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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 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.

- 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.
- 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.

**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).
- 2) Lines 88-89: Seeds came from multiple islands???
- 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.
- 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 seed-derived 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.
- 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.
- 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 enclosure portion of the study).
- 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).
- 8) Lines 197-199: “appeared to come from browsing rather than rooting”? Evidence to support that claim?
- 9) Line 226: Looks like you missed a tracked change?
- 10) Many of your citations are lacking important information on volume, page number, publication venue, etc. (e.g., citations #17 and 21).
- 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  $r^2$  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 that

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.