Response to reviewer comments for Gawel et al.

Responses are italicized

Reviewer 1

Review of Gawel et al. (RSOS-170151): *Contrasting ecological roles of non-native ungulates in*

*a novel ecosystem*

Gawel et al. present an interesting study documenting the roles of two non-native, invasive

ungulates – feral pigs and Philippine deer – on forest communities in Guam in what are today

novel ecosystems (i.e., combination of native and nonnative species dominance). Specifically,

they examine the role that each of these non-native ungulates has on plant community

composition via seed dispersal and seed survival. They combine field and greenhouse studies to

document that deer in this system have pronounced negative impacts on plant communities via

seedling browsing (and lack of seed dispersal). In turn, feral pigs are highlighted as being

important seed dispersers for both native and nonnative plants, while having no negative impacts

on seedlings. The importance of feral pigs as seed dispersers is highlighted given the almost

complete lack of native dispersers (e.g., birds) in Guam today.

Understanding how nonnative ungulates impact native plant communities has received

increasing attention, while few (if any?) studies have examined this important question in a novel

ecosystem that consists of mixtures of native and non-native species. I found the article to be

well-written and concise (perhaps a bit too concise, see below). It is an interesting question that

is not isolated to the island of Guam (although I felt the authors could do a better job of

providing more context for how widespread the issue of nonnative ungulates in novel ecosystems

really is globally). Despite these positive aspects, I feel like the article as currently written needs

attention to a few important items, highlighted below.

**Major Items:**

1) **Lack of information on Study Site**: 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 non-native 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?).

*RESPONSE*

*Thank you, expanding on those details would definitely help place this study in better context. We added a figure to demonstrate the dimensions of our vegetation and scat count belt transects as well as a figure to supplementary material with the locations of our seedling plots and transect sites on Guam, relative to where limestone karst forest is located.* *We also added more details to the “Study area” subsection of our Methods that highlight why these forests are still novel ecosystems, and how we chose them:*

*“We chose sites for this project that were considered native limestone karst forest in order to maintain similarities between sites and maximize the likelihood of discerning differences due to pig and deer abundance rather than other site characteristics like history of disturbance or species composition. Native trees still dominated these sites. However, the relative abundances of vegetation differ from early descriptions of Guam forests [30,31]. This, and especially the absence of native avifauna amongst a mixture of other non-native plants, insects, and mammals [23] provided an ideal setting for investigating roles in a novel ecosystem.” (Lines 81-88)*

*The sites were adjacent, with canopies from individual trees usually overlapping both plots. The species composition of the plots would not differ because there were few other seedlings or adults besides the seedlings that we planted ourselves in each 3.5-m by 5.5-m plot. We added this text under “Effects of ungulates on seedling survival” subsection of the Methods:*

*“Since the paired plots were adjacent, very little differed between them in canopy composition and cover. We also consciously avoided large gaps in canopy cover, depressions in the substrate, or any other features that might have caused a difference between the paired plots outside of our treatments.” (Lines 95-98)*

*END RESPONSE*

Reviewer 1 continued:

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).

*RESPONSE:*

*We added a few details about feral pigs:*

*“Deer were introduced to the wild in Guam in 1772 by Spanish Governor Mariano Tobias as game meat [22], while pigs in the forests of Guam are descended from livestock brought by Spanish colonizers in the 1660’s, and subsequently mixed with other livestock throughout the centuries [20].” (Lines 55-58)*

*We also added new sources and a few more details on limestone karst substrates to Methods, Study Area:*

*“This karst is extremely porous and easily weathered by water, creating sharp and porous features that hold very little topsoil [30,32]. It is extremely rugged and difficult to walk on, with small crevasses and holes throughout.” (Lines 77-79)*

*And in the discussion:*

*“While the novel ecosystems of Guam provide an important context in determining the relative detriment or benefit of these ungulates, the natural limestone karst forest features, which are easier for deer to traverse in, but more difficult for pigs to root and wallow in, also played a large role in determining this. A similar study in the clay soils of Guam would likely produce different results.” (Lines 295-300)*

*END RESPONSE*

Reviewer 1:

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.

*RESPONSE:*

*We agree that ungulate numbers would enhance the paper, but we do not have ungulate densities for sites in Guam, and no natural resource agencies or other researchers have attempted to estimate ungulate densities on a wide scale in Guam. One unpublished study from 2002 estimated deer abundance along abandoned runways on the Air Force Base using spotlight counts from multiple vehicles (Knutson and Vogt 2002 unpublished). They estimated 1.83 deer per hectare (95% confidence interval = 1.44-2.21) and feral pig densities of 0.38 pigs per hectare (95% confidence interval = 0.20-0.55), indicating that they were very dense in this area of Guam. This effort required multiple vehicles spotlighting along open runways. Much of the habitat that we sampled in is closed canopy with distance-limited visibility and no roadsides or open trails. While three of our sites were located on the same Air Force base, we could not reliably use Knutson and Vogt’s numbers for such different habitat types. Further, there are few reliable and feasible methods for estimating ungulate densities in tropical forests without knowing more about the natural history of the animals in this setting – for example, home range or average distance travelled for foraging (Koster and Hart 1988, Jathanna et al. 2003, Carillo et al. 2008). Therefore, we chose to use relative abundances between sites using scat counts (other sign such as tracks are impossible to see on karst substrate). We added this text to our methods section:*

*“**Actual ungulate densities in any habitat in Guam are unknown, but thought to be very high. Estimates have rarely ever been attempted because common methods such as spot*

*lighting, visual counts on transects, and aerial counts are unreliable in dense tropical forests.”(Lines 153-156)*

*We also added this text to the Discussion:*

*“**We know that pigs are present in these forests, and their wallows are abundant in ravine forests. However, unlike other forest types, the forest floor in a limestone karst forest is rocky and rigid [29,31], which would be difficult for pigs to root and wallow in, thereby limiting the extent of their damage to seedlings. In contrast, feral pigs in Hawaii and Malaysia cause seedling mortality, increase erosion, affect biogeochemical cycling, and spread invasive plants [17,37-39]. These damaging processes are unlikely to impact the rocky substrates in limestone karst forests. Removing pigs in Guam could have detrimental effects to plant species that have been limited by the lack of dispersers, especially in limestone karst forests,* *where they are less likely to cause damage through rooting and wallowing.” (Lines 277-283)*

*As for origin of pigs and deer, we added this sentence to the Introduction:*

*“Deer were introduced by a colonial Spanish governor in 1772, and feral pigs are believed to be descended from livestock first brought on Spanish ships in the mid-1600’s [20,27].* *We have no evidence that wild boar have ever been introduced to Guam.” (Lines 55-59)*

*END RESPONSE*

Reviewer 1:

2) **Interpretation of results**: I feel like the authors did a pretty good job of framing this study

as a novel ecosystem consisting of a mixture of native and nonnative trees, and two

nonnative ungulates. However, they go on to interpret almost all of their results based on

native vs. non-native plants, and in doing so I feel like they get away from the novel

ecosystem story and muddy the water. For example, a lot of attention is given to seed

dispersal of native species over nonnative species in Results. Table 2 and Fig. 2 tell me a

different story: that pigs disperse a lot of a single native species (*Morinda citrifolia*), but

primarily disperse non-native species. In the context of a novel ecosystem I think this is fine,

but as presented it comes across as a hold-over from a prior version of the manuscript where

the focus was on native vs. nonnative, and not novel ecosystems? I feel like the authors miss

a really nice opportunity to consider seed dispersal from the viewpoint of life history

characteristics instead of native vs. nonnative, which would fit well into the novel ecosystem

context. For example, it appears that all of the seed dispersed by pigs are from trees with

fleshy fruits (which makes sense for pigs to disperse). Why not present the results then based

on the life history characteristics of the tree species, and not the simply dichotomy of native

vs nonnative? You do a good job of setting this up as an important question to ask in a novel

ecosystem in the Introduction, but then get away from that context in the interpretation of

results.

RESPONSE

*Thank you for these suggestions about how to frame the results in a more compelling manner consistent with our novel ecosystem approach of viewing the ecosystem. We focused on the native/non-native distinction in part because one of the major impacts of pigs in Hawaii is their role in dispersing invasive plants, and therefore we have retained some discussion of the native/non-native distinction. However, we added some information on the properties of these species as well as what we know of species traits to the Discussion.*

*Although no studies that we know of have addressed the questions of natural defences directly, we know that Guam’s native flora have that have evolved in the absence of large herbivores common to continental systems consistent with the native flora of many remote oceanic islands (Courchamp 2003). They have no evident physical defences. We have no definitive answer for why deer avoided these species in our seedling plots and, therefore, do not detail conclusions concerning their chemical composition. However, we included some new citations on species’ traits and chemical composition in a new paragraph of the Discussion:*

*“Beyond ecology or status as native or non-native, traits of the plant species themselves turned out to be predictive of how they were affected by either deer or pigs. As mentioned above,* M. citrifolia*,* Ficus *sp., and* C. papaya *all contain a large number of small seeds per fruit, contributing to the numbers we recorded germinating from pig scats. They are also fleshy-fruited and sweet or pungent when ripe, all suggesting appeal to pigs when encountered in the forest. Evidence also points to small seed size being advantageous to dispersal [37]. While species-specific studies have rarely been done on the chemical traits of species planted in our seedling plots, we assume that these characteristics contribute to their survival in the presence of deer. Studies on other species of deer suggest their selective browsing depends on chemical composition of different plants. For example, they tended to avoid plants with high amounts of tannic acid [38,39]. We do not have chemical composition studies on the two species that were consistently avoided in seedling exclosures (*O. oppositifolia *and* A. mariannensis*). However,* O. oppositifolia *has a thick, milky sap like other Apocynaceae, and other members of the* Aglaia *genus are known to have high tannin content [41,42], potentially contributing to lower palatability by deer.* M. citrifolia*,* P. serratifolia*,* C. papaya, *and other species of* Psychotria *have documented medicinal uses [27,43,44,45], suggestive of potent chemical properties, but, in contrast, were all consumed by deer in our open seedling plots instead of avoided. Since they have no visible physical defences, the chemical composition of the avoided species surely contributes to their defence against herbivory. The other species that were consumed, although medicinal, were more palatable to deer, suggesting that deer have some tolerance of plants with antimicrobial and other medicinal uses. This, rather than just origin or status as native, contributed to their susceptibility in Guam.” (Lines 267-288)*

*END RESPONSE*

*Reviewer 1:*

3) **Over-interpretation of results?:** One of the primary take-home points from the article is

that feral pigs play an important role as seed dispersers in this novel ecosystem. However, I

found this point to be at least somewhat contradictory to other statements in the paper. For

example, the authors state on lines 199-201 that “While the benefits of pigs as seed dispersers

were not evident in the seedling community, neither was a negative role for pigs”. I have a

hard time reconciling that statement with others, for example lines 12-13 in the abstract

stating “…suggesting that pigs provide an ecosystem function – seed dispersal – that has

been lost from Guam”; and lines 213-214 stating “…pigs may be one of the few vertebrate

species moving successional species into edges and gaps”. How is it possible that pigs are

playing an important role as a seed disperser if they have no impact on the plant community?

I find there to be a pretty big difference between lack of a negative role vs. presence of a

positive role. Your evidence seems to point to the former, but most of the attention is on the

latter.

RESPONSE

*We appreciate the feedback from this reviewer that the lack of negative role should be emphasised instead of giving the impression that pigs play a positive role. We soften our language about the role of pigs as dispersers. Instead, we suggest that they are capable of dispersing seeds, but that further studies are needed to truly discern their roles.*

*END RESPONSE*

Reviewer 1:

**More minor items:**

1) I feel like it is important to highlight that you have no true control in this study (i.e., forests

never impacted by deer and feral pigs on Guam).

RESPONSE

*This is an important point relevant to many systems dealing with invasive species -* *when the invader has been present for decades, they have likely impacted the composition of all forests, so we will never know what an invader-free forest would look like. However, using exclosures and gradients, we can study the effects of pig and deer presence & abundance on the current plant community. We have acknowledged this in the paper by saying :*

*"Unfortunately, since both deer and pigs have been present for centuries, we had no true “ungulate-free” control. To remedy this, we used exclosures and gradients of abundance to tease apart what their effects are to plant communities." (Lines 294-296)*

*END RESPONSE*

*Reviewer 1:*

2) Lines 88-89: Seeds came from multiple islands???

*RESPONSE*

*Seedlings were only from Guam. Line was corrected.*

*END RESPONSE*

*Reviewer 1:*

3) Line 100: sounds like some of the outplanted seedlings were in the ground for 15 months,

others only 4. This should be expanded upon in the Results and their interpretation.

*RESPONSE*

*Some seedlings were in the field for longer than others for logistical reasons (fruiting seasons varied, so we staggered seedling planting accordingly. To test whether the effect of ungulates varied by the duration of time seedlings were outplanted, we included length of time in our GLM full model, but it did not improve model fit, so was not included in the best-fit model.*

*END RESPONSE*

*Reviewer 1:*

4) Lines 114-116: I found it odd that the authors appear to have removed all wind-borne seeds

from the seedling/scat greenhouse trial, yet in lines 164-165 refer to a windborne seedderived

seedling in deer scat as being accidentally ingested. How do you reconcile that

apparent discrepancy? Were windborne seeds removed from that experiment or not? This

also goes back to my comment about presenting and interpreting results based on life history

characteristics of the studied species, and not just native vs. nonnative.

RESPONSE

*Only one wind-dispersed seed was included in our counts, it was from deer scats. We added this text to lines 198-199:*

*“The* M. micrantha *seedling, however, was only found in one tray and sprouting directly from one of the deer pellets and so was included.”*

*END RESPONSE*

*Reviewer 1:*

5) Lines 155-158: What is it based on life history characteristics that would make these two

species unaffected by fencing? Thorns? Defense compounds? I feel like you miss an

important opportunity by not looking at the life history characteristics of both those species

impacted and those not impacted by deer browsing. This is particularly important given your

contention that deer are selecting for these species by not browsing on them, and more

information would help bolster that claim.

RESPONSE

*See response above about natural history of* O. oppositifolia *and* A. mariannensis*.*

*END RESPONSE*

Reviewer 1:

6) Line 176: Cause and effect? Why not “Effect of community composition on ungulate

abundance”? This seems like a circular argument to me, and without more information it is

impossible to tell if deer activity is driving seedling dynamics, or seedling dynamics are

driving deer activity (you should be able to tease this apart with the exclosure portion of the

study).

RESPONSE

*There is an extensive body of literature (cited throughout the manuscript) on the severe impacts that deer can have on plant communities from species composition to structure and abundances. We find it highly unlikely that seedling abundance is driving deer abundance instead of vice versa.*

*END RESPONSE*

*Reviewer 1:*

7) Lines 190-191: Be specific that “ungulates” refers to deer. You just made the distinction

between deer and pigs, and now go back to referring to ungulates in general (and the main

point of your paper is that they need to be considered separately).

RESPONSE

*Line changed to state “deer” instead of “ungulates.”*

*END RESPONSE*

Reviewer 1:

8) Lines 197-199: “appeared to come from browsing rather than rooting”? Evidence to support

that claim?

RESPONSE

*Rooting by pigs is very obvious because the rocks and soil are disturbed. Seedlings that have been eaten by deer usually still have the stem present, but leaves have been removed and there is no sign of disturbance to the soil or substrate around the seedlings. We have added this clarification to the Results:*

*“Almost all mortality observed in seedling plots was in the form of deer herbivory – evident by leaves and stems being cut from the seedlings – instead of disturbed by uprooting by pigs.” (Lines 192-194)*

*END RESPONSE*

*Reviewer 1:*

9) Line 226: Looks like you missed a tracked change?

RESPONSE

*Adjusted.*

END RESPONSE

Reviewer 1:

10)Many of your citations are lacking important information on volume, page number,

publication venue, etc. (e.g., citations #17 and 21).

RESPONSE

*Edited so now Literature Cited is complete.*

END RESPONSE

Reviewer 1:

11) Figure 3: It is misleading to put regression lines on non-significant results. At a minimum,

use dotted lines for non-significance (and indicate this in the heading), or simply remove the

regression lines (my recommendation). Also, I would contend that 2 decimal places is

sufficient for r2 values. Finally, for all of the pig scat figures on the left it appears that the

lack of significance is being driven by a single point (far R data point). If you removed that4

point, would you not have the exact same patterns (and significance) as for the deer scat

figures on the R? Is there anything compelling about that data point to warrant it’s inclusion

or exclusion from the analysis? A lot of your interpretation of results relies on this set of

figures, so a bit concerning that a single data point may be driving most of your results.

RESPONSE

*While that point may contribute somewhat more than the other points to the shape of the graph, the results would still be significant with a similar curve shape for the parameters we measured:*

*Total seedlings vs deer scat count: r2 = 0.69*

*Native seedlings vs deer scat count: r2 = 0.62*

*Non-native seedlings vs deer scat count: r2 = 0.78*

*Vines vs deer scat count: r2 = 0.78*

*We have included a redrawn figure with the regression lines without that site to include in the supplementary material for reference. Because there is not much difference between results with and without that site, and because we think that the scat count fairly represents the high deer abundance at that site (site is in a restricted access area of a military base with no hunting), we included our complete dataset.*

*We also revised the figure included with the manuscript to only have 2 decimal places.*

*END RESPONSE*

Reviewer: 2  
  
Comments to the Author(s)  
RSOS-170151  
Review « Contrasting ecological roles of non-native ungulates in a novel ecosystem » by Gawel et al.  
General comments  
Interesting paper that tries to disentangle deer and pig effects on vegetation though different interactions (endozoochory, herbivory at the species and the community level). However it is not possible to establish a definitive statement on the relative effects of both species. I think that the authors should be cautious to push not too far the interpretations of their results. For instance, I am not sure the gradient of pig scat density to be sufficient to really test its effects on vegetation community composition.

RESPONSE

*Thank you for your suggestions. We soften our language about the role of pigs as dispersers. We agree that the lack of negative role should be emphasised instead of giving the impression that pigs play a positive role. Since both deer and pigs have been established for a long time, we resorted to using a gradient of abundances without the presence of a true control (areas of similar forest with no deer or no pigs)*

*END RESPONSE*

Reviwer 2:  
I have tried to access the dryad deposit as the origin of some data (vegetation surveys, number of sites not precisely indicated) is unclear and so it is difficult to interpret the data. However the data are not yet accessible.

*RESPONSE:*

*We will contact RSOS and Dryad to ensure the data is accessible. It is possible it has not been uploaded pending review of the paper. See text from email below:*

*“Thank you for submitting your data package to Dryad for journal review. Please read the following information carefully, so you will know what to expect during the rest of the data archiving process.*

*YOUR DRYAD DOI*

*Your data package has been assigned a unique identifier, called a DOI. This DOI is provisional for now, but may be included in the article manuscript. It will be fully registered with the DOI system when your submission has been approved by Dryad curation staff.*

*doi:10.5061/dryad.sp5ff*

*CITING YOUR DRYAD DATA*

*Ensure that readers can find your data!*

*We recommend that the article include a link to the Dryad data as follows: Data available from the Dryad Digital Repository:* [*http://dx.doi.org/10.5061/dryad.sp5ff*](http://dx.doi.org/10.5061/dryad.sp5ff)*”*

*The link does not seem to be up and working yet. However, we will gladly supply you with the raw csv and R files upon request in the meantime. We also plan to have an open repository on github.*

*END RESPONSE*

\*\*\*\*\*\*\*\*\*\*

Reviewer 2:  
I would advise the authors the following recommendations. The current version of the paper is acceptable pending major revisions  
Specific comments  
First of all, you have to give more details about the protocols:  
- How did you calculate the proportional abundances for vegetation surveys (seedling counts in nature) and for pig scats and deer dungs?

*RESPONSE*

*More detail has been added to both the Methods and Results sections:*

*“Proportional abundance in nature (left hand panel, Figure 3) for each species was calculated by dividing the total count of adults of that species across our fourteen sites and dividing that by the total number of adult trees across all sites. (Total adult count of one species / total adult count of all species counted on vegetation transects). We counted only adult trees in calculations to represent potentially fruiting trees.”*

*(Lines 213-218)*

*END RESPONSE*

Reviewer 2:  
- It is not mentioned how many sites have been sampled for vegetation surveys, looking at figure 3, it seems that there are 14 ? Please clarify

*RESPONSE*

*Thank you, that was a very important detail that we omitted. Number of sites (14) was added to methods and throughout the manuscript when we referred to those sites.*

*END RESPONSE*

Reviewer 2:  
- Concerning deer dung and pig scat counts, they are measured on each site in a square transect of 800m², it is not really clear the way it is described in the material and methods. May be a scheme would help, that present both vegetation and ungulates faeces surveys.

*RESPONSE*

*More detail has been added to the methods section, and we have added an additional figure to clarify methods for both our paired seedling plots and our vegetation and scat transects:*

*“To detect a range of scat abundances, we also surveyed a greater area at each site by including 2-m-wide belt transects encircling the vegetation transects (see Figure 1). These were walked and length estimated using GPS, with total area surveyed amounting to approximately 800 m2. However, since transect lengths used to count scats differed slightly from site to site, scat abundances used in analysis were number of scats per 100 m2.” (Lines 149 – 154)*

*END RESPONSE*

Reviwer 2:  
- We need a map for Guam highlighting the karst forests in global and the eight (14 vegetation surveys ?) ones that have been sampled. That would allow to see how the different samples are spatially organised.

RESPONSE:

*All sites were at least half a kilometer away from each other, and a map was added to supplementary material. We do not believe it contains enough information to justify adding it to the main published figures, but will be in supplementary material for reference.*

*END RESPONSE*

Reviewer 2  
Analysis  
Why did not you consider treatment and species in the same model to explain seedling survival. That will allow to really discuss the differences among species. You should also add a continuous variable for the time the seedlings are exposed to ungulates (varying from 4 to 15 months), the same measures are repeated over time. This would be much more clearer than now, when you are discussing differences among species but without testing for them.  
The dependent variable would be survival (yes=1 or no=0) for a given seedling as a function of time, treatment and species and taking site into account as a random factor.

RESPONSE

*This is a good point. We included length of time in our GLM full model, but it did not improve model fit. We report AICc values in our results:*

*“AICc for the model with the three-way interaction was 672.12, higher than AICc of 612.89 for just the species and treatment interaction.” (Lines 184 – 186)*

*END RESPONSE*

Reviewer 2:  
Figure 1. Put a star for the significant differences for treatment, and ns for the two last ones. Effect of length of monitoring  to be tested ? Order the species according to length of exposures to ungulates. We might expect longer times of exposure to lead to higher differences between treatments for the species concerned.

*RESPONSE*

*There is an asterisk next to each of the species names that had a significant difference along the x axis in Figure 2. Since they are arranged along the x-axis by largest difference between treatments to smallest, all four species with significant treatment effects are to the left, while the two species without treatment effect are on the right.*

*END RESPONSE*

Reviewer 2:  
Figure 3, there are inconsistencies between the r² in the figure and the ones given in the text. In this figure 3 and associated analysis, why did not you use multiple regressions to see if boar and deer have complementary effects on different functional groups abundances?

*RESPONSE*

*This has been corrected in the text.*

*END RESPONSE*

The range for wild boar is 10 times shorter (0-10 dungs/800m²) than the one for deer (0-80/800m²). That is surely the reason why we cannot conclude about any effect from pigs concerning vegetation community composition.

*RESPONSE*

*Pigs defecate less often than deer, and that may have accounted for the smaller range of values in pig scat counts. Pigs are still quite abundant in some of these forests, and we should be able to detect trends, even within a smaller range of scat counts. One unpublished study from 2002 estimated deer abundance along abandoned runways on the Air Force Base using spotlight counts from multiple vehicles (Knutson and Vogt 2002 unpublished). They estimated 1.83 deer per hectare (95% confidence interval = 1.44-2.21) and feral pig densities of 0.38 pigs per hectare (95% confidence interval = 0.20-0.55). So, rather than the smaller range of scat counts, we think that pigs that are present are not inflicting the same amount of damage as deer, therefore contributing:*

*“In contrast to deer, we did not detect strong negative impacts from pigs in the native limestone forest, and pigs are one of the last major vertebrate dispersers on an island that has lost its native dispersers. We know that pigs are present in these forests, and their wallows are abundant in ravine forests. However, unlike other forest types, the forest floor in a limestone karst forest is rocky and rigid [29,31], which would be difficult for pigs to root and wallow in, thereby limiting the extent of their damage to seedlings.” (Lines 302-307)*

*END RESPONSE*

*Reviewer 2:*

Again in Fig 3, it seems that there are 14 sites but it is not said anywhere in the manuscript. Please clarify and correct.

*RESPONSE*

*The number of sites used has been added throughout the manuscript.*

*END RESPONSE*

Reviewer 2:  
Figure 2. It is really unclear how proportional abundance is calculated for native and non-native plants in the field and in both types of dungs. Please clarify and justify in the mat and meth. You could in that figure add native and non-native to the species heading on the left and then avoid the double similar X-axis.

*RESPONSE*

*More detail has been added to both the Methods and Results sections:*

*“Proportional abundance in nature (left hand panel, Figure 3) for each species was calculated by dividing the total count of adults of that species across our fourteen sites and dividing that by the total number of adult trees across all sites. (Total adult count of one species / total adult count of all species counted on vegetation transects). We counted only adult trees in calculations to represent potentially fruiting trees.” We decided to keep the figure as is for easier reading.*

*END RESPONSE*

Reviewer 2:  
Table 1. Please identify the non-native species, but it would be better to do that table according to the full model proposed treatment\*species\*(time of exposure) with main effects and interactions. I do not understand why authors did not analyze these data with the full model.

*RESPONSE*

*We indicated that papaya is an introduced species with an asterisk.*

*END RESPONSE*

Reviewer 2:  
Table 2. Add number of deer and boar samples in the table. Rather than 0, put – in lines without data. Average number of seedlings per dung for a given species with standard errors when it is possible.

*RESPONSE*

*Our caption for Table 2 includes the number of deer and pig scat samples. Because of our many zero counts for each species per dung, the standard error would be, in most cases, larger than the average count of seedlings per species per dung. We thought it was important to include zeroes to show that some species did not appear at all in pigs, while they did in deer, and vice versa. In addition, many of them only appeared in a single scat, therefore, standard error could not be calculated. We did change total seedling counts to average seedling counts per species, however. Thank you for the suggestion.*

*END RESPONSE*

Reviewer 2:  
May be it is worth analysing your “endozoochory” data using hurdle models ? With “seedling species richness”and/or “seedling abundance” as dependent variable, then you might be able to test for differences between ungulate species.

*RESPONSE*

*In previous drafts, we had tried to calculate a selectivity index. Upon consultation with multiple statisticians, however, we decided to consider the results qualitatively rather than conducting a statistical analysis because of the small number of scats that we had collected for each species of ungulate. While a hurdle distribution accounts for zero counts as well as high counts, our total number of scats is still quite small (31 for pigs and 20 for deer). ????*

Reviewer 2:  
Related to that analysis we need the information about the number of seeds per fruit somewhere in the material and method for the different species dispersed (why not converting in fruit numbers, the results of seed dispersal). For the moment that issue is solely in the discussion.

RESPONSE

*We added this text to the Discussion:*

*“We know from unpublished data from a related project that M. citrifolia has an average of 115 seeds per fruit and Ficus sp. and C. papaya both have well over 200 seeds per fruit.*

*END RESPONSE*

Is Rusa marianna a browser or a grazer ? Please clarify.

RESPONSE

*This deer would be considered a browser. “Grazing” is not mentioned anywhere in this paper, and it refers to animals like cows, sheep, buffalo, etc… that clip low-lying vegetation. “Browsing” or removing leaves/bark/fruits from trees, shrubs, and herbs, more accurately describes how most deer feed. We stick to “browsing” in the text.*

*END RESPONSE*

Reviewer 2:   
L11P1 effects instead of impacts

RESPONSE

*Changed.*

END RESPONSE

Reviewer 2:  
L12P1 dungs or pellets instead of scats for deer, here more native species dispersed by pigs but not only native species, may be highlight the relative proportion.

RESPONSE

*“Scat” is commonly used to refer to both pig and deer faeces, and we stick to that terminology throughout the paper. We apologize, but we are unsure what the reviewer means by their native species comment.*

*END RESPONSE*

Reviewer 2:  
The authors speak of seedling abundance L62P3/plant community structureL10P1/plant community characteristics P4L65 (3 different manners which are related to the same analysis in the text but is then unclear). Please use the same wording throughout the text. However the variables used are more related to plant community composition than structure.

RESPONSE

*Thank you for catching that. They have been changed throughout text to “plant community composition.”*

END RESPONSE

Reviewer 2:  
P4L67 whether the presence/the effects instead of impacts

RESPONSE

*Changed.*

END RESPONSE

Reviewer 2:  
P4L83 which one is exotic, please specify

RESPONSE

*Added this text to clarify:*

*“All are common components of Guam’s limestone karst forests, although the non-native C. papaya tends to favor edges, and P. mariannensis is less common than the other species.” (Lines 104-106)*

*END RESPONSE*

Reviewer 2:  
Seedling plot measures roughly 19.25 m². according to the plan, it allows 153 available places for seedlings  for a total of 79 planted seedlings. Can you comment on how seedlings planted were spatially arranged (random ?), this may lead to interspecific neighbouring effets ?

RESPONSE  
We added this text to calrify:

“Seedlings were haphazardly placed within the seedling plot since they had to be planted around rocky karst structures and roots from neighbouring trees.” (Lines 114-116)

END RESPONSE

Reviewer 2:  
P5L88 Why “on the island they have been collected”, please clarify

RESPONSE

*This was a mistake, it’s been deleted.*

END RESPONSE

Reviewer 2:  
P5L96 3 species among the 6 tested planted during drier months, which months? To clarify in relation to times of exposures to ungulates by plant species or group of species.

RESPONSE

*Added explicitly what months constitute “dry season” in Guam – December to May.*

END RESPONSE

Reviewer 2:  
P5L103-4 why separately tested? See above comments on this specific analysis.

*RESPONSE*

*We know that species contributes overwhelmingly to the best fit model. We wanted to test on a species-level the importance of treatment effect.*

END RESPONSE

Reviewer 2:  
P6L116-118 Please clarify how proportional abundances have been calculated in faeces et vegetation surveys. A priori there are 14 sites for vegetation surveys!

RESPONSE

*Details added.*

END RESPONSE

Reviewer 2:  
P6L121 You present different functional groups that are nor used, neither presented later on. Be consistent please or justify why some functional groups are not tested.

RESPONSE

Our analysis focused on seedlings, but we still measured adults. Vine abundance responded to deer abundance, and that was one of several general groups (trees, shrubs, herbs) that we classified. However, to minimize confusion, because we only report on seedlings and vines in the results, we just use the general term “growth form.”

*END RESPONSE*

*Reviewer 2:*

Deer pellet and pig scat abundance is an indicator of animal presence. But keep scat or dung abundance per 100m² in the text and do not use deer abundance or pig abundance in the text because it is false and misleading. Faeces count is only an indicator, because you do not justify how it is really related to animal abundance.

RESPONSE

*We assume that scat abundance is related to animal abundance for a given site. There is support for this in other studies such as Engemen et al. 2013. However, we appreciate the reminder that scat or dung abundance is only an indicator of animal abundance, and have adjusted the text in several places accordingly.*

*END RESPONSE*

Reviewer 2:  
P7L133 You could use multiple linear regressions to test deer and pig effects together, but there is probably a problem of range of faces abundance between ungulates! May be is it simply not possible to test for pig scat abundance effect, because the gradient is too short. So be cautious in the interpretation.

RESPONSE

*Noted. We are sticking with analyzing them separately because the range does vary between ungulates (e.g. deer produce lots of small scats, whereas pigs produce fewer large scats). We recognize that the range of pig scat abundance over which we tested was smaller than that for deer, which may have limited our ability to see a signal of pig abundance. However, we sampled in areas with very high evidence of pig damage as well as areas with low pig damage, and this damage correlated well with scat counts. Therefore, we believe the scat counting approach is a viable indicator for pig density, and that we sampled across the range of pig densities.*

END RESPONSE

Reviewer 2:  
P7L137 Forest characteristics not in agreement with the functional groups defined previously, why ? Native vs. non-native should be crossed with each functional group.

RESPONSE

*We revised our methods to focus on the groups that we present in the results (see response above).*

*END RESPONSE*

Reviewer 2:  
P7L153 the dependant variable is survival or not after 4-15 months exposure to ungulates. See comments above on the model. I really think that time of exposure should be taken into account.

RESPONSE

*As in response above, we included length of time in our GLM full model, but it did not improve model fit. We report AICc values on lines 180-181:*

*“AICc for the model with the three-way interaction was 672.12, higher than AICc of 612.89 for just the species and treatment interaction.”*

END OF RESPONSE

Reviewer 2:  
P8L157 erase did not (twice)

RESPONSE

*Corrected.*

END RESPONSE

Reviewer 2:

P8L159 pellets instead of scats for deer

RESPONSE

*See comment above – we continue to use “scats” instead of pellets.*

END RESPONSE

Reviewer 2:  
P8L160 (4/20) instead of  20%, idem  (25/31) instead of 80.6%. How many species for pigs, how many native and non native ? One unidentified ! All of these informations have to be presented here and not only in the attached table.

RESPONSE:

We added more details to the results:

“Of these, 25 scats had seedlings (80.6%), with a total of 1658 seedlings germinating (Table 2). Eight species germinated from pig scats. They were the native trees *M. citrifolia* (in 20 out of 31 scats), and *Ficus prolixa* (in three scats); the non-native trees *C. papaya* (in 16 scats) and *Leucaena leucocephala* (in one scat); the non-native vines *Passiflora* spp. (in three scats) and *Coccinia grandis* (in three scats); and the non-native herb *Chromolaena odorata* (in one scat). All of these except for *C. odorata* and *L. leucocephala* have edible, fleshy fruits.” (Lines 208-213)

We were unable to identify some of the seedlings, which died before they reached a size where we could more easily identify them.

END RESPONSE

Reviewer 2:  
P8L172 local flora and associated vegetation surveys not described in the mat and meth.  
May be you could test the abundance ranking order between local flora (avoid nature) and dung seedling composition with Spearman correlation tests.

RESPONSE

*More detail has been added to Study area subsection of Methods:*

*“We chose sites for this project that were considered native limestone karst forest in order to maintain similarities between sites and maximize the likelihood of discerning differences due to pig and deer abundance rather than other site characteristics like history of disturbance or species composition. Native trees still dominated these sites. However, the relative abundances of vegetation differ from early descriptions of Guam forests [30,31]. This, and especially the absence of native avifauna amongst a mixture of other non-native plants, insects, and mammals [23] provided an ideal setting for investigating roles in a novel ecosystem.”*

*See response above about analysis of scat seedling composition.*

*END RESPONSE*

Reviewer 2:  
P8L176 effects of ungulates on vegetation community composition (erase abundance)

*RESPONSE:*

*We have erased “abundance.” In paragraph, we changed abundances to scat counts. (Line 227)*

Reviewer 2:  
P9L177 Be more precise: total or per functional group seedling abundance, r² different in text and fig. Please check and correct!

RESPONSE

*Corrected r2 and changed to “forest community abundances.” (Lines 218-220)*

*END RESPONSE*

Reviewer 2:  
P9L184 cylindrocarpa or cylindrica ?

RESPONSE

*Changed to cylindrocarpa – good catch!*

END RESPONSE

Reviewer 2:  
P9L184-187 Proportions given, where do they come from, not clear, please clarify !  
Do you have browsing records for the exclosure experiments ? To what is the survival outside the exclosure related to? Only to browsing? Dryness ? Pleas clarify

RESPONSE

*Percentages given here are calculated from our 14 vegetation transects, same as we calculated proportional abundance (except percent instead of proportion). This was described in results (Lines 205-209):*

*“Proportional abundance in nature (left hand panel, Figure 3) for each species was calculated by dividing the total count of adults of that species across our fourteen sites and dividing that by the total number of adult trees across all sites. (Total adult count of one species / total adult count of all species counted on vegetation transects).” (Lines 214-218)*

*We are unsure what this reviewer means by “browsing records for the exclosure experiments.” Full results from our exclosure experiments are described in the first section of our results and Figure 2, and we elaborate on implications in the Discussion. We controlled for any effects of dryness by watering any seedlings planted during the dry season.*

*END RESPONSE*

Reviewer 2:  
P9L196 Deer signs not described! Browsing and rooting are nor estimated neither described.

RESPONSE

*True, we should stick to the only sign we assessed, changed “sign” to “pellets” for deer.*

END RESPONSE

Reviewer 2:  
P9L197 over interpreted and not comparable as pigs scat abundance represent a much shorter gradient ( by ten times roughly).

RESPONSE

*We soften our language about the role of pigs as dispersers. Instead, we suggest that they are capable of dispersing seeds, but that further studies are needed to truly discern their roles. We agree that the lack of negative role should be emphasised instead of giving the impression that pigs play a positive role.*

END RESPONSE

Reviewer 2:  
P10L202 Please look at Picard et al. 2016 in JVS “Functional traits of seeds dispersed through endozoochory by native forest ungulates” for differences between other deer species and wild boar !

*RESPONSE*

*We appreciate the reviewer sharing this study! We hope to look into functional traits in more detail in the future. For this study, we have little information on functional traits to draw conclusions, but have added a paragraph on traits to the Discussion:*

*“Beyond ecology or status as native or non-native, traits of the plant species themselves turned out to be predictive of how they were affected by either deer or pigs. As mentioned above, M. citrifolia, Ficus sp., and C. papaya all contain a large number of small seeds per fruit, contributing to the numbers we recorded germinating from pig scats. They are also fleshy-fruited and sweet or pungent when ripe, all suggesting appeal to pigs when encountered in the forest. Evidence also points to small seed size being advantageous to dispersal [37]. While species-specific studies have rarely been done on the chemical traits of species planted in our seedling plots, we assume that these characteristics contribute to their survival in the presence of deer. Studies on other species of deer suggest their selective browsing depends on chemical composition of different plants. For example, they tended to avoid plants with high amounts of tannic acid [38,39]. We do not have chemical composition studies on the two species that were consistently avoided in seedling exclosures (O. oppositifolia and A. mariannensis). However, O. oppositifolia has a thick, milky sap like other Apocynaceae, and other members of the Aglaia genus are known to have high tannin content [41,42], potentially contributing to lower palatability by deer. M. citrifolia and P. serratifolia, and other species of Psychotria have documented medicinal uses [27,43,44,45], suggestive of potent chemical properties, but, in contrast, were all consumed by deer in our open seedling plots instead of avoided. Since they have no visible physical defences, the chemical composition of the avoided species surely contributes to their defence against herbivory. The other species that were consumed, although medicinal, were more palatable to deer, suggesting that deer have some tolerance of plants with antimicrobial and other medicinal uses. This, rather than just origin or status as native, contributed to their susceptibility in Guam.” (Lines 267-288)*

P10L203 species richness instead of diversity, pellets/dungs instead of scats.

*Changed to species richness. See comment above about continuing to use “scat.”*

P10L204 many seeded fuits, this information arrives too late please see earlier comments on that point.

*Addressed above.*

P10 L218-220 that is not what is tested please do not overestimate your results (boar vs. deer effects)

*As mentioned above,* *we soften our language about the role of pigs as dispersers. Instead, we suggest that they are capable of dispersing seeds, but that further studies are needed to truly discern their roles. We agree that the lack of negative role should be emphasised instead of giving the impression that pigs play a positive role.*

P10 L226 This suggests Rusa marianna is a grazer, is that true ? to be specified in the mat and meth. And comment on its potential effects on different vegetation functional groups (at least woody versus non woody species). What do we know from its feeding regime ? Must be interesting to precise somewhere in the mat and method.

Rusa marianna *is a browser. See response above on browsing vs. grazing.*

It seems that as Cervus elaphus for instance, it is an intermediate mixed feeder (Hoffmann 1989).  
Following paragraph from <http://www.cabi.org/isc/datasheet/89935>  
[…] Nutrition  
Very little information on diet is available in the Philippines, although a few observations have been published (Balete et al., 2011). Food records from Micronesia are more extensive and reveal a diverse diet comprised of at least 82 plant species, including trees, shrubs, grasses, herbaceous plants, vines, ferns, and mushrooms (Wheeler, 1979; Wiles et al., 1999). Foliage, fruits, shoots, seeds, and tree bark are eaten. Diet includes agricultural plants and fruits. Relative preferences among food plants remain unknown. Conry (1986) reported differences in dietary quality in northern versus southern Guam, based on fecal concentrations of diaminopimelic acid. […]

*We cite Wheeler, Wiles, and Conry in our study. We have not determined chemical differences or composition of the plant species that we tested.*  
  
References list has to be checked as for some of them, we do not have the pages …

*Literature Cited is now correct and complete - thanks for the careful checking!*