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RESEARCH PAPER

Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity

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ABSTRACT

Aim To define biome-scale hotspots of phylogenetic and functional mammalian biodiversity (PD and FD, respectively) and compare them with 'classical' hotspots based on species richness (SR) alone.

Location Global.

Methods SR, PD and FD were computed for 782 terrestrial ecoregions using the distribution ranges of 4616 mammalian species. We used a set of comprehensive diversity indices unified by a recent framework incorporating the relative species coverage in each ecoregion. We built large-scale multifaceted diversity–area relationships to rank ecoregions according to their levels of biodiversity while accounting for the effect of area on each facet of diversity. Finally we defined hotspots as the top-ranked ecoregions.

Results While ignoring relative species coverage led to a fairly good congruence between biome-scale top ranked SR, PD and FD hotspots, ecoregions harbouring a rich and abundantly represented evolutionary history and FD did not match with the top-ranked ecoregions defined by SR. More importantly PD and FD hotspots showed important spatial mismatches. We also found that FD and PD generally reached their maximum values faster than SR as a function of area.

Main conclusions The fact that PD/FD reach their maximum value faster than SR could suggest that the two former facets might be less vulnerable to habitat loss than the latter. While this point is expected, it is the first time that it has been quantified at a global scale and should have important consequences for conservation. Incorporating relative species coverage into the delineation of multifaceted hotspots of diversity led to weak congruence between SR, PD and FD hotspots. This means that maximizing species number may fail to preserve those nodes (in the phylogenetic or functional tree) that are relatively abundant in the ecoregion. As a consequence it may be of prime importance to adopt a multifaceted biodiversity perspective to inform conservation strategies at a global scale.

Keywords

Conservation biogeography, diversity indices, functional diversity–area relationship, Hill's numbers, mammals, phylogenetic diversity–area relationship, species–area relationship.

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INTRODUCTION

Understanding the ecological and evolutionary processes driving the distribution of life on Earth is essential from both applied and theoretical perspectives. The quantification of biodiversity, central to conservation science, has recently moved from a focus on pure species counting (e.g. species richness, SR) to a more integrative approach. Assessments of biodiversity now consider the overall evolutionary history embedded within a set of taxa (i.e. phylogenetic diversity, PD) along with the diversity of ecological traits (i.e. functional diversity, FD). In conservation science, this novel approach has redefined the identification of species of conservation interest by taking their high evolutionary or functional distinctiveness into consideration (Isaac *et al.*, 2007; Mouillot *et al.*, 2013) and has also made it possible to detect unique macroecological assemblages (Forest *et al.*, 2007), for example 'cradles' and 'museums' of life (Chown & Gaston, 2000). Furthermore, the loss of FD or PD per unit of habitat loss is likely to be a better predictor of ecosystem vulnerability than the loss of single species. Indeed, the loss of a given amount of FD or PD, often assumed to be related to particular combinations of functional traits or of a certain lineage, respectively, may threaten the functioning of the ecosystem, whereas the loss of a given single species might not be noticeable if redundant species persist (Loreau *et al.*, 2002; Srivastava *et al.*, 2012).

This new perspective also provides fundamental insights into community assembly at multiple spatial scales (Mouquet *et al.*, 2012). A multifaceted approach may help unravel the different drivers of community structure (e.g. competition or environmental filtering; Webb *et al.*, 2002) or ecosystem functioning (Cadotte *et al.*, 2009; Gravel *et al.*, 2012). In macroecology, contrasting SR, PD and FD offers a potential means for disentangling the processes shaping large-scale diversity distribution (Davies & Buckley, 2011; Safi *et al.*, 2011; Huang *et al.*, 2012). For example, the global latitudinal diversity gradient has recently been re-interpreted from a novel evolutionary perspective, merging Earth's climatic history, phylogenetic diversity and species richness in a unified and testable framework (Hawkins *et al.*, 2012). A multifaceted perspective thus represents a promising avenue for exploring the distribution of diversity because it is at the crossroads between ecology, evolution and conservation biology but also palaeontology and palaeoclimatology (Hawkins *et al.*, 2006).

One of the most striking features of biodiversity is the spatial heterogeneity of its distribution, with some regions harbouring extraordinary levels of biodiversity: the so-called biodiversity hotspots (Reid, 1998; Ceballos & Ehrlich, 2006; Guilhaumon *et al.*, 2008). These have not only fascinated macroecologists, who try to understand their origins (e.g. the historical perspective; Wiens *et al.*, 2011), but also conservationists seeking the best opportunities to allocate the limited resources available for global-scale conservation. For example the biodiversity hotspots concept has been proposed to prevent the extinction of large numbers of endangered species, by protecting places 'where exceptional concentrations of endemic species are undergoing exceptional loss of habitat' (Myers *et al.*, 2000).

The most recent comparisons of the world-wide distribution of hotspots have been limited to different taxonomic groups and components of SR for a given taxon (e.g. endemic, total, endangered; Orme *et al.*, 2005; Ceballos & Ehrlich, 2006; Lamoreux *et al.*, 2006) or when carried out in a multifaceted context, have included only limited functional information [e.g. Huang *et al.* (2012) used only geographic range size and body mass as descriptors of mammal FD to define hotspots]. This lack of relevant trait information makes it difficult to adequately represent the spatial distribution of FD because geographic range size may not properly portray species niches, rather it is mostly influenced by historical biogeography and macroevolution (Gaston, 2003).

Here we identified global hotspots of mammalian taxonomic diversity (TD), PD and FD. We based our analyses on the updated version (Fritz *et al.*, 2009) of the dated phylogeny of Bininda-Emonds *et al.* (2007) and a set of functional traits encompassing important aspects of mammal resource use, selected to represent independent and informative niche dimensions (Safi *et al.*, 2011). We used the world's ecoregions (Olson *et al.*, 2001) to define geographical units harbouring unique species assemblages and ecosystems. Ecoregions have proven valuable for addressing a range of questions in macroecology and more applied conservation issues (Lamoreux *et al.*, 2006; Guilhaumon *et al.*, 2008).

To account for expected area effects on TD (Triantis *et al.*, 2012), PD (Morlon *et al.*, 2011) and FD (Cumming & Child, 2009) we constructed diversity–area relationships (DARs hereafter) for 13 terrestrial biomes (global-scale regions gathering ecoregions experiencing similar environmental conditions such as tundra or mediterranean forests). We used a model-averaging approach that fits 19 mathematical functions to the data (Guilhaumon *et al.*, 2008; Triantis *et al.*, 2012) and then computed an Akaike information criterion (AIC)-weighted average of the 19 predicted curves. To quantify the different types of diversity, we used a set of unified TD, PD and FD indices that weigh species coverage differently (Chao *et al.*, 2010) and correspond to modified versions of Faith PD (Faith, 1992), Phylogenetic entropy (Allen *et al.*, 2009) and Rao quadratic entropy (Rao, 1992) (see Methods). For each diversity index we identified as hotspots those ecoregions with the largest positive deviations from, respectively, SARs (species–area relationships), PDARs (phylogenetic diversity–area relationships) and FDARs (functional diversity–area relationships) and investigated their spatial congruences.

Our global exploration of mammals SARs, PDARs and FDARs reveals important mismatches between the spatial scaling and the geographical extremes of SR, PD and FD, calling for integrative approaches.

METHODS

Dataset

Mammal assemblages

We used the distribution maps provided by the Mammal Red List Assessment (http://www.iucnredlist.org/) for 4616 terrestrial species (for which we have functional traits; see below) to obtain occurrence data for each of the 827 ecoregions defined by Olson *et al.* (2001). We retained 782 ecoregions (mean number of ecoregions per biome = 60.1, SD = 53.3, min. = 17, max. = 223). Ecoregions are a valuable tool for studying multifaceted hotspots because they also serve as the basis of World Wildlife Fund conservation planning (Olson & Dinerstein, 1998), the international efforts of Nature Conservancy (Groves, 2003) and the delineation of Conservation International's Biodiversity Hotspots (Mittermeier *et al.*, 2004) and High Biodiversity Wilderness Areas (Mittermeier *et al.*, 2003). Furthermore, ecoregions have commonly been used to define taxonomic hotspots (Lamoreux *et al.*, 2006; Guilhaumon *et al.*, 2008) because they encompass relatively homogeneous biological systems. We retained ecoregions harbouring more than one mammal species and excluded mangrove ecoregions and large uninhabited parts of Greenland and Antarctica because of low data reliability or availability for these areas (Lamoreux *et al.*, 2006). Domestic mammals were also excluded from the analysis.

For each ecoregion and species, species coverage (C_i) was calculated as the intersected surface (in km^2) between the range of the species and the ecoregion. We then computed, for each species i, the following relative coverage (RC_i, equation 1)

$$RC_i = \frac{C_i}{\sum_i C_i}. \tag{1}$$

Basically a species will have low relative coverage in a given ecoregion if its distribution range is small. The relative coverage was used to calculate diversity indices incorporating relative abundance (see below). By doing this we were able to differentiate a species that is poorly represented in an ecoregion, but with a unique evolutionary history (e.g. a monotreme species) or with unique functional traits (e.g. a top predator), from species with a similar evolutionary history (or functional traits) but with greater occupancy in the ecoregion. This weighting scheme emphasizes species that are well distributed in the ecoregion. Establishing how our measure of relative coverage is important for conservation and ecosystem functioning is not straightforward. Nevertheless we believe that the evolutionary history/functional characteristics of a species that shows a very small distribution range in a given ecoregion should not have the same theoretical influence on PD/FD as a widespread species in this ecoregion. Although it is unlikely that our measure of relative coverage represents a direct measure of local species abundance, it has been shown that a positive relationship between range size and local abundance is common (Gaston *et al.*, 2000). Nevertheless departure from this relationship probably exists. First, we did not use the complete range size of the species but only its extent in the ecoregion. Second, we acknowledge that the potential important residual variation that exists around the relationship may depend on species life-history traits. For example species with high dispersal abilities (or a species at a high level in the trophic hierarchy) may have a large range size but be relatively rare at the local scale. It is also possible that a species with a narrow range may exhibit a high local abundance, for example because it uses an abundant resource that is restricted to a small area of the ecoregion. Nevertheless, we believe that our measure of species coverage was a needed first step to incorporate abundances into the definition of PD/FD hotspots.

Phylogeny and functional traits

We used the calibrated and dated ultrametric phylogenetic tree updated by Fritz *et al.* (2009) from Bininda-Emonds *et al.* (2007). We computed functional diversity indices using body mass (log-transformed), diet (vertebrates, invertebrates, foliage, stems and bark, grass, fruits, seeds, flowers, nectar and pollen, roots and tubers), habits (aquatic, fossorial, ground-dwelling, above-ground-dwelling), activity period (diurnal, nocturnal, cathemeral, crepuscular) and litter size (data from Safi *et al.*, 2011). These traits encompass important aspects of mammal resource use, including the temporal and spatial windows used to get their food. They represent independent and informative niche dimensions for evaluating variability in mammal traits related to important ecosystem processes, such as decomposition and seed dispersal, as well as trophic control (Sekercioglu, 2010).

Diversity indices

A myriad of methods have been proposed in the last years to include species traits in diversity indices (Pavoine & Bonsall, 2011). Here we follow the comprehensive framework from Chao *et al.* (2010), which unifies a set of TD, PD and FD indices based on Hill numbers. There were three reasons for this. First it unifies most of the TD, PD and FD indices used in the literature (see below and Table 1). Second it represents equivalent numbers of species to satisfy the replication principle that ensures intuitive results for ecologists and conservation biologists (Jost, 2006; Chao *et al.*, 2010). For example, if the PD of an assemblage equals d (d being a real positive number), it has the same diversity as a community consisting of d equally abundant and maximally distinct species (i.e. with the maximum distance observed in the phylogeny). Third, we present here one of the only comprehensive and intuitive frameworks that incorporates relative species coverage (or abundance) into biodiversity indices.

Phylogenetic diversity

Consider a phylogenetic tree composed of a set B_t of i branches. PD can be defined as the 'mean diversity of order q over T years' (Chao *et al.*, 2010):

$${}^{q}\bar{D}(T) = \left\{ \sum_{i \in B_T} \frac{L_i}{T} a_i^q \right\}^{1/(1-q)} \tag{2}$$

where L_i is the length of branch i in the set B_t, a_i is the total abundance descended from branch i (i.e. the summed

Table 1 The set of diversity indices used in the analysis.

		Type of indices		
Original version				
Without species differences		SR	Shannon	Simpson
With species differences	Phylo.	PD (Faith, 1992)	Hp	QE*
	Functio.	FD (Petchey & Gaston, 2006)	Not named	QE*
Hill numbers version				
Without species differences		SR	exp (Shannon)	1 / Simpson
With species differences	Phylo.	Faith$_{\text{cor}}$ PD	Allen$_{\text{cor}}$ PD	Rao$_{\text{cor}}$ PD
	Functio.	Faith$_{\text{cor}}$ FD	Allen$_{\text{cor}}$ FD	Rao$_{\text{cor}}$ FD
Link between original and Hill numbers version		Faith$_{\text{cor}}$ PD = PD / T Faith$_{\text{cor}}$ FD = FD / T	Allen$_{\text{cor}}$ PD & FD = exp (Hp/T)	Rao$_{\text{cor}}$ PD & FD = 1/ (1- QE)
q value		0	1	2
Weighting by species' coverage		No	Yes	Yes

For this study we used the Hill numbers version with species differences. These transformed versions obey the replication principle and can be grouped in a unified formula using the *q* parameter (see equation 2 and Chao *et al.*, 2010). The table gives the abbreviations used in the text. It also provides the link between original and transformed indices and indicates if coverage is used in the calculation of the indices.

*QE can be calculated with any distances (phylogenetic or functional) between species.

T represents the height of the phylogenetic tree or the functional dendrogram. PD, Phylogenetic diversity; FD, Functional diversity; Hp, Phylogenetic entropy (Allen *et al.* 2009); QE, Rao quadratic entropy (Rao, 1982); SR, Species richness; Phylo, Phylogenetic; Functio, Functional.

abundance or relative coverage of species descending from this branch) and T is the height of the tree. The parameter q affects the influence of node (or branch segment) abundance on the diversity index: a high q-value gives more weight to nodes with high relative abundances. This general formula encompasses a set of well-known diversity indices. With $q = 0$, Faith$_{\text{cor}}$ PD = PD$_{\text{Faith}}$/T, PD$_{\text{Faith}}$ being the phylogenetic diversity defined by Faith (1992) and Faith$_{\text{cor}}$ PD being the corrected version of the Faith PD. With $q = 1$, Allen$_{\text{cor}}$ PD = $\exp(H_p/T)$, H_p being the phylogenetic entropy as defined by Allen *et al.* (2009) and Allen$_{\text{cor}}$ PD being the corrected version of $H_{p.}$. With $q = 2$, Rao$_{\text{cor}}$ PD = $1/(1 - \text{QE})$, QE being the quadratic entropy defined by Rao (1982) and Rao$_{\text{cor}}$ PD being the corrected version of QE (see Table 1 for details). To summarize, q influences the relative weight of widespread versus rare species in the computation of the diversity index. It gives progressively more weight to widespread species and progressively ignores rare species. This point could be problematic if a species is rare and endemic in this ecoregion because we will progressively ignore this unique species. Nevertheless our study aims to characterize the evolutionary history and the functional characteristics that are widespread in a given ecoregion (and somehow representative), which justifies the use of Chao *et al.*'s (2010) framework.

Functional diversity

We adapted previous indices for FD. First, we calculated functional distance among pairs of species using the Gower distance, which can mix categorical and continuous traits with equal weight and can cope with missing values (some traits were missing for 80 species, representing less than 2% of our dataset). We then applied a hierarchical cluster algorithm to convert the functional distance matrix into a functional dendrogram ensuring the ultrametric property (note that using non-ultrametric functional distances did not change our conclusions) using the unweighted pair group method with arithmetic mean (UPGMA) (function *hclust* in R; R Development Core Team, 2010). The corresponding FD indices were named Faith$_{\text{cor}}$ FD, Allen$_{\text{cor}}$ FD and Rao$_{\text{cor}}$ FD (see Table 1). Note that Faith$_{\text{cor}}$ FD is equivalent to the Petchey & Gaston (2006) definition of FD (i.e. 'the total branch length of a functional dendrogram'). Like Faith$_{\text{cor}}$ PD, Faith$_{\text{cor}}$ FD is intrinsically correlated to SR (Huang *et al.*, 2012). This is the case for all the dendrogram-based approaches for estimating functional volume. Nevertheless it is interesting to use it here because it is directly comparable with Faith$_{\text{cor}}$ PD and represents a diversity volume (or 'richness' *sensu* Pavoine & Bonsall, 2011). In addition we computed FD using body mass only to test to what extent the use of multiple traits influences our results. Note also that the expected correlation between SR and FD/PD based on dendrogram becomes weaker when moving from $q = 0$ to $q = 2$.

Species diversity

For maximally distinct species (i.e. a star phylogeny or star functional dendrogram), these indices actually constitute species diversity indices, namely SR when $q = 0$, the exponential of Shannon entropy when $q = 1$ and the inverse of Simpson diversity when $q = 2$ (see Table 1; Chao *et al.*, 2010). We used these TD indices to compare appropriately PDAR/FDAR with the corresponding SAR (i.e. comparing DARs that are built with diversity indices based on the same q). However, we always compared PD/FD hotspots with those based on SR (and not Simpson or Shannon indices) since a list of hotspots based only on TD indices (i.e only quantifying evenness in abundances) might not be appropriate in a conservation context.

Constructing DARs

To account for expected area effects on SR, PD and FD, we provide a construction of DARs for 13 terrestrial biomes (Olson *et al.*, 2001). Such DARs correspond to a non-overlapping design, i.e. they are built from single data points, which corresponds to a type IV curve in Scheiner's (2003) terminology.

Set of models

A wide range of statistical models have been proposed to describe SARs (Tjørve, 2009). Here, 19 models were selected to fit SAR, PDAR and FDAR following Triantis *et al.* (2012) (see Appendix S1 in Supporting information). Recent attempts to model PDAR only used the power model (Morlon *et al.*, 2011) but, given the uncertainty regarding the shape of PDAR and FDAR, we tested a large spectrum of models. These models were chosen because they vary in form (e.g. sigmoid or convex, including asymptotic relationships) and complexity (two to four parameters).

Model fitting

We constructed 117 datasets (9 indices × 13 biomes) and fitted 19 models to each dataset, for a total of 2223 DARs. We carried out our analyses using another dataset that also adds an 'artificial' point of null diversity and null area (0.001 and 0.001 to avoid computing problems).

Models were fitted using nonlinear regression with minimization of the residual sum of squares. Models were further evaluated by examining the normality and homoscedasticity of residuals. To do so, we applied the Lilliefors's test for normality and a Pearson correlation between squared residuals and area for homoscedasticity. Previous studies (e.g. Guilhaumon *et al.*, 2008) considered a model valid when the *P*-value associated with the normality and homoscedasticity tests exceeded the arbitrary threshold of 5%. All DAR analyses were carried out using an updated version of the 'mmSAR' package (Triantis *et al.*, 2012) for the R statistical and programming environment (R Development Core Team, 2010).

Model averaging

For each dataset, we discriminated between different models using an information-theory framework designed to evaluate multiple working hypotheses (Burnham & Anderson, 2002). The AIC can be used to evaluate the goodness of fit of different non-nested models on a given dataset. The weights of evidence were then derived from the AIC values to evaluate the relative likelihood of each model given the data and the set of models (Burnham & Anderson, 2002). Using these weights we derived averaged DARs for each biome and each diversity index.

Model standardization and comparison

For each DAR, we divided each predicted diversity value by that of the largest ecoregion in the considered biome in order to report the percentage of maximal diversity reached in this largest ecoregion. The resulting standardized DAR therefore ranges between 0 and 1, which makes it possible to compare the scaling of different diversity facets with area (see below).

Hotspot lists and spatial congruence

Hotspot selection

Averaged residuals were calculated from the standardized averaged model (as defined above). A positive residual for a given ecoregion means that observed diversity is higher than expected given its area. Hotspots were defined as those ecoregions with the highest residuals. We ranked ecoregions according to their averaged residuals: the higher the residuals, the higher the concentration of biodiversity in the ecoregion. Note that ranking in terms of original or standardized curve/observed diversity gives exactly the same results because standardization is linear (see Appendix S2). We also derived an averaged rank across SR, PD and FD hotspots to provide an integrative definition of a hotspot by summing up the ranking for each ecoregion across the biodiversity facets (i.e. SR, PD and FD).

Impact of DAR shape on hotspot lists

We investigated whether PDARs and FDARs were different enough from corresponding SAR to deeply modify the hotspot rankings. In other words we wanted to test whether PDARs/FDARs are needed to define hotspots or if SAR is a good proxy for FDAR/PDAR when defining hotspots. SAR, PDAR and FDAR were directly comparable thanks to the standardization procedure explained above (they are all expressed as a proportion of the maximal diversity predicted for the largest ecoregion and thus vary between 0 and 100%). We computed the difference between the standardized PD/FD in each ecoregion and the proportion of diversity predicted by the area using the SAR (and not PDAR/FDAR as previously done) and ranked these differences to compute lists of hotspots. Then, we compared the congruence between PD/FD hotspot lists derived from SAR and the 'natural' PD/FD hotspot lists derived from the PDAR/FDAR (as explained in the previous section). If SARs correctly model the scaling of PD/FD with area, the lists of hotspots should be very similar. In this case, SARs would be well suited to direct modelling of the spatial scaling of PD/FD to define hotspots and it would not be necessary to construct explicit PDAR/FDAR.

RESULTS

We start first by reporting the general results of the statistical procedures related to the DAR estimations and then by describing the outcomes of this procedure for the hotspot lists.

DAR modelling

Convergence, homoscedasticity and normality

One of the 19 models showed unrealistic fits (Epm2, see Appendix S1) and was not considered in the analysis. Of the remaining

2106 model fits (13 biomes × 18 models × 9 indices), 1895 (90%) converged. Amongst the different indices, models fitting Rao-based DAR showed the highest non-normality of residuals (homoscedasticity was not the limiting factor; results not shown). Indeed at the 1% level test of homoscedasticity and normality of the residuals, 53, 68 and 75% of the models were valid for the Rao-, Allen- and Faith-based indices, respectively.

Relative model fit

The variation in diversity indices explained by area was generally high (the median R^2 of the best function in each dataset was 0.5; see Appendix S3) but was quite variable. The R^2 of the best model for each dataset ranged from $R^2 = 0.0001$ (asymptotic model fitting SR in Montane grasslands and shrublands) to $R^2 = 0.95$ (the P2 function fitting Rao_{cor} PD in temperate coniferous forest; see Appendix S3). No single best model outperformed across all data sets, with model selection varying markedly across biomes and diversity indices and revealing substantial levels of uncertainty with different models showing equivalent levels of support (see Appendix S4).

Model shape

To illustrate the difference between the rate of increase in SAR and FDAR/PDAR, we plotted the difference between predicted PDAR/FDAR and the corresponding predicted SAR for four biomes that cover the latitudinal gradient (Fig. 1, Appendix S5). The starting value of the curve was zero in most cases, while differences between PDAR/FDAR tended to zero as area increased. This means that PDAR/FDAR and SAR have the same proportion of diversity when area tends to zero (generally it was 0% of maximum diversity) and also end at the same point because of the standardization (their respective maximum 100%). In the intermediate area between the two extremes, PDAR and FDAR were in general higher than SAR (i.e. a positive difference), indicating that PDAR and FDAR reached their

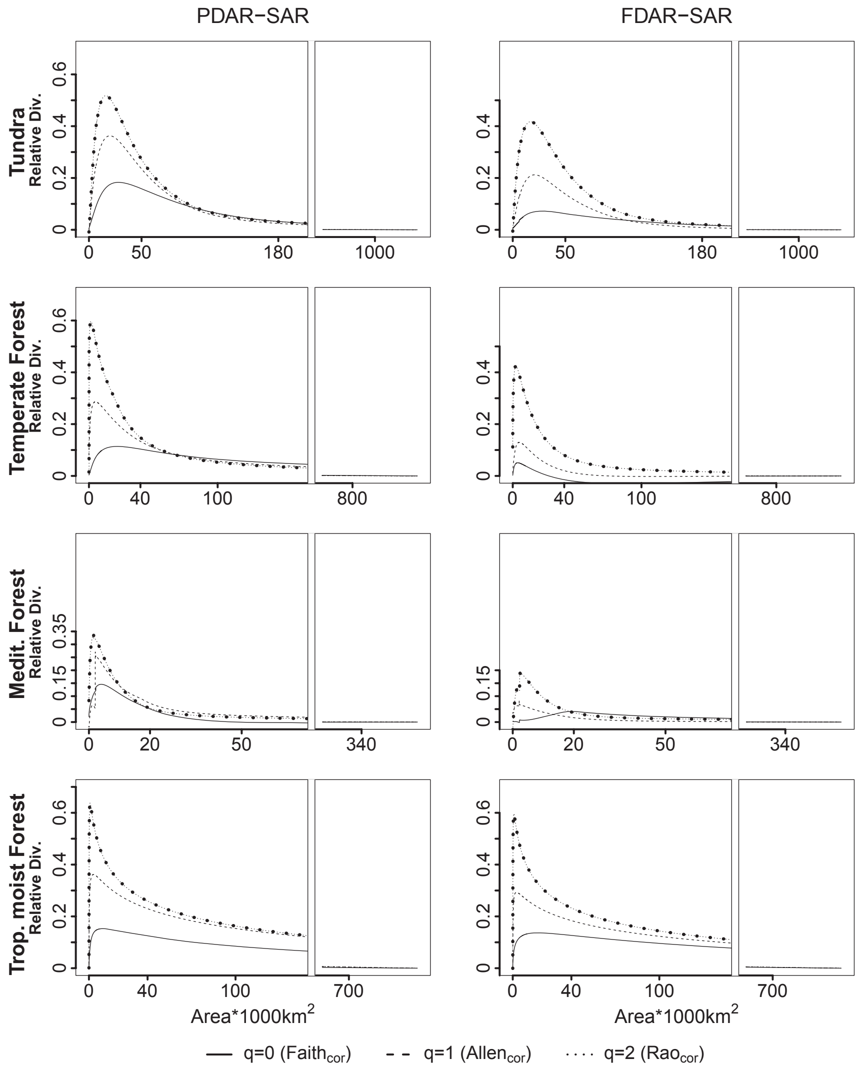

Figure 1 Differences between predicted phylogenetic diversity–area relationship (PDAR)/functional diversity–area relationship (FDAR) values and corresponding predicted species–area relationship (SAR) values. Rows correspond to different biomes, while columns represent differences between diversity–area relationship (DAR): PDAR–SAR and FDAR–SAR. For each plot, the differences between PDAR/FDAR and SAR are represented for three values of q: 0 ($\text{Faith}_{\text{cor}}$ index), 1 ($\text{Allen}_{\text{cor}}$ index) and 2 (Rao_{cor} index). Positive differences mean that PDAR or FDAR are higher than SAR. Area is given in km^2. Trop moist Forest, tropical moist forest; Medit. F., mediterranean forest; Relative Div., relative diversity.

maximum diversity faster than SAR. This difference increased with the *q* parameter defining the weight given to species coverage in the diversity indices ($\text{Faith}_{\text{cor}}$ to Rao_{cor}). PDAR and FDAR had a similar shape in most cases. Results were qualitatively equivalent when fitting DARs without artificial zeros except when area tended to zero: PDAR/FDAR started at a relatively higher percentage of diversity than SARs and thus the difference between PDAR/FDAR and SAR curves tended to start with positive values for some biomes (see Appendix S5).

Functional and phylogenetic hotspots

We extracted residuals (i.e. observed minus predicted diversity) from each averaged DAR and ranked them to define hotspots of diversity. As an example, we mapped diversity ranks for tropical moist forests (Fig. 2; but also see Appendix S6 for all biomes and indices) considering $\text{Allen}_{\text{cor}}$ PD and FD hotspots as well as the traditional SR hotspots. SR rankings were relatively well distributed in the three continents whereas PD $\text{Allen}_{\text{cor}}$ hotspots were much more concentrated in the Afrotropics (and Central America) or in the Afrotropical and Indomalaysian realms for FD $\text{Allen}_{\text{cor}}$ hotspots. Interestingly, when focusing on the five hottest hotspots for this biome (Table 2), two important results emerged: (1) the list of SR hotspots shared few ecoregions with the lists of $\text{Allen}_{\text{cor}}$ PD, FD and integrative hottest hotspots (i.e. two, one and three ecoregions, respectively); and (2) the hottest FD and PD hotspots shared only two ecoregions.

The same hotspot mismatches were found across all biomes (Fig. 3). For example, with the cut-off point for defining a hotspot set at the 5% richest ecoregions we found that congruence ranged from 5% (FD Rao_{cor} hotspots versus SR hotspots) to 74% (PD $\text{Faith}_{\text{cor}}$ hotspots versus SR hotspots). Interestingly, when compared with hotspots defined with SR, hotspots defined with the $\text{Faith}_{\text{cor}}$ index strongly matched, while those defined with Rao_{cor} strongly mismatched; those defined with $\text{Allen}_{\text{cor}}$ fell in between. In other words, the hotspot rankings were significantly correlated – but were not equal – across different indices (see Appendix S7). These differences were robust against the threshold used to define valid DAR models (i.e. the *P*-value threshold used to reject a model based on the non-normality and/or homoscedasticity of its residuals; see Appendix S8) due to the weak influence of this threshold on the definition of hotspots (see Appendix S9). We also explored to what extent the use of multiple traits influences the definition of hotspots. We show that FD hotspots lists based on body mass only differ from FD hotspots defined with our complete set of traits (Appendix S9).

On average, using SAR instead of PDAR/FDAR to define PD/FD hotspots marginally modified the hotspot list (Appendix S10). However, it turns out that there is still high variability between biomes. For some of these, using SAR instead of PDAR/FDAR dramatically changes the hotspot lists. Note also that the nonlinear fit of the power model alone gave fairly similar results to those obtained when using model averaging to define hotspots (Appendix S11).

DISCUSSION

We found considerable geographical mismatches between global mammal hotspots of SR, PD and FD and, quite importantly, found that the magnitude of the mismatches depends on the index considered, which highlights the importance of considering a variety of indices (Huang *et al.*, 2012). Mismatches were higher with Rao-based indices (Rao_{cor}), lower when using the $\text{Faith}_{\text{cor}}$ indices and in between for the $\text{Allen}_{\text{cor}}$ indices, whatever the facet considered. This is not entirely surprising given the correlation between SR and PD/FD (high with $\text{Faith}_{\text{cor}}$, medium with $\text{Allen}_{\text{cor}}$ and weak with Rao_{cor}).

Rodrigues *et al.* (2011) have already pointed out a high congruence between $\text{Faith}_{\text{cor}}$ PD hotspots and SR hotspots. As a result, they concluded that incorporating phylogenetic information is not a major concern in conservation. Nevertheless, incorporating relative species coverage into the definition of multifaceted hotspots alters this conclusion. $\text{Faith}_{\text{cor}}$ indices do not incorporate species abundance or coverage and give equal weight to rare and dominant evolutionary history in a given location (Chao *et al.*, 2010). However, it seems appropriate to give less weight to particular evolutionary histories (i.e. particular branch paths) that are rare in a given ecoregion because they are less representative than a widespread species in this ecoregion. $\text{Allen}_{\text{cor}}$ and Rao_{cor} indices give more weight to a given branch if it is long and well represented in an ecoregion. For instance, hotspots defined using PD Rao_{cor} are mostly concentrated in the Australasian realm because of the presence of marsupials. This group has a unique evolutionary history since they diverged 147 million years ago from placentals (extant eutherians, containing the majority of mammals) and are widely distributed (i.e. have large coverage) through the Australasian ecoregions (and not in South American ecoregions). These results are congruent with those of a recent study revealing important mismatches between global hotspots of mammal trait variance and SR (Huang *et al.*, 2012). Although these authors used a different approach (they used grid cells as geographical units and did not use information about species coverage), these close results are probably explained by the fact that Rao_{cor} indices are linked to a measure of variance (Pavoine & Bonsall, 2011). We also showed that the use of body mass alone to define FD hotspots is not sufficient to match the FD hotspots defined with our complete set of traits, but it still represents an acceptable approximation. We also showed that PD and FD hotspots are not always congruent, suggesting that PD is not necessarily a good surrogate for FD (at least for the functional traits selected here).

As well as defining hotspots, DARs have been shown to be useful in both applied and fundamental ecology. We found that $\text{Faith}_{\text{cor}}$ PDAR and FDAR generally reach their maximum faster than SAR (Cumming & Child, 2009). This result was expected, since $\text{Faith}_{\text{cor}}$ PD and FD explicitly account for redundancy between species while SR does not. More specifically, it is possible that small sample areas already contain a broad set of phylogenetic history and FD (e.g. a mouse and an elephant), whereas large sample areas contain relatively more redundant

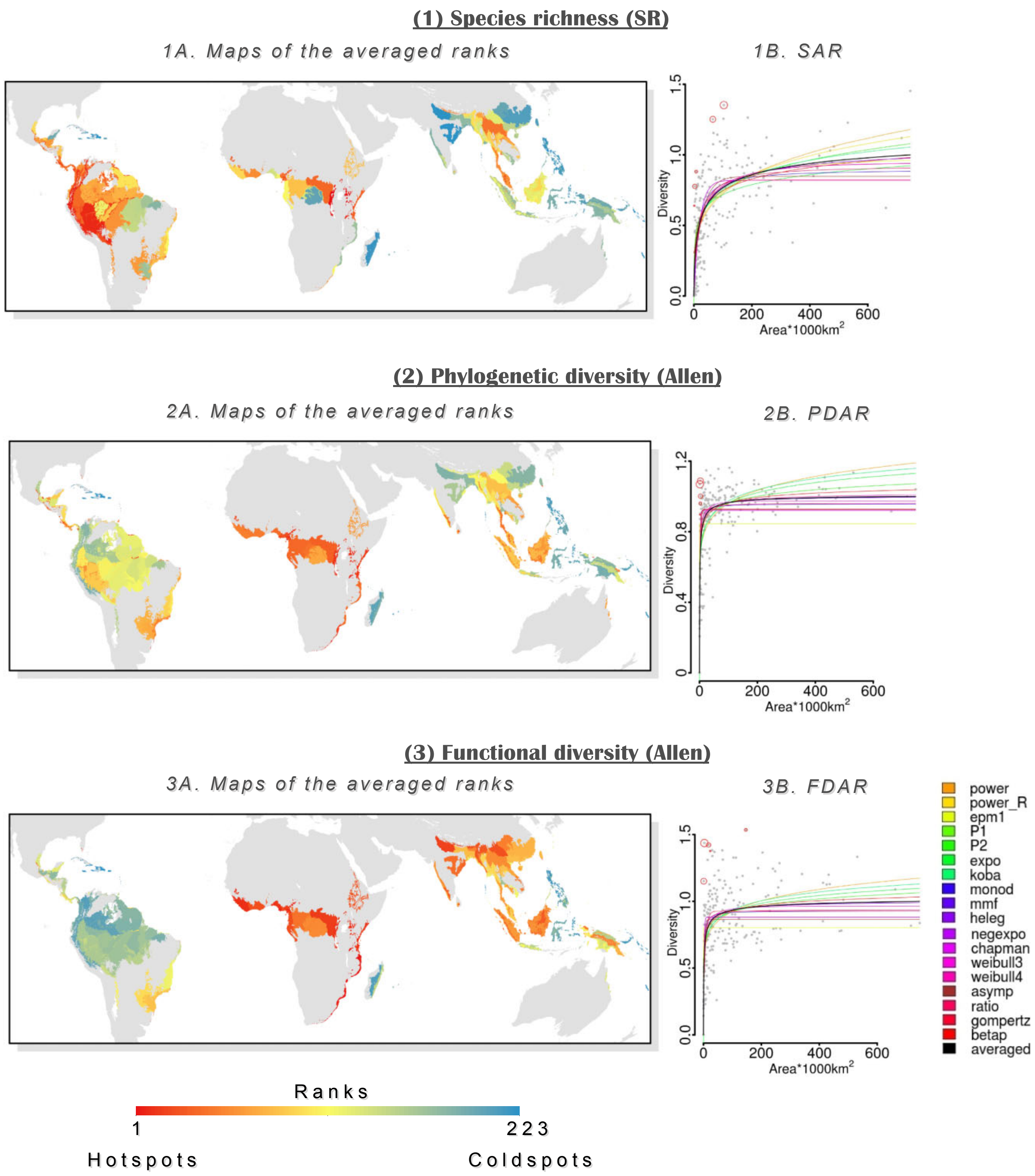

Figure 2 Taxonomic, phylogenetic and functional mammal hotspot selection for tropical moist forests. For each biodiversity facet (1, species richness; 2, phylogenetic diversity ($\mathrm{Allen}_{\mathrm{cor}}$ PD); and 3, functional diversity ($\mathrm{Allen}_{\mathrm{cor}}$ FD)) a map (a) and a diversity area relationship (b) are presented. Graphs (b) represent the species–area relationship (SAR), phylogenetic diversity–area relationship (PDAR) and functional diversity–area relationship (FDAR). Model fits are shown with a coloured curve (see legend) and the averaged fit is presented in black. Red circles indicate hotspots, the larger the diameter, the higher the ranking. Maps (a) represent the derived ranks from the residuals of the averaged model presented in (b).

Table 2 The five hottest hotspots of tropical and subtropical moist broadleaf forest.

Rank	Ecoregions	Area (km^2)	REALM
Traditional hotspots (SR)			
1	Albertine Rift montane forests	103,403	AT
2	East African montane forests	65,199	AT
3	Eastern Panamanian montane forests	3031	NT
4	Atlantic Coast restingas	7850	NT
5	Mount Cameroon and Bioko montane forests	1141	AT
Phylogenetic hotspots (Allen$_{\mathrm{cor}}$ PD)			
1	Mount Cameroon and Bioko montane forests	1141	AT
2	Knysna–Amatole montane forests	3061	AT
3	Peninsular Malaysian peat swamp forests	3610	IM
4	Eastern Panamanian montane forests	3031	NT
5	Chimalapas montane forests	2077	NT
Functional hotspots (Allen$_{\mathrm{cor}}$ FD)			
1	Knysna–Amatole montane forests	3061	AT
2	Mount Cameroon and Bioko montane forests	1141	AT
3	KwaZulu–Cape coastal forest mosaic	17,779	AT
4	Southern Zanzibar–Inhambane coastal forest mosaic	146,463	AT
5	Eastern Arc forests	23,556	AT
Integrative hotspots (Allen$_{\mathrm{cor}}$ PD and FD and SR)			
1	Mount Cameroon and Bioko montane forests	1141	AT
2	Eastern Arc forests	23,556	AT
3	East African montane forests	65,199	AT
4	Albertine Rift montane forests	103,404	AT
5	Peninsular Malaysian peat swamp forests	3610	IM

AT, Afrotropics; IM, Indomalaysian; NT, Neotropics; PD, phylogenetic diversity; FD, functional diversity; SR, species richness. Allen$_{\mathrm{cor}}$ PD and FD correspond to modified version of Allen entropy.

species (e.g. several species of mice) and thus PDAR/FDAR reach their maximum faster than SAR.

Morlon *et al.* (2011) obtained a similar result for PDAR on nested Mediterranean plant communities ranging from 6.25 to 400 m^2 of spatial extent. They used a power law (see Appendix S1) to model PDAR and SAR and found that the rate of increase in Faith PD with area (z_{PDAR}) was slower that in SR (z_{SAR}). When standardizing DARs, PDAR is above SAR if $z_{\mathrm{PDAR}} < z_{\mathrm{SAR}}$. They showed that protected areas in Australian mediterranean-like regions (representing 13% of the regions) capture 72% of PD, but only 56% of SR, indicating that PDAR accumulates total diversity faster than SAR.

Our results show that if only a fraction of the total biome area is protected, the percentage of remaining PD (compared with the initial PD) will be higher than the percentage of remaining species. If we consider that PD or FD are better predictors of ecosystem functioning, resistance or resilience (Cadotte *et al.*, 2009; Gravel *et al.*, 2012) than SR, it means that ecosystem features might be more robust to species loss than previously predicted (but see Mouillot *et al.*, 2013).

We also found that a key feature of a comprehensive measure of diversity is that when rarely represented evolutionary history is progressively removed (i.e. using different values of q), the differences between PDAR/FDAR and SAR increase. In other words, PD/FD of abundant lineages reaches its maximum faster than when considering all lineages having the same coverage. This result suggests that the evolutionary history or functional traits of well-represented taxa are relatively more rapidly sampled when area increases. For example, branches of major mammal lineages (e.g. bats, rodents or carnivores) are probably already well sampled in small ecoregions and thus PD or FD reach their maximum faster than TD in larger sample areas. It follows that well-represented functional/phylogenetic biodiversity might be robust to habitat loss, a point that is not detected when considering all lineages having the same coverage.

Although SARs have been thoroughly investigated (Scheiner, 2003), we have shown that there is not a single best model that fits all the data. Thus the automatic use of a single model (traditionally the linear version of the power model) is not justified. Conversely, to date PDAR and FDAR have been subject to very little investigation (but see Cumming & Child, 2009; Morlon *et al.*, 2011; Wang *et al.*, 2011; Helmus & Ives, 2012). Here, given the important variability across biomes and indices, we also show that a single best model does not exist for PDAR and FDAR. Nevertheless the model-averaging framework allows these uncertainties to be taken into account and we used an averaged prediction to remove the area effect on PD/FD. We also asked whether the averaged SAR could be a good proxy of the averaged PDAR/FADR to remove this area effect to define PD/FD hotspots. We demonstrated that there is a notable difference between PD/FD hotspot lists defined using PDAR/FDAR and those defined using SAR, suggesting that the construction

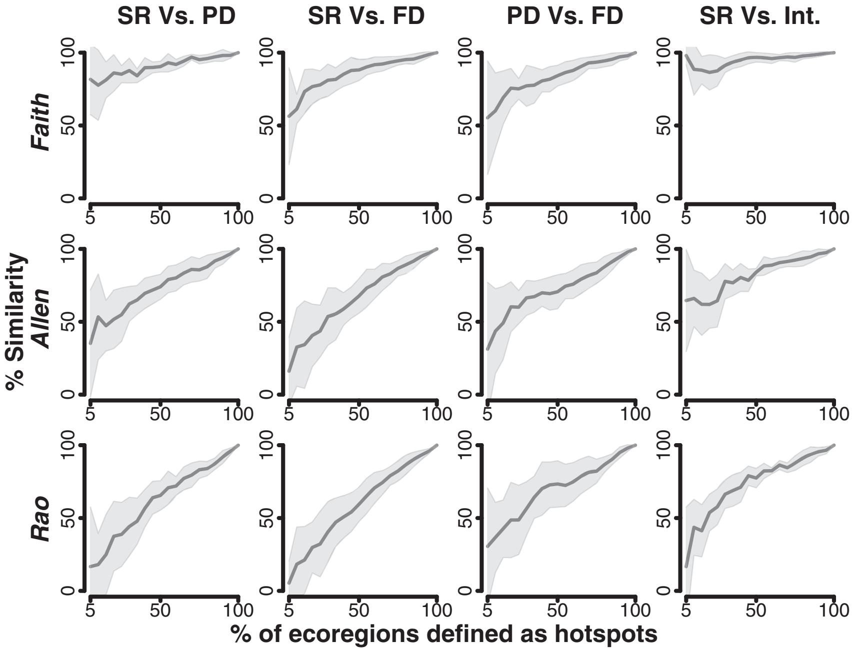

Figure 3 Relationships between the threshold used to define hotspots (expressed in percentage of ecoregion defined as a hotspot) and the similarity between corresponding hotspot lists. From the left to the right columns we compared species richness and phylogenetic diversity hotspots (SR Vs. PD, species richness and functional diversity hotspots (SR Vs. FD), phylogenetic and functional diversity hotspots (PD Vs. FD), species richness and integrative hotspots (agreement between the three facets, SR Vs. Int.). From the top to the bottom row we used $\text{Faith}_{\text{cor}}$, $\text{Allen}_{\text{cor}}$ and Rao_{cor} as PD and FD. The dark continuous line represents the mean percentage of congruence of hotspot lists averaged across biomes; the shaded polygon is the associated standard error of the mean. The relative congruence among hotspot lists of two biodiversity facets was determined as the number of ecoregions identified as hotspots by both, divided by the total number of ecoregions in a group.

of PDAR/FDAR is required to define functionally or phylogenetically based hotspots and that SAR alone cannot be used for this purpose.

We constructed DARs using a particular experimental design (Scheiner, 2003) but we are aware that all methods for constructing DARs have their own drawbacks and we suggest that the next challenge in the study of large-scale multifaceted DARs is to test different methodological designs. For example, the strictly nested design (SNQ) of Storch *et al.* (2012) seems particularly interesting to analyse. Nevertheless, since our work was about delineating hotspots of diversity, we had to construct DARs using a non-overlapping design.

CONCLUSION

Here we used a unified framework for building large-scale DARs for each facet of mammal diversity. The spatial scaling of each facet revealed that PD/FD reach their maximal diversity faster than SAR, suggesting that PD/FD might be less vulnerable than SR to habitat loss. In addition, we extracted the area effect on the diversity of individual terrestrial ecoregions to identify multifaceted hotspots of diversity. We showed that multifaceted hotspots are not necessarily congruent and, thus, that SR, PD and FD are not necessarily good surrogates for each other, especially when considering relative species coverage. Although the identification of global hotspots is important as an initial coarse-scale assessment of the conservation value of different regions (Lamoreux *et al.*, 2006), several challenges would need to be addressed before our results could be directly transferred into conservation planning actions.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Diversity–area relationship model list.
Appendix S2 Proof of rank invariance after standardization.
Appendix S3 Variance explained by the diversity–area relationships.
Appendix S4 Species–area relationship, phylogenetic diversity–area relationship and functional diversity-area relationship model selection patterns.
Appendix S5 Analysing model shape by plotting differences in diversity–area relationships.
Appendix S6 Maps of taxonomic, phylogenetic and functional mammal hotspots.
Appendix S7 Correlation of ranks between facets.
Appendix S8 Relationships between the threshold used to define hotspots and the congruence between hotspots.
Appendix S9 Robustness of the hotspots lists to choice of diversity–area relationship model.
Appendix S10 Congruence between functional diversity hotspots defined with different sets of functional traits.
Appendix S11 Importance of diversity–area relationship construction for defining multifaceted hotspots.
Appendix S12 Comparing model averaging and the power model alone to define hotpots.

BIOSKETCH

F. Mazel is a PhD student mostly interested in macroecology and macroevolution. Specifically, he aims to describe and understand the distribution of biodiversity in the light of ecology, evolution, palaeontology and palaeoclimatology.

Author contributions: F.M., F.G., N.M., V.D., D.G., D.M. and W.T. designed the study. J.R. collected and formatted distribution data. M.V.C., R.L. and J.A.F.D.F. provided the functional traits database. F.M. ran the analysis and wrote the first draft of the manuscript; all authors contributed substantially to revisions.

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