & Monroe, B.L., Jr (1990) *Distribution and taxonomy of birds of the world*. Yale University Press, New Haven, CT.

Vaughan, T.A. (1986) *Mammalogy*, 3rd edn. Saunders College Publishing, Philadelphia, PA.

Wallace, A.R. (1876) *The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface*. Harper, New York.

Webb, S.D. (2006) The Great American Interchange: patterns and processes. *Annals of the Missouri Botanical Garden*, **93,** 245–257.

Weir, J.T. & Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates in birds and mammals. *Science*, **315,** 1574–1576.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28,** 453–470.

Wiens, J.J. (2007) Global patterns of species richness and diversification in amphibians. *The American Naturalist*, **170,** S86–S106.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, **19,** 639–644.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist*, **168,** 579–596.

Wiens, J.J., Sukumaran, J., Pyron, R.A. & Brown, R.M. (2009) Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution*, **63,** 1217–1231.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. & Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13,** 1310–1324.

Wiens, J.J., Pyron, R.A. & Moen, D.S. (2011) Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecology Letters*, **14,** 643–652.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, **34,** 273–309.

Wilson, D.E. & Reeder, D.M. (eds) (2005) *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Johns Hopkins University Press, Baltimore, MD.

Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 66–74. University of Chicago Press, Chicago, IL.

Zhou, Z. (2007) *Cretaceous bird radiation*. AccessScience, McGraw-Hill Co. Available at: http://www.accessscience.com.

SUPPORTING INFORMATION

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

Appendix S1 Basal and derived families of birds and mammals used to examine diversity gradients of groups originating before and after the Eocene–Oligocene climate shift.

Appendix S2 Geographical patterns of mean root distance (MRD_F) for mammal species using seven classification systems generated by assigning family rank to all currently extant clades at seven, 10-Myr time periods, ranging from 20 to 80 Ma.

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BIOSKETCH

Our Niche Conservatism and Diversity Gradients Working Group is composed of a set of ecologists, biogeographers and phylogeneticists who share an interest in understanding how evolutionary mechanisms interact with ecological processes to generate species richness gradients across spatial and temporal scales.

Author contributions: B.A.H. conceived the idea during the working group discussions; analyses were conducted by B.A.H. and J.D.; B.A.H. C.M.M. and J.D. led the writing; and all participants contributed throughout the process during working group and draft discussions.

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