TITLE: Contrasting ecological roles of non-native ungulates in a novel ecosystem

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**Summary**

Conservation has long focused on preserving or restoring pristine ecosystems. However, understanding and managing novel ecosystems has grown in importance as they outnumber pristine ecosystems worldwide. While non-native species may be neutral or detrimental in pristine ecosystems, it is possible that even notorious invaders could play beneficial roles in novel ecosystems. We examined the effects of two long-established non-native species – Philippine deer (*Rusa marianna*) and feral pigs (*Sus scrofa*) – in Guam, Micronesia, where native vertebrate frugivores are functionally absent leaving forests devoid of seed dispersers. We compared the roles of deer and pigs on seedling survival, seed dispersal, and plant community structure in limestone karst forests. Deer, even at low abundances, had pronounced negative impacts on forest communities by decreasing seedling and vine abundance. In contrast, pigs showed no such relationship, and more seeds were found in pig scats than deer scats, 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 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, non-native trees have been used 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]. Similarly damaging, 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, albeit with unique challenges. One of the world’s most infamous invasive species is 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]. While snakes are a relatively recent introduction, Philippine deer (*Rusa marianna*) (referred to as deer from here on) and feral pigs (*Sus scrofa*) (referred to as pigs from here on) have been established for centuries in Guam [20,22,27]. Deer density in Guam has been correlated with reduced seedling recruitment in some species of native trees [21,28]. Pigs in Guam, similar to pigs in other systems, alter habitats by rooting and wallowing [20], which can disrupt forest regeneration. However, the effects from deer and pigs 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 non-native 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 experimentally tested whether deer and pigs affect seedling survival of a specific subset of native and non-native plants. We also tested the capabilities of deer and pigs for dispersing seeds by germinating scats collected in the wild. Finally, we compared plant community characteristics (e.g. native and non-native seedling abundance, vine abundance) across a range of relative ungulate densities to assess whether the impacts of ungulates as herbivores or dispersers is evident in the forest.

**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. The dominant forest type of Guam is limestone karst forest. 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].

*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. 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 [31]. 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 in the corresponding model [32].

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

*Effects of ungulate abundance on community composition*

We surveyed the community composition of karst forest sites by using 100-m by 1-m belt transects at 14 different sites across northern Guam, where limestone karst dominates the forest types. All plants within these transects were identified to species and categorized as vines, trees, shrubs, or herbs, and as native or non-native. Plants were considered seedlings if they appeared to be within their first year of growth – for woody species, they had no woody stem yet, or were less than 0.5-m tall.

To estimate relative ungulate abundance among sites, scats from pigsand deer were counted along the vegetation transects. The 100-m by 1-m belt transects proved too small to detect differences between sites as represented by ungulate scats. Therefore, we surveyed a greater area at each site by also including 2-m-wide belt transects encircling the vegetation transects. 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. Although they do not give exact population abundance, counts of scats can be used as an index to compare abundance of ungulates between sites [33] . 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. Deer abundance and pig abundance were considered as separate independent factors, and forest characteristics as dependent factors. The forest characteristics that we investigated were total seedling abundance, native seedling abundance, non-native seedling abundance, and vine abundance. For each correlation, we report r2 values.

*Permissions and licenses*

We applied for and received special use permits to conduct research on U.S. Fish and Wildlife Service (Department of Interior) Wildlife Refuge property in 2010. This was coordinated through Refuge Manager Joseph Schwagerl ([Joseph\_Schwagerl@fws.gov](mailto:Joseph_Schwagerl@fws.gov)) and Refuge Biologist Cari Eggleston ([cari\_eggleston@fws.gov](mailto:cari_eggleston@fws.gov)). For study sites on Government of Guam property, we received approval from Guam Department of Agriculture for use of the Anao Conservation Area, and approval from the Chamorro Land Trust for use of Chamorro Land Trust lands. In addition, surveys carried out on Department of Defense property were coordinated with permission from U.S. Air Force, 36th Wing Civil Engineering Squadron, Environmental Flight.

**Results**

*Effects of ungulates on seedling survival*

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 (see Table 1 for AICc values). 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), with higher survival of seedlings when protected from ungulates. For *A. mariannensis* and *O. oppositifolia*, AICc values were <2 between models including and not including treatment (Table 1), indicating that these two species did not did not benefit from protection from ungulates.

*Germination from scats*

We collected and observed germination from a total of 20 deer scats. Only four of the 20 deer scats collected produced seedlings (20%). Only 13 individual seedlings, from four different species of non-native plants and two unknown species germinated from 20 deer scats (Table 2, Figure 2). Eight *Passiflora suberosa* seedlings germinated from one pellet group. In addition, one *C. papaya*, 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.

Many more seedlings emerged from the 31 pig scats that we collected from four different sites. Of these, 25 scats had seedlings (80.6%), with a total of 1658 seedlings germinating (Table 2). The species that germinated from pig scats were comprised of the native trees *M. citrifolia*, and *Ficus prolixa,* the non-native trees *C. papaya* and *Leucaena leucocephala*, the non-native vines *Passiflora* spp. and *Coccinia grandis*, and the non-native herb *Chromolaena odorata*. All of these except for *C. odorata* and *L. leucocephala* have edible, fleshy fruits.

We used data from our vegetation surveys to compare the most abundant species that germinated from scats to the most abundant species found in nature (Figure 2). 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. We only counted adult trees to represent only potentially fruiting trees. We used a similar approach to calculate the proportional abundance of seedling species found in pigs scats and deer pellets. The species found in the highest proportion of scats for both deer and pigs did not reflect the most abundant species in nature, suggesting that pigs are selectively dispersing certain species.

*Effects of ungulate abundance on 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), non-native 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.

The two species for which seedling survival was unaffected by the ungulate exclosure treatment in the experiment above, *O. oppositifolia* and *A. marianennsis*, are also dominant in nature. After *Meiogyne cylindrocarpa*, they comprise the top three most common tree species for adults across all sites, accounting for over 30% of adult tree species surveyed for this study (Figure 2, top panel). In addition, together, they accounted for over 60% of seedlings recorded in our transects in Guam, and were present even in the areas with the high deer 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. Ungulates selectively browse four of the six species tested while avoiding the other two (Figure 1), and as a result, have potential to shape forest community diversity through herbivory. When assessing seed dispersal, we found that deer dispersed very few seeds, while pigs dispersed large numbers of predominantly native seeds, potentially replacing the function of extirpated native birds and bats. However, the negative effects of deer were evident across the forest, as there were far more seedlings in areas with few deer than in areas with moderate or high signs of deer, whereas 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. While the benefits of pigs as seed dispersers were not evident in the seedling community, neither was a negative role for pigs; herbivory by deer is likely to mask any benefits provided via dispersal by pigs.

Both native and non-native species germinated from pig scats, while a smaller number and diversity of seedlings that only included non-native 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 *C. papaya* fruit contributes to the likelihood of germinating from scat once the fruit is encountered by a pig in the forest. Both *M. citrifolia* and *C. papaya* are known to grow easily in disturbed or edge areas [34,35]. Although *C. papaya* is not a native plant, it is naturalized and not considered invasive in the Marianas [36]. It is similarly common in Guam in previously disturbed areas and edges but not in deeper forests [29,36], indicating that it may be important for primary or secondary succession and forest regrowth in disturbed areas. This, coupled with the results of our seedling plots indicating that both *C. papaya* and *M. citrifolia* are browsed by deer, suggests that while deer can inhibit regrowth in disturbed areas, pigs may be one of the few vertebrate species moving successional species into edges and gaps.

Because deer and pigs 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). The two most common tree seedlings across all of our survey sites and two of the most common adult species in the forests on Guam (after *Meiogyne cylindrocarpa*). are the two species that survived just as well outside our seedling exclosures as they did inside – *O. oppositifolia* and *A. mariannensis*. This suggests the browsing preferences have long been shaping the forest species composition on Guam. Our findings are consistent with many studies on the detrimental effects of invasive deer, primarily through selective browsing [10,11,14]. We anticipate that deer eradication or control to very low abundance would prove beneficial on Guam, which has never had native grazing herbivores.

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. These results are inconsistent with studies conducted in Hawaii and Malaysia, which show that pigs cause seedling mortality, increase erosion, affect biogeochemical cycling, and spread invasive plants [17,37-39]. Unlike other forest types, however, the forest floor in a limestone karst forest is rocky and rigid [29,36], which would be difficult for pigs to root and wallow in, thereby limiting the extent of their damage to seedlings. Removing pigs could have detrimental effects to plant species that have been limited by the lack of dispersers. We recognize pigs would likely have a greater impact in areas, such as secondary forest or volcanic forest, with more soil. However, the role of non-native species must be evaluated on the basis of each habitat and ecological situation, rather than on a species basis.

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 [40-42], there are a few examples where they play beneficial roles [43,44] or have unexpectedly insignificant effects on native flora [45,46]. Ungulate eradication is an important restoration tool, especially in island environments where ungulates are considered destructive invasive species [47]. 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 [15,48] or reduced seed dispersal [43]. Natural resource managers would be aided by discerning which non-native species serve important functions and which species are especially destructive in a particular habitat type, before implementing conservation actions in a novel ecosystem.

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 [49,50]. In the Marianas, management plans are focused on eradicating ungulates, and pigs are frequently the targeted ungulate species. However, removing invasive species could have negative consequences if these species play important ecological roles otherwise missing from the novel system [51]. If restoration of native species is a future possibility, non-native species may act as a temporary placeholder until species reintroductions can occur. Restoring a functioning ecosystem rather than the exact original complement of species, or considering restoration an iterative process with strategic and temporary use of non-natives, may be more feasible for highly degraded ecosystems [52].

**Ethics**

No animal or human subjects were used to carry out this study. This study was designed and written solely by the authors listed. See Methods section for permissions for use of government properties.

**Competing Interests**

We have no competing interests.

**Data Availability**

Complete datasets are available at <http://dx.doi.org/10.5061/dryad.sp5ff>.

**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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