

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

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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 (110×110 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) (Biknevicus *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 110×110 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 19th
201 century (Nowak, 1999) and the last wild specimen of the species globally died in the 20th
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_{err} 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-R² throughout the paper even though several
236 different estimates of model fit are frequently referred to as pseudo-R² (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

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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
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462 **Jens-Christian Svenning** is a professor at Aarhus University. He is a broadly based
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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

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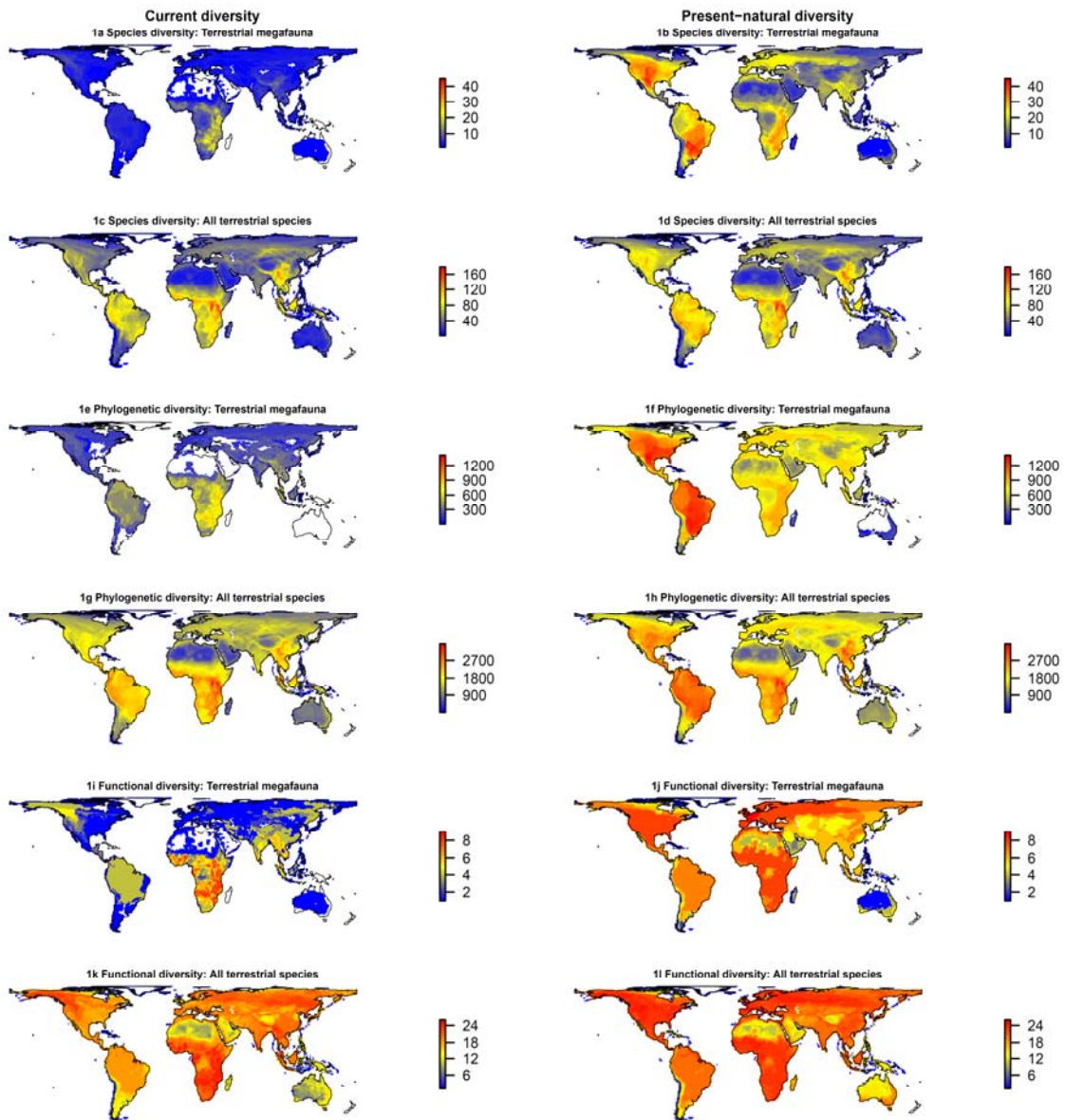
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612 **Figures**

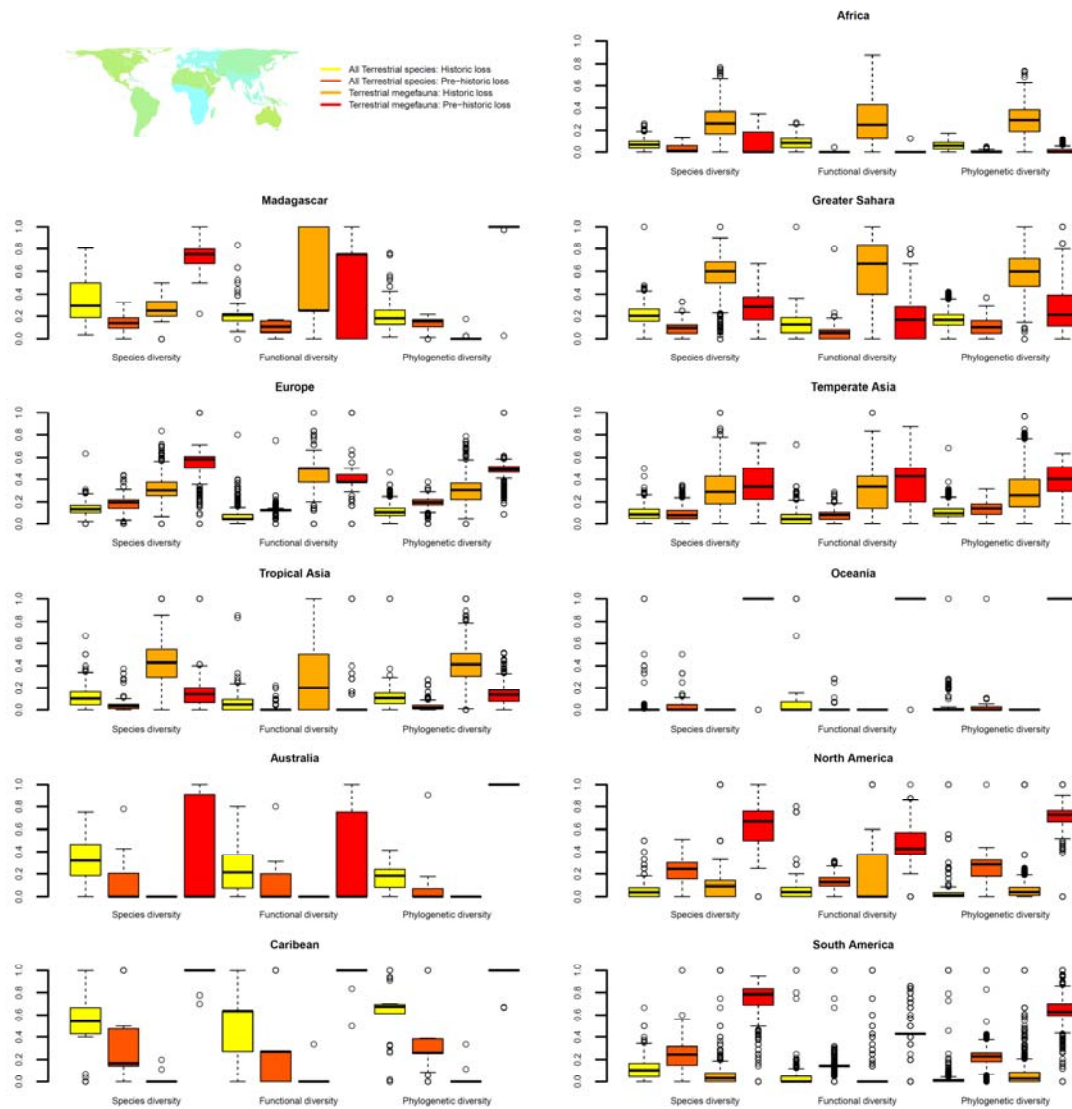
613 **Figure 1**



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.

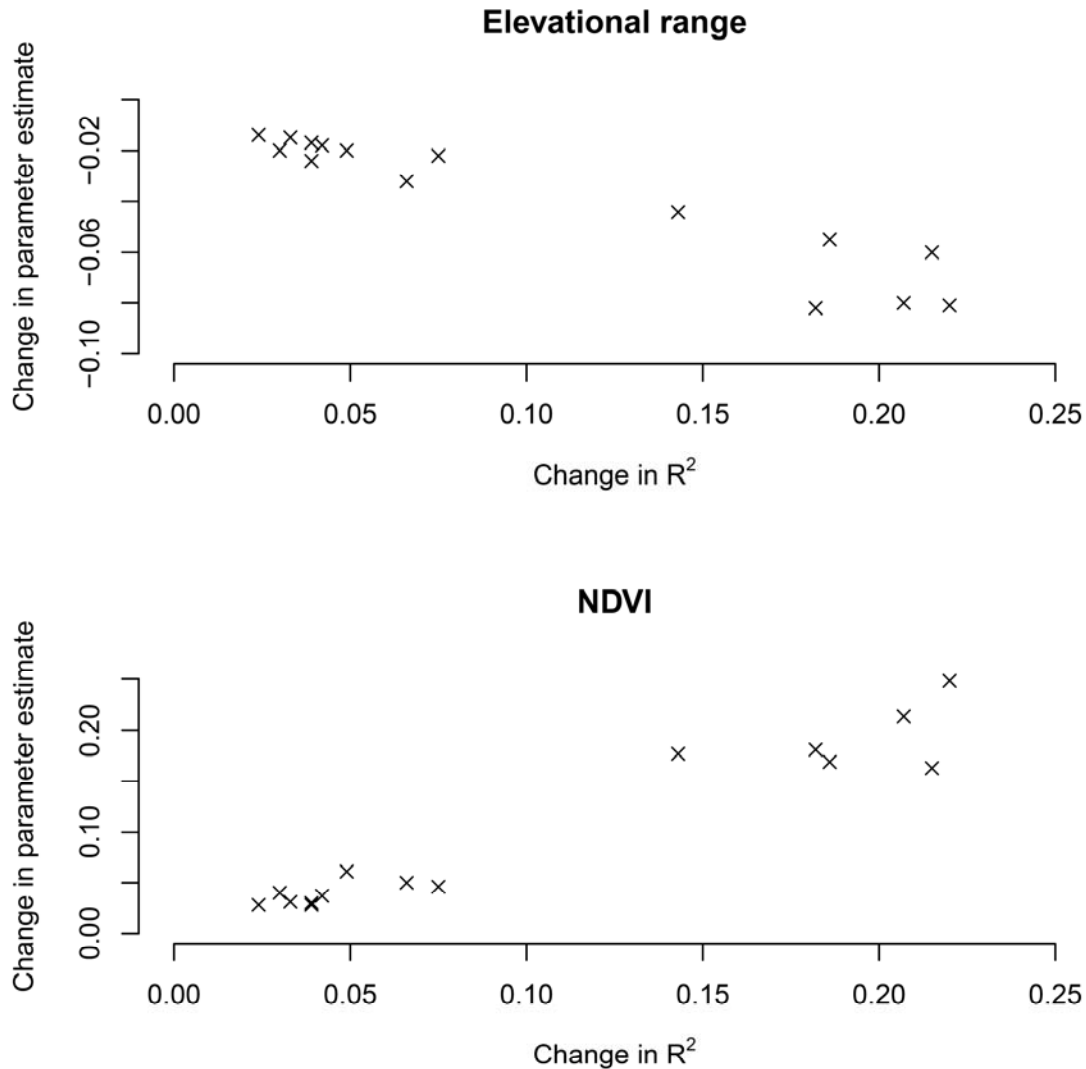
619 **Figure 2**



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-R² 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).