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Exploring the phylogenetic history of mammal species richness

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ABSTRACT

Aim At broad geographical scales, species richness is a product of three basic processes: speciation, extinction and migration. However, determining which of these processes predominates is a major challenge. Whilst palaeontological studies can provide information on speciation and extinction rates, data are frequently lacking. Here we use a recent dated phylogenetic tree of mammals to explore the relative importance of these three processes in structuring present-day richness gradients.

Location The global terrestrial biosphere.

Methods We combine macroecological data with phylogenetic methods more typically used in community ecology to describe the phylogenetic history of regional faunas. Using simulations, we explore two simple phylogenetic metrics, the mean and variance in the pairwise distances between taxa, and describe their relationship to phylogenetic tree topology. We then use these two metrics to characterize the evolutionary relationships among mammal species assemblages across the terrestrial biome.

Results We show that the mean and variance in the pairwise distances describe phylogenetic tree topology well, but are less sensitive to phylogenetic uncertainty than more direct measures of tree shape. We find the phylogeny for South American mammals is imbalanced and ‘stemmy’ (long branches towards the root), consistent with recent diversification within evolutionarily disparate lineages. In contrast, the phylogeny for African mammals is balanced and ‘tippy’ (long branches towards the tips), more consistent with the slow accumulation of diversity over long times, reflecting the Old World origin of many mammal clades.

Main conclusions We show that phylogeny can accurately capture biogeographical processes operating at broad spatial scales and over long time periods. Our results support inferences from the fossil record – that the New World tropics are a diversity cradle whereas the Old World tropics are a museum of old diversity.

Keywords

Diversification, latitudinal diversity gradient, migration, phylogeny, species richness.

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INTRODUCTION

Diversity tends to peak in tropical (warm and wet) climates and tapers towards the poles, generating a latitudinal gradient in species richness. At broad geographical scales there is high congruence in species richness among disparate clades, from birds and mammals to plants and amphibians (Currie, 1991; Grenyer *et al.*, 2006). The ubiquity of the latitudinal diversity gradient suggests a common process, and there has been much specula-

tion with regard to casual mechanisms (e.g. see reviews by Willig *et al.*, 2003 and Mittelbach *et al.*, 2007). In 1974 the botanist G. L. Stebbins (Stebbins 1974) first posed the question of whether the tropics represent a cradle of diversity (faster rates) or a museum of diversity (longer time and lower extinction) – the answer is still being debated. The increasingly availability of phylogenetic data has generated renewed interest in historical explanations and, in particular, whether regional richness can be explained by the length of time of occupancy (Wiens &

Donoghue, 2004) – the time for speciation effect (Pianka, 1966) – versus faster rates of diversification linked to greater environmental energy (Davies *et al.*, 2004; Allen *et al.*, 2006) – the evolutionary rates theory (Rohde, 1992).

Evaluating historical explanations using information on present-day diversity patterns is challenging. For clades with a good fossil record, such as marine bivalves, palaeontological data can provide georeferenced estimates of extinction and speciation rates through time (e.g. Jablonski *et al.*, 2006). However, for taxa with poor or sporadic fossil records, as is the case for most taxa, even large-bodied groups such as terrestrial mammals, we are, at best, restricted to estimating global accumulation curves (e.g. Alroy, 2000), or exploring trends over only the relatively recent past (i.e. tens of thousands to hundreds of thousands of years; e.g. FAUNMAP, http://gcmd.nasa.gov/records/GCMD_Faunmap.html). Nonetheless, present-day diversity can still provide insights into historical processes. One approach has been to contrast predictors of species richness between regions with different biogeographical histories but similar current climates (e.g. Qian & Ricklefs, 2000). An alternative approach is to include data from historical climate models in models exploring variation in diversification rates, assuming the recent past can be extrapolated over evolutionary time-scales (e.g. Jansson & Davies, 2008; Davies *et al.*, 2011). Although such methods might suggest different regions have been shaped by different evolutionary histories, they do not directly evaluate evolutionary dynamics, and remain broadly correlative in approach. Here we develop a novel approach using information on the evolutionary relationships among regional species assemblages.

A sophisticated set of phylogenetic metrics has been developed to infer the evolutionary history of clades (e.g. see Purvis, 1996; Mooers & Heard, 1997). More recently, there has been increasing interest in the utility of phylogenetic methods in community ecology (e.g. see Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Vamosi *et al.*, 2009), and a separate set of metrics has been developed to help unravel the processes structuring ecological communities (see Webb *et al.*, 2002; Kembel, 2009). To date, progress in interpreting regional patterns has lagged (but see Heard & Cox, 2007), and regional studies have been largely limited to mapping the distribution of phylogenetic diversity [e.g. in mammals (Sechrest *et al.*, 2002; Schipper *et al.*, 2008) and flowering plants (Forest *et al.*, 2007)]. Here we aim to help fill this gap. We combine methods developed for analysing the phylogenetic structure of clades with those for describing the structure of ecological communities to explore regional diversity patterns for terrestrial mammals.

Regional diversity is a product of speciation, extinction and migration. Recent studies have demonstrated that distinguishing between alternative models of speciation and extinction regimes using phylogeny is challenging (e.g. Rabosky, 2009; Fitz-John, 2010; Rabosky & McCune, 2010). Attempting to estimate extinction or speciation from an incomplete phylogeny, such as that representing a regional species pool, where migration has also shaped species membership, is likely to be very difficult, if not impossible. Nonetheless, we can still make strong a priori

hypotheses on the expected phylogenetic structure of regional assemblages using our knowledge of mammalian historical biogeography. We use the practically complete dated phylogenetic tree for mammals from Bininda-Emonds *et al.* (2007) to evaluate the structure of regional phylogenies. We focus on three aspects of phylogenetic tree shape: tree depth (the age of the most recent common ancestor for the set of species), tree imbalance (differences in diversity between sister clades) and tree ‘stemminess’ [the distribution of branch lengths from the root to the tips of the phylogeny as an indicator of the timing of the evolutionary diversification of a given set of species; see Rohlf *et al.* (1990) and Mooers *et al.* (2007)]. However, because mammalian phylogeny is incompletely resolved (46.7% resolved compared with a fully bifurcating tree), direct measures of tree imbalance and stemminess are unreliable. Therefore, we extend one well-defined metric from the community phylogenetics literature – the pairwise phylogenetic distances between community members (see Webb *et al.*, 2002; Kembel, 2009) – to characterize tree structure. First, we use simulations to describe the relationship between tree shape and the mean and variance in pairwise phylogenetic distances (MPD and VPD, respectively). Second, we map the empirical distribution of MPD and VPD for mammals to compare with predictions from our understanding of mammalian biogeography.

As an illustration, we contrast patterns for Amazonia and central Africa. In South America, much of the extant diversity is thought to be a product of recent immigration and radiation, following the formation of the Isthmus of Panama and the Great American Biotic Interchange (Webb, 1976; Webb 2006). In contrast, mammalian diversity in Africa may have accumulated more gradually over a longer time (Davies *et al.*, 2008; Davies & Buckley, 2011). Assuming that immigrating lineages are evolutionarily distinct from the native fauna and recent *in situ* diversification, we predict the phylogeny for Amazonian fauna to be imbalanced and ‘stemmy’ (longer branches towards the root). In Africa, with relatively slower recent net diversification rates and fewer immigrating lineages, we predicted more balanced and ‘tippy’ (longer branches towards the tips) regional phylogenies.

METHODS

Traditional metrics of tree shape, such as Colless’ measure of imbalance (Colless, 1982) and Pybus & Harvey’s (2000) gamma statistic (γ), are sensitive to phylogenetic resolution (Fig. S1 in Appendix S1 in Supporting Information). We therefore explored alternative metrics derived from the community phylogenetics literature that describe the distribution of pairwise phylogenetic distances between tip taxa (Kembel, 2009): mean pairwise phylogenetic distance (MPD), and variance in pairwise phylogenetic distances (VPD).

Phylogenetic simulations

We used computer simulations implemented in R (<http://www.r-project.org>) to evaluate the relationship between tree

shape (depth, imbalance and stemminess) and the distribution of phylogenetic distances between species.

First, we generated 5000 ultrametric (all terminal nodes equidistant from the root) trees of various depths (root-to-tip distance) using a pure-birth model in which all lineages have an equal probability of diversifying (function `birthdeath.tree` in R package Geiger: $b = 0.04$, $d = 0$, `taxa.stop = 100`). We arbitrarily assumed the maximum likelihood birth (speciation) rate (b) for the crown group of mammals, estimated as $\ln(n/2)/t$, where n is the number of extant species and t is the age of the crown group; however, our results are not qualitatively affected by b (Fig. S2 in Appendix S1). By assuming a pure-birth model we constrain the likely range of tree balance and stemminess, but allow tree depth to vary. For consistency, we used a constant tree size, $n = 100$, approximating the diversity of mammals within a moderately species-rich $1^\circ \times 1^\circ$ cell. We consider the implications of relaxing this constraint of fixed tree size on estimates of MPD and VPD below.

Second, we generated a range of tree shapes to span empirical values of imbalance and stemminess using the following heuristic: 10,000 random branching topologies of size $n = 100$ were generated by randomly splitting edges (function `rtree` in R package `ape`). Branch lengths were assigned to each edge from a random uniform distribution (option `br = runif`). Trees were made ultrametric using nonparametric rate smoothing as implemented in R (function `chronogram` in R package `ape`). Last, trees were scaled to a unit depth (function `rescaleTree` in R package Geiger).

We characterized the topology of each tree using three commonly used metrics.

1. Tree depth, representing the total root-to-tip distance for the tree (i.e. tree age).
2. Branching symmetry using Colless' index of imbalance, I_c (Colless, 1982), estimated as the sum of absolute differences in species richness between sister clades at each internal node, which is the most commonly used imbalance metric (Mooers *et al.*, 2007). Although I_c can be sensitive to tree size, i.e. number of tips, our simulations are unbiased because we held species richness constant.
3. Tree 'stemminess' using Pybus & Harvey's (2000) gamma statistic (γ), to characterize the distribution of branching events within the tree (following Mooers *et al.*, 2007). Trees with $\gamma < 0$ have relatively longer inter-nodal distances towards the tips of the phylogeny (\approx tippy trees), whereas trees with $\gamma > 0$ have relatively longer inter-nodal distances towards the root of the phylogeny (\approx stemmy trees). Tippy trees would be consistent with an ancient radiation and a subsequent slow-down in diversification rates towards the present, whereas stemmy trees might reflect a recent radiation of evolutionary distinct lineages.

The latter two indices capture complementary axes of tree shape, although, for ultrametric trees, they are not independent – balanced trees tend to be more stemmy (Mooers, 2004).

For both sets of simulations, we generated a matrix of the pairwise phylogenetic distances between tip taxa on the phylogeny. We then calculated two summary statistics (MPD and VPD)

on this matrix, representing the mean and variance respectively (see also Webb *et al.*, 2002 and Kembel 2009). We take the square root of variance (equivalent to the standard deviation) so that both mean and variance scale linearly with tree depth.

Our simulations were parameterized so as to generate a range of tree shapes that reflected the distribution of empirical trees topologies. However, because tree space is very large, it remains possible that our simulated trees represent a particular biased subset. We therefore re-evaluated the relationship between MPD and VPD with I_c and γ on a set of 242 published phylogenetic trees from McPeck & Brown (2007). For the majority of trees branch lengths were present as the number of molecular substitutions. We therefore first transformed branch lengths to make trees ultrametric using penalized likelihood with $\lambda = 0$ (Sanderson, 2002). McPeck & Brown (2007) reportedly used the mean path lengths method of Britton *et al.* (2002); however, we found that the non-clock-like substitution rates evident in many of the trees resulted in negative branch lengths using this method.

Mapping MPD and VPD

The empirical distribution of MPD and VPD for mammals was calculated for a global grid at a resolution of $100 \text{ km} \times 100 \text{ km}$ using the database of mammalian distributions from Grenyer *et al.* (2006) and the complete species-level phylogenetic tree for mammals published by Bininda-Emonds *et al.* (2007). For each cell, we extracted the list of species with overlapping ranges, and pruned the mammal phylogeny to just this subset. We then derived the pairwise distances, in millions of years, between species from the pruned subtree. Cells with fewer than five species were excluded from the analysis. We map MPD and VPD rather than I_c and γ directly, because MPD and VPD are more robust (but, of course, still somewhat sensitive) to phylogenetic uncertainty (see Fig. S1 in Appendix S1). To explore broad regional patterns, we compare the per-cell estimates of MPD and VPD between Africa, South America and Australia. Although our focus is primarily on contrasting the Old World versus New World tropical biodiversity hotspots, we include Australia because it represents a unique, but relatively well-studied, phylogeographical outlier. To assess scale sensitivity, we also generate equivalent plots using World Wildlife Fund (WWF) ecoregions as the basic spatial unit.

Because tree depth can have a large influence on both MPD and VPD, we performed the following sensitivity analyses. First, we re-scaled trees to unit length and estimated MPD and VPD in units of relative time not directly comparable between cells. Second, we repeated the analysis but excluding the marsupials plus monotremes: the early divergence event between eutherians (placentals), metatherians (marsupials) and prototherians (monotremes) is likely to skew mean divergence times for cells in which two or more clades are represented (e.g. Australia and South America). Last, we evaluated the sensitivity of our metrics to variation in species richness. We generated a set of 1000 trees between size $n = 5$ and $n = 250$, matching variation in per-cell mammalian species richness across the globe, by selecting taxa

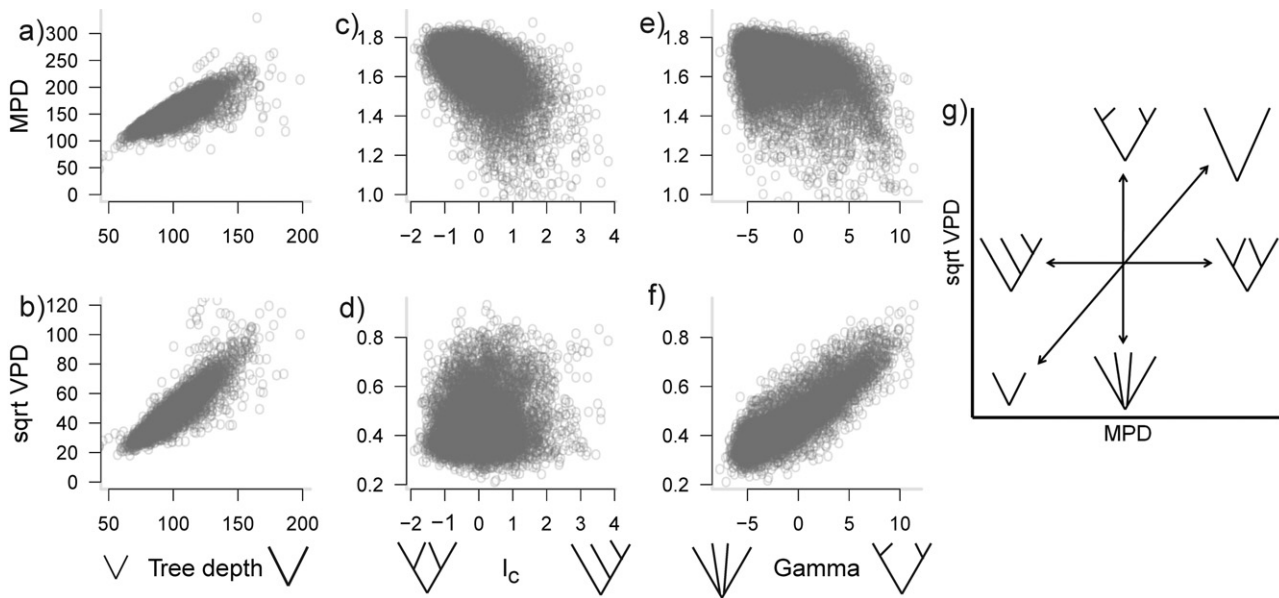


Figure 1 Mean and variance in phylogenetic distance (MPD and VPD, respectively) as a function of: (a, b) tree depth (total root-to-tip distance, my); (c, d) imbalance (I_c); and (e, f) stemminess (γ) for 5000 (a, b) and 10,000 (c–f) simulated trees. High VPD is indicative of old stemmy trees, whereas high MPD is indicative of old balanced trees (g).

at random from the complete mammalian phylogeny and extracting the minimum spanning trees connecting them. We then calculated MPD and VPD on each of the subtrees.

Environmental correlates of VPD and MPD

We test for a relationship between the distribution of the various tree-shape metrics and environment by regressing VPD and MPD with two key climate variables that typically correlate strongly with species richness: mean annual temperature and actual evaporation (AET) (Currie, 1991). We derived geographical information systems (GIS) layers for mean annual temperature (dataset A03; http://www.ngdc.noaa.gov/ecosys/ged_toc.shtml) and AET (dataset GNV183; <http://www.grid.unep.ch/data/>) from remote-sensing data at a resolution of $0.5^\circ \times 0.5^\circ$ following Buckley *et al.* (2010). We focus on these two variables because they link to two alternative mechanisms thought to be important in shaping species richness gradients. First, AET is closely linked to productivity and the biomass or carrying capacity (numbers of individuals and hence numbers of species) a region may be able to support (Currie, 1991; Willig *et al.*, 2003). Second, temperature is linked with evolutionary rates, for example, through variation in molecular substitution rates (Rohde, 1992) or, more generally, the metabolic theory of ecology (Brown *et al.*, 2004).

We construct separate linear and maximum-likelihood spatial autoregressive (SAR) models (R package *spdep*; Bivand, 2005) for MPD and VPD against temperature and AET to assess whether the relationship with environment differs between the two metrics. We implemented error-dependence models to account for spatial autocorrelation in the error term (Haining, 2003). Longitude and latitude were used to develop a neigh-

bourhood with a threshold distance of 2000 km, which was selected by examining correlograms. Neighbours were weighted a priori using row standardization, such that the weights of all neighbours within the threshold distance sum to 1 (Haining, 2003). To assess model sensitivity to neighbourhood distance, we also explored models with a 4000-km threshold distance. We used 25% of the database for spatial analysis due to memory limitations on size of the covariance matrix, sampling one in every four cells using an evenly spaced lattice. Spatial autocorrelation of the model residuals was evaluated using Moran's I as implemented in the `Moran.test` function in the R *spdep* library. We used the same neighbourhood (distance and spatial weights) for calculating the Moran's I -values as we did for the SAR models.

RESULTS

MPD and VPD

From simulations, we show a close relationship between tree shape and the distribution of evolutionary distances (MPD and VPD) separating taxa (Fig. 1a–f). Our initial set of simulations demonstrate that tree depth (root-to-tip distances) is strongly and positively correlated with both MPD ($r = 0.84$; Fig. 1a) and VPD ($r = 0.89$; Fig. 1b). Our second set of simulations, that held tree depth constant, show that MPD correlates most strongly with tree imbalance (slope + 95% CI = $-0.09 + 0.004$, $r = -0.50$ and slope + 95% CI = $0.02 + 0.004$, $r = 0.13$, from the correlation of I_c with MPD and VPD, respectively; Figs 1c & 2d). However, we note that the relationship between MPD and tree imbalance is complex; for example, MPD is invariant when setting branch lengths using the method of Grafen (1989), irre-

spective of tree balance (data not shown). In contrast, VPD is by far the stronger predictor of tree stemminess (γ) (slope + 95% CI = 0.02 + 0.004, $r = 0.86$ and slope + 95% CI = -0.01 + 0.004, $r = -0.37$; from the correlation of γ with VPD and MPD, respectively; Figs 1e & 2f). Importantly, trends across the empirical set of phylogenetic trees match the trends from simulations (Fig. S3 in Appendix S1). Hence the two metrics capture largely complementary aspects of tree shape relevant for describing the structure of empirical phylogenetic trees.

The negative correlation between MPD and I_c indicates that for trees of similar depth there is, on average, a larger distance separating taxa in more balanced (symmetrical) evolutionary

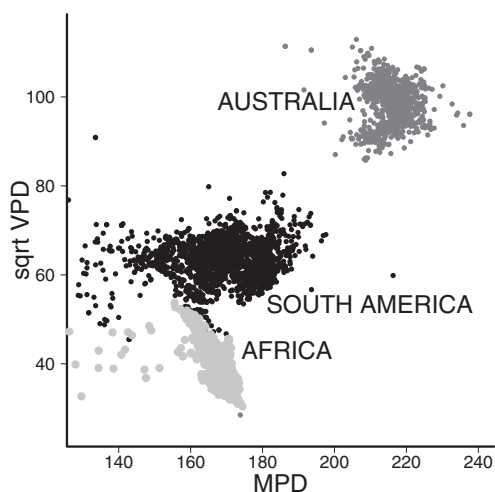


Figure 2 Mean and variance in phylogenetic distance (MPD and VPD, respectively) for grid cells within our focal areas.

trees, although this relationship is of course sensitive to the particular distribution of branch lengths in the tree (see above). The positive correlation between VPD and γ indicates that there is greater variance in evolutionary distances between species for trees with more stemmy (longer branches towards the root) topologies. High VPD is then indicative of old stemmy trees, whereas high MPD is indicative of old balanced trees (Fig. 1g).

New World versus Old World patterns

We show differences in MPD and VPD for New World versus Old World mammalian faunas (Fig. 2). The distribution of MPD for South American cells spans values for Africa, and the means are statistically indistinguishable (mean MPD for cells = 168 for both South America and Africa, $t = -0.982$, $P = 0.326$). There is less overlap in VPD, with higher values across most of South America (mean VPD for cells = 4007 versus 1460, for South America and Africa respectively, $t = 183.094$, $P < 2.2 \times 10^{-16}$). Australia is evidently distinct, with no overlap in per-cell MPD or VPD values. Globally (Fig. 3a), we show that South America and Australia have high VPD and MPD, consistent with old trees and/or stemmy plus balanced topologies. Africa has high MPD but low VPD, inconsistent with a simple explanation related to tree depth alone. Similar spatial trends were observed at the scale of ecoregions (Fig. S4 in Appendix S1). Our findings suggest the phylogenetic tree for Africa is balanced and tippy. We find no bias in our tree-shape metrics with species richness (Fig. S5 in Appendix S1), and in any case, per-cell species richness is similar for the New World and Old World tropics.

Controlling for tree depth by rescaling trees to unit length (Fig. 3b) or excluding marsupials plus monotremes from the

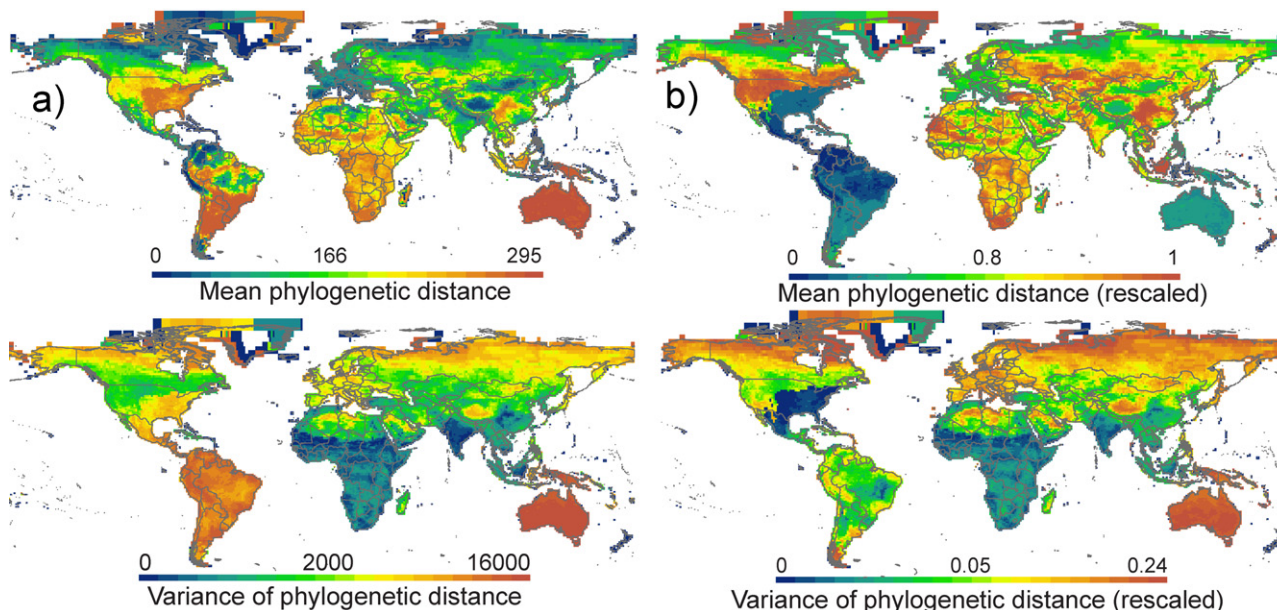


Figure 3 (a) Mean and variance in pairwise phylogenetic distances (MPD and VPD, respectively) between the mammal fauna within 100 km × 100 km grid cells. Distances are estimated from the dated phylogenetic tree for mammals from Bininda-Emonds *et al.* (2007). In (b), trees are re-scaled to unit length. Map projection: geographical (unprojected). Data were divided into 20 quantiles.

Table 1 Regression of tree shape characterized by the mean and variance of pairwise phylogenetic distances between tip taxa (MPD and VPD, respectively) against temperature and actual evapotranspiration (AET), assuming a linear model with normal errors (lm) and after adjusting for spatial autocorrelation (errorSAR). All models and included terms are significant at $P < 0.001$.

Model	Response	r^2	Predictor	Coefficient	t -value or z -value	Moran's I
lm	MPD	0.21	AET	-1.04×10^{-4}	-46.3*	0.75
			Temperature	-9.79×10^{-5}	-12.6*	
errorSAR	MPD	0.87‡	AET	-7.46×10^{-6}	-3.2†	0.06
			Temperature	-1.10×10^{-4}	-7.3†	
lm	VPD	0.17	AET	-1.19×10^{-5}	-14.3*	0.45
			Temperature	-1.08×10^{-4}	-37.5*	
errorSAR	VPD	0.57‡	AET	-7.7×10^{-6}	-5.1†	0.02
			Temperature	-8.99×10^{-5}	-9.3†	

* t -value from linear regression models.

† z -value from spatial autoregressive (SAR) models.

‡Pseudo r^2 estimated as the fit of predicted against observed values.

analysis (see Fig. S6 in Appendix S1) had important but qualitatively similar effects on regional patterns of MPD and VPD. The re-scaled phylogenies for Africa and South America show opposite trends [high MPD (balanced) and low VPD (tippy) for Africa versus low MPD (imbalanced) and high VPD (stemmy) for South America], and differ significantly in both mean MPD (mean re-scaled MPD for cells = 0.582 and 0.857, for South America and Africa, respectively, $t = -212.814$, $P < 2.2 \times 10^{-16}$) and mean VPD (mean re-scaled VPD for cells = 0.048 and 0.038, for South America and Africa, respectively, $t = 40.899$, $P < 2.2 \times 10^{-16}$). We note that P -values should be interpreted cautiously because adjacent cells sample similar sets of species from the regional pool and hence capture similar variation in phylogenetic tree structure (spatial correlograms are shown in Fig. S7 in Appendix S1) – which we explore further below in our spatial regressions.

In summary, our results indicate that the phylogenetic trees connecting the regional mammalian fauna in both South America and Australia is deep (old, because it include the basal splits between monotremes, marsupials and placentals), imbalanced and stemmy. In contrast, the phylogenetic tree connecting the regional mammal fauna in Africa is shallower (younger, because all species are nested within Eutheria), balanced and tippy.

Environmental predictors of tree shape

We find a significant relationship between environment and both tree-shape indices (Table 1); however, the strength of the relationship was markedly less than that typically observed for correlations with species richness ($r^2 = 0.21$ – 0.17 for the linear regression of temperature and AET on re-scaled MPD and re-scaled VPD, respectively). The SAR models reduce Moran's I -values to near zero, but the values remain significant given the large number of grid cells in the analysis (Table 1; also compare correlograms in Fig. S7 in Appendix S1). The results were qualitatively similar for the 2000-km and 4000-km neighbourhoods, so we present only those for the 2000-km neighbourhood. Environmental energy correlates negatively with both indices, and temperature is consistently the stronger predictor of VPD,

although precise coefficient estimates vary with model structure (Table 1). Imbalanced trees are therefore characteristic of more energy-rich environments generally, whereas tippy trees typify warmer regions. Although it is possible that additional environmental parameters and their interaction terms might also correlate with tree shape, we suspect the additional variance explained is likely to be low (given the generally weak explanatory power of the models), and we retain focus here on the variables most commonly correlated with species richness.

DISCUSSION

Phylogenetic trees can provide information on macroevolutionary rates (speciation and extinction) (Harvey *et al.*, 1994; Nee *et al.*, 1994) and also on the processes structuring ecological communities (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009). Our analysis illustrates the potential for phylogenetic trees to inform inquiries into the origin of diversity patterns at regional scales. Here, using diversity metrics more typically applied to ecological communities, we present a novel phylogenetic framework to help reconstruct the evolutionary history of extant mammalian richness patterns. Using a practically complete species-level phylogenetic tree for mammals (Bininda-Emonds *et al.*, 2007), we show large differences in the evolutionary relationships among species for New and Old World diversities that capture well the evolutionary and biogeographical hypotheses inferred from fossil data. Our results demonstrate the utility of phylogenetic approaches in providing an independent quantitative test of macroecological as well as macroevolutionary theory, and perhaps their potential to reveal new insights into mammalian biogeography.

The mammalian fauna of the New World tropics matches trends for Australian mammals – a fauna largely assembled from radiations within ancient marsupial lineages (Johnson, 2007). Both faunas share two distinct phylogenetic signatures (although the regional phylogeny for Australian mammals is much deeper). First, large variation in the number of extant species between sister clade (phylogenetic imbalance) – reflected in the mean pairwise phylogenetic distance among taxa. Second, several young but evolutionarily distinct (separated by long stem

branches) clades with high species richness (separated by short evolutionary distances) – reflected in the variance in pairwise phylogenetic distances among taxa. In contrast, the evolutionary branches connecting Old World diversity in tropical Africa are characteristic of symmetrical (balanced) and tippy phylogenetic trees. The differences in tree topologies between Old and New World faunas fits well with current understanding of mammalian phylogeography.

Despite early mammalian diversification in the Mesozoic (Cox, 2000; Springer *et al.*, 2003), current mammalian richness is largely a product of diversification within the last 100 Myr (Bininda-Emonds *et al.*, 2007). Clades characteristic of Africa (e.g. Afrotheria) and the Americas (e.g. Xenarthra) split *c.* 100–90 Ma following the final separation of Africa and South America *c.* 120–100 Ma (Murphy *et al.*, 2001; Wildman *et al.*, 2007). However, due to extinctions among old lineages, much of present-day South American diversity can be attributed to recent radiation of clades with Central and North American origins that migrated following the formation of the Isthmus of Panama (e.g. sigmodontine rodents with more than 300 species) (Webb, 1976; Cox, 2000) or across the shallow seas that predated it over the preceding few millions of years (Eisenberg, 1981). The filtering effect of migration resulted in many evolutionarily distinct lineages that subsequently diversified rapidly, including noctilionoid bats (Simmons, 2005), Canidae, Mustelidae, Cervidae and Muridae (Webb, 2006). This biogeographical history is reflected in the long stem branches subtending from clades with young crown ages and many closely related (recently diversified) species (stemmy trees).

In contrast to data on the origins of New World diversity, the record of the early African mammalian fauna is surprisingly poor. Although several lineages are thought to have crossed shallow seas separating Africa from Asia and Europe that occurred approximately 55 and 30 Ma (Cox, 2000), the high tropical species richness in Africa is more consistent with a model of gradual accumulation of over a long period of time. In particular, diversity is striking within large-bodied lineages (Nieto *et al.* 2005) which escaped the Pliocene and Pleistocene extinctions that resulted in the loss of much of the South American megafauna (Webb, 1976, 2006), and suggests that most modern African diversity may be within clades of ancient African origin, leading to more tippy regional phylogenetic trees.

Differences in biogeographical histories are also reflected in the symmetry of the regional phylogenies. Phylogenetic imbalance appears to be a common feature of the tree of life (Heard, 1992; Purvis & Agapow, 2002), and is typically interpreted as representing differences in net diversification rates (speciation – extinction) (Heard, 1996; Purvis, 1996; Mooers & Heard, 1997). At large spatial scales there is a tendency for mammalian assemblages to demonstrate phylogenetic imbalance, reflecting the overall phylogenetic imbalance of the mammalian tree of life (Purvis *et al.*, 2011). However, within regional phylogenies, imbalance might also indicate differences in migration patterns between regions (Heard & Cox, 2007). For example, a lineage might be relatively species poor within a region either because it

has diversified slowly or because it has only recently migrated and represents a part of a more species-rich clade. Here we use information on mean pairwise distances to infer greater imbalance in the phylogenetic trees for the New World. Our results somewhat conflict with a recent analysis by Purvis *et al.* (2011) using a different metric of tree shape, that indicated more balanced phylogenetic trees for the mammalian fauna of the Amazonian Basin. We suggest that this discrepancy is probably explained by the difference in weighting applied to the incontrovertible imbalance of deep nodes versus greater balance of young nodes representing *in situ* radiations. Detailed phylogeographical data are required to fully unravel the likely complex history of speciation, extinction and migration captured in the regional phylogenies; nonetheless environment might also be informative.

If, as we suggest, stemmy trees are indicative of recent speciation, and speciation rates are influenced by environmental energy (Rohde, 1992; Davies *et al.*, 2004; Allen *et al.*, 2006), then we might also expect a correlation between tree shape and environment. We explored two key environmental variables, temperature and AET. We revealed a significant correlation with both axes of tree shape, but with warm temperatures and productive environments associated with more tippy trees; hence, we did not find evidence supporting a role of environmentally mediated diversification shaping tree topology. Different aspects of the environment were better at predicting our indices of stemminess and imbalance; however, any spatially structured variable is likely to covary with some aspect of the environment (Buckley *et al.*, 2010). We therefore interpret our results cautiously, as differences in regional biogeographical histories might also give rise to significant correlations between environment and tree shape.

CONCLUSION

The shape of the evolutionary tree-of-life for regions with different floras and faunas is highly variable (Heard & Cox, 2007), and can reveal the historical processes that have shaped current diversity gradients. Here we used pairwise distances to characterize the evolutionary relationships within regional faunas. We show that pairwise measures capture key aspects of tree shape well, but are less sensitive to phylogenetic uncertainty. We find large differences between New World and Old World tropics in the distribution of evolutionary branch lengths connecting their regional mammal faunas. African mammals tend to be relatively old, disparate (see also Davies *et al.*, 2008) and evenly distributed on the local tree-of-life. African tropical diversity accumulated slowly over long periods of time, and reflects the Old World origin of eutherian lineages (Lillegraven *et al.*, 1987) and their steady phylogenetic radiations. In contrast, South American species tend to be young and clustered within several evolutionarily distinct clades. These results reflect the recent diversification of evolutionarily disparate lineages within the New World. Our analysis supports fossil evidence suggesting that the New World tropics are a cradle of recent diversification

whereas the Old World tropics represent a museum of old diversity.

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SUPPORTING INFORMATION

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

Appendix S1 Figures S1–S7.

Figure S1 Relationship between the various tree-shape metrics and tree resolution.

Figure S2 Relationship between MPD and VPD, and tree depth.

Figure S3 Relationship between the various phylogenetic metrics for empirical trees.

Figure S4 Mean and variance in pairwise phylogenetic distance within ecoregions.

Figure S5 Relationship between species richness and tree shape.

Figure S6 Mean and variance in pairwise phylogenetic distance excluding marsupials and monotremes.

Figure S7 Correlograms depicting spatial autocorrelation structure in re-scaled VPD and MPD.

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