1   **Full Title: Introduced megafauna are rewilding the Anthropocene**

2   **Short title: Anthropocene megafauna**

3   **Authors:** Erick J. Lundgren[1,2], Daniel Ramp[2], William J. Ripple[3], Arian D. Wallach[2]

4   **Affiliations:**

5   [1] Arizona State University, School of Life Sciences, Tempe, Arizona, 85287, USA.

6   [2] Centre for Compassionate Conservation, School of Life Sciences, University of

7   Technology Sydney, Broadway, NSW, 2007, Australia.

8   [3] Global Trophic Cascades Program, Department of Forest Ecosystems and Society,

9   Oregon State University, Corvallis, Oregon, 97331, USA

10

11   **Correspondence to**:

12   Erick Lundgren; PO Box 123, Broadway, NSW 2007; elundgr2@asu.edu;
13   (585) 645.9974
14   ORCID: 0000-0001-9893-3324
15

16   **Keywords:** Anthropocene, Conservation Ethics, Invasion Biology, Megafauna,

17   Pleistocene, Rewilding

18

19

20

21

22

23 **ABSTRACT**

24 Large herbivorous mammals, already greatly reduced by the late-Pleistocene extinctions,

25 continue to be threatened with decline. However, many herbivorous megafauna (body

26 mass ≥ 100 kg) have populations outside their native ranges. We evaluate the

27 distribution, diversity and threat status of introduced terrestrial megafauna worldwide and

28 their contribution towards lost Pleistocene species richness. Of 76 megafauna species, 22

29 (~29%) have introduced populations; of these ten (45%) are threatened or extinct in their

30 native ranges. Introductions have increased megafauna species richness by between 10%

31 (Africa) and 100% (Australia). Furthermore, between 15% (Asia) and 67% (Australia) of

32 extinct species richness, from the late Pleistocene to today, have been numerically

33 replaced by introduced megafauna. Much remains unknown about the ecology of

34 introduced herbivores, but evidence suggests that these populations are rewilding modern

35 ecosystems. We propose that attitudes towards introduced megafauna should allow for

36 broader research and management goals.

37

38

39

40

41

42

43

44

45

INTRODUCTION

46

47   Terrestrial herbivorous megafauna are undergoing severe declines around the

48   world. Of 74 extant large terrestrial herbivorous mammal species with body masses ≥ 100

49   kg, 44 (~60%) are threatened with extinction (Ripple et al. 2015). The decline of this

50   functional group began 10,000-50,000 years ago, most likely due to overhunting by

51   humans during the late Pleistocene (Barnosky et al. 2004, Bartlett et al. 2015).

52   Large (≥ 100 kg) herbivorous megafauna (henceforth 'megafauna') perform

53   distinct roles that contribute to the functioning of ecological systems. Megafauna

54   consume fibrous vegetation, which can benefit smaller herbivores, reduce fire risk,

55   accelerate rates of nutrient cycling by orders of magnitude, and shift plant community

56   structure by facilitating coexistence between different plant functional types. Due to their

57   large size, these organisms cause physical disturbance and disperse large seeds and

58   nutrients great distances (Ripple et al. 2015). The considerable loss of this functionality at

59   the end of the Pleistocene had dramatic effects on plant community structure, fire

60   regimes, nutrient and mineral cycling across landscapes, and community assembly

61   (Bakker et al. 2016a, Gill et al. 2009, Doughty et al. 2016a, Doughty et al. 2016b,

62   Doughty et al. 2016c, Ripple & Van Valkenburgh 2010, Smith et al. 2015, Malhi et al.

63   2016). Modern declines have similar consequences for terrestrial ecosystems and

64   community dynamics (Ripple et al. 2015) and have led to broad international calls for

65   immediate action to conserve the world's remaining mammalian megafauna (Ripple et al.

66   2016, Ripple et al. 2017).

67   Less well considered is the role of megafauna introductions on their conservation

68   and on ecosystem function. Since the advent of the Anthopocene, particularly in the past

69 200 years, megafauna have been moved to new regions and between continents.

70 Introductions of megafauna worldwide may have inadvertently provided refuge for

71 threatened megafauna, increased regional large herbivore species richness, and restored

72 or added ecological functions. Acknowledgement of this possibility is being fostered by

73 the burgeoning concept of 'rewilding,' which includes efforts to proactively introduce

74 species in order to provide refuge and to restore lost ecological processes (Donlan et al.

75 2006, Svenning et al. 2016). However, much remains unknown about the contribution of

76 already introduced populations to global conservation goals.

77   Given that introduced populations are often unwanted and considered components

78 of anthropogenic harm, the existence of populations that are simultaneously introduced

79 and threatened or extinct in their native ranges has been highlighted as a conservation

80 paradox (Marchetti and Engstrom 2015). Indeed, the considerable redistribution of biota

81 that characterizes the Anthropocene may be a countercurrent to the extinction crisis by

82 providing refuge and new opportunities for threatened species (Wallach et al. 2015).

83 However, comprehensive analyses of the interaction between the processes of extinction

84 and redistribution have not been conducted.

85   To assess the potential conservation values of introduced megafauna we compiled

86 current information on their threat statuses and population trends in their native ranges,

87 their relative population sizes in and out of their native ranges, and their functional roles.

88 To understand how introduced megafauna have potentially rewilded the world, we

89 assessed the contribution of introduced megafauna to continental assemblages, and the

90 contribution of introduced megafauna to Anthropocene richness relative to the Holocene

91 and Pleistocene epochs.

92

METHODS

94   We searched for introduced populations of herbivorous megafauna (mammals

95   only) with body masses ≥ 100 kg based on Ripple et al. (2015) using Long (2003) and

96   supplemented with online searches (Google Scholar and Google) using the terms "feral",

97   "introduced", "invasive", "exotic" and "non-native". We used grey literature (e.g.

98   government reports) and journalism sources (e.g. The New York Times) alongside peer-

99   reviewed literature to identify megafauna populations outside their native ranges. Data

100   collection concluded in July, 2017. While some native megafauna populations live in

101   fenced and managed conditions (e.g. Kruger National Park), only free-roaming wild

102   introduced populations were included because it was not clear if fenced/managed

103   introduced populations are ecologically viable in their new homes.

104   To understand to what extent introduced megafauna represent the taxonomic

105   diversity of the world's remaining megafauna, we calculated the number of large

106   herbivore families represented by introduced species, the number of genera of each

107   family represented by introduced species, and the percentage of species with introduced

108   populations within each taxonomic family.

109   To determine the potential conservation value of introduced megafauna as refuge

110   populations, we compiled IUCN (2017) Red List threat statuses and trends in each

111   species' historic native ranges and the proportion of each population that is currently

112   outside of its native range (Supplementary material Appendix 2, Table A1). Wild post-

113   domestic species were assigned the threat status of their pre-domestic ancestor. For

114   example, introduced wild dromedary camels (*Camelus dromedarius*) originate from the

115   domesticated form of an extinct camel species (possibly *C. thomasi*), and were therefore

116   considered extinct in the wild in their native range.

117   To understand to what geographic extent introduced megafauna have rewilded the

118   world, we calculated megafauna species richness by Taxonomic Databases Working

119   Group level 3 countries (henceforth TDWG), which are bio-geographic units defined by

120   political (nation, state, province, or district) boundaries at a biologically relevant scale

121   (Brummitt 2001). Inter- and intra-continental introductions were included in this

122   comparison. The distributions of introduced megafauna were determined from literature

123   and Google searches (Supplementary material Appendix 1, Data A1). Geographic ranges

124   for native megafauna were downloaded from the IUCN (2017) Red List. The percentage

125   of each TDWG country's megafauna assemblage that is introduced was calculated and

126   compared between continents to understand how introductions have altered continental

127   megafauna assemblages.

128   We assessed how Anthropocene megafauna richness compares to those of past

129   geological epochs. For each continent, we compared megafauna species richness and

130   conservation status between the late Pleistocene (50,000 – 10,000 BP), Holocene

131   (<10,000 BP), and Anthropocene (past ~ 200 years) epochs. Only inter-continental

132   introduced megafauna were included.

133   Pleistocene species were classified as 'extinct', 'extirpated' or 'survived' based on

134   their fate through the late-Pleistocene extinction. Pleistocene megafauna presence was

135   based on Sandom et al. (2014) and body masses ($\geq 100kg$) were confirmed through

136   literature searches. The Holocene included species from the end of the Pleistocene until

137   the Anthropocene. Holocene species included 'survived' taxa, natural immigrants, and

138 species that went extinct during the Holocene (e.g. aurochs *Bos primigenius* and

139 dromedary camel), while Anthropocene genera included 'survived', 'survived,

140 threatened', 'introduced', and 'introduced, threatened' species, reflecting their current

141 IUCN (2017) threat statuses (Supplementary material Appendix 3, Table A2).

142   To describe the range of functional traits of introduced megafauna, we reviewed

143 their average body masses, habitat types, dietary types (grazer, browser, or intermediate),

144 and other unique traits using the IUCN (2017) and published literature.

145

146 **RESULTS**

147   Twenty-two (32%) of the 76 extant megafauna species have established wild

148 populations outside their native ranges (Supplementary material Appendix 2, Table A1).

149 Sixteen are inter-continental introductions, two are intra-regional but overcame oceanic

150 barriers, and four are intra-continental. By including post-domesticates of extinct

151 heritage, an additional two species (the dromedary camel and cattle, *Bos taurus*) are

152 added to the 74 remaining native megafauna. Six additional species were excluded from

153 analysis: three species because they appear to be confined to game ranches, one because

154 introduced populations are described as semi-wild, and two because of uncertain

155 taxonomic relation to already included species.

156   Six (55%) of the eleven families containing megafauna species have established

157 populations outside their native ranges. Introduced species represent between 29%

158 (Equidae) and 56% (Cervidae) of the megafauna species within their families (Fig. 1).

159 Likewise, introduced populations represent between 50% (Camelidae) and 100%

160 (Equidae) of the megafauna genera within their families.

161   Of the 22 species with introduced populations, ten (45%) are threatened or extinct

162   in their native ranges (Fig. 2). This includes three (~14%) Vulnerable non-domesticated

163   species, four (18%) post-domestics whose progenitors are Endangered, two (9%) post-

164   domestic species whose wild progenitors are Extinct, and one (~5%) post-domestic

165   whose progenitor is Critically Endangered. All seven post-domestic species are extinct or

166   threatened in their native ranges. Of the remaining twelve introduced megafauna, three

167   (14%) are Near Threatened, and nine are ranked as Least Concern in their native ranges,

168   of which 66% have stable population trends, 22% are increasing, and 11% are declining

169   (Fig. 2). Of the 20 introduced species with surviving native populations, ten (50%) are

170   declining in their native ranges, seven (35%) are stable, and three (15%) are increasing

171   (Supplementary material Appendix 2, Table A1). In all, 59% of introduced megafauna

172   are threatened or declining in their native ranges (Fig. 2).

173   On average, over 38% (ranging between <1% and 100%) of megafauna

174   populations are outside of their native ranges. Whereas two species have relatively small

175   (possibly ~100 individuals) populations outside their native ranges (hippopotamus,

176   *Hippopotamus amphibius,* and Asian elephant, *Elephas maximus*), twelve populations are

177   estimated in the thousands and up to over 1 million individuals (Fig. 3, Supplementary

178   material Appendix 2, Table A1).

179   By including introduced megafauna, the worldwide distribution of megafauna

180   species richness increases significantly (Fig. 4). Introduced megafauna have substantially

181   increased continental megafauna richness and TDWG-country-scale species richness

182   within each continent: 62% of South American (mean = 37%, SD = 34%), 57% of North

183   American (TDWG: mean = 24%, SD = 37%), 33% of European (mean = 36%, SD =

184 33%), 11% of Asian (mean = 17%, SD = 34%), and 11% of African (mean = 10%, SD =

185 27%) megafauna are introduced. Introduced megafauna comprise at least 75% of the

186 megafauna assemblages of 56 of the 369 (15%) TDWG countries.

187   Strikingly, the entire continental megafauna assemblage of Australia is composed

188 of introduced species. Australia lost all megafauna species during the Pleistocene

189 extinctions, yet has become home to eight introduced species in the Anthropocene,

190 including the Endangered Banteng (*Bos javanicus*), the world's only population of wild

191 dromedary camel, the Vulnerable sambar deer (*Rusa unicolor*), and the water buffalo

192 (*Bubalus bubalis*), the descendant of the Endangered water buffalo (*B. arnee*). Wild

193 donkeys (*Equus asinus*), whose progenitor, the African wild ass (*E. africanus*) is

194 Critically Endangered, and Endangered horses (*E. ferus caballus*), have also found refuge

195 in Australia, as well as in North America, South America, and Europe.

196   Late Pleistocene losses of megafauna species (100% for Australia, 89% for South

197 America, 89% for North America, 53% for Europe, 41% for Asia, and 27% for Africa)

198 and Holocene losses (14% for Europe, 5% for Asia, and 3% for Africa) were substantial.

199 Following the Pleistocene, North American species richness increased from 4 to 6 due to

200 immigration of wapiti (*Cervus canadensis*) and moose (*Alces alces*) from Eurasia

201 concurrent with the arrival of the first humans to the continent (Meiri *et al*. 2014,

202 Hundertmark *et al*., 2002). Reductions in species richness on all continents since the

203 Pleistocene have been counteracted by gains from introduced megafauna in the

204 Anthropocene, so that there are currently more megafauna species per continent than at

205 the end of the Holocene. Introduced megafauna have numerically replaced extinct species

206 richness in Australia by 67%, in South America by 21%, in North America by 26%, in

207 Europe by 33%, in Asia by 15%, and in Africa by 31% (Fig. 5, Table 1).

208   Megafauna are likely to have significant functional roles in their introduced

209 ranges. Their average body masses ranges from 109 to 3,270 kg (median = 256 kg, mean

210 = 526 kg, SD = 697 kg) (Table 2), which is representative of the native megafauna body

211 mass distribution ranging from 100 to 3,825 kg (median = 238 kg, mean = 496 kg, SD =

212 666 kg). Introduced megafauna are primarily grazers (45% of species) or intermediate

213 grazers and browsers (41% of species), and three species (14%) are primarily browsers

214 (Table 1). Introduced megafauna are adapted for habitats ranging from Arctic tundra

215 (muskox *Ovibos moschatus*) to tropical forest (sambar deer) and deserts (dromedary

216 camels) (Table 1). Although there is little known about the specific ecological

217 functionalities of several introduced megafauna, many introduced species are known for

218 unique traits, such as the ability to drink brackish water and consume halophytic plants

219 (dromedary camel) or to survive without surface water (gemsbok *Oryx gazella*) (Table 2).

220

221 **DISCUSSION**

222   Introduced megafauna represent a significant proportion of the remaining

223 taxonomic diversity of their functional group and are themselves significantly threatened

224 in their historic native ranges. This raises the question of how to assign conservation

225 value in an era of extinction and redistribution. Conservation biology is a field driven by

226 a plurality of values, which offer various visions at different scales and times (Sandbrook

227 et al. 2011). Many current schools of thought prioritize the conservation of species

228 considered to be native at the local and regional scale. However, given the ongoing global

229 extinction process, more research and dialogue is needed to understand when these values

230 may undermine other conservation goals and values.

231   While many introduced populations were formerly domesticated, they may still

232 effectively represent their wild relatives. Introduced populations of Endangered banteng

233 in northern Australia have maintained high genetic fidelity to their pre-domestic

234 ancestors (Bradshaw et al. 2005). Likewise, domesticated horses retain a substantial

235 component of the genetic diversity of extinct Holarctic horse lineages (Lippold et al.

236 2011). Given that the closest wild relatives of all six post-domestic megafauna are

237 Endangered or extinct, it appears that domestication has provided a crucial bridge for

238 certain species from the pre-pastoral wild landscapes of the early Holocene to the post-

239 industrial wild landscapes of the Anthropocene.

240   Evolutionary and ecological change has also been witnessed in post-domestic

241 populations. Wild goats (*Capra aegragus*) on Aldabra Atoll regularly drink saltwater

242 when freshwater is absent (Burke 1990). Wild sheep (*Ovis aries*) show higher resistance

243 to local parasites than sympatric domestic sheep. Wild Ossabaw island pigs (*Sus scrofa*)

244 have unique lipid structures (Van Vuren and Hedrick 1989). Wild cattle in Mexico do not

245 linger in riparian areas like their sympatric domestic cousins due to altered predation

246 threats (Hernandez et al. 1999). Native Torresian crows (*Corvus orru*) appear to have

247 developed a mutualistic grooming behavior on introduced banteng in Australia

248 (Bradshaw and White 2006).

249   Like all herbivores, introduced megafauna can exert strong grazing or browsing

250 pressure to the detriment of other species, most notably where apex predators are

251 extirpated or continue to be persecuted (Wallach et al. 2010). Unfortunately, much of the

252   research to document these effects has ignored the ecological context of predator control,

253   which is to ignore an important explanatory variable for the density-dependent effects of

254   all herbivores. Indeed, wild horses in the United States may be limited by mountain lions

255   (Turner and Morrison 2001) and dingoes appear to suppress populations of wild donkeys

256   in Australia (Wallach et al. 2010). The potential to influence the ecologies of introduced

257   megafauna by protecting or restoring large predators is an important topic for further

258   research.

259   In the Pleistocene, the ecological influences of herbivorous megafauna on

260   disturbance regimes, seed dispersal, nutrient cycling, and community structure were

261   ubiquitous. Introduced megafauna have potentially augmented this lost functional and

262   taxonomic diversity across most continents, particularly in those regions most depleted:

263   Australia, North America, and South America (Fig. 4); Asia and Africa have retained

264   many Pleistocene megafauna and have fewer introduced species. Several of these

265   introductions restore taxonomic analogues to extinct Pleistocene species. For example,

266   introduced donkeys are morphologically similar to congeneric extinct North American

267   and South American stilt-legged horses, and the modern wild horse is the same species as

268   the horse of the Holarctic Pleistocene (Weinstock et al. 2005).

269   The late Pleistocene extinctions in Australia included all megafauna and many

270   browsing herbivores, the loss of which appears to have led to increased fire frequency

271   and altered plant community structure (Miller et al. 2005, Rule et al. 2012). Introduced

272   megafauna, especially browsers such as dromedary camels, may reverse these ecological

273   state shifts. However, determining how introductions of taxonomically dissimilar species

274   restore or add new functionalities within insular ecosystems (there are no surviving

275   taxonomic analogues to Australia's Pleistocene marsupial megafauna) requires further

276   research into the relative importance of co-evolutionary history versus ecological context

277   in determining species coexistence and ecosystem function (Wallach et al. 2015).

278   Introduced megafauna vary in body mass considerably, which influences their

279   ability to open thickets and digest coarse fibrous vegetation and thus their relation to

280   plant communities and other herbivores. Introduced megafauna also possess unique

281   functional adaptations that may be of ecological significance in their new ranges. For

282   example, introduced camels are capable of ingesting brackish water and consuming

283   halophytic plants (Root-Bernstein & Svenning 2016), which in conjunction with their

284   large home ranges (Spencer et al. 2012) may contribute to the megafaunal redistribution

285   of terrestrial salts (Doughty et al. 2016a). Likewise, the ability of gemsbok (*Oryx gazella*)

286   to survive without surface water (Hamilton et al. 1977) likely allows it to occupy novel

287   niches in the North American deserts in which it now lives.

288   There is substantial and growing evidence that introduced species can perform

289   significant and desirable ecological roles (Schlaepfer et al. 2011). Bighorn sheep forage

290   more efficiently, with less time invested in vigilance behaviors in mixed herds with

291   introduced wild horses (Coates and Schemnitz 1994). Giant tortoises introduced onto

292   oceanic islands as substitutes for extinct species are dispersing large-seeded endemic

293   plants and shaping plant communities through grazing (Hansen et al. 2010). Intentional

294   introductions of horses and cattle in the Oostvaardersplassen nature reserve in the

295   Netherlands have created Pleistocene-like savanna conditions in a temperate deciduous

296   forest environment (Vera 2009). In North America and Australia, the drying and

297   constriction of desert springs and the extinction of several endemic fish populations was

298 linked to the removal of wild introduced megafauna whose grazing appeared to maintain

299 open-water habitat (Kodric-Brown and Brown 2007).

300   Likewise, our own ongoing research is yielding similarly surprising observations.

301 For example, in the Sonoran Desert of North America, wild donkeys ('burros', *E. asinus*)

302 dig groundwater wells of more than a meter in depth (Supplementary material Appendix

303 4, Movie A1). These wells are common wherever groundwater approaches the surface,

304 have been recorded in use by more than thirty mammal and bird species, and in certain

305 conditions become nurseries for riparian trees (Fig. 6). It is possible that by creating new

306 water sources across the landscape, maintaining access to receding water-tables during

307 droughts, and providing conditions ideal for the germination of riparian trees, wild

308 donkeys play a facilitative role, one that may improve the resilience of these arid

309 ecosystems to climate change. Furthermore, given the ubiquity of taxa whose

310 contemporaries dig wells, such as Proboscideans (Ramey et al. 2013) and other equids

311 (Feh et al. 2002) in the North American Pleistocene, it is likely that introduced donkeys

312 have restored a functionality lost from these landscapes.

313   Unfortunately, little more is known about the ecological functions of megafauna

314 outside their native ranges because the majority of studies are conducted on the premise

315 that introduced species are harmful and should be suppressed or eradicated. Future

316 research on the ecological functions of introduced megafauna, under varying ecological

317 contexts (e.g. predator control, landscape connectivity), will be essential to understand

318 the novel megafaunal communities of the Anthropocene.

319   Reassessing conservation attitudes towards introduced megafauna may find

320 synergy with other conservation goals. Introduced megafauna are likely vulnerable to

321   similar threats as native megafauna as they require large tracts of land and may be

322   vulnerable to exploitation. Valuing introduced megafauna as umbrella or flagship species

323   in efforts to expand protected areas or establish movement corridors would contribute to

324   important conservation goals. Broadening the range of wildlife valued and protected by

325   conservation practitioners could also help form alliances with public advocates of

326   introduced megafauna, who are often alienated by projects that treat these species as

327   pests. Conflicts between these groups and conservation professionals erode trust and

328   undermine conservation efficacy (Crowley et al. 2017), yet these groups are natural allies

329   in their concern for the welfare and persistence of non-human life (Bruskotter et al.

330   2017). It is likely that incorporating broader value systems towards these organisms

331   would offer a range of practical benefits towards conservation objectives and could

332   strengthen the diversity and inclusiveness of the conservation community.

333   The introduced megafauna of the world have restored species richness across

334   many continents to levels approaching the Pleistocene, contribute fascinating and

335   potentially important ecological functions, and are an important refuge for their

336   functional group. We propose that further research and dialogue on how introduced

337   megafauna interact with and without potential predators in the novel ecosystems of the

338   Anthropocene will be essential in reconciling the concerns of local managers with global

339   conservation efforts and will bring new attention to the emerging eco-evolutionary

340   trajectories of these populations.

341

342   **REFERENCES**

343 Ajmone-Marsan, P., et al. 2010. On the origin of cattle: how aurochs became cattle and

344   colonized the world. — Evolutionary Anthropology: Issues, News, and Reviews

345   19: 148-157.

346 Ali, R. 2004. The effect of introduced herbivores on vegetation in the Andaman Islands.

347   — Current Science 86: 1103-1112.

348 Alroy, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal

349   mass extinction. — Science 292: 1893-1896.

350 Álvarez-Romero, J. et al. 2008. Animales exóticos en México: una amenaza para la

351   biodiversidad. — Comisión Nacional para el Conocimiento y Uso de la

352   Biodiversidad.

353 Almador-del Ángel, L. E., et al. 2015. Fauna exótica establecida e invasora en el Área de

354   Protección de Flora y Fauna Laguna de Términos, Campeche: estado actual,

355   impactos, necesidades y perspectivas. — In: Almador-del Ángel, L. E., and Frutos

356   Cortés, M. (eds). Problemas contemporáneos regionales del Sureste Mexicano. El

357   caso del estado de Campeche. Universidad Autónoma del Carmen.

358 Australian Government. 2009. Camel fact sheet. —

359   <http://155.187.2.69/biodiversity/invasive/publications/pubs/camel-

360   factsheet.pdf>, accessed April 2017.

361 Bakker, E. S., et al. 2016a. Combining paleo-data and modern exclosure experiments to

362   assess the impact of megafauna extinctions on woody vegetation. — Proc. Natl.

363   Acad. Sci. USA 113: 847-855.

364   Bakker, E. S. et al. 2016b. Assessing the role of large herbivores in the structuring and

365   functioning of freshwater and marine angiosperm ecosystems. — Ecography 39:

366   162-179.

367   Barnosky, A. D., et al. 2004. Assessing the causes of late Pleistocene extinctions on the

368   continents. — Science 306: 70-75.

369   Bartlett, L. J., et al. 2015. Robustness despite uncertainty: regional climate data reveal the

370   dominant role of humans in explaining global extinctions of Late Quaternary

371   megafauna. — Ecography 39: 152-161.

372   BBC News. 15 February, 2004. "Buffalo improve wildlife habitat". — BBC News.

373   Blouch, R., et al. 1998. Deer: status survey and conservation action plan. In: IUCN/SSC

374   Action Plans for the Conservation of Biological Diversity.

375   Bobe, R. 2006. The evolution of arid ecosystems in eastern Africa. — Journal of Arid

376   Environments 66: 564-584.

377   Bradshaw, C. J. A., et al. 2005. Conservation value of non-native banteng in Northern

378   Australia. — Conservation Biology 20: 1306-1311.

379   Bradshaw, C. J. A., and W. W. White. 2006. Rapid development of cleaning behavior by

380   Torresian crows Corvus orru on non-native banteng Bos javanicus in northern

381   Australia. — Journal of Avian Biology 37: 409-411.

382   Brummitt, R. K. 2001. World geographical scheme for recording plant distributions, 2nd

383   ed. — Hunt Institute for Botanical Documentation.

384   Bruskotter, J. T., et al. 2017. "Animal Rights and Wildlife Conservation Conflicting or

385   Compatible?" — The Wildlife Professional July/August 2017.

386   Burke, M. G. 1990. Seawater consumption and water economy of tropical feral goats. —

387   Biotropica 22: 416-419.

388   Burns, J. A. 2010. Mammalian faunal dynamics in Late Pleistocene Alberta, Canada. —

389   Quaternary International 217: 37-42.

390   CABI. Invasive Species Compendium — <http://www.cabi.org/isc/>, accessed April

391   2017.

392   Coates, K. P., and S. D. Schemnitz. 1994. Habitat use and behavior of male mountain

393   sheep in foraging associations with wild horses. — Great Basin Naturalist 54: 86-

394   90.

395   Constible, J. M., et al. 2005. Dispersal of non-native plants by introduced bison in an

396   island ecosystem. — Biological Invasions 7: 699-709

397   Cossíos, E. D. 2010. Vertebrados naturalizados en el Perú: historia y estado del

398   conocimiento. — Revista Peruana de Biología 17: 179-189.

399   Crowley, S. L. et al. 2017. Conflict in invasive species management. — Frontiers in

400   Ecology and the Environment 15: 133-141.

401   California Wildlife Habitat Relationships System Staff. 2005. Sambar Deer *Cervus*

402   *unicolor.* — In: California's Wildlife Vol. I-III. California Department of Fish and

403   Game.

404   Dahdouh-Guebas, F. et al. 2006. Short-term mangrove browsing by feral water buffalo:

405   conflict between natural resources, wildlife and subsistence interests? —

406   Environmental Conservation 33: 157-163.

407   Department of Veterinary Integrative Biosciences. Mitochondrial DNA analysis of

408   donkeys from Bonaire Island. — Texas A & M University Memo.

409 Donlan, C. J., et al. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first
410   century conservation. — The American Naturalist 168: 660-681.

411 Doughty, C. E. et al. 2016a. Interdependency of plants and animals in controlling the
412   sodium balance of ecosystems and the impacts of global defaunation. —
413   Ecography 39: 204-212.

414 Doughty, C. E., et al. 2016b. Global nutrient transport in a world of giants. — Proc. Natl.
415   Acad. Sci. USA 113: 868-873.

416 Doughty, C. E. et al. 2016c. Megafauna extinction, tree species range reduction, and carbon
417   storage in Amazonian forests. — Ecography 39: 194-203.

418 Faith, J. T. 2014. Late Pleistocene and Holocene mammal extinctions on continental
419   Africa. — Earth-Science Reviews 128: 105-121.

420 Faurby, S., and J. C. Svenning. 2015. Historic and prehistoric human-driven extinctions
421   have reshaped global mammal diversity patterns. — Diversity and Distributions
422   12: 1155-1166.

423 Feh, C., et al. 2002. Status and action plan for the Asiatic wild ass (Equus hemionus). —
424   In: Equids: Zebras, Asses and Horses. Cambridge, UK: IUCN Publication
425   Services Unit.

426 Florida State Parks. Welcome to Paynes Prairie Preserve State Park. —
427   <https://www.floridastateparks.org/park/Paynes-Prairie>, accessed April 2017.

428 Frisina, M. R. and Frisina, R. M. 2013. Phenotype evaluation of free-ranging European
429   moufflon. — Taprobanica 5: 157-162.

430 Gill, J. L., et al. 2009. Pleistocene megafaunal collapse, novel plant communities, and
431   enhanced fire regimes in North America. — Science 326: 1100-1103.

432   Global Invasive Species Database. 2017. — <www.iucngisd.org/gisd>, accessed April

433   2017.

434   Grubb, P. 2005. *Rangifer tarandus*. — In: Wilson & Reeder's Mammal Species of the

435   World, 3rd Edition.

436   Hamilton, W. J. III et al. 1977. Intersexual dominance and differential mortality of

437   Gemsbok *Oryx gazella* at Namib Desert waterholes. — Madoqua 10: 5-19.

438   Hamrick, R. G. et al. 2005. Feral donkey *Equus asinus* populations on the Karpaz

439   peninsula, Cyprus. — European Journal of Wildlife Research 51: 108-116.

440   Hansen, D. M., et al. 2010. Ecological history and latent conservation potential: large and

441   giant tortoises as a model for taxon substitutions. — Ecography 33: 272-284.

442   Hernandez, L., et al. 1999. A note on the behavior of feral cattle in the Chihuahuan

443   Desert of Mexico. — Applied Animal Behaviour Science 63: 259-267.

444   Hundertmark, K. J., et al. 2002. Mitochondrial phylogeography of moose (*Alces alces*):

445   late Pleistocene divergence and population expansion. — Molecular

446   Phylogenetics and Evolution 22: 375-387.

447   Invasive Species South Africa. 2017. — <http://www.invasives.org.za/>, accessed April

448   2017.

449   IUCN 2017. The 2017 IUCN Red List of Threatened Species. —

450   <http://www.iucnredlist.org>, accessed April 2017.

451   Jaksic, F.M. Vertebrate invaders and their ecological impacts in Chile. — Biodiversity

452   and Conservation 7: 1427

453   Jesser, P. et al. 2008. Invasive animal risk assessment: Water buffalo *Bubalus bubalis*.

454   — State of Queensland.

455   Johnsingh, A. J. T. et al. 2007. Preparations for the reintroduction of Asiatic lion

456   *Panthera leo persica* into Kuno Wildlife Sanctuary, Madhya Pradesh, India. —

457   Oryx 41: 93-96.

458   Johnson, C. N., and G. J. Prideaux. 2004. Extinctions of herbivorous mammals in the late

459   Pleistocene of Australia in relation to their feeding ecology: no evidence for

460   environmental change as cause of extinction. — Austral Ecology 29: 553-557.

461   Jones, K. E. et al. 2009. PanTHERIA: a species-level database of life history, ecology,

462   and geography of extant and recently extinct mammals. — Ecology 90: 2648-

463   2648.

464   Kerkdijk, H. 2012. Where did the wild horse go? Rewilding Europe. —

465   <https://www.rewildingeurope.com/blog/where-did-the-wild-horse-go/>,

466   accessed April 2017

467   Knapp, A. K. et al. 1999. The keystone role of bison in North American tallgrass prairie: bison

468   increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem

469   processes. — BioScience 49: 39-50.

470   Kodric-Brown, A., and J. H. Brown. 2007. Native fishes, exotic mammals, and the

471   conservation of desert springs. — Frontiers in Ecology and the Environment 5:

472   549-553.

473   Leslie, D. M. Jr. 2008. *Boselaphus tragocamelus* (Artiodactyla: Bovidae). — Mammalian

474   Species 813: 1-16.

475   Lippold, S., N. J. Matzke, M. Reissmann, and M. Hofreiter. 2011. Whole mitochondrial

476   genome sequencing of domestic horses reveals incorporation of extensive wild

477   horse diversity during domestication. — BMC evolutionary biology 11: 328.

478   Lizarralde, M. 2016. Especies exóticas invasoras (EEI) en Argentina: categorización de

479   mamíferos invasores y alternativas de manejo. — Mastozoología Neotropical 23:

480   1-11.

481   Long, C. A., and C. J. Yahnke. 2011. End of the Pleistocene: elk-moose (*Cervalces*) and

482   caribou (*Rangifer*) in Wisconsin. — Journal of Mammalogy 92: 1127-1135.

483   Long, J. L. 2003. Introduced mammals of the world: their history, distribution &

484   influence. CSIRO PUBLISHING, Collingwood, VIC, Australia.

485   Malhi, Y. et al. 2016. Megafauna and ecosystem function from the Pleistocene to the

486   Anthropocene. — Proc. Natl. Acad. Sci. USA 113: 838-846.

487   Malo, J. E. et al. 2016. Low habitat overlap at landscape scale between wild camelids and

488   feral donkeys in the Chilean desert. — Acta Oecologica 70: 1-9.

489   Marchetti, M. P., and T. Engstrom. 2015. The conservation paradox of endangered and

490   invasive species. — Conservation Biology 38: 434-437.

491   Meiri, M., et al. 2014. Faunal record identifies Bering isthmus conditions as constraint to

492   end-Pleistocene migration to the New World. — Proc. R. Soc. B. 281: 20132167.

493   Miller, G. H. 2005. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal

494   extinction. — Science 309: 287-290.

495   Moriarty, A. 2004. The liberation, distribution, abundance and management of wild deer

496   in Australia. — Wildlife Research 31: 291-299.

497   Naiman, R. J. and Rogers, K. H. 1997. Animals and system-level characteristics in river

498   corridors. — BioScience 47: 521-529.

499   National Research Council 2013. Using Science to Improve the BLM Wild Horse and

500   Burro Program: A Way Forward. — The National Academies Press.

501   Naundrup, P. J. and Svenning, J. C. 2015. A Geographic Assessment of the Global Scope

502   for Rewilding with Wild-Living Horses (*Equus ferus*). — PLoS One 10:

503   e0132359.

504   New Zealand Department of Conservation. Facts about Kaimanawa horses. — <

505   http://www.doc.govt.nz/nature/pests-and-threats/animal-pests/kaimanawa-

506   horses/>, accessed April 2017.

507   Novillo, A. and Ojeda, R. A. 2008. The exotic mammals of Argentina. — Biological

508   Invasions 10: 1333-1344.

509   Palmqvist, P. et al. 1996. Prey selection by terrestrial carnivores in a lower Pleistocene

510   paleocommunity. — Paleobiology 22: 514-534.

511   Palo, R. T. 1993. Usnic acid, a secondary metabolite of lichens and its effect on *in vitro*

512   digestibility in reindeer. —Rangifer 13: 39-43.

513   Pastor, J. et al. 1988. Moose, microbes, and the boreal forest. — BioScience 38: 770-777.

514   Pereira-Garbero, R. et al. 2013. Mamíferos invasores en Uruguay, historia, perspectivas y

515   consecuencias. — Revista Chilena de Historia Natural 86: 403-421.

516   Pushkina, D., and P. Raia. 2008. Human influence on distribution and extinctions of the

517   late Pleistocene Eurasian megafauna. — Journal of Human Evolution 54: 769-

518   782.

519   Ramey, E. M., et al.. 2013. Desert-dwelling African elephants (Loxodonta africana) in

520   Namibia dig wells to purify drinking water. — Pachyderm 53: 66-72.

521   Ramírez-Chaves, H. E. et al. 2011. History of exotic mammal species in Colombia. —

522   Boletín Científico Museo de Historia Natural 15: 139-156.

523   Reus, M. L. et al. 2014. Trophic interactions between the native guanaco (Lama

524   guanicoe) and the exotic donkey (Equus asinus) in the hyper-arid Monte desert

525   (Ischigualasto Park, Argentina). — Studies on Neotropical Fauna and

526   Environment 49: 159-168.

527 Ripple, W.J. and Van Valkenburgh, B., 2010. Linking top-down forces to the Pleistocene

528   megafaunal extinctions. — BioScience, 60: 516-526.

529 Ripple, W. J., et al. 2015. Collapse of the world's largest herbivores. — Science

530   Advances 1:e1400103.

531 Ripple, W.J., et al. 2016. Saving the world's terrestrial megafauna. — BioScience, 66:

532   807-812.

533 Ripple, W. J., et al. 2017. Conserving the World's Megafauna and Biodiversity: The

534   Fierce Urgency of Now. — Bioscience, 67: 197-200

535 Roberts, R. G., et al.. 2001. New ages for the last Australian megafauna: continent-wide

536   extinction about 46,000 years ago. — Science 292: 1888-1892.

537 Romero, S. Sept. 10, 2009. "Colombia Confronts Drug Lord's Legacy: Hippos". — The

538   New York Times.

539 Root-Bernstein, M. and Svenning, J.-C. 2016. Prospects for rewilding with camelids. —

540   — Journal of Arid Environments 130: 54-61.

541 Rule, S. et al. 2012. The aftermath of megafaunal extinction: ecosystem transformation in

542   Pleistocene Australia. — Science 335: 1483-6.

543 Salter, R. E. 2006. Wild Horses. The Canadian Encyclopedia. Accessed: April, 2017

544 Sánchez, O., et al. 2016. Mamíferos de Guanajuato: actualización taxonómica y

545   diagnóstico de conservación — In: Briones-Salas, M. et al. (eds), Riqueza y

546   Conservación de los Mamíferos en México a Nivel Estatal, Universidad Nacional

547   Autónoma de México.

548   Sandbrook, C., et al. 2011. Value plurality among conservation professionals. —

549   Conservation Biology 33: 285-374.

550   Sandom, C. et al. 2014. Global late Quaternary megafauna extinctions linked to humans,

551   not climate change. — Proc. R. Soc. B. 281: 20133254.

552   Scauzillo, S. Oct. 22, 2013. "Cows gone wild: feral cattle scaring hikers in Chino Hills

553   State Park". — San Gabriel Valley Tribune.

554   Schlaepfer, M. A., et al. 2011. The potential conservation value of non-native species. —

555   Conservation Biology 25: 428-437.

556   SCI Online Record Book. — <http://www.scirecordbook.org/>, accessed June, 2017.

557   Smith, F. A., et al. 2003. Body mass of late Quaternary mammals. — Ecology 84: 3403-

558   3403.

559   Smith, F. A. et al. 2015. Unraveling the consequences of the terminal Pleistocene megafauna

560   extinction on mammal community assembly. — Ecography 39: 223-239.

561   Spencer, P. B. S. et al. 2012. Identification and management of a single large population

562   of wild dromedary camels. — The Journal of Wildlife Management 76: 1254-

563   1263.

564   Stuart, A. J. 1993. The failure of evolution: late Quaternary mammalian extinctions in the

565   Holarctic. — Quaternary International 19: 101-107.

566   Svenning, J. C., et al. 2016. Science for a wilder Anthropocene: Synthesis and future

567   directions for trophic rewilding research. — Proc. Natl. Acad. Sci. USA 113: 898-

568   906.

569   te Beest, M. et al. 2016. Reindeer grazing increases summer albedo by reducing shrub abundance

570   in Arctic tundra. — Environmental Research Letters 11: 125013.

571   Texas Parks and Wildlife Facts about feral burros at Big Bend Ranch State Park. Texas

572   Parks and Wildlife Department.

573   The Ethiopian News Agency. January 9, 2008. Wild horses exist in Ethiopia, but face

574   danger of extinction: Exploratory Team. — The Ethiopian News Agency.

575   Thórisson, S. 1984. The history of reindeer in iceland and reindeer study 1979-1981. —

576   Rangifer 4: 22-38.

577   Timmins, R. et al. 2015. *Rusa unicolor.* The IUCN red List of Threatened Species.

578   Turner, J. W., Jr., and M. L. Morrison. 2001. Influence of predation by mountain lions on

579   numbers and survivorship of a feral horse population. — The Southwestern

580   Naturalist 46: 183-190.

581   Van Vuren, D., and P. W. Hedrick. 1989. Genetic conservation in feral populations of

582   livestock. — Conservation Biology 3: 312-317.

583   Vera, F. W. M. 2009. Large-scale nature development—The Oostvaardersplassen. —

584   British Wildlife 20: 28-36.

585   Vigne, J.-D. 1992. Zooarchaeology and the biogeographical history of the mammals of

586   Corsica and Sardinia since the last ice age. — Mammal Review 22: 87-96.

587   Vikoren, T. et al. 2008. A severe outbreak of contagious ecthyma (orf) in a free-ranging

588   musk ox (*Ovibos moschatus*) population in Norway. — Veterinary Microbiology

589   127: 10-20.

590   Wallach, A. D. et al. 2010. Predator control promotes invasive dominated ecological

591   states. — Ecology Letters 13: 1008-1018.

592   Wallach, A. D. et al. 2015. Novel trophic cascades: apex predators enable coexistence. — Trends

593   in Ecology & Evolution 30: 146-53.

594   Weinstock, J., E. et al. 2005. Evolution, systematics, and phylogeography of Pleistocene

595   horses in the New World: a molecular perspective. — PLoS Biology 3: e241.

596   West, P. 2011. National mapping of the abundance of established, new and emerging pest

597   animals to improve decision-making and the assessment of government

598   investment programs. — Australian Pest Animal Research Program. NSW

599   Department of Primary Industries.

600   Wildlife Partners 2017. Nilgai Antelope. http://wildlifepartners.com/species/nilgai-

601   antelope/ Accessed: April, 2017.

602

607

608

609

610

611 Table 1. Changes in megafauna species richness from the Pleistocene to the Anthropocene. In column 2, percent survived is the

612 percent of megafauna to survive the late Pleistocene extinctions; in column 3, percent lost/gained is the percent change in Holocene

613 species richness due to extinction/immigration during the Holocene; in column 4, percent replaced is the percent of all extinct

614 megafauna richness (Pleistocene and Holocene) to be numerically replaced by introductions in the Anthropocene. * indicates natural

615 immigration from Eurasia to North America during the early Holocene.

Continent	Pleistocene species richness	Holocene species richness (percent survived)	Holocene extinctions/immigration (percent lost/gained)	Anthropocene richness (percent replaced)
Africa	44	32 (73%)	-1 (-3%)	35 (31%)
Asia	61	36 (59%)	-2 (-6%)	38 (14%)
Europe	15	7 (47%)	-1 (-14%)	9 (33%)
North America	35	4 (11%)	+2 (+33%)*	14 (26%)
South America	44	5 (11%)	0 (0%)	12 (18%)
Australia	12	0 (0%)	N/A	8 (67%)

616

617

618 Table 2. Functional traits of introduced megafauna. ABM is average body mass (Jones et al. 2009); foraging type is 'B' is browser, 'G' is

619 grazer, and G/B are intermediate; habitats are derived from IUCN Redlist species accounts (give web address here).

Species	Common Name	ABM	Type	Habitat	Known or potential unique ecological functions
Alces alces	Moose	541	B	Woodlands, tundra, montane forests	Browse at heights up to 2m, affecting stand height and canopy composition (Pastor et al. 1988).
Bison bison	Bison	625	G	Grasslands, open forests	Create wallows that become ephemeral pools, serve as fire breaks, and increase landscape scale plant diversity (Knapp et al. 1999).
Bos javanicus	Banteng	636	G/B	Open dry forests	
Bos taurus	Cattle	613	G	Numerous	
Boselaphus tragocamelus	Nilgai	182	G/B	Open grasslands	Open trails in dense shrubland, capable of jumping 2.5m high- potentially sustaining seed/nutrient dispersal in fenced landscapes (Leslie 2008).
Bubalus bubalis	Water buffalo	919	G/B	Moist grasslands, marshes	Used for conservation grazing to maintain open water habitat for birds and fish (BBC News).
Camelus dromedarius	Dromedary camel	488	B	Desert scrub	Salt-tolerant (Root-Bernstein & Svenning 2016); large home ranges (Spencer et al. 2012), may redistribute sodium (Doughty et al. 2016a).
Cervus elaphus	Red deer	241	G/B	Generalist	
Connochaetes gnou	Black wildebeest	157	G	Short-grass grasslands	
Elephas maximus	Asian elephant	3270	G/B	Tropics	Ecological engineer in native range by dispersing large seeds and removing trees (Donlan et al. 2006)
Equus asinus	Donkey	180	G/B	Deserts	Digs wells used by other species
Equus caballus	Horse	400	G	Grasslands, open forests	Feeds on coarse, abrasive grasses (Naundrup & Svenning 2015)
Hippopotamus amphibius	Hippopotamus	1536	G	Aquatic daytime refuge; grasslands	Maintain grazing meadows, fertilize riparian systems (Bakker et al. 2016b), unstudied in introduced range
Hippotragus niger	Sable antelope	236	G/B	Woodland edges	
Kobus ellipsiprymnus	Waterbuck	204	G	Savanna woodlands	Riparian grazer, likely influences riparian vegetation and river geomorphology (IUCN 2017, Naiman & Rogers 1997)
Oryx gazella	Gemsbok	188	G	Desert scrub, desert grassland	Dig wells used by other species (Hamilton et al. 1977)
Ovibos moschatus	Muskox	313	G	Arctic tundra	Few other herbivores adapted to extreme arctic environment (Schmidt et al. 2015)
Ovis ammon	Argali	114	G	Steep, rocky environments	

Rangifer tarandus	Reindeer	109	G/B	Mountains, arctic tundra	Grazing can alter arctic albedo, causing temperature reductions that may counteract climate change (te Beest et al. 2016). Uniquely capable of digesting lichens (Palo 1993).
Rucervus duvaucelii	Barasingha	171	G	Forests, riparian grasslands	Riparian grazer, likely influences riparian vegetation and river geomorphology (IUCN 2017, Naiman & Rogers 1997)
Rusa unicolor	Sambar	178	G/B	Generalist	

620

621

622

623

624

625

626

627

628

629

630

631

632

633

634

FIGURE CAPTIONS

636

637 Figure 1. Threatened megafauna species are finding refuge outside their native ranges.
638 Percentage of megafauna in each family with introduced populations, colored by IUCN
639 threat categories in their native ranges. Number within parentheses indicates total number
640 of megafauna within each family.

641

642 Figure 2. The number of introduced megafauna species by IUCN (2017) threat status and
643 population trends in their native ranges. The majority (59%) of introduced megafauna are
644 threatened or have declining populations in their native ranges.

645

646 Figure 3. Percent of global populations of megafauna that are introduced. Color indicates
647 IUCN (2017) status. Bars indicate high and low estimates if multiple estimates were
648 found. Includes only species with known population sizes in native and non-native ranges
649 and thus excludes *Tragelaphus eurycerus* (NT), *Kobus ellipsiprymnus* (LC), *Hippotragus*
650 *niger* (LC), *Rusa unicolor* (VU), *Rucervus duvaucelii* (VU), *Alces alces* (LC), and *Ovis*
651 *ammon* (NT). * indicates post-domestic species.

652

653 Figure 4. Contribution of introduced megafauna to TDWG-country species richness. (a)
654 Native megafauna species richness (b) introduced megafauna species richness, (c) all
655 megafauna species richness, and (d) percent contribution of introduced species to
656 TDWG-country megafauna assemblages. Inter- and intra-continental introductions were
657 included. Native richness was derived from IUCN (2017) species distribution data.
658 Introduced species distributions are available in Supplementary materials Appendix 1,
659 Data A1.

660

661 Figure 5. Megafauna species richness per epoch by continent. 'Extinct' indicates species
662 that went extinct in the wild on all continents; 'extirpated' are species that survived
663 elsewhere; 'immigrated' are species that immigrated without human intervention;
664 'introduced' indicates species introduced by humans; 'introduced, threatened' are
665 introduced species threatened in their native ranges; 'survived' are species that were still
666 present into the following epoch; 'survived, threatened' are threatened native species
667 (Supplementary materials Appendix 3, Table A2).

668

669 Figure 6. Wild donkeys (*Equus asinus*) increase surface water availability in the Sonoran
670 Desert. (a) Wild donkey digging well to water table ('burro well'), (b) troop of javelina
671 (*Pecari tajacu*) bathing and drinking in burro wells, and (c) several-year-old Fremont's
672 cottonwood (*Populus fremontii*) growing in an abandoned burro well on a high channel
673 bar.

674

675

676

677

678

679

680

681 **SUPPLEMENTARY MATERIAL APPENDIX CAPTIONS**

682 Supplementary material Appendix 1, Data A1. Shapefile of introduced megafauna ranges

683 with references.

684

685 Supplementary material Appendix 2, Table A1. The introduced large ($\geq$ 100kg)

686 herbivorous mammals of the world. Data from Ripple *et al.* (2015), Long (2003), and the

687 Large Herbivore Network (2015) unless otherwise noted.

688

689 Supplementary material Appendix 3, Table A2. Large ($\geq$ 100kg) herbivore species status

690 by continent (Africa, Australia, Eurasia, North America, South America), by epoch

691 (Pleistocene, Holocene, Anthropocene).

692

693 Supplementary material Appendix 4, Movie A1. Digging by wild donkeys ('burros')

694 creates water resources used by other species in the Sonoran Desert. In addition to the

695 four species shown here, from trail cameras and direct observations we have documented

696 an additional twenty-six vertebrate species utilizing 'burro wells' including, bobcats

697 (*Lynx rufus*), badgers (*Taxidea taxus*), black-tailed jackrabbits (*Lepus californicus*),

698 striped skunks (*Mephitis mephitis*), ringtail cats (*Bassariscus astutus*), rock squirrels

699 (*Spermophilus variegatus*), Common Ravens (*Corvus corax*), Hooded Orioles (*Icterus*

700 *cucullatus*), Yellow Warblers (*Setophaga petechia*), Black-throated Sparrows

701 (*Amphispiza bilineata*), Gila Woodpeckers (*Melanerpes uropygialis*), Gambel's Quail

702 (*Callipepla gambelii*), Mourning Doves (*Zenaida macroura*), and various plant,

703 amphibian and invertebrate species.