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1 Mammalian phylogenetic diversity-area relationships at a continental scale

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Abstract

37

38 In analogy to the species-area relationship (SAR), one of the few laws in Ecology, the
39 phylogenetic diversity-area relationship (PDAR) describes the tendency of phylogenetic
40 diversity (PD) to increase with area. Although investigating PDAR has the potential to
41 unravel the underlying processes shaping assemblages across spatial scales and to predict PD
42 loss through habitat reduction, it has been little investigated so far. Focusing on PD has
43 noticeable advantages compared to species richness (SR) since PD also gives insights on
44 processes such as speciation/extinction, assembly rules and ecosystem functioning. Here we
45 investigate the universality and pervasiveness of the PDAR at continental scale using
46 terrestrial mammals as study case. We define the relative robustness of PD (compared to SR)
47 to habitat loss as the area between the standardized PDAR and standardized SAR (i.e.
48 standardized by the diversity of the largest spatial window) divided by the area under the
49 standardized SAR only. This metric quantifies the relative increase of PD robustness
50 compared to SR robustness. We show that PD robustness is higher than SR robustness but
51 that it varies among continents. We further use a null model approach to disentangle the
52 relative effect of phylogenetic tree shape and non random spatial distribution of evolutionary
53 history on the PDAR. We find that for most spatial scales and for all continents except
54 Eurasia, PDARs are not different from expected by a model using only the observed SAR and
55 the shape of the phylogenetic tree at continental scale. Interestingly, we detect a strong
56 phylogenetic structure of the Eurasian PDAR that can be predicted by a model that
57 specifically account for a finer biogeographical delineation of this continent. In conclusion,
58 the relative robustness of PD to habitat loss compared to species richness is determined by
59 the phylogenetic tree shape but also depends on the spatial structure of PD.

60

61 Keywords: species area-relationship, strict nested design, null models, phylogenetic

62 **diversity**

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63 **Introduction**

64

65 The species area relationship (SAR) describes the tendency of species richness (SR) to
66 increase with area (Rosenzweig 1995). This relationship is documented for a wide range of
67 taxonomic groups and ecosystems (Guilhaumon et al. 2008, Triantis et al. 2012) and its
68 understanding is central to ecology and conservation biogeography (Rosenzweig 1995,
69 Whittaker et al. 2005). For instance, the SAR is a key tool to estimate species extinctions
70 from habitat destruction and climate change (Pimm and Raven 2000, Thomas et al. 2004,
71 Pereira et al. 2010, Matias et al. 2014). Nevertheless a SAR approach reduces biological
72 diversity to species richness only and fails to include the amount of evolutionary history in
73 species assemblages (Mouquet et al. 2012). To fill this gap, the Phylogenetic Diversity Area
74 Relationship (PDAR hereafter; Morlon et al. 2011) can help unravel the processes assembling
75 communities across spatio-temporal scales and provides complementary tools for conserving
76 the Tree of Life (Mazel et al. 2014). For instance, translating SAR into PDAR allows to
77 predict the loss of PD through habitat destruction. This prediction is essential since the loss of
78 a given amount of PD or the loss of an entire lineage could have strong negative ecological
79 consequences since distinct lineages are likely to perform different functions (Cadotte et al.
80 2008, Mouquet et al. 2012).

81

82 Several mechanisms have been proposed to explain the SAR, such as sampling effects
83 (Rosenzweig 1995), the effect of habitat size on extinction rates (MacArthur and Wilson
84 1967), the scaling of environmental heterogeneity with area (Kadmon and Allouche 2007) or
85 dispersal limitation (Hubbell 2001). In complement to the SAR, the PDAR brings unique
86 information about the different processes structuring biodiversity at different spatial scales,
87 helping, for example, to quantify the effects of biotic interactions at small scales versus

88 biogeographical processes at large scale. A particular feature of the PDAR is that the shape of
89 the phylogenetic tree ultimately drives its relative position to the SAR. A star phylogeny
90 would produce a PDAR proportional to the SAR, while a complete and recent polytomy at
91 the tips of the tree would produce an extreme PDAR that would reach its maximum from the
92 smallest area (see Figure 1.A). In addition to those mechanisms, biogeographic history
93 together with ecological processes should also influence the PDAR (see Fig. 1.B). Allopatric
94 speciation and/or competition between close relative species would result in a relatively
95 higher PD than expected for a given SR ('overdispersion'; Webb et al. 2002, O'Dwyer et al.
96 2012). Coexistence theory indeed predicts that similar species will compete more strongly
97 than dissimilar species, leading to the exclusion of one of the similar species
98 (HilleRisLambers et al. 2012). If we assume that niche differences are properly portrayed by
99 phylogenetic differences, we predict a phylogenetic overdispersion (i.e. distantly related
100 species co-occur) under competitive interactions (Webb et al. 2002, but see Mayfield and
101 Levine 2010). Reciprocally, low PD may be expected if close relative species tend to co-
102 occur because of shared environmental niches and/or geographic isolation of land mass
103 (phylogenetic clustering; Webb et al. 2002, O'Dwyer et al. 2012, see Fig. 1.B). Overall the
104 difference between SAR and PDAR curves is thus very informative on the way the
105 phylogenetic structure of assemblages varies across spatial scales.

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

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

137 might be more robust than SR to habitat loss but that this higher robustness differs across

138 continents for different reasons.

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140 **Methods**

141 **1. Datasets and diversity metrics**

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

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

151 To characterize the PD of an assemblage we used the Faith's measure (Faith 1992). This
152 metric represents a 'richness' or 'volume' of diversity (Pavoine and Bonsall 2011) and
153 simply sums up branch lengths of the given species assemblage phylogeny (Rodrigues and
154 Gaston 2002). Faith's measure is an intuitive and relatively simple measure of PD. It is also,
155 by construction, generally highly correlated with SR (Huang et al. 2012, Tucker and Cadotte
156 2013). The use of any PD metric theoretically linked with SR in the description of PDAR has
157 been criticized because PDAR would be biased by "spurious artefacts of a statistical
158 relationship between species richness and area "(Helmus and Ives 2012). Here the
159 comparison of the SAR and the PDAR we propose, i.e. with the standardisation and the null
160 model that removes the effect of SR on PD (see section describing our null model approach)
161 avoid this artefact while it allows a simple interpretation of the results.

162

163 **2. Constructing SAR & PDAR**

164 Median and Median absolute deviance (MAD) of SR/PD were reported for each spatial scale
165 (from 110*110 km up to 2200*2200 km) by using the framework proposed by Storch et al.
166 (2012). We do not use mean SR and PD as the data was highly non-normal (see Appendix A
167 for examples of distributions of diversity). It uses a strictly nested quadrat design where a
168 moving window (Leitner and Rosenzweig 1997, Lennon et al. 2001) reports the SR/PD of all
169 possible windows of a given size within a continent. The median and MAD of SR/PD are
170 then computed for each spatial scale. This procedure implies that some cells are counted
171 several time for a given spatial windows and thus some pseudo-replication is inevitably
172 introduced. Nevertheless all designs have their own drawbacks and SNQ have several
173 important advantages (Storch et al. 2012). We implemented the algorithm within a reduced
174 subset of the five continents (see Appendix B for further details) to avoid some border effect:
175 i.e. for each scale (whatever its size) all pixels of the selected area of the continent will be
176 sampled at least one time. The spectrum of spatial scale analysed was set between 1*1 to
177 14*14 cells for Australia (i.e. from approximately 110*110 km to 1540*1540 km) and from
178 1*1 to 20*20 cells for North and South America, Africa and Eurasia (i.e. from approximately
179 110*110 km to 2200*2200 km) following Storch et al. (2012). Note that the resulting curve
180 corresponds to a type I curve in the terminology proposed by Scheiner (2003).

181

182 **3. Analysing SAR & PDAR**

183 3.1. Comparing the relative shape of SAR & PDAR

184 We compared the shape of PDAR and SAR using two complementary approaches. First we
185 fitted a power model (Rosenzweig 1995) to each SAR and PDAR. We then reported the slope
186 (z) value of the linear model in a log-log space. These values were then used to depict in a
187 simple way the relative shape of PDAR and SAR. Because PDAR and SAR are not
188 necessarily best modelled by a power function (Guilhaumon et al. 2008, Mazel et al. 2014)

we also (1) fitted alternative statistical models (see Appendix C) 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

214 unchanged the distribution of range size and the local species richness (Hardy 2008). By
215 repeating this procedure n times (see below), we were able to assess the significance of the
216 observed PDAR relative to our null expectation (using a two-sided test).

217 In other words, for each randomization, we (1) shuffled the tips of the phylogeny within a
218 given species pool (see below). The resulting randomized phylogeny was used to (2) compute
219 null PD values for each basic grid cells (approximately 110*110 km) and we (3) applied the
220 methodology described above to compute the resulting null median and MAD PDARs. Such
221 null model may help unravel the determinants of the PDAR. For example we may expect
222 competition (Pigot and Tobias 2013) or environmental filtering to occur at smaller scale,
223 potentially leading to phylogenetic overdispersion or clustering respectively (Webb et al.,
224 2002; but note that competition may also lead to clustering, see Mayfield & Levine, 2010).
225 Also, phylogenetic clustering could be detected at larger scales because of biogeographical
226 effect (Rosenzweig 1995). We used two null models that use either a (1) continental or a (2)
227 biogeographic pool of species. We restricted the analysis of the biogeographic pool of species
228 for Eurasia only because it is the only continent in our design that is a mix of distantly related
229 zoogeographic regions (Wallace 1876, Holt et al. 2013).

230 **(1) Continental pool of species**

231 This null model simply shuffles the tips within the entire continental phylogeny. The
232 significance of the observed values of PDAR was assessed by comparing observed values
233 with 1000 randomized PDARs. We further confirmed this simulation approach by using
234 analytical expectations of PD based on the framework of Nipperess and Matsen (2013,
235 Appendix D)

236 **(2) Biogeographical pool of species**

237 First we defined zoogeographic regions following the methodology of Holt et al. (2013). To
238 do so we computed phylogenetic beta diversity values between each pair of grid cells from

239 the Eurasian continent by using an index independent of species richness (Lennon et al. 2001,
240 Holt et al. 2013):

$$241 \quad \beta = 1 - \frac{a}{\min(b, c) + a} \quad (\text{Eq. 1})$$

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

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

$$255 \quad P_{i,k} = \frac{C_{i,k}}{\sum_K C_{i,k}} \quad (\text{Eq. 2})$$

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

259

260 **Results & Discussion**

261 To visually compare the PDAR and the SAR of mammals we standardized the two curves by
262 the maximal diversity reached in the data set. The two resulting curves are thus expressed in
263 % of maximal diversity and are directly comparable (Fig. 3). We show that PDARs approach
264 their maximum faster than SARs for all continents (Fig. 3). To describe the rate of PD and
265 SR accumulation as a function of area, we estimated local derivatives and show that PDARs
266 accelerate much faster than SARs for small areas and that this tendency reverses for large
267 areas (see subplots of Fig. 3). We show that the power model is among the best model to fit
268 the dataset (Appendix F) but fails to model the upward acceleration of PD on a log-log scale
269 (e.g. Fig. 4). The slope of the power model is lower for the PDARs than for the SAR ($z_{\text{PDAR}} <$
270 z_{SAR} , see Appendix G). The last point has been previously reported at this scale (Mazel et al.
271 2014) but with a different PDAR/SAR reconstruction based on non-overlapping ecoregions
272 (Olson et al. 2001). This result is thus independent of the sampling procedure and
273 approaches, and is, overall, not surprising. Indeed the SAR fully represents the PDAR in the
274 case of a star phylogeny (in this case the PD is proportional to SR). As the phylogenetic tree
275 departs from a star phylogeny (i.e. as some branches start to be shared between species), the
276 relationship between PD and SR becomes concave and the PDAR deviates from the SAR
277 (because redundancies between species are introduced, see Fig. 1.A).

278 As a consequence, AUC_r values are positives but we find that they differ across continents
279 (see Fig. 2-3). The use of the SAR to predict species extinction from habitat loss (Pimm and
280 Raven 2000, Thomas et al. 2004, Halley et al. 2014) has been questioned (He and Hubbell
281 2011) but remains useful (e.g. Axelsen, Roll, Stone, & Solow, 2013; Hanski & Zurita, 2013;
282 Matias et al., 2014), especially when species ranges are randomly distributed (He and
283 Hubbell 2011). If we assume that the SAR and the PDAR can be used to predict the loss of
284 species and PD, respectively, through habitat loss (Mazel et al. 2014), the AUC_r (Fig. 2) then

285 represents the relative robustness of PD (compared to SR) to habitat destruction. In this case,
286 we show, for example, that the Australian PD will be relatively more robust –at the
287 continental scale- than the Eurasian PD to habitat loss (note that at the global scale, the
288 evolutionary history of Australia is particularly unique; Holt et al., 2013). This difference
289 could be explained by the different structure of the two trees (see Fig. 1.A) and/or by
290 different eco-evolutionary processes leading to a different spatial pattern of PD (e.g. either
291 clustered, random or overdispersed; see Fig. 1.B). Teasing apart these two mechanisms called
292 for using appropriate null models.

293 For all continents except Eurasia and for most of the spatial scales, we find that PD values are
294 not significantly different from those obtained with the null model randomizing the
295 phylogenetic relationships among species (Fig. 4 and Appendix H). This means that the only
296 significant phylogenetic effect that influences the PDAR is the shape of the observed
297 continental tree. Several non-mutually exclusive hypotheses can be proposed to explain this
298 result. First, we use here an averaged phylogenetic structure across a whole continent and
299 different assembly processes may have been mixed. In North America for example we could
300 expect a phylogenetic clustering at high elevation in the Rocky Mountains (e.g. due to
301 environmental filtering) while overdispersion could be found in the lowland forest (e.g. due
302 to competition, Graham and Parra 2009), resulting in higher MAD of PD than expected by
303 chance (see Appendix I). Such distribution may likely compensate each other during the
304 sampling process, resulting in a null random distribution when averaged across assemblages.
305 Second, the spatial and phylogenetic scale of our analysis is perhaps too large to detect any
306 effect of repulsion/attraction of species. Indeed, at the smallest resolution we have used
307 (110*110 km), co-occurring species do not necessarily interact with each other (probably
308 because this scale is still very large) and may, for example, use different habitats (Araújo and
309 Rozenfeld 2014, but see Cardillo 2011). Also, specific group of mammals may show

310 repulsion or attraction while others not, blurring the overall pattern (see e.g. Pedersen et al.
311 2014).

312 The Eurasian PDARs is however much lower than expected by chance at all spatial scales,
313 indicating phylogenetic clustering (Fig. 4 and Appendix H). This continent is a mosaic of
314 biogeographic realms with diverging biogeographic history (Wallace 1876, Holt et al. 2013)
315 and thus mixes very different faunas: there are many strict Palearctic species (e.g. the
316 wolverine, *Gulo gulo*) and strict oriental species (e.g. the asiatic elephant, *Elephas maximus*).

317 The continental null model mixes all these faunas and thus tends to overestimate the expected
318 median PD of assemblages. For example *Elephas maximus* represents the only afrotherian
319 species present in our data set so it has a very high distinctiveness at the continental scale and
320 will considerably increase relative local PD. We consequently develop a biogeographical null
321 model that takes into account the historical origin of taxa. We show that this null model
322 progressively decreases the random PD expectations (Fig 5) and that 15 realms were
323 sufficient to correctly predict most of the spatial scale median PD and observed c value (Fig.
324 5 and Appendix J-K). Our approach may sound circular at first glance because we use spatial
325 and phylogenetic data (to define zoogeographic regions) to explain spatial and phylogenetic
326 data (the PDAR). Nevertheless the aim of any null models is rather to ask how much
327 synthetic information we need from the initial data to parsimoniously explain this data. The
328 null model is necessarily constrained by the initial data but if this constrain is too high (i.e. a
329 lot of the initial data is used) the null model will necessarily be plausible (the “narcissus
330 effect”; Gotelli 2001). Here our aim is to quantify how much synthetic information is needed
331 to parsimoniously explain the Eurasian PDAR. Finally it is not directly possible to conclude
332 from the biogeographic null model that the effect we detected is purely ‘historic’, i.e. that it
333 derives from the mix of fauna due to continental drift. Indeed Eurasia has also a steep North-
334 South gradient in term of climate (and SR) and we cannot reject the hypothesis of a

335 phylogenetic clustering due to environmental filtering (Webb et al. 2002). One potential
336 future avenue could be to contrast the relative predictive power of biogeographic null model
337 versus a climate based null model.

338 We also find that PD at small scale tends to be higher than expected by chance for South
339 America (phylogenetic overdispersion, Fig. 4), leading to a significantly low z value for the
340 PDAR ($p < 0.005$, Appendix H). This observation may result from allopatric speciation events
341 and/or competition at the smallest scale (Pigot and Tobias 2013) but more work is needed to
342 test these hypotheses. For Eurasia, on the contrary, we observe that small scale PD tends to
343 be relatively lower than expected by chance (phylogenetic clustering, Fig. 4) leading to a
344 significant high z value ($p < 0.01$, Appendix H). This could be a possible product of
345 environmental filtering occurring only at small scale.

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

359

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369 **References**

370 Araújo, M., and A. Rozenfeld. 2014. The geographic scaling of biotic interactions.

371 *Ecography* 37:406–415.

372 Axelsen, J., U. Roll, L. Stone, and A. Solow. 2013. Species-area relationships always

373 overestimate extinction rates from habitat loss: comment. *Ecology* 94:761–763.

374 Belmaker, J., and W. Jetz. 2011. Cross-scale variation in species richness–environment

375 associations. *Global Ecology and Biogeography*.

376 Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R.

377 Grenyer, S. A. Price, R. A. Vos, J. L. Gittleman, and A. Purvis. 2007. The delayed rise

378 of present-day mammals. *Nature* 446:507–12.

379 Cadotte, M. W., B. J. Cardinale, and T. H. Oakley. 2008. Evolutionary history and the effect

380 of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences*

381 of the United States of America 105:17012–7.

382 Cardillo, M. 2011. Phylogenetic structure of mammal assemblages at large geographical

383 scales: linking phylogenetic community ecology with macroecology. *Philosophical*384 *Transactions of the Royal Society of London, Series B* 366:2545–2553.385 Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. *Biological*386 *Conservation* 61:1–10.

387 Fritz, S. A., O. R. P. Bininda-Emonds, and A. Purvis. 2009. Geographical variation in

388 predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology*389 *letters* 12:538–49.

- 390 Gotelli, N. 2001. Research frontiers in null model analysis. *Global Ecology and*
391 *Biogeography* 10:337–343.
- 392 Graham, C. H., J. L. Parra, C. Rahbek, and J. A. McGuire. 2009. Phylogenetic structure in
393 tropical hummingbird communities. *Proceedings of the National Academy of Sciences*
394 *of the United States of America* 106 Suppl:19673–19678.
- 395 Guilhaumon, F., O. Gimenez, K. J. Gaston, and D. Mouillot. 2008. Taxonomic and regional
396 uncertainty in species-area relationships and the identification of richness hotspots.
397 *Proceedings of the National Academy of Sciences of the United States of America*
398 105:15458–15463.
- 399 Halley, J., V. Sgardeli, and K. Triantis. 2014. Extinction debt and the species–area
400 relationship: a neutral perspective. *Global Ecology and Biogeography* 23:113–123.
- 401 Hanski, I., and G. Zurita. 2013. Species–fragmented area relationship. *Proceedings of the*
402 *National Academy of Sciences of the United States of America* 110:12715–12720.
- 403 Hardy, O. 2008. Testing the spatial phylogenetic structure of local communities: statistical
404 performances of different null models and test statistics on a locally neutral community.
405 *Journal of ecology* 96:914–926.
- 406 He, F., and S. Hubbell. 2011. Species-area relationships always overestimate extinction rates
407 from habitat loss. *Nature* 473:368–371.
- 408 Helmus, M. R., and A. R. Ives. 2012. Phylogenetic diversity–area curves. *Ecology* 91:31–43.
- 409 HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012.
410 Rethinking Community Assembly through the Lens of Coexistence Theory. *Annual*
411 *Review of Ecology, Evolution, and Systematics* 43:227–248.

- 412 Holt, B. G., J. P. Lessard, M. K. Borregaard, S. A. Fritz, M. B. Araújo, D. Dimitrov, P. H.
413 Fabre, C. H. Graham, G. R. Graves, K. A. Jønsson, and Others. 2013. An Update of
414 Wallace's Zoogeographic Regions of the World. *Science* 339:74–78.
- 415 Huang, S., P. R. Stephens, and J. L. Gittleman. 2012. Traits, trees and taxa: global
416 dimensions of biodiversity in mammals. *Proceedings of the Royal Society, Series B.*
417 279:4997–5003.
- 418 Hubbell, S. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton
419 University Press.
- 420 Jenkins, C. N., S. L. Pimm, and L. N. Joppa. 2013. Global patterns of terrestrial vertebrate
421 diversity and conservation. *Proceedings of the National Academy of Sciences of the*
422 *United States of America* 110:E2602–2610.
- 423 Kadmon, R., and O. Allouche. 2007. Integrating the effects of area, isolation, and habitat
424 heterogeneity on species diversity: a unification of island biogeography and niche
425 theory. *The American Naturalist* 170:443–454.
- 426 Leitner, W., and M. Rosenzweig. 1997. Nested species-area curves and stochastic sampling: a
427 new theory. *Oikos*:503–512.
- 428 Lennon, J. J., P. Koleff, J. J. D. Greenwood, and K. J. Gaston. 2001. The geographical
429 structure of British bird distributions: diversity, spatial turnover and scale. *Journal of*
430 *Animal Ecology* 70:966–979.
- 431 MacArthur, R., and E. Wilson. 1967. *The theory of island biogeography*. Princeton, New jersey.
- 432 Matias, M., D. Gravel, F. Guilhaumon, P. Desjardins-Proulx, M. Loreau, T.
433 Mu nkemu ller, and N. Mouquet. 2014. Estimates of species extinctions from species–
434 area relationships strongly depend on ecological context. *Ecography* 37:001–012.

- 435 Mayfield, M., and J. Levine. 2010. Opposing effects of competitive exclusion on the
436 phylogenetic structure of communities. *Ecology letters* 13:1085–1093.
- 437 Mazel, F., F. Guilhaumon, N. Mouquet, V. Devictor, D. Gravel, J. Renaud, R. L. Marcus
438 Vinicius Cianciaruso, J. A. F. Diniz-Filho, D. Mouillot, and W. Thuiller. 2014.
439 Multifaceted diversity–area relationships reveal global hotspots of mammalian species,
440 trait and lineage diversity. *Global Ecology and Biogeography* 23:836–847.
- 441 Morlon, H., D. W. Schwilk, J. A. Bryant, P. A. Marquet, A. G. Rebelo, C. Taus, B. J. M.
442 Bohannan, and J. L. Green. 2011. Spatial patterns of phylogenetic diversity. *Ecology*
443 *letters* 14:141–149.
- 444 Mouquet, N., V. Devictor, C. N. Meynard, F. Munoz, L.-F. F. Bersier, J. Chave, P. Couteron,
445 A. Dalecky, C. Fontaine, D. Gravel, O. J. Hardy, F. Jabot, S. Lavergne, M. Leibold, D.
446 Mouillot, T. Münkemüller, S. Pavoine, A. Prinzing, A. S. L. Rodrigues, R. P. Rohr, E.
447 Thébault, W. Thuiller, and Others. 2012. Ecophylogenetics: advances and perspectives.
448 *Biological Reviews* 87:769–785.
- 449 Nipperess, D., and F. Matsen. 2013. The mean and variance of phylogenetic diversity under
450 rarefaction. *Methods in Ecology and Evolution* 4:566–572.
- 451 O’Dwyer, J., S. Kembel, and J. Green. 2012. Phylogenetic diversity theory sheds light on the
452 structure of microbial communities. *PLoS computational biology* 8:e1002832.
- 453 Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, V. N. P. George, E. D.
454 Underwood, J. D’amico, I. Itoua, H. E. Strand, J. C. Morrison, G. V. N. Powell, E. C.
455 Underwood, J. a. D’amico, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F.
456 Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial Ecoregions
457 of the World: A New Map of Life on Earth. *BioScience* 51:933–938.

- 458 Pavoine, S., and M. B. Bonsall. 2011. Measuring biodiversity to explain community
459 assembly: a unified approach. *Biological Reviews* 86:792–812.
- 460 Pedersen, R. Ø., B. Sandel, and J.-C. Svenning. 2014. Macroecological evidence for
461 competitive regional-scale interactions between the two major clades of mammal
462 carnivores (Feliformia and Caniformia). *PloS one* 9:e100553.
- 463 Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F.
464 Fernandez-Manjarrés, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, Others,
465 L. Chini, H. D. Cooper, E. L. Gilman, S. Guénette, G. C. Hurtt, H. P. Huntington, G. M.
466 Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, and M.
467 Walpole. 2010. Scenarios for global biodiversity in the 21st century. *Science* 330:1496–
468 1501.
- 469 Pigot, A. L., and J. A. Tobias. 2013. Species interactions constrain geographic range
470 expansion over evolutionary time. *Ecology letters* 16:330–8.
- 471 Pimm, S., and P. Raven. 2000. Biodiversity: extinction by numbers. *Nature* 403:843–845.
- 472 R Development Core Team. 2014. *R: A Language and Environment for Statistical*
473 *Computing*. Vienna, Austria.
- 474 Rodrigues, A. S. L., and K. J. Gaston. 2002. Maximising phylogenetic diversity in the
475 selection of networks of conservation areas. *Biological Conservation* 105:103–111.
- 476 Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press.
- 477 Scheiner, S. M. 2003. Six types of species-area curves. *Global Ecology and Biogeography*
478 12:441–447.
- 479 Storch, D., P. Keil, and W. Jetz. 2012. Universal species-area and endemics-area
480 relationships at continental scales. *Nature* 488:78–81.

- 481 Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham,
482 B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.
483 S. van Jaarsveld, G. F. Midgley, L. Miles, M. a. Ortega-Huerta, a. T. Peterson, O. L.
484 Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature*
485 427:145–148.
- 486 Triantis, K. A., F. Guilhaumon, and R. J. Whittaker. 2012. The island species-area
487 relationship: biology and statistics. *Journal of Biogeography* 39:215–231.
- 488 Tucker, C., and M. Cadotte. 2013. Unifying measures of biodiversity: understanding when
489 richness and phylogenetic diversity should be congruent. *Diversity and Distributions*
490 19:845–854.
- 491 Wallace, A. 1876. *The geographical distribution of animals*. Cambridge Univ. Press,
492 Cambridge.
- 493 Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and
494 Community Ecology. *Annual Review of Ecology, Evolution, and Systematics* 33:475–
495 505.
- 496 Whittaker, R. J., M. B. Araújo, J. Paul, R. J. Ladle, J. E. M. Watson, K. J. Willis, and P.
497 Jepson. 2005. Conservation Biogeography: assessment and prospect. *Diversity and*
498 *Distributions* 11:3–23.
- 499
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501

Supplemental materials

502

503 Appendix A. Distribution of species richness and phylogenetic diversity values.

504 Appendix B. Details on the grain and extent of the study

505 Appendix C. Alternative statistical models list and fitting procedure

506 Appendix D. Congruence between analytical and null model approach

507 Appendix E. The biogeographic species pool model: illustration of the clusters

508 Appendix F. Results from the multi-model fits

509 Appendix G. Power model parameters for observed median SARs and PDARs

510 Appendix H. Null C and Z values under the continental null model

511 Appendix I. Null and observed Median absolute deviation (MAD) of PDARs

512 Appendix J. Detailed results of the biogeographical null models

513 Appendix K. Null C and Z values under the biogeographical null

514 Appendix L. Null and observed AUC_r for median PDAR/SAR

515 **FIGURES LEGENDS**

516 **Figure 1. Expected variation of the standardized PDAR given (1.A) different tree shapes**

517 **and (1.B) different eco-evolutionary processes.** (A) The three standardized PDARs

518 correspond to the three trees depicted above the graph. Note that the red PDAR also

519 corresponds to the observed SAR as the red tree is a star phylogeny. (B) Different eco-

520 evolutionary processes may change the PDAR if they act differently among spatial scales.

521 We expect that competition and/or allopatric speciation may relatively increase the PD at

522 small scale while environmental filtering and/or geographic isolation of biotas may relatively

523 decrease the PD at small scale.

524

525 **Figure 2. Hypothetical example to quantify the relative robustness of PD (compared to**

526 **SR) to habitat loss (AUC_r) using PDAR and SAR.** The example shows how to quantify the

527 relative PDAR shape by measuring the Area between the two curves (SR, PD and Area are

528 expressed in %) and computing AUC_r .

529

530 **Figure 3. Observed rescaled median SARs and median PDARs.** For each continent, we

531 report the SAR & the PDAR rescaled by the value of the maximum SR and PD respectively.

532 The two curves are both expressed in percentage of maximum diversity and thus directly

533 comparable. We also report the corresponding AUC_r values (see Fig. 2). In the lower-right

534 corner subplots we show the corresponding local derivatives.

535

536 **Figure 4. Median PDARs obtained from the continental null model.** For each continent,

537 the envelope corresponding to 1000 null continental PDARs is shown in black while the

538 observed PDAR is in red. In the corner of each panel, we plot the relative rank of observed

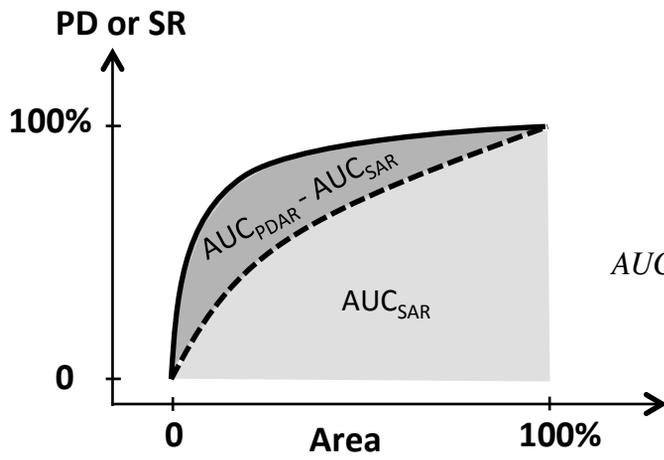
539 PD value within the null PD distribution as a function of log Area. For each spatial scale, it is

540 computed as the percentage of null PD values that are lower than the observed value (a value
541 of 0.5 indicates that observed PD equals the median of the null distribution). The dashed lines
542 correspond to a relative rank of 2.5% and 97.5%. When the computed relative ranks fall out
543 of this 95% envelope, a * is reported in the main panel (see Appendix 8 for the relative ranks
544 associated with power model parameters).

545

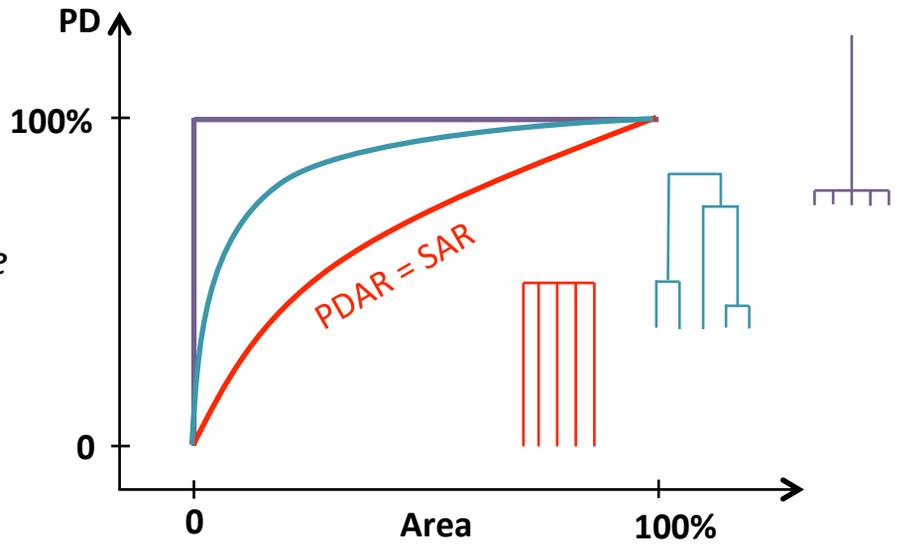
546 **Figure 5. Median PDARs obtained from the Eurasian biogeographical null models.** The
547 biogeographical null models shuffle the tips of the phylogeny according to biogeographical
548 origin (see methods). We present the results from null models containing different numbers
549 of biogeographical regions. The top panel presents the median PDAR obtained for different
550 number of biogeographic regions (see legend). The four other panels represent the details of
551 four biogeographic null models that used 1 (=continental null model), 2, 15 or 30
552 biogeographic regions, respectively. The * indicates if the relative rank of observed PD value
553 within the null PD distribution is lower (or higher) than 0.025 (or 0.975) for a given area.

554

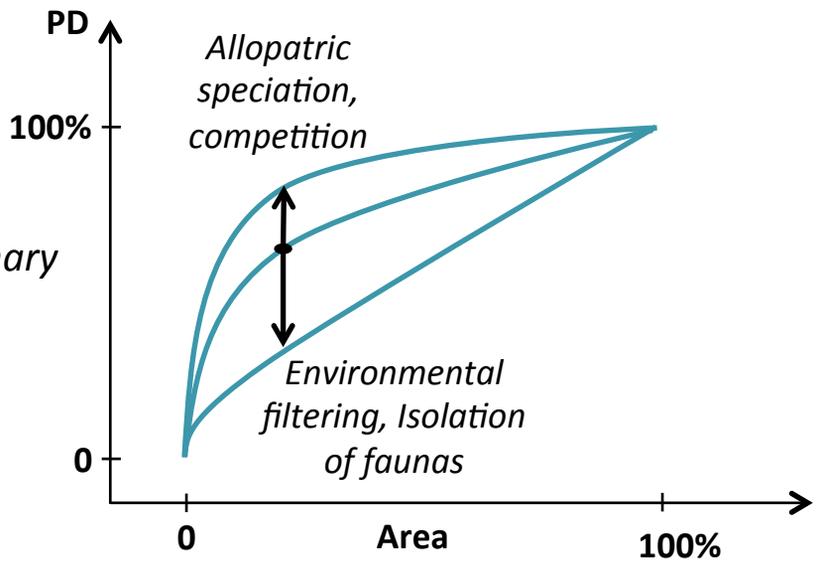


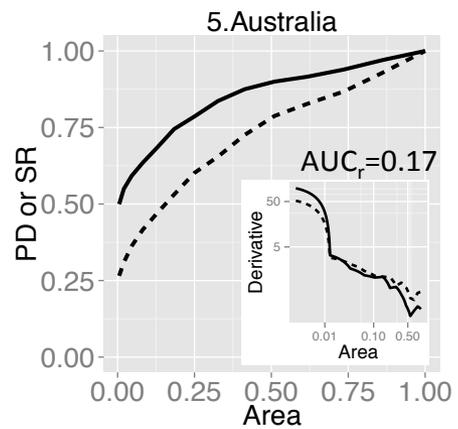
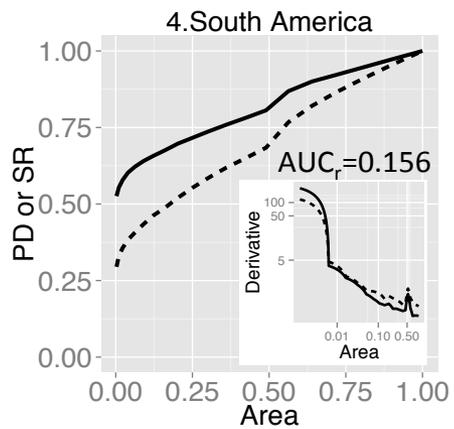
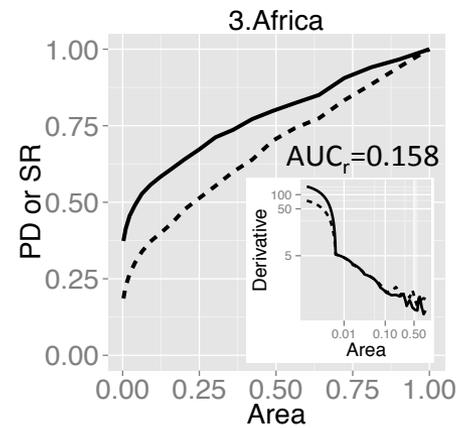
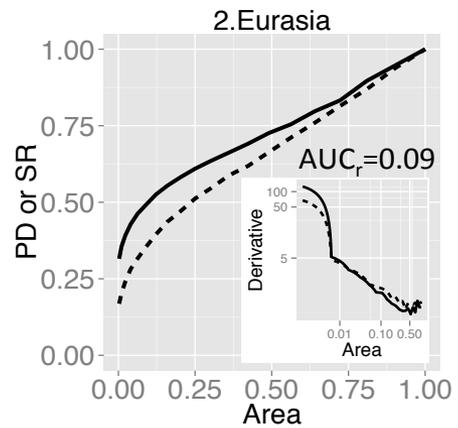
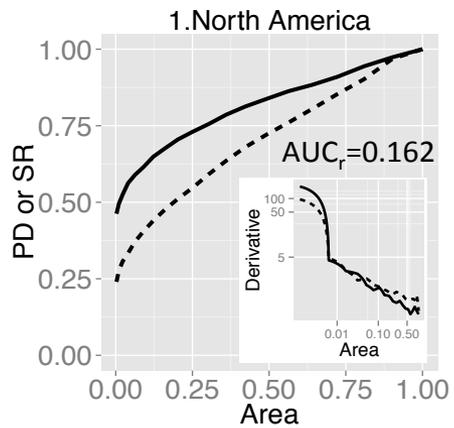
$$AUC_r = \frac{AUC_{PDAR} - AUC_{SAR}}{AUC_{SAR}}$$

A. Effect of tree shape on PDAR



B. Effect of eco-evolutionary processes on PDAR





--- Species Richness
— Phylogenetic Diversity

