



Species and functional diversity accumulate differently in mammals

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ABSTRACT

Aim Whether the gradients of global diversity conform to equilibrium or non-equilibrium dynamics remains an unresolved question in ecology and evolution. Here, we evaluate four prominent hypotheses which invoke either equilibrium (more individuals, niche diversity) or non-equilibrium dynamics (diversification rate, evolutionary time) to explain species richness and functional diversity of mammals worldwide.

Location Global.

Methods We combine structural equation modelling with simulations to examine whether species richness and functional diversity are in equilibrium with environmental conditions (climate, productivity) or whether they vary with non-equilibrium factors (diversification rates, evolutionary time). We use the newest and most inclusive phylogenetic, distributional and trait data for mammals.

Results We find that species richness and functional diversity are decoupled across multiple regions of the world. While species richness correlates closely with environmental conditions, functional diversity depends mostly on non-equilibrium factors (evolutionary time to overcome niche conservatism). Moreover, functional diversity plateaus with species richness, such that species-rich regions (especially the Neotropics) host many species that are apparently functionally redundant.

Main conclusions We conclude that species richness depends on environmental factors while functional diversity depends on the evolutionary history of the region. Our work further challenges the classic notion that highly productive regions host more species because they offer a great diversity of ecological niches. Instead, they suggest that productive regions offer more resources, which allow more individuals, populations and species to coexist within a region, even when the species are apparently functionally redundant (the more individuals hypothesis). Together these findings demonstrate how ecological (the total amount of resources) and evolutionary factors (time to overcome niche conservatism) might have interacted to generate the striking diversity of mammals and their life histories.

Keywords

Conservatism, diversification, ecological limits, niche filling, saturation, time for speciation.

Even after decades of research, the mechanisms that shape global diversity patterns remain elusive and controversial. Much of the controversy revolves around the relative importance of equilibrium and non-equilibrium processes. Equilibrium hypotheses argue that regional richness is set by environmental conditions, which constrain the amount of resources and the diversity of niches (Hutchinson, 1959; MacArthur, 1972; Wright, 1983; Rabosky, 2009). Non-equilibrium hypotheses claim that the number of species in a region depends mostly on diversification rates and evolutionary time (i.e. assemblage age, time for speciation; Wallace, 1876; Fischer, 1960; Wiens *et al.*, 2011). Both classes of hypotheses are normally tested with data on species richness, but they may be better assessed with complementary information on species traits which captures functional diversity and the partitioning of niches. Here, we integrate phylogenetic, geographical and trait data for mammals to evaluate the two sets of hypotheses and uncover the mechanisms that have likely shaped global mammalian diversity.

Under equilibrium hypotheses, total resource availability and niche diversity together regulate the number of species in a given region (MacArthur, 1972; Rabosky, 2009). Resource availability may govern species richness by setting the number of individuals, viable populations and species that can regionally coexist, irrespective of their functional similarity. This mechanism, known as the “more individuals hypothesis” (Brown, 1981; Wright, 1983; Currie *et al.*, 2004) (Table 1a, Fig. 1a), has received limited attention as it allows for regional coexistence of functionally redundant species, which seems to contradict the principle of competitive exclusion that has received support mostly from local-scale studies (MacArthur & Pianka, 1966; Cavender-Bares *et al.*, 2009). The alternative and more broadly accepted explanation

argues that highly productive regions are species-rich because they afford a great diversity of ecological niches (Simpson, 1953; MacArthur & Pianka, 1966; Evans *et al.*, 2005) (Table 1b, Fig. 1a), such that species richness and functional diversity are expected to be correlated. In either case, species richness depends on environmental conditions, such as temperature, precipitation and regional productivity (Hawkins *et al.*, 2003; Currie *et al.*, 2004).

Under non-equilibrium hypotheses, species richness depends mostly on evolutionary time (i.e. time for speciation, assemblage age) and diversification rates (i.e. speciation minus extinction) (Wallace, 1876; Fischer, 1960; Wiens *et al.*, 2011; Harmon & Harrison, 2015). The time-for-speciation hypothesis posits that species gradually accumulate over time, such that regions that were colonized earlier will have higher richness (Wallace, 1876; Fischer, 1960; Wiens *et al.*, 2011) (Table 1c, Fig. 1b). Moreover, if species tend to retain their ancestral niches, conforming to niche conservatism *sensu* Wiens & Graham (2005), early colonized regions should host functionally diverse suites of species because of the long time for ecological divergence. In contrast, regions that were colonized recently should host relatively few, functionally redundant species (Table 1c, Fig. 1b). The diversification rates hypothesis (Table 1d) further suggests that regions become species rich because they rapidly accumulate species. Rapid diversification within regions that are highly diverse (especially the tropics) has been reported across many taxa (e.g. Rohde, 1992; Mittelbach *et al.*, 2007). In some cases, diversification coincides with the divergence in functional traits (e.g. adaptive radiations and punctuated equilibria; Simpson, 1953; Eldredge & Gould, 1972; Schluter, 2000), but it may also proceed without any obvious phenotypical change (Rundell & Price, 2009). In the latter case, niche conservatism presumably constrains trait evolution and results in

Table 1 Equilibrium and non-equilibrium hypotheses of biological diversity. Each hypothesis is introduced together with its predictions regarding species richness and functional diversity.

Hypothesis	Prediction		
	General mechanism	Species richness (SR)	Functional diversity (FD)
(a) Equilibrium: resource availability	High productivity and resource availability can sustain more individuals, more viable populations and more species (i.e. the more individuals hypothesis; Brown, 1981; Wright, 1983; Currie <i>et al.</i> , 2004)	SR correlates positively with productivity	FD correlates weakly, if at all, with productivity
(b) Equilibrium: niche diversity	Productive environments support more species because they afford a greater diversity of niches, facilitating species coexistence (MacArthur & Pianka, 1966; Schluter, 2000; Evans <i>et al.</i> , 2005)	SR correlates positively with productivity	FD correlates strongly and positively with productivity
(c) Non-equilibrium: evolutionary time	Evolutionary time allows assemblages to gradually accumulate high diversity (Wallace, 1876; Fischer, 1960; Stephens & Wiens, 2003)	SR correlates positively with evolutionary time	FD correlates positively with evolutionary time
(d) Non-equilibrium: diversification rates	High diversity results from a fast accumulation of species due to high speciation and/or low extinction, especially in the tropics (Fischer, 1960; Stebbins, 1974; Mittelbach <i>et al.</i> , 2007).	SR correlates positively with diversification rates	If diversification is coupled with trait divergence, FD correlates positively with diversification rates

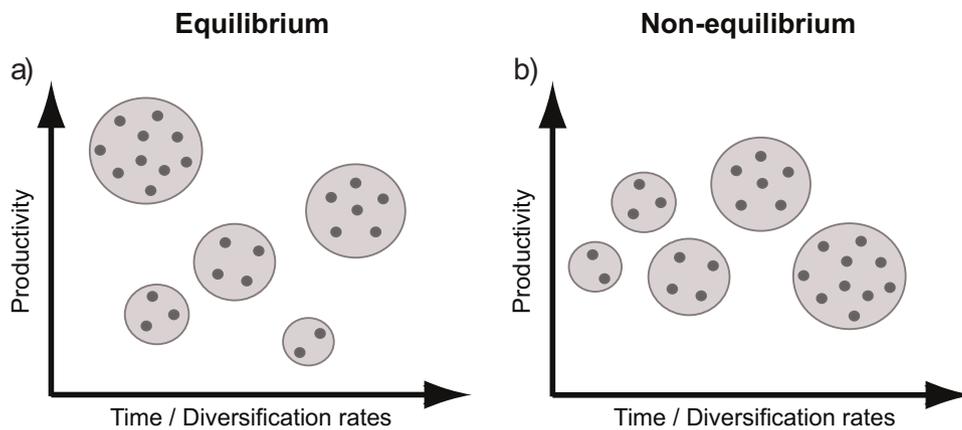


Figure 1 Schematic representation of equilibrium and non-equilibrium hypotheses. Under equilibrium hypotheses, species richness (the dark dots represent different species) and functional diversity (grey circles) are determined by environmental conditions, independently of evolutionary history. In contrast, under non-equilibrium hypotheses, evolutionary time and diversification rates are the key determinants of species richness and functional diversity. The hypotheses are further explained in Table 1.

functional redundancy among regionally coexisting species (Rundell & Price, 2009) (Table 1d).

While equilibrium and non-equilibrium hypotheses have received considerable attention in the literature (Wiens *et al.*, 2011; Cornell, 2013; Rabosky 2013; Rabosky & Hurlbert, 2015; Harmon & Harrison, 2015) and some empirical support (e.g. Stephens & Wiens, 2003; Rabosky & Glor, 2010; Hawkins *et al.*, 2012; Hutter *et al.*, 2013), it remains unknown whether they can explain the diversity of species and their traits alike. It is also unresolved whether these two classes of hypotheses are necessarily mutually exclusive or whether they merely reflect different phases of similar processes (e.g. Phillimore & Price 2008; Cornell 2013), such that equilibrium and non-equilibrium dynamics may prevail in different regions depending on their evolutionary history. By integrating information on species richness and functional diversity, we aim to address these issues and shed light on the mechanisms that generated the diversity of mammals and their life histories (Table 1, Fig. 1).

METHODS

Data

Our phylogeny for mammals was extracted from the newly assembled and smoothed time tree of life (Hedges *et al.*, 2015). With 5363 species and approximately 70% resolution, our phylogeny represents arguably the most complete and most resolved mammalian tree to date (Hedges *et al.*, 2015). Our analyses included all extant terrestrial mammals, including aquatic and marine species born on land (e.g. sea otters, polar bears).

Trait data were taken from a newly compiled dataset for mammals that combines multiple sources and databases (e.g. PanTHERIA, Jones *et al.*, 2009; EltonTraits 1.0, Wilman *et al.*, 2014; Davidson *et al.*, 2009; Arregoitia *et al.*, 2013; Pacifici *et al.*, 2013). From this dataset, we selected the seven

most complete ($57 \pm 16\%$) ecologically relevant traits: body mass (log-transformed), habitat mode (aquatic, arboreal, fossorial, terrestrial, marine born on land and volant), habitat breadth (number of habitat modes used by a species), trophic level (omnivore, herbivore, carnivore), diet breadth (includes over 20 categories), activity cycle (diurnal, nocturnal, both) and litter size (log number of offspring born per female per litter). These traits are generally believed to reflect many important dimensions of the ecological niche in mammals (e.g. Davidson *et al.*, 2009; Jones *et al.*, 2009; Safi *et al.*, 2011). Missing values were imputed using the nonparametric version of the random forest algorithm which considers traits only ('R' package missForest; Stekhoven & Bühlmann, 2012). This algorithm performs comparably to or better than its alternatives, even without phylogenetic information (Penone *et al.*, 2014).

Range maps for mammals were taken from Rondinini *et al.* (2011). These maps are based on 'extent of suitable habitat' models (ESH) that control for species-specific habitat preferences within species ranges (Rondinini *et al.*, 2011). We transformed all range maps into presence/absence grids and compiled species assemblages for each grid cell. We used the Mollweide equal-area projection to ensure that all grid cells covered the same geographical area (100 km^2) regardless of their latitudinal position. Assemblages that lacked both phylogenetic and trait data or contained fewer than five species were discarded (Hortal *et al.*, 2011). Our final combined dataset comprised 11,712 grid cells with 4500 mammal species ($87.66 \pm 4.04\%$ of the totally available distributional, phylogenetic and trait data); grid cell richness correlated closely with that of the raw distributional data (Pearson's $r = 0.99$; $P < 0.001$).

We used climatic variables and actual evapotranspiration (AET) to capture environmental energy and resource availability. AET is a measure of plant biomass and environmental productivity, which has been hypothesized to correspond

with the carrying capacity of a region (Hawkins *et al.*, 2003). AET data were taken from the United Nations Environment Programme (Ahn & Tateishi, 1994; available at <http://www.grid.unep.ch/data/data.php>). We also used 19 bioclimatic variables (Hijmans *et al.*, 2005) representing temperature, precipitation and seasonality, which are likely to correspond with regional resources (Rohde, 1992; Hawkins *et al.*, 2003; Mittelbach *et al.*, 2007). We used principal component analysis (PCA) to combine all 19 variables into a single composite variable (PC1), which explained 60% of the variation in the climatic data and captured a gradient from cold and seasonal to warm and non-seasonal conditions. PC1 and AET were highly correlated (Pearson's $r = 0.72$, $P = 0.001$), and this collinearity motivated us to use only AET in further analyses (Anderson & Burnham, 2002).

Phylogenetics: evolutionary time and diversification rates

An increasing number of phylogenetics have been proposed to capture the evolutionary history and phylogenetic structure of species assemblages (Faith, 1992; Webb, 2000; Redding & Mooers, 2006; Cavender-Bares *et al.*, 2009; Davies & Buckley, 2012; Tucker *et al.*, 2016); however, there is little consensus on the biological interpretation of many of these metrics. For example, mean root distance (MRD), or the mean number of nodes separating the tips from the root of a phylogeny, has been interpreted as a measure of two very distinct variables: evolutionary time (e.g. Algar *et al.*, 2009; Hawkins *et al.*, 2012) and diversification rates (e.g. Fritz & Rahbek, 2012; Qian *et al.*, 2015). In addition, MRD often reaches extreme values in species-poor assemblages (Fritz & Rahbek, 2012), suggesting that it might be sensitive to species richness. It remains largely untested whether other phylogenetics have similar issues.

Given this lack of guidance in the literature, we conducted simulations to evaluate which of the most commonly used phylogenetics [e.g. MRD, mean phylogenetic distance (MPD), species-level diversification rate (DivRate)] (see Table S1 in the Supporting Information for the complete list) are least sensitive to assemblage richness and most accurately represent evolutionary time and diversification rates. To this end, we simulated phylogenetic trees under a range of birth rates (λ), death rates (μ), evolutionary times (t) and richness values (n). The baseline parameter values for the simulation were inferred from the mammalian phylogeny (tree size = 5000, $\lambda = 0.2$, $\mu = 0.14$, $t = 180$) (Hedges *et al.*, 2015). These values were varied across our simulations but left constant within any particular simulation (diversification slowdowns, accelerations, etc., were not considered).

In a first round of simulations, we identified the phylogenetics that were least sensitive to assemblage richness. We used the previously inferred parameters to simulate 5000 phylogenies (tree size = 5,000, $\lambda = 0.2$, $\mu = 0.14$, $t = 180$) and varied the degree of tree pruning across the phylogenies to obtain 5000 assemblages, which differed in their phylogenetic

composition but had similar richness to the empirical assemblages of mammals (mean = 100, SD = 38). We calculated 11 different phylogenetics for each simulated assemblage (Table S1) and identified the metrics that were least influenced by assemblage richness.

These metrics were further examined in the second round of simulations, where we evaluated how well they captured either evolutionary time or diversification rates. This time, we varied evolutionary time across our simulations (mean = 100, SD = 20; equivalent to the estimated ages of mammalian assemblages) while diversification rates and relative branch lengths within the simulated phylogenies were held constant (see Davies & Buckley, 2012). Next, we held evolutionary time constant ($t = 40$) while varying rates of diversification, selecting speciation (λ) and extinction rates (μ) at random from the exponential (mean = 0.5) and the constant distribution ($\mu = 0.14$), respectively. These statistical distributions were chosen to match speciation and extinction rates observed across mammalian clades and in the fossil record, which suggests that speciation rates varied against the background of stationary extinction within this group (Alroy, 1996). The resultant assemblages were therefore simulated either under constant time or constant diversification, and we evaluated which of the phylogenetics correlated closely and most exclusively with these variables. The script used for the simulations is accessible from the GitHub repository (https://github.com/oliveirab/simulation_phylogenetics).

The simulations were parameterized with values extracted from the mammalian tree (Hedges *et al.*, 2015), but we found that other parameter values and their various combinations (e.g. different means of the exponential distribution, differentially fixed tree age) yielded very similar results. The results may therefore be transferable to other taxa, at least to the extent that the phylogenies of these taxa are similar to the mammalian tree (in terms of tree topology, branching time distributions or tree shape). The script can be easily adapted for different types of trees as well.

Functional diversity metrics

There are many metrics of functional diversity (Petchey & Gaston, 2002; Laliberté & Legendre, 2010; Schleuter *et al.*, 2010; Pavoine & Bonsall, 2011), each suited for different purposes, with their own sensitivities to outliers and species richness. Therefore, we again used simulations to compare the performance of the five most suitable candidate indices (FRic, FEve, FDiv, FDis, Q; see Table S3). We avoided dendrogram-based metrics because they vary dramatically, even when applied to the same data, depending on the choice of the distance measure and the clustering algorithm (Mouchet *et al.*, 2008). Because we aimed to capture the spread of species within their multidimensional trait space, we tested how the five candidate metrics correlated with the range and the standard deviation of trait values. Both the range and the standard deviation measure trait spread, but the range is more sensitive to outliers.

Following Laliberté and Legendre (2010), we generated a pool of 5000 simulated species from which we randomly assembled 20,000 assemblages (simul.dbFD routine in the 'R' package FD) (Laliberté *et al.*, 2014). The simulated assemblages contained between 5 and 100 species, spanning the range of richness values observed for mammals, from species-poor (e.g. the Sahara Desert) to species-rich regions (e.g. the Neotropics). Each species within each simulated assemblage was assigned five different traits whose values were selected at random from several statistical distributions (normal, log-normal and exponential), which we parameterized to approximate the empirical values observed across mammals. This procedure ensured that we compiled a realistic collection of phenotypes and functional spaces (Laliberté & Legendre, 2010, Laliberté *et al.*, 2014). The metrics that perform poorly across the simulated data need to be interpreted cautiously when applied to mammals or other taxonomic groups of similar functional diversity (Laliberté & Legendre, 2010, Laliberté *et al.*, 2014). The script for these simulations is accessible at https://github.com/oliveirab/simulation_traits.

Statistical analysis

To evaluate the effects of equilibrium (AET) and non-equilibrium factors (diversification rates, evolutionary time) on species richness and functional diversity, we used structural equation modelling (SEM), in which causal relationships among the variables of interest are statistically defined and evaluated in the form of mutually interconnected equations (e.g. Shipley, 2009). The SEM models were implemented within the generalized least-squares (GLS) and the mixed-effects framework (LME) to account for spatial autocorrelation (Lefcheck, 2016). The former framework allows full spatial error terms to be fitted, while the latter incorporates realm identity as a random effect. Inspection of model residuals indicated that the autocorrelation was significantly better accommodated under the LME (Fig. S1), so we only present those results (Shipley, 2009; Lefcheck, 2016).

Due to the distinct faunas of Australia and Oceania (monotremes and marsupials), most of the inferred phylogenetics had a clearly bimodal distribution, so we split our dataset and reran our analyses for Australia–Oceania and the rest of the world separately (following Holt *et al.*, 2013). In addition, we investigated whether regions with relatively young and relatively old faunas supported differential dynamics (non-equilibrium versus equilibrium). In particular, we divided the 100-km² grid cells containing the mammalian assemblages into four quartiles, depending on the estimated age of their faunas, to identify regions with the youngest (25th quartile) and the oldest (75th quartile) mammal faunas. Then, we reran our statistical analyses for these regions separately.

The phylogenetic and the functional metrics used across our analyses were only minimally influenced by assemblage richness (see Results and Tables S2 & S4). However, to elimi-

nate any remaining and potentially confounding effects of richness, we used null models to estimate their standard effect sizes (SES). SES compare the observed values of the metrics with the values expected for random species assemblages [$SES = \text{observed} - \text{mean}(\text{null}) / \text{SD}(\text{null})$] (Webb, 2000; Swenson, 2014), which we generated by selecting species at random from the pool of all mammals (Webb, 2000; Swenson, 2014). SES are completely independent of assemblage richness but may be hard to interpret biologically (Swenson, 2014). For these reasons, we repeated our analyses for both raw values and SES of the employed metrics.

Finally, we performed a series of outlier analyses to evaluate the robustness of our findings. We used Bonferroni's test of Studentized residuals to identify outliers and determine if their removal from our analyses influenced the results (Cook & Weisberg, 1982). To satisfy the statistical assumptions of normality and linearity across our analyses, we log-transformed richness and square-root transformed AET. All SEM models were built using the piecewise SEM package (Lefcheck, 2016) implemented in the statistical environment 'R' (R Core Team, 2015).

RESULTS

Phylogenetics: evolutionary time and diversification rates

We examined the statistical properties of 11 different phylogenetics (Table S1) to assess which of them were least confounded by species richness and most accurately represented evolutionary time and diversification rates. We found that evolutionary time was best approximated by MPD (Table S2), mathematically defined as the mean of all pairwise phylogenetic distances among species within an assemblage (Webb, 2000). MPD increases with the degree of phylogenetic divergence between species within an assemblage, which makes it easily interpretable in terms of evolutionary time. Diversification rates were best predicted by DivRate. DivRate is an inverse of the mean fair proportion measure, which represents the proportion of branch lengths shared between the focal species and all the other species in the tree (Redding & Mooers, 2006; Isaac *et al.*, 2007). For example, species within rapidly diversifying clades are typically connected with short branches that are only partially shared across the many species within the clade, which produces high values of DivRate (Jetz *et al.*, 2012). The other examined phylogenetics (PD, MNTD, RBL, ED, etc., see Table S1 for definitions) often confounded the effects of diversification rates and time across our simulations. Many were also sensitive to assemblage richness (Table S2).

Functional diversity metrics

The range and the standard deviation of trait values across the simulated assemblages were most accurately approximated by functional dispersion (FDIs) (Table S4), which measures the mean distance of species from the centroid of

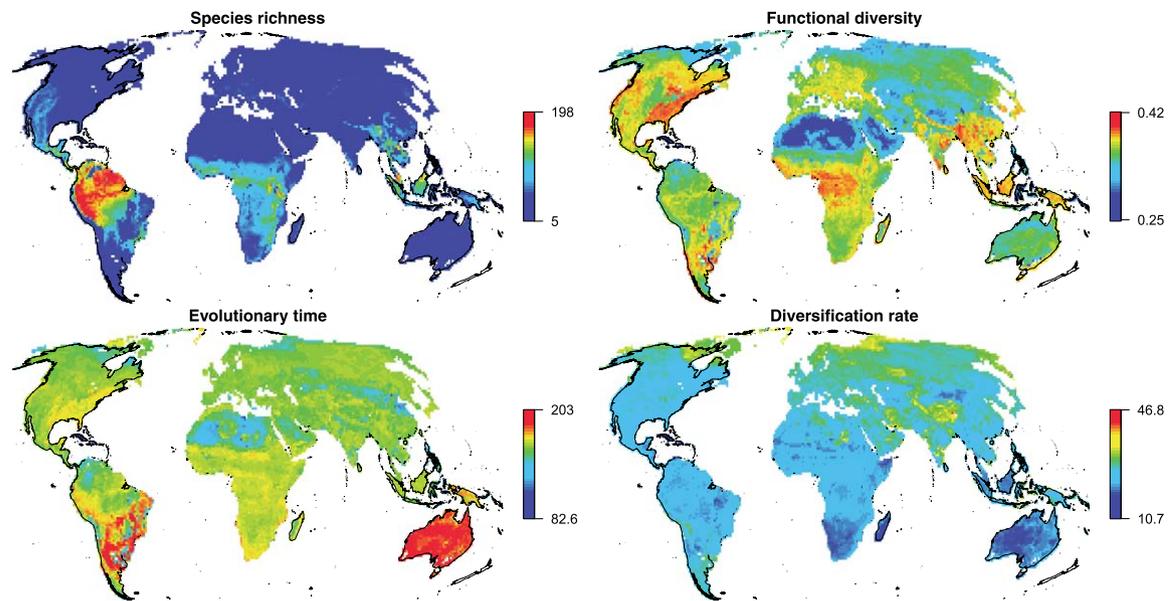


Figure 2 Geographical variation in species richness, functional diversity, evolutionary time and diversification rates. Functional diversity was measured as functional dispersion (FDis; Laliberté & Legendre, 2010). Evolutionary time corresponded to the mean phylogenetic distance (MPD; Webb, 2000) and diversification rates to the inverse of the fair-proportion measure (DivRate; Redding & Mooers, 2006; Isaac *et al.*, 2007; Jetz *et al.*, 2012).

the assemblage trait space (Laliberté & Legendre, 2010). FDis was largely independent of species richness while the other indices (FDiv, FRic, FEve; see Tables S3 & S4) were correlated with the range, but not the standard deviation, of trait values, or showed high sensitivity to assemblage richness.

Empirical results

Species richness and functional diversity varied substantially across continents (Fig. 2). In the Old World, they correlated with each other and reached their highest values in the tropics of Africa and Southeast Asia. In the New World, however, species richness and functional diversity were decoupled. Species richness increased towards the tropics, but functional diversity peaked at high latitudes in the Americas (Fig. 2).

Worldwide, functional diversity increased asymptotically [polynomial function; $R^2 = 0.43$, Akaike information criterion (AIC) = $-56,580$, $P < 0.001$] rather than linearly with species richness ($R^2 = 0.20$, AIC = $-52,557$, $P < 0.001$; Fig. 3a), suggesting functional redundancy in species-rich regions (especially in the tropics of the New World; Fig. 2). The same results were supported when we removed outliers from the analysis (Fig. S2). After we statistically accounted for the effect of species richness (Fig. 3b,c, Table S5), we found that functional diversity significantly increased with evolutionary time (global model, $R^2 = 0.22$, $P < 0.001$; Australian model, $R^2 = 0.34$, $P < 0.001$) (Fig. 3b,c), suggesting disproportionately high functional diversity across old assemblages (compare Fig. 2 with Fig. S3).

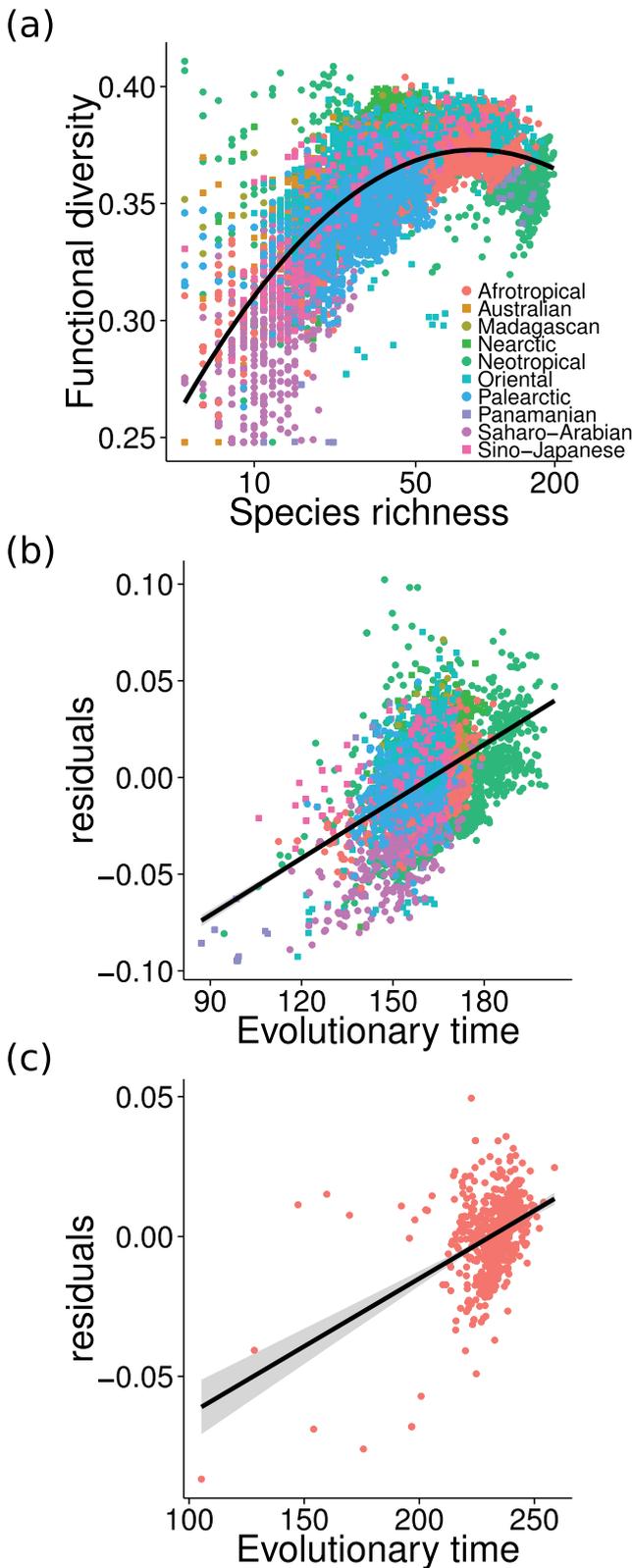
Species richness correlated closely with AET ($\beta = 0.64$, $P < 0.001$), but only loosely with evolutionary time

($\beta = 0.08$, $P < 0.001$) and diversification rates ($\beta = -0.19$, $P < 0.001$) (Fig. 4a), indicating that species richness may be influenced primarily by environmental conditions. The same results were supported by the global and the Australian models (Fig. 4a,b) and across regions with relatively young and relatively old mammalian faunas (Fig. 4c,d). Moreover, diversification rates were generally low in species-rich regions (e.g. in the tropics; see Fig. 2), as further corroborated by the negative path coefficients between diversification rates and species richness (Fig. 4). The same results were supported regardless of whether evolutionary time was expressed in terms of MPD or SES-MPD (Figs S4 & S5).

Functional diversity, in contrast, was better explained by evolutionary time ($\beta = 0.54$, $P < 0.001$), as compared with the diversification rate ($\beta = -0.05$, $P < 0.001$) or AET ($\beta = 0.34$, $P < 0.001$) (Fig. 4a), indicating non-equilibrium dynamics. The strong correlation with evolutionary time (but not with diversification rate) (see Fig. 4) suggests that the accumulation of functional diversity lags behind the diversification process. These results were again supported for the global and the Australian models (Fig. 4a,b) and across regions with young and old mammalian assemblages (Fig. 4c,d). Similar results were supported regardless of whether we measured functional diversity as FDis or SES-FDis (Figs S4 & S5), suggesting that our findings were not confounded by species richness.

DISCUSSION

Species richness and functional diversity seem to be decoupled across multiple regions of the world and are likely governed by different mechanisms. Specifically, species



richness conforms to equilibrium dynamics and correlates closely with environmental factors (climate, AET) but not with evolutionary factors, such as diversification rates and time (Fig. 4). In fact, regions with high mammalian richness

Figure 3 Predictors of functional diversity. Functional diversity plateaued with increasing species richness (a), suggesting functional redundancy in species-rich regions. After we subtracted the effects of species richness (a), the residuals in functional diversity increased linearly with evolutionary time for both (b) the global and model (c) the Australian model. Evolutionary time was measured as mean phylogenetic distance (Webb, 2000); the colours/shades indicate different biogeographical realms (see key) (Holt *et al.*, 2013).

show relatively slow diversification (Fig. 2). Functional diversity follows non-equilibrium dynamics and gradually increases over time. Old mammalian assemblages are typically functionally diverse, regardless of how many species they contain (Fig. 2), while young assemblages tend to consist of functionally redundant species (especially in the Neotropics) (Figs 3b,c & 4). These findings together indicate that environmental factors constrain the accumulation of species within a region, while the time needed to overcome niche conservatism constrains their functional divergence.

The relationship between species richness and environmental conditions is well documented (Wright, 1983; Hawkins *et al.*, 2003; Currie *et al.*, 2004; Evans *et al.*, 2005). The most common explanation for this relationship is that environmental conditions reflect available resources, niche diversity or both. Our results do not support the hypothesis that high richness within highly productive regions results from the great diversity of niches that these regions afford (Simpson, 1953; Evans *et al.*, 2005). Instead, regional richness seems to be governed by the total amount of resources which species need to maintain viable populations (i.e. the more individuals hypothesis *sensu* Evans *et al.*, 2005). This conclusion is consistent with the lack of correlation between mammalian richness and functional diversity (Fig. 3) despite the strong relationship between mammalian richness and productivity (Fig. 4) (Evans *et al.*, 2005; Willig, 2011; Hurlbert & Stegen, 2014). It also hinges on the assumption that our life-history traits capture the range of ecological strategies across mammals. While this is difficult to demonstrate definitively, it seems safe to infer that mammals in some regions (e.g. the Neotropics) are more functionally redundant than their counterparts in other, equally species-rich and productive regions (the Afrotropics and Southeast Asia) (Figs 2 & S4), in agreement with the conclusion that total resources, rather than niche diversity, limit regional richness in mammals.

Unlike species richness, functional diversity depended mostly on evolutionary time (Fig. 4a–d), which was further corroborated by the fact that the residuals from the relationship between functional diversity and species richness increased with evolutionary time (Fig. 3b,c). This indicates that mammalian assemblages which include relatively old lineages have disproportionately high functional diversity, given their richness. These findings are consistent with the niche conservatism hypothesis, which posits that species tend to retain their ancestral traits (Wiens & Graham, 2005; Pyron

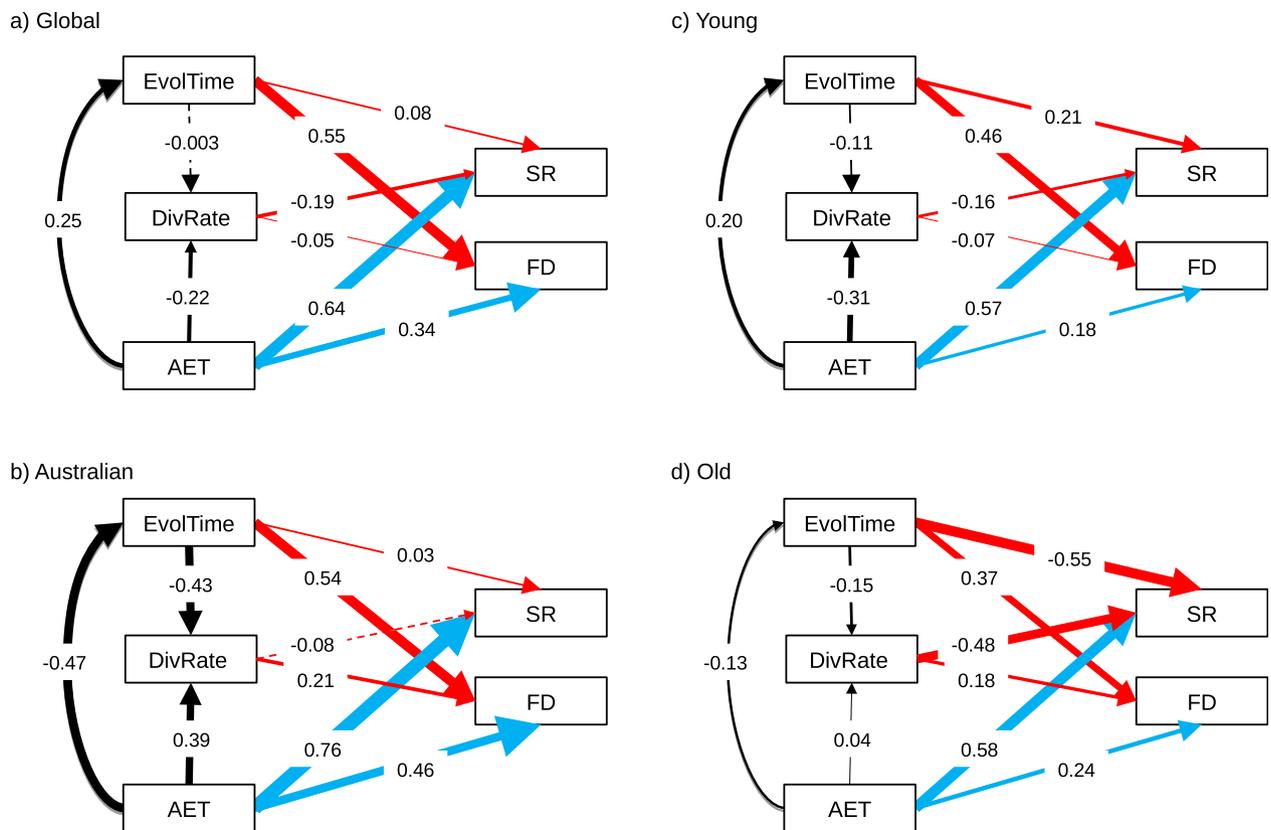


Figure 4 Path models of species richness (SR) and functional diversity (FD). Non-equilibrium effects are indicated by red arrows: EvolTime (evolutionary time, MPD; Webb, 2000), DivRate (diversification rate; Redding & Mooers, 2006; Isaac *et al.*, 2007; Jetz *et al.*, 2012). Equilibrium effects are indicated by blue arrows: AET (environmental productivity captured by the actual evapotranspiration). Path coefficients give the strength of partial correlations (= standardized β -coefficients from piecewise SEM) (Lefcheck, 2016). Dashed arrows indicate non-significant effects ($P \geq 0.05$). Path thickness reflects the values of β -coefficients. All variables are explained in the text.

et al., 2015), such that assemblages become increasingly functionally diverse over time. In addition, these findings shed new light on the somewhat perplexing conclusion that functional diversity is subject to strong environmental filtering in the tropics (e.g. Lamanna *et al.*, 2014) as the surprisingly low functional diversity in the tropics could be simply the outcome of rapid accumulation of species with little time for ecological divergence.

The lack of relationship between species richness and functional diversity has been previously reported for some taxa and regions (Shepherd, 1998; Stevens *et al.*, 2003; Safi *et al.*, 2011; Ricklefs, 2012). For example, low functional diversity despite high species richness occurs in tropical mammals (Safi *et al.*, 2011) and tropical trees (Lamanna *et al.*, 2014) while Neotropical bats show highest functional diversity at moderate species richness (Stevens *et al.*, 2003). In mammals and birds, regional richness rarely reflects niche diversity (Belmaker & Jetz, 2015; Fergnani & Ruggiero, 2015). Multiple mechanisms have been suggested to explain these surprising results. Specifically, latitudinal differences in the strength of niche conservatism might hinder functional divergence in tropical species (Wiens & Donoghue, 2004; Buckley *et al.*,

2010; Cooper & Purvis, 2010) while low tropical seasonality and high resource availability might together facilitate the coexistence of functionally redundant species (Weir & Schluter, 2007; Safi *et al.*, 2011). Here, we unrecovered the possible evolutionary mechanism, namely that species and their functional traits are generated differently. Species richness accumulates relatively fast, regulated by diversity-dependent mechanisms associated with environmental conditions and resource availability. Functional diversity lags behind species richness, presumably because of the time necessary for traits to ecologically diverge. Such differential dynamics can explain why comparably species-rich regions host functionally very different suites of mammals (Fig. 2).

We recognize that equilibrium and non-equilibrium dynamics are not necessarily mutually exclusive. Many regions may show some mixture of these dynamics and different dynamics may prevail across regions, depending on their evolutionary history. Still, our analyses recovered very similar dynamics across regions. The same dynamics were recovered globally (Fig. 4a), for Australia–Oceania (Fig. 4b) and for different biogeographical realms (Fig. 3) despite their dramatically different geological, evolutionary and

colonization history. In addition, the same results were recovered for regions with relatively young (Fig. 4c) and relatively old mammalian faunas (Fig. 4d), suggesting that equilibrium and non-equilibrium dynamics might not represent different phases of the same process. Regions hosting ancient faunas are no more likely to have reached their equilibrium than regions with relatively young faunas (Fig. 4c,d). These findings together corroborate that species richness follows equilibrium dynamics, governed by climate and productivity, while functional diversity follows non-equilibrium dynamics, dependent mostly on the evolutionary time to overcome niche conservatism, across regions with very different histories (Figs 4 & S5, Table S5).

We also recovered some potentially important findings for phylometrics, which have been used extensively to study the effects of evolutionary time and diversification rates on regional richness (e.g. Algar *et al.*, 2009; Davies & Buckley, 2012; Hawkins *et al.*, 2012; Qian *et al.*, 2015). Yet, how accurately a given phylometric captures time and diversification rates or how sensitive it is to richness has rarely been formally assessed. Our simulations suggest that many of the widely used phylometrics confound time and diversification rates (Table S2). Moreover, even the phylometrics mathematically defined to be independent of species richness are empirically correlated with it (Table S2). For example, MRD, employed across many previous studies, proved to be strongly dependent on assemblage richness across our simulations while being only weakly related to evolutionary time or diversification rates (Table S2). These findings may have important implications for the validity of previous studies and phylometrics in general (e.g. Algar *et al.*, 2009; Hawkins *et al.*, 2012; Fritz & Rahbek, 2012). In addition to illuminating their potential pitfalls, our simulations identified phylometrics that approximate evolutionary time (MPD; Webb, 2000) and diversification rate (DivRate; Redding & Mooers, 2006; Isaac *et al.*, 2007; Jetz *et al.*, 2012) reasonably well and therefore maximize the chances of teasing the effects of these two variables apart.

We recognize that species assemblages are not constant, and the suites of geographically co-occurring species may change over time. Yet, the turnover of species across the geographical scales assessed in our study appears to be relatively low and most species tend to remain within their biogeographical realms while showing only limited dispersal between them (Dynesius & Jansson, 2000; Wiens & Donoghue, 2004; Crisp *et al.*, 2009). Historical dispersals may still have introduced some noise to our analyses, but we were able to recover the well-known biogeographical patterns (the distinct assemblages of Australia and New Guinea, basal marsupial lineages in South America and the comparatively younger fauna of Africa), indicating that our study captured the key trends in the composition of mammalian assemblages (Fig. 2).

We further acknowledge that our estimates of functional diversity, and the following conclusions, reflect our choice of functional traits. We used traits that are generally believed to

capture many of the important dimensions of the ecological niche in mammals, including their body mass, reproduction, diet, activity cycle and habitat mode (Jones *et al.*, 2009; Davidson *et al.*, 2009; Safi *et al.*, 2011). Nevertheless, the ecological significance of any particular trait might vary across mammalian taxa, and the selection of ecologically relevant traits is always somewhat subjective and dependent on data availability.

Taken together, our results reveal that species richness and functional diversity are often decoupled, probably because different processes generate these two dimensions of biological diversity. Species richness seems to converge on an equilibrium determined by environmental conditions, such that regions with different evolutionary histories often show conspicuously similar species richness gradients (Davies & Buckley, 2012; Hawkins *et al.*, 2012). In contrast, functional diversity, controlled mostly by time to overcome niche conservatism, shows different patterns across regions, depending on their history. These findings together illustrate that the evolution of life histories may be decoupled from species origination. They also underscore that slow functional evolution may prevent some mammals from keeping pace with rapid environmental changes.

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AUTHOR CONTRIBUTIONS

B.F.O., A.M., G.C.C., and C.H.G. conceived and designed the research. B.F.O. performed the analyses with input from A.M. B.F.O., A.M., G.C.C. and C.H.G. wrote the manuscript. A.D.D. and C.R. contributed data. All authors contributed to the discussion of the results and to the editing of the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website:

Table S1 Definition of the phylometrics examined in our study.

Table S2 Simulation results for the phylometrics.

Table S3 Definition of the functional diversity metrics examined in our study.

Table S4 Simulation results for the functional diversity metrics, with trait values selected at random from different statistical distributions (normal, log-normal, exponential).

Table S5 Results for functional diversity, after accounting for the potentially confounding effects of species richness.

Figure S1 Spatial autocorrelation in the residuals of the SEM models, constructed under the mixed-effects (LME) and generalized least-squares frameworks (GLS).

Figure S2 Outlier analysis performed for the relationship between species richness and functional diversity.

Figure S3 Geographical variation in species richness, functional diversity (SES–FDis), evolutionary time (SES–MPD), and diversification rates.

Figure S4 Geographical variation in the residuals from the relationship between species richness and functional diversity.

Figure S5 Path models fitted for functional diversity (SES–FDis) and evolutionary time (SES–MPD) corrected for the effects of species richness.

BIOSKETCH

Brunno F. Oliveira is a PhD student with an interest in macroecology, macroevolution and biodiversity. His research integrates phylogenetic and biogeographical approaches across temporal and spatial scales.

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