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 ecoystem*

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 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.

*We 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.”*

*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 feathers that might have caused a difference between the paired plots outside of our treatments.”*

*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). 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 a different habitat type. Further, there are few reliable and feasible methods for estimating ungulate densities in tropical forests without knowing much of the natural history of either animal in this setting – for example, home range or average distance travelled for foraging. Therefore, we determined that getting relative abundances through scat counts (other sign such as tracks are impossible to see on karst substrate) was sufficient to draw comparisons between sites. Admittedly, this might not have been a good estimate for pig abundance, which did not correlate with any of the plant community characteristics that we estimated. We added this text to our methods section (p. 7):*

Actual ungulate densities in any habitat in Guam are unknown and estimates have rarely ever been attempted because common methods such as spotlighting, visual counts on transects, and aerial counts are challenging in dense tropical forests.

*We also added this text to the Discussion (p. 13):*

We acknowledge that pig scat may not be a good proxy for abundance in these forest types, and this may have played a role in our inability to detect correlations between pig scat abundance and plant community characteristics. Still, 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.

*As for origin of pigs and deer, we added this sentence to the Introduction (p. 3)*

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].

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.

*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), the little we do know about Guam’s plants suggests that they have few chemical or physical defences such as strong toxins or thorns.* Ochrosia oppositifolia *and* Aglaia mariannensis *both have medicinal uses (Safford 1905), and we have observed some evidence of deer herbivory on their leaves, suggesting they are not highly toxic. 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 include speculations or guesses in the absence of solid information on their chemical composition. We simply point out that they survived in our ungulate-accessible plots, and they are also among the most numerous adults and seedlings in our vegetation surveys, leading us to believe that deer either avoid them or select for other species.*

*Added this text to Discussion (p. 12):*

*Further studies would be needed to determine if pigs are actually dispersing these species in to disturbed edges and gaps, but both tree species are very common in secondary forests that were formerly cleared land (which were not surveyed for this study) that also have evidence of pig presence like scat, wallows, and rooting.*

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.

*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.*

**More minor items:**

3

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).

*A few large-scale ungulate-exclusion fences were put up after our study, but at the time of our study, none existed outside of a small (220m by 220m) snake-proof enclosure where US Geological Survey scientists had been monitoring changes in vegetation inside versus outside the fence. We look forward to those results and ours helping inform the role that deer and pigs play in Guam. We settled on comparing relative abundances across based on scat counts. Based on the strong signal in the seedling communities we were able to detect across sites, this index was sufficient at capturing differences in deer abundances. Our seedling plots, however, were truly exempt from deer herbivory and any effects from pig rooting.*

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

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

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.

*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.”

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.

*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.”*

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.

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

6) Line 176: Cause and effect? Why not “Effect of community compoistion 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).

*We find it highly unlikely that seedling abundance is driving deer abundance instead of vice versa. We tried our best to find forest sites that were similar in structure so that differences in composition could be tied to ungulate abundance and not habitat type or historic use. Some sites are more popular as hunting sites than others, while sites on the military base or National Widlife Refuge that have more restricted hunting access had medium to high deer scat counts.*

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).

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

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

that claim?

Rooting by pigs is very obvious because the rocks and soil are disturbed.

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

Adjusted.

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

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

Edited so now Literature Cited is complete.

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.

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.  
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.  
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?  
- 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  
- 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.  
- 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.  
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.  
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.  
  
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?  
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. Again in Fig 3, it seems that there are 14 sites but it is not said anywhere in the manuscript. Please clarify and correct.  
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.  
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.  
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.  
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.  
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.  
Is Rusa marianna a browser or a grazer ? Please clarify.  
L11P1 effects instead of impacts  
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.  
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.  
P4L67 whether the presence/the effects instead of impacts  
P4L83 which one is exotic, please specify  
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 ?  
P5L88 Why “on the island they have been collected”, please  clarify  
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.  
P5L103-4 why separately tested? See above comments on this specific analysis.  
P6L116-118 Please clarify how proportional abundances have been calculated in faeces et vegetation surveys. A priori there are 14 sites for vegetation surveys!  
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.  
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.  
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.  
P7L137 Forest characteristics not in agreement with the functional groups defined previously, why ?Native vs. non-native should be crossed with each functional group.  
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.  
P8L157 erase did not (twice)  
P8L159 pellets instead of scats for deer  
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.  
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.  
P8L176 effects of ungulates on vegetation community composition (erase abundance)  
P9L177 Be more precise: total or per functional group seedling abundance, r² different in text and fig. Please check and correct!  
P9L184 cylindrocarpa or cylindrica ?  
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  
P9L196 Deer signs not described ! Browsing and rooting are nor estimated neither described.  
P9L197 over interpreted and not comparable as pigs scat abundance represent a much shorter gradient ( by ten times roughly)  
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 !  
P10L203 species richness instead of diversity, pellets/dungs instead of scats.  
P10L204 many seeded fuits, this information arrives too late please see earlier comments on that point.  
P10 L218-220 that is not what is tested please do not overestimate your results (boar vs. deer effects)  
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.  
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. […]  
  
References list has to be checked as for some of them, we do not have the pages …