

1 Meta-analysis shows that wild large
2 herbivores shape ecosystem properties and
3 promote spatial heterogeneity

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32 Abstract

33 Megafauna (animals ≥ 45 kg) have likely shaped the Earth's terrestrial ecosystems for millions
34 of years with pronounced impacts on biogeochemistry, vegetation, ecological communities,
35 and evolutionary processes. However, a quantitative and global synthesis of megafauna effects
36 on ecosystems and their generality is lacking. Here, we conducted a meta-analysis on 297
37 studies and 5,990 individual observations across six continents to determine how wild
38 herbivorous megafauna influence ecosystem structure, ecological processes, and spatial
39 heterogeneity and whether these impacts depend on body size and environmental factors.
40 Despite large variability in megafauna effects, we show that megafauna significantly alter soil
41 nutrient availability, promote open vegetation structure, and reduce the abundance of smaller
42 animals. Other responses (14 out of 26), including soil respiration and soil carbon, were not
43 significantly affected. Further, megafauna significantly increase ecosystem heterogeneity by
44 affecting spatial heterogeneity in vegetation structure and the abundance and diversity of
45 smaller animals. Given that spatial heterogeneity is considered an important driver of
46 biodiversity across taxonomic groups and scales, these results support the hypothesis that
47 megafauna may promote biodiversity at large scales. Megafauna declined precipitously in
48 diversity and abundance since the Late Pleistocene, and our results indicate that their
49 restoration would substantially influence Earth's terrestrial ecosystems.

50 Main text

51 Large mammalian herbivores (≥ 45 kg body mass^{1,2}, henceforth megafauna) have shaped
52 Earth's ecosystems for more than 35 million years^{3,4}. However, in the Late Pleistocene and
53 Early Holocene (50,000 - 7,000 years ago), terrestrial megafauna suffered a global wave of
54 declines and extinctions, strongly linked to the worldwide expansion of humans⁵⁻⁸. These
55 extinctions led to extreme global body size downgrading to levels not seen since the extinction
56 of dinosaurs 66 million years ago⁴ with profound consequences for ecosystem processes^{3,9-11}.

57
58 Megafauna are considered disproportionately important for biosphere functioning, because of
59 their ability to access resources that are not available to smaller consumers, to digest high
60 amounts of low-quality biomass, to shape fire dynamics and to move over very large
61 distances¹²⁻¹⁴. This enables large animals to increase nutrient cycling, contribute to seed and
62 nutrient dispersal¹⁵, and reshape vegetation^{13,16} with direct and indirect effects on soil
63 properties and processes^{17,18}, plant diversity, productivity and structure^{12,19} and animal
64 abundance and diversity^{20,21}. These effects are predicted to be modulated by body size^{22,23} and
65 environmental conditions such as nutrient availability²⁴ and productivity^{14,25}.

66
67 One of the key hypothesized impacts of megafauna is the promotion of ecosystem
68 heterogeneity²⁶, for example by creating local nutrient hotspots^{16,27} and heterogeneity in
69 vegetation structure through physical disturbance²⁸. This can translate to increased diversity of
70 vegetation types on landscape scales¹². In general, biodiversity increases with environmental
71 heterogeneity across spatial scales, biomes and taxonomic groups²⁹, both by increasing
72 available niche space (allowing more species to coexist) and by promoting species persistence
73 via the provision of refuges during environmental fluctuations²⁹⁻³¹. By preventing one or a few
74 species from dominating³² and therefore enabling species with similar ecological attributes to
75 coexist in the same ecosystem, this heterogeneity may also lead to functional redundancies and
76 thus promote ecosystem resilience³³⁻³⁵.

77
78 Although there is strong case-specific evidence and conceptual expectations that large
79 herbivores influence soil properties, vegetation community and structure and other animal¹²⁻
80 ¹⁴, a formal quantitative test for the generality of these impacts across ecosystems and
81 taxonomic groups is lacking¹⁴. As megafauna are particularly affected by past, current and
82 potential future defaunation⁹, addressing this knowledge gap is important.

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Using a meta-analytic approach, we compiled and analyzed an extensive global database to quantify the effects of megafauna on ecosystems. Further, we employed a meta-analytic effect size measure that allows estimation of effects on variability, to test their effect on the heterogeneity within each ecosystem response³⁶.

Specifically, we sought to investigate the effect of large mammalian herbivores on the diversity and abundance of different taxa (plants, birds, small mammals, invertebrates), vegetation structure and nutrient concentrations, soil nutrients and properties and biogeochemical processes. Moreover, we tested if megafauna promote spatial heterogeneity in these ecosystem responses and if these effects vary predictably with herbivore body mass and environmental covariates.

97 Results

98 We conducted a systematic literature search to find studies investigating the impact of wild
99 large mammalian herbivores on ecosystems. Studies included contrasts in megafauna density
100 and megafauna presence/absence, with >89 % being exclosure experiments (Fig. S1).
101 Comparisons of areas with high and low megafauna density were only included if those areas
102 were adjacent and were the result of management decisions (e.g., a hunting area vs a protected
103 area). Herbivore effects were calculated as standardized mean difference (Hedges' g) while
104 within-treatment heterogeneity was estimated using the log-ratio between two coefficients of
105 variation ($\ln\text{CVR}$)³⁶. The final dataset consisted of 5,990 data points from 297 studies (each
106 representing, for example, one comparison between an exclosure and control) representing 26
107 ecosystem responses (Table S1, Table S2). The dataset was geographically biased towards
108 Europe, North America, South Africa, and Australia (Fig. S2, Fig. S3), towards the Afrotropics
109 (Fig. S4A) and temperate forests (Fig. S4C), and against areas with low temperatures and/or
110 high precipitation (Fig. S4B).

111 The median area of measurement (i.e., plot size) was 1 m² [95% CI: 0.002 - 25,000 m²]
112 (Fig. S5A), the median treatment duration was 2190 days [95% CI: 365 - 21,900 days] (Fig
113 S5B), the median number of data points per study was 11 [95% CI: 1 - 97] and the median
114 number of studies per response was 15 [95% CI: 6 - 108].

115 Effects of herbivorous megafauna

116 We used random effects meta-analytic models³⁷ to investigate the overall effect of megafauna
117 on 26 different ecosystem responses and their heterogeneity. Despite high variability in the
118 effects of megafauna, we found a significant impact on 50% of the investigated responses. If
119 not stated otherwise, these are the ones presented in the results.

120 Effects on soil

121 Megafauna moderately decreased soil labile phosphorous (P) (Hedges' g of 0.2 can be
122 interpreted as small effect, 0.4 as medium effect and ≥ 0.8 as large effect³⁸; Fig. 1A, Fig 2A,
123 Table 1). Megafauna also slightly increased soil compaction and strongly increased bare
124 ground cover while strongly decreasing litter cover (Fig. 1A, Fig 2A, Table 1). Megafauna
125 decreased heterogeneity in bare ground cover (Fig. 1B, Fig 2B, Table 1).

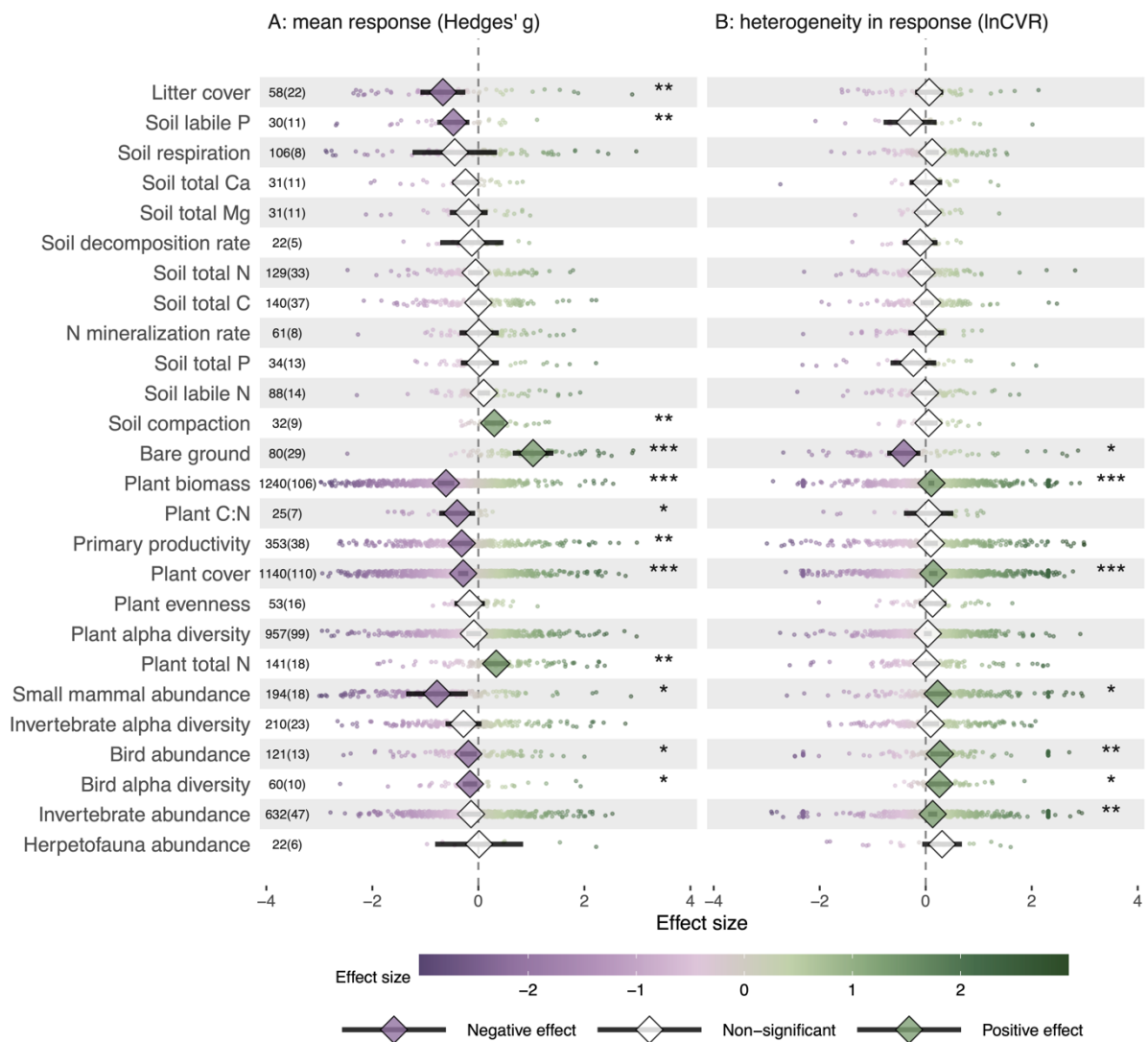
126 Effect on vegetation

127 Megafauna had moderate positive effects on plant nitrogen (N) content (Fig. 1A, Fig 2, Table
 128 1), moderately reducing plant carbon (C):N ratios (Fig. 1A, Fig 2, Table 1). Moreover, they
 129 moderately reduced plant cover and plant biomass and slightly reduced primary productivity
 130 (Fig. 1A, Fig 2A, Table 1). Further, megafauna increased heterogeneity in plant cover and plant
 131 biomass (Fig. 1B, Fig 2B, Table 1).

132 Effect on other animals

133 Megafauna strongly reduced the abundance of small mammals and had weak negative effects
 134 on bird alpha diversity and abundance (Fig. 1A, Fig 2A, Table 1). They also increased
 135 heterogeneity in the abundance of small mammals, invertebrates, and birds, as well as in bird
 136 alpha diversity (Fig. 1B, Fig 2B, Table 1).

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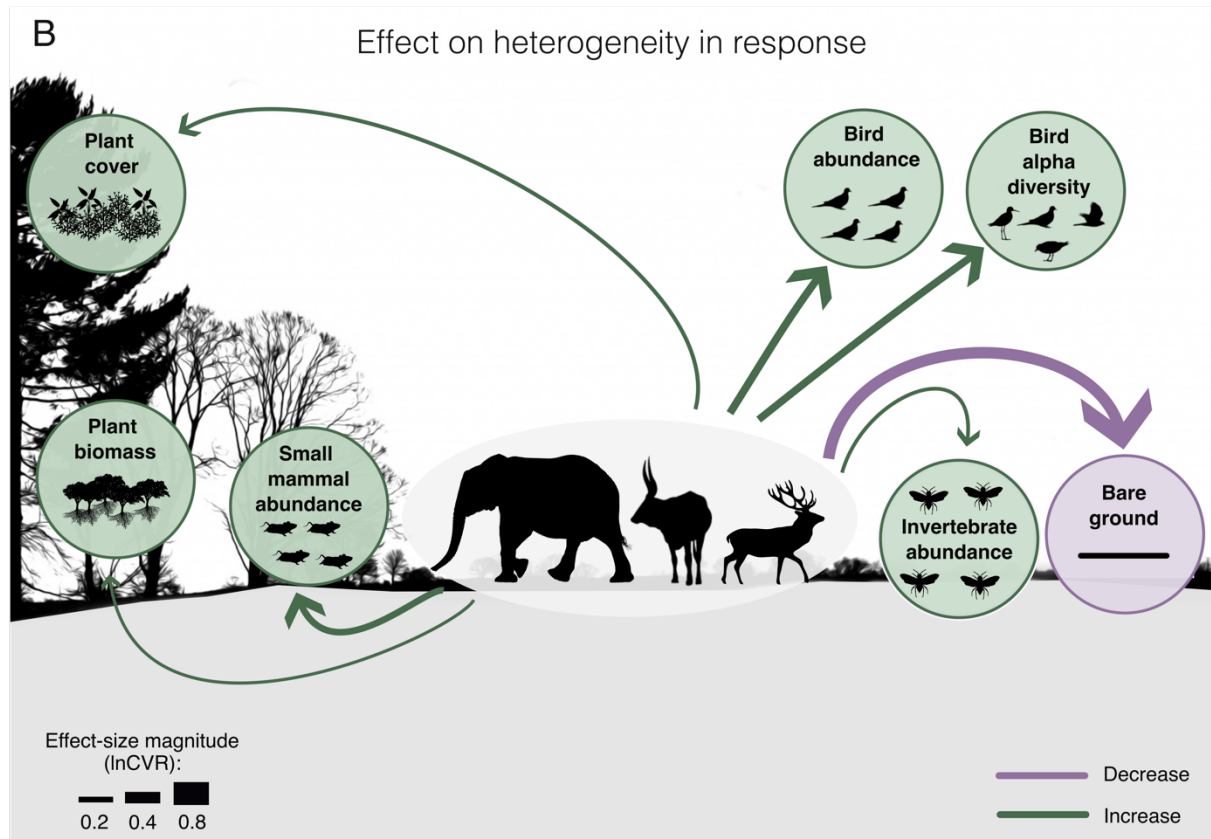
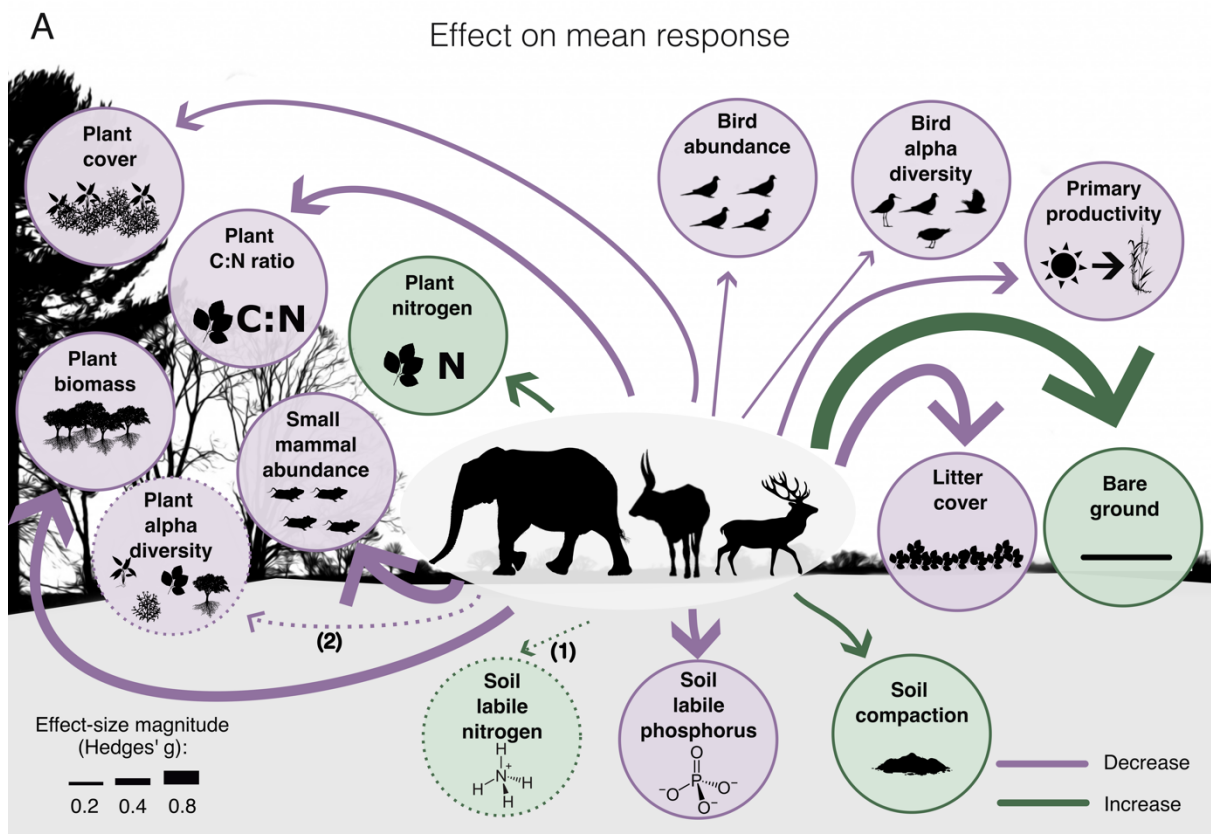


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139 **Fig. 1 Effects of herbivorous megafauna on mean ecosystem responses and heterogeneity**
140 **within these responses.** Model estimates (\pm 95% confidence intervals) for the different
141 response categories, derived from random-effects meta-analytic models³⁷; see methods for
142 details. Purple symbols indicate a significant negative impact, green symbols a significant
143 positive impact, and white symbols a non-significant impact of large herbivores. Stars indicate
144 different significance thresholds: * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$. Each point in the
145 background indicates a data point (i.e., a pairwise comparison in a study such as enclosure vs
146 control) used in the analysis of the respective response. The numbers after each label on the y
147 axis provide information about the sample size of the measured response: number of data points
148 (number of studies). **A:** effect on mean response (Hedges g); **B:** effect on heterogeneity in
149 response (lnCVR).
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152 Notable null results

153 We found no significant mean effect of megafauna on the 14 of 26 tested responses, and on
154 the heterogeneity of 19 tested responses ([min, max]: Hedges' g =[-0.27, 0.14], lnCVR=[-0.23,
155 0.23], p =[0.06, 0.96], Fig. 1). Among the more notable responses for which we detected no
156 statistically significant effect on the overall mean response (but see Fig. 2a and *Results:*
157 *Influence of body mass and environmental variables on megafauna impacts*) were total and
158 labile soil N and N mineralization rate, soil total C, and plant alpha diversity and evenness.



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Fig. 2. Impacts of herbivorous megafauna on different ecosystem responses and their heterogeneity. Shown here are the statistically significant impacts of megafauna. All tested responses and their estimates can be found in Fig. 1. Numeric results of the significant models

163 can be found in Table 2. Green indicates an increase and violet a decrease of the mean response
 164 or the heterogeneity in the response; arrow widths are scaled by effect-size magnitude. Note
 165 that **(1)** the positive effect on soil labile N is only significant in megafauna communities with
 166 species ≥ 100 kg body mass (Fig. S7) and **(2)** the negative effect in plant alpha diversity is
 167 only significant in megafauna communities without species ≥ 100 kg body mass (Fig. S7).
 168 As a rule of thumb, a hedges' g of 0.2 can be interpreted as small effect, 0.4 as medium effect
 169 and 0.8 as large effect³⁸. **A:** Mean effect of megafauna herbivores on ecosystem responses. **B:**
 170 Effect of megafauna herbivores on spatial heterogeneity in these ecosystems.

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173 **Table 1: Results of significant models.** Model estimates (\pm 95% confidence intervals) for the
 174 different significant response categories, derived from random-effects meta-analytic models³⁷.
 175 Here we used intercept only models which provide a mean estimate of the effect size weighted
 176 by the inverse of the sampling variance and under consideration of the included random
 177 structure (see method for details). The effect size type 'Hedges g' refers to the standardized
 178 mean difference between low and high megafauna herbivore density (or presence/absence)
 179 while lnCVR quantifies differences in spatial heterogeneity. CI = 95 % confidence interval

| Measured response | Effect size type | Estimate | Lower CI | Upper CI | p value |
|------------------------|------------------|----------|----------|----------|----------|
| Litter cover | Hedges g | -0.67 | -1.10 | -0.25 | 0.004 |
| Soil labile P | Hedges g | -0.47 | -0.78 | -0.17 | 0.006 |
| Soil compaction | Hedges g | 0.30 | 0.11 | 0.49 | 0.006 |
| Bare ground | Hedges g | 1.03 | 0.65 | 1.41 | <0.0001 |
| Bare ground | lnCVR | -0.41 | -0.73 | -0.10 | 0.01 |
| Plant biomass | Hedges g | -0.61 | -0.77 | -0.45 | 0.0001 |
| Plant C:N | Hedges g | -0.40 | -0.73 | -0.06 | 0.0002 |
| Primary productivity | Hedges g | -0.31 | -0.51 | -0.11 | 0.003 |
| Plant cover | Hedges g | -0.29 | -0.38 | -0.19 | < 0.0001 |
| Plant total N | Hedges g | 0.34 | 0.11 | 0.56 | 0.0005 |
| Plant biomass | lnCVR | 0.11 | 0.05 | 0.16 | 0.0002 |
| Plant cover | lnCVR | 0.14 | 0.06 | 0.22 | 0.0001 |
| Small mammal abundance | Hedges g | -0.78 | -1.36 | -0.19 | 0.01 |
| Bird alpha diversity | Hedges g | -0.15 | -0.29 | -0.02 | 0.03 |
| Small mammal abundance | lnCVR | 0.23 | 0.02 | 0.43 | 0.03 |
| Bird abundance | Hedges g | -0.19 | -0.35 | -0.03 | 0.02 |
| Bird alpha diversity | Hedges g | -0.16 | -0.30 | -0.02 | 0.03 |
| Bird abundance | lnCVR | 0.27 | 0.08 | 0.45 | 0.008 |
| Bird alpha diversity | lnCVR | 0.26 | 0.05 | 0.47 | 0.02 |
| Invertebrate abundance | lnCVR | 0.13 | 0.05 | 0.2 | 0.003 |

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181 **Influence of body mass and environmental variables**

182 The effects of megafauna are predicted to be dependent on body size^{22,23} and environmental
183 conditions such as nutrient availability²⁴ and productivity²⁵. Therefore, we added body mass
184 (both mean and maximum body size of the community, weighted by relative biomass per
185 species for responses with sufficient sample size (>10 studies); see methods for details) and a
186 variety of environmental factors (Table S3) as variables to our models. We added each
187 covariate as a single variable and compared the single-term model to its intercept only model,
188 using a likelihood ratio test (LRT). If the covariate significantly improved model quality, we
189 considered it as explaining some of the variability in the effects of megafauna. Moreover, for
190 those responses with sufficient sample size, we divided our data in communities including
191 megaherbivores (≥ 1000 kg) vs communities without megaherbivores (Fig. S6) and
192 communities including herbivores ≥ 100 kg vs without those species (Fig. S7) and analyzed
193 their impact separately.

194 **Body mass**

195 Larger-bodied megafauna communities were more likely to increase heterogeneity in total soil
196 N (Fig 3A, Table 2). In this case, the body mass variable here reflects the body size of the
197 biggest animal in the community (i.e., not weighted by relative biomass). Megafauna
198 communities comprising larger-bodied species (body mass weighted by relative biomass per
199 species) were also more likely to increase plant alpha diversity (Fig. 3B, Table 2). None of the
200 other tested effects on ecosystem responses were significantly affected by megafauna body
201 mass (Likelihood ratio test [LRT]=[0.00, 5.97], p =[0.10, 0.99]).

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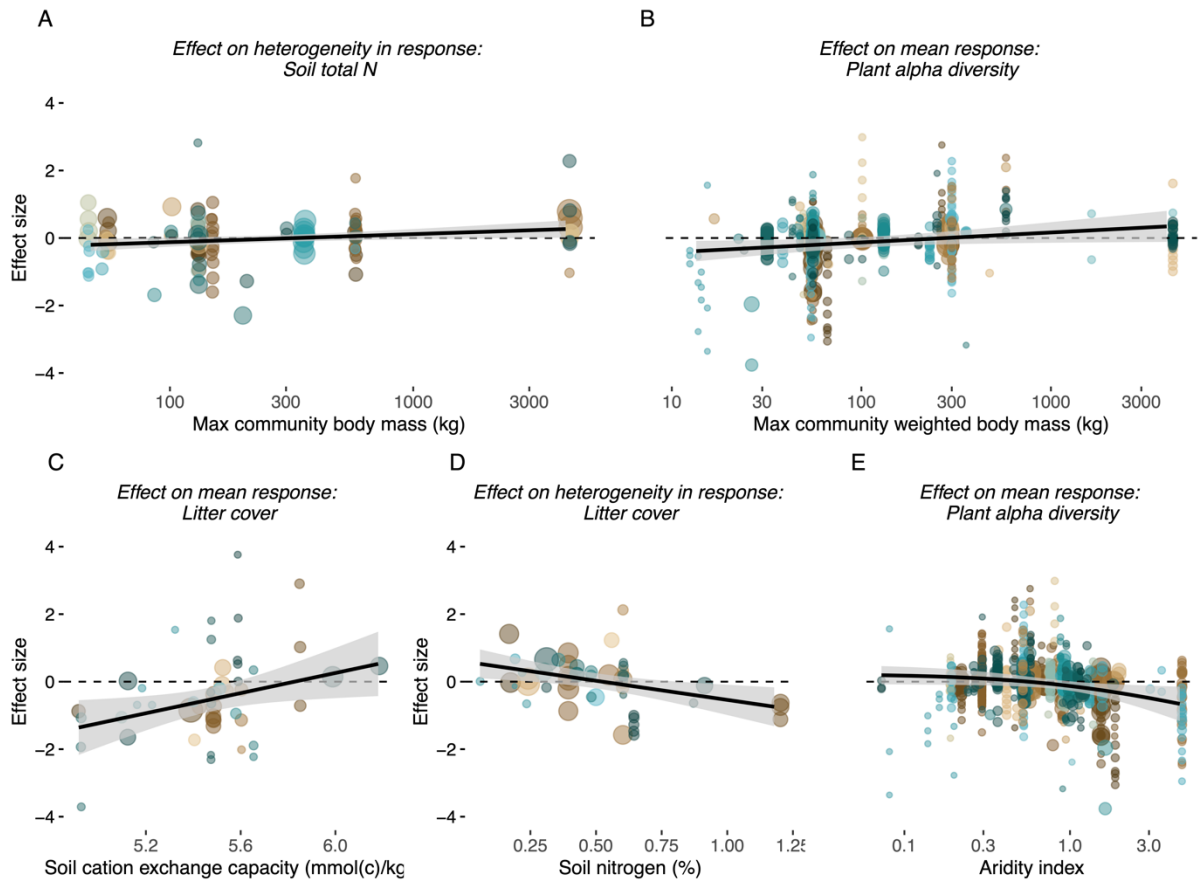
203 Moreover, megafauna communities that included herbivores ≥ 100 kg significantly increased
204 soil labile N (Fig. S7) and communities without herbivores ≥ 100 kg significantly decreased
205 plant alpha diversity (Fig. S7).

206 **Environmental covariates**

207 Negative effects on litter cover were observed mainly in soils with lower cation exchange
208 capacity (Fig 3C, Table 2), while positive effects on heterogeneity in litter cover occurred
209 more frequently in soils with lower nitrogen content (Fig 3D, Table 2).

210

211 The response of plant alpha diversity was slightly more negative in more humid areas (Fig. 3E,
 212 Table 2). None of the other tested effects on ecosystem responses was significantly affected by
 213 our environmental covariates (Likelihood ratio test [LRT]=[0.00, 3.76], p =[0.06, 1.00]).
 214



215
 216 **Fig. 3 Predictions of significant covariates** Estimates (\pm confidence intervals) of covariates
 217 which are significantly improving model quality. Different point colors and shades indicate
 218 different studies. Point size is determined by $1/\text{sampling variance}$ to indicate its weight in the
 219 model. All explanatory variables are log transformed and scaled. **A.** Impact of megafauna
 220 herbivore body mass on the extent to which herbivores influence the spatial heterogeneity of
 221 soil total N. Note that body size in this case is not community weighted to maintain a sample
 222 size > 10 studies; **B.** Impact of community-weighted megafauna herbivore body mass on the
 223 effect of megafauna herbivores on plant diversity. **C.** Impact of soil cation exchange capacity
 224 on megafauna herbivores' effects on litter cover (however, we note that the used soil covariates
 225 represent regional averages rather than fine scaled gradients in soil properties); **D.** Impact of
 226 soil nitrogen content on the effect of megafauna herbivores on heterogeneity in litter cover; **E.**
 227 Impact of aridity on the effect of megafauna herbivores on plant diversity. Note that a smaller
 228 aridity index indicates arid systems while a higher aridity index indicates more humid systems.
 229 We fitted all models in a linear framework, however, when plotting the back-transformed
 230 predictions the relationship may appear non-linear.
 231

232 **Table 2: Model results of significant covariates.** The p-value here refers to the likelihood
 233 ratio test which compares the null model with the univariate model in terms of model quality
 234 (i.e., explanatory power). $p < 0.05$ indicates significant improvement of the assembly model
 235 compared to the intercept only null model; test is one-sided. CI = 95 % Confidence interval.

| Measured response | Effect size type | Tested covariate | Estimate | Lower CI | Upper CI | LRT | p value |
|--|------------------|-------------------------------|----------|----------|----------|------|---------|
| Influence of body mass | | | | | | | |
| Soil total N | lnCVR | Body mass | 0.13 | -0.03 | -0.23 | 5.40 | 0.02 |
| Plant alpha diversity | Hedges g | Weighted body mass | 0.14 | 0.01 | 0.29 | 4.30 | 0.04 |
| Influence of environmental covariates | | | | | | | |
| Litter cover | Hedges g | Soil cation exchange capacity | 0.40 | 0.07 | 0.72 | 5.20 | 0.02 |
| Litter cover | lnCVR | Soil nitrogen content | -0.29 | -0.49 | -0.09 | 6.42 | 0.01 |
| Plant alpha diversity | Hedges g | Aridity index | -0.18 | -0.33 | -0.03 | 5.10 | 0.02 |

236

237 Discussion

238 Our meta-analysis of 297 studies across six continents shows that herbivorous megafauna
 239 shape ecosystems by affecting ecosystem properties and processes across trophic levels and by
 240 increasing ecosystem heterogeneity. We confirmed that body size influenced megafauna
 241 effects on soil labile N and plant alpha diversity, but that the effect was relatively small and
 242 variable. Some environmental factors¹⁴ modulated megafauna effects on ecosystem responses
 243 such as plant alpha diversity, and litter cover, whereas we found no evidence for others.
 244 Interestingly, and contrary to former meta-analysis and theory^{39,40}, we did not find NPP to
 245 explain variation in the effects of megafauna on any tested response. While some responses
 246 had clear and generalizable patterns (e.g., the decrease in soil labile P and plant biomass), we
 247 found large variability in others (e.g., invertebrate abundance and soil total C).

248

249 Of the 13 soil responses, four were significantly affected by megafauna. Notably, megafauna
 250 did not alter the absolute amount of soil C, P and N, but rather the bioavailable forms of N and
 251 P (sample size was insufficient to include labile C). Herbivores larger than 100 kg tended to
 252 increase the amount of available nitrogen. At the same time, megafauna in general tended to
 253 decrease labile P, supporting suggestions that megafauna may push systems towards a higher
 254 degree of P-limitation⁴¹. While the increase of N-availability may be explained by megafauna

255 accessing N otherwise locked away in plant biomass and providing it in bioavailable forms via
256 excreta⁴², P may be stored away in skeletons for longer periods⁴¹. Alternatively, the increased
257 availability of soil labile N may stimulate plant growth until P becomes limiting^{43,44} with the
258 consequence that more available P may be stored in vegetation compared to soils not affected
259 by megafauna.

260

261 Of the seven plant responses, five were significantly impacted. Megafauna increased plant
262 nitrogen content, which could be driven by a combination of elevated soil nitrogen availability
263 from direct megafauna inputs and reduced C:N ratios in young (regrowing) plant tissue^{45,46}
264 (e.g., less “dilution” by structural carbon). Higher plant nitrogen content should have various
265 ecosystem consequences, e.g., by increasing litter quality⁴⁷ or favoring phytophagous insects⁴⁸
266 and their associated food webs (although we detected no general effect on invertebrate
267 abundance or diversity).

268

269 Megafauna significantly and strongly decreased plant biomass and cover, litter cover while
270 increasing bare ground cover. These effects are expected through biomass consumption,
271 trampling and wallowing^{49,50}. The increase in bare soil may result in increased day-time soil
272 temperature and reduced moisture due to increased exposure to solar radiation and increased
273 runoff⁵¹, which may have cascading consequences on other soil properties. However, despite
274 the changes in organic matter (i.e., reduced quantity of biomass, increased quality of litter) and
275 increased soil compaction, we did not find consistent changes in bulk soil C, or soil
276 decomposition and respiration, which is in line with previous meta-analyses^{52,53}.

277

278 Our results confirm the ability of megafauna to promote open and semi-open habitats at the
279 plot scale by decreasing plant biomass and cover^{12,14,54}. Moreover, megafauna increased
280 heterogeneity in vegetation structure between plots, which suggests that megafauna increase
281 vegetation structural diversity also on the landscape scale. However, most enclosure
282 experiments, and vegetation sampling methods, are too small to quantify megafauna impacts
283 at larger spatial scales directly.

284

285 Overall, megafauna significantly decreased primary productivity. However, this result is
286 difficult to interpret since variables used to quantify NPP vary widely among studies. One
287 possible reason may be that plants might shift some of their productivity belowground,
288 resulting in e.g., increased fine root biomass and root exudation (which may ultimately

289 contribute to the accumulation of persistent soil organic matter¹⁷), highlighting the need for
290 more research on the below-ground impacts of large animals.

291

292 Consistent with previous work^{14,54}, the overall effect of megafauna—from deer to elephants—
293 on plant alpha diversity was non-significant. However, we found that smaller-bodied (i.e.,
294 < 100 kg) megafauna communities tended to have more negative effects on plant alpha
295 diversity while larger-bodied herbivore communities tended to have slight positive effects. This
296 could be because larger animals can eat lower-quality food^{55,56} such as branches and stems,
297 which may result in proportionally greater impacts on dominant plant species and thus release
298 less competitive plants from competition^{25,57}. The negative effect of smaller megafauna may
299 reflect lack of predation pressure due to anthropogenic predator-removal⁵⁸, which allows
300 smaller species to access more risky habitats. Furthermore, the differential impact of
301 megafauna of different size classes supports the principle that smaller herbivores cannot
302 substitute for larger megafauna¹⁴ and suggests that the anthropogenically simplified and
303 smaller-bodied herbivore communities^{59,60} currently found in large parts of the world lack
304 important functions.

305

306 Megafauna effects on other animals were measured using six variables, of which four were
307 significantly impacted. Consistent with previous work, megafauna strongly reduced the
308 abundances of small mammals (i.e., rodents)¹⁴ at small scales, but simultaneously increased
309 heterogeneity in this response. A decrease in small mammals in the presence of megafauna
310 might in part be due to lower vegetation cover or trampling of burrows, although evidence
311 suggests that feeding competition is the main mechanism of control²⁰. A reduction of
312 competition and increase of vegetation cover in exclosures may also lead smaller consumers to
313 actively move into these relatively small patches that now provide habitat of a higher quality
314 (greater cover from predators, more food abundance) for smaller consumers compared to the
315 surroundings⁶¹. These larger numbers of smaller animals may in turn have knock-on effects on
316 the rest of the system, e.g., by affecting plant species whose seeds are eaten primarily by
317 rodents, resulting in lower recruitment than in areas with large herbivores²⁰.

318

319 The decrease of bird alpha diversity and abundance could potentially be explained by
320 decreasing nesting spaces on small scales and may seem counterintuitive as both bird
321 abundance and diversity are known to increase with increasing habitat heterogeneity⁶², for
322 which we also find evidence. However, the exact shape of heterogeneity-diversity relationships

323 can differ between taxonomic groups, trophic levels and across scales⁶³ and depends on other
324 factors such as resource availability and environmental conditions⁶⁴ This suggests that the
325 megafauna-induced increases in heterogeneity may lead to non-linear effects on bird
326 abundance and diversity. Additionally, the effect of megafauna on the abundance and diversity
327 of birds is most likely to be positive at intermediate disturbance levels but can be negative at
328 higher levels⁶⁵. However, more research is needed to disentangle the relationship between
329 increased heterogeneity and decreased bird alpha diversity such as found here.

330

331 A key outcome of our study is the demonstration of pervasive positive impacts of megafauna
332 on heterogeneity (not consistently statistically significant, but almost never significantly
333 negative; Fig. 1b). By increasing heterogeneity in vegetation structure, for example, megafauna
334 may increase the amount of available habitat types and structural complexity, allowing more
335 species to coexist⁶⁶. Given that heterogeneity is known as a key driver of biodiversity across
336 scales and taxonomic groups^{29,35,67}, megafauna have the potential to contribute diversity at
337 larger scales. Moreover, increased heterogeneity in vegetation structure may also lead to
338 microclimatic variation which has also been shown to be an important driver of community
339 functional diversity⁶⁸. Therefore, it has been suggested that small-scale environmental
340 heterogeneity (such as studied here) is a strong predictor of functional diversity⁶⁸. Previous
341 work has also shown that megafauna may prevent one or a few species from dominating all
342 available niches within its ecological range and thus allow different species with both similar
343 and different ecological roles to coexist^{29,32}. Hence, megafauna could contribute to the
344 establishment of functional redundancies in ecological roles and subsequently to ecosystem
345 resilience^{35,69}. This becomes particularly important as ecosystem heterogeneity has been shown
346 to increase the adaptive capacity of ecosystems to respond to climate change³⁵.

347 **Limitations and recommendations for future studies**

348 Small plot sizes in exclosure experiments along with the spatial scale at which responses were
349 measured are a major limitation to unraveling megafauna impacts at larger scales. Additionally,
350 we found significant signs of publication bias in the studies analyzed here (Fig. S8, Table S4)
351 and spatial bias towards better-funded and researched parts of the world^{64,70} (Fig. 4, Fig. S2-
352 S4), which may hamper generalisations⁷¹. Despite these biases, our results are in line with
353 theory and recent reviews^{13,14} (which likely suffer from the same biases). Although it is
354 plausible that some of the observed effects on megafauna translate to larger spatial scales -
355 such as the positive effects on heterogeneity - the results presented here only provide reliable

356 information about effects at the plot scale. Consequently, studying the impact of megafauna on
357 ecosystems at larger scales (i.e., landscape scale and larger) is a major challenge and will
358 contribute significantly to our understanding of megafauna effects. Since setting up
359 experiments on landscape scales is challenging, better use of natural experiments and
360 counterfactuals and available landscape-extent data (e.g., from remote sensing⁷²), will be key
361 avenues in further quantifying the role of megafauna in the Earth system.

362

363 Despite testing a broad range of environmental covariates and megafauna body size, a large
364 amount of the observed variation in megafauna impacts on ecosystems remains unexplained.
365 Moreover, most of the covariates that significantly improved model quality had only small
366 effect sizes. Part of this unexplained variation may be due to variation in megafauna densities
367 and herbivory pressure, which was not reported in most studies. Other context dependencies
368 related to historic megafauna extinctions or historic human land-use may also affect both the
369 starting conditions when enclosure experiments were initiated and subsequent trajectories in
370 response variables, e.g. through impacts on regional species pools, soil seed banks, fire regimes
371 or hydrology⁷³.

372 **Conclusion and outlook**

373 The results presented here show that megafauna have strong effects on ecosystems. By
374 modifying soil and plant nutrients, vegetation structure and altering consumer populations,
375 megafauna are expected to have numerous other downstream effects on ecosystem functioning
376 and community structure. Moreover, by increasing heterogeneity megafauna may promote
377 biodiversity at landscape scales, thus favoring diverse ecosystems that may be more
378 ecologically resilient^{35,69}. However, we found no evidence for other hypothesized effects of
379 megafauna, such as on soil respiration and total soil C content, or for a modulating effect of
380 NPP on megafauna effects. Likewise, we found high variability in megafauna effects, indicating
381 underlying contextual complexity and highlighting the need for globally distributed
382 experiments⁷⁴.

383

384 Our results provide quantitative evidence for some findings in a recent extensive review of
385 several megafauna effects¹⁴, such as the importance of body size in modulating the impact of
386 herbivores, top-down trophic effects on vegetation, the importance of megafauna to nutrient
387 cycling, the suppression of smaller animals and increased ecosystem heterogeneity when
388 megafauna are present. These general patterns in how megafauna affect ecosystems,

389 biodiversity and Earth system functioning underpin the global importance of megafauna and
390 highlight the need for process-based work that allows predictions of megafauna impacts,
391 specifically with regard to ecosystem restoration in a rapidly changing world¹⁴.

392

393 Considering the variety of effects we could confirm in this meta-analysis, we argue that
394 ecosystems that lost their wild megafauna during the late Quaternary are likely missing key
395 processes^{3,8,10,75}. This loss is expected to continue given ongoing declines of large-bodied
396 species^{9,58,76}. Therefore, we advocate for their carefully planned and implemented restoration
397 through actions such as trophic rewilding⁷⁷; actions that may become increasingly important in
398 the face of future environmental change.

399

400 Methods

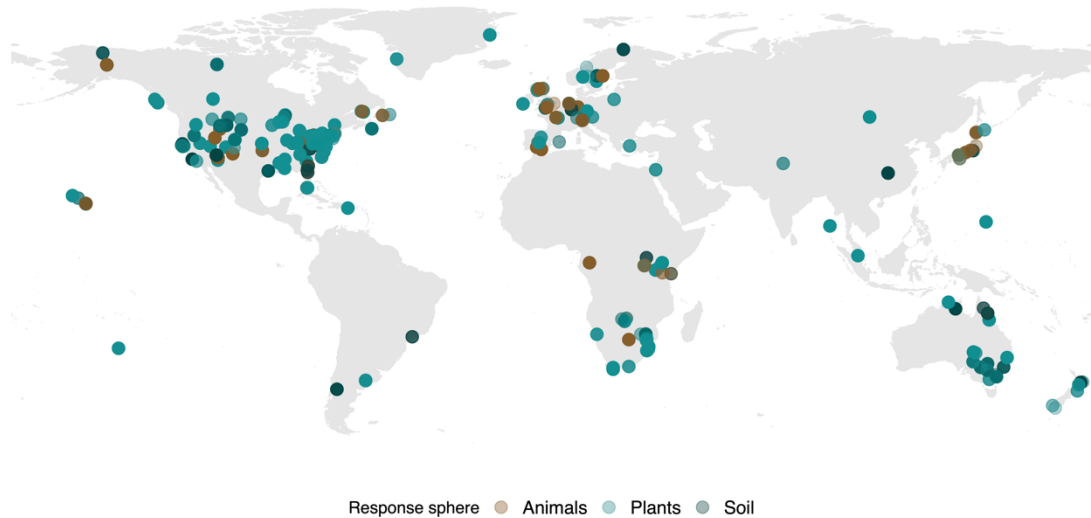
401 Literature search and digitization

402 This meta-analysis is part of a larger project aiming to understand how large (> 45 kg body
403 weight) terrestrial mammalian herbivores can affect different aspects of ecosystems (e.g.,
404 Lundgren et al., in revision]). We searched Web of Science (www.webofscience.com) on 18th
405 February 2021 with a string of search terms that included the common names and latin genera
406 of all terrestrial mammalian megafauna species (common names from HerbiTraits v1.2 ⁷⁸)
407 separated with an 'OR' operand, combined with the following search terms: "disturb*, graz*,
408 brows*, impact*, effect, affect, disrupt, facilitate, invasi*, ecosystem*, vegetat*, plant*,
409 fauna*, reptil*, amphib*, bird*, rodent*, fish*, invertebrat*, insect*, soil*, carbon, climate,
410 albedo, river*, riparian, desert*, forest*, tundra, decomposition, grassland*, savanna*,
411 chaparral, scrub, shrub, diversity, heterogeneity, extinction, richness, environment, reptile*,
412 ecolog*, hydrolog*, disturbance, density, biodiversity, response*, ecosystem, herbaceous,
413 canopy, germination, cover, pollinator*, tree, nutrient*, understory, erosion, grass*, vegetation,
414 community, exclosure, competition, effect*, abundance, productivity" in combination with the
415 topic filter: "WC=(Ecology OR Zoology OR Environmental Sciences OR Biodiversity
416 Conservation OR Evolutionary Biology OR Geography Physical OR Remote Sensing OR Plant
417 Sciences OR Multidisciplinary Science OR Forestry OR Entomology OR Marine & Freshwater
418 Biology OR Mycology OR Biology OR Oceanography OR Ornithology OR Behavioral
419 Sciences OR Fisheries" After removing duplicate studies with the function

420 `find_duplicates` of the R package ‘revtools’⁷⁹, this led to 62,628 hits. After screening all
421 titles and removing obviously unsuitable articles, this number was reduced to 2369 studies.
422 The literature list was extended by studies used in other meta-analyses e.g.,^{39,80} and found in
423 reference lists of studies we downloaded. We supplemented the list further with focused
424 Google Scholar searches on the 15th of July 2022, using the following terms: “ungulate impacts
425 island*”, “introduced goat impact island*”, “introduced deer impact*”, “feral camel impact*”,
426 “wild OR feral boar OR hog OR pig OR feral pig OR swine impact*”, “feral cattle impact*”,
427 “invasive ungulate hawaii OR guam OR new zealand OR pacific island OR new caledonia OR
428 galapagos OR caribbean OR oceanic island” and a Web of Science search on the 22nd of
429 December 2022 using the search string “herbivore* AND (plant* OR soil) AND nutrient*
430 AND response*”. This led to the addition of 38 and 15 studies respectively (Fig. S9 for Prisma
431 chart).

432

433 Considering that ecosystem responses can differ drastically between wild and domesticated
434 animals^{20,81}, we only considered studies investigating wild megafauna populations. We
435 excluded studies investigating only herbivores < 45 kg. Further, we only included studies that
436 compared adjacent areas of low (mostly no megafauna) and high megafauna densities due to
437 known factors like exclosures, policy-driven differences (hunting versus no-hunting in adjacent
438 properties), and differences in introduction or eradication histories (adjacent islands with and
439 without megafauna). Given that adding nativeness to our models never improved model fit
440 (LRT=[0.00, 3.62], p=[0.12, 0.95], Fig. S10), except for plant cover (LRT = 4.03, p = 0.04, but
441 with the same effect direction for both introduced ($g = -0.42$ [-0.58, -0.26]) and native
442 megafauna ($g = -0.22$ [-0.32, -0.11]), Fig. S11), we also included non-native megafauna in our
443 analysis.



444

445 **Fig. 4 Locations of the studies used in this meta-analysis.** Points appear darker if there are
 446 several studies at the same location. More detailed maps including response directions can be
 447 found in Fig. S1 and Fig. S2.

448

449 In grouping the individual ecosystem responses, we attempted to find a compromise between
 450 maximizing sample size and ecological accuracy. Apart from obviously incorrect groupings
 451 (e.g., NDVI as measurement for PP), we have essentially followed the categories used by the
 452 authors of the respective studies. For example, primary productivity responses are mainly
 453 composed of various growth rate measurements (such as tree growth rate, total crown growth,
 454 leaf growth rate, etc.). All included types of measurements for each response can be found in
 455 the `Data and supplementary files` folder on Figshare (file name:
 456 “measured_responses_R1.csv”).

457 We exclude all before-after comparisons (e.g., a plot measured prior to construction of an
 458 enclosure and then again afterwards) due to the high rates of change in many ecological systems
 459 over time, such as afforestation, climate shifts, and succession. Studies investigating plant
 460 nutrients but reporting nutrient values in units per area were also excluded because any
 461 differences possibly rather reflect biomass removal due to megafauna foraging than actual
 462 changes in nutrient concentrations.

463

464 We digitized measures of central tendency (mean, median), variability (standard deviation,
 465 interquartile ranges), error (standard error, confidence intervals) and sample sizes for each

466 response in each study. We used the ‘Figure_Calibration’ plugin ⁸² in ImageJ 1.53k
467 (www.imagej.nih.gov/ij/) to extract data from figures.

468

469 We also digitized relevant information associated with each observation, which included time
470 since treatment (e.g., exclosure construction or island colonization), study location (latitude,
471 longitude; Fig. 4), reported density of megafauna (converted to biomass per hectare),
472 megafauna nativeness and relative abundance of megafauna (in the case of multispecies
473 megafauna communities). However, not all studies reported these variables and in most cases
474 sample size was too small to test for them specifically (i.e., only 172 out of 297 studies reported
475 megafauna densities).

476 **Covariates**

477 Covariates were selected based on *a priori* hypotheses and were expected to influence
478 ecosystem responses to megafauna.

479 Environmental covariates were extracted for each study location using the function
480 `exact_extract` from the R package ‘exactextractr’ version 0.8.2 ⁸³ and the `extract`
481 function from the ‘terra’ package version 1.7-3 ⁸⁴. These variables included maximum annual
482 temperature (MAT) ⁸⁵, net primary productivity (NPP) ⁸⁶ and the aridity index (AI)⁸⁷.
483 Moreover, we extracted soil pH, soil cation exchange capacity, soil nitrogen and soil clay
484 content from the SoilGrids database ⁸⁸.

485

486 Megafauna body mass was extracted from the HerbiTraits v1.2 database ⁷⁸ for all species in
487 our dataset (including herbivores < 45 kg that were part of the experimental manipulation, Fig.
488 S12). Many studies manipulated multiple megafauna species simultaneously. To account for
489 this, we calculated community-weighted body mass by multiplying species-specific body mass
490 (BM) by the proportional contribution of that species’ biomass to the total biomass of the
491 community(RB). For example, a megafauna community consisting of two species, one with a
492 body weight of 100 kg that accounts for 80% of the biomass of the entire community, and the
493 second species with a weight of 1000 kg that accounts for 20% of the biomass of the
494 community. The unweighted mean body mass of the community would be 550, while the
495 weighted body mass of the community would be 140 kg, which is calculated as in equation (1)
496 and exemplified in equation (2):

497

498
$$(BM_{species\ 1} \times RB_{species\ 1} + \dots + BM_{species\ n} \times RB_{species\ n})/n \quad (1)$$

499

500
$$(100 \times 0.8 + 1000 \times 0.2)/2 \quad (2)$$

501

502 Relative biomass estimations were computed based on either the relative abundance or absolute
503 density estimates per species. However, as using only these community-weighted variables in
504 some cases reduced our sample size drastically, and weighted and unweighted covariates were
505 strongly correlated ($\rho = 0.94$, $p < 0.0001$), we decided to use the unweighted body mass in
506 cases where using the weighted covariate would reduce sample size to < 10 studies.

507 **Data analysis**

508 All data analysis was performed in R version 4.2.2⁸⁹. We calculated the effect size and
509 corresponding sampling variance of the megafauna treatment (low vs. high density) as
510 standardized mean difference, also known as Hedges' g (g)⁹⁰. Hedges' g is a unitless
511 measurement⁹¹. As a rule of thumb, a value of 0.2 can be interpreted as small effect, 0.4 as
512 medium effect and 0.8 as large effect. However, given the context dependency of the
513 importance of those categories, the exact values should be interpreted with care^{38,91}. To
514 investigate if megafauna has an impact on the variability of the parameters of interest we further
515 calculated the log transformed coefficient of variation ratio (lnCVR)^{36,92}. This effect size
516 quantifies the between-plot heterogeneity within each reported comparison between high and
517 low megafauna density. It therefore primarily reflects variation among plots, i.e. spatial
518 heterogeneity within an enclosure or control site, uncorrected for differences in spatial grain
519 (plot size) and extent (study area) between studies. First we transformed all medians to means
520 and error measurements to standard deviation (SD) with the function `qe.mean.sd` from the
521 R package 'estmeansd' version 1.0.0⁹³. Then we employed the `escalc` function of the
522 'metafor' package version 3.5-12³⁷ which is using the observed mean, SD and group size of
523 both treatment groups to calculate effect size and variation³⁷.

524

525 To account for potential non-independence in the effect size (i.e., due to repeated measures in
526 the same study) we fit random-effects meta-analytic models with the `rma.mv` function of the
527 'metafor' package³⁷ and added citation as random effect. Because some of the studies reported
528 time series data, we also included an ordered time series variable for each individual
529 experiment ID (e.g., a specific nutrient response per study) in our random effects.

530 We modeled the response variable (hedges g or $\ln\text{CVR}$), either against the intercept
531 only or against one covariate of interest at a time and used the sampling variance to weigh each
532 data point. Studies with larger sample sizes and/or lower variance thus have higher weight in
533 models³⁷. For modeling purposes, we took the natural logarithm of those covariates without
534 normal distribution and standardized all covariates using the `scale` function in base R (R core
535 team 2022) to approach a normal distribution and to account for the different units and thus
536 magnitude differences between the variables.

537

538 To test the influence of sample size, we selected the five responses with the largest sample size
539 and bootstrapped the model 1000 times for different numbers of studies ($n = 3, 5, 8, 10, 15$,
540 Fig. S13). We find that as the number of included studies increases, the frequency distribution
541 of estimates narrows considerably toward the confidence interval of the model with the full
542 sample size (Fig. S13). While we observe a large variation for models with 5 or fewer studies,
543 we notice a stabilization toward a sample size of 10 studies, which is why we excluded
544 responses with fewer than 10 studies from the covariate analysis. Nativeness was only tested
545 on ecosystem responses with ≥ 5 studies with introduced and ≥ 5 studies with native species.

546

547 We compared the assembly model of each covariate with the respective intercept only model,
548 using a likelihood ratio test via the `anova` function of the 'metafor' package^{37,94}.

549 After running all models we followed a leave-one-out approach to identify influential studies
550 (Cook's Distance $> 1^{95}$) using the `cooks.distance` function of the 'metafor' package^{37,96},
551 and removed studies that showed cook's distance of larger than 1.

552

553 For those responses which have a sufficient sample size we also tested the effect of treatment
554 duration (Fig. S14) and area of measurement (Fig. S15). We further tested the effect of biomass
555 lost due to treatment (as proxy of megafauna density) on the effect size magnitude of responses
556 with sufficient sample size but did not find it to improve model quality for any tested response.

557 To account for the specific characteristics of megaherbivores (terrestrial megafauna herbivores
558 (≥ 1000 kg)²³, we performed an additional sensitivity analysis where we tested the effects of
559 megaherbivores and megafauna herbivores < 1000 kg on those responses with sufficient
560 sample size separately (Fig. S6). We further performed a similar analysis for large herbivores
561 ≥ 100 kg vs smaller megafauna herbivores (< 100 kg) (Fig. S7). Moreover, we tested the effect
562 of megafauna in different biome categories (namely temperate forests, temperate grasslands,

563 tropical forests, tropical grasslands, and mediterranean forests) separately for those responses
564 with sufficient sample size (Fig. S16, Fig. S17).

565

566 To check for publication bias we used funnel plots⁹⁷ via the `funnel` function of the ‘metafor’
567 package³⁷ (Fig. S8). We further performed regression correlation tests for funnel plot
568 asymmetry⁹⁸ via the `regtest` function from the ‘metafor’ package³⁷ to adjust for the overall
569 mean⁹⁹ (Table S4).

570

571 Data availability

572 All data are available on figshare:
573 [https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_w](https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_world_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031)
574 [ild_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031](https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_world_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031)¹⁰⁰

575

576 Code availability

577 All core analysis and figure scripts are available on figshare:
578 [https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_w](https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_world_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031)
579 [ild_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031](https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_world_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031)¹⁰⁰

580

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592

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604

605 Competing Interests Statement

606 The authors declare no competing interests.

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608

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