Mammalian phylogenetic diversity-area relationships at a continental scale

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Abstract

In analogy to the species-area relationship (SAR), one of the few laws in Ecology, the phylogenetic diversity-area relationship (PDAR) describes the tendency of phylogenetic diversity (PD) to increase with area. Although investigating PDAR has the potential to unravel the underlying processes shaping assemblages across spatial scales and to predict PD loss through habitat reduction, it has been little investigated so far. Focusing on PD has noticeable advantages compared to species richness (SR) since PD also gives insights on processes such as speciation/extinction, assembly rules and ecosystem functioning. Here we investigate the universality and pervasiveness of the PDAR at continental scale using terrestrial mammals as study case. We define the relative robustness of PD (compared to SR) to habitat loss as the area between the standardized PDAR and standardized SAR (i.e. standardized by the diversity of the largest spatial window) divided by the area under the standardized SAR only. This metric quantifies the relative increase of PD robustness compared to SR robustness. We show that PD robustness is higher than

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SR robustness but that it varies among continents. We further use a null model approach to disentangle the relative effect of phylogenetic tree shape and non random spatial distribution of evolutionary history on the PDAR. We find that for most spatial scales and for all continents except Eurasia, PDARs are not different from expected by a model using only the observed SAR and the shape of the phylogenetic tree at continental scale. Interestingly, we detect a strong phylogenetic structure of the Eurasian PDAR that can be predicted by a model that specifically account for a finer biogeographical delineation of this continent. In conclusion, the relative robustness of PD to habitat loss compared to species richness is determined by the phylogenetic tree shape but also depends on the spatial structure of PD.

Keywords

species area-relationship; strict nested design; null models; phylogenetic diversity

Introduction

The species area relationship (SAR) describes the tendency of species richness (SR) to increase with area (Rosenzweig 1995). This relationship is documented for a wide range of taxonomic groups and ecosystems (Guilhaumon et al. 2008, Triantis et al. 2012) and its understanding is central to ecology and conservation biogeography (Rosenzweig 1995, Whittaker et al. 2005). For instance, the SAR is a key tool to estimate species extinctions from habitat destruction and climate change (Pimm and Raven 2000, Thomas et al. 2004, Pereira et al. 2010, Matias et al. 2014). Nevertheless a SAR approach reduces biological diversity to species richness only and fails to include the amount of evolutionary history in species assemblages (Mouquet et al. 2012). To fill this gap, the Phylogenetic Diversity Area Relationship (PDAR hereafter; Morlon et al. 2011) can help unravel the processes assembling communities across spatio-temporal scales and provides complementary tools for conserving the Tree of Life (Mazel et al. 2014). For instance, translating SAR into PDAR allows to predict the loss of PD through habitat destruction. This prediction is essential since the loss of a given amount of PD or the loss of an entire lineage could have strong negative ecological consequences since distinct lineages are likely to perform different functions (Cadotte et al. 2008, Mouquet et al. 2012).

Several mechanisms have been proposed to explain the SAR, such as sampling effects (Rosenzweig 1995), the effect of habitat size on extinction rates (MacArthur and Wilson 1967), the scaling of environmental heterogeneity with area (Kadmon and Allouche 2007) or dispersal limitation (Hubbell 2001). In complement to the SAR, the PDAR brings unique information about the different processes structuring biodiversity at different spatial scales, helping, for example, to quantify the effects of biotic interactions at small scales versus biogeographical processes at large scale. A particular feature of the PDAR is that the shape of the phylogenetic tree ultimately drives its relative position to the SAR. A star phylogeny would produce a PDAR proportional to the SAR, while a complete and recent polytomy at the tips of the tree would produce an extreme PDAR that would reach its maximum from the smallest area (see Figure 1.A). In addition to those mechanisms, biogeographic history together with ecological processes should also influence the PDAR (see Fig. 1.B). Allopatric

speciation and/or competition between close relative species would result in a relatively higher PD than expected for a given SR ('overdispersion'; Webb et al. 2002, O'Dwyer et al. 2012). Coexistence theory indeed predicts that similar species will compete more strongly than dissimilar species, leading to the exclusion of one of the similar species (HilleRisLambers et al. 2012). If we assume that niche differences are properly portrayed by phylogenetic differences, we predict a phylogenetic overdispersion (i.e. distantly related species co-occur) under competitive interactions (Webb et al. 2002, but see Mayfield and Levine 2010). Reciprocally, low PD may be expected if close relative species tend to co-occur because of shared environmental niches and/or geographic isolation of land mass (phylogenetic clustering; Webb et al. 2002, O'Dwyer et al. 2012, see Fig. 1.B). Overall the difference between SAR and PDAR curves is thus very informative on the way the phylogenetic structure of assemblages varies across spatial scales.

In summary the PDAR is ultimately influenced by (1) the shape of the SAR that depends on species range placement over space (e.g. either 'clumped' or random), (2) the structure of the phylogenetic tree and (3) the species range placement in regards to the phylogeny (that ultimately depends on eco-evolutionary processes). Since the pioneering work by Morlon et al. (2011), that first introduced PDAR, no study has tried to explain large scale PDARs and to disentangle the relative influence of these three factors.

In this paper we report the first large-scale analysis of PDAR over the globe for mammal assemblages. We used the calibrated and dated ultrametric phylogenetic tree updated by Fritz et al. (2009) from Bininda-Emonds et al. (2007). We extracted the distribution maps provided by the Mammal Red List Assessment (http://www.iucnredlist.org/) for 4616 terrestrial species to obtain occurrence data on worldwide grid cells of approximately 110*110 km and used a strictly nested design recently published (SNQ; Storch et al. 2012) to produce median SAR and PDAR at a continental scale (i.e. we computed median SR and PD over each spatial scale to produce median SAR and PDAR respectively). First we ask whether PDAR differs from the SAR at a continental scale and how this difference may affect the robustness of PD to habitat loss. To do so we define the relative robustness of PD (compared to SR) to habitat loss as the area between the standardized PDAR and standardized SAR (i.e. standardized by the diversity of the largest spatial window) divided by the area under the standardized SAR only (named 'relative Area Under the Curve', AUC_r). This metric quantifies the relative increase of PD robustness compared to SR robustness (Fig. 2). Second, we ask whether PDARs is a simple consequence of the observed SAR and a random sampling of species on the phylogenetic tree or if it also depends on eco-evolutionary processes. Assuming that the continental SAR for mammals can be adequately modelled by a random placement model of species ranges (Storch et al. 2012), we derive PDAR expectations that only rely on the phylogenetic tree shape. To do so we use a tip-shuffling null model that keeps the observed species range distribution, SAR and phylogenetic tree shape while shuffling the phylogenetic relationships among species. Third we ask whether AUC_r depends on the phylogenetic tree shape only (see Fig. 1.A) or if it is also an outcome of eco-evolutionary processes (see Fig. 1.B). To do so we take advantage of our null model approach to produce null AUC_r expectations. More specifically we estimate the effect of tree structure (see Fig. 1.A) on the relative robustness of PD to

habitat loss across continents. Our analyses confirm that PD might be more robust than SR to habitat loss but that this higher robustness differs across continents for different reasons.

Methods

1. Datasets and diversity metrics

We used the distribution maps provided by the Mammal Red List Assessment (http://www.iucnredlist.org/) for 4616 terrestrial species to obtain occurrence data on worldwide grid cells of approximately 110*110 km. The best resolution to use the IUCN maps is still under discussion in the literature (Storch et al. 2012, Jenkins et al. 2013). We here used the resolution commonly used at global scale (Belmaker and Jetz 2011, Storch et al. 2012). This was our basic unit to construct SAR and PDAR. Domestic, aquatic and semi aquatic mammals were excluded from the analysis.

We used the calibrated and dated ultrametric phylogenetic tree updated by Fritz et al. (2009) from Bininda-Emonds et al. (2007).

To characterize the PD of an assemblage we used the Faith's measure (Faith 1992). This metric represents a 'richness' or 'volume' of diversity (Pavoine and Bonsall 2011) and simply sums up branch lengths of the given species assemblage phylogeny (Rodrigues and Gaston 2002). Faith's measure is an intuitive and relatively simple measure of PD. It is also, by construction, generally highly correlated with SR (Huang et al. 2012, Tucker and Cadotte 2013). The use of any PD metric theoretically linked with SR in the description of PDAR has been criticized because PDAR would be biased by "spurious artefacts of a statistical relationship between species richness and area "(Helmus and Ives 2012). Here the comparison of the SAR and the PDAR within the standardisation and the null model that removes the effect of SR on PD (see section describing our null model approach) we propose avoid this artefact while it allows a simple interpretation of the results.

2. Constructing SAR & PDAR

Median and Median absolute deviance (MAD) of SR/PD were reported for each spatial scale (from 110*110 km up to 2200*2200 km) by using the framework proposed by Storch et al. (2012). We do not use mean SR and PD as the data was highly non-normal (see Supplementary Material 1 for examples of distributions of diversity). It uses a strictly nested quadrat design where a moving window (Leitner and Rosenzweig 1997, Lennon et al. 2001) reports the SR/PD of all possible windows of a given size within a continent. The median and MAD of SR/PD are then computed for each spatial scale. This procedure implies that some cells are counted several time for a given spatial windows and thus some pseudo-replication is inevitably introduced. Nevertheless all designs have their own drawbacks and SNQ have several important advantages (Storch et al. 2012). We implemented the algorithm within a reduced subset of the five continents (see Supp. Mat. 2 for further details) to avoid some border effect: i.e. for each scale (whatever its size) all pixels of the selected area of the continent will be sampled at least one time. The spectrum of spatial scale analysed was set between 1*1 to 14*14 cells for Australia (i.e. from approximately 110*110 km to 1540*1540 km) and from 1*1 to 20*20 cells for North and South America, Africa and

Eurasia (i.e. from approximately 110*110 km to 2200*2200 km) following Storch et al. (2012). Note that the resulting curve corresponds to a type I curve in the terminology proposed by Scheiner (2003).

3. Analysing SAR & PDAR

3.1. Comparing the relative shape of SAR & PDAR—We compared the shape of PDAR and SAR using two complementary approaches. First we fitted a power model (Rosenzweig 1995) to each SAR and PDAR. We then reported the slope (z) value of the linear model in a log-log space. These values were then used to depict in a simple way the relative shape of PDAR and SAR. Because PDAR and SAR are not necessarily best modelled by a power function (Guilhaumon et al. 2008, Mazel et al. 2014) we also (1) fitted alternative statistical models (see Supp. Matt. 3) and (2) directly compared PDAR and SAR without an a-priori function. As PD is expressed in units of times while SR in number of species, they are not directly comparable. Therefore we used a basic standardization procedure by rescaling each sampling windows PD/SR value by the value reached at the maximum sample size (Mazel et al. 2014). This gives a relative diversity value for each sampling windows, compared to the largest one (that thus represents 100%). We define the relative robustness of PD (compared to SR) to habitat loss as the area between the standardized PDAR and standardized SAR divided by the area under the standardized SAR only (eq. 1 and Fig. 2).

$$AUCr = \frac{AUC_{PDAR} - AUC_{SAR}}{AUC_{SAR}} \quad \text{Eq.1}$$

If we define the absolute robustness of PD/SR as the AUC under the PDAR/SAR, our metric quantifies the relative increase of absolute PD robustness compared to absolute SR robustness (Fig. 1). To study the relative increase of PD and SR with area we simply computed the local slope (or derivative) of PDAR & SAR on the standardized coordinates assuming a first point of null diversity and area. Indeed when area tends to zero, diversity also necessarily tends to zero (as sampled area becomes smaller than a single individual).

3.2. Understanding the absolute value of PDAR—Second we used a null model approach to describe and investigate the absolute value of PDAR. This approach allows to compare null expectations with the observed PDAR and avoids the bias caused by the correlation between PD and SR.

We chose to use the observed SAR as a starting point because it has already been shown to be modelled by a simple null model where species ranges are randomly distributed within the continent (Storch *et al.* 2012). Assuming the SAR, we computed a null PDAR expectation by randomly shuffling the tips of the phylogeny within a given pool of species. This procedure breaks the link between species range size/position and phylogenetic relationships but keep unchanged the distribution of range size and the local species richness (Hardy 2008). By repeating this procedure *n* times (see below), we were able to assess the significance of the observed PDAR relative to our null expectation (using a two-sided test).

In other words, for each randomization, we (1) shuffled the tips of the phylogeny within a given species pool (see below). The resulting randomized phylogeny was used to (2) compute null PD values for each basic grid cells (approximately 110*110 km) and we (3) applied the methodology described above to compute the resulting null median and MAD PDARs. Such null model may help unravel the determinants of the PDAR. For example we may expect competition (Pigot and Tobias 2013) or environmental filtering to occur at smaller scale, potentially leading to phylogenetic overdispersion or clustering respectively (Webb et al., 2002; but note that competition may also lead to clustering, see Mayfield & Levine, 2010). Also, phylogenetic clustering could be detected at larger scales because of biogeographical effect (Rosenzweig 1995). We used two null models that use either a (1) continental or a (2) biogeographic pool of species. We restricted the analysis of the biogeographic pool of species for Eurasia only because it is the only continent in our design that is a mix of distantly related zoogeographic regions (Wallace 1876, Holt et al. 2013).

(1) Continental pool of species: This null model simply shuffles the tips within the entire continental phylogeny. The significance of the observed values of PDAR was assessed by comparing observed values with 1000 randomized PDARs. We further confirmed this simulation approach by using analytical expectations of PD based on the framework of Nipperess and Matsen (2013, Supp. Mat. 4)

(2) Biogeographical pool of species: First we defined zoogeographic regions following the methodology of Holt et al. (2013). To do so we computed phylogenetic beta diversity values between each pair of grid cells from the Eurasian continent by using an index independent of species richness (Lennon et al. 2001, Holt et al. 2013):

$$\beta = 1 - \frac{a}{\min(b,c) + a} \quad \text{(Eq. 1)}$$

where a = the branch lengths shared by the two grid cells and b and c represent the branch lengths unique to each grid cell.

Then we identified group of grid cells (=zoogeographic regions) using the unweighted pair group method with arithmetic mean (UPGMA, function *hclust* in R; R Development Core Team 2014). We varied the number of delimited zoogeographic regions from 1 to 30 (see Supp. Mat. 5 for examples). We then used these regions to construct a biogeographical null model of the PDAR. While we were shuffling species within the entire continental pool of species in the previous null model, we shuffled here species within the pool of species belonging to a specific zoogeographic region. Because all species are not restricted to one unique zoogeographic region, we adopted a probabilistic approach where, for each randomization independently, a zoogeographic region k is assigned to a species i with a probability of $P_{i,k}$ depending on its coverage $C_{i,k}$ in this region with respect to its total coverage across all regions:

$$P_{i,k} = \frac{C_{i,k}}{\sum\limits_{K} C_{i,k}} \quad \text{(Eq. 2)}$$

where K represents the entire set of regions (from 2 to 30). For each randomization, we computed a null PDAR and tested significance by comparing the observed PDAR and 100 null PDAR for each number of zoogeographic regions defined.

Results & Discussion

To visually compare the PDAR and the SAR of mammals we standardized the two curves by the maximal diversity reached in the data set. The two resulting curves are thus expressed in % of maximal diversity and are directly comparable (Fig. 3). We show that PDARs approach their maximum faster than SARs for all continents (Fig. 3). To describe the rate of PD and SR accumulation as a function of area, we estimated local derivatives and show that PDARs accelerate much faster than SARs for small areas and that this tendency reverses for large areas (see subplots of Fig. 3). We show that the power model is among the best model to fit the dataset (Supplementary Mat. 6) but fails to model the upward acceleration of PD on a log-log scale (e.g. Fig. 4). The slope of the power model is lower for the PDARs than for the SAR ($z_{PDAR} < z_{SAR}$, see Supplementary Mat. 7). The last point has been previously reported at this scale (Mazel et al. 2014) but with a different PDAR/SAR reconstruction based on non-overlapping ecoregions (Olson et al. 2001). This result is thus independent of the sampling procedure and approaches, and is, overall, not surprising. Indeed the SAR fully represents the PDAR in the case of a star phylogeny (in this case the PD is proportional to SR). As the phylogenetic tree departs from a star phylogeny (i.e. as some branches start to be shared between species), the relationship between PD and SR becomes concave and the PDAR deviates from the SAR (because redundancies between species are introduced, see Fig. 1.A). As a consequence, AUC_r values are positives but we find that they differ across continents (see Fig. 2-3). The use of the SAR to predict species extinction from habitat loss (Pimm and Raven 2000, Thomas et al. 2004, Halley et al. 2014) has been questioned (He and Hubbell 2011) but remains useful (e.g. Axelsen, Roll, Stone, & Solow, 2013; Hanski & Zurita, 2013; Matias et al., 2014), especially when species ranges are randomly distributed (He and Hubbell 2011). If we assume that the SAR and the PDAR can be used to predict the loss of species and PD, respectively, through habitat loss (Mazel et al. 2014), the AUC_r (Fig. 2) then represents the relative robustness of PD (compared to SR) to habitat destruction. In this case, we show, for example, that the Australian PD will be relatively more robust–at the continental scale-than the Eurasian PD to habitat loss (note that at the global scale, the evolutionary history of Australia is particularly unique; Holt et al., 2013). This difference could be explained by the different structure of the two trees (see Fig. 1.A) and/or by different eco-evolutionary processes leading to a different spatial pattern of PD (e.g. either clustered, random or overdispersed; see Fig. 1.B). Teasing apart these two mechanisms called for using appropriate null models.

For all continents except Eurasia and for most of the spatial scales, we find that PD values are not significantly different from those obtained with the null model randomizing the phylogenetic relationships among species (Fig. 4 and Supplementary Mat. 8). This means that the only significant phylogenetic effect that influences the PDAR is the shape of the observed continental tree. Several non-mutually exclusive hypotheses can be proposed to explain this result. First, we use here an averaged phylogenetic structure across a whole continent and different assembly processes may have been mixed. In North America for

example we could expect a phylogenetic clustering at high elevation in the Rocky Mountains (e.g. due to environmental filtering) while overdispersion could be found in the lowland forest (e.g. due to competition, Graham and Parra 2009), resulting in higher MAD of PD than expected by chance (see Supp. Mat. 9). Such distribution may likely compensate each other during the sampling process, resulting in a null random distribution when averaged across assemblages. Second, the spatial and phylogenetic scale of our analysis is perhaps too large to detect any effect of repulsion/attraction of species. Indeed, at the smallest resolution we have used (110*110 km), co-occurring species do not necessarily interact with each other (probably because this scale is still very large) and may, for example, use different habitats (Araújo and Rozenfeld 2014, but see Cardillo 2011). Also, specific group of mammals may show repulsion or attraction while others not, blurring the overall pattern (see e.g. Pedersen et al. 2014).

The Eurasian PDARs is however much lower than expected by chance at all spatial scales, indicating phylogenetic clustering (Fig. 4 and Supplementary Mat. 8). This continent is a mosaic of biogeographic realms with diverging biogeographic history (Wallace 1876, Holt et al. 2013) and thus mixes very different faunas: there are many strict Palearctic species (e.g. the wolverine, *Gulo gulo*) and strict oriental species (e.g. the asiatic elephant, *Elephas maximus*). The continental null model mixes all these faunas and thus tends to overestimate the expected median PD of assemblages. For example *Elephas maximus* represents the only afrotherian species present in our data set so it has a very high distinctiveness at the continental scale and will considerably increase relative local PD. We consequently develop a biogeographical null model that takes into account the historical origin of taxa. We show that this null model progressively decreases the random PD expectations (Fig 5) and that 15 realms were sufficient to correctly predict most of the spatial scale median PD and observed c value (Fig. 5 and Supp. Mat. 10-11). Our approach may sound circular at first glance because we use spatial and phylogenetic data (to define zoogeographic regions) to explain spatial and phylogenetic data (the PDAR). Nevertheless the aim of any null models is rather to ask how much synthetic information we need from the initial data to parsimoniously explain this data. The null model is necessarily constrained by the initial data but if this constrain is too high (i.e. a lot of the initial data is used) the null model will necessarily be plausible (the "narcissus effect"; Gotelli 2001). Here our aim is to quantify how much synthetic information is needed to parsimoniously explain the Eurasian PDAR. Finally it is not directly possible to conclude from the biogeographic null model that the effect we detected is purely 'historic', i.e. that it derives from the mix of fauna due to continental drift. Indeed Eurasia has also a steep North-South gradient in term of climate (and SR) and we cannot reject the hypothesis of a phylogenetic clustering due to environmental filtering (Webb et al. 2002). One potential future avenue could be to contrast the relative predictive power of biogeographic null model versus a climate based null model.

We also find that PD at small scale tends to be higher than expected by chance for South America (phylogenetic overdispersion, Fig. 4), leading to a significantly low z value for the PDAR (Supp. mat. 8, p<0.005). This observation may result from allopatric speciation events and/or competition at the smallest scale (Pigot and Tobias 2013) but more work is needed to test these hypotheses. For Eurasia, on the contrary, we observe that small scale PD

tends to be relatively lower than expected by chance (phylogenetic clustering, Fig. 4) leading to a significant high z value (p<0.01, Supp. Mat. 8). This could be a possible product of environmental filtering occurring only at small scale.

These last two results shed light on the discrepancy between observed and null AUC_r (Supp. mat. 12 black and red lines respectively). Indeed the robustness of PD to habitat loss depends on the structure of the phylogenetic tree (represented here by the null model mean expectation) and also on the spatial pattern of phylogenetic structure (represented by the departure of the observed PDAR from the mean null model, see subplots in Fig. 4). We indeed find that Australian observed AUC_r is higher than predicted by the continental tree structure because small scale Australian PD tends to be relatively higher than expected by chance (see Supp. Mat. 12), providing a buffer against the loss of PD. In contrast, observed Eurasia AUC_r is lower than expected by the tree shape (see Supp. Mat. 12). This is because Eurasian PD is disproportionately low at small scale, reducing the area between the PDAR and the SAR compared to random expectations and thus being more vulnerable to habitat reduction. Overall, we demonstrate that the additional robustness of PD to habitat loss compared to species richness is determined by the phylogenetic tree shape but also depends on the spatial structure of PD.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

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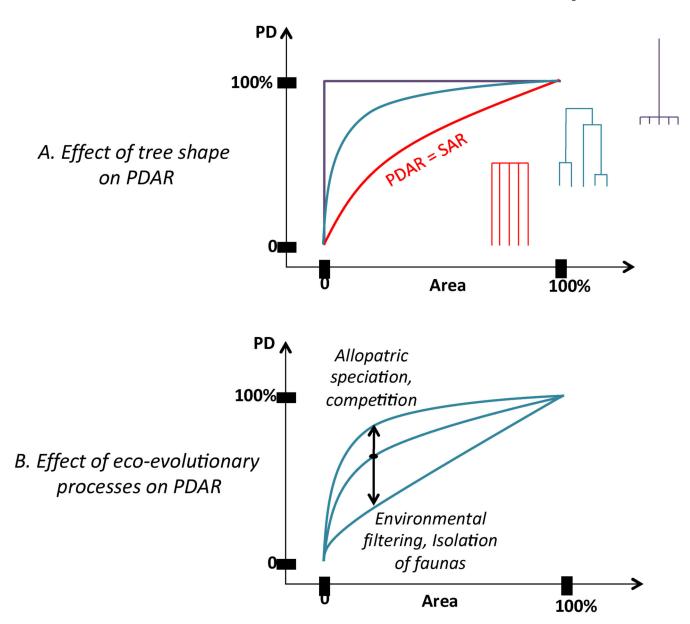
Figure 1. Expected variation of the standardized PDAR given (1.A) different tree shapes and (1.B) different eco-evolutionary processes
(A) The three standardized PDARs correspond to the three trees depicted above the graph. Note that the red PDAR also corresponds to the observed SAR as the red tree is a star phylogeny. (B) Different eco-evolutionary processes may change the PDAR if they act differently among spatial scales. We expect that competition and/or allopatric speciation may relatively increase the PD at small scale while environmental filtering and/or geographic isolation of biotas may relatively decrease the PD at small scale.
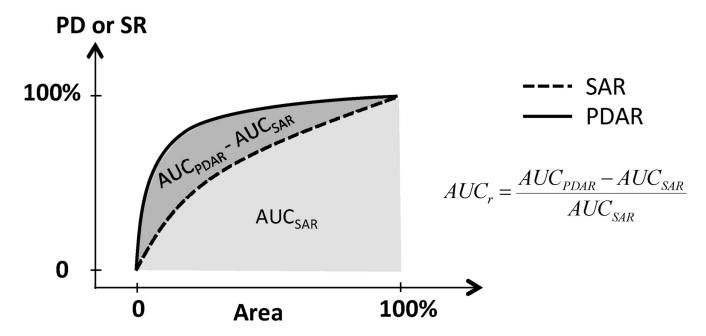
Figure 2. Hypothetical example to quantify the relative robustness of PD (compared to SR) to habitat loss (AUC$_r$) using PDAR and SAR

The example shows how to quantify the relative PDAR shape by measuring the Area between the two curves (SR, PD and Area are expressed in %) and computing AUC$_r$.
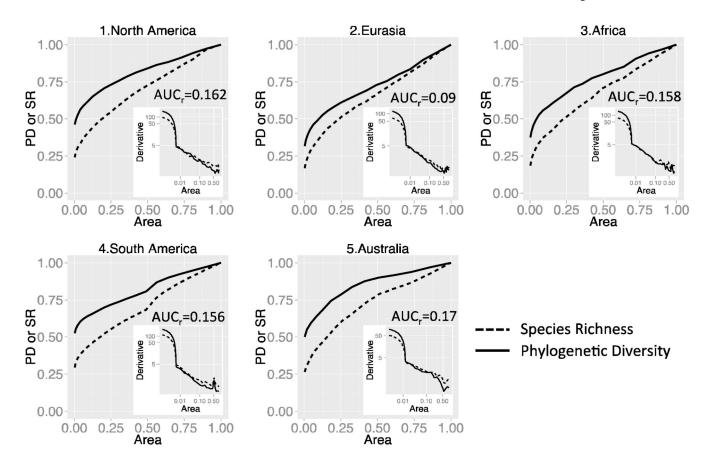
Figure 3. Observed rescaled median SARs and median PDARs

For each continent, we report the SAR & the PDAR rescaled by the value of the maximum SR and PD respectively. The two curves are both expressed in percentage of maximum diversity and thus directly comparable. We also report the corresponding AUC_r values (see Fig. 2). In the lower-right corner subplots we show the corresponding local derivatives.
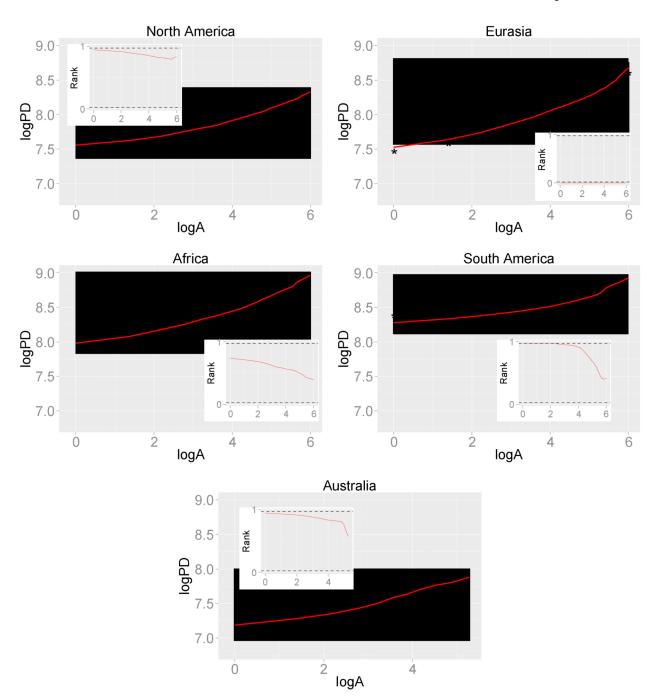
Figure 4. Median PDARs obtained from the continental null model
For each continent, the envelope corresponding to 1000 null continental PDARs is shown in black while the observed PDAR is in red. In the corner of each panel, we plot the relative rank of observed PD value within the null PD distribution as a function of log Area. For each spatial scale, it is computed as the percentage of null PD values that are lower than the observed value (a value of 0.5 indicates that observed PD equals the median of the null distribution). The dashed lines correspond to a relative rank of 2.5% and 97.5%. When the

computed relative ranks fall out of this 95% envelope, a * is reported in the main panel (see Supp. Mat. 6 for the relative ranks associated with power model parameters).
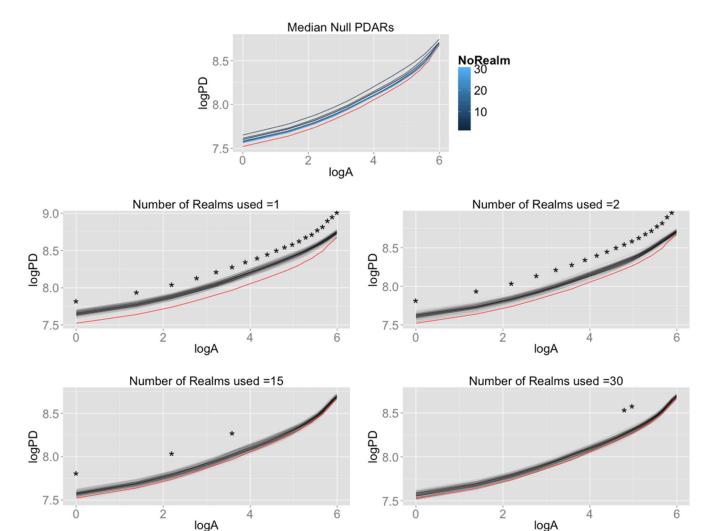
Figure 5. Median PDARs obtained from the Eurasian biogeographical null models

The biogeographical null models shuffle the tips of the phylogeny according to biogeographical origin (see methods). We present the results from null models containing different numbers of biogeographical regions. The top panel presents the median PDAR obtained for different number of biogeographic regions (see legend). The four other panels represent the details of four biogeographic null models that used 1 (=continental null model), 2, 15 or 30 biogeographic regions, respectively. The * indicates if the relative rank of observed PD value within the null PD distribution is lower (or higher) than 0.025 (or 0.975) for a given area.