

1 Extinctions have strongly reduced the 2 mammalian consumption of primary 3 productivity 4

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13 Abstract

14 Herbivorous mammals are important for natural ecosystems even today, but how much stronger would
15 there effects be without human-linked extinctions and extirpations? The ranges of many mammal species
16 have contracted and numerous species have gone extinct due to human pressures, so herbivore impacts in
17 even seemingly natural ecosystems likely deviate from their pre-anthropogenic state. However, such
18 effects remain poorly understood and often unrecognized. To address this issue, we here quantified and
19 mapped plant consumption by all terrestrial mammals in natural areas based on both current and
20 estimated natural ranges. We then compared the estimated consumption rates to current plant net
21 primary productivity, and summarised the results for global ecosystem types both broadly and in the
22 wildest remaining natural areas around the world (the Last of the Wild). We found that wild mammals
23 consume 7.3% (95% interquartile range: 0.85% - 26%) of net primary productivity in current natural areas,
24 and that this would be much higher in the absence of extinctions and extirpations, namely 13% (95%
25 interquartile range: 1.7% - 40%), i.e., a >50% higher consumption rate. Marked human-linked declines in
26 herbivory were seen even in the wildest remaining natural areas, where mammals now consume a mean of
27 9% (95% interquartile range: 2.2% - 26%) of plant primary productivity, which is only 60% of no-extinction
28 level. Our results show that mammalian herbivores naturally play an important part in ecosystems at a
29 global scale, but that this effect has been strongly reduced by extinctions and extirpations.

30 Introduction

31 There is wide evidence that large herbivorous mammals can strongly shape vegetation¹⁻³. Nevertheless, the
32 general importance of such effects is poorly understood, with several studies reporting that mammalian
33 herbivores consume a surprisingly small amount of the net primary production⁴. At the same time, large
34 herbivore assemblages have been strong affected by human activities^{5,6}, meaning that we have poor
35 understanding of natural levels of herbivory and their vegetation effects. During the last 100,000 years,
36 modern humans have spread across the whole world and with their arrival a large part of the megafauna
37 has disappeared^{7,8}. Only parts of Africa and small parts of Asia have retained megafauna assemblages
38 comparable to those which once roamed the whole planet⁶. When these megafauna have been released
39 from human pressures in protected conservancies, they have a large effect on ecosystem and vegetation
40 structure^{5,9}.

41 The ecosystem impact of a species tends to scale with body mass making the changes in ecosystems
42 following megafauna extinctions larger than the changes in mammal diversity. Large animals can both have
43 major direct structural effects (e.g. when elephants knock over trees¹⁰), but are also disproportionately
44 important in indirect ways like overall vegetation consumption since a species' energy requirements over a
45 given area tends to increase with body mass^{11,12}. The exact consequences of the prehistoric and historic
46 megafauna range contractions extinctions on vegetation structure and ecosystem function is poorly known,
47 albeit a rising number of studies point to widespread major effects: South American savannas would have
48 been much more open like the African savannas¹³. Beetle assemblages from Great Britain indicate both a
49 larger proportion of dung and more open and diverse mixture of vegetation cover in the Last Interglacial
50 than Early Holocene¹. A study from Queensland showed that megafauna extinction and subsequent
51 increased wildfires led to the shift from mixed savanna including fire-sensitive trees to fire-tolerant
52 sclerophyll vegetation¹⁴, and strong vegetation changes have also been coupled to megafauna losses in
53 northeastern North America¹⁵. However, the large and cascading effects of large herbivores are also
54 evident from the remaining species⁵, and the few areas with well-developed wild herbivore faunas that still
55 exist (e.g. extirpation of the large herbivores in Mozambique led to an expansion in an invasive species and
56 reintroductions took the invasive back to pre-extirpation occurrence¹⁶, re-establishment of bison numbers in
57 Yellowstone National Park are limiting the woody plant communities¹⁷, enclosure experiments in temperate
58 forests have shown that saplings have a hard time escaping herbivores both under closed forest canopy
59 and in large gaps¹⁸, and long-term elephant use decreases vegetation height and increases vegetation
60 height variability¹⁹). It is obvious that large herbivores have a unique importance in ecosystem function and
61 are irreplaceable by smaller species and this has implications for nature restoration^{5,20}. Even though the
62 extinct Late Pleistocene terrestrial megafauna only made up a small fraction of the global species diversity
63 of mammals (3.9%), their effect on vegetation seem likely to have been substantial³.

64 A review of consumption studies on current mammalian terrestrial fauna have shown them to have a highly
65 variable, but often quite small effect on total net primary productivity (NPP), consuming only a median of
66 2%, although varying from <1% to 29%⁴. A few macroecological studies have made rough estimates of the
67 effect of extinctions on the consumption patterns and have estimated that the extinction of megafauna
68 have decreased mammalian consumption by 2.2% - 5.3% of NPP²¹. Earlier studies, however, use broad
69 allometric scaling equations for density and consumption estimates based on a limited number of data
70 points, even though we know that different functional and taxonomic groups can scale widely different¹².
71 Here we use taxonomically wide datasets and use phylogenetic models to estimate individual species
72 density and metabolic rates. So even though the impact of megafauna seems small, there has clearly been
73 a significant drop in impact as a consequence of the megafauna extinctions. Only few studies have tried to
74 address and understand the importance of mammals for regulating vegetation growth at a global scale.
75 How important would they be, if there had been no megafauna extinctions and extirpations in the late
76 Quaternary?

77 Here, we assess the potential global impact of herbivory by current and present-natural mammalian fauna
78 (i.e., under current climatic conditions but in the absence of anthropogenic late-Quaternary extinctions and
79 extirpations). We have assembled and combined data on ranges, metabolic demands, population densities,
80 and diets for all mammals extant throughout the last 130,000 years. Putting this together enabled us to
81 estimate the overall consumption of the planet's vegetation production by mammals.

82 We compare this to estimates of current plant productivity to estimate how large effects mammals with
83 and without megafauna losses have on the ecosystems. Even though only a small part of the mammalian
84 fauna has gone extinct, we (1) expect that the extinctions have had a strong impact on vegetation
85 consumption. We compare the losses across realms and biomes, to assess how consistent the patterns are
86 geographically and ecologically. We (2) expect to see a consistent pattern geographically, with least impact
87 in the Afrotropics which still has the most extant megafauna. Forested areas have been least impacted by
88 humans and we could therefore (3) expect a smaller impact in those ecosystems. The wildest places left on

89 earth, have not been immune to megafauna extinctions and we therefore (4) expect to see the same
90 patterns even there.

91 Results and discussion

92 Wild mammal biomass

93 We estimated wild mammal biomass across the globe, assuming total coverage and full natural density
94 within each 96 km × 96 km grid cell. This was done for current-day non-introduced ranges for all extant
95 mammal species, as well as for present-natural ranges of all late-Quaternary mammal species, i.e., without
96 any late-Quaternary extinctions or any human-driven range modifications.

97 We estimate present-natural terrestrial mammal carbon stock (outside deserts) to be 0.32 PgC (95%
98 interquartile range: 0.047 PgC -2.9 PgC). This is substantially higher than previous estimates. A study²² of
99 mammal biomass through time estimated the pre-extinction biomass to be around 0.03 PgCs, but using
100 different methods and cruder ranges. A study of current global carbon in livestock estimate 0.1 PgC in
101 livestock and 0.003 PgC in wild mammal populations²³. So current-day mammal biomass including livestock
102 is comparable to the potential-natural carbon stock in wild animals, just with a near-complete shift from
103 wild to domestic animals. We note that these numbers only concern standing biomass and not biomass
104 flux, a faster turn-over rate in domestic animals would mean a much higher consumption per kg farmed
105 biomass relative to wild biomass.

106 Mapping total mammal biomass, we get comparable estimates to what others have found before, based on
107 empirical local animal counts²⁴. Fløjgaard et al.²⁴ report a bimodal distribution of empirical large-herbivore
108 biomass in Europe with the high numbers, from rewilding sites, in line with our estimates. Comparing to the
109 empirical values from their study based on animal counts we find that our theoretical estimates are broadly
110 in agreement, but for most areas in the Afrotropics tend to be higher than those observed empirically (Fig
111 S6). The latter can likely be attributed to reduced megafauna densities due to hunting and other human
112 pressures^{25,26}. The top-level empirical from the Afrotropics, such as from the Maasai Mara, Kenya with its
113 nearly intact megafauna, are close to ours, despite even these areas being affected by anthropogenic
114 megafauna declines²⁷, further supporting that our estimates are reasonable equilibrium estimates in the
115 absence of human pressures.

116 Current vegetation consumption by wild mammals

117 When we estimate current plant consumption by wild mammals, we note that this is meant for *natural*
118 *areas*. We state this to highlight that most places are under anthropogenic use, and that our numbers are
119 applicable where wild animal species occur within the cell at their natural densities. Our estimates suggest
120 that current plant consumption by wild mammals in natural areas varies greatly across the globe, with the
121 highest consumption in western North America, central and eastern Africa, as well as a large spike in
122 central Asia (Fig 2). This pattern largely follows the current diversity of large mammals across the globe⁶,
123 with the most diverse areas having the highest consumption. We compared how our estimates of mammal
124 plant consumption compares to net primary productivity (NPP), and found the median consumption by wild
125 mammal populations was only around 7.3% (mean 9.1%) (95% interquartile range: 0.85% - 26%) (Fig 2-4).
126 Areas like tropical South America and coastal Australia have very few extant large mammal species but high
127 plant productivity, therefore almost none of the NPP is currently being consumed by mammals in these
128 ecosystems. Our estimate of current consumption as a percentage of NPP fits well with empirical studies: A
129 review on NPP consumption in modern terrestrial ecosystems found that across 21 studies, animals eat
130 0.24% - 29% of the total production with a median of 1.9%⁴.

131 In a study²⁸ on one of the most megafauna rich ecosystems today, the Serengeti National Park, Tanzania,
132 large-herbivore consumption at the grazed sites was found to be median 163 Mg Carbon / km² / year
133 (range 36-462, n = 28, extracted from figures in the paper), i.e., 15% of our estimate of total NPP for the
134 area (1115 Mg Carbon / km² / year). Our estimate from the same area is that that 112 Mg Carbon / km² /

135 year is currently consumed, i.e., 10% of total NPP. Hence, our estimate is close the empirical estimates in
136 intact ecosystems.

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138 Differences between current and present-natural vegetation consumption

139 Global plant consumption by mammals in natural areas is very different now compared to what it would
140 have been today had a large part of the mammalian megafauna not been lost (Fig 1), with especially large
141 differences in parts of the Americas and Australia, where >50% of the present-natural mammalian
142 consumption is missing today (Fig. 1 and 3), i.e., considering only native species and ignoring the impacts of
143 introduced species²⁹. Wild areas in Africa and Asia where more of the megafauna has been preserved are
144 much closer to present-natural consumption. The global median fraction of NPP consumed for present-
145 natural distributions is 13% (mean 15%) (95% interquartile range: 1.7% - 40%) of NPP, i.e., 1.8 times the
146 current level (Fig 2-4).

147 As increased mammal density may sometimes increase NPP, our use of current NPP might in some areas
148 underestimate of present-natural NPP. Several insect studies have shown increased productivity in the
149 presence of increased herbivory and viceversa^{30,31}. Mammals have also been shown to increase
150 productivity. Arctic tundra ecosystems are nutrient-limited and mammals increase nutrient turnover and in
151 turn increase the productivity of grasslands – which they likely did so much more in the past³². Further,
152 both in Africa and South America grazing lawns are being kept by large herbivores, again increasing
153 productivity³³, and a grazing study in Serengeti, showed that cutting and grazing stimulated productivity²⁸.
154 Hence, in such situations our estimated present-natural proportional consumption rates may be
155 overestimates.

156 Only 7.4% of all terrestrial mammal species have gone extinct since the Late Pleistocene, but a massive 54%
157 of terrestrial megafauna mammal species (≥ 45 kg body mass) have been lost across the same period^{34,35}.
158 Our results show that this have strongly changed NPP consumption levels. The current mammal fauna
159 accounts for an average of 9.1% of plant consumption in natural areas, with megafauna accounting for 13%
160 hereof. In the absence of extinctions and extirpations, the present-natural fauna would consume an
161 average of 15% of plant consumption in natural areas, with megafauna accounting for a 45% hereof, i.e.,
162 megafauna loss accounts for 93% of the overall decrease in NPP consumption. As discussed earlier, there
163 are current and paleoecological examples of how large herbivores can be very important for the
164 environment and how their loss may cause large vegetation shifts across the world's biomes³. This is
165 reaffirmed in our consumption estimates with a 44% reduction in NPP consumption (13% to 7.3%).

166 Some regions are particular affected. For example, Australia's native megafauna diversity is extremely
167 impoverished compared to the present-natural diversity. Out of the 33 late-Quaternary species of strict
168 herbivorous ($\geq 90\%$ plant diet) marsupials > 20 kg, only 8 are left (21 kg - 31 kg and one of 46 kg) of whom
169 one is classified as threatened by IUCN (International Union for Conservation of Nature). While the median
170 body size of the extinct fauna was 131 kg, and the heaviest 2700 kg^{35,36}. This causes the extreme drops in
171 consumption we see in the temperate grasslands, shrublands and forests of Australasia (Fig. 4), though
172 some of this effect might be mitigated by introduced species that were not included in this study²⁹.

173 Reduced herbivore effects even in natural areas

174 In the areas with the lowest human footprint ('Last of the Wild'³⁷), the median fraction of NPP consumed is
175 9.0% (95% interquartile range: 2.2% - 26%) and 15% (95% interquartile range: 3.4% - 40%) for current and
176 present-natural ranges, respectively (Fig. 3c). It has previously been highlighted that there is poor overlap
177 between human footprint and faunistic intactness³⁸. Our finding of strongly reduced large-herbivore
178 consumption in the Last of the Wild areas shows that many of these apparently low-impact areas are not
179 only substantially modified in their species composition, but also in their functional ecology.

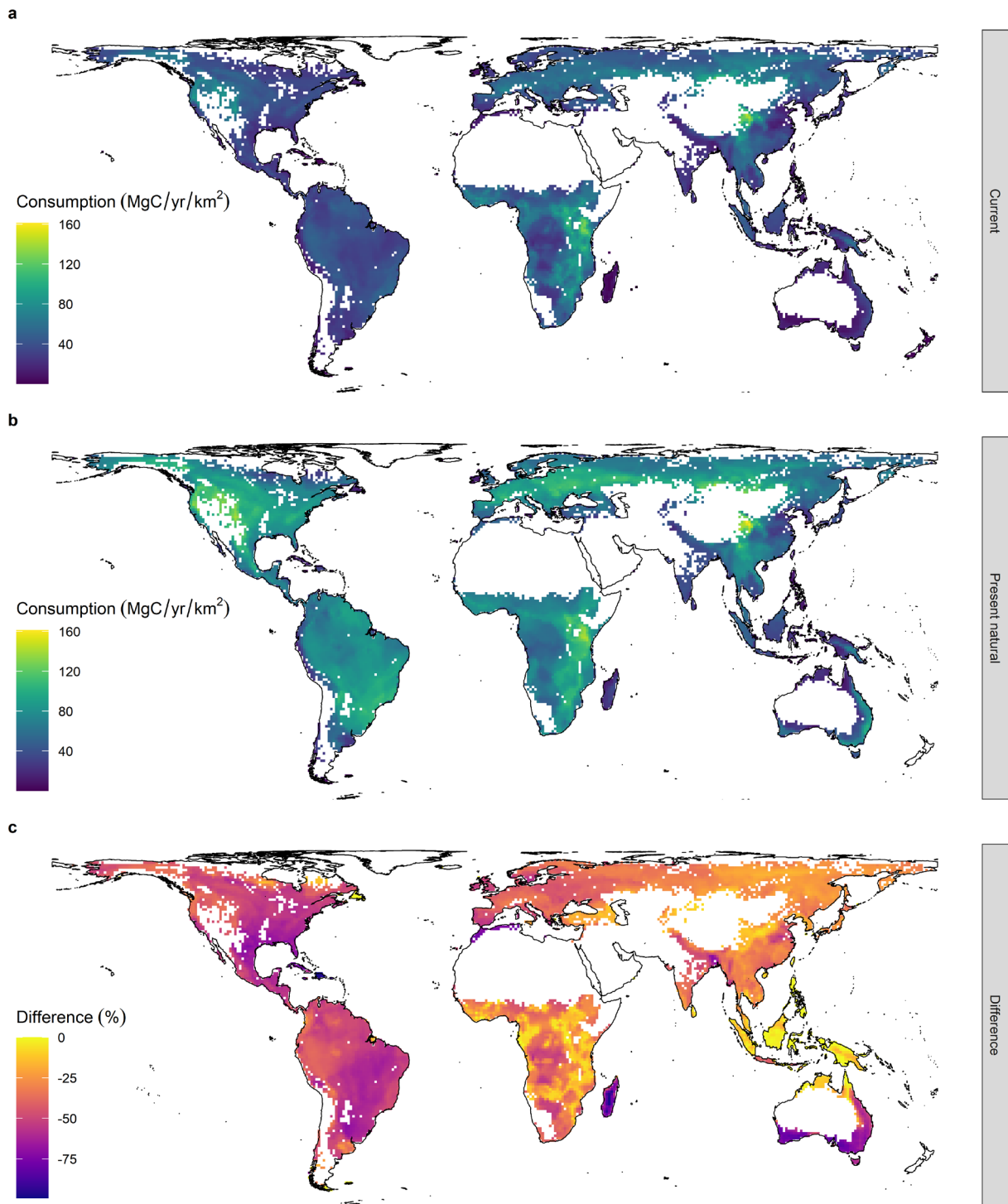
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181 Perspective

182 The ecological implications of our findings are complex and will depend both on biomes and the ecological
183 characteristics of the herbivores that has been lost. The consequences of reduced large mammal herbivory
184 for woody vegetation and fire risk for instance depends of the relative dominance of browser vs grazers.
185 The loss of many large browsers in the Americas could have reduced the fire risk, since browsers create
186 woody debris and promote semi-open grasslands with flammable grasses³⁹. On the other hand, we see in
187 our model, that the full Pleistocene community would have consumed a much larger fraction of the plant
188 productivity likely leading to much lower fuel loads, which should have decreased fire severity⁴⁰. A dramatic
189 loss of consumption of the plant productivity would also lead to a promotion of competitive plant species,
190 and less seed dispersal^{41,39}, potentially leading to reduced plant diversity (either at the landscape scale,
191 due to vegetation composition shift⁴² or locally due to decreased connectivity⁴³). Several studies have
192 found that the extinction of megafauna have led to ecosystem impacts such as loss of open mosaic
193 vegetation^{1,17} and increased fire⁴⁴. The extinction of arctic megafauna likely led to an increase in *Betula*
194 cover, with potential effects on global climate^{32,45}. As an example changes in fire regimes a study in
195 Australia found that the extinction of extinction megafauna preceded an increased fire regime which again
196 preceded a vegetation shift from mixed savanna with both rainforest and sclerophyll trees to purely
197 sclerophyll vegetation¹⁴. A review of current elephant impact found that while elephants decreases tree
198 abundance, they do not affect their diversity and increases herb diversity, and found no consistent
199 cascading effects on either abundance or diversity other animals⁴⁶.

200 Whenever we look to seemingly pristine ecosystems³⁷, we have to keep in mind that even those
201 ecosystems are affected by human-linked ecological changes. With a large proportion of the terrestrial
202 megafauna extinct or extirpated across the globe⁶, a large part of the mammal function has been lost^{47,48}.
203 As this study shows, even the “least impacted” environments on the planet, have also experienced a large
204 reduction in mammal vegetation consumption. The mammal communities have been impoverished to such
205 an extent that introduced species make up an important part of their functional space²⁹. These extinctions
206 must have had an effect on the ecosystems: Decreased mammal consumption leading to a variety of effects
207 including, but not limited to on changes in community composition and structure^{1,13,16,17,19} or changes in fire
208 frequency and intensity^{14,15,39}. Our work cannot with certainty identify how ecosystems would have
209 functioned prior to the late-Quaternary megafauna losses, but highlights that even remote ecosystems are
210 likely fundamentally changed relative to a pre-extinction baseline²¹. The world we live in is drastically
211 different from one without human impacts even in seemingly pristine landscapes. In consequence, our
212 findings also have strong implications for ecosystem restoration, notably trophic rewilding⁴⁹. Notably, they
213 highlight that it is important to consider the strong down-sizing of large-herbivore assemblages since the
214 Late Pleistocene and associated reduction in NPP consumption rates in efforts to restore self-sustaining
215 ecosystems, e.g., via active megafauna restoration⁴⁹.

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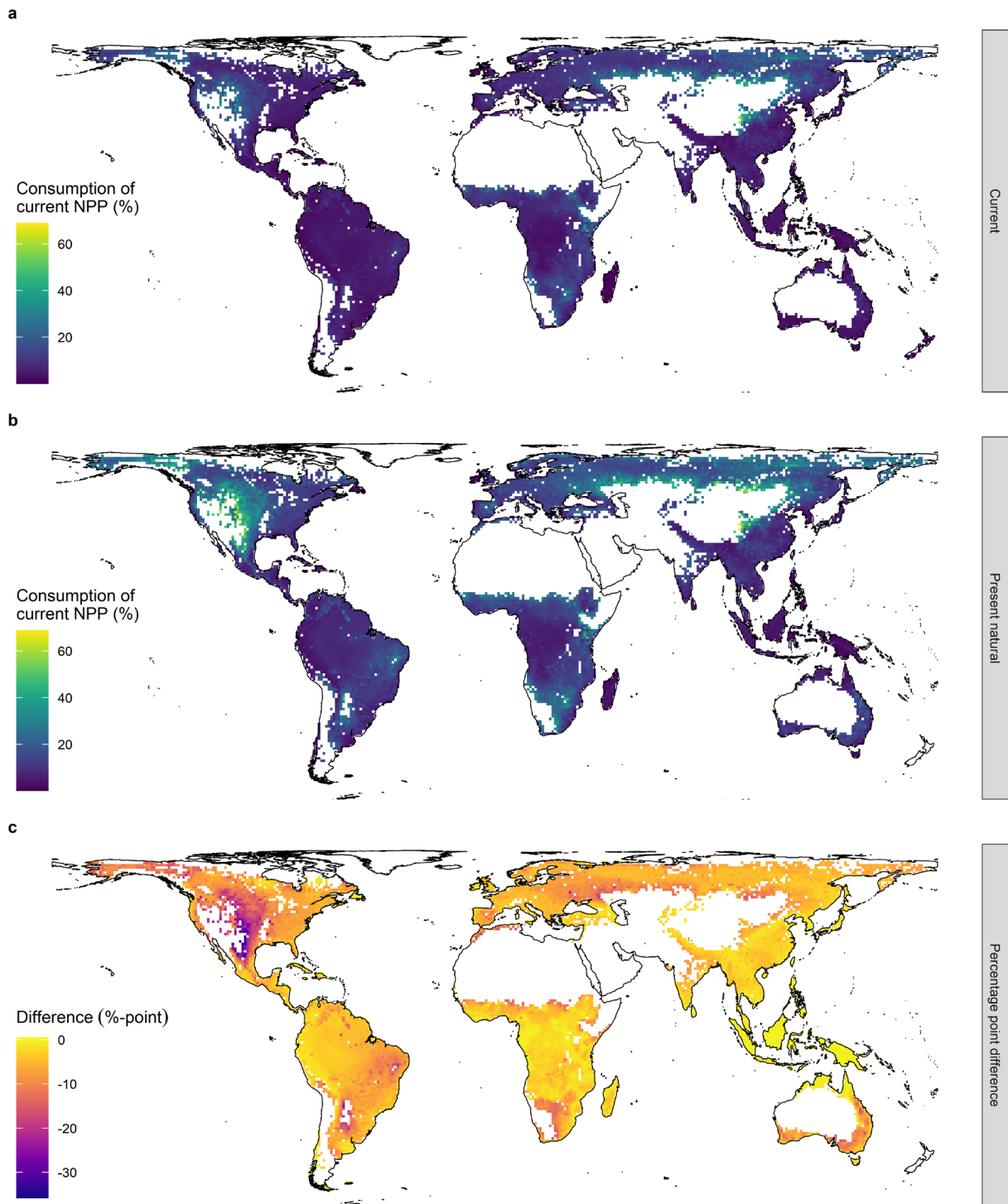
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Fig 1: Mammal consumption of plant carbon globally. a) Average terrestrial mammal consumption by current mammals (current ranges of extant species). b) shows present natural consumption (potential present day ranges with no human presence). c) shows the percentage lower consumption of current ranges compared to present natural. Blank pixels represents areas excluded from the analyses due to very low NPP or high variability in NPP. (See Fig S1 for included low NPP regions.)



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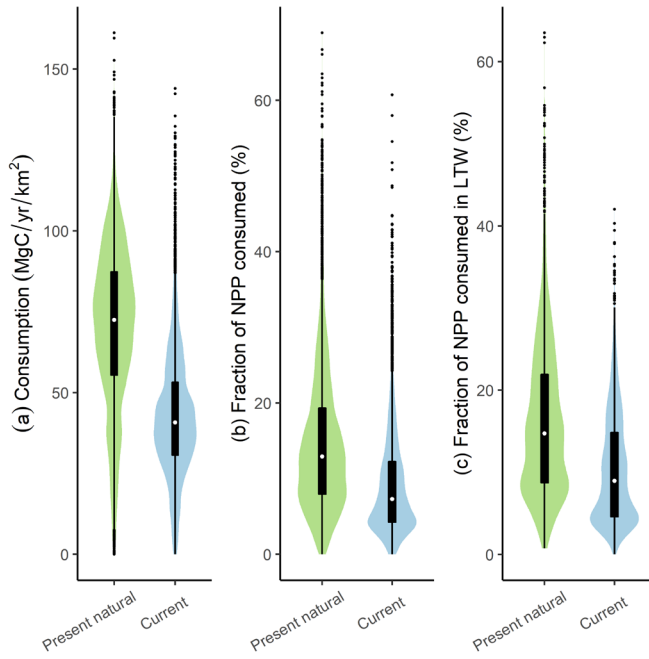
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Fig 2: Estimated mammal consumption of net primary productivity (NPP) globally. a) Consumption by current mammals (current ranges of extant species). b) Present natural consumption (potential present day ranges with no human presence). c) Percentage-point consumption difference between present natural and current consumption. Blank pixels represents areas excluded from the analyses due to very low NPP or high variability in NPP. (See Fig S2 for included low NPP regions.)

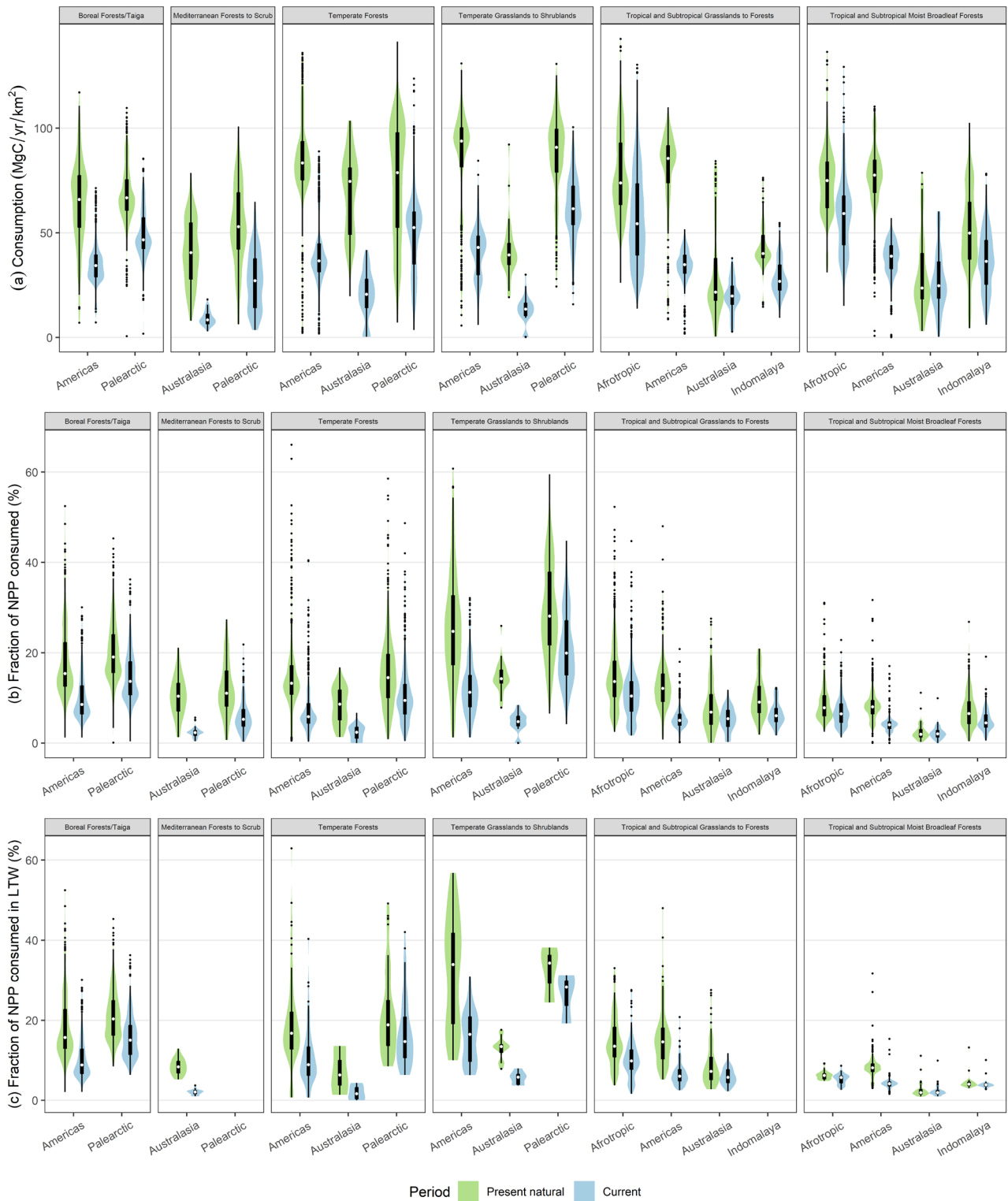
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234 **Fig 3:** Global consumption summary. Boxplot with underlying violins with kernel density scaled to width. **a)** Total
235 consumption of carbon. **b)** Fraction of net primary productivity (NPP) consumed. **c)** Fraction of net primary
236 productivity (NPP) consumed in the areas designated as 'last of the wild'^{37,50}. (See Fig S3 for included low NPP
237 regions.)

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Fig 4: Consumption summary for large ecological units based on realms and biomes⁵¹. Boxplot with underlying violins

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with kernel density scaled to width. Neotropics and Nearctic are merged to the Americas and Madagascar is excluded

242

from the Afrotropics for biome modifications see Fig S5. **a)** Total consumption of carbon. **b)** Fraction of net primary

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productivity (NPP) consumed. **c)** Fraction of net primary productivity (NPP) consumed in the areas designated as 'last

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of the wild'^{37,50}. (See Fig S4 for included low NPP regions.)

245

246 Methods

247 The goal of this paper was to estimate the total consumption by wild mammals in a non human-dominated
248 world. To do this we estimated densities and energetic needs for all mammals and combined this with
249 previously gathered information on diet and current and natural range size of all mammals.
250 To estimate the total impact of consumption by mammals globally and to what degree this must be
251 affected by the human impacts, we needed information on species distributions with and without human
252 presence impacts, population densities, energetic needs, and diet.

253 Consumption

254 Taxonomic scope

255 We followed the mammalian species list in PHYLACINE^{34,35} (v.1.2.1) which follows the IUCN Red List⁵² for
256 extant species. This list was filtered to include only terrestrial not primarily marine species i.e. excluding
257 bats, whales, pinnipeds and sea cows, and three marine carnivores (*Enhydra lutris*, *Lontra felina*, and *Ursus*
258 *maritimus*). Bats do forage on land and have an impact, but we felt that they are too different to be reliably
259 modelled along the rest – and therefore excluded them from our study. Further their ranges have not been
260 documented to be affected by the expansion on the globe, and therefore wouldn't change between current
261 and present natural maps.

262 Densities

263 We estimated population density for all species. We used population densities from the PanTHERIA⁵³ and
264 body masses from PHYLACINE 1.2^{34,35} and underlying sources^{54,55}. We build an allometric model of density
265 as a function of body mass using a Bayesian approach based on species level phylogeny from
266 PHYLACINE^{34,35,56}, where estimates are weighted by closer phylogenetic relationships. Further explanation
267 on the methods and overview of the imputed density results can be found in Appendix S1, with the
268 estimates available in Table S2. In the further model we used the estimated densities for all species, to
269 avoid biases by mixing known values and estimated values. To estimate the unbiased uncertainty we used
270 1000 of the sampled results for each species throughout the model.

271 Our consumption estimates are based on single population densities across a species range, which is fine
272 for most species on average as there is no tendency for central abundance neither climatically or
273 geographically⁵⁷ – but estimates for individual species might be error prone. An example is the Capybara
274 (*Hydrochoerus hydrochaeris*) a grazer which is highly connected to water, a resource not homogenously
275 found across its large range^{58,59}. Using a single density across its range limits our study's geographic specific
276 accuracy. We model density to 55/km² – on par with an average (51/km²) previously found⁶⁰, though
277 densities between 1/km² and 200/km² have been reported⁶⁰. Further, our models do not directly take
278 species interactions into account, or density compensation by other species in a community if one goes
279 extinct. Therefore, more species equates to more consumption in general. Some density compensation
280 likely occurs in impoverished assemblages, while present-natural species assemblages probably more
281 accurately reflect real densities and consumption.

282

283 Metabolic rates

284 We estimated field metabolic rates for all species. We first compiled a dataset of metabolic rates (MR)
285 (Table S1). We gathered data on both basal metabolic rate (BMR) and field metabolic rate (FMR). FMR and
286 BMR are closely related, and therefore known values of one could help pin down the value of the other
287 estimate. FMR and BMR are tightly related to body mass even within each species, therefore we in the
288 dataset often have several body mass/metabolic rate (MR) pairs for each species. We built an allometric
289 model of MR as a function of body mass using a Bayesian approach based on the species-level phylogeny
290 from PHYLACINE^{34,35,56}, where estimates are weighted by closer phylogenetic relationships. Further
291 explanation on the methods and overview of the imputed density results can be found in Appendix S2, with
292 the estimates available in Table S3. In the further model we used the estimated densities based on the

293 body masses from PHYLACINE for all species. To estimate the unbiased uncertainty we used 1000 of the
294 sampled results for each species throughout the model.

295 Species energy needs and plant carbon consumption

296 For each species we calculated the species energy need (Equation 1), by multiplying FMR with density. By
297 doing so we make the assumption that populations occur at stable densities across time, and that every
298 animal eats at consumes the average needed energy for the species. This is assumption is wrong for young
299 and suckling animals which require less energy and for pregnant and nursing animals which require more.
300 On average these effects will at least partly cancel each other out.

301 Since not all species in our model only eat plants we corrected by the plant diet (Diet.Plant) percentage
302 based on the PHYLACINE diet^{34,35,61,62}. This will remove all strict non-plant eaters from impact, and reduce
303 all not strict herbivores as well. Assuming that the plant diet percentage is equal to energy consumed is not
304 necessarily correct, but plant diets percentages are calculated in a number of ways and a better solution is
305 not available. And species affected by this counts only in the minority of the model anyway.

306 Equation 1

307 $\text{SpeciesEnergyNeeds} [\text{kJ} / \text{km}^2 / \text{yr}] = \text{FMR} [\text{kJ} / \text{day}] \times 365.25 [\text{day} / \text{yr}] \times \text{density} [1 / \text{km}^2] \times \text{Diet.Plant}$

308 We were only interested in the animal's impact on primary productivity and therefore weighted each
309 species impact with its plant diet percentage (Equation 2). Several studies have shown that about 50% of
310 the gross available energy is digested the rest is excreted again, and absorbed energy is ranges from 6.4-9.6
311 MJ/kgDM across wild monkeys, kangaroos and sheep⁶³⁻⁶⁵. We did not find enough species specific data for
312 this factor, to differentiate between species. A study of diet selection in wild foraging sheep measured the
313 metabolic energy (ME) available in the selected diet⁶⁵. This study provided a measured of ME = 8.5 MJ / kg
314 Dry-matter with an uncertainty (sd = 1.4). The uncertainty of the number was propagated through our
315 models, by sampling this distribution (n = 1000). Further to translate kg Dry-matter to kg Carbon we need
316 estimates for carbon content in vegetation. Vegetation contains about 45% (SD = 5.23) carbon (CC) [kgC /
317 kgDM], which is does not vary much between plant 'organ' (fruit, stem, leaf, and root) or between life
318 forms (e.g. herbs, broad-leaved trees, conifers, etc.), where the mean of any combination of life form and
319 organ varied between 42% (herb-root) and 51% (conifer-stem)⁶⁶. We used the mean vegetation CC for our
320 model, and carried the uncertainty by sampling a normal distribution with the given parameters 1000
321 times.

322 Equation 2

323 $\text{SpeciesPlantConsumption} [\text{kgC} / \text{km}^2 / \text{yr}] =$
324 $\text{SpeciesEnergyNeeds} [\text{kJ} / \text{km}^2 / \text{yr}] \times \text{CC} [\text{kgC} / \text{kgDM}] / \text{ME} [\text{kJ} / \text{kgDM}]$

325 Mapping the consumption

326 To compare estimate the human impact on natural consumption we used current range maps and present-
327 natural range maps from PHYLACINE^{6,34,35,52}. Present-natural range maps are counterfactual range maps
328 with no mammal extinctions within the last 130 000 years. These maps are the baselines for all mapping
329 the this paper, which are projected in a Berhman projection i.e. a 'cylindrical equal' area projection with
330 standard parallel at 30° with a projected cell size of 96.5 km × 96.5 km, which is approximately 1° × 1° at 30°
331 N and S.

332 For each grid cell we summed the species plant consumption for all species in that cell. By doing so we are
333 making the assumption that each species occur at a uniform density across its full range. This is of course
334 not the case, but basing it on any other distribution would introduce even more assumptions. Further, any
335 comparisons between the current and the present natural will be minimally impacted by such an
336 assumption. Still, the maps in PHYLACINE are very inclusive (i.e., if even a tiny part of a species range is in
337 the cell, the whole cell is counted as range), and therefore we mitigate some of this by reducing species
338 populations at range edges (defined using rook's case). We do this based on the theoretical mean

339 expectations if a grid is put on top of square ranges of random size. We focus on the number of rook's case
340 neighbours included in the range. Cells with no neighbors are weighted as $1/9^{\text{th}}$, endpoints (one neighbour)
341 as $1/6^{\text{th}}$, bridges and corners (two neighbours) as $1/4^{\text{th}}$, and flat edges (three neighbours) as $1/2$.

342 Global consumption of primary productivity

343 We compared our consumption estimates with primary productivity based on a mean dataset of corrected
344 MODIS 17A3 NPP data from 2000-2015⁶⁷. This was resampled to the same projection as the range maps.
345 Species were scored as presence/absence within each cell (except for $1/2$ at the range boundaries), which is
346 generally justifiable for relatively homogeneous areas but it is increasingly problematic for more
347 heterogeneous areas. We therefore removed the cells with most variable NPP from the analysis.
348 Specifically we calculated the standard deviation of $\log_{10}(\text{NPP}(\text{g Carbon}/\text{m}^2/\text{yr})+1)$ within each cell and
349 excluded the upper 5% quantile of cells. Further we believe our estimates of mammal densities to be highly
350 inaccurate in low production areas and therefore removed them, which has also been done in similar
351 studies²¹. We defined low production as cells with $\text{NPP} < 200 \text{ g Carbon}/\text{m}^2/\text{yr}$, which is equivalent to most
352 ($3/4$ -quantile) of the WWF biome Deserts and Xeric Shrublands a balance between not removing too much or
353 too little.

354 Our estimates do not take the domestic mammals into account, or current modern land use. Therefore our
355 numbers are solely estimated densities that are not farmed or domestically grazed – or in other ways
356 influenced by human use. I.e. our current maps estimates densities in natural areas where population sizes
357 are at their natural equilibrium for the species still present in the areas. Further we assume that all species
358 occur across each full cell (except range edges where we assume 50%), and that they are not affected by
359 poorer habitat. Finally we note that we are only mapping species within their native ranges and e.g. does
360 not include the wild dromedaries in Australia⁶⁸ since no systematic range estimate is available mapping the
361 introduced ranges of all mammals.

362 To summarise our findings across the wildest remaining places on earth, we downloaded the ‘Last of the
363 Wild’^{37,50} dataset (Downloaded from <http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-last-of-the-wild-geographic>). This map was resampled and projected to match the maps from PHYLACINE 1.2, and
364 extracted to ecoregions and biomes c.f. WWF⁵¹. The map includes all the areas with a human footprint of
365 maximum 10 (out of 100)⁵⁰.

367

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374 We assembled data mostly from larger databases and it was therefore not possible to cite all the original
375 underlying studies, but we are grateful for all the preceding efforts in primary data collection and in data
376 integration and harmonization, which enabled us to carry out this study.

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524 [Supplementary materials overview](#)

525 [Appendices:](#)

526 Appendix S1: Imputation of density

527 Appendix S2: Imputation of metabolic rate

528 [Tables:](#)

529 Table S1a: Metabolic rate data. Column explanations.

Column name	Column explanation
Binomial.1.2	Phylacine Taxonomy
Order.1.2	Phylacine Taxonomy
Family.1.2	Phylacine Taxonomy
Binomial.Source	Binomial used in source
BM	Mass for measured individual in gram
MR	Metabolic rate kJ/day
log10BM	Log10 Mass for measured individual in gram
log10MR	Log10 Metabolic rate kJ/day
MR.type	Basal or field metabolic rate (BMR/FMR)
Source	Reference to source
Comment	Comment for single species sources

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531 Table S1b: Metabolic rate data.

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533 Table S2a: Imputed density. Column explanations.

Column name	Column explanation
Binomial.1.2	Phylacine Taxonomy
Order.1.2	Phylacine Taxonomy
Family.1.2	Phylacine Taxonomy
log10BM	Log10 Mass in gram
log10.density.median	Log10 Density median in individuals/km ²
log10.density.mean	Log10 Density mean in individuals/km ²
sd	Standard deviation density on log scale
log10.lower.95hpd	Lower confidence interval for 95% highest posterior distribution on log scale
log10.upper.95hpd	Upper confidence interval for 95% highest posterior distribution on log scale
density.median	Density median in individuals/km ² transformed from log
density.mean	Density mean in individuals/km ² transformed from log
lower.95hpd	Lower confidence interval for 95% highest posterior distribution transformed from log
upper.95hpd	Upper confidence interval for 95% highest posterior distribution transformed from log

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535 Table S2b: Imputed density.

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538 Table S3a: Imputed metabolic rate. All estimates are for the average species body mass from PHYLACINE.
539 Column explanations.

Column name	Column explanation
Binomial.1.2	Phylacine Taxonomy
Order.1.2	Phylacine Taxonomy
Family.1.2	Phylacine Taxonomy
log10BM	Log10 Mass in gram
log10.bmr.median	Log10 median basal metabolic rate in kJ/day
log10.bmr.mean	Log10 mean basal metabolic rate in kJ/day
sd.bmr	Standard deviation BMR on log scale
log10.bmr.lower.95hpd	Lower confidence interval for 95% highest posterior distribution BMR on log scale
log10.bmr.upper.95hpd	Upper confidence interval for 95% highest posterior distribution BMR on log scale
log10.fmr.median	Log10 median field metabolic rate in kJ/day
log10.fmr.mean	Log10 mean field metabolic rate in kJ/day
sd.fmr	Standard deviation FMR on log scale
log10.fmr.lower.95hpd	Lower confidence interval for 95% highest posterior distribution FMR on log scale
log10.fmr.upper.95hpd	Upper confidence interval for 95% highest posterior distribution FMR on log scale
bmr.median	Median basal metabolic rate in kJ/day
bmr.mean	Mean basal metabolic rate in kJ/day
bmr.lower.95hpd	Lower confidence interval for 95% highest posterior distribution BMR transformed from log
bmr.upper.95hpd	Upper confidence interval for 95% highest posterior distribution BMR transformed from log
fmr.median	Median field metabolic rate in kJ/day
fmr.mean	Mean field metabolic rate in kJ/day
fmr.lower.95hpd	Lower confidence interval for 95% highest posterior distribution FMR transformed from log
fmr.upper.95hpd	Upper confidence interval for 95% highest posterior distribution FMR transformed from log

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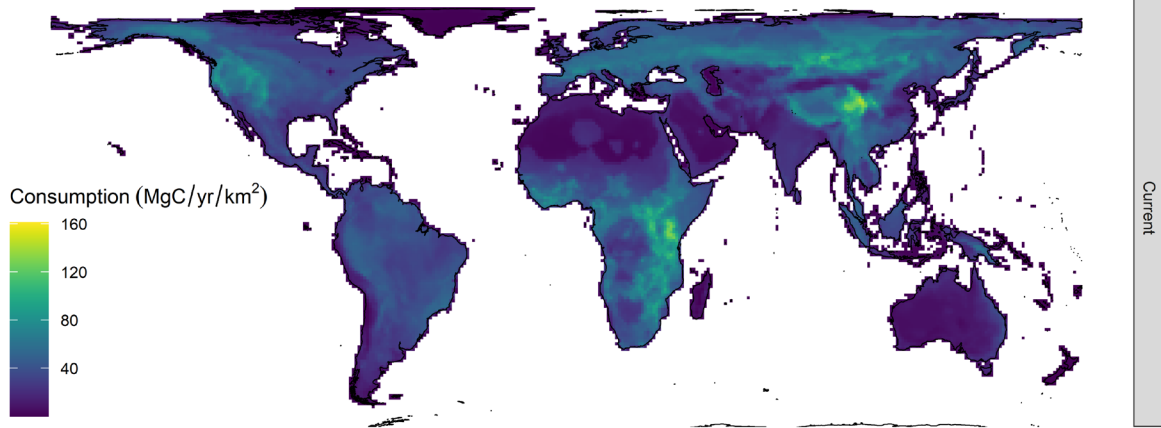
541 Table S3b: Imputed metabolic rate. All estimates are for the average species body mass from PHYLACINE.

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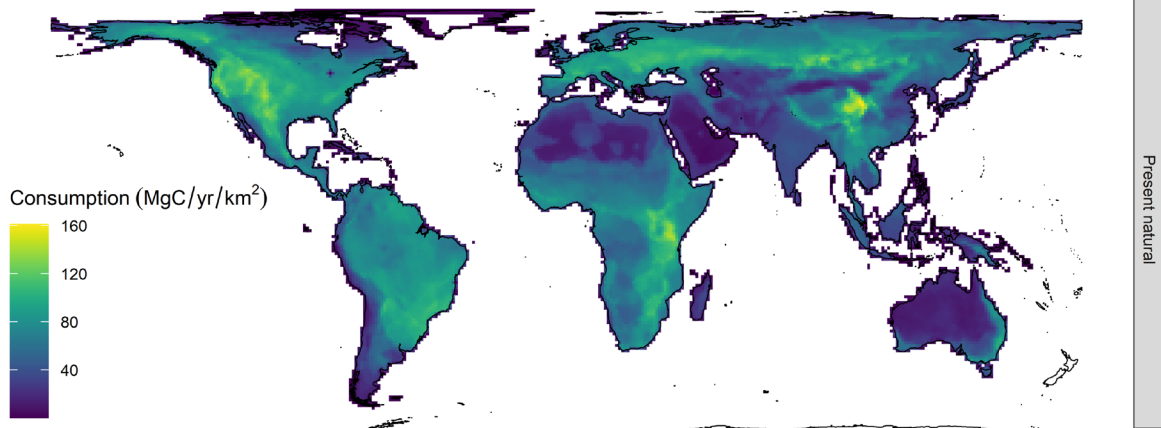
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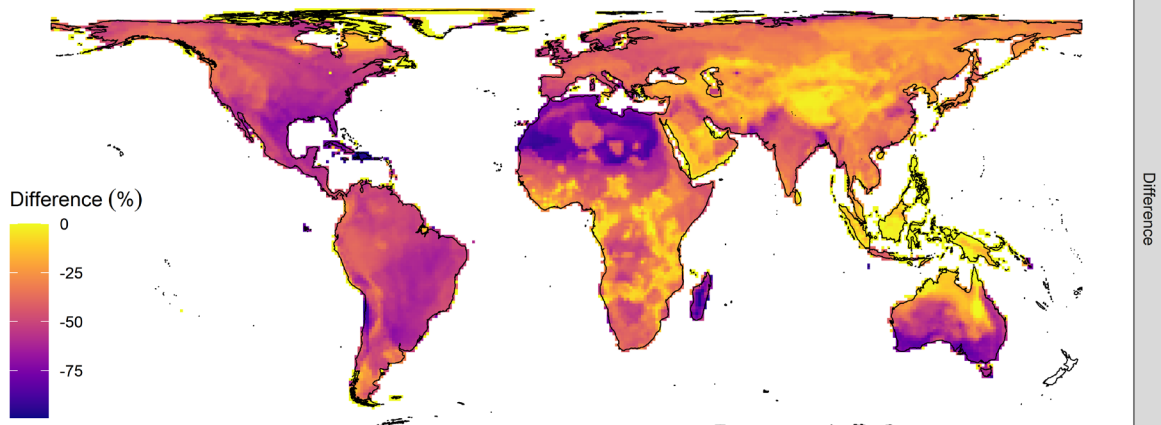
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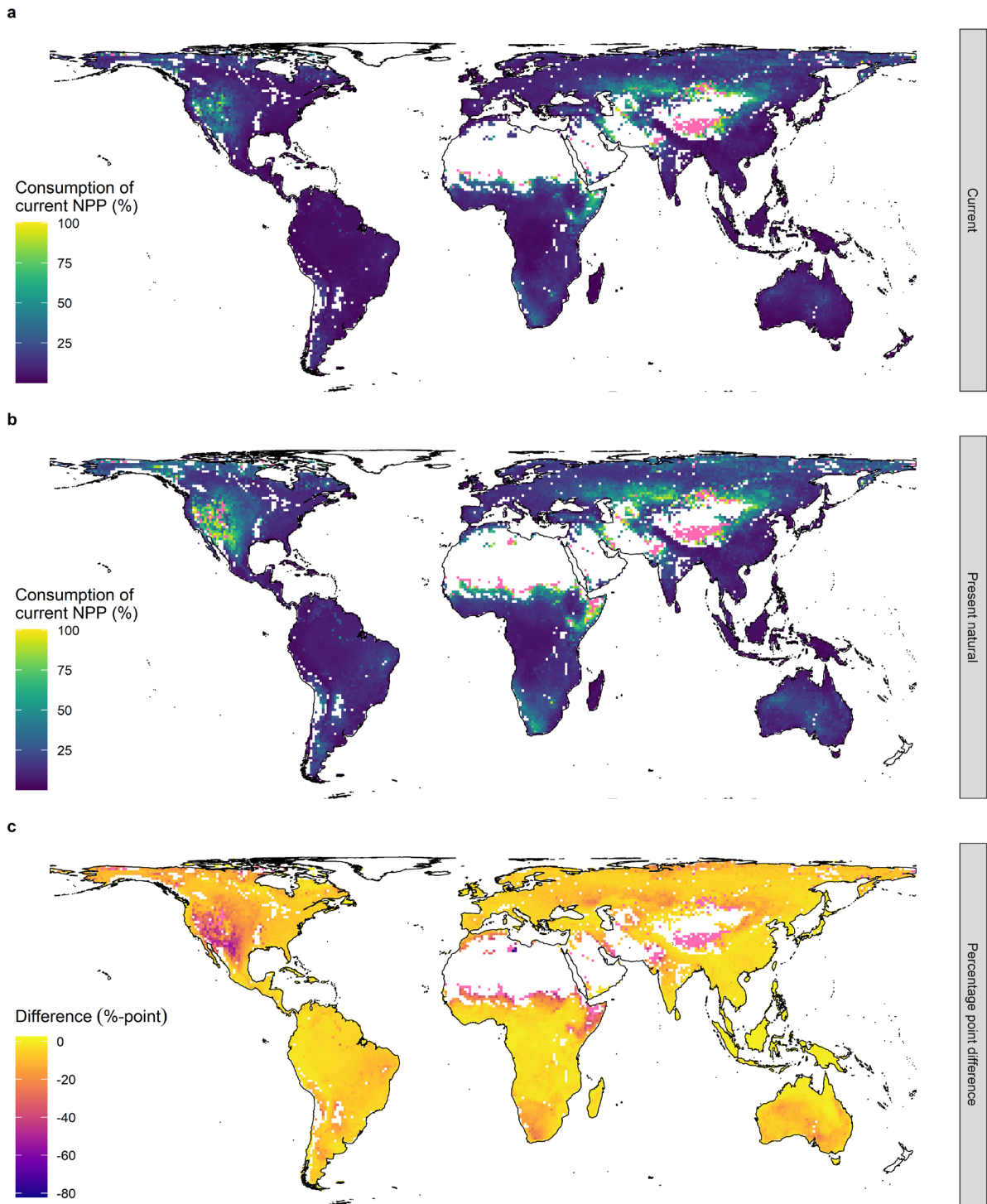
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546 **Fig S1:** Mammal consumption of plant carbon globally. Same as Fig 1, but no areas removed. a) Average terrestrial
547 mammal consumption by current mammals (current ranges of extant species). b) shows present natural consumption
548 (potential present day ranges with no human presence). c) shows the percentage lower consumption of current
549 ranges compared to present natural ranges.

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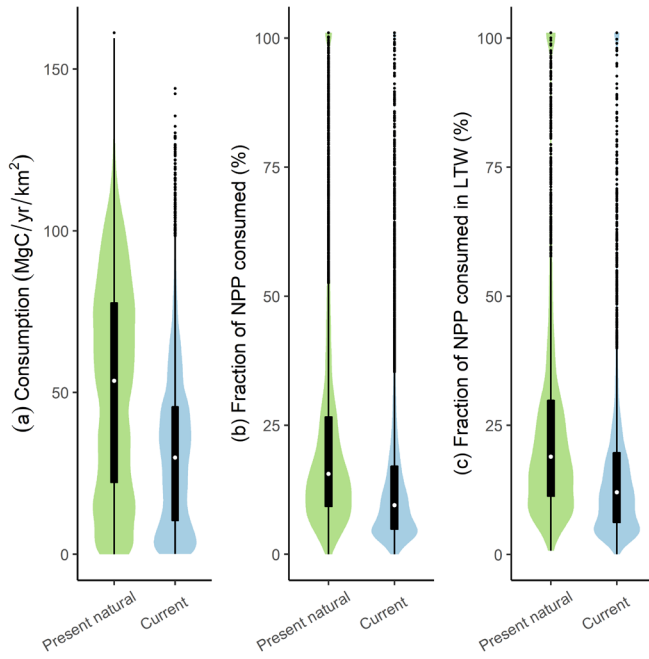


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552 **Fig S2:** Estimated mammal consumption of net primary productivity (NPP) globally. Same as Fig 2 but including the low
553 NPP areas where our model likely causes overestimations of densities. a) Consumption by current mammals (current
554 ranges of extant species). b) Present natural consumption (potential present day ranges with no human presence). c)
555 Percentage-point consumption difference between present natural and current consumption. Blank pixels are either
556 unknown or high variability in NPP and pixels in hot pink are where consumptions exceeds 100%.

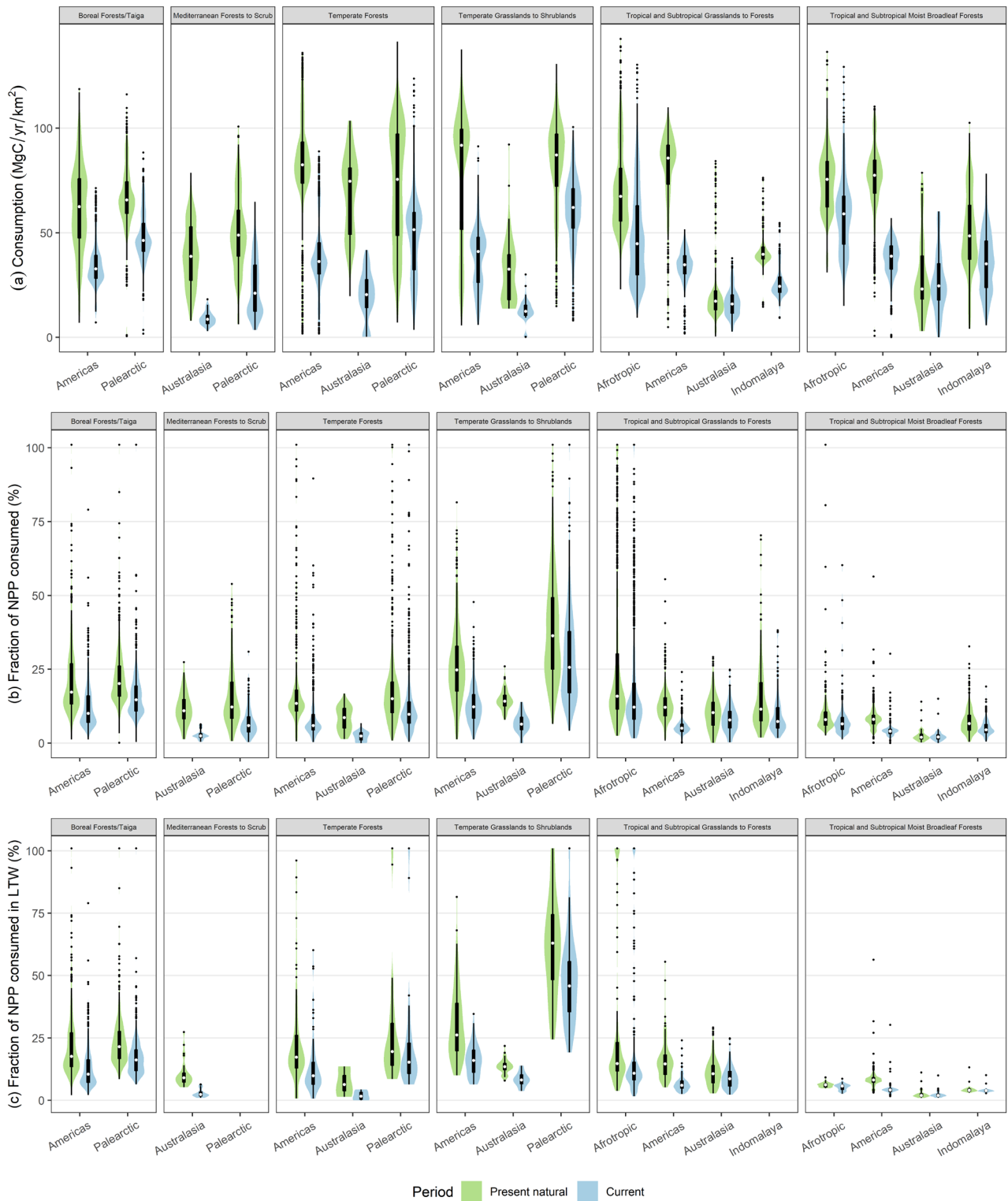
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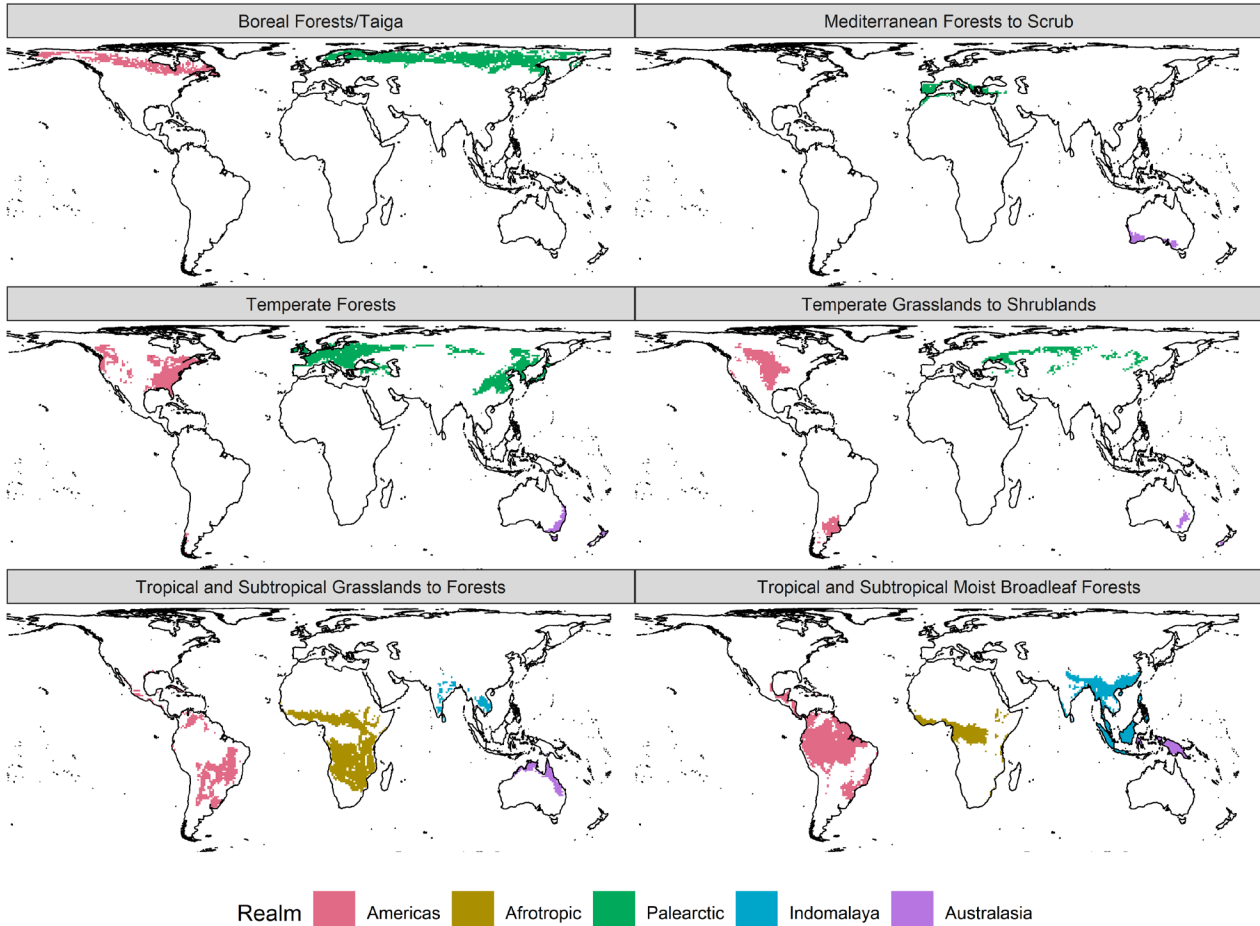
560 **Fig S3:** Global consumption summary. Same as Fig 3, but low NPP areas not removed. Boxplot with underlying violins
561 with kernel density scaled to width. **a)** Total consumption of carbon. **b)** Fraction of net primary productivity (NPP)
562 consumed. **c)** Fraction of net primary productivity (NPP) consumed in the areas designated as 'last of the wild'^{37,50}.
563 Values above 100% are truncated to 101%.



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Fig S4: Consumption summary for large ecological units based on realms and biomes⁵¹. Same as Fig 4, but low NPP areas not removed. Boxplot with underlying violins with kernel density scaled to width. Neotropics and Nearctic are merged to the Americas and Madagascar is excluded from the Afrotropics for biome modifications see Fig S5. **a)** Total consumption of carbon. **b)** Fraction of net primary productivity (NPP) consumed. **c)** Fraction of net primary productivity (NPP) consumed in the areas designated as 'last of the wild'^{37,50}. Values above 100% are truncated to 101%.

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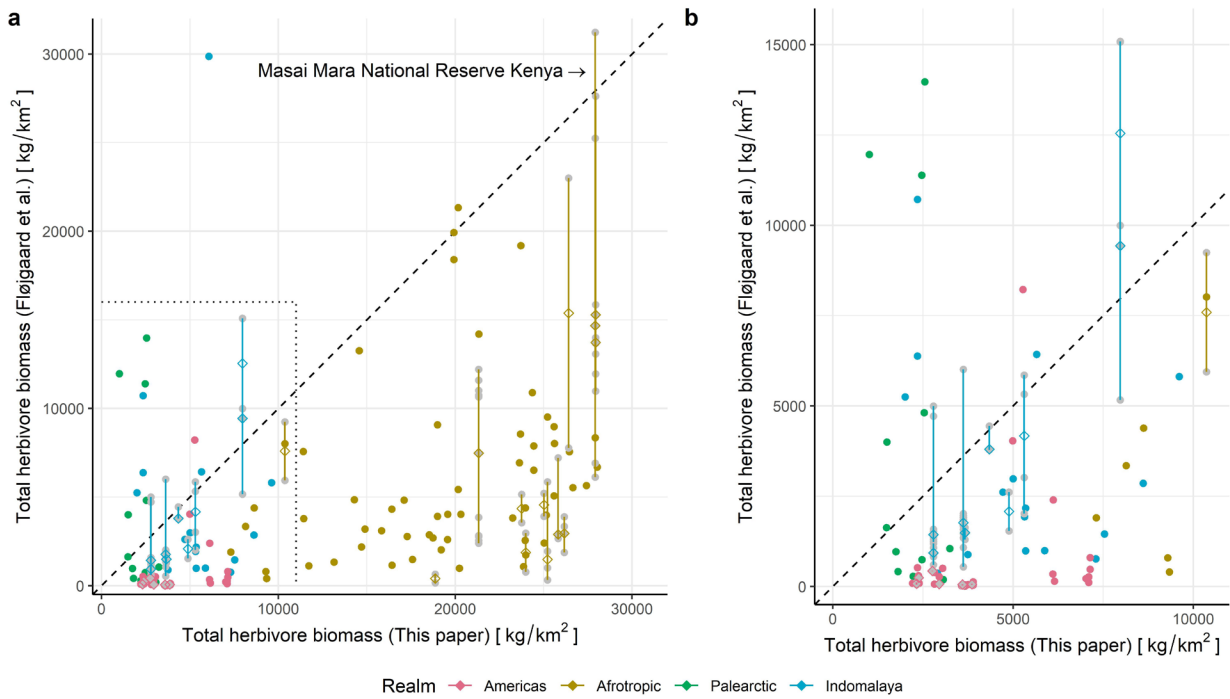
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Fig S5: Global ecological units based on realms and biomes⁵¹. Neotropics and Nearctic are merged in the Americas and Madagascar is excluded from the Afrotropics. “*Temperate Broadleaf and Mixed Forests*” and “*Temperate Coniferous Forests*” are merged to “*Temperate Forests*”. “*Tropical and Subtropical Dry Broadleaf Forests*” and “*Tropical and subtropical grasslands, savannas, and shrublands*” are merged to “*Tropical and Subtropical Grasslands to Forests*”. We changed the name of “*Temperate Grasslands, Savannas, and Shrublands*” to “*Temperate Grasslands to Shrublands*”, and changed “*Mediterranean Forests, Woodlands, and Scrub*” to “*Mediterranean Forests to Scrub*” for plotting purposes.



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Fig S6: Total current biomass in protected areas. Data of herbivore biomass estimates based on population counts from Fløjgaard et al.²⁴ mapped against this study's median results in the same areas (for their current fauna). (a) Is all global data and (b) is a zoomed region showing more detailed info outside the Afrotropics. Areas that have been estimated across several years are shown as line-ranges with median diamonds and grey points for yearly estimates. In areas where there are multiple estimates from Fløjgaard et al. we often see that our estimate is within the observed range. The Maasai Mara National Reserve in Kenya (line) have been highlighted as an example of an area with close to intact megafauna.