

Research

Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals

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Phylogenetic diversity (PD) captures the shared ancestry of species, and is increasingly being recognized as a valuable conservation currency. Regionally, PD frequently covaries closely with species richness; however, variation in speciation and extinction rates and/or the biogeographic history of lineages can result in significant deviation. Locally, these differences may be pronounced. Rapid recent speciation or high temporal turnover of lineages can result in low PD but high richness. In contrast, rare dispersal events, for example, between biomes, can elevate PD but have only small impact on richness. To date, environmental predictors of species richness have been well studied but global models explaining variation in PD are lacking. Here, we contrast the global distribution of PD versus species richness for terrestrial mammals. We show that an environmental model of lineage diversification can predict well the discrepancy in the distribution of these two variables in some places, for example, South America and Africa but not others, such as Southeast Asia. When we have information on multiple diversity indices, conservation efforts directed towards maximizing one currency or another (e.g. species richness versus PD) should also consider the underlying processes that have shaped their distributions.

Keywords: evolutionary history; conservation; diversification; Great American Interchange; megafaunal extinction

1. INTRODUCTION

Recent efforts have provided us with an increasingly nuanced understanding of the relationship between biodiversity, ecosystem function and ecological stability [1–6]; however, at the same time, there is mounting evidence that we are losing elements of biodiversity at a rapid rate [7,8]. There is, therefore, increasing pressure to identify conservation priorities to maximize returns on limited conservation dollars (e.g. [9,10]). While there is general consensus (at least in the scientific community) that urgent action is essential, there remains debate regarding the currency that should be maximized, complicating conservation efforts [11,12]. There is a bewildering array of diversity metrics from which to choose (see [13,14]), each considering different and sometimes only marginally overlapping aspects of biodiversity (e.g. [12,15–17]). At large geographical scales, diversity is most commonly described using metrics that maximize the sum of some conservation unit—typically counts of total species richness or endemism, and areas of high conservation value have been termed biodiversity hotspots [9,18]. At finer, ecological,

scales, diversity indices might also consider the representation of species, for example, by accounting for variation in abundances (e.g. Shannon–Weiner index, Simpson’s index, Pielou’s index; see [19]). Recently, much emphasis has been placed upon the link between diversity and ecosystem function [6,20], valuing the services that intact ecosystems provide (e.g. water purification, erosion control or crop pollination). Because it is difficult to partition contribution to ecosystem services across multiple habitats and biomes, at larger spatial scales, counting species remains the most common approach to quantifying diversity, and even then there remain many challenges (see [21]). However, if we assume that more closely related species are also more functionally similar, phylogenetic metrics can allow us to consider both richness and function simultaneously [22–25].

Phylogenetic diversity (PD) represents the summed branch lengths of the evolutionary tree connecting species within a set, frequently defined by geographical proximity [23,26]. While a completely sampled phylogeny depicts the evolutionary divergences between extant taxa, allowing us to reconstruct ancestral states and diversification rates, the sub tree includes only species within a given sample; hence not all diversification events are represented, but the evolutionary distances separating included taxa are preserved. Faith

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One contribution of 10 to a Theme Issue ‘Biogeography and ecology: two views of one world’.

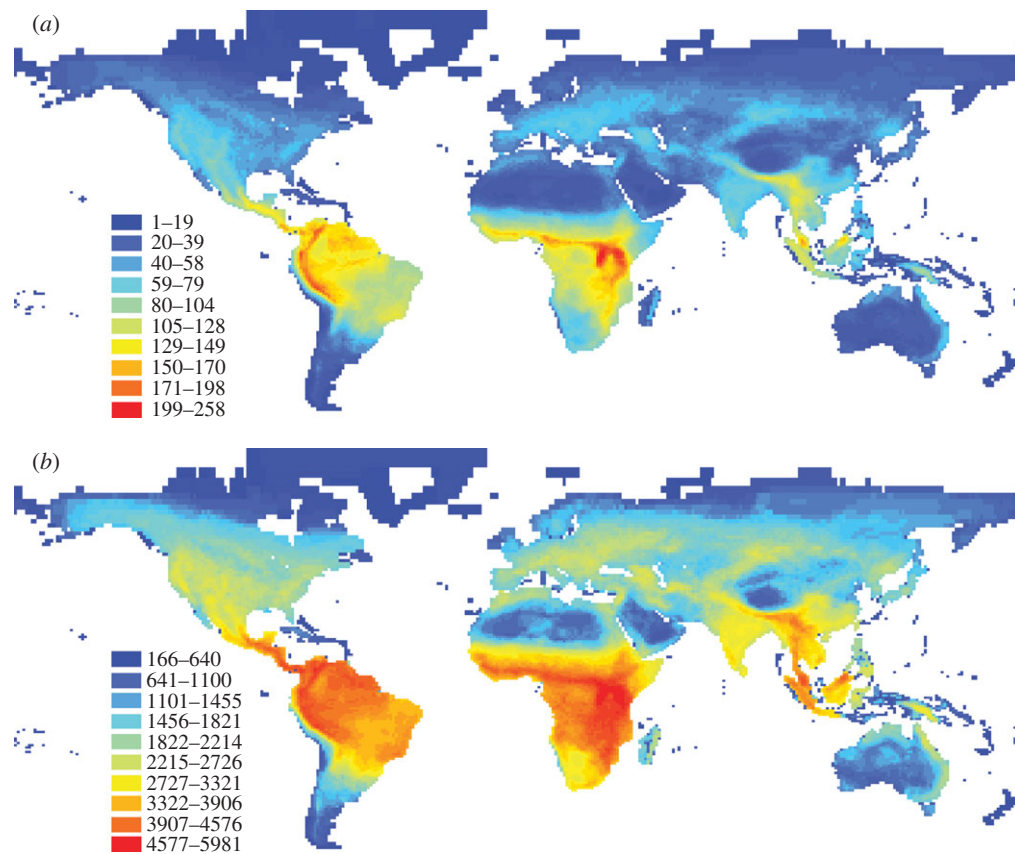


Figure 1. (a) Mammal species richness and (b) mammal phylogenetic diversity (millions of years). Data are depicted divided into 32 classes using natural breaks.

[23] was perhaps the first to describe explicitly the utility of PD for conservation, but Crozier [25] and Vane-Wright *et al.* [22] were also to publish related concepts contemporaneously, perhaps precipitated by the increasing availability of phylogenetic data made possible through advances in molecular sequencing technology [27]. As ecologists have been aware since Darwin, closely related species tend, on average, to share similar physiologies and ecologies as a consequence of their shared evolutionary histories [28], although their relative abundances and range distributions might differ. As a result, two species separated by a short evolutionary distance may perform similar ecosystem functions and provide similar ecosystem services. Therefore, if we wish to maximize functional or feature diversity, one approach would be to maximize the preservation of PD [23,25]. In addition, PD offers a number of advantages over simple species-richness counts; for example, it can be useful when the taxonomy of a clade is poorly understood or species are difficult to identify and, as a corollary, it is less biased by taxonomic revisions [29,30]. In most instances, phylogeny reconstruction will still rely upon appropriate taxonomic sampling [31], new metagenomics approaches do away with even this constraint [32]. The loss of PD, quantified in millions of years, provides a resonant symbol of the current biodiversity crisis [33]. Finally, PD might be particularly sensitive to the addition of non-native species to a local flora or fauna. For example, if invasive species are only distantly related to natives, they would add significantly to total PD, perhaps indicating large ecosystem effect. Evidence suggests that non-natives

grasses less related to natives are more invasive [34]. Hence, we might be concerned with both the loss and gains of PD.

Although the justifications for considering PD have been made strongly (e.g. [23,35–37]), it typically covaries closely with species richness at regional to global scales, and conservation decision making based on richness or PD might be largely indistinguishable [38]. However, empirical studies have shown that the relationship between PD and richness can vary biogeographically, probably reflecting differences in patterns of diversification and migration (e.g. [39]). Here, we consider the global distribution of PD for terrestrial mammals relative to species-richness patterns as a way to illustrate the different perspectives on diversity (figure 1). Previous work has shown that, like mammal species richness, mammal PD is unevenly distributed across the globe [17,40], and that hotspots of species richness might capture more PD than expected by chance [41,42]. However, our understanding of the underlying mechanisms that were important in shaping the distribution of PD versus species richness remains rudimentary. We predict that regions where speciation has been rapid and immigration rare will tend to have low PD relative to species richness, but where diversification has been slow and long-distant immigrations frequent, regions will tend to have high relative PD. Here, we deconstruct the global gradients in mammal species richness and PD. First, we describe the contribution of ancestral lineages to the structuring of contemporary species-richness gradients. Second, we develop a simple model describing the relationship

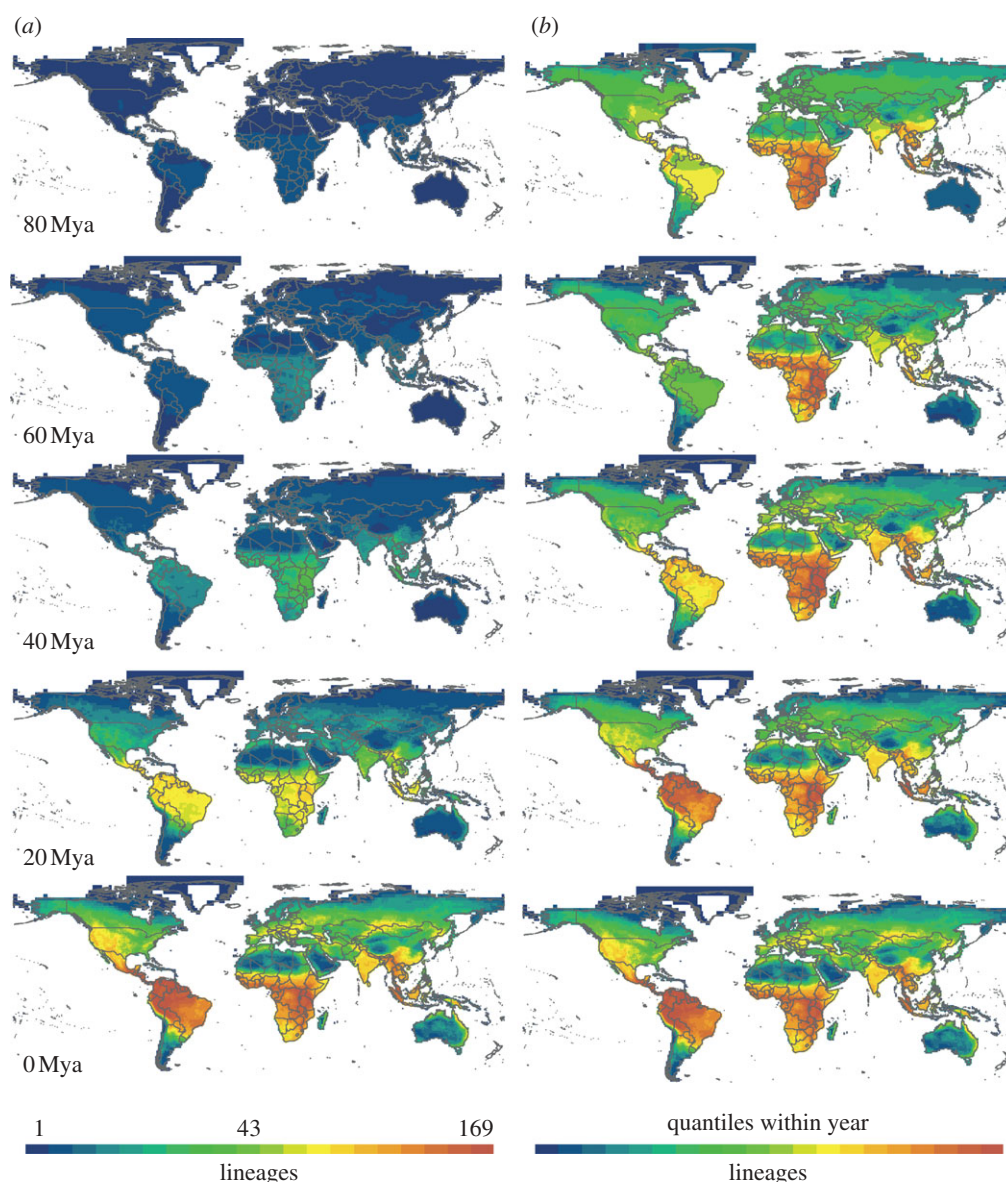


Figure 2. Local lineage through time plots depicts the accumulation of mammal lineages since 80 Mya. Data are depicted (a) divided into 20 quantiles across all age classes and (b) divided into 20 quantiles within each age class.

between environment and diversification, and use it to help explain the disparity in the distributions of PD and species richness. We discuss the implications of our results on the utility of PD as a currency for conservation biology.

2. THE PHYLOGENETIC DEPTH OF PRESENT-DAY DIVERSITY GRADIENTS

Global hotspots of species richness and endemism have been well characterized (e.g. [9,18,43]), and typically environment–richness models explain spatial variation in species richness well (frequently of the order of 70–90% [44]). However, the relationship between the environment and species richness varies between biogeographic regions, indicating that historical factors, such as dispersal events and local speciation and extinction regimes were probably important in shaping the environment–richness relationship [45–49]. These historical factors should be apparent in the phylogenetic relationships among extant species ([50], T. J. Davies

& L. B. Buckley 2011, unpublished data), and will therefore also shape the geographical distribution of PD. To illustrate the phylogenetic depth of present-day diversity gradients, we determined the richness of ancestral lineages at various time slices through a recent, dated phylogenetic tree for mammals [51]. Importantly, the richness of ancestral lineages does not necessarily correspond to historical richness of standing diversity, but simply represents the number of lineages within each time slice that are direct ancestors to the extant species within the region. For example, South American diversity might have matched closely African diversity over evolutionary time, but the richness of lineages ancestral to extant diversity at various time slices may differ because many South American lineages were lost during the megafaunal extinction at the end of the last ice age (*ca* 15 000–10 000 years ago) [52,53], whereas fewer megafaunal extinctions occurred in Africa [54].

Using an equal area (100 × 100 km) grid, we plot the richness of ancestral lineages through time for the sub tree representing the set of species in each cell (figure 2).

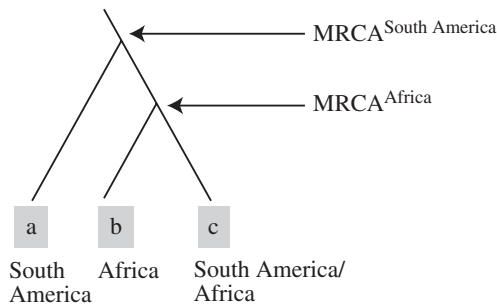


Figure 3. Phylogenetic tree connecting three taxa (a, b and c), with distributions in South America (taxon a), Africa (taxon b) and across both regions (taxon c), respectively. For this set of taxa, the most recent common ancestor (MRCA) for the South American regional species pool ($MRCA^{\text{South America}}$) is older (further toward the root of the tree) than the African species pool ($MRCA^{\text{Africa}}$).

Regions for which the phylogenetic tree of local fauna includes many early diverging lineages are predicted to have high relative PD. Because most modern mammals can be traced back to just a few lineages older than 80 Mya (i.e. representing the stem groups for monotremes, marsupials and the early splits within Placentalia, including Euarchontoglires (rodents and primates), Laurasiatheria (bats, horses and carnivores), Xenarthra (anteaters and sloths) and Afrotheria (elephants and elephant shrews)), we focus upon more recent diversification. We show extant species in tropical Africa can be traced back to multiple ancestral lineages deep in the phylogenetic tree, with divergence time greater than 60 Mya, whereas richness of ancestral South American tropical lineages only approaches that of tropical Africa and Asia, when we consider more recent divergences, within the last 20 Mya. Lineage richness at high latitudes remains low through to the present day. Because the local phylogenies do not sample diversity for the entire clade, they capture information on both variation in migration and diversification (speciation and extinction). For example, the most recent common ancestor of a species within South America might have a non-South American distribution (figure 3). Hence, the presence of many old divergences might represent either ancient speciation or multiple immigration from disparate clades. A preponderance of young divergences is most probably explained by recent *in situ* speciation, although it remains possible that co-immigration of multiple species from one or a few clades might also generate similar patterns—as may have occurred during the Great American Interchange [52], discussed below.

(a) Local lineages through time

To better compare the relative richness of ancestral lineages between the Old and New World, we generate local lineage through time (LLTT) plots for each region (figure 4). As described above, these plots represent the ancestors of the extant species within the region, irrespective of the true geographical origins for the clade. Because immigrating lineages will always have deeper evolutionary links that connect them with indigenous fauna, it is difficult to detect the signal of migrations directly from the LLTT

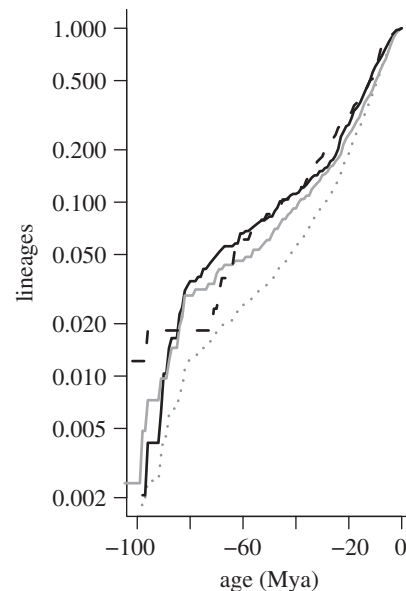


Figure 4. The number of regional lineages through time plotted as a proportion of total lineages summed across a continent and globally. Dotted line, global; black solid line, Africa; grey solid line, South America; dashed line, Australia.

plots—i.e. a recent migration will result in the addition of an old ancestral lineage if there are currently no close relatives of the immigrating lineages in the native biota. Nonetheless, rapid diversification may succeed invasion because new environments make available new ecological opportunities [55], as exemplified by the adaptive radiation of honeycreepers (Drepanididae) and *Drosophila* in Hawaii following their initial invasion and establishment [56]. Therefore, we might still expect to detect increases in regional diversification coincident with major immigration events. However, the LLTT plots illustrate that the accumulation of lineages through time for Africa and South America is approximately linear on a log scale between approximately 80 and 25 Mya (figure 4), suggesting that the more ancient immigration events that determined the global distribution of major mammal clades left little impression on rates of lineage accumulation, at least for lineages ancestral to extant clades.

Contrasting with patterns deeper in time, we find a significant acceleration in diversity curves for both South America and Africa within the last 25 Mya (support for fitting a breakpoint in LLTT plots for Africa at approx. 24 Mya; $\Delta AIC = -278.451$, and South America at approx. 28 Mya; $\Delta AIC = -208.755$). If long-distant dispersal is rare relative to speciation, we might predict a greater proportion of relatively recent evolutionary splits will represent *in situ* diversification, consistent with the recent steepening of the LLTT slopes, an expectation from complete phylogenetic trees [57,58]. We also observe that the slope of lineage accumulation from 80 Mya until Present for South America is significantly different from the corresponding slope for Africa ($\Delta AIC = -111.924$ for comparison of regression models with and without fitting separate LLTT slopes for Africa and South America), consistent with a more rapid recent diversification of lineages that

is thought to have accompanied the uplift of the Andes from approximately 25 Mya [59], and more recently following the formation of the Isthmus of Panama and the Great American Interchange [52].

By exploring the phylogenetic depth of the gradient in species richness, we can help unravel the complex history of speciation, extinction and migration that shaped the present-day distribution of biodiversity. The presence of old lineages might be attributed to ancient diversification or migration. We suggest the more parsimonious explanation for high richness of old lineages is old diversification, as found for Africa, whereas the lower richness of old lineages in South America might be a product of extinction and/or long-distance dispersal of lineages that had already diversified elsewhere. Evidence from the fossil record indicates that both extinction and immigration were probably important in shaping South American biodiversity, for example, immigration and diversification of the sigmodontine rodents (more than 300 species) following the formation of the Isthmus of Panama [52,60], and the extinction of many large-bodied mammals during the Quaternary megafaunal extinction event at the end of the last glacial period [52,53]. Irrespective of mechanism, our analysis of the richness of old lineages helps explain some of the mismatch between hotspots of species richness and hotspots of PD. In particular, where there are few old lineages, there will be proportionately less unique (unshared) evolutionary history captured by lineages towards the tips of the tree. Next, we consider the processes that have shaped the distribution and diversity of young lineages.

3. DIVERSITY AND DIVERSIFICATION

Many hypotheses have been proposed to explain the uneven distribution of species richness (e.g. Palmer [61] recognizes over 120). Explanations can be variously categorized, with ecological explanations linked to species coexistence and assembly rules, the focus at finer spatial scales, and biogeographic processes, including species–area relationships and environment–richness gradients, the focus at larger regional scales [21]. Here, we consider evolutionary explanations, which fall into two broad classes, (i) a longer time for speciation [62–64], and (ii) faster net diversification (speciation–extinction) [65,66]. Without detailed phylogenetic data, these two explanations are largely indistinguishable. The strong correlation between species richness and environmental energy has been linked to evolutionary rates and diversification [65,67], but is also predicted by alternative models based on variation in environmental carrying capacity (see review by Willig *et al.* [68]). Furthermore, covariation among environmental variables makes differentiating between alternative models problematic. While more sophisticated analytical tools (e.g. [69]) have increased the precision with which we have modelled the relationship between species richness and environment, they have generally only confirmed known patterns. However, detailed phylogenetic data allow net diversification rates to be estimated directly [57,58,70], and comparisons of

species richness between sister clades provide a robust model to evaluate the drivers of diversification [71].

In comparison with the wealth of data on models of species richness, the search for environmental correlates of diversification is just beginning. To date, results have been mixed, for example, Cardillo *et al.* [72,73] and Ricklefs [74] reported faster rates of diversification at lower latitude in birds, but Wiens *et al.* [75] reported no such correlation for hylid frogs, nor did Farrell & Mitter [76] for herbivorous insects. However, most such studies have focused on one or a few variables (i.e. latitude), and have not considered the geographical area a clade occupies. Larger areas are predicted to have higher speciation rates and lower extinction rates because larger areas can support larger population sizes and provide greater opportunity for allopatric speciation [77,78]. Area by far explains the most variation in diversification models for plants [79–81], but significant additional variation in rates is explained by environmental energy [80,82].

(a) *Predicting diversification rates from environment*

Using the phylogenetic tree for mammals from Bininda-Emonds *et al.* [51] and the 100 × 100 km grid described above along with mammal distribution data from Grenyer *et al.* [83], we develop a simple climate model explaining differences in species richness between sister clades. We characterize the mean annual climate for each cell using three key environmental variables that integrate abiotic and biotic factors: temperature, actual evapotranspiration (AET) and net primary productivity (NPP). Geographical Information Systems (GIS) layers for temperature (dataset A03; http://www.ngdc.noaa.gov/ecosys/ged_toc.shtml; mean monthly values, 1931–1960 [84]) and AET (dataset GNV183; <http://www.grid.unep.ch/data/>; mean monthly values 1920–1980 [85]) were derived from remote-sensing data at a resolution of 0.5° × 0.5°; for further details see Davies *et al.* [48]. The dataset for NPP (Global Production Efficiency Model; <http://www.glc.f.umd.edu/data/glopem/>; 1981–2000 [86,87]) is derived from the Advanced Very High Resolution Radiometer (AVHRR) images at a resolution of 8 km, in 10 day periods. For each node in the tree with total richness greater than 20, we calculate the contrast in species richness between sister clades as: $\log(n_1) - \log(n_2)$, where n_1 and n_2 are the species richness for the respective sister clades. Because sister clades are by definition the same age, contrasts in species richness reflect differences in net diversification rates [71]. Next, we estimated the geographical range of each clade by summing the union of occupied cells. Area was square root transformed prior to further analysis. For each of the three climatic variables, we estimated the weighted mean for the clade as: \bar{x}_{ij} , for climate variable x across the set of i species with occurrence in j cells. We then used regression through the origin [28] to model contrast in species richness against differences in environment including area.

Our modelling approach is a simple extension of independent contrasts but differs slightly from traditional approaches (e.g. phylogenetically independent contrasts

Table 1. Regression through the origin on contrasts in species richness, area and various environmental variables (model $p \ll 0.001$, model adjusted $r^2 = 0.65$, $^{**}p < 0.01$, $^{***}p < 0.001$).

predictor	coefficient	<i>t</i> -value	<i>p</i> -value
sqrt(area)	0.05	14.38	$< 2e-16^{***}$
temperature	0.01	2.80	0.01 **
AET	< 0.01	0.72	0.47
NPP	< 0.01	0.55	0.58
latitude	0.05	2.81	0.01 **

[88] and phylogenetic regressions [89–91]), because we estimate nodal values directly from the data on species' distributions, rather than assuming some model (typically Brownian motion) of evolutionary trait change. While our approach provides a straightforward and intuitive solution to the particularities of modelling species richness–environment relationships across phylogeny, it does not fully correct for non-independence of nested nodes; we therefore generated an equivalent model using only non-nested nodes to explore model sensitivity (appendix A). We use the full model (including all nodes) in subsequent analyses because we argue that it better encapsulates trends across the entire phylogeny, whereas considering only a subset of nodes might omit significant relationships; for example, maximizing the number of non-nested nodes constrains the model to relatively recent divergences, ignoring differences between earlier diverging clades.

As shown for flowering plants, geographical area is the strongest predictor of clade richness (table 1), but when we consider all nodes, climate is also important, with a highly significant positive relationship between species richness and temperature, also consistent with results for plants [80,82] and birds [74,92]. The full model explains 65 per cent of the variation in species richness between sister clades, approaching explanatory power of models for spatial gradients in species richness [44]. Variables that are expected to correlate most closely with biomass and, by extension, productivity (i.e. AET and NPP), were not significant. Interestingly, the residual relationship with latitude, quantified as degrees from the Equator, is positive, indicating higher net diversification rates at higher latitudes, providing some corroboration for a recent study suggesting rapid species turnover at these latitudes [93]. Our results are consistent with a role for climate in mediating diversification, with greater clade richness in warmer but not necessarily more productive environments. Fast diversification would result in high species richness but low relative PD (i.e. short evolutionary branches separating species). Might climate-mediated diversification, therefore, help explain the residual mismatch between hotspots of species richness and hotspots of PD (figure 5a)?

(b) *The relationship between evolutionary rates and phylogenetic diversity*

That lineages have diversified at different rates in different biogeographic regions is widely appreciated,

and has been suggested as contributing towards the latitudinal gradient in species richness (reviewed in [66]). We have shown for mammals that environment is a significant predictor of evolutionary rates, even after correcting for area. If hotspots of species richness and endemism reflect regions that have been particularly conducive to speciation, then we might predict that they will tend to capture less PD than regions with similar numbers of species that diversified more slowly or originated elsewhere. Previous work has shown that Africa and Asia capture much PD even after correcting for species richness [17] (figure 5a), consistent with a long history of slow diversification as implied by the high richness of old lineages described above. In contrast, the equally speciose New World tropics is relatively phylogenetically depauperate (figure 5a). We suggest this is because much of present-day species richness (we do not consider here the diversity of lineages that were subsequently lost to extinction within the relatively recent evolutionary past) is a product of recent radiations within a few evolutionary disparate clades [52,60]. We illustrated above the relative paucity of old lineages; here, we explore geographical variation in diversification rates.

Using the model describing the relationship between climate and diversification rates, we derive a per-cell expectation of diversification rate (figure 5b). Although our model was derived from contrast analyses, model coefficients can be reliably estimated by forcing an intercept (see [94]). We did not include area in the model predictions because all cells are the same size. We show that diversification rates are predicted to be low in the Nearctic and Palaearctic biomes, reflecting low mean annual temperatures. Globally, tropical rates are predicted to be high, but with faster rates in the Neotropics, supporting evidence that they represent a speciation pump for many taxa (e.g. plants [95–97], insects [98,99], birds [73,100], fish and mammals [52,60], T. J. Davies & L. B. Buckley 2011, unpublished data). However, our model also predicts fast rates in Southeast Asia, which has a high richness of old lineages. In addition, the per-cell estimates of diversification rate correlate positively, albeit weakly, with high residual PD from a LOESS regression of PD against species richness (figure 5; see [17]; $r = 0.18$, $p < 0.001$ and $p = 0.4$ adjusting degrees of freedom to account for spatial autocorrelation [101]).

Why do we predict fast diversification in regions with both low and high PD? First, other factors linked to reproductive isolation, for example, topographical heterogeneity, are also probably important in influencing speciation rates. Second, our diversification rate model indicated that geographical area was by far the best predictor of rates; however, area was not included in grid-cell model predictions. It is likely that much of the variation in diversification rates is, therefore, explained by geographical area constraints that operate at larger scales than the grid-cell size of our analysis. The large contiguous landmass of South America may have provided greater opportunity for speciation or reduced probability of extinction, whereas the fragmented landmasses that comprise southern Asia and Australasia placed tighter limits on clade diversification. Third, it remains possible

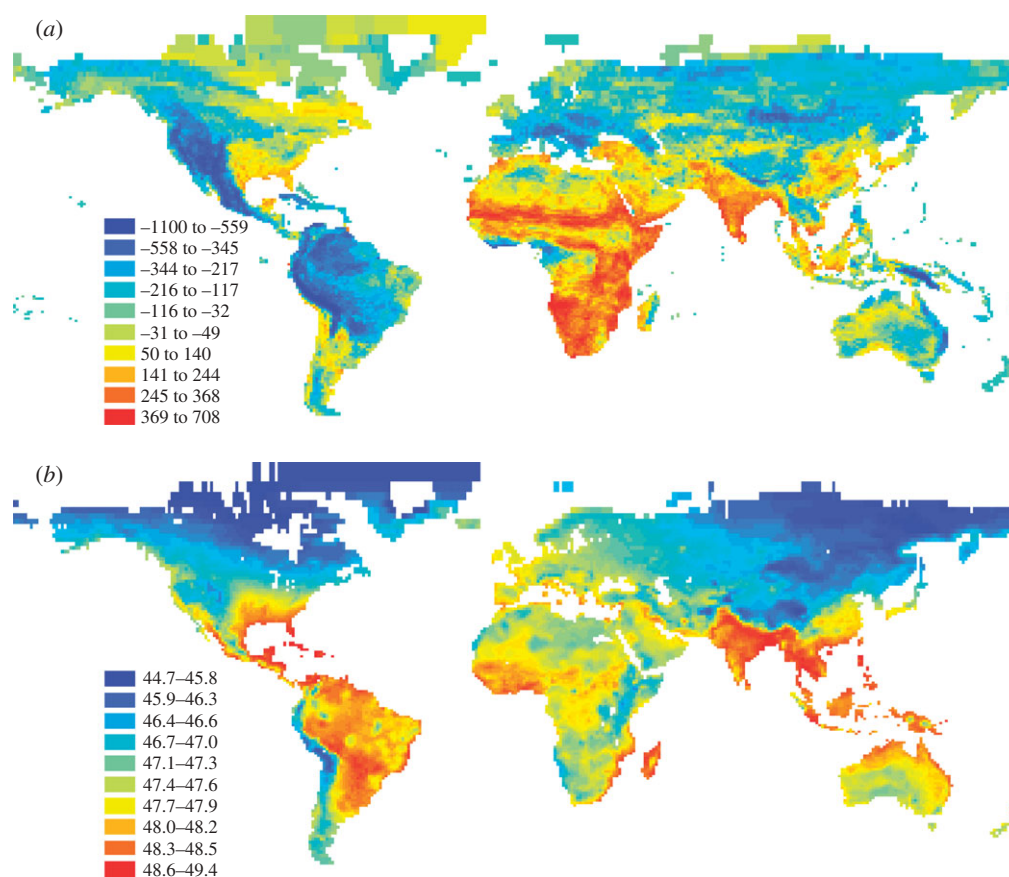


Figure 5. (a) Residuals (millions of years) from a LOESS regression of cell PD against cell species number, data from Davies *et al.* [17]; (b) Expected diversification from the model of species richness and environment using contrasts between sister clades (values are dimensionless, and represent relative rates, see text and table 1 for further details). Data are depicted divided into 32 classes using natural breaks.

that species' range shifts and migrations misalign our per-cell estimates of diversification to current richness patterns.

4. DISCUSSION

What can the distribution of mammal PD reveal about the evolutionary history of extant mammal richness? We show that PD is unevenly distributed in space, mirroring patterns observed for species-richness gradients, but while species richness and PD covary closely ($r = 0.98$), the latter exhibits a more diffuse distribution. The residual variation in PD after adjusting for species richness is more spatially complex, and provides insights into the historical processes by which contemporary species-richness gradients arose. Africa and Southeast Asia contain greater PD than predicted from species richness, while South America and western North America capture less PD than predicted from species richness. Using plots of the richness of ancestral lineages through time, we show that Africa has a greater diversity of old lineages, probably reflecting the early African origins of many major clades of extant mammals [102]. By contrast, South America shows low richness of old lineages, with tropical lineage diversity only approaching that for Africa within the last 20 Mya. We suggest the paucity of old lineages in the New World tropics is explained by the extra-tropical origins of clades that subsequently diversified

in South America following successive migration events and the formation of the Isthmus of Panama over the past few millions of years [52,60] and multiple extinctions from within a previously more diverse Quaternary mammal fauna composed of older radiations (e.g. ground sloths, giant armadillos and tapirs) towards the end of the Pleistocene [52,53]. We are fortunate in that the historical biogeography of modern mammals is relatively well understood. For less well-studied clades, our approach might help bring to the light previously undescribed biogeographic histories. However, additional data, for example, from the palaeontological record, would still be required to differentiate among alternative scenarios.

We used contemporary climate data and mammal distributions to develop a predictive model of clade diversification. Over the course of mammal evolution, climate has changed considerably, and current range distributions are unlikely to match those historically. Furthermore, multiple additional factors, including plate tectonics, topographic heterogeneity and biotic interactions, were also likely to have influenced the processes of speciation, extinction and migration over these long time periods. However, assuming some evolutionary conservatism in the climatic niche, which seems likely [103,104], species may track changing climates, so that the relationship between species distributions and environment is evolutionarily conserved (i.e. species within clades with tropical origins are likely to have

tropical distributions). Critically, if current distributions do not reflect past conditions or if other processes not included in our models were more important determinants of clade richness, the relationship between contemporary environment and clade diversification would probably be masked; hence our models are conservative. That we can explain approximately two-thirds of the variation in evolutionary rates suggests our approach is useful in helping understand present-day diversity gradients. We show that geographical area is by far the best predictor of diversification rates; nonetheless, we also find that rates have been faster in warmer climates, consistent with energy-diversification theory [65,67,80]. Our results contrast with some previous work in which no relationship between rates and latitude (which covaries closely with temperature) was detected (e.g. [75,76]). We suggest this discrepancy might in part be explained by the large contribution of geographical area to explanations for variation in diversification.

Fast diversification translates into short evolutionary distances between taxa; therefore, we suggest climate-driven rate variation might explain some of the additional residual variation in PD. We predict that where rates have been fast, species richness will be high but PD will be relatively low, and that this might explain low-residual PD observed for South America. We used the model coefficients describing diversification rate differences between sister clades to generate a map of expected diversification. Consistent with our predictions, we show South America to have high expected diversification from climate. In addition, we show that the expected diversification rates for Africa are lower than those for the New World, supporting a model of slow accumulation of diversity through evolutionary time. However, we also show fast expected rates in Southeast Asia and Oceania, which otherwise demonstrate phylogenetic trends more similar to Africa, with a high richness of old lineages and high residual PD. We suggest that variation in geographical area might also explain this apparent mismatch.

We have shown how phylogeny can help inform models of evolutionary and biogeographic histories that underlie present-day diversity gradients. Hotspots in species richness can be a product of either recent radiations or long times for speciation. By deconstructing the gradient in PD, we have illustrated how it is possible to differentiate between them. Critically, our analysis demonstrates that conservation strategies aimed at maximizing species richness may depart significantly from those aimed at preserving PD. Within the Neotropics, conservation efforts directed towards maximizing species richness are likely to be suboptimal for maximizing representation of PD. As illustration, consider two equally species-rich but evolutionary distinct clades; a phylogenetically informed approach would select one species from each clade to maximize representation of PD. However, if we consider only species richness, we are just as likely select two species from within the same clade, missing the internal phylogenetic branch lengths linking the two clades. By contrast, within the Old World tropics, species richness might provide a good surrogate for PD, and there is

likely to be less redundancy in the species required to capture ancestral lineages represented by deep branches in the phylogenetic tree; therefore richness-based conservation strategies may be sufficient. We suggest that because the evolutionary histories of local biotas differ regionally, so might the optimal conservation strategy. For example, in the Cape of South Africa, the flora of the eastern Cape has captured significantly greater PD than equal numbers of species from the western Cape [39]. The gain from considering PD as part of any conservation strategy is therefore relatively high in the eastern flora, but might not be worth the extra investment for the western flora.

While many challenges remain in accurately characterizing species diversity [21], the inclusion of phylogenetic information is providing additional insight into diversity gradients. Here, we demonstrate how phylogenetic information can be applied to infer the dynamics of diversity gradients through time. This dynamic perspective reveals limitations to conservation approaches aimed at maximizing PD. For example, immigrations of phylogenetically distinct species from other regions can dramatically enhance PD. By contrast, regions with rapid diversification and many species will tend to have low PD. Thus, a strategy to conserve areas with high PD might favour the conservation of areas experiencing biotic homogenization rather than *in situ* diversification. These spatial mismatches in patterns of species, functional and phylogenetic diversity are increasingly being documented (e.g. [105]). While theories for spatial scaling of species diversity are well established, analogous theory for PD is just emerging [106].

The dynamic perspective on diversity gradients explored here reflects regional scale diversification and movement in an environmental context over long timescales. Insights from regional scale PD differ from those derived by analysis of local community composition [107]. At local scales, patterns of phylogenetic over- and under-dispersion are frequently used to infer ecological processes structuring community composition; for example, competition or environmental filtering [108]. Recent efforts have moved towards incorporating evolutionary history within diversity metrics relevant at ecological scales [21,109,110]. While PD is complementary to other species' diversity metrics [21], applying PD to inform local conservation strategies can be problematic. For example, should a functionally similar, phylogenetically clustered community in a stressful local environment receive a lower conservation priority than an over-dispersed community in a stable environment? Might preserving the phylogenetic structure of a community be an important conservation goal, irrespective of total PD or phylogenetic dispersion? Our analysis suggests that phylogenies can be effectively applied to infer the temporal dynamics of diversity gradients at biogeographic scales. Such a phylogenetically informed biogeographic perspective may be an important component of integrated conservation strategies considering the taxonomic, functional and phylogenetic components of diversity. Merging these various components across biogeographical and ecological scales will be a future challenge [21].

We thank D. Jenkins and R. Ricklefs for the invitation to contribute to this volume, and the International Biogeography Society for supporting the *Biogeography and Ecology—two lenses in one telescope* symposium.

APPENDIX A

Regression through the origin on contrasts in species richness, area and various environmental variables, non-nested nodes (all included sister contrasts have a divergences time less than 20 Mya). Model $p \ll 0.001$, model-adjusted $r^2 = 0.74$, $***p < 0.001$.

predictor	coefficient	t-value	p-value
sqrt(area)	0.04	7.36	$< 2e-16^{***}$
temperature	0	-0.69	0.50
AET	0	1.88	0.07
NPP	0	-0.89	0.38
latitude	0.03	1.00	0.33

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