TITLE: Non-native ungulates take on alternative roles in a novel ecosystem that has lost ecological functions

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**Abstract**

Conservation has long focused on preserving or restoring pristine ecosystems. However, understanding and managing novel ecosystems has grown in importance as these systems outnumber pristine ecosystems worldwide. We examined species interactions in the novel ecosystems of the island of Guam. While non-native species may be neutral or detrimental in pristine ecosystems, it is possible that even notorious invaders could play a beneficial role in novel ecosystems. We examined the effects of two invasive species Micronesia, where native vertebrate frugivores are functionally absent. This study compared the roles of long-established ungulates – Philippine deer (*Rusa marianna*) and feral pigs (*Sus scrofa*) – on seedling survival, seed dispersal, and plant community structure in limestone karst forests. We found that deer, even at low abundances, had pronounced negative impacts on forest communities through selective browsing. Deer negatively impacted forests by decreasing seedling and vine abundance. In contrast, pigs showed no relationship to seedling abundance or diversity, and more seeds were found in pig feces than deer feces, suggesting that pigs provide an ecosystem function – seed dispersal – that has been lost from Guam. Our study presents a surprising discrepancy between the roles of two non-native species that are traditionally managed as a single entity, suggesting that ecological function, rather than identity as a native or non-native, may be more important to consider in managing novel systems.

**Introduction**

The extent of human influence is so pervasive that the earth today is comprised mostly of novel ecosystems (1) – anthropogenically modified systems with species compositions and relative abundances that have not been previously observed (2). Species introductions create and maintain novel ecosystems both by adding new species and by removing native ones (1). Novel ecosystems typically still harbour many native species (3); however, effective management of these systems is challenging due to the potentially new ecological roles of the remnant native and introduced species that comprise them.

Although the negative impacts of introduced species are extensive, some may also play beneficial roles (4). Introduced species can be preferred candidates for restoring severely degraded habitats (5). For example, in Puerto Rico, planting non-native trees in abandoned pastures where the native plants would not have originally facilitated the return of native plant communities (6). Some introduced species may provide desirable ecological functions such as seed dispersal or food sources for native species (7). The introduced Japanese white-eyes (*Zosterops japonica*) in Hawaii are seed dispersers for native plants that previously relied on now extinct or rare native birds (8). Finally, invasive species may slow or reverse negative ecological effects from other anthropogenic impacts. Cascading ecological effects from overfishing in Cape Cod salt marshes are being reversed by green crabs (*Carcinas maenas*), which are normally considered a harmful invasive (9).

The negative effects of introduced deer and pigs have been well documented in ecosystems across the globe (10-13). Deer alter forest structure by browsing on seedlings and saplings, and suppressing forest regeneration (14). Introduced deer in New Zealand had effects on understory and forest composition that persisted even after control of deer (*Cervus elaphas*) populations (15). Pigs are known to affect regeneration and recruitment in a number of forest systems. For example, feral pigs have a pronounced effect on regeneration in lowland forests of Malaysia, by direct predation on seeds and by soil-rooting (16,17). Rooting kills or physically damages seedlings and can alter soil properties (18,19). Similarly, ungulates are thought to have negative effects on plant communities in Guam (20-22).

The southernmost island of the Mariana Archipelago, Guam, as with many islands around the world, has had a long history of species introductions (23), making its forest prime examples of novel ecosystems with unique challenges. One of the most infamous invasive species, the brown treesnake (*Boiga irregularis*), which was unintentionally introduced to Guam on military cargo at the end of World War II (24). It is responsible for the extinction of most of Guam’s native birds between 1945 and 1985 (25,26), functionally leaving the island bereft of native vertebrate nectarivores, frugivores, or insectivores (23). Deer and pigs have been established for centuries in Guam (20,22,27) Philippine deer (*Rusa marianna*) density in Guam has been correlated with reduced seedling recruitment in some species of native trees (21,28). Feral pigs (*Sus scrofa*) in Guam, similar to pigs in other systems, alter habitats by rooting and wallowing (20), which can disrupt forest regeneration. However, these effects are occurring within novel rather than pristine ecosystems, therefore a more thorough examination of the role of each species within the larger ecological context is needed to make appropriate management decisions.

We investigated the ecological role of invasive ungulates in the novel ecosystems of Guam, by examining the influence of non-native deer and feral pigs on seedling survival, seed dispersal, and seedling abundance in limestone karst communities. First, we tested for effects to a specific subset of native and non-native plants by planting seedlings in fenced and unfenced plots. We also tested their capabilities of dispersing seeds by germinating scats from both deer and pigs. Finally, we surveyed sites to determine relative ungulate densities and plant community structure to draw comparisons between ungulate abundance and a number of variables such as native and non-native seedling abundance.

**Methods**

*Study Area*

Guam (13.5° N, 144.8° E; 544 km2) is the largest and southernmost island of the Mariana Island Archipelago in the Western Pacific. Guam, especially northern Guam, is comprised mostly of limestone karst forests. Plant communities in these forests are growing on top of calcareous rock – the brittle, fossilized remains of ancient marine organisms. Guam contains a variety of habitats, but karst forests were chosen as the focus of this study because they contain a larger variety of native and endemic tree species relative to other habitats, such as savannah or ravine forest (29,30). The substrate in this habitat is fossilized remnants of coral reef organisms, which is sharp and brittle with little topsoil.

*Effect of ungulates on seedling survival*

To assess ungulate effects on seedling survival, we set up paired plots in eight selected karst forest sites in northern Guam. At each site, we erected a 1.8-m tall chicken-wire fence around one plot, and left the adjacent plot unfenced, allowing ungulate access. The fenced and unfenced plots were placed so that individual pairs had similar canopy cover, rockiness, and forest structure. Each seedling plot covered an area of about 3.5 m x 5.5 m.

We selected six species for this experiment encompassing a variety of common native and one introduced tree that occur in Guam’s karst forests: *Carica papaya*, *Morinda citrifolia*, *Ochrosia oppositifolia* (synonym *Neisosperma oppositifolia*), *Aglaia mariannensis*, *Premna serratifolia*, and *Psychotria mariannensis*. For each species we collected seeds from at least five trees and at least four different sites to minimize maternal effects and effects of local adaptation. The date of seed collection and subsequent out-planting was staggered by species due primarily to differences in fruiting phenology. Seeds were planted on the island from which they were collected under 60% shadecloth at a nursery in Guam, and allowed to grow in these conditions until they had fully rooted and grown their first true leaves. At this point, the seedlings were transported to the exclosure sites for out-planting.

Seedlings of each species were out-planted in the control and treatment areas at each site on the same day. Seedlings were placed at least 0.3 m apart from each other, and at least 0.5 m away from the fences in fenced treatments. Fourteen seedlings of each species were planted in each treatment at each site, except for *O. oppositifolia*, a tree with large fruits and seeds, which had only nine seedlings planted per treatment. The seedlings planted during drier months (*C. papaya, M. citrifolia,* and *O. oppositifolia*) were watered about every other day during the first few weeks following transplanting to ensure they successfully established. After transplanting, seedlings were monitored monthly for survival until July 2011 (15 months after the first species was transplanted and four months after the last).

Fourteen seedlings of each species were planted in each treatment at each site, except for two species, where a lack of seedlings limited the number we were able to plant. *O. oppositifolia* had only seven seedlings planted per treatment on Guam and 9 seedlings per treatment on Rota, and11 seedlings of *Carica papaya* were planted in each plot on Rota, compared to the 14 planted per plot on Guam. The seedlings planted during drier months (*C. papaya, M. citrifolia,* and *O. oppositifolia*) were watered regularly during the first few weeks following transplanting to ensure they successfully established. We monitored seedling mortality monthly, but final counts used in analysis were recorded in July 2011, or 15 months after the first species was transplanted and four months after the last.

Seedling survival was compared for each planted species between fenced and unfenced plots, using generalized linear mixed effects models (lme4 package) in R statistical software (R package cite). Fencing was considered a fixed effect, whereas site was considered a random effect. We analysed seedling survival for each species separately. Factors were considered to have a significant effect on seedling survival if they reduced Akaike Information Criterion, corrected for smaller sample sizes (AICc), scores by more than 2 (31) in the corresponding model.

*Germination from scats*

We collected scats from deer and pigs from limestone karst forest sites to determine if either species dispersed viable seeds via endozoochory. We collected throughout the year, through both rainy and dry seasons from four sites in northern Guam. Scats were layered on top of a 50% perlite and 50% peat moss soil mix in germination trays. The trays were kept outdoors at a nursery under shade cloth. Deer pellets were admixed at the surface, pig scats were broken up and mixed at the surface. Trays were watered regularly before and after seedlings emerged from scats. Seedlings were then identified and counted. Because the nursery was open air, species that were known to be wind-dispersed and that germinated across all seedling trays, including adjacent experiments at the nursery, were not counted.

We compared the occurrence of species germinating from scat to their presence in vegetation surveys from those same sites.

*Vegetation transects and scat counts*

We surveyed the community composition of karst forest sites by using 100-m by 1-m belt transects. All plants within these transects were identified to species and categorized as vines, trees, shrubs, or herbs. Seedlings were counted as plants that appeared to be within their first year of growth – woody tree shrub species usually had no woody stem yet, or were less than 0.5-m tall.

To estimate relative ungulate abundance among sites, faecal groups from pigsand deer were counted along the vegetation transects, as well as in a 2-m wide square-shaped belt transect that centred along the vegetation transects. Although they do not give exact population abundance, counts of faecal groups can be used as an index to compare abundance of ungulates between sites (32) . Each transect covered an area of about 800 m2. We used scat as an indicator of ungulate abundance because other sign, such as animal tracks, are rarely visible in karst forest terrain and the detectability of other sign such as trails and grazing varies widely even in similar habitats (21).

We used linear regressions to determine whether ungulate scat abundance covaried with forest characteristics measured on vegetation transects. We used deer abundance and pig abundance as separate independent factors, and forest characteristics as dependent factors. The forest characteristics that we investigated were total seedling abundance, native seedling abundance, exotic seedling abundance, and vine abundance. We also determined *r2* and *P-values* for each regression. To select the best-fit linear models, *F-statistics* and *P-values* were also calculated.

**Results**

*Do ungulates affect forest recruitment?*

Seedling survival in seedling plots varied depending on species and fencing treatment. The best fit model predicting survival strongly depended on species. However, when we looked at each species specifically, we saw that treatment did affect survival. For four species, *C. papaya*, *M. citrifolia*, *P. serratifolia*, and *P. mariana*, fencing treatment contributed to the best-fit model explaining proportion alive (Figure 1). For *A. mariannensis* and *O. oppositifolia*, AICc values were <2 between models including and not including treatment. Therefore, treatment (fenced or not fenced) for these two species did not predict survival better than random effects alone.

*Do ungulates act as seed dispersers?*

We collected and observed germination from a total of 20 deer faecal groups. Only four of the 20 deer faecal groups collected produced seedlings (20%). Eight *C. papaya* seedlings germinated from one pellet group. In addition, one *Passiflora suberosa*, one *Vitex parviflora,* and one *Mikania micrantha* seedling each emerged from separate pellet groups. The *Mikania micrantha* may have been ingested by the deer accidentally, as this species has wind-borne seeds lacking a fruit.

A greater abundance and diversity of seedlings emerged from the 31 pig faecal groups that we collected from four different sites. Of these, 25 faecal groups had seedlings (80.6%), with a total of 1657 seedlings germinating. The species that germinated from pig scats were comprised of the native trees *M. citrifolia*, and *Ficus prolixa,* the introduced trees *C. papaya* and *Leucaena leucocephala*, the introduced vines *Passiflora* spp. and *Coccinia grandis*, and the introduced herb *Chromolaena odorata*. All of these except for *C. odorata* and *L. leucocephala* have edible, fleshy fruits.

A total of nine species germinated from pig and deer scats, seven exotic and two native species in addition to several unidentified species that died before they could be keyed to species (Table 2). Only five individual seedlings, from four different species of exotic plants germinated from 20 deer scats (Table 2). Pig scats, however, contained a larger variety of germinating species in much higher numbers (Table 2). The three species that germinated in the highest numbers from pig scats, *Ficus* sp., *Morinda citrifolia*, and *Carica papaya* all have high seed counts per fruit. This likely accounted for the large abundance of seeds that germinated of these particular species.,

*How does ungulate abundance relate to forest community composition?*

Strong negative loglinear relationships were detected between the following forest characteristics and deer abundance: total seedling abundance (r2 = 0.710, P < 0.001), native seedling abundance (r2 = 0.648, P < 0.001), exotic seedling abundance (r2 = 0.770, P < 0.001), and vine abundance (r2 = 0.751, P <0.001) (Figure 3). In contrast, no correlations were detected between these characteristics and pig abundance.

**Discussion**

We found that a group of invasive species often managed as a single entity – ungulates – differ in their effects at a species level. Based on results from an experiment that excluded both pigs and deer, we conclude that ungulates selectively browse four of the six species tested while avoiding the other two (Figure 1), and as a result, shape forest community diversity. However, deer abundance alone was negatively correlated with overall seedling abundance, including native and exotic seedling abundance, and vine abundance, while no such correlations were detected with pig abundance (Figure 3). This, in combination with the observation that most mortality in the exclosure study appeared to come from browsing rather than rooting, indicates that deer have a greater impact on seedling mortality than do pigs. Our findings are consistent with numerous other studies on the detrimental effects of invasive deer (10,11,14). In addition, deer dispersed very few seeds, while pigs dispersed large numbers of native seeds. Thus, we conclude that, in our study systems, deer and pigs have different ecological functions, and management of these ungulates should consider the extreme detrimental effects that deer have on seedlings and the potential seed dispersal function that pigs provide.

Most conservation goals emphasise reintroducing reduced or extirpated native species to historical abundances, and efforts that have focused on removing invasive species and reintroducing native species have yielded many positive results (33,34). However, removing invasive species could have negative consequences if these species play important ecological roles otherwise missing from the novel system (35). Likewise, reintroducing reduced or extirpated native species may prove unsuccessful or detrimental if persistent threats and current conditions are poorly understood (25,36). Restoring a functioning ecosystem rather than the exact original complement of species may be more feasible for highly degraded ecosystems (37).

A variety of both native and non-native species germinated from pig scats, while a smaller number and diversity of seedlings that only included exotic species germinated from deer scats. The most abundant seedlings in pig scats were from many-seeded fruit species with small seeds. The high number of seeds per fruit in a given *M. citrifolia, Ficus* sp., or *Carica papaya* fruit contributes to the likelihood of germinating from scat once the fruit is encountered by a pig in the forest. In addition, smaller seeds tend to have higher toughness {Fricke:2016hz}, which in turn could contribute to higher likelihood of surviving both mastication and gut passage. We encourage future studies incorporating feeding and germination trials to

Because these invasive species are being managed within the context of a highly degraded novel ecosystem, these functional differences suggest that different management strategies should apply to each species, especially in limestone karst forests. Deer are not replacing a lost ecological function, but instead have a strongly negative impact on forest communities by hindering forest regeneration (Figure 3). We anticipate that eradication or control to very low abundance would prove beneficial. In contrast, pigs are one of the last major vertebrate dispersers on an island that has lost its native dispersers. Removing pigs could have detrimental effects to native plant species that have been limited by the lack of dispersers in limestone karst forests, where we did not detect strong negative impacts from pigs. The forest floor in a limestone karst forest is rocky and rigid, which would be difficult for pigs to root and wallow in, thereby limiting the extent of their damage to seedlings. However, pigs could have more impact in other forest types with softer soils. Therefore, more detailed studies of their roles in other forest types should guide management in those habitats, and any negative impacts weighed with potential benefits, even if these benefits are a temporary placeholder until species reintroductions can occur.

Invasive species are normally managed with the goal of control or eradication, but in novel ecosystems with multiple species and factors contributing to ecological changes, a blanket approach may not be wise. Feral ungulates are components of novel ecosystems around the world, and although their negative effects are well-documented (38-40), there are a few examples where they play beneficial roles (41,42) or have unexpectedly insignificant effects on native flora (43,44). Ungulate eradication is an important restoration tool, especially in island environments where ungulates are considered destructive invasive species (45). Although this may still be the preferred management tool for Guam’s systems, there may be unintended consequences. These include the release of invasive plant species (15,46) or reduced seed dispersal (41). Natural resource managers would be aided by discerning which non-native species serve important functions in certain habitat types, and which species are especially destructive before implementing conservation actions in a novel ecosystem.

**Competing Interests**

We have no competing interests.

**Author’s Contributions**

Ann Marie Gawel helped to design the study, set up the experiments, collect data, analyse and draft the manuscript. Haldre Rogers helped design and coordinate the study, set up experiments, and aided in analysis and drafting the manuscript. Alexander Kerr aided in designing and coordinating the study, reviewing the analysis, and drafting and reviewing the manuscript. Ross Miller aided in designing and coordinating the study and reviewing the manuscript. All authors gave final approval for publication.

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