

1     **Title: Historic and prehistoric human-driven extinctions have reshaped**  
2                                    **global mammal diversity patterns**

3     **Authors:** S. Faurby<sup>1\*</sup>, J-C. Svenning<sup>1</sup>

4     **Affiliations:**

5     <sup>1</sup> Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus  
6     University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark

7     \*Correspondence to: [soren.faurby@bios.au.dk](mailto:soren.faurby@bios.au.dk)

8

9     **Abstract:**

10    **Aim:** To assess the extent to which humans have reshaped Earth's biodiversity, by  
11    estimating natural ranges of all late Quaternary mammalian species, and to compare  
12    diversity patterns based on these with diversity patterns based on current distributions.

13    **Location:** Globally

14    **Methods:** We estimated species, functional and phylogenetic diversity patterns based on  
15    natural ranges of all mammalian species (n=5747 species) as they could have been today  
16    in the complete absence of human influence through time. Following this we compared  
17    macroecological analyses of current and natural diversity patterns to assess if human-  
18    induced range changes bias for evolutionary and ecological analyses based on current  
19    diversity patterns.

20 **Results:** We find that current diversity patterns have been drastically modified by  
21 humans, mostly due to global extinctions and regional to local extirpations. Current and  
22 natural diversities exhibit marked deviations virtually everywhere outside sub-Saharan  
23 Africa. These differences are strongest for terrestrial megafauna, but also important for  
24 all mammals combined. The human-induced changes led to biases in estimates of  
25 environmental diversity drivers, especially for terrestrial megafauna, but also for all  
26 mammals combined.

27 **Main conclusions:** Our results show that fundamental diversity patterns have been  
28 reshaped by human-driven extinctions and extirpations, highlighting humans as a major  
29 force in the Earth system. We thereby emphasize that estimating natural distributions and  
30 diversities is important to improve our understanding of the evolutionary and ecologically  
31 drivers of diversity as well as for providing a benchmark for conservation.

32 **Keywords**

33 **Extinction, functional diversity, macroecology, mammals, megafauna, phylogenetic**  
34 **diversity**

35 **(A). Introduction**

36 Human activities increasingly affect the whole Earth system (Crutzen, 2002), driving an  
37 ongoing global mass extinction (Barnosky *et al.*, 2011) and massive global environmental  
38 changes (IPCC, 2013), with a looming planetary biosphere state shift on the horizon  
39 (Barnosky *et al.*, 2011). A largely overlooked consequence of these anthropogenic global  
40 transformations is that they may also influence our ability to understand the factors that  
41 have generated and maintained Earth's biodiversity, one of the most important questions  
42 for contemporary science (Pennisi, 2005). Mammals represent one of the most studied  
43 organism groups, and the current diversity and general distribution of most mammal  
44 groups is well known (Schipper *et al.*, 2008). This knowledge has been used in numerous  
45 studies analyzing patterns in species, functional, or phylogenetic diversity (Safi *et al.*,  
46 1011; Huang *et al.*, 1012; Jetz & Fine, 2012; Mazel *et al.*, 2014), as well as conservation  
47 studies (Sodhi *et al.*, 2010). However, mammals are also one of the organism groups that  
48 have been influenced the most by human activities, such as habitat loss and hunting  
49 (Schipper *et al.*, 2008; Spear & Chown, 2008; Sandom *et al.*, 2014). Therefore, it is not  
50 clear to what extent the current diversity patterns still reflect natural patterns or are biased  
51 by anthropogenic extinctions, extirpations, and introductions. The extent to which our  
52 knowledge on the natural drivers of mammal diversity is biased by these human-induced  
53 changes is unknown.

54 There is ample evidence that human activities have strongly the distributions of a number  
55 of mammal species during the last few thousand years. These modifications involve

56 range contractions (Short & Smith, 1994; Laliberte & Ripple 2004), but also extinctions,  
57 notably on islands (Turvey & Fritz, 2011), and to a lesser extent also old introductions of  
58 species that are now thought of as native (Bover & Alcover, 2008). In addition,  
59 accumulating evidence indicates that humans have been a major driver of severe Late  
60 Pleistocene and early Holocene large-mammal extinctions (Sandom *et al.*, 2014). These  
61 human-induced changes raise the question of how diversity patterns would look today  
62 without any human modifications of species distributions in the Late Pleistocene, early  
63 Holocene, or historic time, i.e., given the present-natural ranges *sensu* Peterken (1977)  
64 for all late Quaternary mammals. The term “present-natural” refers to the state that a  
65 phenomenon would be in today in the complete absence of human influence through  
66 time; for simplicity, we hereafter refer to this concept by the term ‘natural’.

67 The majority of basic ecological and evolutionary studies on diversity patterns in  
68 mammals have aimed to test hypotheses for natural diversity patterns, but testing them on  
69 current diversity patterns (Sandom *et al.*, 2013). The potential problems that such  
70 anthropogenic effects may cause for macro-ecological studies have previously been  
71 pointed out (Blackburn & Gaston, 1998). Yet, no previous study has systematically  
72 estimated the natural distribution of all species within larger clades, and empirical studies  
73 have been forced to ignore this issue. If current diversity patterns have been re-shaped by  
74 human activities, this may confound conclusions from studies of natural drivers.

75 Therefore, knowing how different current diversity patterns are from the natural patterns  
76 is important, but no study has assessed this. The goal of this paper is to estimate natural  
77 diversity patterns of mammals (i.e., as they would have been given the natural

78 distributions of all species) in order determine how much human activities have reshaped  
79 contemporary diversity patterns. Understanding how current diversity patterns are shaped  
80 by human activities is not just crucial for diversity studies, but also essential for  
81 conservation management, notably for providing base-lines for restoration efforts  
82 (Donlan *et al.*, 2005).

83 As argued by Devictor *et al.* (2010), no single diversity measure fully captures all  
84 biologically relevant elements of diversity; therefore, we estimated natural patterns not  
85 just for taxonomic diversity (species richness), but also for phylogenetic and functional  
86 diversity. The use of multiple diversity measures is especially interesting in this context  
87 because all previous analyses of pre-historic faunal losses have focused solely on  
88 taxonomic richness (Sandom *et al.*, 2014; Johnson, 2002). We also analyzed the effects  
89 of human-induced changes in diversity on estimates of relationships between diversity  
90 and key environmental factors in order to investigate the extent to which analyses based  
91 on current diversity patterns may be biased. We expect that the largest differences will be  
92 found for larger animals because both the Late Pleistocene extinctions and the more  
93 recent range contractions have disproportionately affected larger species (Koch &  
94 Barnosky, 2006; Ripple *et al.*, 2014). We also expect pronounced geographic variation in  
95 the difference between current and natural diversity due to variation in human impact  
96 between geographic regions (De Thoisy *et al.*, 2010), as well as higher sensitivity of  
97 island or island-like faunas (Sandom *et al.*, 2014; Duncan *et al.*, 2013). In addition, some  
98 habitat types may have higher sensitivity than others, with large, dense forests and steep

99 mountainous areas being less vulnerable (Johnson, 2002) and desert regions being more  
100 vulnerable (Yeakel, 2014).

101

## 102 **(A) Materials and methods**

### 103 **(B) Range modifications**

104 The taxonomy for this study is the same as in a recent mammal phylogeny (Faurby &  
105 Svenning, 2015). For all species, we attempted to estimate their potential current  
106 distributions as they would potentially be today if they had not been modified by humans,  
107 i.e., their natural ranges (Peterken, 1977). Climatic data were used to estimate this range  
108 for some species, but this is not identical to the climatic potential range because we only  
109 aimed to identify the areas the species would have been able to inhabit without human  
110 interference, not the entire possible potential range based on the estimated niche.  
111 Therefore, natural dispersal constraints, biotic constraints, and non-climatic abiotic  
112 limiting factors were also taken into account when estimating natural ranges. We  
113 systematically inspected the IUCN ranges (Schipper *et al.*, 2008) of all species suspected  
114 to have had anthropogenically-induced range changes based on red-list category (red-  
115 listed as vulnerable, endangered, critically endangered, extinct, extinct in the wild, or data  
116 deficient: 2302 species), body size (all species larger than 1 kg: 627 additional species),  
117 or occurrence in large isolated island-like systems (Australia, New Guinea, or  
118 Madagascar: 340 additional species). These ranges were modified accordingly when  
119 evidence for anthropogenic range changes was found. The remaining species were not

120 systematically investigated, but their ranges were modified whenever we found evidence  
121 for human-caused range changes. We modified the ranges of 1085 species, though for 85  
122 of them the range modifications were too small to affect our analyses at our chosen grid  
123 size ( $110 \times 110$  km cells). A total of 260 species were not covered by IUCN because they  
124 went extinct prior to 1500 AD, but were included in our analysis because they have gone  
125 extinct within the last 130,000 years. By doing this we implicitly assumed that all global  
126 and continental extinctions during this period were caused by humans rather than natural  
127 phenomena, such as climatic variations. We acknowledge that this may not be true in all  
128 cases, as the probability of extinction prior to human contact seems high for a few  
129 species, such as the giant Caribbean rodent *Amblyrhiza inundata* (blunt-toothed giant  
130 hutia) (Biknevics *et al.*, 1993). Still, the evidence is overwhelming for strong human  
131 involvement in most of these extinctions (Sandom *et al.*, 2014; Turvey & Fritz 2011).  
132 Our methodology did of course allow for natural regional extinctions, notably due to  
133 climate changes, e.g., the disappearance of *Ovibos moschatus* (musk-ox) and *Gulo gulo*  
134 (wolverine) and other cold-adapted species from Southern Europe after the end of the ice  
135 age (Álvarez-Lao & García, 2010).

136 Overall, the modifications led to a change from a total of 1,983,482 occurrences to  
137 2,212,446 occurrences in  $110 \times 110$  km cells (1,073,129 to 1,298,365 occurrences for  
138 non-marine mammals and 67,306 to 242,960 occurrences for megafauna). A detailed  
139 explanation of the different types of modifications can be found in supplementary  
140 methods.

141

142 **(B) Estimated diversity**

143 All diversities were estimated on a Behrman projection of the world with equally sized  
144 grid cells with 360 columns (i.e., 1° by 1° cells at the equator, roughly equal to 110 × 110  
145 km grid cells). Diversities were estimated for five mammalian subgroups: 1) *all species*,  
146 2) *non-marine species*, 3) *terrestrial species*, 4) *large terrestrial species*, and 5)  
147 *terrestrial megafauna*. For *non-marine species*, species coded as exclusively marine by  
148 IUCN (most whales and two manatees), as well as pinnipeds coded as “marine and  
149 terrestrial” and three effectively marine non-pinniped carnivores (*Ursus maritimus* (polar  
150 bear), *Enhydra lutris* (sea otter) and *Lontra felina* (marine otter)), were removed, whereas  
151 species coded as “freshwater and marine”, such as *Phoca vitulina* (harbor seal) or  
152 manatees of the genus *Trichechus*, were deleted from all fully or partially marine cells.  
153 For *terrestrial species* all manatees, whales, pinnipeds, and bats were removed from *non-*  
154 *marine species*, and this list was further restricted in *large terrestrial species* to only  
155 include species larger than 10 kg, the definition of megafauna used by Sandom *et al.*  
156 (2014), and in *terrestrial megafauna* to only include species greater than 44.5 kg, the  
157 classical definition of megafauna used by many studies (Barnosky *et al.*, 2004).  
158 Analyses were performed on species, phylogenetic, and functional diversity. The  
159 phylogenetic diversity of each cell was defined as the median tree length of the species in  
160 the cell based on 100 trees from the posterior distribution of the phylogeny (Faurby &  
161 Svenning, 2015). Our treatment of functional diversity is a multidimensional version of



162 the bin-filling approach of (Huang *et al.*, 2012). For the functional diversity analyses of  
163 *all species* and *non-marine species*, we focused on the three dimensions of niche space,  
164 habitat, body size, and diet, whereas the analysis of the three terrestrial subsets only  
165 focused on body size and diet. Details of the estimation can be found in supplementary  
166 methods.

167 Three diversities were estimated for each cell: 1) current diversity, 2) natural diversity of  
168 historically extant species, and 3) total natural diversity. *Current diversity* was defined as  
169 the diversity following IUCN, excluding species ranges coded as introduced and species  
170 ranges coded as extinct or possibly extinct (5). *Natural diversity of historically extant*  
171 *species* was generally the natural diversity of all species accepted by IUCN, meaning that  
172 species ranges coded as extinct or possibly extinct by IUCN, as well as our modified  
173 ranges of species accepted by IUCN, were included, but species that went globally  
174 extinct prior to 1500 AD were not included. In addition, for species that went  
175 continentally extinct (with Europa and Asia considered the same continent) prior to 1500  
176 AD, the natural distributions on these continents were removed. Therefore, the natural  
177 distribution of *Equus ferus* in North America, South America, and Africa, *Camelus*  
178 *dromedarius* in Africa and Eurasia, *Cuon alpinus* and *Saiga tatarica* in North America,  
179 *Bos primigenius* in Africa, and *Crocuta crocuta*, *Hippopotamus amphibius*, *Macaca*  
180 *sylvanus*, and *Ovibos moschatus* in Eurasia were removed. *Total natural diversity*  
181 included the natural distribution of all species accepted by IUCN, including the ranges on  
182 the continents mentioned above, but also included the natural distribution of the 260 pre-  
183 historically extinct species. In the main article we focus on the differences between

184 *current diversity* and *total natural diversity*, and we refer to *total natural diversity* simply  
185 as *natural diversity* throughout the main article. Separate maps showing the patterns for  
186 *Natural diversity of historically extant species* are shown in the supplementary figures.

187 We also estimated the total deficit (the difference between *current diversity* and *total*  
188 *natural diversity* relative to the *total natural diversity*), the historic loss (the difference  
189 between *current diversity* and *natural diversity of historically extant species* relative to  
190 the *total natural diversity*), and the pre-historic loss (the difference between the *natural*  
191 *diversity of historically extant species* and the *total natural diversity* relative to the *total*  
192 *natural diversity*). These terms are defined temporally, and the vast majority of pre-  
193 historic loss occurred earlier than historic loss, but we note that a limited temporal  
194 overlap between the two exists. For example, the massive pre-historic loss in the  
195 Caribbean mainly occurred within the middle to late Holocene (Steadman *et al.*, 2005),  
196 whereas most of the range contractions of *Panthera pardus* in Europe occurred earlier  
197 (Sommer & Benecke, 2006). In addition, for some species the loss in range was a slow  
198 and gradual process, perhaps best exemplified by *Equus ferus*. The decline in this species  
199 started near the end of the last ice age with continental extinctions in North and South  
200 America (Sandom *et al.*, 2014), whereas the last wild specimen in Europe died in the 19<sup>th</sup>  
201 century (Nowak, 1999) and the last wild specimen of the species globally died in the 20<sup>th</sup>  
202 century (Schipper *et al.*, 2008).

203

204 **(B) Statistical analysis of diversity**

205 We analyzed the geographic variation in diversity for a total of 45 different analyses: all  
206 combinations of the three diversities (species, phylogenetic, and functional), five datasets  
207 (terrestrial megafauna, large terrestrial mammals, all terrestrial mammals, non-marine  
208 mammals, and all mammals) and current, IUCN natural, and total natural diversity. Our  
209 analysis had nine variables comprising seven main effects and two interactions. The  
210 effects were: 1) elevation range, 2) annual temperature (Hijmans *et al.*, 2005), 3)  
211 logarithm transformed annual precipitation (Hijmans *et al.*, 2005), 4) precipitation  
212 seasonality (Hijmans *et al.*, 2005), 5) temperature seasonality (Hijmans *et al.*, 2005), 6)  
213 NDVI (Tucker *et al.*, 2005), and 7) “open areas”. The last was a dummy variable  
214 separating all non-forest cells (defined as areas with Tropical and Subtropical Grasslands,  
215 Savannas and Shrublands, Temperate Grasslands, Savannas and Shrublands, Flooded  
216 Grasslands and Savannas, Montane Grasslands and Shrublands, Tundra, or Deserts and  
217 Xeric Shrublands (Olson, 2001)) from forest cells (defined as Tropical and Subtropical  
218 Moist Broadleaf Forests, Tropical and Subtropical Dry Broadleaf Forests, Tropical and  
219 Subtropical Coniferous Forests, Temperate Broadleaf and Mixed Forests, Temperate  
220 Coniferous Forest, Boreal Forests/Taiga, Mediterranean Forests, Woodlands and Scrubs,  
221 or Mangroves (Olson, 2001)). The interactions were: 8) annual temperature and open  
222 areas and 9) annual temperature and annual precipitation. The interactions were intended  
223 to take into account that diversity may be different in forest and non-forest biomes,  
224 especially for megafauna because such species may not have access to the plant resources  
225 in the canopy. All parameters except “open areas” were standardized to have a mean of 0  
226 and a standard deviation of 1.

227 In order to remove spatial autocorrelation in the data, we analyzed the data based on the  
228 SAR<sub>err</sub> model, which has been suggested to be a suitable method of minimizing  
229 autocorrelation (Kissling & Carl, 2008). SAR models are computing intensive; therefore,  
230 for computational reasons, we chose to perform them using cells equivalent to 4° squares  
231 at the equator. We tried neighborhoods for each SAR model of between 1 and 8  
232 neighbors and selected the best model based on AIC (the chosen models had between 4  
233 and 6 neighbors). Next, we estimated the overall model performance by calculating the  
234 square of the correlation between the predicted (only the predictor, not the spatial parts)  
235 and raw values. We refer to this as pseudo-R<sup>2</sup> throughout the paper even though several  
236 different estimates of model fit are frequently referred to as pseudo-R<sup>2</sup> (UCLA: Statistical  
237 Consulting Group, 2014). All p-values were calculated by Wald's tests. In order to make  
238 comparisons between different models easier, we kept all parameters in the models, even  
239 if they were not significant. In order to make parameter values for *current diversity* and  
240 *natural diversity* comparable, the neighborhoods in the SAR analyses that minimized the  
241 AIC for the corresponding *total natural diversity* were used for *current diversity* and  
242 *natural diversity of historically extant species*.

243

## 244 (A) Results

### 245 (B) Diversity gradients

246 We here focus on the patterns for all terrestrial species (n = 4465) and terrestrial  
247 megafauna (n = 330). Three other datasets (large terrestrial species ≥10 kg (n=570) with

248 results similar to those for megafauna; non-marine species (n= 5635), and all species  
249 (n=5747) with results overall similar to all terrestrial species) are reported in the appendix  
250 (Fig S1-S10). Overall the differences between current and natural diversities were  
251 substantially larger for megafauna than for all terrestrial species (Fig. 1). The changes in  
252 species, phylogenetic and functional diversity were overall similar although there were  
253 some differences which we will discuss later.

254

### 255 **(B) Geographic variation in diversity deficits**

256 Geographic patterns in the difference between current and natural diversity (hereafter for  
257 simplicity referred to as deficits) in species, phylogenetic and functional diversity exhibit  
258 similar geographic patterns (Fig. 2). The largest deficits in megafauna diversity occur on  
259 islands (Madagascar, Caribbean, Oceania) and the island-like continent Australia (Fig. 2).  
260 Strong deficits are also found in the Americas and Greater Sahara, whereas deficits are  
261 only minor in Africa and tropical Asia and intermediate in the remaining regions. The  
262 temporal patterns of the losses behind these deficits are radically different. Some regions,  
263 such as Australia, New Guinea and the Caribbean islands, and the New World, have had  
264 almost exclusively pre-historic losses, others have had mainly historic losses, such as  
265 Greater Sahara and Africa, whereas still other regions - most noticeably Europe – have  
266 had both large historic and pre-historic losses. In all regions, the relative deficits for all  
267 terrestrial species are substantially smaller than the megafauna losses, but the difference  
268 between the two varied among regions.

269

270 **(B) Biases in the inference in diversity drivers**

271 The substantial and geographically variable anthropogenic diversity deficits could have  
272 large effects on our ability to understand macroscale diversity patterns. In order to assess  
273 the magnitude of this problem, we compared the results of parallel standard  
274 macroecological analyses of current and natural diversity patterns. A striking result was  
275 that the explanatory power (pseudo- $R^2$ ) was consistently lower for current diversity than  
276 for natural diversity for all studied mammal groups. In addition, the models for natural  
277 diversity based only on historically extant species consistently had intermediate pseudo-  
278  $R^2$  values between the two (Tables S1-S3). The decreases in pseudo- $R^2$  were especially  
279 large for terrestrial megafauna; the pseudo- $R^2$  values for all three diversity measures were  
280 approximately 0.2 lower for current diversity than for natural diversity. The higher  
281 explanatory power for the natural diversity is especially noteworthy given that these are  
282 known with less certainty than the current diversity, and these uncertainties would be  
283 expected to reduce the pseudo- $R^2$  values.

284 Two other consistent changes were seen in analyses of current vs. natural diversity. In all  
285 analyses, the normalized difference vegetation index (NDVI), an indicator of vegetation  
286 productivity (Wang *et al.*, 2004), was the strongest predictor of diversity, with higher  
287 diversity in areas with higher NDVI, but its predictive power was always lower for  
288 current diversity than for natural diversity. Elevation range was a weaker, but consistent,  
289 predictor (with higher diversity with higher elevation range), but with a consistently

290 stronger effect on current diversity relative to natural diversity. The changes in pseudo-  
291  $R^2$ , NDVI, and elevation range were strikingly regular, with a larger change in pseudo- $R^2$   
292 also corresponding to a larger change in the effect sizes of NDVI and elevation range  
293 (Fig. 3).

294

## 295 (A) Discussion

### 296 (B) Diversity gradients

297 For terrestrial megafauna, the pattern in natural species diversity is radically different  
298 from the current pattern (Fig. 1A and B). Current species diversity exhibits a well-known  
299 peak in Sub-Saharan Africa, whereas Africa's natural species diversity is similar to other  
300 continents, as suggested previously (Owen-Smith, 2013). For natural diversity, the  
301 highest values are observed in the southern Rocky Mountains and Mexico and in northern  
302 Argentina, whereas most of the Americas and large parts of Eurasia have diversities  
303 similar to the most diverse areas in sub-Saharan Africa (Fig. 1A and B). Differences  
304 between current and natural diversities for all terrestrial species (i.e., irrespective of body  
305 size) are smaller than for megafauna, with the largest changes occurring on islands  
306 (including the island-like continent Australia) and some temperate areas in Europe and  
307 North America (Fig. 1C and D). The patterns in phylogenetic diversity are similar to the  
308 patterns in species diversity (Fig. 1E-H versus Fig. 1A-D). The major difference is that  
309 natural phylogenetic diversity is elevated in the Americas relative to Africa and Southeast

310 Asia, reflecting greater diversity at deep phylogenetic levels in South America, as seen by  
311 tabulating the number of mammalian orders containing terrestrial megafauna.

312 The natural and current megafauna in Africa belong to six orders, whereas the natural  
313 megafauna diversity in South America belongs to nine orders, only five of which have  
314 extant megafauna species in South America. The high natural phylogenetic diversity of  
315 the New World can likely be seen as a consequence of the former isolation of South  
316 America, followed by the effects of the Great American Biotic Interchange (GABI)  
317 (Simpson, 1980). Even though many of the formerly endemic South American  
318 mammalian groups went extinct due to competition with invading Northern Hemisphere  
319 clades, a number of groups survived until the Late Pleistocene or early Holocene  
320 (Sandom *et al.*, 2014). However, the species diversity within many of these clades was  
321 low during the Late Pleistocene, with only a few species, even though they were formerly  
322 diverse clades (Billet, 2011), creating a pattern of long branches separating species and  
323 high phylogenetic diversity. The GABI is expected to influence the phylogenetic  
324 diversity, but it could potentially also influence species diversity. As already suggested  
325 by Darwin (1859), related species are often thought to compete more with each other, and  
326 two areas of equal productivity may potentially support more species if they are distantly  
327 related rather than closely related. The evidence for this is limited (Cahill *et al.*, 2008),  
328 but a functional coupling between the high megafauna ordinal diversity in the Americas  
329 and the region's very high species diversity in the absence of human-driven extinctions  
330 and extirpations is still possible.



331 The most striking difference between the patterns in functional diversity (Fig. 1I-L) and  
332 the other patterns is that the differences in functional diversity between current and  
333 natural diversity are clearly visible in all areas for both all terrestrial species and  
334 megafauna, as opposed to being much more evident for megafauna. This is at least partly  
335 a logical consequence of the highly size-selective nature of the extinctions and range  
336 contractions affecting our size-based metric for functional diversity. Though we mainly  
337 focus on patterns that are different between natural and current patterns, the functional  
338 diversity patterns also highlight the constancy of some patterns. One such constant  
339 pattern is the relative steepness of the gradient between temperate and tropical regions of  
340 functional and species diversity. For both current and natural diversity, the gradient is  
341 substantially less steep in functional diversity than in the other diversity measures, which  
342 corresponds to studies from other taxa (Mouillot *et al.*, 2014).

343

#### 344 **(B) Geographic variation in diversity deficits**

345 The regional differences in faunal deficits are consistent with higher sensitivity of island  
346 regions and open areas to human pressures compared to continental forest regions. Only  
347 some of the island regions (Caribbean, Madagascar, and Australia) have large deficits  
348 among all terrestrial species, with Oceania having a much smaller deficit, similar to that  
349 of tropical Asia. The cause for the low deficits in Oceania is unknown, but it could be  
350 related to a higher survival in closed forest environments (Johnson, 2002) due to lower  
351 accessibility to humans. The large deficits in the Greater Sahara (Fig. 2) and the desert

352 regions of Australia (Figs. S6-S10) despite low human footprint in these regions  
353 (Wildlife Conservation Society, 2015) point to a higher sensitivity of arid faunas to  
354 human-driven extirpation either directly via hunting or indirectly via higher sensitivity of  
355 arid vegetation to anthropogenic degradation. There is evidence for high pre-historic or  
356 historic hunting pressure in certain arid regions, such as the Middle East (Bar-Oz *et al.*,  
357 2011). Further, a number of species formerly inhabiting these regions used were at their  
358 environmental extremes here, and such marginal populations could potentially be more  
359 sensitive to increased human pressures.

360 Anthropogenic diversity losses in an area within a given time period may depend on  
361 losses during preceding periods. Africa experienced a rather large Early Pleistocene  
362 extinction, which was potentially caused by early *Homo* species (Werdelin & Lewis,  
363 2013), and this has been suggested to be a contributing factor to the low loss of  
364 megafauna in Africa in the Late Pleistocene (Short & Smith, 1994). Similarly, the  
365 relatively low historic losses in North and South America may reflect that the massive  
366 pre-historic loss already had removed most sensitive species. Conversely, the lower pre-  
367 historic loss in South-East Asia and potential survival of relatively sensitive species could  
368 explain its large historic losses and higher fraction endangered species compared to  
369 America (Sodhi *et al.*, 2010).

370 The patterns in phylogenetic diversity deficits are similar to those for species diversity,  
371 although generally smaller (Fig. 2). This is most striking in Australia, which appears to  
372 have suffered substantially lower phylogenetic losses relative to its species losses. A

373 potential reason may be that marsupials appear to have a higher evolutionary ecological  
374 plasticity than placental mammals, so that phylogenetic clades are less ecologically  
375 specialized and thus less consistently sensitive to the same pressures. Exemplifying this,  
376 the two largest extinct marsupial predators belongs to two different orders  
377 (Dasyuromorphia and Diprotodontia), with the latter showing large variation in body  
378 size, from <10 g to >1 ton. The cause of this large plasticity is unknown, but it could  
379 potentially be a corollary of the more limited scope for ecological specialization in  
380 marsupials caused by only having one set of teeth (Werdelin, 1987). Irrespective of the  
381 underlying cause, selective removal of species based on ecological characteristics, such  
382 as body size, would remove a relatively lower amount of phylogenetic history for  
383 marsupials than for placental mammals.

384

#### 385 **(B) Biases in the inference in diversity drivers**

386 The findings of this paper suggest that analyses of current patterns may lead to a biased  
387 understanding of the drivers of diversity. Importantly, our results suggest that mammal  
388 diversity was more strongly linked to vegetation productivity before being reshaped by  
389 human activities and that analyses of current diversity patterns underestimate this  
390 relationship. This is likely a consequence of the strong correlation between productivity  
391 and human population density (Evans & Gaston, 2004). The differences in the  
392 importance of elevation range also suggest an anthropogenic bias in the current patterns.  
393 All current diversities exhibited significant positive correlations between diversity and

394 elevation ranges, whereas this relationship was not significant for the natural diversity of  
395 megafauna and large species diversity. Habitat accessibility for humans may be highly  
396 correlated with elevation range as suggested by a strong correlation between elevation  
397 slope and remaining tree cover across the globe (Sande & Svenning, 2013). Importantly,  
398 steep mountainous terrain has been proposed to have offered some megafauna species a  
399 refuge from pre-historic hunting (Johnson, 2002) and to provide protection against human  
400 activities today (Gavashelishvili & Lukarevskiy, 2008). Therefore, our results suggest  
401 that the positive effect of elevation range on the current diversity of terrestrial megafauna  
402 may largely be an anthropogenic artefact rather than a natural phenomenon, as it is not a  
403 significant predictor of natural diversity. On the other hand, the still significant effect of  
404 elevational range for the natural diversity of all terrestrial species (Tables S1-S3) suggest  
405 that the effect on overall diversity represent a natural phenomenon, e.g., reflecting habitat  
406 heterogeneity.

407 The performance of models of diversity drivers is often judged based on their explanatory  
408 power (Jetz & Fine, 2012), and changes in  $R^2$  values may change our understanding of  
409 how well we understand diversity patterns. There is still substantial debate over the  
410 causes of the overall diversity gradients (Brown, 2014). Part of the reason why no  
411 explanation has been universally accepted could be that the models are designed to  
412 explain natural diversity, but are applied to current diversity. The observed increases in  
413 pseudo- $R^2$  values when shifting to natural diversity suggest that we are actually better  
414 able to explain diversity gradients than we thought, at least for mammals, if we remove  
415 the human-induced biases.

416 We have only focused on overall diversity patterns rather than clade- or region-specific  
417 patterns, but there is no reason to assume that the overall patterns are especially sensitive  
418 to human impact. One could even assume that the patterns we investigated in this paper  
419 may be some of the geographic patterns least influenced by anthropogenic modifications.  
420 Many studies have documented a strong human impact on smaller-scale distribution and  
421 diversity patterns (Laliberte & Ripple, 2004). Therefore, we suggest that researchers  
422 working on macroecological or macroevolutionary analyses of natural ecological and  
423 evolutionary drivers of diversity should focus on natural rather than current distributions  
424 whenever possible (maps of all distributions are available as appendix 2-7, but the data  
425 can also be downloaded in a readily useable format at [http://bios.au.dk/om-](http://bios.au.dk/om-instituttet/organisation/oekoinformatik-biodiversitet/data/)  
426 [instituttet/organisation/oekoinformatik-biodiversitet/data/](http://bios.au.dk/om-instituttet/organisation/oekoinformatik-biodiversitet/data/) (DATAWILL BE  
427 UPLOADED UPON ACCEPTANCE).

428 More fundamentally, the results of the present study illustrate that we now live in the  
429 Anthropocene (Crutzen, 2002), a human-dominated epoch in which few biological  
430 patterns and processes are not substantially modified by humans (Helmus *et al.*, 2014;  
431 Dirzo *et al.*, 2014). Therefore, it is important to integrate the potential effects of humans  
432 into any type of analysis, including ones often thought of as being little influenced by  
433 humans, such as the diversity gradients discussed here. The estimated natural  
434 distributions for all late-Quaternary mammals will also be highly useful for applied  
435 conservation projects and studies, enabling managers and researchers to use present  
436 natural diversity as a baseline, e.g., for selecting species for rewilding projects or  
437 reintroductions (Donlan *et al.*, 2005; Hayward 2009).

438

439 **Supplementary Materials:**

440 Supplementary Materials and Methods

441 Supplementary Figures S1-S11

442 Supplementary Tables S1-S3

443 Supplementary Data 1-8

444

445 **Acknowledgments**

446 JCS was supported by the European Research Council (ERC-2012-StG-310886-  
447 HISTFUNC). SF was supported by the Danish Natural Science Research Council (#11-  
448 115750). SF estimated the natural distributions of all species with input from JCS. SF  
449 performed the analyses. SF and JCS wrote the paper.

450

451 **Data accessibility.**

452 The data reported in this paper are provided in the electronic supplementary material as  
453 pdf files and in a readily useable format from [http://bios.au.dk/om-](http://bios.au.dk/om-instituttet/organisation/oekoinformatik-biodiversitet/data/)  
454 [instituttet/organisation/oekoinformatik-biodiversitet/data/](http://bios.au.dk/om-instituttet/organisation/oekoinformatik-biodiversitet/data/) (DATAWILL BE  
455 UPLOADED UPON ACCEPTANCE).

456

457 **Biosketches**

458 **Søren Faurby** is a postdoc at Aarhus University. He is an evolutionary biologist  
459 interested in the development, maintenance, and consequences of geographic variation  
460 within and between species, and he has investigated these subjects in a wide variety of  
461 taxa.

462 **Jens-Christian Svenning** is a professor at Aarhus University. He is a broadly based  
463 ecologist, with core research interests including community and vegetation ecology,  
464 macroecology, biogeography, and physical geography. His work ranges from addressing  
465 basic ecological and evolutionary questions to investigating applied ecology,  
466 conservation biology, and global change.

467

468 **REFERENCES**

469 Álvarez-Lao, D.J. & García, N. (2010) Chronological distribution of Pleistocene cold-  
470 adapted large mammal faunas in the Iberian Peninsula. *Quaternary International*,  
471 **212**,120-128.

472 Bar-Oz, G., Zeder, M. & Hole, F. (2011) Role of mass-kill hunting strategies in the  
473 extirpation of Persian gazelle (*Gazella subgutturosa*) in the northern Levant. *Proceedings*  
474 *of the National Academy of Sciences*, **108**, 7345-7350.

475 Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L.& Shabel, A.B. (2004) Assessing  
476 the causes of Late Pleistocene extinctions on the continents. *Science*, **306**, 70-75.

- 477 Barnosky, A.D., *et al.* (2011) Has the Earth's sixth mass extinction already arrived?  
478 *Nature*, **471**, 51-57.
- 479 Biknevicus, A.R., McFarlane, D.A. & MacPhee, R.D.E. (1993) Body size in *Amblyrhiza*  
480 *inundata* (Rodentia: Caviomorpha), an extinct megafaunal rodent from the Anguilla  
481 Bank, West Indies: estimates and implications. *American Museum Novitates*, **3079**, 1-25.
- 482 Billet, G. (2011) Phylogeny of the Notoungulata (Mammalia) based on cranial and dental  
483 characters. *Journal of Systematic Palaeontology*, **9**, 481-497.
- 484 Blackburn, T.M. & Gaston, K.J. (1998) Methodological issues in macroecology.  
485 *American Naturalist*, **151**, 68-83.
- 486 Bover, P.P. & Alcover, J.A. (2008) Extinction of the autochthonous small mammals of  
487 Mallorca (Gymnesic Islands, Western Mediterranean) and its ecological consequences.  
488 *Journal of Biogeography*, **35**, 1112-1122.
- 489 Brown, J.M. (2014) Why are there so many species in the tropics? *Journal of*  
490 *Biogeography*, **41**, 8-22.
- 491 Cahill, J.F., Kembela, S.W., Lamba, E.G. & Keddy, P.A. (2008) Does phylogenetic  
492 relatedness influence the strength of competition among vascular plants? *Perspectives in*  
493 *Plant Ecology, Evolution and Systematics*, **10**, 41-50.
- 494 Crutzen, P.J. (2002) Geology of mankind. *Nature*, **415**, 23-23.
- 495 Darwin, C. (1859) *The Origin of Species*. John Murray, London.



- 496 De Thoisy, B., Richard-Hansen, C., Goguillon, B., Joubert, P., Obstancias, J., Winterton,  
497 P. & Brosse, S. (2010) Rapid evaluation of threats to biodiversity: human footprint score  
498 and large vertebrate species responses in French Guiana. *Biodiversity Conservation*,  
499 **19**,1567–1584.
- 500 Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010)  
501 Spatial mismatch and congruence between taxonomic, phylogenetic and functional  
502 diversity: the need for integrative conservation strategies in a changing world. *Ecology*  
503 *Letters*, **13**, 1030–1040.
- 504 Dirzo, R., *et al.* (2014) Defaunation in the Anthropocene. *Science*, **345**, 401-406.
- 505 Donlan, J., *et al.* (2005) Re-wilding North America. *Nature*, **436**, 913–914.
- 506 Duncan, R.P., Boyer, A.G. & Blackburn, T.M. (2013) Magnitude and variation of  
507 prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of*  
508 *Sciences*, **110**, 6436-6441.
- 509 Evans, K.L. & Gaston, K.J. 2004 People, energy and avian species richness. *Global*  
510 *Ecology and Biogeography*, **14**, 187-196.
- 511 Faurby, S. & Svenning, J.C. (2015) A species-level phylogeny of all extant and late  
512 Quaternary extinct mammals using a novel heuristic-hierarchical bayesian approach.  
513 *Molecular Phylogenetics and Evolution*, **84**, 14-26.

- 514 Gavashelishvili, A. & Lukarevskiy, V. (2008) Modelling the habitat requirements of  
515 leopard *Panthera pardus* in west and central Asia. *Journal of Applied Ecology*, **45**, 579-  
516 588.
- 517 Hayward, M.W. (2009) Conservation management for the past, present and future.  
518 *Biodiversity and Conservation*, **18**,765-775.
- 519 Helmus, M.R., Mahler, D.L. & Losos, J.B. (2014) Island biogeography of the  
520 Anthropocene. *Nature* **513**, 543-546.
- 521 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A. (2005) Very high  
522 resolution interpolated climate surfaces for global land areas. *International Journal of*  
523 *Climatology*, **25**, 1965-197.
- 524 Huang, S., Stephens, P.R. & Gittleman, J.L. (2012) Traits, trees and taxa: global  
525 dimensions of biodiversity in mammals. *Proceedings of the Royal Society B*, **279**, 4997-  
526 5003.
- 527 IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of*  
528 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*  
529 *Climate Change* (ed. by Stocker, T.F., *et al.*). Cambridge University Press, Cambridge.
- 530 Jetz, W. & Fine, P.V.A. (2012) Global gradients in vertebrate diversity predicted by  
531 historical area-productivity dynamics and contemporary environment. *PLoS Biology*, **10**,  
532 e1001292.

- 533 Johnson, C.N. (2002) Determinants of loss of mammal species during the Late  
534 Quaternary ‘megafauna’ extinctions: life history and ecology, but not body size.  
535 *Proceedings of the Royal Society of London B*, **269**, 2221–2227.
- 536 Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of  
537 simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59–71.
- 538 Koch, P.L. & Barnosky, A.D. (2006) Late Quaternary extinctions: State of the debate.  
539 *Annual Reviews of Ecology Evolution and Systematics*, **37**, 215-250.
- 540 Laliberte, A.S. & Ripple, W.J. (2004) Range contractions of North American carnivores  
541 and ungulates. *BioScience*, **154**, 123-138.
- 542 Mazel, F., *et al.* 2014 Multifaceted diversity–area relationships reveal global hotspots of  
543 mammalian species, trait and lineage diversity. *Global Ecology and Biogeography*, **23**,  
544 836-847.
- 545 Mouillot, D., *et al.* (2014) Functional over-redundancy and high functional vulnerability  
546 in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences*,  
547 **111**, 13757-13762.
- 548 Nowak, R.M. (1999) *Walker's Mammals of the World*. The Johns Hopkins University  
549 Press, Baltimore.
- 550 Olson, D.M. (2001) Terrestrial ecoregions of the world: A new map of life on Earth.  
551 *BioScience*, **51**, 933-938.

- 552 Owen-Smith, N. (2013) Contrasts in the large herbivore faunas of the southern continents  
553 in the late Pleistocene and the ecological implications for human origins. *J. Biogeogr.* **40**,  
554 1215-1224.
- 555 Pennisi, E. (2005) What determines species diversity? *Science*, **309**, 90.
- 556 Peterken, G.F. (1977) Habitat conservation priorities in British and European woodlands.  
557 *Biodiversity Conservation*, **11**, 223-236.
- 558 Ripple, W.J., *et al.* (2014) Status and ecological effects of the world's largest carnivores.  
559 *Science*, **343**, 1241484 (2014).
- 560 Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho,  
561 J.A.F. (2011) Understanding global patterns of mammalian functional and phylogenetic  
562 diversity. *Philosophical Transactions of the Royal Society B*, **366**, 2536-2544.
- 563 Sandel, B. & Svenning, J.C. (2013) Human impacts drive a global topographic signature  
564 in tree cover. *Nature Communications* **4**, 2474.
- 565 Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W.D., Lenoir, J., Sandel, B., Trøjelsgaard,  
566 K., Ejrnæs, R. & Svenning, J.C. (2013) Mammal predator and prey species richness are  
567 strongly linked at macroscale. *Ecology*, **94**, 1112-1122.
- 568 Sandom, C., Faurby, S., Sandel, B. & Svenning, J.C. (2014) Global late Quaternary  
569 megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal*  
570 *Society B*, **281**, 20133254.

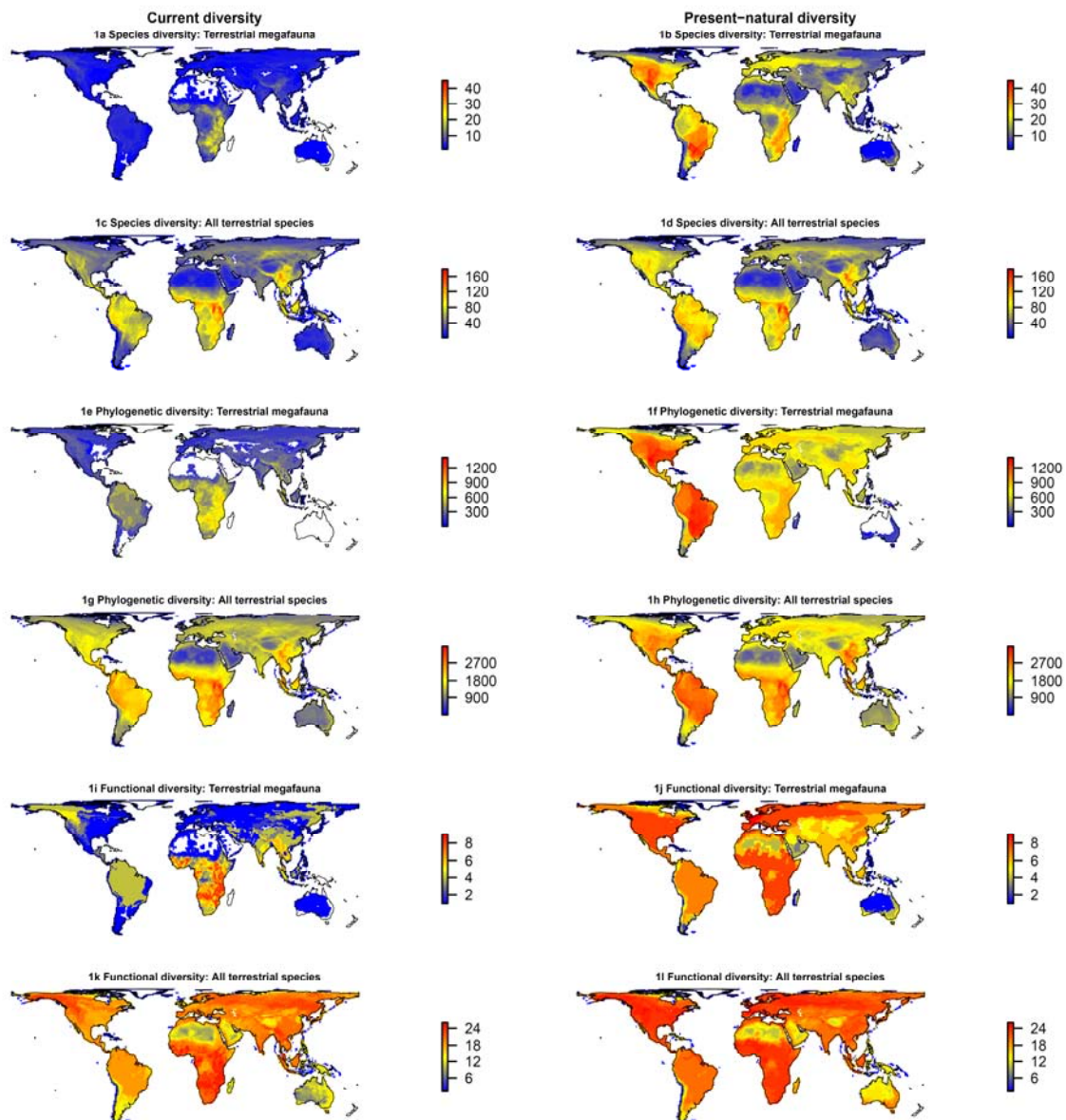
- 571 Schipper, J. *et al.* (2008) The status of the world's land and marine mammals: Diversity,  
572 threat, and knowledge. *Science*, **322**, 225-230.
- 573 Short, J., Smith, A. (1994) Mammal decline and recovery in Australia. *Journal of*  
574 *Mammalogy*, **75**, 288-297.
- 575 Simpson, G.G. (1980) *Splendid isolation: the curious history of South American*  
576 *mammals*. Yale University Press.
- 577 Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh, L.P. & Brook, B.W. (2010) The  
578 state and Conservation of Southeast Asian biodiversity. *Biodiversity Conservation*, **19**,  
579 317-218.
- 580 Sommer, R.S., Benecke, N. (2006) Late Pleistocene and Holocene development of the  
581 felid fauna (Felidae) of Europe: a review. *Journal of Zoology*. **269**, 7-19.
- 582 Spear, D. & Chown, S.L. (2008) Taxonomic homogenization in ungulates: patterns and  
583 mechanisms at local and global scales. *Journal of Biogeography*, **35**, 1962-1975.
- 584 Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods,  
585 C.A., Iturralde-Vinent, M. & Hodgins, G.W.L. (2005) Asynchronous extinction of late  
586 Quaternary sloths on continents and islands. *Proceedings of the National Academy of*  
587 *Sciences*, **102**, 11763–11768.
- 588 Tucker, C.J., Pinzon, J.E., Brown, M.E., Slayback, D.A., Pak, E.W., Mahoney, R.,  
589 Vermote, E.F. & El Saleous, N. (2005) An Extended AVHRR 8-km NDVI Data Set

- 590 Compatible with MODIS and SPOT Vegetation NDVI Data. *International Journal*  
591 *Remote Sensing*, **26**, 4485–4498.
- 592 Turvey, S.T. & Fritz, S.A. (2011) The ghosts of mammals past: biological and  
593 geographical patterns of global mammalian extinction across the Holocene. *Philosophical*  
594 *Transactions of the Royal Society B*, **366**, 2564–2576.
- 595 UCLA: Statistical Consulting Group. (2014) *FAQ: What are pseudo R-squareds?*  
596 (Available at [http://www.ats.ucla.edu/stat/mult\\_pkg/faq/general/Psuedo\\_RSquareds.htm](http://www.ats.ucla.edu/stat/mult_pkg/faq/general/Psuedo_RSquareds.htm)).  
597 (Accessed: 12th February 2015).
- 598 Wang, J., Rich, P.M., Price, K.P. & Kettle, W.D. (2004) Relations between NDVI and  
599 tree productivity in the central Great Plains. *International Journal of Remote Sensing*, **25**,  
600 3127-3138.
- 601 Werdelin, L. (1987) Jaw geometry and molar morphology in marsupial carnivores:  
602 analysis of a constraint and its macroevolutionary consequences. *Paleobiology*, **13**, 342-  
603 350.
- 604 Werdelin, L & Lewis, M.E. (2013) Temporal change in functional richness and evenness  
605 in the eastern African Plio-Pleistocene carnivoran guild. *PLoS ONE*, **8**, e57944.
- 606 Wildlife Conservation Society - WCS, and Center for International Earth Science  
607 Information Network - CIESIN - Columbia University. (2015) *Last of the Wild Project*,  
608 *Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic)*. (Available at  
609 <http://dx.doi.org/10.7927/H4M61H5F>). (Accessed: 12th February 2015).

- 610 Yeakel, J.D. (2014) Collapse of an ecological network in Ancient Egypt. *Proc. Natl.*  
611 *Acad. Sci. U. S. A.* **111**, 14472-14477.

612 **Figures**

613 **Figure 1**

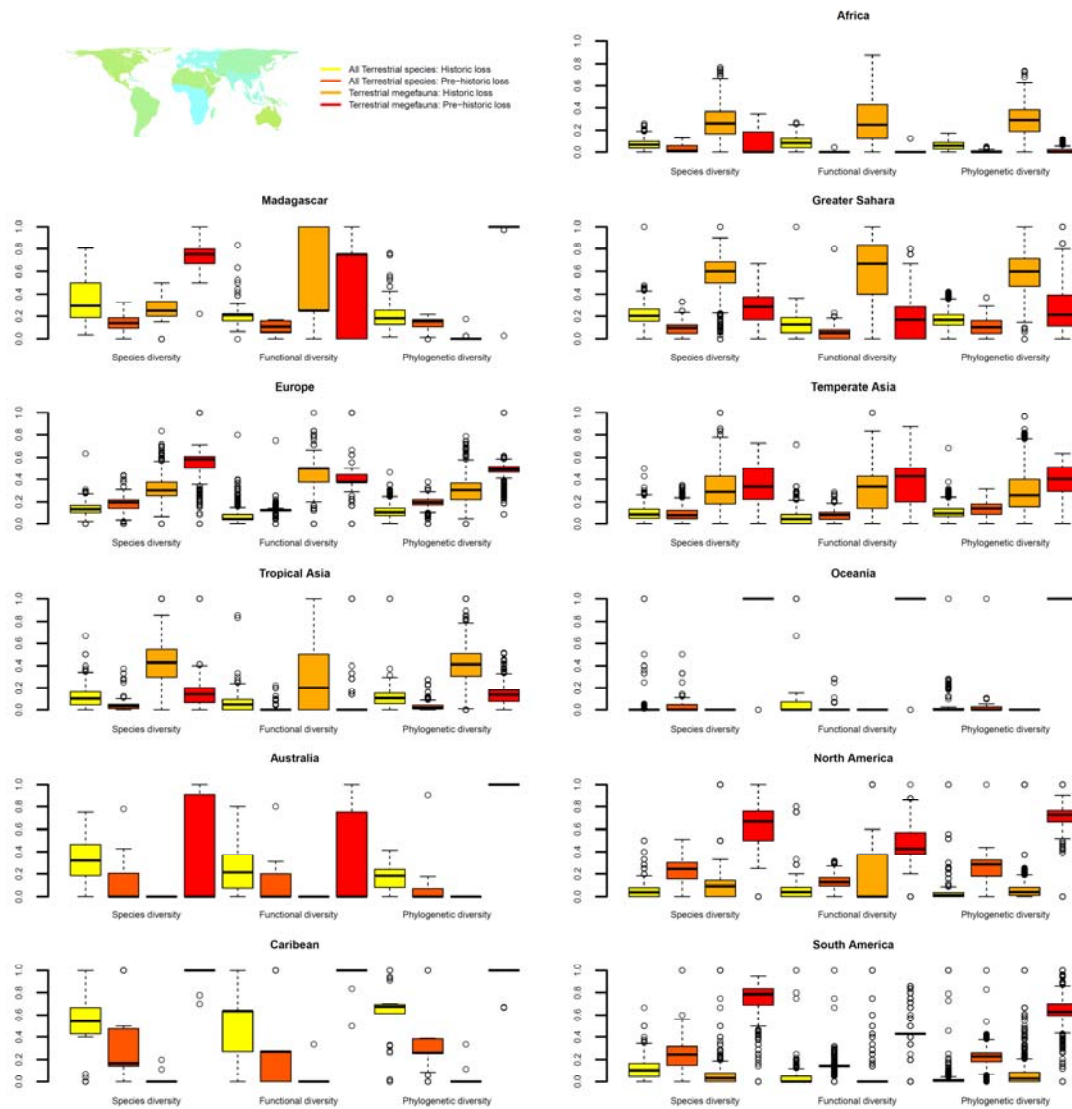


614

615 Current diversity and natural species, phylogenetic, and functional diversities for all  
616 terrestrial mammal species and for terrestrial mammal megafauna (body size > 10 kg).  
617 Colors are standardized horizontally so the same values in are given the same color in all  
618 panels.



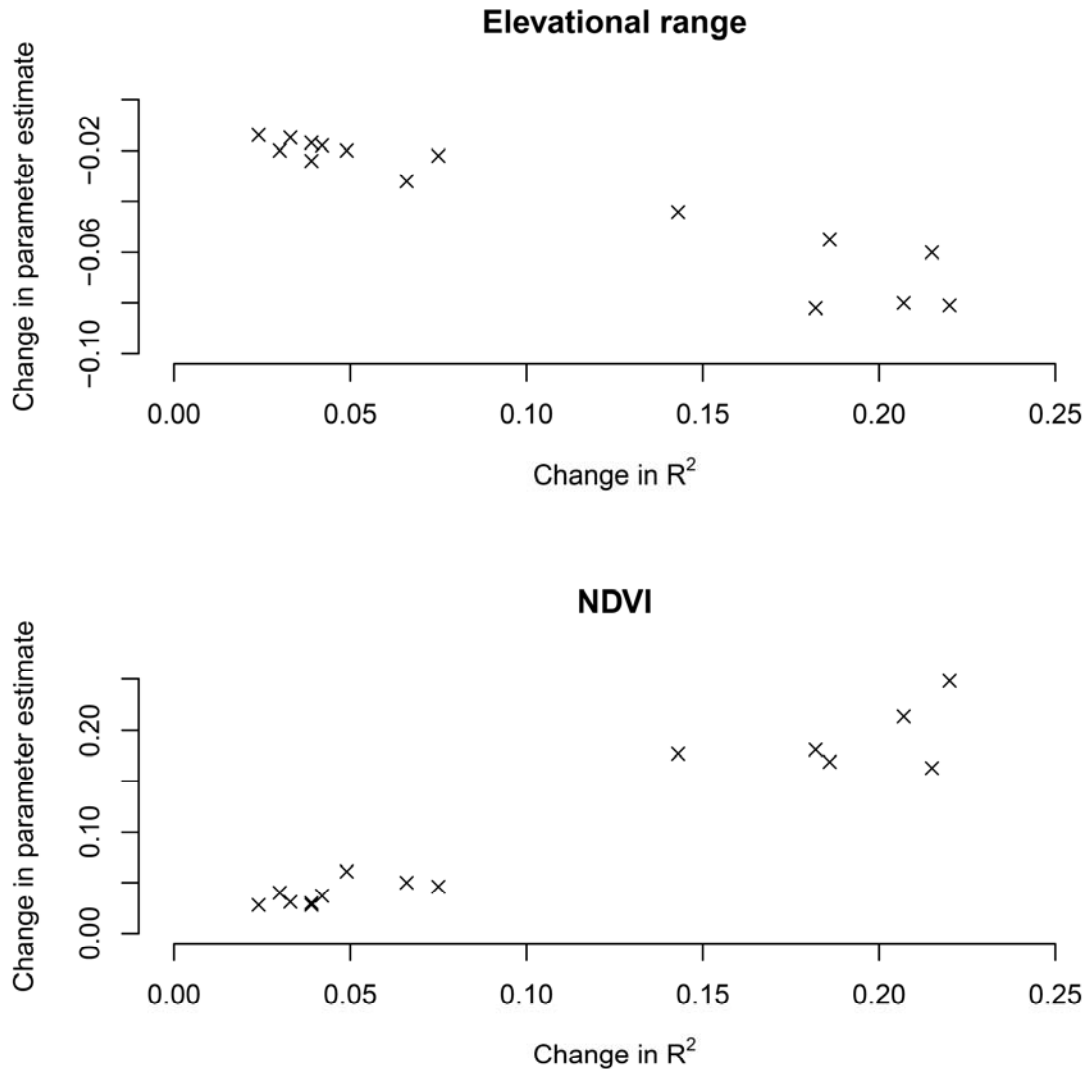
619 **Figure 2**



620

621 Estimated deficits in natural species, phylogenetic, and functional diversity for all  
622 terrestrial mammal species and terrestrial mammal megafauna species. The deficits are  
623 divided into those resulting from historic losses (the difference between current diversity  
624 and the present natural diversity of all species accepted by IUCN) and those resulting  
625 from pre-historic losses (the difference between the natural diversity for all species and  
626 for species accepted by IUCN). The thick middle line and box represent the median and  
627 first to third quartiles, respectively, and whiskers extend to the furthest datapoint that is  
628 no more than 1.5 times the interquartile range away from the median.

629 **Figure 3**



630

631 Relationship between the difference in pseudo-R<sup>2</sup> for the models of natural and current  
632 mammal diversity and the corresponding difference between the standardized estimates  
633 for the effect size of NDVI or elevation range. The 15 circles represent the difference for  
634 each combination of one of the three diversities (species diversity, phylogenetic diversity,  
635 functional diversity) and one of the five datasets (all species, non-marine species, all  
636 terrestrial species, large terrestrial species, and terrestrial megafauna).