

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

Corresponding Author: Dr Erick Lundgren

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors present a well-written and compelling manuscript investigating the effects of native and introduced megafauna and investigate whether nativeness can be used to predict ecological impacts. The study uses a strong meta-analytic framework and found introduced species have similar reported effects to vertebrates, invertebrates, and ecosystems as native ones. The study is of broad relevance to conservation globally as introduced species have proliferated across the globe due to human activity.

The manuscript would benefit from increased clarity terminology and use of explicit definitions. The authors investigate whether there is support for biological nativeness – but do not articulate distinctions between various definitions (e.g., species which have coevolved vs a description of dispersal history) or how each may be empirically evaluated.

Perhaps related to a lack of clear definitions, I struggle with terming nativeness a “biological attribute”. Generally, biological attributes include physiological, behavioral, or genetic characteristics and evolutionary adaptations, etc. whereas nativeness is typically used a descriptive classification. Explicit definitions for these terms may alleviate this issue.

The authors posit that targeting of introduced species by conservation eradication programs is “[...] predicated upon the hypothesis that nativeness is a biological attribute of populations that shapes their ecological effects.” However, numerous rational such as biological nativeness, dispersal history, or ecological effects (regardless of native status) could underly these policies. Thus, this assertion needs greater support.

Related to the discussion, while the magnitude of effects may be similar for native and introduced megafauna – is there varied ecological significance? For example, both native and introduced megafauna are correlated with reductions in small mammal abundance – are there ecological communities where this is a greater concern?

Compelling evidence is provided that biological nativeness on its own poorly predicts the impact of species. However, the discussion would also benefit from greater acknowledgment that ecosystem effects (i.e., as measured) are not the only reason conservation decisions may target introduced species and how nativeness as a category may (or may not) offer ongoing utility for ecology.

This manuscript provides a valuable contribution our understanding how native and non-native megafauna affect ecosystems and highlights erroneous wide-spread preconceptions. I believe greater clarity – as noted above – would greatly enhance the clarity and utility of the manuscript but do not represent flaws in the analysis or interpretation.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

General comments:

This manuscript, entitled “Native and introduced megafauna have convergent effects on animals and ecosystems” by the

authors presents a systematic assessment of the ecological impacts of native and introduced/invasive megafauna on local animal abundance, diversity, and ecosystem features. Specifically, the authors applied multilevel random-effect meta-analysis testing whether the impacts depend on nativeness / 'invasiveness', and also testing different impacts from intact African assemblages and introduced megafauna. The authors used a previously published dataset and conducted this study on the basis of 2,162 observations across 186 studies worldwide. The results generally find no discernible difference between the effects of introduced/invasive megafauna and native megafauna on animal and ecosystem features. These findings highlight that nativeness has limited explanatory power for understanding the ecological impacts of megafauna. Although the authors claimed that native and introduced/invasive megafauna have similar patterns of ecological impacts, from the main figures, there are still significant doubts that cannot be ignored, which pose a challenge to the 'no discernible difference...' / 'no evidence...' in the Abstract/conclusion. For example, from Fig. 1 to Fig. 3, there are significant impacts of native megafauna and intact African assemblages on animals and ecosystems, but no significant impacts from introduced or invasive megafauna (see details in specific comments). In addition, publication bias is crucial for the reliability of conclusions on whether native or introduced/invasive megafauna have an impact, and the author also points out that 9 out of 25 response indicators have bias, which may be another reason for challenging 'no evidence...'.

Except for my main concern mentioned above, there are still some of would be worthwhile to explicitly mention, such as

(1) Why did the authors distinguish non-native megafauna into 'introduced' and 'invasive' levels for analysis?

(2) Did the authors control the phylogenetic relationship between native and introduced/invasive megafauna and then compare different impacts on the same response variable? Because it should be much more reasonable to compare ecological impacts at their same family or genus level.

(3) The data collection period for analysis is until 2022. The author may consider further collecting literature data from the period of 2022-2025 to conduct a more comprehensive analysis.

(4) The author should conduct a detailed discussion and speculation based on the findings of this study, and control the length to extend the possible levels of ecological and social impacts if there is little difference in the ecological impacts of native and introduced/invasive megafauna.

(5) Finally, some necessary citations for supporting the Methods are lacking; inconsistent information, such as 24/25?

Response variables were used for analysis; publication bias results or mentioned bias issues are not found in the results, discussion, or supplementary information.

As a result, I believe this study is exploring a key question about how the role of nativeness/invasiveness contributes to the variances of ecological impacts, which is necessary to inform the protection and resource utilization of megafauna. However, the manuscript in its present form does not meet the standard for publishing in Nature Communications. I suggest a "major revision" to this work. I would like to see a new version of this work after fixing key flaws by the authors. I also strongly suggest improving the language and the unclear writing of the manuscript.

Specific comments:

Line 65: What is the purpose of distinguishing the non-native species into 'introduced' and 'invasive' groups? Please add some words to briefly show your intention, which is important for readers to follow the results.

Line 67: Please cite literature to support why the '3 studies' are a threshold to judge whether there is sufficient sample size.

Line 80-81: What is the 'LRT'? I suggest showing the full name when the abbreviation emerges for the first time in the text. In addition, how did you perform this analysis? I suggest you add some words at the last paragraph in the Introduction section. It is better to show your Important step(s) and illustrate that your comparison is reasonable, and it would be best to have a supplementary table or figure to show more detailed results.

Line 83-84: I read the first part of the Results section. I am wondering whether you have determined the non-significant/significant effects of megafauna on animals on the basis of 'cross-hatched error bars' encompassing/not encompassing zero. If yes, is it inconsistent with the summary in the Abstract about 'no discernible difference between megafauna impacts...' (Line 19)? For example, the native megafauna had a negative effect on vertebrate herbivore abundance, but 'introduced' or 'invasive' did not. A similar issue is also found for small mammal abundance, detritivore abundance.

Line 103: How did you perform this contrast t-tests? Is it paired t-tests? I also suggest you add some words at the last paragraph in the Introduction section to show the rationality of the comparison.

Line 111-112: There is a similar issue to the suggestion for Line 80-81.

Line 109-110: From Fig. 2A, I notice the estimated CIs for native megafauna may encompass zero, but introduced megafauna may not. Does this mean the native and introduced megafauna have different effects on soil total Ca and Mg? If yes, I suggest you can double-check the results here.

Line 116-117: Only from Fig. 2A, the estimated CIs for native megafauna may encompass zero. I am not sure how you found that the native megafauna had a negative effect on soil Ca.

Line 135-138: This is better to move the short background into the Introduction section, and you can also show your assumption based on this background. In addition, please avoid citing references in the Results section (e.g., Line 141).

Line 145: Please cite a supplementary table or figure here to show the sample sizes for each of the ecological response

variables.

Line 146: When I read your result text about Fig. 3B, D, and F, you mentioned no difference between introduced and African assemblages. However, I STILL have doubts about the estimated mean effect sizes with CIs of the African assemblages and introduced megafauna (Fig. 3A, C, and E) showing different effects on vertebrate abundance, vertebrate herbivore abundance, small mammal abundance, invertebrate herbivore abundance (maybe), and bare ground. Thus, it is unclear to me, and please specify this.

Line 167: I suggest you double-check the above results before saying the general point of 'no evidence that...'.

Line 168-169: I am not clear what you mean about 'still provide some explanatory power'. If your main points are correct, the nativeness and 'invasiveness' had no significant power in explaining variations in animal and ecosystem variables. Please specify this.

Line 170: I am sorry, I cannot follow the meaning of 'reduced total variance by a mean of 0.05'. Please specify this.

Line 178-179: Please cite a supplementary table/figure to show details of the 'reduced total model variance'.

Line 179-182: I see you have applied the null model approach to test whether there is a difference between observed and randomized nativeness/invasiveness model. I suggest you add a supplementary table/figure to show your testing results, which is beneficial for understanding your description here.

Line 212: I see the 'sample size' may be one of the limitations for exploring the roles of biological nativeness in influencing local animals and ecosystems. However, I suggest you can link your results to briefly discuss the rationale and limitations of your findings.

Line 228: I read the subsection 'Spontaneous rewilding and the moralization of nature' in your Discussion section. In my view on this study, I suggest some words can be used to discuss the potential reasons for differences and similarity effects of native vs. introduced/invasive megafauna on animal abundance, diversity, and ecosystem features. Based on your current version, I think there are some deviations from the problem you want to study, and there are not many detailed discussions and speculations based on your results.

Line 265: I see the largest dataset publishing with two top Journal literature. However, as you mentioned the last searching date was stopped by 2022. I suggest you use the same searching terms to conduct a new round of literature collection, setting dates from July 2022 to now.

Line 275: add supporting literature for 'a prior threshold of 3 studies...'

Line 276: In the Abstract and Introduction section, it's mentioned '24 responses' (Line 20) / '24 ecological responses' (Line 66). However, in the Methods section, it's mentioned '25 ecological response categories'. Inconsistent number? Please have a double-check. Another suggestion is to cite a supplementary table to show these response variables and original data sources for collecting their information.

Line 284-286: Intact African megafauna definitively depends on the local species lists. In addition, I notice the size-specific condition of megafauna is also a key to assessing the assemblages and their impacts. I am not sure how the species list of introduced megafauna was handled and filtered to meet the impacts' comparisons between Intact vs. introduced megafauna. Please specify this.

Line 292-295: add necessary supporting literature and a more detailed explanation for why you chose Hedges' g and log-transformed ratio parameters for calculating effect size.

Line 295-296: It's unclear how they were calculated. Please rephrase the sentence.

Line 301-304: Please add necessary citation(s), and add words to specify how the model comparisons were conducted and what the t-tests were used for.

Line 310-311: I am not clear what basic principle was considered in designing these random-effect structures in your multilevel random-effect meta-analytic model fitting. Please specify this. In addition, please cite necessary literature to support your approach to determine the optimal random effect structure.

Line 312-316: As I mentioned above, what is your main principle and intention in comparing these three types of random effect structures?

Line 318-319: I am sorry, I am not clear what the nativeness or 'invasiveness' includes. Did you mean the nativeness for classifying the megafauna into native/non-native, and 'invasiveness' for introduced/invaded megafauna? Please specify this.

Line 320-322: It's unclear for 'planned contrast tests'. How did you perform the 't-tests in relation to the reference level of interest'? In addition, please cite necessary supporting literature.

Line 343: The 'outside the 95% confidence intervals of these randomized distributions' is unclear. If you applied a null model approach to test whether the observed values had a significant difference from the random values, I suggest you can add words and necessary citations to improve this paragraph.

Line 352: As you found evidence of publication bias in 9 of 25 responses, you need to be careful to describe the results and summarize the different effects of native, introduced, and invasive megafauna on animal and ecosystem variables. Please add a supplementary table to show Egger's test results.

Line 360: When you described the 'Influence analysis' subsection, I suggest you cite the necessary literature to support the analysis you applied.

Figures:

In Fig. 1A, the 'cross-hatched error bar' is hard to read in categories, such as vertebrate diversity, bird diversity under native megafauna; in Fig. 1B, predator abundance under native megafauna.

In Fig. 1D and Fig. 2B, I notice there are different widths of the error bars. Is there any other meaning? In addition, in Fig. 2B, the error bar of 'introduced' megafauna on bare ground at the right side has a different style compared to the others.

In Fig. 4, how can the 'all nativeness and 'invasiveness' models were within the 95%...' be read from the figure? Please specify this.

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

In this paper the authors report the results of a meta-analysis looking at the effects of large herbivores on ecological responses such as species diversity and soil structure/composition. The authors find that generally large herbivores have an effect on these responses, and the responses are of similar magnitude in systems where the herbivore/herbivores is/are native or introduced. The biological component of this paper is outside my area of expertise, and I was invited to review the methodological aspects of the analysis. Generally, the analyses appear to have been thoroughly conducted and documented, and I have only three major comments.

1. The dataset is a little on the older side (last updated 2022) and analyses of these responses appear to have featured in several other high-profile papers. I am not familiar with the rate of publication for the primary literature here, but in other areas of the life sciences it would be expected to update such an old literature search prior to finalisation.

2. I didn't see any discussion of heterogeneity from the models. As far as I can tell, it's not actually possible to calculate heterogeneity at the level which one would find most interesting in this analysis; that is the heterogeneity in the difference in effect of native vs non-native herbivores among different systems. This seems to be a limitation of the dataset which is not discussed; we do not have comparisons between natives vs non-natives at the same sites. In the absence of this ideal heterogeneity, it might be worth reporting whether the total heterogeneity in effects is larger/same/smaller for analyses stratified by natives vs non-natives. This would at least let us know whether non-natives have more unpredictable effects on ecosystems than natives.

3. More generally, I would have liked to see comprehensive reporting of the main model outputs shown in the figures. I checked the supp matts and the model tables including variance components do not seem to be there.

(Remarks on code availability)

The code appears to be fully accessible and well documented. I would recommend adding a few sentences on the author's use of the 'groundhog' package in their code to the README.

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

This is my second time reviewing this manuscript. The authors offer a substantial revision of their manuscript, investigating contrasting the effects of native and introduced megafauna. The authors' revisions satisfactorily addressed changes I suggested and, in particular, more clearly utilize terminology and define their hypotheses. Notably, in addressing additional reviewer feedback, the authors have also updated their dataset (now articles published during 2022–2025) and conducted a

full reanalysis, which is welcome. Overall, I believe the authors' revisions have yielded a substantially improved article.

As a minor point, I suggest the abstract would benefit from the addition of a clear and concise distillation of how the authors' results contribute to our understanding of whether or not nativeness should be considered a biological attribute (for large herbivores and/or other species). Fully recognizing that abstracts are strictly limited in length, making the final sentence more concise may allow space for such an addition.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

Thank you so much for the great efforts from the authors to improve the manuscript. Congratulations! I have no further comments in this round.

(Remarks on code availability)

Reviewer #3

(Remarks to the Author)

The authors have addressed all of my comments.

(Remarks on code availability)

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REVIEWER COMMENTS

Reviewer #1 (Remarks to the Author):

The authors present a well-written and compelling manuscript investigating the effects of native and introduced megafauna and investigate whether nativeness can be used to predict ecological impacts. The study uses a strong meta-analytic framework and found introduced species have similar reported effects to vertebrates, invertebrates, and ecosystems as native ones. The study is of broad relevance to conservation globally as introduced species have proliferated across the globe due to human activity.

Thank you for supportive comments and your helpful feedback. We believe they have considerably improved the manuscript.

The manuscript would benefit from increased clarity terminology and use of explicit definitions. The authors investigate whether there is support for biological nativeness – but do not articulate distinctions between various definitions (e.g., species which have coevolved vs a description of dispersal history) or how each may be empirically evaluated.

Thank you for this comment. We used the IUCN's definition of nativeness, which is whether a species was introduced somewhere by human beings. We have also clarified in the introduction that coevolution is presupposed from being native—we only rarely have direct evidence that species have coevolved. We have added text on L312-315 of the methods of how we designated species as native or introduced, and we have added text to the Introduction on L46-51.

Perhaps related to a lack of clear definitions, I struggle with terming nativeness a “biological attribute”. Generally, biological attributes include physiological, behavioral, or genetic characteristics and evolutionary adaptations, etc. whereas nativeness is typically used a descriptive classification. Explicit definitions for these terms may alleviate this issue.

Yes, we agree that nativeness is an odd biological attribute, yet this is exactly what many invasion biologists argue. There are also numerous analyses which include nativeness as an actual functional trait. We have added an additional quote from a recent invasion biology article (published in NatComms about introduced megafauna) to this point on L43-44.

The authors posit that targeting of introduced species by conservation eradication programs is “[...] predicated upon the hypothesis that nativeness is a biological attribute of populations that shapes their ecological effects.” However, numerous rationals such as biological nativeness, dispersal history, or ecological effects (regardless of native status) could underly these policies. Thus, this assertion needs greater support.

The most tangible reason for these programs, which is rarely transparently admitted to, is the normative value of nativism—that communities should be the way they were in the past. Unfortunately, discussing nativism is out of scope of this manuscript. We have instead added a paragraph in the conclusion arguing that indeed, lethal management

may sometimes be necessary for both introduced and native species. See L254-261 of the Discussion.

Related to the discussion, while the magnitude of effects may be similar for native and introduced megafauna – is there varied ecological significance? For example, both native and introduced megafauna are correlated with reductions in small mammal abundance – are there ecological communities where this is a greater concern?

This may be the case, but the burden of proof would be on invasion biologists to generate mechanisms or defenses for which are also transparent to the breadth of ecological history. For example, some literature has argued, for instance, that the fire-suppressing effects of feral pigs in Florida (see Brown et al. 2024 Biological Invasions) are unnatural, given that those ecosystems are fire-adapted. However, this is a question of baselines: Florida was a hotspot of megafauna during the Late Pleistocene (including pig-like peccaries) (and with a resurgence of bison in the early Holocene). Prehistoric fire patterns do appear to support that the prehistoric losses of these animals led to the development of modern fire regimes (Perrotti 2018 Quaternary International, Karp et al. 2021 Science).

Compelling evidence is provided that biological nativeness on its own poorly predicts the impact of species. However, the discussion would also benefit from greater acknowledgment that ecosystem effects (i.e., as measured) are not the only reason conservation decisions may target introduced species and how nativeness as a category may (or may not) offer ongoing utility for ecology.

Given the length of the discussion, and the ethical/normative nature of that discussion, we are hesitant to dive into this in depth. However, this is a topic that has been discussed in detail elsewhere and we now refer to those discussions on L256.

This manuscript provides a valuable contribution our understanding how native and non-native megafauna affect ecosystems and highlights erroneous wide-spread preconceptions. I believe greater clarity – as noted above – would greatly enhance the clarity and utility of the manuscript but do not represent flaws in the analysis or interpretation.

Thank you for your very helpful comments. We hope our revisions assuage your concerns.

Reviewer #2 (Remarks to the Author):

General comments:

This manuscript, entitled “Native and introduced megafauna have convergent effects on animals and ecosystems” by the authors presents a systematic assessment of the ecological impacts of native and introduced/invasive megafauna on local animal abundance, diversity, and ecosystem features. Specifically, the authors applied multilevel random-effect meta-analysis testing whether the impacts depend on nativeness / ‘invasiveness’, and also testing different impacts from intact African assemblages and introduced megafauna. The authors used a previously published

dataset and conducted this study on the basis of 2,162 observations across 186 studies worldwide. The results generally find no discernible difference between the effects of introduced/invasive megafauna and native megafauna on animal and ecosystem features. These findings highlight that nativeness has limited explanatory power for understanding the ecological impacts of megafauna.

Thank you for your constructive comments. We believe they have considerably improved the manuscript.

Although the authors claimed that native and introduced/invasive megafauna have similar patterns of ecological impacts, from the main figures, there are still significant doubts that cannot be ignored, which pose a challenge to the ‘no discernible difference...’ / ‘no evidence...’ in the Abstract/conclusion. For example, from Fig. 1 to Fig. 3, there are significant impacts of native megafauna and intact African assemblages on animals and ecosystems, but no significant impacts from introduced or invasive megafauna (see details in specific comments).

Thank you for this comment. Indeed, this is a question of what hypothesis we are testing. We are not testing whether the effects of native or introduced megafauna are differently different than 0. We are testing whether the effects of native and introduced megafauna are different from each other with planned contrast tests (also called posthoc tests).

The panel A of each figure shows the raw data and the overall effects. To evaluate whether native and introduced megafauna have different impacts, one must compare the overlapping CIs of each nativeness level in panel A or look at the panel B, which shows the estimated difference and CIs—if these CIs are different from 0 then there is statistical support that the effects of native and introduced (or ‘invasive’) megafauna are different.

We write this more explicitly now in the introduction on L71: “In each case, we report planned contrast comparisons to test whether the effects of introduced or invasive megafauna are different from those of native megafauna.” and have added additional text to the figure captions. Moreover, we added clarifying text to the methods (L347-352).

Finally, we also report differences beyond the traditional <0.05 threshold, and employ the ‘language of evidence’ to avoid binary significance language. As such, we believe you’ll find the revised version of the manuscript to be more circumspect and cautious in our conclusions.

In addition, publication bias is crucial for the reliability of conclusions on whether native or introduced/invasive megafauna have an impact, and the author also points out that 9 out of 25 response indicators have bias, which may be another reason for challenging ‘no evidence...’.

Thank you for this comment. The earlier version of this manuscript used out-dated methods to test publication bias. We have updated the analytic approach (now based on Nakagawa et al. 2022, Method Eco Evo) to use multilevel models and evaluate the influence of effective sample size on overall estimates. See L380-391 of the methods. We have now identified publication bias for only two responses: soil pH and vertebrate diversity, for which there was no difference between native and introduced megafauna.

Except for my main concern mentioned above, there are still some of would be worthwhile to explicitly mention, such as

(1) Why did the authors distinguish non-native megafauna into 'introduced' and 'invasive' levels for analysis?

It is often claimed that not all introduced species are problematic, only a special subset of 'invasive' species (Pysek et al. 2020 Biological Reviews). For that reason we evaluated both introduced and 'invasive' species separately. We detail this rationale on L40-42 and L66-67 of introduction.

(2) Did the authors control the phylogenetic relationship between native and introduced/invasive megafauna and then compare different impacts on the same response variable? Because it should be much more reasonable to compare ecological impacts at their same family or genus level.

Ideally we would have controlled for phylogenetic covariate between megafauna. However, many (43 %) of our megafauna communities are mixed species. While some studies present comparisons with size-selective exclosures, these still exclude herbivores by body size and not by phylogenetic group. We have clarified this in the methods on L371-375.

(3) The data collection period for analysis is until 2022. The author may consider further collecting literature data from the period of 2022-2025 to conduct a more comprehensive analysis.

We agree and conducted a systematic update, which identified an additional 90 studies and 1,778 responses. We have detailed the specifics of our literature update, including a PRISMA diagram, in the Methods (see L284-399 and Fig S1).

(4) The author should conduct a detailed discussion and speculation based on the findings of this study, and control the length to extend the possible levels of ecological and social impacts if there is little difference in the ecological impacts of native and introduced/invasive megafauna.

Thank you for this comment. It is always nice to be encouraged to speculate! Our discussion is quite long but we have added brief reference to social dimensions (including normative values) and how our results suggest the need for value transparency as well as increased empirical rigor (see L249-256).

(5) Finally, some necessary citations for supporting the Methods are lacking; inconsistent information, such as 24?/25? Response variables were used for analysis; publication bias results or mentioned bias issues are not found in the results, discussion, or supplementary information.

Thank you for pointing these out. We have clarified the exact number of responses consistently throughout (which has increased to 32, thanks to the update of the dataset). In our previous submission, the publication bias tests were reported with funnel plots in the supplementary materials. We have updated our publication bias test methods following more statistically robust methods (see Nakagawa et al. 2022, Method Eco Evo). We report multilevel metaregressions that evaluate publication bias by regressing effect

sizes against effective sample size. We found publication bias in only one response: soil pH and vertebrate diversity. These results are reported Supplementary Table 5. We have also added two additional tables to clarify the nesting levels of the responses and the sample sizes of all responses, including those for which we did not have sufficient sample size to analyze (see Supplementary Tables 3 and 4).

As a result, I believe this study is exploring a key question about how the role of nativeness/invasiveness contributes to the variances of ecological impacts, which is necessary to inform the protection and resource utilization of megafauna. However, the manuscript in its present form does not meet the standard for publishing in Nature Communications. I suggest a “major revision” to this work. I would like to see a new version of this work after fixing key flaws by the authors. I also strongly suggest improving the language and the unclear writing of the manuscript.

Thank you for your comments, we really appreciate the time you put into this review. As detailed above and below, we gave our best to amend your concerns and we believe the revised manuscript is significantly clearer.

Specific comments:

Line 65: What is the purpose of distinguishing the non-native species into ‘introduced’ and ‘invasive’ groups? Please add some words to briefly show your intention, which is important for readers to follow the results.

We have specified this in two places in the Introduction (as specified above). Some invasion biologists have argued that not all introduced species are problematic, but only those that are qualify as ‘invasive’. We have thus evaluated those that are categorized as such separately, to test, if, indeed, ‘invasive’ megafauna have truly aberrant impacts.

Line 67: Please cite literature to support why the ‘3 studies’ are a threshold to judge whether there is sufficient sample size.

We selected 3 as the bare minimum threshold. It takes 1 degree of freedom to calculate means and an additional degree of freedom to calculate standard deviation. A sample size of 3 thus leaves us with one degree of freedom to conduct our analyses—which is the bare minimum for any type of statistical rigor.

Line 80-81: What is the ‘LRT’? I suggest showing the full name when the abbreviation emerges for the first time in the text. In addition, how did you perform this analysis? I suggest you add some words at the last paragraph in the Introduction section. It is better to show your Important step(s) and illustrate that your comparison is reasonable, and it would be best to have a supplementary table or figure to show more detailed results.

Thank you for catching that we did not define ‘LRT’ (Log-likelihood ratio test). We have now defined it at first mention. We have also added a sentence at the end of the introduction regarding the use of log-likelihood ratio tests. We had included this with a Table of all model results, see Table S1.

Line 83-84: I read the first part of the Results section. I am wondering whether you have determined the non-significant/significant effects of megafauna on animals on the basis of 'cross-hatched error bars' encompassing/not encompassing zero. If yes, is it inconsistent with the summary in the Abstract about 'no discernible difference between megafauna impacts...' (Line 19)? For example, the native megafauna had a negative effect on vertebrate herbivore abundance, but 'introduced' or 'invasive' did not. A similar issue is also found for small mammal abundance, detritivore abundance.

Thank you for pointing out the potential source of confusion. We are not testing whether the effects of introduced or native megafauna are different from 0. We are testing whether introduced and native megafauna have impacts different from each other. This is done with planned contrast (also called posthoc tests), which compare a reference level to the factor of interest. The lack of difference indicates that even if group A is significantly different from 0, the group B is within the range of impacts of group A. This is a common and well used statistical practice to understand if different categorical treatments have different outcomes. We have added clarifying sentences to the introduction, as specified above.

Line 103: How did you perform this contrast t-tests? Is it paired t-tests? I also suggest you add some words at the last paragraph in the Introduction section to show the rationality of the comparison.

A paired t-test would not be appropriate for multilevel meta-analytic data. The t in question refers to the statistical distribution used to conduct significance testing in the hierarchical multilevel meta-analytic models. Two options are available for these types of tests: the z distribution and the t distribution. The z distribution requires higher sample sizes and assumes a known population standard deviation. The t distribution is robust to lower sample sizes and does not assume a known population standard deviation (used a given degree of freedom). We have made this clearer in the Introduction and in the methods on L344-346.

Line 111-112: There is a similar issue to the suggestion for Line 80-81.

We believe it is standard practice to define statistical acronyms at first mention and then to use the acronyms throughout. We have added the definition of LRT to its first mention and we also made sure to only report these results after reporting their interpretation in plain english.

Line 109-110: From Fig. 2A, I notice the estimated CIs for native megafauna may encompass zero, but introduced megafauna may not. Does this mean the native and introduced megafauna have different effects on soil total Ca and Mg? If yes, I suggest you can double-check the results here.

Thank you for this comment. Again, we are evaluating whether there is a difference between the effects of introduced and native megafauna. Not whether they are differently different from 0. This is the same type of statistical comparison that is core to nearly every contrast between categorical groups (e.g., in an ANOVA).

Line 116-117: Only from Fig. 2A, the estimated CIs for native megafauna may encompass zero. I am not sure how you found that the native megafauna had a negative effect on soil Ca.

Apologies for the confusion. We believe it stems from the fact that these results are for all megafauna combined, given that there was no evidence that native or introduced megafauna had impacts different from each other. Lumping native and introduced did, indeed, cause some responses to tip over the edge to becoming significantly different from 0. We have revised the paragraph in question and we hope the language is now clearer.

Line 135-138: This is better to move the short background into the Introduction section, and you can also show your assumption based on this background. In addition, please avoid citing references in the Results section (e.g., Line 141).

With all due respect, we believe that weaving some introductory content is standard practice in Letter-style articles. We believe that this breaks up the tediousness of the results and allows us to justify this comparison, which indeed, reflected an additional analysis not initially planned when conducting this research. If the editors concur that this section should be moved into the Introduction for stylistic reasons, we will happily do so, but we would prefer to leave this as is.

Line 145: Please cite a supplementary table or figure here to show the sample sizes for each of the ecological response variables.

The original supplementary table S1 included sample sizes for each group but we have also added an additional table (Supp Table 4) with all sample sizes.

Line 146: When I read your result text about Fig. 3B, D, and F, you mentioned no difference between introduced and African assemblages. However, I STILL have doubts about the estimated mean effect sizes with CIs of the African assemblages and introduced megafauna (Fig. 3A, C, and E) showing different effects on vertebrate abundance, vertebrate herbivore abundance, small mammal abundance, invertebrate herbivore abundance (maybe), and bare ground. Thus, it is unclear to me, and please specify this.

As described above, we are testing whether the effects of introduced megafauna are different from African megafauna. As you can see, the error bars in panel A overlap in all cases but with soil Magnesium. Panel B indicates that all differences (and CIs) overlap 0 (no difference between African megafauna and introduced megafauna) except for soil magnesium responses.

Line 167: I suggest you double-check the above results before saying the general point of 'no evidence that...'.

We hope that our additional text and our explanations in this response have clarified this concern. We remain open to adding additional clarifying text if there is a clearer way to describe what we believe is fairly common practice in statistical analysis.

Line 168-169: I am not clear what you mean about 'still provide some explanatory power'. If your main points are correct, the nativeness and 'invasiveness' had no significant power in explaining variations in animal and ecosystem variables. Please specify this.

We have removed this section due to length constraints.

Line 170: I am sorry, I cannot follow the meaning of 'reduced total variance by a mean of 0.05'. Please specify this.

We have removed this section due to length constraints but we still report total variance reduction in the methods and supplementary figures. Please see L423-441 where we describe this calculation and Fig. S6 for a breakdown of the extent to which nativeness and 'invasiveness' reduced model variance.

Line 178-179: Please cite a supplementary table/figure to show details of the 'reduced total model variance'.

We have removed this section, but we have included supplementary figures and tables with how much nativeness/invasiveness reduced model variance.

Line 179-182: I see you have applied the null model approach to test whether there is a difference between observed and randomized nativeness/invasiveness model. I suggest you add a supplementary table/figure to show your testing results, which is beneficial for understanding your description here.

We have removed this analysis because it led to confusion among coauthors and some external friends we asked for third party opinions.

Line 212: I see the 'sample size' may be one of the limitations for exploring the roles of biological nativeness in influencing local animals and ecosystems. However, I suggest you can link your results to briefly discuss the rationale and limitations of your findings.

We have significantly expanded upon the tenuous results from our new analyses on L197-217 of the Discussion. Indeed, many of these patterns are not resilient to the exclusion of influential data and others can be explained by functional patterns in the underlying megafauna communities.

Line 228: I read the subsection 'Spontaneous rewilding and the moralization of nature' in your Discussion section. In my view on this study, I suggest some words can be used to discuss the potential reasons for differences and similarity effects of native vs. introduced/invasive megafauna on animal abundance, diversity, and ecosystem features. Based on your current version, I think there are some deviations from the problem you want to study, and there are not many detailed discussions and speculations based on your results.

We have added some additional discussion of the one response, which is now significantly different. Given the number of responses, we do not think it would be cogent to discuss slight differences in whether introduced or native megafauna impacts overlap 0 or not — which is not the question we are asking.

Line 265: I see the largest dataset publishing with two top Journal literature. However, as you mentioned the last searching date was stopped by 2022. I suggest you use the same searching terms to conduct a new round of literature collection, setting dates from July 2022 to now.

Thank you for this comment. We agree. We have updated our meta-analysis, which added an additional 90 studies and 1,778 observations.

Line 275: add supporting literature for 'a prior threshold of 3 studies...'

We have added justification for this threshold.

Line 276: In the Abstract and Introduction section, it's mentioned '24 responses' (Line 20) / '24 ecological responses' (Line 66). However, in the Methods section, it's mentioned '25 ecological response categories'. Inconsistent number? Please have a double-check. Another suggestion is to cite a supplementary table to show these response variables and original data sources for collecting their information.

Thank you for catching this discrepancy. Now that we have updated the underlying dataset, we were able to analyze 32 responses, which have been consistently reported throughout.

Line 284-286: Intact African megafauna definitively depends on the local species lists. In addition, I notice the size-specific condition of megafauna is also a key to assessing the assemblages and their impacts. I am not sure how the species list of introduced megafauna was handled and filtered to meet the impacts' comparisons between Intact vs. introduced megafauna. Please specify this.

Thank you for this comment, but we do not understand what Reviewer 2 meant. African assemblages were in African parks and were filtered to only include experimental comparisons that manipulated the entire megafauna community (as opposed to just excluding the largest herbivores). We do not know what is meant in regards to the introduced megafauna species list. And indeed, body mass is intrinsic to the definition of megafauna, but we are sorry that we were unable to interpret your comment. Potentially you are asking for clarification on how species nativeness was defined. We have added a paragraph to this effect in the Methods on L307-313.

Line 292-295: add necessary supporting literature and a more detailed explanation for why you chose Hedges' g and log-transformed ratio parameters for calculating effect size.

We write on L334-341 that we chose to use Hedges' g because the log-transformed ratio of means cannot be calculated for negative values or 0s, which would exclude a considerable amount of data. We had written this and cited the appropriate literature in the initial version so we are somewhat confused about what else the reviewer requires.

Line 295-296: It's unclear how they were calculated. Please rephrase the sentence.

We apologize for the typo—the R package was missing from the original sentence. Thank you for catching this, we have corrected it.

Line 301-304: Please add necessary citation(s), and add words to specify how the model comparisons were conducted and what the t-tests were used for.

We have considerably elaborated on how the models were conducted and on the use of the t distribution (which can also be called a t test but is perhaps more confusing that way). We hope that the revised text is clearer, and we thank you for your attention to detail.

Line 310-311: I am not clear what basic principle was considered in designing these random-effect structures in your multilevel random-effect meta-analytic model fitting. Please specify this. In addition, please cite necessary literature to support your approach to determine the optimal random effect structure.

We describe how these random effect structures accommodate for non-independence in the dataset, which varied between responses. We have elaborated on this section and now cite key literature regarding the use of information-theoretic approaches to evaluate between multiple plausible candidate models.

Line 312-316: As I mentioned above, what is your main principle and intention in comparing these three types of random effect structures?

The main principles and intentions are laid out on L358-370: "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 was complex, 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 but also to avoid overfitting, we evaluated a suite of alternative random effect structures and chose the optimal random effect structure based on BIC."

Line 318-319: I am sorry, I am not clear what the nativeness or 'invasiveness' includes. Did you mean the nativeness for classifying the megafauna into native/non-native, and 'invasiveness' for introduced/invaded megafauna? Please specify this.

We have revised this sentence to clarify that nativeness or 'invasiveness' are the variables we are including in the model.

Line 320-322: It's unclear for 'planned contrast tests'. How did you perform the 't-tests in relation to the reference level of interest'? In addition, please cite necessary supporting literature.

Planned contrast tests are the same as posthoc comparisons: comparing the estimates for two discrete groups. These are commonplace and part of basic statistical practice. Nonetheless we have revised the paragraph for increased clarity.

Line 343: The 'outside the 95% confidence intervals of these randomized distributions' is unclear. If you applied a null model approach to test whether the observed values had a significant difference from the random values, I suggest you can add words and necessary citations to improve this paragraph.

We removed this analysis.

Line 352: As you found evidence of publication bias in 9 of 25 responses, you need to be careful to describe the results and summarize the different effects of native, introduced, and invasive megafauna on animal and ecosystem variables. Please add a supplementary table to show Egger's test results.

We have added supplementary tables of all publication bias tests (Supp Table 5). We only found two significant publication bias test results (for soil pH and vertebrate diversity) with our updated analysis.

Line 360: When you described the 'Influence analysis' subsection, I suggest you cite the necessary literature to support the analysis you applied.

We are confused by this comment because we did indeed cite the relevant literature. However, we have updated our approach to use more modern and supported methods and cite the relevant literature to support them.

Figures:

In Fig. 1A, the 'cross-hatched error bar' is hard to read in categories, such as vertebrate diversity, bird diversity under native megafauna; in Fig. 1B, predator abundance under native megafauna.

We have removed prediction intervals to make the confidence intervals more visible.

In Fig. 1D and Fig. 2B, I notice there are different widths of the error bars. Is there any other meaning? In addition, in Fig. 2B, the error bar of 'introduced' megafauna on bare ground at the right side has a different style compared to the others.

It's very difficult to get identical error bar widths when there are such different numbers of groups in each plot. We have done our best to make them more visually consistent in the revision.

In Fig. 4, how can the 'all nativeness and 'invasiveness' models were within the 95%...' be read from the figure? Please specify this.

We have removed this analysis, but indeed, the points were inside the 95% error bars, which is evidence of being within the 95% confidence intervals.

Reviewer #3 (Remarks to the Author):

In this paper the authors report the results of a meta-analysis looking at the effects of large herbivores on ecological responses such as species diversity and soil structure/composition. The authors find that generally large herbivores have an effect on these responses, and the responses are of similar magnitude in systems where the herbivore/herbivores is/are native or introduced. The biological component of this paper is outside my area of expertise, and I was invited to review the methodological aspects of the analysis. Generally, the analyses appear to have been thoroughly conducted and documented, and I have only three major comments.

Thank you very much for the helpful and constructive comments. We really appreciate the time you invested in the review.

1. The dataset is a little on the older side (last updated 2022) and analyses of these responses appear to have featured in several other high-profile papers. I am not familiar with the rate of publication for the primary literature here, but in other areas of the life sciences it would be expected to update such an old literature search prior to finalisation.

This is a very fair point. We have updated our meta-analysis, which added 90 studies and 1,778 observations.

2. I didn't see any discussion of heterogeneity from the models. As far as I can tell, it's not actually possible to calculate heterogeneity at the level which one would find most interesting in this analysis; that is the heterogeneity in the difference in effect of native vs non-native herbivores among different systems. This seems to be a limitation of the dataset which is not discussed; we do not have comparisons between natives vs non-natives at the same sites. In the absence of this ideal heterogeneity, it might be worth reporting whether the total heterogeneity in effects is larger/same/smaller for analyses stratified by natives vs non-natives. This would at least let us know whether non-natives have more unpredictable effects on ecosystems than natives.

Thank you for this comment. Indeed, we do not have the proper comparisons to know whether natives or non-natives have different (or more variable) impacts at the same study sites, unfortunately. We have considerably expanded our supplementary reporting of heterogeneity and variance explained. We now report in figures (as well as in Table S1 and see Supp Figure 6-9) on the proportional reduction in total variance when including nativeness or 'invasiveness', on total heterogeneity (I^2), and R^2 . For some responses, we had surprisingly low heterogeneity, leading to R^2 values of 100%—despite there being 0 difference between native and introduced megafauna. We thus also report what we refer to as R^{2*} — which is the proportion of variance in effect sizes explained by our predictors and β_1 coefficient.

3. More generally, I would have liked to see comprehensive reporting of the main model outputs shown in the figures. I checked the supp matts and the model tables including variance components do not seem to be there.

Thank you for this comment. Table S1 did include I^2 and proportional variance reduction but the format was dense and difficult to read. We have reformatted Table S1 to be clearer and have added R^2 and R^{2*} .

Reviewer #3 (Remarks on code availability):

The code appears to be fully accessible and well documented. I would recommend adding a few sentences on the author's use of the 'groundhog' package in their code to the [READ.ME](#).

Thank you. We have added a description of this package to the READ.ME.

REVIEWERS' COMMENTS

Reviewer #1 (Remarks to the Author):

This is my second time reviewing this manuscript. The authors offer a substantial revision of their manuscript, investigating contrasting the effects of native and introduced megafauna. The authors' revisions satisfactorily addressed changes I suggested and, in particular, more clearly utilize terminology and define their hypotheses. Notably, in addressing additional reviewer feedback, the authors have also updated their dataset (now articles published during 2022–2025) and conducted a full reanalysis, which is welcome. Overall, I believe the authors' revisions have yielded a substantially improved article.

Thank you for your constructive comments and we are glad that our revision addressed your concerns.

As a minor point, I suggest the abstract would benefit from the addition of a clear and concise distillation of how the authors' results contribute to our understanding of whether or not nativeness should be considered a biological attribute (for large herbivores and/or other species). Fully recognizing that abstracts are strictly limited in length, making the final sentence more concise may allow space for such an addition.

We added a clear and concise sentence (“Our results suggest that nativeness is unlikely to be a biological attribute of megafauna.”) to the abstract following your recommendation.

Reviewer #2 (Remarks to the Author):

Thank you so much for the great efforts from the authors to improve the manuscript. Congratulations! I have no further comments in this round.

Thank you for your support and your helpful comments!

Reviewer #3 (Remarks to the Author):

The authors have addressed all of my comments.

Thank you for your constructive review.