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.

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 disproportionally 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-R^2 throughout the paper even though several

236   different estimates of model fit are frequently referred to as pseudo-R^2 (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 c*urrent 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 decifits**

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 decifits**

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-

426   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

Supplementary Materials:

440   Supplementary Materials and Methods

441   Supplementary Figures S1-S11

442   Supplementary Tables S1-S3

443   Supplementary Data 1-8

444

Acknowledgments

450

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-

454   instituttet/organisation/oekoinformatik-biodiversitet/data/ (DATAWILL BE

455   UPLOADED UPON ACCEPTANCE).

456

Biosketches

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

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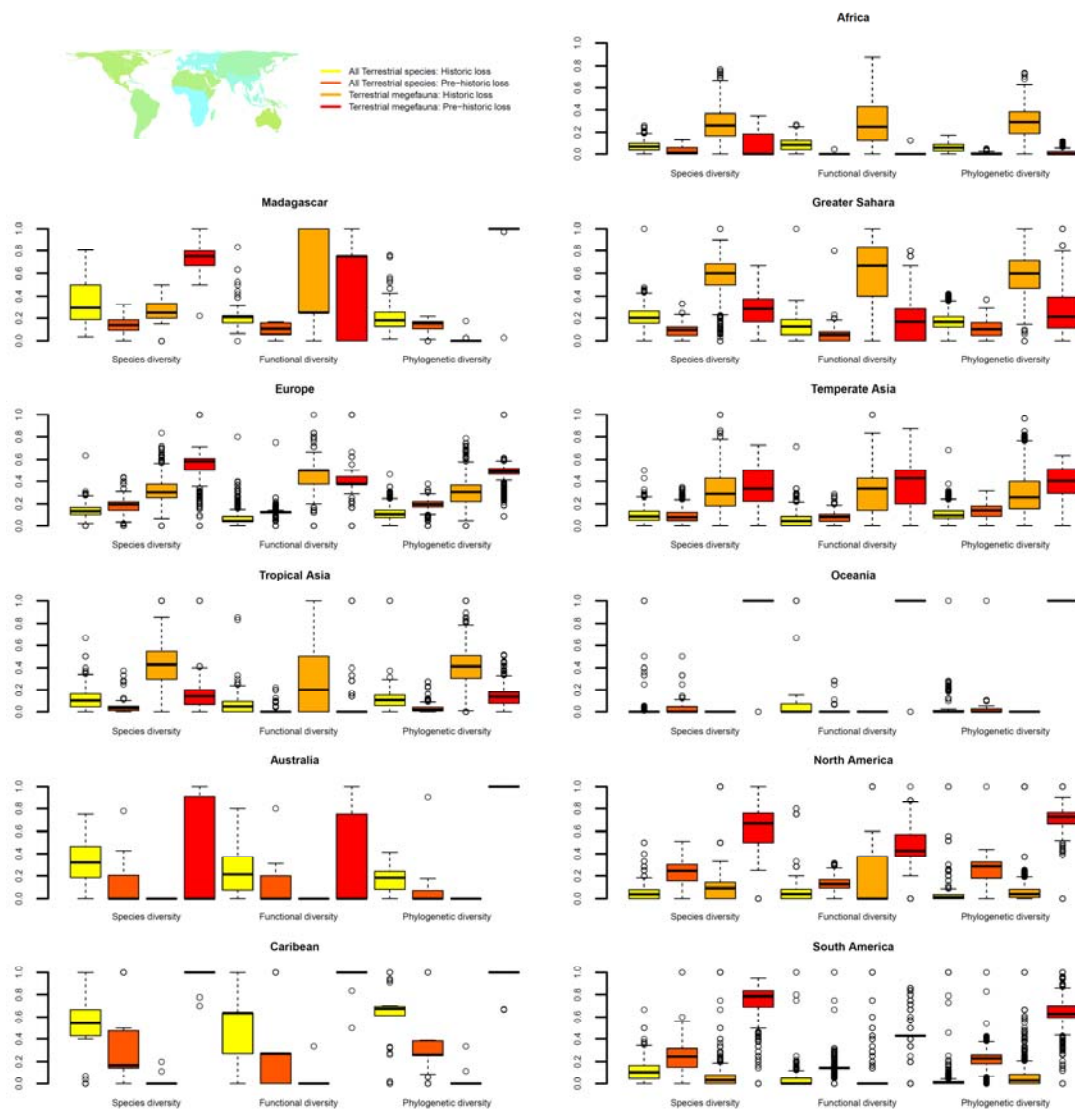
611   *Acad. Sci. U. S. A.* **111**, 14472-14477.

612   **Figures**

613   **Figure 1**

614
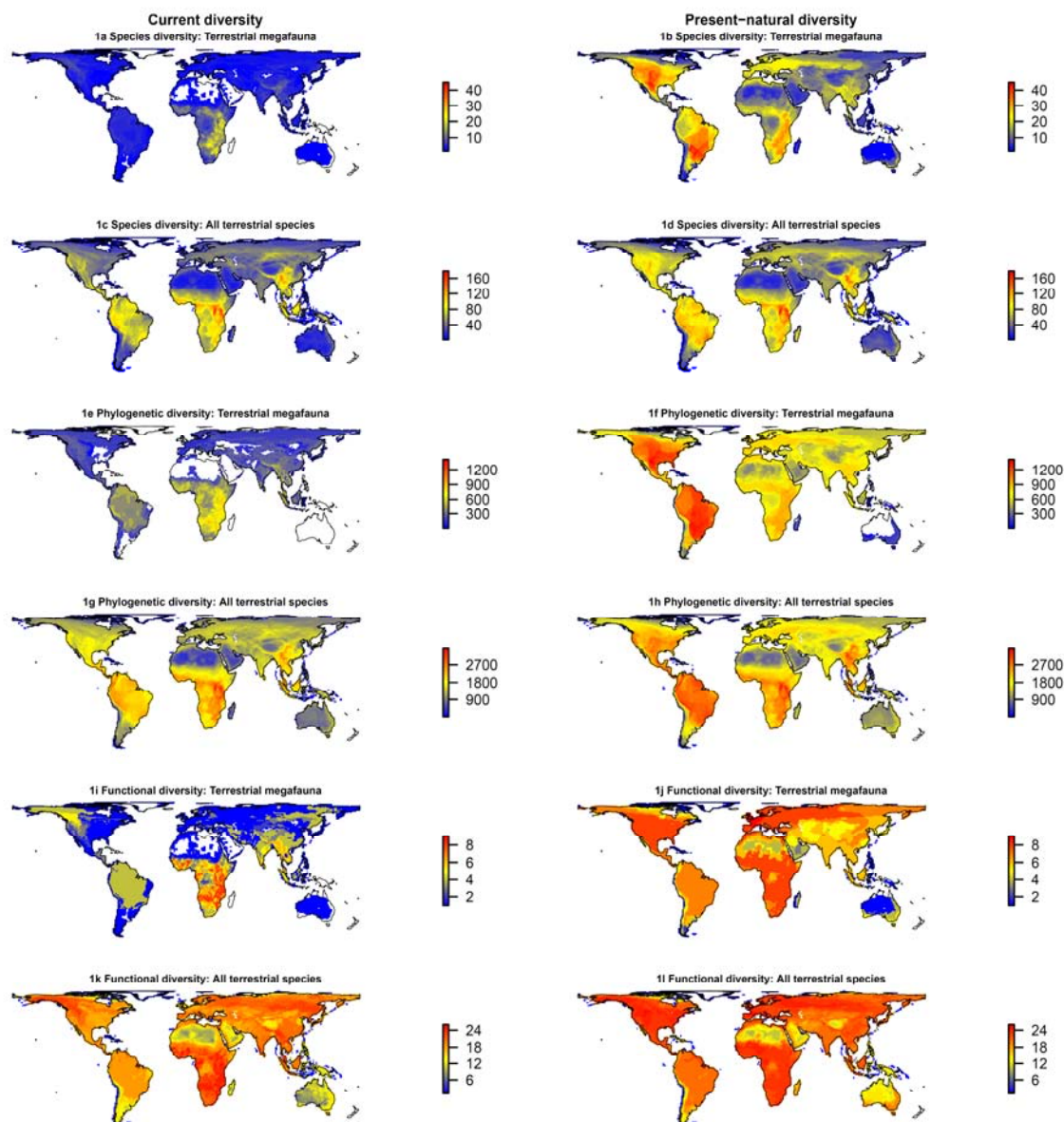
615   Current diversity and natural species, phylogenetic, and functional diversities for all
616   terrestrial mammal species and for terrestrial mammal megafauna (body size > 10 kg).
617   Colors are standardized horizontally so the same values in are given the same color in all
618   panels.

Figure 2

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

629   **Figure 3**
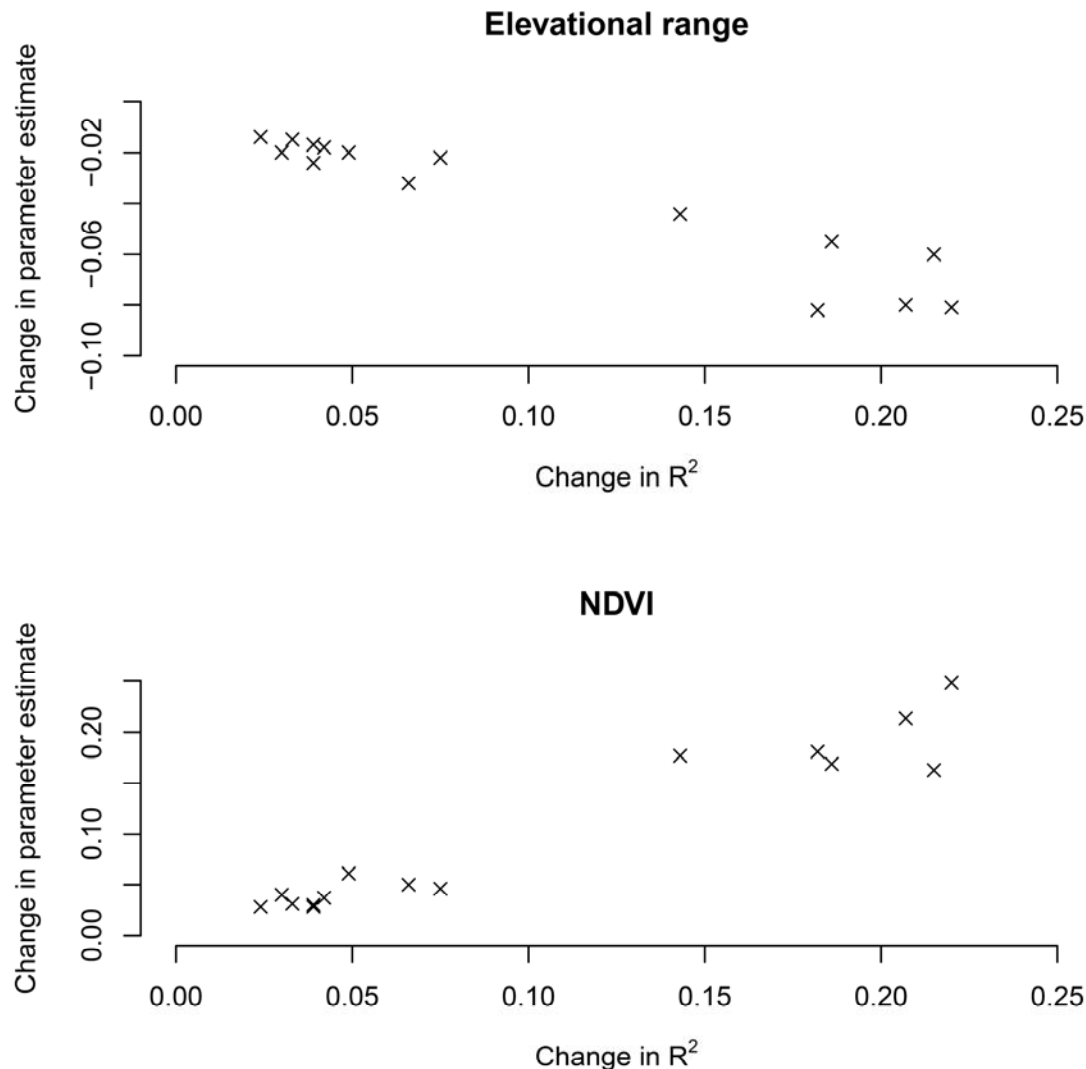
630

631   Relationship between the difference in pseudo-R^2 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).