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Native and introduced megafauna have convergent effects on animals and ecosystems: a meta-analysis

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Introduced large herbivores (henceforth megafauna) are thought to have 'harmful' effects on ecosystems by disrupting coevolutionary dynamics. If this is the case, their effects should be distinct from those of native megafauna. We use a systematic meta-analytic dataset of 3,532 observations from 235 articles to test whether there is any difference between the effects of native, introduced, and invasive megafauna on animals, soil, and a variety of ecosystem processes. Among 32 ecological responses, we only find moderate evidence that invasive megafauna has more neutral effects on soil compaction than native megafauna. We then compare the effects of introduced megafauna to intact African megafauna assemblages, the closest proxies for the communities that dominated Earth's continents for millions of years. We find moderate evidence that introduced megafauna reduces soil magnesium more than African megafauna, but no differences among the other responses. Our results suggest that nativeness is unlikely to be a biological attribute of megafauna. While the effects of introduced megafauna may seem unusual in reference to modern defaunated baselines, we suggest that broader lenses—and objective research across the cascading indirect effects of megafauna—will help us better understand the role of introduced megafauna in a time of rising global novelty.

For ~55 million years, a diversity of large terrestrial herbivores (henceforth megafauna) exerted top-down influences on ecosystems across all continents and many islands. In the Late Pleistocene (~12,000 years ago), human-caused extinctions and declines of these animals led to dramatic changes in Earth's ecosystems, including shifts in vegetation structure, increases in wildfire, and the loss of nutrient and seed dispersal[1–4]. The only mammal communities largely reflective of the evolutionary contexts of the Cenozoic persist in Africa and parts of Asia[5], where these animals are increasingly threatened by habitat loss and overexploitation[6].

However, a countercurrent of refaunation has emerged over the last centuries as humans have reshuffled species across the world, including some of the world's remaining megafauna[7,8]. While many of these introduced species are threatened in their native ranges[9], they are largely considered pests and targeted for eradication or culling[10,11]. This is particularly true for those described as invasive [i.e., species that are thought to spread rapidly or be particularly 'harmful'[12,13]].

These policies are predicated on the hypothesis that "the introduction of species outside their native range mostly disrupts

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established eco-evolutionary dynamics"[14], which is justified by the proposition that "many of the species that constitute natural communities are the products of coevolutionary processes"[15,16]. However, it is rarely possible to directly measure whether species have coevolved[17]. Instead, coevolutionary history is presupposed from dispersal history. This overlooks the strong possibility that many species can coexist due to ecological mechanisms [e.g., predation[18]] and that many communities may have assembled simply from processes of ecological fitting, with coevolution playing a less important role than usually considered[19,20].

Since the 1990s, nativeness and invasiveness have become axiomatic to conservation policy and to ecological thought[21]. However, for a category like nativeness to be supported by science, it must be empirically measurable[22–25]. Therefore, to claim that nativeness is biologically real, one must compare the effects of similar native and introduced organisms and find that they differ. Otherwise, nativeness would remain simply a description of dispersal history, agnostic to (co) evolutionary mismatches.

In a recent study, we found no difference in the effects of native or introduced megafauna on plant diversity and abundance[26]. However, we did not test the importance of nativeness across the spectrum of megafauna impacts, including many of potential conservation concern —such as impacts on other vertebrates, invertebrates, soil compaction, soil nutrients, and so on[27,28].

We here employ a meta-analytic dataset of 3532 observations from 235 studies to evaluate whether there is evidence to claim that native, introduced, or invasive megafauna (≥45 kg) have distinct effects on ecosystems (Supplementary Fig. 1). We analyze the effect of megafauna on 32 ecological responses for which we had sufficient sample size (3 articles per nativeness category). We ran models with invasiveness separately, and thus estimates for invasive megafauna [based on the Global Register of Introduced and Invasive Species (GRIIS)[29]] represent the subset of introduced megafauna that have been labeled especially 'harmful'. We then compare the effects of introduced megafauna with those of intact African megafauna assemblages, where megafauna diversity and composition remain most analogous to the prehistoric compositions of the world's continents[5].

Results

We report planned contrast comparisons to test whether the effects of introduced or invasive megafauna are different from those of native megafauna. We report results following the language of evidence[30], thus highlighting results with p values between 0.01 and 0.05 as 'moderate evidence' and p values between 0.05 and 0.1 as 'weak evidence'. We also report if results were resilient to the exclusion of influential articles or observations (based on Cook's distance[31]). Throughout, we report from log-likelihood ratio tests on whether including nativeness or invasiveness improved model quality relative to intercept-only models.

Effects on other animals

Multilevel meta-analytic models found little statistical evidence ($p < 0.05$) that the effects of introduced or invasive megafauna differed from the effects of native megafauna on animal abundance or diversity (planned contrast $t_{8-56} = [-1.81, 1.79]$, $p = 0.09–0.91$, Fig. 1A–D, see Supplementary Data 1 for full statistical results per response). However, there was weak evidence ($0.05 \leq p \leq 0.1$) that invasive megafauna increased the abundance of invertebrate detritivores more than native megafauna ($t_{18} = -1.79$, $p = 0.089$, Supplementary Data 1), that introduced megafauna increased small mammal abundance more than native megafauna ($t_{12} = -1.79$, $p = 0.095$, Supplementary Data 1), and that introduced megafauna reduced vertebrate diversity more than native megafauna ($t_{12} = 1.79$, $p = 0.099$, Supplementary Data 1).

All of these differences faded when influential articles were excluded ($p > 0.1$, Supplementary Figs. 1, 2, Supplementary Data 2) and nativeness and invasiveness did not improve model quality relative to intercept-only models (log-likelihood ratio test (LRT) = [0.01, 3.22], p = 0.07–0.90, Supplementary Data 1).

Collectively, we found evidence that native and introduced megafauna reduced the abundance and diversity of other vertebrates (Hedges' g ± 95%CIs: abundance g = −0.21 ± [−0.36, −0.06], $t_{33} = -2.9$, $p = 0.006$, diversity g = −0.18 ± [−0.28, −0.09], $t_{13} = -4.22$, $p = 0.001$); reduced mammal abundance (g = −0.33 ± [−0.63, −0.05], $t_{16} = -2.46$, $p = 0.03$) and small mammal abundance (g = −0.47 ± [−0.77, −0.18], $t_{13} = -3.43$, $p = 0.004$), reduced bird diversity (g = −0.18 ± [−0.30, −0.07], $t_9 = -3.72$, $p = 0.005$), reduced invertebrate diversity (g = −0.34 ± [−0.64, −0.04], $t_{25} = -2.33$, $p = 0.03$), and reduced invertebrate herbivore abundance (g = −0.28 ± [−0.54, −0.03], $t_{24} = -2.27$, $p = 0.03$).

Effects on ecosystems & soils

We found moderate evidence ($0.01 \leq p < 0.05$) that invasive megafauna have more neutral effects on soil compaction than native megafauna (planned contrast: $t_{10} = 2.26$, $p = 0.047$; Fig. 2, Supplementary Data 1) and invasiveness improved model quality for this response (LRT = 4.03, $p = 0.04$). However, these results were no longer significant when excluding influential observations ($p = 0.12$) or articles ($p = 0.24$, Supplementary Fig. 2, nd Supplementary Data 2).

We also found weak evidence ($0.05 \leq p < 0.1$) that introduced megafauna had more neutral effects on plant growth rates than native megafauna ($t_{16} = -2.02$, $p = 0.06$, Supplementary Data 1); increased bare ground cover more than native megafauna ($t_{74} = -1.86$, $p = 0.07$); reduced dead vegetation abundance ($t_{48} = 1.89$, $p = 0.06$) and litter cover ($t_{41} = 1.81$, $p = 0.08$) more than native megafauna; and that invasive megafauna reduced soil magnesium concentrations more than native megafauna ($t_{12} = 1.89$, $p = 0.08$). With the exception of litter cover, all of these differences faded ($p > 0.1$) when influential articles were excluded (Supplementary Fig. 3 and Supplementary Data 2).

There was no evidence that megafauna nativeness or invasiveness explained the other 19 ecosystem and soil responses and did not improve model quality relative to intercept-only models ($t_{8\text{-}190} = [-1.46, 1.69]$, $p = 0.12\text{-}0.96$, Fig. 2A, B, LRT = [0.002, 2.73], $p = 0.1–0.96$).

In general, we found evidence that megafauna—native or otherwise—increased bare ground cover (g = 0.92 ± [0.62, 1.22], $t_{34} = 6.22$, $p < 0.0001$), reduced dead vegetation and litter cover (−0.53 ± [−0.70, −0.36], $t_{49} = -6.18$, $p < 0.0001$; −0.57 ± [−0.79, −0.35], $t_{42} = -5.24$, $p < 0.0001$), and reduced plant growth rates (−0.38 ± [−0.57, −0.18], $t_{17} = -3.56$, $p < 0.0001$). Megafauna also increased soil compaction (0.42 ± [0.06, 0.77], $t_{14} = 2.49$, $p = 0.03$), reduced soil calcium availability (−0.30 ± [−0.55, −0.05], $t_{13} = -2.61$, $p = 0.02$), and increased soil labile Nitrogen (0.24 ± [0.07, 0.41], $t_{21} = 2.96$, $p = 0.0007$).

The effects of the last 'intact' megafauna communities

A potential caveat with the results reported above is that many native megafauna communities have experienced substantial extinctions since the Late Pleistocene, have lost their predators, or are occurring in landscapes heavily modified by human activity—all of which may lead to native megafauna having unusual impacts on ecosystems[32]. We thus compared the effects of introduced megafauna globally with those of 'intact' megafauna communities in Africa—communities that are the most functionally similar to the megafauna communities that were pervasive on every continent for ~35 million years until the Late Pleistocene extinctions[5]. We defined these communities as assemblages with megaherbivores (>1000 kg) as well as smaller herbivores, thus excluding data from African parks missing their megaherbivores and excluding particular size-selective exclosure treatments (e.g., mesoherbivore comparisons at the Mpala or UHURU exclosure

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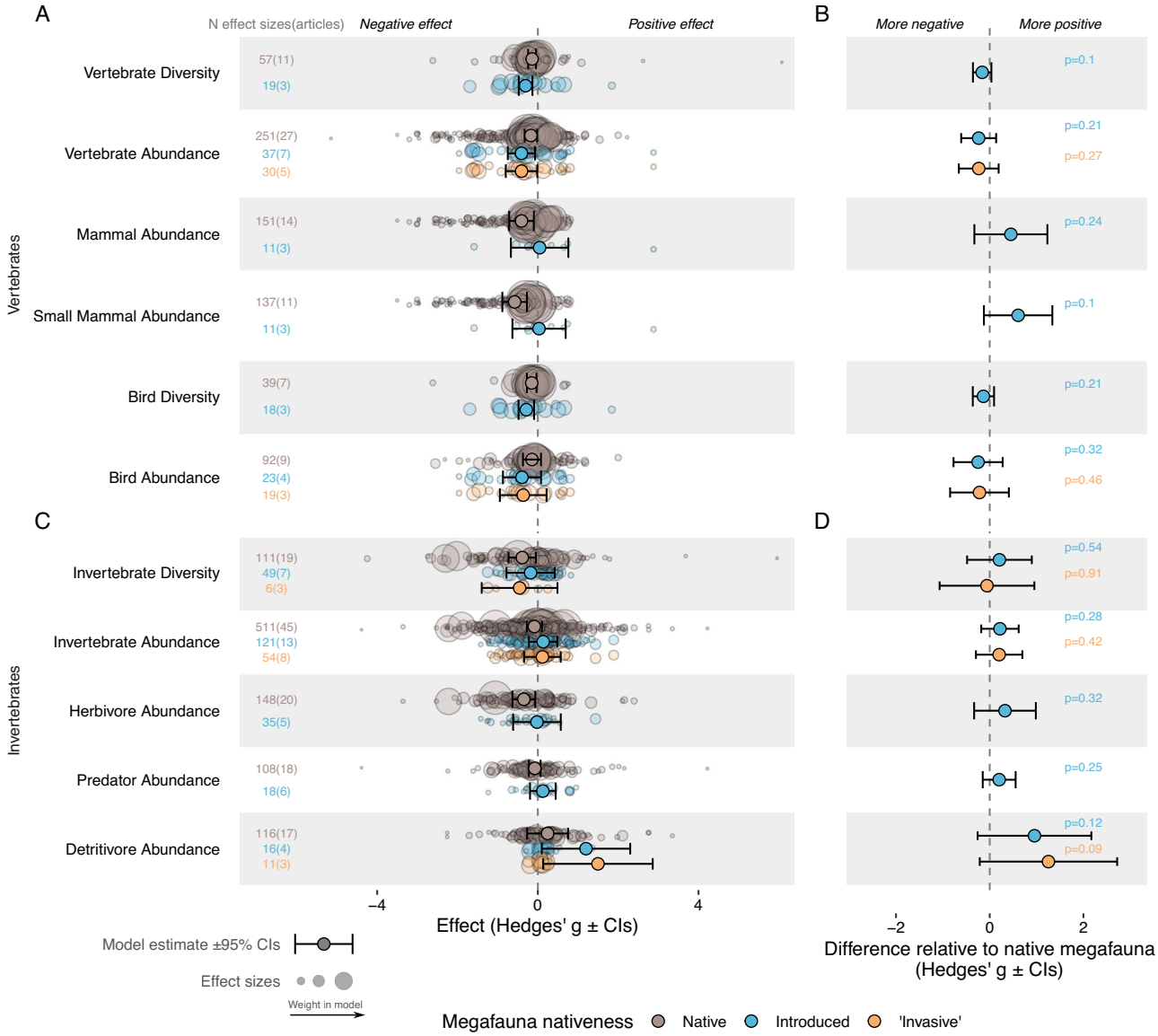


Fig. 1 | Effects of native, introduced, and invasive megafauna on other animals. Overall effects of native, introduced and invasive megafauna on vertebrates (**A**) and invertebrates (**C**). The x-axis indicates the effect size (calculated as standardized mean difference or Hedges' g). Meta-analytic model estimates are indicated with larger points with 95% confidence intervals (error bars). Individual effect sizes are plotted as semi-translucent points, with larger points having less sampling variance and thus higher influence on model estimates. Numeric annotations indicate sample size in terms of effect sizes and articles (in parentheses), which are also in Supplementary Data 3. **B**,**D**. Planned contrast comparisons between the effects of introduced and invasive megafauna relative to native megafauna. Point and error bars indicate estimated difference in impact (±95% confidence intervals). *P*-values (from two-tailed planned contrast tests with the t-distribution) are indicated with text annotations for each comparison (see Supplementary Data 1 for model statistics and summaries). Introduced megafauna (blue) include all introduced megafauna, while those defined as invasive megafauna (gold) contain the subset locally registered as invasive by GRIIS[29] and were produced in separate models. The data and scripts used to produce the analyses are provided on Github[77].

experiments). Sample sizes limited us to 16 ecological responses (Supplementary Data 3).

We found moderate evidence that introduced megafauna reduce soil magnesium concentrations more than African megafauna ($t_5 = -2.67$, $p = 0.04$, Supplementary Data 1, and Fig. 3). However, this was not significant after excluding influential articles (Supplementary Fig. 3, Supplementary Data 2). We also found weak evidence that introduced megafauna had more neutral effects on plant growth rates than African megafauna ($t_8 = 0.27$, $p = 0.05$, Supplementary Data 1), which became stronger after excluding influential articles and observations ($p = 0.01$–0.04, Supplementary Fig. 4, Supplementary Data 2). Including nativeness only improved model quality for soil magnesium responses (magnesium: LRT = 5.5, $p = 0.02$, Supplementary Data 1).

We found no further evidence that introduced megafauna have different effects than intact African assemblages for the other 14 responses ($t_{4\text{-}21} = [-1.28, 1.82]$, $p = 0.11$–0.94, Supplementary Data 1) and nativeness did not improve model quality for any other model (LRT = [0.005, 2.96], $p = 0.08$–0.94, Supplementary Data 1).

Discussion

Invasion biology treats nativeness as a biologically meaningful category shaped by long-term evolutionary history, leading to introduced organisms having categorically different ecological impacts from native species. We evaluated a broad spectrum of megafauna impacts [and see ref. 26] and found that the effects of introduced and invasive megafauna are largely similar to those of

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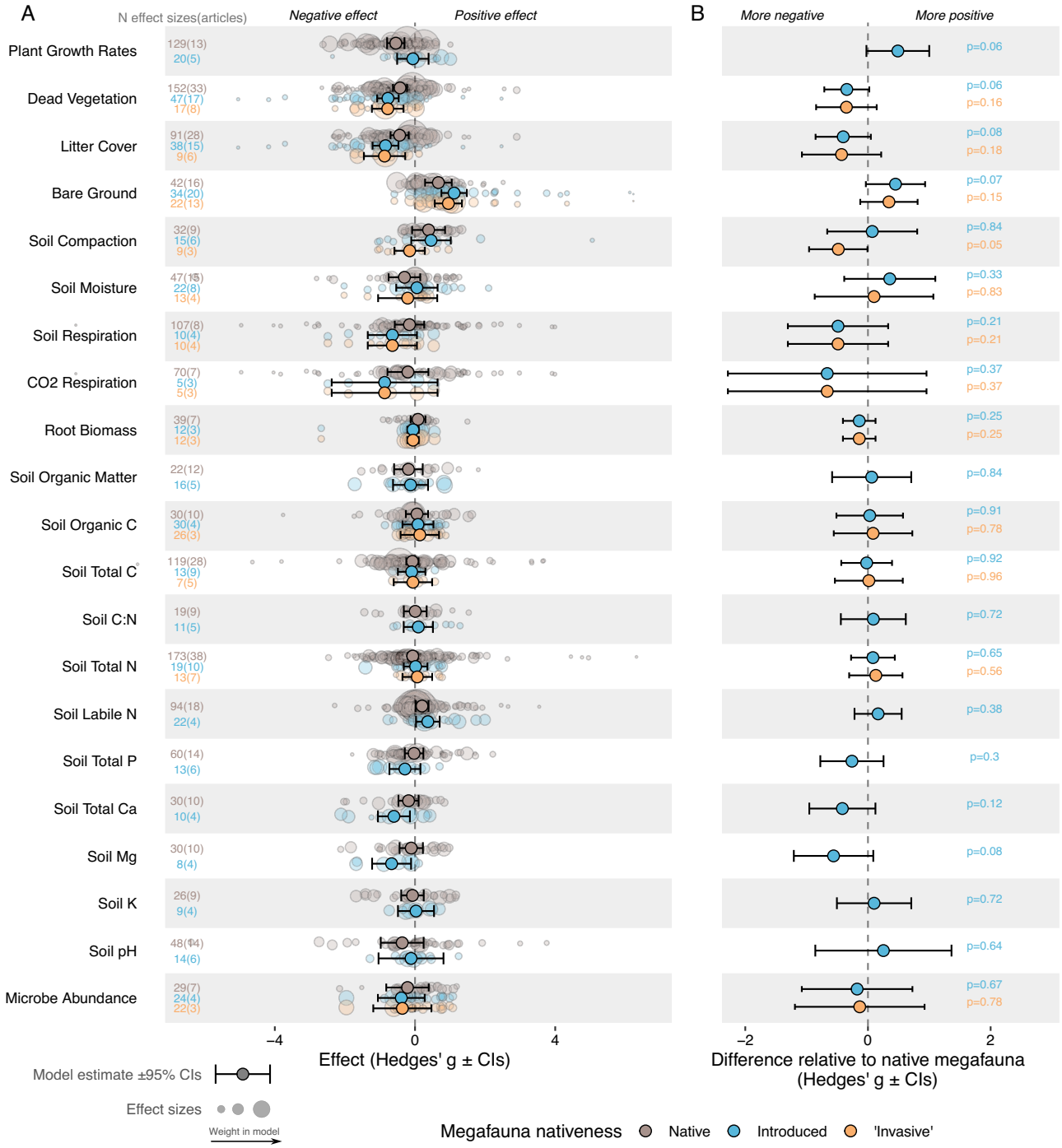


Fig. 2 | Effects of native, introduced, and invasive megafauna on soils. A Overall effects of native, introduced and invasive megafauna on ecosystems and soils. The x-axis indicates the effect (Hedges' g) on ecosystem response (y-axis). Meta-analytic model estimates are indicated with larger points with 95% confidence intervals (error bars). Observations are plotted as semi-translucent points, with larger points having less sampling variance and thus higher influence on model estimates. Numeric annotations indicate sample size in terms of observations and citations (in parentheses), which are also in Supplementary Data 3. **B** Planned contrast comparisons between the effects of introduced and invasive megafauna relative to native megafauna. Point and error bars indicate estimated difference in impact (± 95% confidence intervals). *P*-values (from two-tailed planned contrast tests with the t-distribution) are indicated with text annotations for each comparison (see Supplementary Data 1 for model statistics and summaries). Numeric annotations indicate sample size in terms of observations and articles (in parentheses). The data and scripts used to produce the analyses are provided on Github[77].

native megafauna—though the points of difference deserve attention and further investigation.

We found moderate statistical evidence ($0.01 \leq p < 0.05$) that introduced megafauna had more neutral effects on soil compaction than native megafauna and that introduced megafauna reduced soil magnesium concentrations more than African megafauna. Both of these results appear to reflect differences in megafaunal functional traits, which we did not have sufficient sample size to model directly. In particular, these differences appear to be driven by pigs (Suidae). Feral pigs (*Sus scrofa*) were the focus of most of the introduced megafauna articles in both responses (75% of soil magnesium articles, 66% of soil compaction articles), but Suidae were only a subdominant member of

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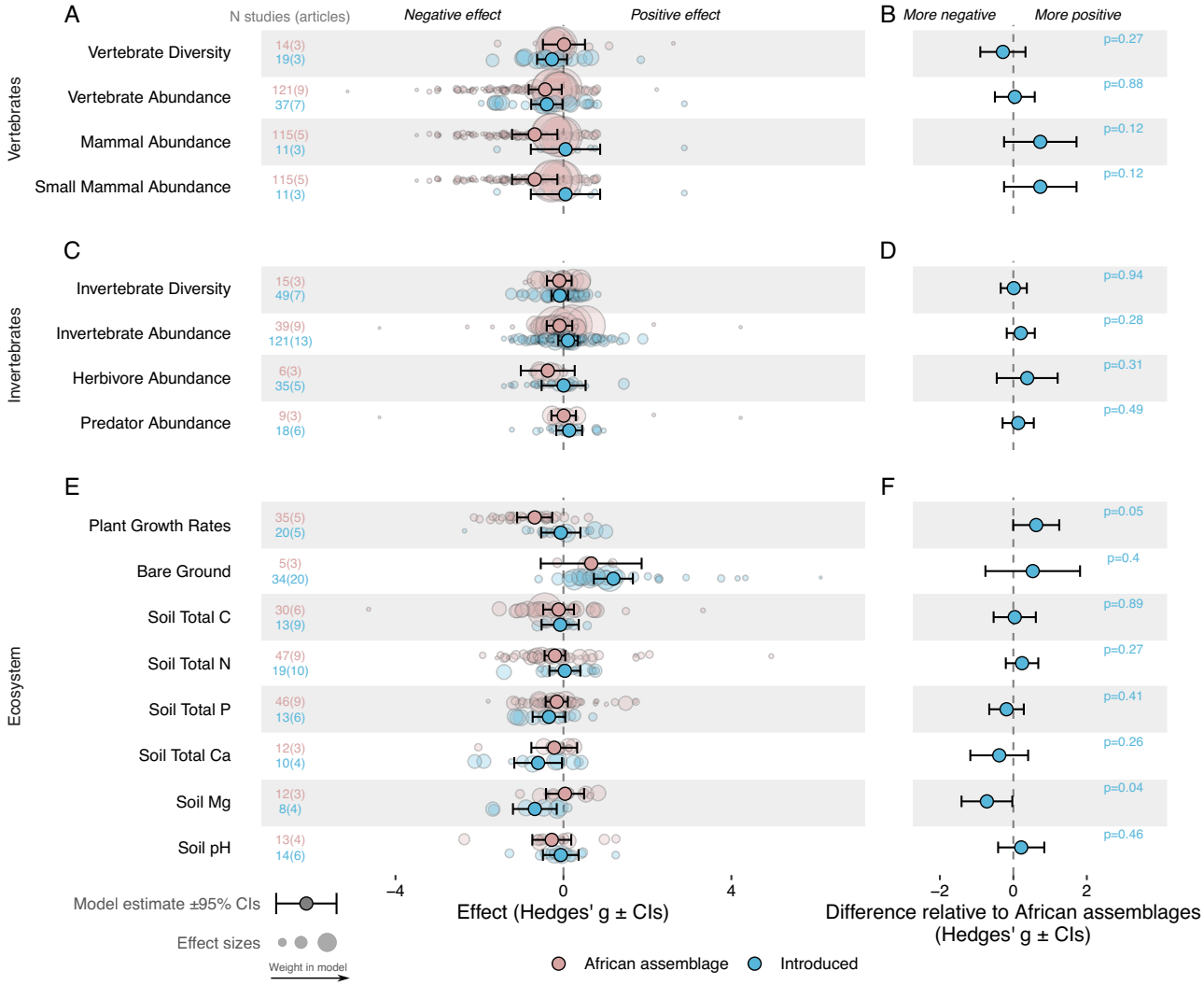


Fig. 3 | Effects of introduced herbivores relative to intact African megafauna communities. A,**C**,**E**. Overall effects of intact African megafauna communities and introduced megafauna on (**A**) vertebrates, (**C**) invertebrates, and (**E**) ecosystems. The x-axis indicates the effect (Hedges' g) on ecosystem response (y-axis). Meta-analytic model estimates are indicated with larger points with confidence intervals (error bars). Observations are plotted as semi-translucent points, with larger points having less sampling variance and thus higher influence on model estimates. Numeric annotations indicate sample size in terms of observations and citations (in parentheses), which are also in Supplementary Data 3. **B**,**D**,**F**. Planned contrast comparisons between the effects of introduced megafauna relative to African megafauna on (**B**) vertebrates, (**D**) invertebrates, (**F**) ecosystems. We found no statistical evidence for significant differences between the effects of introduced herbivores and African megafauna communities. Point and error bars indicate estimated difference in impact (±95% confidence intervals). P-values (from two-tailed planned contrast tests with the t-distribution) are indicated with text annotations for each comparison (see Supplementary Data 1 for model statistics and summaries). Numeric annotations indicate sample size in terms of observations and articles (in parentheses). The data and scripts used to produce the analyses are provided on Github[77].

one native megafauna article on soil compaction (of 9 articles) and minor components of the African articles that evaluated soil magnesium responses. In their native and introduced ranges, pig rooting can reduce soil compaction[33,34]) and, by mixing soil layers and leaf litter, can lead to increased nutrient leaching rates[34–37] and increased plant nutrient uptake rates and plant growth rates[38], all of which can lead to lower soil concentrations of certain mineral nutrients[34–37].

There were some other responses for which weak but non-significant evidence ($0.05 \leq p < 0.1$) might suggest differences between the effects of native and introduced megafauna. However, with the exception of litter cover, these differences faded once influential articles were excluded, and there was no difference between the effects of introduced megafauna and African megafauna assemblages on these responses. While future empirical work may discover that some introduced megafauna have impacts that are only explainable due to their nativeness, the burden of proof rests on claims that nativeness is biologically meaningful—evidence which, for megafauna, is largely absent or weak.

To claim that introduced species have distinct impacts, one must compare their impacts to the proper controls: similar native organisms. Unfortunately, most invasion biology impact literature, and dominant methodologies, such as IUCN's EICAT framework[39], consist of tabulations of the impacts of introduced organisms without comparison to similar native species[40] [e.g., see refs. 14,41]. Under these lines of circular reasoning, is there any way for an organism to not be 'harmful'? After all, all organisms must take up space and consume resources, thereby negatively affecting at least some other species.

Regardless, many of the impacts of megafauna, both native and introduced, can, at first glance, be interpreted as ecological 'harms'. These impacts, however, may have downstream and broader-scale consequences that we may find desirable. For example, while reducing leaf litter and dead vegetation can increase soil surface temperatures

and reduce habitat for invertebrates and small vertebrates[42], it can also facilitate the germination of many plant species and reduce wildfire frequency and intensity[43–45]—one of the notable ways megafauna have impacted ecosystems throughout the Cenozoic[46–48]. Indeed, several articles in our meta-analysis found that both native (e.g., ref. 49,) and introduced megafauna[50] reduced wildfire intensity.

Similarly, while megafauna appear to reduce the abundance of many vertebrates at the plot scale—most likely through competition[51,52]—megafauna can also facilitate vertebrates at other temporal or spatial scales by maintaining water availability, reducing wildfire, as prey or carrion, and by creating unique resources and habitats through herbivory and disturbance[32,53,54]. Finally, reductions in small mammal abundance can be seen as both 'harmful' and 'beneficial' as high rodent abundance can suppress the germination of some plant species and can promote ticks and tick-borne pathogens[55–57].

As such, our results suggest caution when applying moral mathematics to the messy, multivariate world of ecology. Taking the sum of the 'beneficial' and 'harmful' effects of an organism to derive some moral value is common for both native and introduced species (e.g., ref. 58). However, this not only exceeds the powers of science (which can only describe what *is*, not what is *good*[22]) but also prevents us from openly studying organisms across the full spectrum and cascading consequences of their effects and interactions. Moral mathematics yields simplistic stories of heroes and villains, eclipsing rich and nuanced stories of ecological complexity[59,60].

This is not to say that native and introduced megafauna may not come into conflict with important conservation goals, such as preventing extinctions. In some cases, interventions—including lethal ones—may be considered necessary, especially in some isolated biota (e.g., islands) or if addressing underlying ecological drivers (such as predator persecution) is impossible. However, our results suggest that nativeness itself is a poor justification for these decisions and that conservation decisions would be better justified with honesty about ultimate drivers[61], transparency towards normative values[62,63], and increased attention to the underlying ecological conditions that promote coexistence[64].

Wild introduced megafauna have restored trait combinations and ecological functions that were once ubiquitous[8,65]. This unintentional and spontaneous rewilding may change the way ecosystems look and function relative to the defaunated landscapes of the Holocene. However, these changes appear to be rarely different than the effects of native megafauna and, if anything, are less dramatic than the effects of intact African megafauna assemblages—the closest proxies to the evolutionary conditions under which most modern biodiversity evolved[5]. Given these findings, we suggest that introduced megafauna merit open-minded, evidence-based study and conservation consideration, rather than categorical dismissal based solely on their dispersal histories. Further interrogation of the concept of nativeness is essential to maintain the rigor of our disciplines, to improve our understanding of the interplay of (co)evolution and ecology, and to envision pragmatic ways to respond to ongoing and incoming species reshuffling and landscape change[9,63].

Methods

Data compilation

We here analyzed an updated version of the systematic meta-analytic dataset published in refs. 26,52. The original dataset derives from a literature review originally completed on the 19th of February 2021. This dataset consists of comparisons between areas with high and low megafauna densities, as provided by exclosures, natural experiments (e.g., islands with and without megafauna), and density contrasts within a landscape resulting from known management actions (e.g., differences in hunting pressure). We included data from all experimental designs that presented discrete comparisons between adjacent areas with high and low megafauna densities, including before/after contrasts, in order to maximize the number of responses we could include.

We excluded articles of semi-domestic animals whose movements were controlled by managers or who were fed supplementary food. We also excluded density contrasts that were caused by unknown drivers—e.g., comparing an area with high megafauna density to an area with low megafauna density without a reasonable explanation of some quasi-experimental mechanism behind these density differences.

We updated this dataset with a modified search string in Web of Science for all records between February 19th 2021 and October 9th 2025. Using the original search string from refs. 26,52 returned >50,000 records (similar to the number of records from the initial search in 2021). We thus modified the search string to return more relevant and tractable results (see Supplementary Table 1 for modified search string). The modified search string returned 4876 records (see Supplementary Fig. 1 for PRISMA diagram). Title screening reduced this to 263 records for which we evaluated full texts and extracted data. In sum, we were able to add 90 articles and 1778 observations to our database. In all cases, plots were the unit of replication.

We included all article types, including theses and reports and extracted data from main text and figures. Screening and extraction were conducted by four individuals (EJL, SR, JT, SN) and extraction was done with metaDigitise v1.0.1[66]. All extracted data was double-checked by EJL. To be consistent with[52], we did not contact authors for missing data nor did we impute missing data.

We also re-screened the records in Trepel et al. 2024[52], focusing on any effect size with a coefficient of variation >3. In doing so, we identified 18 articles from populations that were heavily managed like livestock and 2 that had improper designs (e.g., comparing distant areas with mixed grazing histories of livestock and wild herbivores). After excluding these and synthesizing the two databases, our full dataset consisted of 384 articles and 8554 effect sizes, which was filtered to 235 articles and 3532 effect sizes to focus on responses not published in Lundgren et al. 2024[26].

We set an a priori threshold of three articles per nativeness category and ecological response category, which limited us to 32 ecological response categories. Unfortunately, we had insufficient data to analyze these responses when stratified by oceanic islands, islands, and continents [e.g., as in ref. 26]. We chose a priori threshold of three articles because calculating means and standard deviation for each treatment level requires 2 degrees of freedom, which leaves an additional degree of freedom for the comparison. See Supplementary Data 3 for the sample sizes of all responses included in the final dataset, including those for which we lacked sufficient sample size.

While Trepel et al. 2024[52] reported the responses of many similar ecological response categories as us, we categorized responses into finer scales, including into body size bins and taxonomic classes. As such, we here analyzed several nested responses (e.g., small mammal abundance nested within total vertebrate abundance). For these, the same effect sizes were used in separate models. We categorized mammals as "small mammals" as reported by study authors. Invertebrate dietary guilds (herbivore, predator, and detritivore) were derived from ref. 67. For a full table of response categories (including nesting levels) see Supplementary Data 4.

Megafauna nativeness was derived from author descriptions, which aligned with IUCN Red List guidelines which define any species that has been moved by human beings (intentionally or otherwise) as introduced[68]. In ambiguous cases, we consulted with IUCN Red List distribution maps to determine nativeness. Megafauna invasiveness, e.g., whether they are considered particularly harmful and problematic, was determined from the Global Register of Introduced and Invasive Species (GRIIS), which provides country-level (iso3) invasiveness designations[29]. We integrated GRIIS data by intersecting the study coordinates with country polygons and merging in GRIIS status code. All spatial analyses were done with R package 'sf'[69].

Intact African assemblages were assessed based on the species lists reported by the study authors and consisted of studies within African protected areas that possessed megaherbivores as well as smaller megafauna. We excluded size-specific exclosure treatments that evaluated only the effects of megaherbivores or of medium-sized herbivores. The final studies of intact African assemblages derive from Kruger National Park (South Africa), Hluhluwe-iMfolowzi (South Africa), Serengeti National Park (Tanzania), Mpala Research Center (Kenya), Murchison Falls National Park (Uganda), Sanbona Wildlife Reserve (South Africa), Phinda Private Game Reserve (South Africa), Ivindo National Park (Gabon), Chobe National Park (Botswana), Lake Naivasha (Kenya), and the Endarakwai Ranch (Tanzania).

In order to maximize sample size, we calculated effect sizes as Hedges' g[70], a measure of standardized mean difference. Alternative effect sizes for discrete comparisons, such as log-transformed ratio of means, would require excluding >400 unique effect sizes due to negative values[71]. We used the 'escalc' function in the R package 'metafor' [version 4.8-0[71]] to calculate effect sizes and associated sampling variance. Sampling variances are used as model weights for each effect size and are derived from the standard deviation and sample size. Given high coefficients of variation and heteroscedasticity between treatments, we used the 'SMDH' formulation of Hedges' g[72]. All analyses were conducted in R (version 4.5.0).

Model specification

We fitted multilevel random-effect meta-analytic models with the function 'rma.mv' in the R package 'metafor'[71]. These models account for sampling variance and the non-independence structure among observations to produce overall model estimates, in this case, of the effects of native, introduced, and invasive megafauna. Models were fitted using a maximum-likelihood estimator to enable model comparisons and were specified to use the *t*-distribution for statistical tests. The *t* distribution is recommended over the *z* distribution when population standard deviation is unknown and with small sample sizes[73].

Our a priori hypotheses were that introduced or invasive megafauna would have different effects than native megafauna. We evaluated this hypothesis with planned contrast tests (i.e., post hoc tests), which were conducted by comparing the second level of each nativeness model to the intercept of each model (default output of 'rma.mv'). Importantly, our aim was not to evaluate whether each nativeness level was different from 0 but whether nativeness explained the variance in impacts *between* megafauna. See Supplementary Data 1 for model coefficients, random effect structures, planned contrast test statistics, and fit statistics (including I^2 and R^2).

The overall effects of megafauna, which we report when significantly different from 0 and if there was no difference between native and introduced or invasive megafauna, were derived from the overall estimates derived from intercept-only models.

To control for non-independence between observations, all models included an observation ID (unique for each data point) nested within an article ID. However, our data had complex non-independence structures, with some responses including different articles from the same study systems, repeated time series measurements, and repeated measurements of the same species or taxonomic group within the same article. To control for these sources of non-independence and avoid overfitting, we evaluated a suite of alternative random-effects structures and selected the optimal one based on BIC.

These alternative random effects structures included 1) a crossed random effect that controlled for articles at the same location (a 'site-id' for articles within 100 km of each other); 2) a time series random effect (with an autoregressive correlation structure); and 3) an additional nesting level within our main random effects of the particular response species as reported by the authors. We selected the random effect structure with the lowest BIC[74] for each ecological response after screening out models with σ^2 of 0 [as indicative for overfitting[74],].

Ideally, we would have included a phylogenetic covariance matrix to control for phylogenetic differences between megafauna communities. However, 43% of the articles evaluated the effects of multi-species megafauna communities, which prevents the calculation of phylogenetic dissimilarity. Future methodological development is necessary to control for phylogenetic non-independence in mixed-species comparisons.

To assess whether including nativeness or invasiveness variables improved model quality and thus added information value, we used log-likelihood ratio tests relative to an intercept-only model with the same random effect structure.

Influence analysis

We screened influential data by calculating Cook's distance for each article and observation, which measures how much the model predictions change when each article or observation is excluded. We then filtered out articles and observations with a Cook's distance greater than 4 divided by sample size (in this case, the number of observations or articles, respectively)[31,75]. We then reran all models without these influential observations and articles and compared the planned contrast results from these revised models to our main text results.

The removal of influential data led to introduced megafauna having more negative effects on vertebrate diversity when influential observations were excluded ($p = 0.03$, see Supplementary Data 2 for model statistics) but not when influential articles were excluded ($p = 0.2$); significantly more positive effects on plant growth rates when observations were excluded ($p = 0.03$) but not when influential articles were excluded ($p = 0.19$); significantly more positive effects on bare ground cover ($p = 0.02$) when influential observations were excluded but not when influential articles were excluded ($p = 0.12$); significantly more negative effects on soil Magnesium when influential articles were excluded ($p = 0.04$) but not when influential observations were excluded ($p = 0.15$, Supplementary Figs. 2-4, see Supplementary Data 2 for model results).

Excluding influential data for the comparison between introduced megafauna and intact African communities led to introduced megafauna having significantly more positive effects on the abundance of mammals and small mammals ($p = 0.02$) when influential articles were excluded but not when influential observations were excluded ($p = 0.17$); significantly more positive effects on plant growth rates (observations excluded: $p = 0.01$, articles: $p = 0.04$); significantly more positive effects on soil total Nitrogen when significant observations were excluded ($p = 0.03$) but not when influential articles were excluded ($p = 0.59$, Supplementary Fig. 5 and Supplementary Data 2).

We screened all articles and observations flagged as influential to ensure that the data were entered correctly and that the study design was correctly assessed. Since they were, we elected to maintain these articles in the main dataset and main text results.

Model heterogeneity and variance explained

To understand whether nativeness or invasiveness provided information value, we calculated the proportion of model variance reduced by these factors relative to an intercept-only model (Eq. 1, Supplementary Fig. 6). Total model variance was estimated by summing σ^2 across all hierarchical random effect levels for each model.

$$\frac{sum(\sigma^2_{null}) - sum(\sigma^2_{model})}{sum(\sigma^2_{null})} \quad (1)$$

σ^2 was calculated as the sum of model variance across all random effect levels for each model and compared between intercept-only models and models with either nativeness or invasiveness.

To understand how well nativeness and invasiveness explained heterogeneity in megafauna impacts, we calculated several statistics. First, we report total unexplained heterogeneity in each model (I^2), including both null intercept-only models and full models with our factors of interest (Supplementary Fig. 7). We also report total heterogeneity explained by our fixed effects ($R^2_{conditional}$, Eqs. 2–4). Conditional R^2 was calculated by taking the variance of the coefficient from our nativeness models multiplied by a [0, 1] vector corresponding to our predictor. This variance was then divided by the total model variance, which was the sum of this variance as well as σ^2 and τ^2 (for models that included a time series random effect).

$$s^2_{fixed-effect} = Var(\beta_1 x) \tag{2}$$

$$s^2_{total-variance} = s^2_{fixed-effect} + sum(\sigma^2) + \tau^2 \tag{3}$$

$$R^2_{conditional} = \frac{s^2_{fixed-effect}}{s^2_{total-variance}} \tag{4}$$

Surprisingly, some models (root biomass with nativeness and invasiveness) had an $R^2_{conditional}$ of 100% (Supplementary Fig. 8) due to an absence of heterogeneity ($I^2 < 0.0001$). We thus also calculated an alternative of R^2 (denoted R^{2*}) which used total variance in effect sizes as its denominator instead of summing model variance components (Eqs. 5–7, Supplementary Fig. 9).

$$s^2_{fixed-effect} = Var(\beta_1 x) \tag{5}$$

$$s^2_{yi} = Var(yi) \tag{6}$$

$$R^2_{conditional}{}^{*} = \frac{s^2_{fixed-effect}}{s^2_{yi}} \tag{7}$$

Publication bias

We used multilevel publication bias tests [following[76]] to evaluate small-sample publication bias, which is generally expected for high variance, low sample size studies, which are less likely to be published if the results do not support their hypotheses[76]. To evaluate this, we modeled the relationship between effect sizes and the square root of effective sample size (Eq. 8). Effective sample size (N_0) pools n from each group (e.g., n_1, n_2) and thus accounts for unbalanced sampling.

$$N_0 = \frac{4 n_{1i} n_{2i}}{(n_{1i} + n_{2i})} \tag{8}$$

We found evidence for small-sample publication bias in 1 of 69 models. This model (soil pH and African versus introduced megafauna) had a significant slope for the square root of effective N ($7.6 \pm [0.52, 14.81]$, $p = 0.04$), indicating that the estimated effects were related to sampling effort. For this model, we then ran a second model with effective N (not its square root) to estimate a corrected overall effect of megafauna on soil pH. This corrected estimate ($g = -1.01 \pm [-1.98, -0.04]$, $p = 0.04$) was more negative than the uncorrected intercept-only estimate for soil pH ($g = -0.16 \pm [-0.47, 0.15]$, $p = 0.27$). See Supplementary Data 5 for all publication bias test results, including corrected estimates.

Reporting summary

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

Data availability

The meta-analytic data generated in this study have been deposited in Zenodo at https://zenodo.org/records/20261849 and on github at (https://github.com/ejlundgren/ecosystem_metamega.git)[77]. Supplementary Data 1-6 include, respectively, (1) main text model summaries and fit statistics, (2) influence analysis results, (3) sample sizes across all response categories, (4) the nesting structure of response categories, (5) publication bias test results, and (6) all studies included in meta-analysis. The data and code to reproduce the figures are available on github at (https://github.com/ejlundgren/ecosystem_metamega.git)

Code availability

All code used in this study have been deposited in Zenodo at https://zenodo.org/records/20261849 and on github at (https://github.com/ejlundgren/ecosystem_metamega.git)[77]

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Author contributions

E.J.L., J.-C.S., J.T., E.R., and E.I.F.W. conceived of manuscript; E.J.L., J.T., and S.R. collected data; E.J.L., J.T., and S.N. analyzed data; all authors contributed equally to writing and editing manuscript.

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Competing interests

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