Dear Editor,

We thank you for the opportunity to revise our manuscript, *Contrasting ecological roles of non-native ungulates in a novel ecosystem*, for potential publication in Royal Society Open Science. We have revised our manuscript in response to the comments from the two reviewers, who have provided helpful suggestions. We provide detailed responses to the reviewers' comments below, after three asterisks (***).

Thank you for again considering our manuscript for publication.

Sincerely, Ann Marie Gawel

Associate Editor Comments to Author:

Comments to the Author:

Before this paper can be accepted for publication, referee #1's concerns need to be fully and adequately addressed.

*** We have fully addressed referee #1's concerns, as described below.

REVIEWER 1 COMMENTS:

I reviewed the first version of this manuscript several months ago. In that review, I found the article to be well-written and concise, to address an important question (role of nonnative ungulates as seed dispersers vs. herbivores in novel tropical ecosystems), and to largely be sound. I had suggestions for revisions that centered around: (a) lack of information on study sites (vegetation and soil characteristics); (b) interpretation of results (in a native vs. nonnative context, instead of a novel ecosystem context); and (c) over interpretation of results (primarily of feral pigs playing a beneficial role vs. not having a negative impact).

In general, I feel like the authors did a good job of addressing these concerns and suggested revisions. *** Thank you for this positive feedback. Your suggestions have greatly improved the manuscript.

I still feel like too much importance is placed on native vs. nonnative in the Discussion, but the authors do eventually provide text and discussion placing the results in a novel ecosystem context.

*** We have added this sentence to the end of the first paragraph (L. 270-274) to bring up the concepts of functionally important species in novel ecosystems sooner:

"In a novel ecosystem completely lacking native seed dispersers, the negative effects of nonnative deer on seedling presence and abundance and the potential for non-native pigs to fill a missing ecological function provide support for a management approach based on functional roles rather than native/non-native status."

The one area where I feel the authors still need to improve is on details of the study site,

specifically information on vegetation composition and importance in the 8 study sites (fenced vs. unfenced). I originally wrote:

"The article is concise, and I appreciate that. However, I feel like there is some pretty important information missing, largely from the Methods (although at 4x the length of the Introduction, I found the Methods section to already be long compared to other sections). First, I feel like the authors need to provide a fair bit more information on the species composition of the "novel ecosystem" within which they are working. For example, it would be very informative to know the average densities and importance (e.g., via basal area) of the dominant species, both the native and the nonnative components of the overall community. Also, what proportion of the forest do the selected study species make up? As currently written there is a lot of attention on this being a novel ecosystem, but zero information to support that and zero information to support the importance of the selected study species. In addition to information on the overall study site species composition, I feel that the authors need to do the same for the small fenced exclosures they studied. As written, they simply say on lines 79-81 that the fenced and unfenced plots "had similar canopy cover, rockiness, and forest structure", but provide no data to support this. A table of the dominant species with densities and some estimate of importance (e.g., basal area, biomass, etc.) is warranted at a minimum, but it should also be pretty easy to run some analyses to see just how similar they were (t-test of species composition in paired fenced vs. unfenced sites?). Second, the authors should provide a lot more information on the soils in the study site, particularly to help couch the results about feral pigs. It strikes me that these are very unique soils (karst; "calcareous rock – the brittle, fossilized remains of ancient marine organisms"), and the primary way in which feral pigs impact other ecosystems is via rooting and wallowing. If they are unable to root in these soils, it likely has a huge impact on the results seen (and potential comparisons to other studies). Finally, the authors provide no information on ungulate densities for deer and pigs in the study area. It is very difficult to interpret the results (and compare to other studies) without this information. Also for feral pigs, what are the animals on Guam descendant from (e.g., are they true feral pigs that escaped from domestication, wild boar introduced, or something else?). All three of these items are basic aspects that you would expect to find in the Methods section of any scientific paper, such that the absence from this one is quite striking."

I feel that the authors did an adequate job addressing lack of information on soils (although soil taxonomy for the study sites, if it exists (?), remains conspicuously lacking) and ungulate densities (although I encourage the authors to include the information (and caveats) on ungulate density estimates from the one study in Guam that estimated deer and pig densities that was included in the response to reviewers, but not the actual manuscript).

*** To address concerns about lack of information on soil types, we added this to the Study Area subsection of our Methods (L. 85-88):

"While a variety of karst types exist in northern Guam, our seedling plot and transect sites all occurred on reef facies and detrital facies of what is classified as Mariana Limestone – that is, Plio-Pleistocene reef and lagoon that comprises 75% of Guam's karst formations [32]."

In contrast, I feel the authors still do not provide adequate information on vegetation composition in the study plots. So I repeat that I feel that the authors need to provide more information on the vegetation of the small fenced exclosures they studied. As written, they simply say on lines 94-

96 that the fenced and unfenced plots "had similar canopy cover, rockiness, and forest structure", but provide no data to support this (i.e., the same text provided in the original version, still with no data to support it). A table of the dominant species with densities and some estimate of importance (e.g., basal area, biomass, etc.) is warranted at a minimum, but it should also be pretty easy to run some analyses to see just how similar they were (t-test of species composition in paired fenced vs. unfenced sites?). I feel this needs to be done to be able to interpret these data (L. 96-107).

***We carefully selected sites to be paired in biotic and abiotic characteristics, as we recognize the potential for bias in site selection to lead to biased results, however we agree that we didn't present data on these characteristics. We have rewritten the paragraph describing how we chose paired plots in the Methods section to include comparisons between fenced and unfenced treatments. It now reads:

"The fenced and unfenced plots were placed so that individual pairs had similar canopy cover, rockiness, slope, and ground cover, as well as similar adult tree composition, density, heights, and diameters. While species composition of adult trees already present was almost impossible to match exactly, species composition often overlapped. Using linear mixed effect models and the lsmeans package for posthoc comparisons, we compared the fenced and unfenced treatments and found no significant differences in numbers of adult trees (p=0.22), canopy cover (p=0.92), average diameter at breast height (p=0.78), and average height of adult trees (p=0.85) between paired plots. We avoided gaps, depressions in the substrate, or any other features that might have caused a difference between the paired plots outside of our treatments." (L. 103-112)

We have added tables and figures to the Supplementary Section 3 (Tables 1-3, and Figure 3)to further demonstrate the similarity between the treatment and control plots. We hope this additional data convinces the reviewer that treatment differences are not due to systematic bias in plot selection.

REVIEWER 2 COMMENTS

Dear authors,

Thank you for your answers to our questions. After a second evaluation of your paper, I still think that there are major revisions to bring to it. Please see my suggestions, comments and questions below.

Table 1 and model results

The authors should really present the complete results testing species, time and treatment in a single model and then provide the model retained after the selection process, with the weight and AICc of each model and of the model retained.

The treatment effect for each species is already presented in figure 2.

Full model: Species+Treatment+Species:Treatment+time+time:Treatment (to test for the different time length of exposure to ungulates) and not the other interactions time:species as it is not fully crossed, and same for the 3rd order interaction.

*** Thank you for this feedback. We agree that the full model selection process should be included in the table, therefore, we have changed Table 1a to show the results accordingly. We

have kept the species-level model comparison results as Table 1b, because they show the relative strength of each model, and support Figure 2.

Table 2

Pb average seedlings/scat is not an accurate measure, the frequency of presence is a more relevant measure or the average seedling/scat should be assessed only when the species has been consumed (within presence).

Please reshape this table with frequency of occurrence, recalculated average seedling (to be linked to the number of seeds produced per fruit of each species).

*** We have revised Table 2 to include these parameters.

L 39Elaphus not elaphas.

***Changed.

L88-89 Please clarify and rephrase, I do not understand ...and especially the absence of scat amongst ????

*** The text has been revised to state "...the absence of birds..." instead of "scat."

L122-124 if this is the case, then time will not be significant in the final model. So I do not understand why you put these results in the mat and method section

*** We removed that line and this information is now presented in the Results.

L159 among instead of between

*** Corrected.

L 189 P. mariannensis not mariana

*** Corrected – the species is Psychotria mariana. Not sure how that got mixed up, thank you for pointing it out.

L231 metrics instead of numbers

*** Corrected.

Figure 1. is OK

Figure 2. is OK put the * on top of the bars, and ns for the last two species. If there is a species effect, please show it on the figure with letters (a, b, c ...) species sharing the same letter are not different ...

*** Figure 2 has been changed as recommended.

Figure 3.

The data in that figure are not accurate, because the proportional abundances (as they are defined in the material and methods) of the different species dispersed by wild pigs do not sum to 1 (it is more than 1) and for deer, there is a similar problem (the sum is less than 1)

For the species present in the local flora however (left panel), the data presented seem to be OK.

*** Thank you very much for pointing this discrepancy out. We made an error in describing the way that the values in that panel (scat) were calculated. We revised in the text in the Methods to state:

"We used a similar approach to calculate the proportional abundance of seedling species found in pig and deer scats: the total number of scats that has a given species of seedling germinating from it, divided by the total number of either deer or pig scats that we had collected." (L. 159-162)

"We used a similar approach to calculate the proportional abundance of seedling species found in pig and deer scats: the total number of scats that has a given species of seedling germinating from it, divided by the total number of either deer or pig scats that we had collected. For example, Carica papaya seeds germinated in 16 out of 31 pig scats. Therefore, the proportional abundance was 16 divided by 31, or 0.52. Because multiple species occurred in some single scats, the values for proportional abundance in scats do not necessarily add up to 1." (in Results L. 231-236)

Figure 4.

Concerning defecation rate, please check Picard et al. 2015 (http://onlinelibrary.wiley.com/doi/10.1002/ece3.1512/abstract), where you will see that your statement does not hold as defecation rate is not so different among animal species (for instance between red deer and wild boar).

The density of scats for pigs is very small (from 0 up to 4 per 800m² and an outlier with 10 scats per 800m²) and variable at all. Putting pig and deer on different X scales lead to ambiguous reading of the results.

I would erase that figure or present it with two boxplots: with and without pig scat. In no manner you can use these results to determine that wild boar has or has no effect on the vegetation.

*** We appreciate the reviewer's concerns about the comparison between pigs and deer.

Because there are only three out of 14 sites that have zero pig scats, we did not include the box plots with the binary comparison as suggested. However, a binary comparison would likely provide qualitatively similar results to the linear model, with no relationship between pig presence and the seedling community, as the three sites without pig scat contain low, medium, and high values of seedling and vine abundance.

The ideal situation would allow a direct per capita comparison between the two species, but assessing pig and deer abundance is problematic, therefore we had to rely on scat counts to assess relative abundance. The reviewer suggested that we could directly relate seedling metrics to deer and pig scat counts on the same graph, which suggests that one scat from a pig is equivalent to one scat from a deer. However, studies focused on wild boar and multiple species of deer consistently report that deer have higher daily defecation rates (DDR), with boar producing 3.8-5.8 defecations per day (Ferretti et al 2015; Plhal et al 2014), and deer producing 11-34 defecations per day (Dinerstein and Dublin 1982; Rogers 1987; Sawyer et al 1990; Smith 1964). The Picard et al. 2015 paper suggested by the reviewer supports the idea that defecation rates are lower for pigs than for deer, as it states that "Defecation probability ... was lower in wild boar (median = 0.38) than in roe deer (0.70 ...) and red deer (0.74..., posterior probability that pdef_{i,t wild boar} < pdef_{i,t ruminants} was 99.5 +/- 3%)", although it also states that the daily defecation rates for roe deer was 6.3 and for red deer was 5.4, which is well below the daily defecation rates from other literature. The daily defecation rate in Picard et al 2015 for boar

was 4.0, which is within the range reported elsewhere. It would be ideal to have data on the Philippine deer defecation rates, but we were unable to locate it. Since the existing data show higher defecation rates for deer than pigs, with a lot of variation, we chose to keep pigs and deer on separate graphs.

Wild Boar

Ferretti, F., Storer, K., Coats, J. and Massei, G., 2015. Temporal and spatial patterns of defecation in wild boar. Wildlife Society Bulletin, 39(1), pp.65-69. (DDR 3.8-4.3)

Plhal, R., Kamler, J. & Homolka, M. Acta Theriol .2014. Faecal pellet group counting as a promising method of wild boar population density estimation. Acta Theriologica. 59: 561. https://doi.org/10.1007/s13364-014-0194-9. (DDR 4.2-5.8)

Deer

Captive axis deer

Dinerstein, E. and Dublin, H.T., 1982. Daily defecation rate of captive axis deer. The Journal of Wildlife Management, 46(3), pp.833-835. (DDR: >13)

White-tailed deer

Rogers, L.L., 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. The Journal of Wildlife Management, pp.330-333. (DDR: 34 in wild, 11-14 in captivity)

White-tailed deer (wild females)

Sawyer, T.G., Marchinton, R.L. and Lentz, W.M., 1990. Defection rates of female white-tailed deer in Georgia. Wildlife Society Bulletin (1973-2006), 18(1), pp.16-18. (DDR: 26.9)

Mule deer

Smith, A.D., 1964. Defecation rates of mule deer. The Journal of Wildlife Management, pp.435-444. (DDR: 13-15)

As I pointed out in my first review I would suggest using linear regressions with both types of scats to see if wild boar can significantly explain something once deer has been taken into account

***We performed linear regressions with both types of scats, and added the model comparison results to the supplementary information (Section 4). We state:

"Deer scat abundance was consistently part of the best fit model to explain seedling abundances and vine abundance, while the models with pig scat abundance and both pig and deer scat abundance were not."

The fact that boar do not wallow on limestone karst forest and are not browsing animals just mean that you can not really assess their direct role in this kind of forest. Then I would conclude that the comparison you do between deer and pigs role is not really relevant.

*** We seek to understand the impact of non-native pigs and deer in limestone forest, and thus our conclusions are only relevant for this forest type. Both species are present in these forests, as indicated by the scat counts, other signs (e.g. rooting in locations where possible, tree damage), and frequent observations of animals while conducting research, therefore a qualitative comparison between the role of pigs and deer in this forest type is relevant. Since we are unable

to assess the per capita impact, we refrain from quantitative comparisons between the two species, but believe qualitative comparisons of their impacts are warranted in the discussion.