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

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

Large mammalian herbivores (≥45 kg body mass[1,2], henceforth mega-fauna) have shaped Earth's ecosystems for more than 35 Myr[3,4]. However, in the late Pleistocene and early Holocene, terrestrial megafauna suffered a global wave of declines and extinctions strongly linked to the worldwide expansion of humans[5–8]. These extinctions (50,000–7,000 years ago) led to extreme global body size downgrading to levels not seen since the extinction of dinosaurs 66 million years ago[4] with profound consequences for ecosystem processes[3,9–11].

Megafauna are considered disproportionately important for biosphere functioning because of their ability to access resources that are not available to smaller consumers, digest high amounts of low-quality biomass, shape fire dynamics and move over very large distances[12–14]. This enables large animals to increase nutrient cycling, contribute to seed and nutrient dispersal[15], and reshape vegetation[13,16], with direct and indirect effects on soil properties and processes[17,18], plant diversity, productivity and structure[12,19], and animal abundance
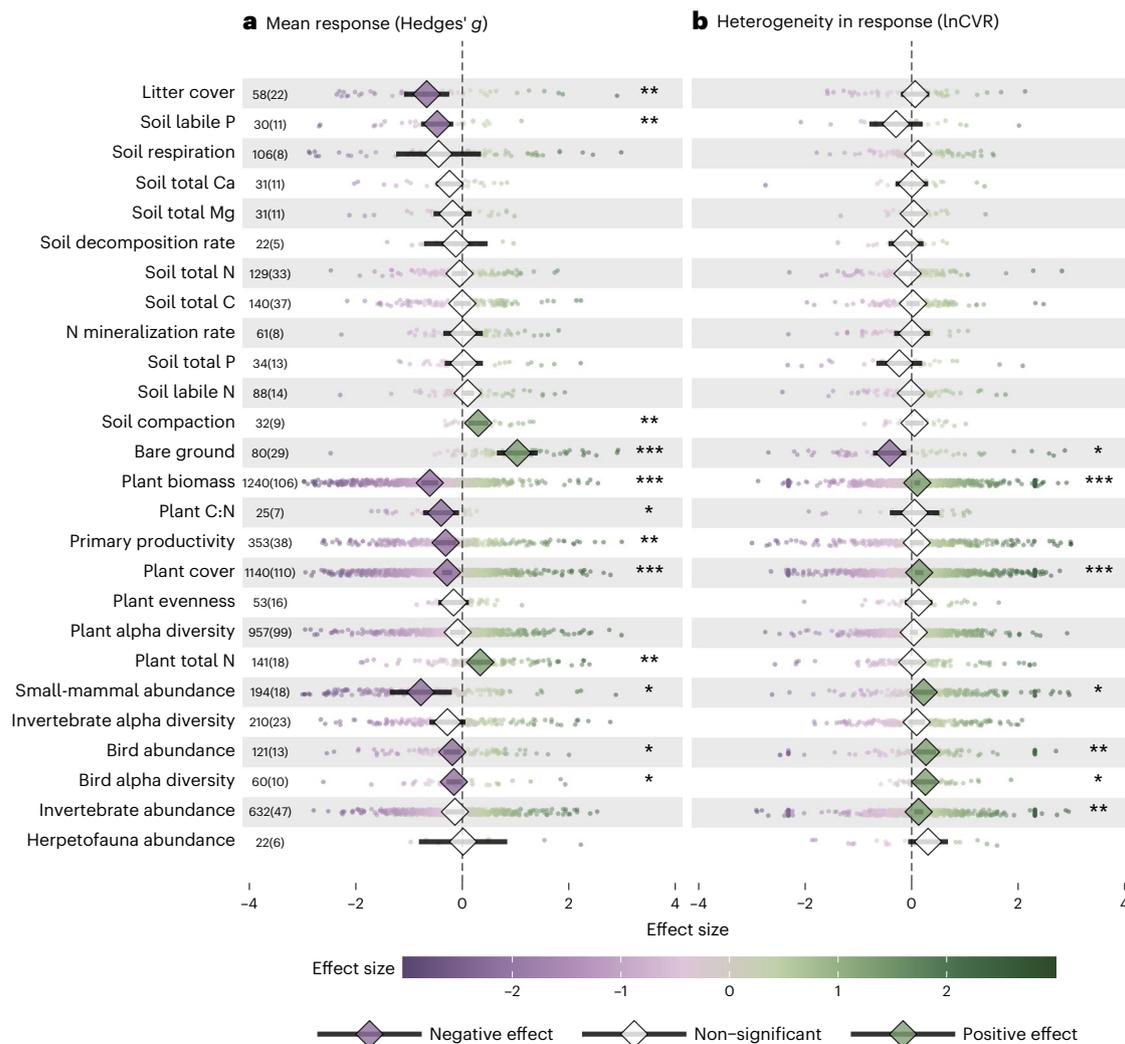
Fig. 1 | Effects of herbivorous megafauna on mean ecosystem responses and heterogeneity within these responses. Model estimates (±95% confidence interval (CI)) for the different response categories, derived from random-effects meta-analytic models[37] (see Methods for details). Purple symbols indicate a significant negative impact, green symbols a significant positive impact and white symbols a non-significant impact of large herbivores. Stars indicate different significance thresholds: *$P \le 0.05$; **$P \le 0.01$; ***$P \le 0.001$. Each point in the background indicates a datapoint (that is, a pairwise comparison in a study such as exclosure vs control) used in the analysis of the respective response. The numbers after each label on the y axis provide information about the sample size of the measured response, that is, number of datapoints, with the number of studies enclosed in brackets. **a**, Effect on mean response (Hedges' g); **b**, Effect on heterogeneity in response (lnCVR).

and diversity[20,21]. These effects are predicted to be modulated by body size[22,23] and environmental conditions such as nutrient availability[24] and productivity[14,25].

One of the key hypothesized impacts of megafauna is the promotion of ecosystem heterogeneity[26], for example, by creating local nutrient hotspots[16,27] and heterogeneity in vegetation structure through physical disturbance[28]. This can translate to increased diversity of vegetation types at landscape scales[12]. In general, biodiversity increases with environmental heterogeneity across spatial scales, biomes and taxonomic groups[29] by both increasing available niche space (allowing more species to coexist) and promoting species persistence via the provision of refuges during environmental fluctuations[29–31]. By preventing one or a few species from dominating[32] and therefore enabling species with similar ecological attributes to coexist in the same ecosystem, this heterogeneity may also lead to functional redundancies and thus promote ecosystem resilience[33–35].

Although there is strong case-specific evidence and conceptual expectations that large herbivores influence soil properties, vegetation

community and structure and other animals[12–14], a formal quantitative test for the generality of these impacts across ecosystems and taxonomic groups is lacking[14]. As megafauna are particularly affected by past, current and potential future defaunation[9], addressing this knowledge gap is important.

Using a meta-analytic approach, we compiled and analysed 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 response[36].

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 whether megafauna promote spatial heterogeneity in these ecosystem responses and whether these effects vary predictably with herbivore body mass and environmental covariates.

Results

We conducted a systematic literature search to find studies investigating the impact of wild large mammalian herbivores on ecosystems. Studies included contrasts in megafauna density and megafauna presence/absence, with >89% being exclosure experiments (Supplementary Fig. 1). Comparisons of areas with high and low megafauna density were only included if those areas were adjacent and were the result of management decisions (for example, a hunting area vs a protected area). Herbivore effects were calculated as standardized mean difference (Hedges' g), while within-treatment heterogeneity was estimated using the log-ratio between two coefficients of variation (lnCVR)[36]. The final dataset consisted of 5,990 datapoints from 297 studies (each representing, for example, one comparison between an exclosure and a control) representing 26 ecosystem responses (Supplementary Tables 1 and 2). The dataset was geographically biased towards Europe, North America, South Africa and Australia (Supplementary Figs. 2 and 3), towards the Afrotropics (Supplementary Fig. 4a) and temperate forests (Supplementary Fig. 4c), and against areas with low temperatures and/or high precipitation (Supplementary Fig. 4b).

The median area of measurement (that is, plot size) was 1 m^2 (95% confidence interval (CI): 0.002–25,000 m^2) (Supplementary Fig. 5a), the median treatment duration was 2,190 d (95% CI: 365–21,900 d) (Supplementary Fig. 5b), the median number of datapoints per study was 11 (95% CI: 1–97) and the median number of studies per response was 15 (95% CI: 6–108).

Effects of herbivorous megafauna

We used random-effects meta-analytic models[37] to investigate the overall effect of megafauna on 26 different ecosystem responses and their heterogeneity. Despite high variability in the effects of megafauna, we found a significant impact on 50% of the investigated responses. Unless stated otherwise, these are the ones presented in the results.

Soil responses. Megafauna moderately decreased soil labile phosphorous (P), slightly increased soil compaction and strongly increased bare ground cover while strongly decreasing litter cover (Figs. 1a and 2a, and Table 1). Megafauna decreased heterogeneity in bare ground cover (Figs. 1b and 2b, and Table 1).

Vegetation responses. Megafauna had moderate positive effects on plant nitrogen (N) content (Figs. 1a and 2, and Table 1), moderately reducing plant carbon:nitrogen (C:N) ratios (Figs. 1a and 2, and Table 1). Moreover, they moderately reduced plant cover and plant biomass and slightly reduced primary productivity (Figs. 1a and 2a, and Table 1). Further, megafauna increased heterogeneity in plant cover and plant biomass (Figs. 1b and 2b, and Table 1).

Other animals' responses. Megafauna strongly reduced the abundance of small mammals and had weak negative effects on bird alpha diversity and abundance (Figs. 1a and 2a, and Table 1). They also increased heterogeneity in the abundance of small mammals, invertebrates and birds, as well as in bird alpha diversity (Figs. 1b and 2b, and Table 1).

Notable null results. We found no significant mean effect of megafauna on 14 of 26 tested responses and on the heterogeneity of 19 tested responses ((minimum, maximum): Hedges' g = (−0.27, 0.14), lnCVR = (−0.23, 0.23), P = (0.06, 0.96); Fig. 1). Among the more notable responses for which we detected no statistically significant effect on the overall mean response (but see Fig. 2a and 'Results: Influence of body mass and environmental variables on megafauna impacts') were total and labile soil N and N mineralization rate, soil respiraton and total C, and plant alpha diversity and evenness.

Influence of body mass and environmental variables

The effects of megafauna are predicted to be dependent on body size[22,23] and environmental conditions such as nutrient availability[24]

and productivity[25]. Therefore, we added body mass (both mean and maximum body size of the community, weighted by relative biomass per species for responses with sufficient sample size (>10 studies); see Methods for details) and a variety of environmental factors (Supplementary Table 3) as variables to our models. We added each covariate as a single variable and compared the single-term model to its intercept-only model, using a likelihood ratio test (LRT). If the covariate significantly improved model quality, we considered it as explaining some of the variability in the effects of megafauna. Moreover, for those responses with sufficient sample size, we divided our data into communities including megaherbivores (≥1,000 kg) vs communities without megaherbivores (Supplementary Fig. 6) and communities including herbivores ≥100 kg vs without those species (Supplementary Fig. 7) and analysed their impacts separately.

Body mass. Larger-bodied megafauna communities were more likely to increase heterogeneity in total soil N (Fig. 3a and Table 2). In this case, the body mass variable here reflects the body size of the biggest animal in the community (that is, not weighted by relative biomass). Megafauna communities comprising larger-bodied species (body mass weighted by relative biomass per species) tended to increase plant alpha diversity (Fig. 3b and Table 2). None of the other tested effects on ecosystem responses were significantly affected by megafauna body mass (LRT = (0, 5.97), P = (0.10, 0.99)).

Moreover, megafauna communities that included herbivores ≥100 kg significantly increased soil labile N (Supplementary Fig. 7) and communities without herbivores ≥100 kg significantly decreased plant alpha diversity (Supplementary Fig. 7).

Environmental covariates. Negative effects on litter cover were observed mainly in soils with lower cation exchange capacity (Fig. 3c and Table 2), while positive effects on heterogeneity in litter cover occurred more frequently in soils with lower nitrogen content (Fig. 3d and Table 2).

The response of plant alpha diversity was slightly more negative in more humid areas (Fig. 3e and Table 2). None of the other tested effects on ecosystem responses was significantly affected by our environmental covariates (LRT = (0.00, 3.76), P = (0.06, 1.00)).

Discussion

Our meta-analysis of 297 studies across six continents shows that herbivorous megafauna shape ecosystems by affecting ecosystem properties and processes across trophic levels and by increasing ecosystem heterogeneity. We confirmed that body size influenced megafauna effects on soil labile N and plant alpha diversity, but that the effect was relatively small and variable. Some environmental factors[14] modulated megafauna effects on ecosystem responses such as plant alpha diversity and litter cover, whereas we found no evidence for others. Interestingly, and contrary to former meta-analysis and theory[38,39], net primary productivity (NPP) did not explain variation in the effects of megafauna on any tested response. While some responses had clear and generalizable patterns (for example, the decrease in soil labile P and plant biomass), we found large variability in others (for example, invertebrate abundance and soil total C).

Of the 13 soil responses, 4 were significantly affected by megafauna. Notably, megafauna did not alter the absolute amount of soil C (which is noteworthy given the ongoing debate around climate impacts of megafauna (for example, refs. 40,41), P and N, but rather the bioavailable forms of N and P (sample size was insufficient to include labile C). Herbivores larger than 100 kg tended to increase the amount of available nitrogen. At the same time, megafauna in general tended to decrease labile P, supporting suggestions that megafauna may push systems towards a higher degree of P limitation[42]. While the increase in N availability may be explained by megafauna accessing N otherwise locked away in plant biomass and providing it in bioavailable forms
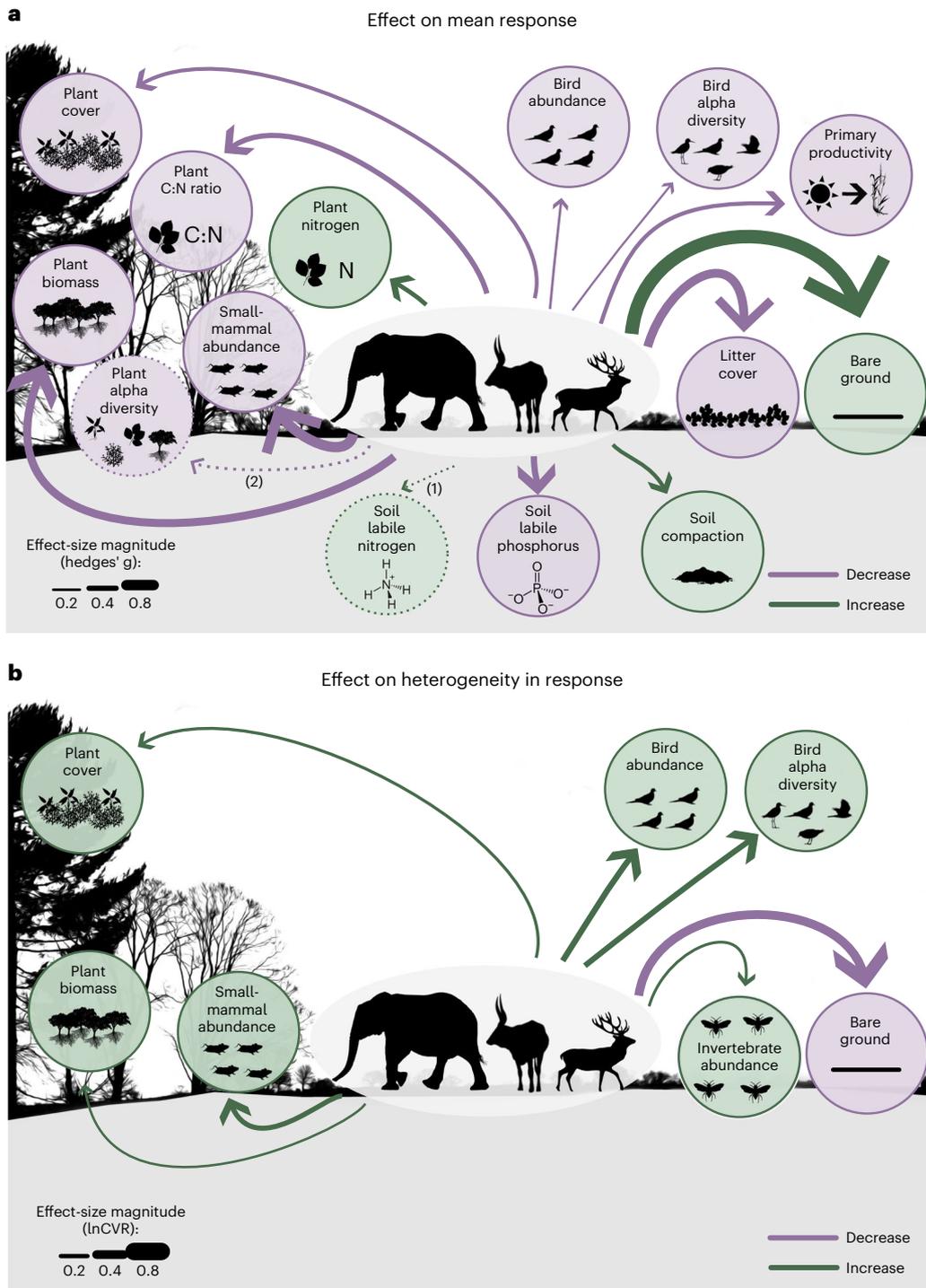
Fig. 2 | Impacts of herbivorous megafauna on different ecosystem responses and their heterogeneity. Shown here are the statistically significant impacts of megafauna. All tested responses and their estimates can be found in Fig. 1. Numeric results of the significant models can be found in Table 2. Green indicates an increase and violet a decrease in the mean response or the heterogeneity in the response; arrow widths are scaled by effect-size magnitude. Note that (1) the positive effect on soil labile N is only significant in megafauna communities

with species with ≥100 kg body mass (Supplementary Fig. 7) and (2) the negative effect in plant alpha diversity is only significant in megafauna communities without species with ≥100 kg body mass (Supplementary Fig. 7). As a rule of thumb, a Hedges' g of 0.2 can be interpreted as a small effect, 0.4 as a medium effect and 0.8 as a large effect[94]. **a**, Mean effect of megafauna herbivores on ecosystem responses. **b**, Effect of megafauna herbivores on spatial heterogeneity in these ecosystems.

via excreta[43], P may be stored away in skeletons for longer periods[42]. Alternatively, the increased availability of labile soil N may stimulate plant growth until P becomes limiting[44,45], with the consequence that more available P may be stored in vegetation compared with soils not affected by megafauna.

Of the seven plant responses, five were significantly impacted. Megafauna increased plant nitrogen content, which could be driven by a combination of elevated soil nitrogen availability from direct megafauna inputs and reduced C:N ratios in young (regrowing) plant tissue[46,47] (for example, less 'dilution' by structural carbon). Higher

Table 1 | Results of significant models

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

Model estimates (±95% CIs) for the different significant response categories, derived from random-effects meta-analytic models[37]. Here we used intercept-only models which provide a mean estimate of the effect size weighted by the inverse of the sampling variance and under consideration of the included random structure (see Methods for details). The effect-size type 'Hedges' g' refers to the standardized mean difference between low and high megafauna herbivore density (or presence/absence), while lnCVR quantifies differences in spatial heterogeneity. Hedges' g of 0.2 can be interpreted as a small effect, 0.4 as a medium effect and ≥0.8 as a large effect[94] (Figs. 1a and 2a).

plant nitrogen content should have various ecosystem consequences, for example, by increasing litter quality[48] or favoring phytophagous insects[49] and their associated food webs (although we detected no general effect on invertebrate abundance or diversity).

Megafauna significantly and strongly decreased plant biomass and cover, and litter cover while increasing bare ground cover. These effects are expected through biomass consumption, trampling and wallowing[50,51]. The increase in bare soil may result in increased day-time soil temperature and reduced moisture due to increased exposure to solar radiation and increased run-off[52], which may have cascading consequences on other soil properties. However, despite the changes in organic matter (that is, reduced quantity of biomass, increased quality of litter) and increased soil compaction, we did not find consistent changes in bulk soil C or soil decomposition and respiration, which is in line with previous meta-analyses[53,54].

Our results confirm the ability of megafauna to promote open and semi-open habitats at the plot scale by decreasing plant biomass and cover[12,14,55]. Moreover, megafauna increased heterogeneity in vegetation structure between plots, which suggests that megafauna increase vegetation structural diversity also on the landscape scale. However, the scale of most exclosure experiments and vegetation sampling methods is too small to enable quantification megafauna impacts at larger spatial scales directly.

Overall, megafauna significantly decreased primary productivity. However, this result is difficult to interpret since variables used to quantify NPP vary widely among studies. One possible reason may be that plants might shift some of their productivity belowground, resulting in, for example, increased fine root biomass and root exudation (which may ultimately contribute to the accumulation of persistent soil organic matter[17]), highlighting the need for more research on the belowground impacts of large animals.

Consistent with previous work[14,55], the overall effect of megafauna— from deer to elephants—on plant alpha diversity was non-significant. However, we found that smaller-bodied (that is, <100 kg) megafauna communities tended to have negative effects on plant alpha diversity, while larger-bodied herbivore communities tended to have slight positive effects. This could be because larger animals can eat lower-quality food[56,57] such as branches and stems, which may result in proportionally greater impacts on dominant plant species and thus release less competitive plants from competition[25,58]. The negative effect of smaller megafauna may reflect reduced predation pressure due to anthropogenic predator removal[59], which allows smaller species to build high densities and access more risky habitats. Furthermore, the differential impact of megafauna of different size classes supports that smaller herbivores cannot substitute for larger megafauna[14] and suggests that the anthropogenically simplified and smaller-bodied herbivore communities[60,61] currently found in large parts of the world lack important functions.

Megafauna effects on other animals were measured using six variables, of which four were significantly impacted. Consistent with previous work, megafauna strongly reduced the abundances of small mammals (notably rodents)[14] at small scales, but simultaneously increased heterogeneity in this response. A decrease in small mammals in the presence of megafauna might in part be due to lower vegetation cover or trampling of burrows, although evidence suggests that feeding competition is the main mechanism of control[20]. A reduction of competition and increase of vegetation cover in exclosures may also lead smaller consumers to actively move into these relatively small patches that now provide habitat of a higher quality (greater cover from predators, more food abundance) for smaller consumers compared with the surroundings[62]. These larger numbers of smaller animals may in turn have knock-on effects on the rest of
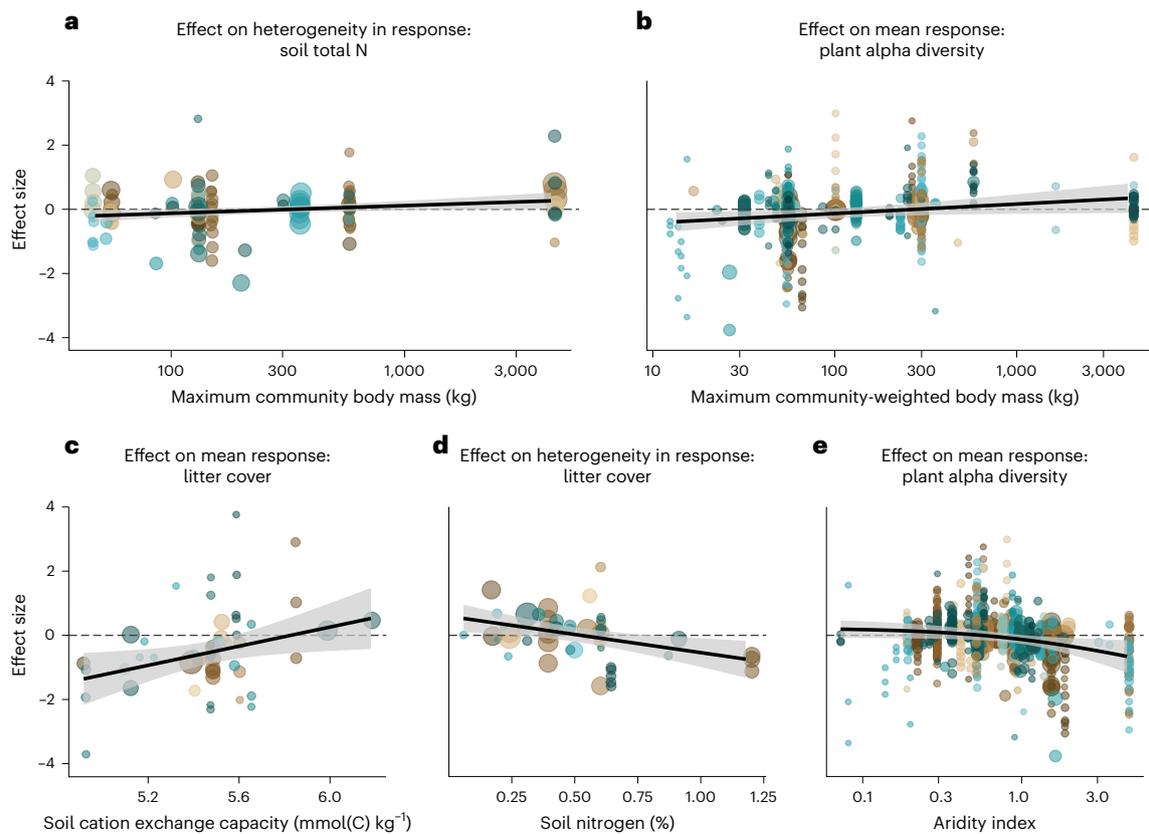
Fig. 3 | Predictions of significant covariates. Estimates (±95% CI) of covariates which are significantly improving model quality. Different point colours and shades indicate different studies. Point size is determined by 1/sampling variance to indicate its weight in the model. All explanatory variables are log transformed and scaled. **a**, Impact of megafauna herbivore body mass on the extent to which herbivores influence the spatial heterogeneity of soil total N. Note that body size in this case is not community weighted to maintain a sample size >10 studies. **b**, Impact of community-weighted megafauna herbivore body mass on the effect of megafauna herbivores on plant diversity. **c**, Impact of soil cation exchange capacity on megafauna herbivores' effects on litter cover (however, we note that the used soil covariates represent regional averages rather than fine-scaled gradients in soil properties). **d**, Impact of soil nitrogen content on the effect of megafauna herbivores on heterogeneity in litter cover. **e**, Impact of aridity on the effect of megafauna herbivores on plant diversity. Note that a smaller aridity index indicates arid systems, while a higher aridity index indicates more humid systems. We fitted all models in a linear framework; however, when plotting the back-transformed predictions, the relationship may appear nonlinear.

Table 2 | Model results of significant covariates

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

The P value here refers to the LRT which compares the null model with the univariate model in terms of model quality (that is, explanatory power). $P < 0.05$ indicates significant improvement of the assembly model compared with the intercept-only null model; test is one-sided.

the system, for example, by affecting plant species whose seeds are eaten primarily by rodents, resulting in lower recruitment than in areas with large herbivores[20].

The decrease in bird alpha diversity and abundance could potentially be explained by decreasing nesting spaces on small scales and may seem counterintuitive as both bird abundance and diversity are known to increase with increasing habitat heterogeneity[63], for which we also find evidence. However, the exact shape of heterogeneity–diversity relationships can differ between taxonomic groups, trophic levels and across scales[64], and depends on other factors such as resource availability and environmental conditions[65]. This suggests that the megafauna-induced increases in heterogeneity may lead to nonlinear effects on bird abundance and diversity. In addition, the effect of megafauna on the abundance and diversity of birds is most likely to be positive at intermediate disturbance levels but can be negative at higher levels[66]. However, more research is needed to disentangle the relationship between increased heterogeneity and decreased bird alpha diversity such as found here.
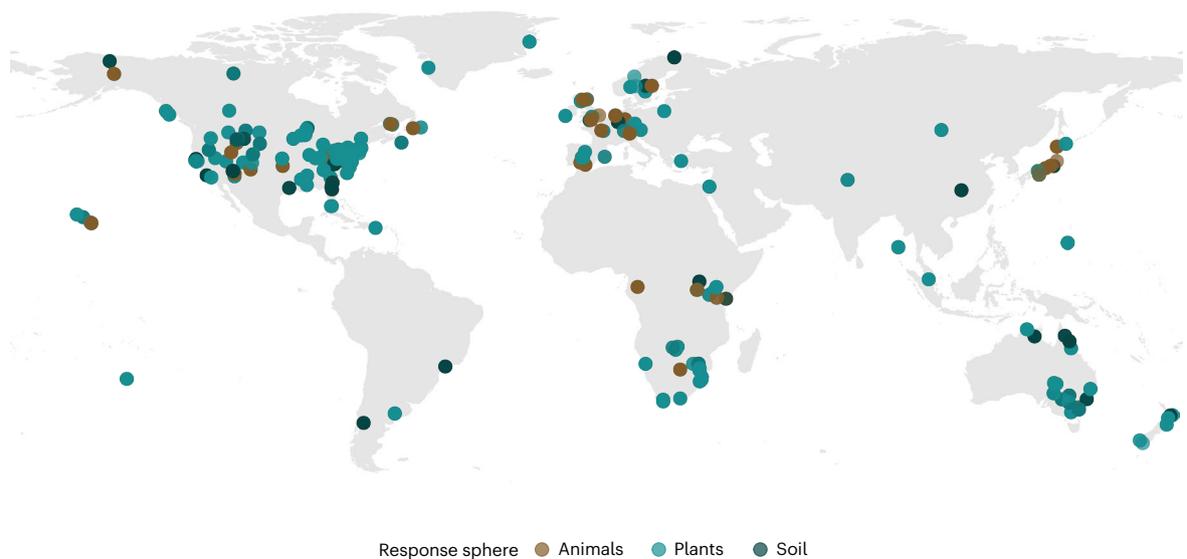
Fig. 4 | Locations of the studies used in this meta-analysis. Points appear darker if there are several studies at the same location. More detailed maps including response directions can be found in Supplementary Figs. 1 and 2.

A key outcome of our study is the demonstration of pervasive positive impacts of megafauna on heterogeneity (not consistently statistically significant, but almost never significantly negative; Fig. 1b). By increasing heterogeneity in vegetation structure, for example, megafauna may increase the amount of available habitat types and structural complexity, allowing more species to coexist[67]. Given that heterogeneity is known as a key driver of biodiversity across scales and taxonomic groups[29,35,68], megafauna have the potential to contribute to diversity at larger scales. Moreover, increased heterogeneity in vegetation structure may also lead to microclimatic variation, which has also been shown to be an important driver of community functional diversity[69]. Therefore, it has been suggested that small-scale environmental heterogeneity (such as studied here) is a strong predictor of functional diversity[69]. Previous work has also shown that megafauna may prevent one or a few species from dominating all available niches within its ecological range and thus allow different species with both similar and different ecological roles to coexist[29,32]. Hence, megafauna could contribute to the establishment of functional redundancies in ecological roles and subsequently to ecosystem resilience[35,70]. This becomes particularly important as ecosystem heterogeneity has been shown to increase the adaptive capacity of ecosystems to respond to climate change[35].

Limitations and recommendations for future studies
Small plot sizes in exclosure experiments along with the spatial scale at which responses were measured are a major limitation to unravelling megafauna impacts at larger scales. In addition, we found significant signs of publication bias in the studies analysed here (Supplementary Fig. 8 and Table 4) and spatial bias towards better-funded and researched parts of the world[65,71] (Fig. 4 and Supplementary Figs. 2–4), which may hamper generalizations[72]. Despite these biases, our results are in line with theory and recent reviews[13,14] (which probably suffer from the same biases). Although it is plausible that some of the observed effects on megafauna translate to larger spatial scales, such as the positive effects on heterogeneity, the results presented here only provide reliable information about effects at the plot scale. Consequently, studying the impact of megafauna on ecosystems at larger scales (that is, landscape scale and larger) is a major challenge and will contribute substantially to our understanding of megafauna effects. Since setting up experiments on landscape scales is challenging, better use of natural experiments

and counterfactuals and available landscape-extent data (for example, from remote sensing[73]), will be key avenues in further quantifying the role of megafauna in the Earth system.

Despite testing a broad range of environmental covariates and megafauna body size, a large amount of the observed variation in megafauna impacts on ecosystems remains unexplained. Moreover, most of the covariates that significantly improved model quality had only small effect sizes. Additionally, our environmental variables were derived from layers with global extent (that is, refs. 74,75,76,77), which may have caused a scale mismatch and thus influenced effect size and significance. Part of this unexplained variation may be due to variation in megafauna densities and herbivory pressure, which was not reported in most studies. Other context dependencies related to historic megafauna extinctions or historic human land use may also affect both the starting conditions when exclosure experiments were initiated and subsequent trajectories in response variables, for example, through impacts on regional species pools, soil seed banks, fire regimes or hydrology[78].

Conclusion and outlook
The results presented here show that megafauna have strong effects on ecosystems. By modifying soil and plant nutrients, vegetation structure and altering consumer populations, megafauna are expected to have numerous other downstream effects on ecosystem functioning and community structure. Moreover, by increasing heterogeneity, megafauna may promote biodiversity at landscape scales, thus favouring diverse ecosystems that may be more ecologically resilient[35,70]. However, we found no evidence for other hypothesized effects of megafauna, such as on total soil C content, or for a modulating effect of NPP on megafauna effects. Likewise, we found high variability in megafauna effects, indicating underlying contextual complexity and highlighting the need for globally distributed experiments[79].

Our results provide quantitative evidence for some findings in a recent extensive review of several megafauna effects[14], such as the importance of body size in modulating the impact of herbivores, top–down trophic effects on vegetation, the importance of megafauna to nutrient cycling, the suppression of smaller animals and increased ecosystem heterogeneity when megafauna are present. These general patterns in how megafauna affect ecosystems, biodiversity and Earth system functioning underpin the global importance of megafauna and

highlight the need for process-based work that allows predictions of megafauna impacts, specifically with regard to ecosystem restoration in a rapidly changing world[14].

Considering the variety of effects we could confirm in this meta-analysis, we argue that ecosystems that lost their wild megafauna during the late Quaternary are probably missing key processes[3,8,10,80]. This loss is expected to continue, given ongoing declines of large-bodied species[9,59,81]. Therefore, we advocate for carefully planned and implemented restoration through actions such as trophic rewilding[82]—actions that may become increasingly important in the face of future environmental change.

Methods

Literature search and digitization

This meta-analysis is part of a larger project aiming to understand how large (>45 kg body weight) terrestrial mammalian herbivores can affect different aspects of ecosystems (for example, ref. [83]). We searched Web of Science (www.webofscience.com) on 18 February 2021 with a string of search terms that included the common names and latin genera of all terrestrial mammalian megafauna species (common names from HerbiTraits (v.1.2)[84]) separated with an 'OR' operand, combined with the following search terms: "disturb*, graz*, brows*, impact*, effect, affect, disrupt, facilitate, invasi*, ecosystem*, vegetat*, plant*, fauna*, reptil*, amphib*, bird*, rodent*, fish*, invertebrat*, insect*, soil*, carbon, climate, albedo, river*, riparian, desert*, forest*, tundra, decomposition, grassland*, savanna*, chaparral, scrub, diversity, heterogeneity, extinction, richness, environment, reptile*, ecolog*, hydrolog*, disturbance, density, biodiversity, response*, ecosystem, herbaceous, canopy, germination, cover, pollinator*, tree, nutrient*, understory, erosion, grass*, vegetation, community, exclosure, competition, effect*, abundance, productivity" in combination with the topic filter: "WC = Ecology OR Zoology OR Environmental Sciences OR Biodiversity Conservation OR Evolutionary Biology OR Geography Physical OR Remote Sensing OR Plant Sciences OR Multidisciplinary Science OR Forestry OR Entomology OR Marine & Freshwater Biology OR Mycology OR Biology OR Oceanography OR Ornithology OR Behavioral Sciences OR Fisheries". Removing duplicate studies using the 'find_duplicates' function of the R package 'revtools'[85] led to 62,628 hits. After screening all titles and removing obviously unsuitable articles, this number was reduced to 2,369 studies.

The literature list was extended by studies used in other meta-analyses, for example, refs. [38,86], and found in reference lists of studies we downloaded. We supplemented the list further with focused Google Scholar searches on 15 July 2022, using the following terms: "ungulate impacts island*", "introduced goat impact island*", "introduced deer impact*", "feral camel impact*", "wild OR feral boar OR hog OR pig OR feral pig OR swine impact*", "feral cattle impact*", "invasive ungulate hawaii OR guam OR new zealand OR pacific island OR new caledonia OR galapagos OR caribbean OR oceanic island" and a Web of Science search on 22 December 2022 using the search string "herbivore* AND (plant* OR soil) AND nutrient* AND response*". This led to the addition of 38 and 15 studies, respectively (see Supplementary Fig. 9 for Prisma chart).

Considering that ecosystem responses can differ drastically between wild and domesticated animals[20,87], we only considered studies investigating wild megafauna populations. We excluded studies investigating only herbivores <45 kg. Further, we only included studies that compared adjacent areas of low (mostly no megafauna) and high megafauna densities due to known factors such as exclosures, policy-driven differences (hunting versus no-hunting in adjacent properties) and differences in introduction or eradication histories (adjacent islands with and without megafauna). Given that adding nativeness to our models never improved model fit (LRT = (0, 3.62), P = (0.12, 0.95), Supplementary Fig. 10), except for plant cover (LRT = 4.03, P = 0.04, but with the same effect direction for both introduced (g = −0.42 (−0.58, −0.26)) and

native megafauna (g = −0.22 (−0.32, −0.11)), Supplementary Fig. 11), we also included non-native megafauna in our analysis.

In grouping the individual ecosystem responses, we attempted to find a compromise between maximizing sample size and ecological accuracy. Apart from obviously inprecise groupings (for example, the normalized difference vegetation index as measurement for PP), we have essentially followed the categories used by the authors of the respective studies. For example, primary productivity responses are mainly composed of various growth rate measurements (such as tree growth rate, total crown growth, leaf growth rate and so on). All included types of measurement for each response can be found in the 'Data and supplementary files' folder on Figshare (file name: 'measured_responses_R1.csv').

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

We digitized measures of central tendency (mean, median), variability (standard deviation, interquartile ranges), error (standard error, confidence intervals) and sample sizes for each response in each study. We used the 'Figure_Calibration' plugin[88] in ImageJ1.53k (www.imagej.nih.gov/ij/) to extract data from figures.

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

Covariates

Covariates were selected on the basis of a priori hypotheses and were expected to influence ecosystem responses to megafauna.

Environmental covariates were extracted for each study location using the function 'exact_extract' of the R package 'exactextractr' (v.0.8.2)[89] and the extract function of the 'terra' package (v.1.7-3)[90]. These variables included maximum annual temperature[74], NPP[75] and the aridity index[76]. Moreover, we extracted soil pH, soil cation exchange capacity, soil nitrogen and soil clay content from the SoilGrids database[77].

Megafauna body mass was extracted from the HerbiTraits v.1.2 database[84] for all species in our dataset (including herbivores <45 kg that were part of the experimental manipulation; Supplementary Fig. 12). Many studies manipulated multiple megafauna species simultaneously. To account for this, we calculated community-weighted body mass by multiplying species-specific body mass (BM) by the proportional contribution of that species' biomass to the total biomass of the community (RB). For example, for a megafauna community consisting of two species, one with a body weight of 100 kg that accounts for 80% of the biomass of the entire community and the second species with a weight of 1,000 kg that accounts for 20% of the biomass of the community, the unweighted mean body mass of the community would be 550, while the weighted body mass of the community would be 140 kg, which is calculated as in equation (1) and exemplified in equation (2):

$$(BM_{species1} x \, RB_{species1} + \ldots + BM_{speciesn} \, x \, RB_{speciesn})/n \quad (1)$$

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

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

Data analysis

All data analysis was performed in R (v.4.2.2)[91]. We calculated the effect size and corresponding sampling variance of the megafauna treatment (low vs high density) as standardized mean difference, also known as Hedges' g (g)[92]. Hedges' g is a unitless measurement[93]. As a rule of thumb, a value of 0.2 can be interpreted as a small effect, 0.4 as a medium effect and 0.8 as a large effect. However, given the context dependency of the importance of these categories, the exact values should be interpreted with care[94,93]. To investigate whether megafauna have an impact on the variability of the parameters of interest, we further calculated the lnCVR[36,95]. This effect size quantifies the between-plot heterogeneity within each reported comparison between high and low megafauna density. It therefore primarily reflects variation among plots, that is, spatial heterogeneity within an exclosure or control site, uncorrected for differences in spatial grain (plot size) and extent (study area) between studies. First, we transformed all medians to means and error measurements to standard deviation using the 'qe.mean.sd' function of the R package 'estmeansd' (v.1.0.0)[96]. Then we employed the 'escalc' function of the 'metafor' package (v.3.5-12)[37], which uses the observed mean, standard deviation and group size of both treatment groups to calculate effect size and variation[37].

To account for potential non-independence in the effect size (that is, due to repeated measures in the same study), we fitted random-effects meta-analytic models using the 'rma.mv' function of the 'metafor' package[37] and added citation as random effect. Because some of the studies reported time-series data, we also included an ordered time-series variable for each individual experiment ID (for example, a specific nutrient response per study) in our random effects.

We modelled the response variable (Hedges' g or lnCVR) either against the intercept only or against one covariate of interest at a time and used the sampling variance to weigh each datapoint. Studies with larger sample sizes and/or lower variance thus have higher weight in models[37]. For modelling purposes, we took the natural logarithm of those covariates without normal distribution and standardized all covariates using the 'scale' function in base R[91] to approach a normal distribution and to account for the different units and thus magnitude of differences between the variables.

To test the influence of sample size, we selected the five responses with the largest sample size and bootstrapped the model 1,000 times for different numbers of studies (n = 3, 5, 8, 10, 15; Supplementary Fig. 13). We found that as the number of included studies increases, the frequency distribution of estimates narrows considerably towards the confidence interval of the model with the full sample size (Supplementary Fig. 13). While we observed a large variation for models with 5 or fewer studies, we noticed a stabilization towards a sample size of 10 studies, which is why we excluded responses with fewer than 10 studies from the covariate analysis. Nativeness was only tested on ecosystem responses with ≥5 studies with introduced and ≥5 studies with native species.

We compared the assembly model of each covariate with the respective intercept-only model, using a likelihood ratio test via the 'anova' function of the 'metafor' package[37,97].

After running all models, we followed a leave-one-out approach to identify influential studies (Cook's distance >1 (ref. 98)) using the 'cooks.distance' function of the 'metafor' package[37,99] and removed studies that showed Cook's distance >1.

For those responses with sufficient sample size, we also tested the effect of treatment duration (Supplementary Fig. 14) and area of measurement (Supplementary Fig. 15). We further tested the effect of biomass lost due to treatment (as a proxy of megafauna density) on the effect-size magnitude of responses with sufficient sample size but did not find it to improve model quality for any tested response. To account for the specific characteristics of megaherbivores (terrestrial megafauna herbivores (≥1,000 kg)[23]), we performed an additional sensitivity analysis where we tested the effects of megaherbivores and megafauna herbivores <1,000 kg on those responses with sufficient sample size separately (Supplementary Fig. 6). We further performed a similar analysis for large herbivores ≥100 kg vs smaller megafauna herbivores (<100 kg) (Supplementary Fig. 7). Moreover, we tested the effect of megafauna in different biome categories (namely, temperate forests, temperate grasslands, tropical forests, tropical grasslands and mediterranean forests) separately for those responses with sufficient sample size (Supplementary Figs. 16 and 17).

To check for publication bias, we used funnel plots[100] via the 'funnel' function of the 'metafor' package[37] (Supplementary Fig. 8). We further performed regression correlation tests for funnel plot asymmetry[101] via the 'regtest' function of the 'metafor' package[37] to adjust for the overall mean[102] (Supplementary Table 4).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data are available on figshare: https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_wild_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031 ref. 103.

Code availability

All core analysis and figure scripts are available on figshare: https://figshare.com/projects/Data_and_scripts_for_manuscript_Worldwide_evidence_that_wild_megafauna_shape_ecosystem_properties_and_promote_spatial_heterogeneity_/180031 ref. 103.

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Author contributions
J.T., E.J.L., E.l.R., A.J.A., J.-C.S and J.A.K. conceptualized the project. J.T. and E.J.L. developed the methodology. J.T., E.J.L. and M.T. performed data analysis. J.T., E.J.L. and J.A.K. conducted investigations. J.T. and E.J.L. performed visualization. J.T., E.J.L. and J.-C.S. administered the project. E.l.R., E.J.L. and J.-C.S. mainly supervised the project. A.J.A. and J.K. co-supervised the project. J.T., E.l.R., J.A.K. and E.J.L. wrote the original draft. J.T., E.l.R., A.J.A., R.B., J.K., J.A.K., M.T., E.J.L. and J.-C.S. reviewed and edited the manuscript.

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Ecological, evolutionary & environmental sciences study design

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Study description	We conducted a systematic literature search to find studies investigating the impact of wild megafauna on ecosystems. Studies included contrasts in megafauna density and megafauna presence/absence, with >89 % being exclosure experiments (Fig. S1). Comparisons of high and low density were only included if those areas were adjacent and were the result of management decisions (e.g., a hunting area vs a protected area). Megafauna effects were calculated as standardized mean difference (Hedges' g) while within-treatment heterogeneity was estimated using the logarithmized ratio between two coefficients of variation (lnCVR) 35. The final dataset consisted of 5,990 data points (i.e., a comparison between an exclosure and control) across 26 ecosystem responses from 297 studies (Table S1, Table S2). The dataset was geographically biased towards Europe, North America, South Africa, Australia (Fig. S2, Fig. S3), towards the Afrotropics (Fig. S4A) and temperate forests (Fig. S4C), and against areas with low temperatures and/or high precipitation (Fig. S4B).
	The median of the area of measurement (i.e., plot size) was 1 m2 [Q2.5: 0.002 m2; Q97.5: 25,000 m2] (Fig. S5A), the median treatment duration was 2190 days [Q2.5: 365 days, Q97.5: 21,900 days] (Fig S5B), the median number of data points per study was 11 [Q2.5: 1, Q97.5: 97] and the median number of studies per response was 15 [Q2.5: 6 , Q97.5: 108].
	We used random effects meta-analytic models36 to investigate the mean effect of megafauna on 26 different ecosystem responses and their heterogeneity.
	The effects of megafauna are predicted to be dependent on body size21,22 and environmental conditions such as nutrient availability23 and productivity24. Therefore, we added body mass (weighted by relative biomass per species for responses with sufficient sample size (>10 studies), see methods for details) and a variety of environmental factors (Table S3) as variables to our models. We added each covariate as a single variable and compared the single-term model to its intercept only model, using a likelihood ratio test (LRT). If the covariate significantly improved model quality, we considered it as explaining some of the variability in the effects of megafauna. Moreover, for those responses with sufficient sample size, we divided our data in communities including megaherbivores (>=1000 kg) vs communities without megaherbivores (Fig. S6) and communities including large herbivores >=100 kg vs without large herbivores (Fig. S7) and analyzed their impact separately.
Research sample	The final dataset consisted of 5,990 data points (i.e., a comparison between an exclosure and control) across 26 ecosystem responses from 297 studies
Sampling strategy	We searched Web of Science (www.webofscience.com) on 18th February 2021 with a string of search terms that included the common names and latin genera of all terrestrial mammalian megafauna species (common names from HerbiTraits v1.2 74) separated with an 'OR' operand, combined with the following search terms: "disturb*, graz*, brows*, impact*, effect, affect, disrupt, facilitate, invasi*, ecosystem*, vegetat*, plant*, fauna*, reptil*, amphib*, bird*, rodent*, fish*, invertebrat*, insect*, soil*, carbon, climate, albedo, river*, riparian, desert*, forest*, tundra, decomposition, grassland*, savanna*, chaparral, scrub, shrub, diversity, heterogeneity, extinction, richness, environment, reptile*, ecolog*, hydrolog*, disturbance, density, biodiversity, response*, ecosystem, herbaceous, canopy, germination, cover, pollinator*, tree, nutrient*, understory, erosion, grass*, vegetation, community, exclosure, competition, effect*, abundance, productivity" in combination with the topic filter: "WC=(Ecology OR Zoology OR Environmental Sciences OR Biodiversity Conservation OR Evolutionary Biology OR Geography Physical OR Remote Sensing OR Plant Sciences OR Multidisciplinary Science OR Forestry OR Entomology OR Marine & Freshwater Biology OR Mycology OR Biology OR Oceanography OR Ornithology OR Behavioral Sciences OR Fisheries" After removing duplicate studies with the function find_duplicates of the R package 'revtools' 75, this led to 62,628 hits. After screening all titles and removing obviously unsuitable articles, this number was reduced to 2369 studies.
	The literature list was extended by studies used in other meta-analyses e.g., 38,76 and found in reference lists of studies we downloaded. We supplemented the list further with focused Google Scholar searches on the 15th of July 2022, using the following terms: "ungulate impacts island*", "introduced goat impact island*", "introduced deer impact*", "feral camel impact*", "wild OR feral boar OR hog OR pig OR feral pig OR swine impact*", "feral cattle impact*", "invasive ungulate hawaii OR guam OR new zealand OR pacific island OR new caledonia OR galapagos OR caribbean OR oceanic island" and a Web of Science search on the 22nd of December 2022 using the search string "herbivore* AND (plant* OR soil) AND nutrient* AND response*". This led to the addition of 38 and 15 studies respectively.

Considering that ecosystem responses can differ drastically between wild and domesticated animals 19,77, we only considered studies investigating wild megafauna populations. We excluded studies investigating only herbivores < 45 kg. Further, we only included studies that compared adjacent areas of low (mostly no megafauna) and high megafauna densities due to known factors like exclosures, policy-driven differences (hunting versus no-hunting in adjacent properties), and differences in introduction or eradication histories (adjacent islands with and without megafauna). Given that adding nativeness to our models never improved model fit (LRT=[0.00, 3.62], p=[0.12, 0.95], Fig. S9), except for plant cover (LRT = 4.03, p = 0.04, but with the same effect direction for both introduced (g = -0.42 [-0.58, -0.26]) and native megafauna (g = -0.22 [-0.32, -0.11]), Fig. S10), we also included non-native megafauna in our analysis.

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Data collection	We digitized measures of central tendency (mean, median), variability (standard deviation, interquartile ranges), error (standard error, confidence intervals) and sample sizes for each response in each study. We used the 'Figure_Calibration' plugin 78 in ImageJ 1.53k (www.imagej.nih.gov/ij/) to extract data from figures. We also digitized relevant information associated with each observation, which included time since treatment (e.g., exclosure construction or island colonization), study location (latitude, longitude; Fig. 4), reported density of megafauna (converted to biomass per hectare), megafauna nativeness and relative abundance of megafauna (in the case of multispecies megafauna communities). However, not all studies reported these variables and in most cases sample size was too small to test for them specifically (i.e., only 172 out of 297 studies reported megafauna densities).
Timing and spatial scale	Included studies report data from 1977 - 2022 and are globally distributed
Data exclusions	Considering that ecosystem responses can differ drastically between wild and domesticated animals 19,77, we only considered studies investigating wild megafauna populations. We excluded studies investigating only herbivores < 45 kg. Further, we only included studies that compared adjacent areas of low (mostly no megafauna) and high megafauna densities due to known factors like exclosures, policy-driven differences (hunting versus no-hunting in adjacent properties), and differences in introduction or eradication histories (adjacent islands with and without megafauna). Given that adding nativeness to our models never improved model fit (LRT=[0.00, 3.62], p=[0.12, 0.95], Fig. S9), except for plant cover (LRT = 4.03, p = 0.04, but with the same effect direction for both introduced (g = -0.42 [-0.58, -0.26]) and native megafauna (g = -0.22 [-0.32, -0.11]), Fig. S10), we also included non-native megafauna in our analysis. In grouping the individual ecosystem responses, we attempted to find a compromise between maximizing sample size and ecological accuracy. Apart from obviously incorrect groupings (e.g., NDVI as measurement for PP), we have essentially followed the categories used by the authors of the respective studies. For example, primary productivity responses are mainly composed of various growth rate measurements (such as tree growth rate, total crown growth, leaf growth rate, etc.). All included types of measurements for each response can be found in the `Data and supplementary files` folder on Figshare (file name: "measured_responses_R1.csv"). We exclude all before-after comparisons (e.g., a plot measured prior to construction of an enclosure and then again afterwards) due to the high rates of change in many ecological systems over time, such as afforestation, climate shifts, and succession. Studies investigating plant nutrients but reporting nutrient values in units per area were also excluded because any differences possibly rather reflect biomass removal due to megafauna foraging than actual changes in nutrient concentrations.
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Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s)	*Specify: functional, structural, diffusion, perfusion.*
Field strength	*Specify in Tesla*
Sequence & imaging parameters	*Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*
Area of acquisition	*State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI   ☐ Used   ☐ Not used

Preprocessing

Preprocessing software	*Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*
Normalization	*If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*
Normalization template	*Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*
Noise and artifact removal	*Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*

Volume censoring	*Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

Model type and settings	*Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).*

Effect(s) tested	*Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.*

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference	*Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.*

(See Eklund et al. 2016)

Correction	*Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).*

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	*Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).*

Graph analysis	*Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*

Multivariate modeling and predictive analysis	*Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*