

**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, Micronesia, where native vertebrate frugivores are functionally absent, and Rota, a neighbouring island that retains native frugivores. This study compared the roles of long-established ungulates – Philippine deer (*Rusa mariannae*) 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 in Guam by decreasing seedling and vine abundance. In contrast, our study suggests that pigs provide an ecosystem service – seed dispersal – that has been functionally lost from Guam. This service may be less desirable in Rota, where native species still perform this function. 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; 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 (3). Introduced species can be preferred candidates for restoring severely degraded habitats (4). 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 (5). Some introduced species may provide desirable ecological functions such as seed dispersal or food sources for native species (6). 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 (7). 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 (*Carcinus maenas*), which are normally considered a harmful invasive (8).

The negative effects of introduced deer and pigs have been well documented in ecosystems across the globe. (9-12). Deer alter forest structure by browsing on seedlings and saplings, and suppressing forest regeneration (13). Introduced deer in New Zealand had effects on understory and forest composition that persisted even after control of deer (*Cervus elaphas*)

populations (14). 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 (15). Rooting kills or physically damages seedlings and can alter soil properties (15-16). Similarly, ungulates are thought to have negative effects on plant communities in the Marianas (17-18).

The southernmost islands of the Mariana Archipelago, Guam and Rota, as with many islands around the world, have had a long history of species introductions (19) making them prime examples of novel ecosystems with unique management challenges. One of the most infamous invasive species occurs in Guam, the brown treesnake (*Boiga irregularis*), which was unintentionally introduced on military cargo at the end of World War II (20). It is responsible for the extinction of most of Guam's native birds between 1945 and 1985 (21-22), functionally leaving the island bereft of native vertebrate nectarivores, frugivores, or insectivores (19). The adjacent island of Rota has nearly identical flora and fauna to Guam, lacks the brown treesnake, and has retained limestone karst forests that are relatively more pristine (23). Deer and pigs have been established for centuries in both islands (18, 24-25). Philippine deer (*Rusa mariannae*) density in Guam has been correlated with reduced seedling recruitment in some species of native trees (17, 26). Similar to their effects in other islands, feral pigs (*Sus scrofa*) in Guam alter habitats by rooting and wallowing (25), 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 investigate the ecological role of invasive ungulates in the two novel ecosystems of Guam and Rota. We examine the influence of non-native deer and feral pigs on seedling

survival, seed dispersal, and overall plant community composition. We contrast their role in the bird-free forests of Guam to that in the nearby forests of Rota which still maintain avian populations.

## Methods

### *Study Area*

Guam (13.5° N, 144.8° E; 544 km<sup>2</sup>) is the largest and southernmost island of the Mariana Island Archipelago in the Western Pacific. Rota (14.15° N, 145.21° E; 85 km<sup>2</sup>) is located 76 km north of Guam and has less than 2% of the population of Guam. Both islands have large areas of native limestone karst forest with similar species compositions. Plant communities in these types of forests are growing on top of calcareous rock – the brittle, fossilized remains of ancient marine organisms. These islands contain 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 (27-28).

### *Effect of ungulates on seedling survival*

To assess ungulate effects on seedling mortality, we set up paired plots in karst forest sites in northern Guam and in Rota. Eight sites were selected in Guam and seven sites in Rota. 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 introduced trees found in forests of the Mariana Islands: *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. After seeds were collected, fleshy fruit was removed, and they were planted in a mixture of 50% perlite and 50% peat moss, and fertilized using Osmocote®. All seeds were planted in the island from which they were collected. The seed trays were placed under 60% shade cloth at nurseries in either Guam or Rota, 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 enclosure 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*, which had only seven seedlings planted per treatment in Guam and nine seedlings per treatment in Rota. In addition, 11 seedlings per plot of *Carica papaya* were planted in Rota. 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).

#### *Germination from faecal samples*

We collected faeces from *R. marianna* and *S. scrofa* from limestone karst forest sites to determine if either ungulate species dispersed viable seeds via endozoochory. We collected throughout the year, through both rainy and dry seasons from four sites in northern Guam. Faecal

samples 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. *R. marianna* pellets were admixed at the surface, and *S. scrofa* scat samples were broken up and mixed at the surface. Trays were watered regularly before and after seedlings emerged from faeces. Seedlings were then identified and counted. Because the nursery was open air, species that were known to be wind-dispersed and that germinated in most of the other seedling trays at the nursery were not counted.

#### *Vegetation transects and scat counts*

We surveyed the community composition of karst forest sites in Guam and Rota by using 100-m by 1-m belt transects. All plants within these transects were identified and recorded, seedlings were identified and counted, and plants were categorized as either adults or seedlings, and as vines, trees, shrubs, or herbs.

To estimate relative ungulate abundance among sites, faecal groups from *S. scrofa* and *R. marianna* 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 (29). Each transect covered an area of about 800 m<sup>2</sup>. We used scat as an indicator of ungulate abundance since 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 (17).

#### *Statistical analyses*

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 (30). Fencing and island were considered fixed effects, while 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.

To determine if pigs exhibited selectivity for either native or exotic species, we collected scat from multiple sites in Guam and compared the abundance of species that germinated from scat to their abundances in vegetation surveys from those same sites. We calculated the Manly Selectivity Index (32) for native and for exotic species

$$B = (o_i / \pi_i) / \sum o_j / \pi_j,$$

Where  $o$  is the proportion of seedlings from scat of either native or exotic seedlings amongst all seedlings from scats from each season (wet/dry), and  $\pi$  is the proportion of native or exotic adult plants at the site. Because nearly all fern spores are dispersed by wind, and not by ungulates, (33), they were excluded from this analysis. Standard error was calculated by using

$$se = \sqrt{\{ o_i(1 - o_i) / (u_{tot}\pi_i) \}}.$$

Where  $u_{tot}$  is the total number sampled (number of faecal groups collected).

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  $r^2$  and  $P$ -values



for each regression. To select the best-fit linear models, *F-statistics* and *P-values* were also calculated. All tests were performed using R (30).

## Results

### *Do ungulates affect forest recruitment?*

Seedling survival in seedling plots varied depending on species, island, and fencing treatment. 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). The best-fit model for *P. mariana* also had an interaction between island and species: although survival for *P. mariana* was higher inside plots in both islands, the difference in survival between fenced and unfenced *P. mariana* seedlings was greater in Guam than in Rota. Island was a factor that contributed to the best-fit model for *M. citrifolia* in addition to fencing treatment, but interaction was not; overall survival both inside and outside fenced plots was higher in Guam than in Rota. For *A. mariannensis* and *O. oppositifolia*, island and species interacted for the best-fit model explaining proportion alive (Figure 1): *A. mariannensis* and *O. oppositifolia* both had better survival inside rather than outside fenced plots in Guam, but better survival outside rather than inside fenced plots in Rota.

### *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* (Table 4). All of these except for *C. odorata* and *L. leucocephala* have edible, fleshy fruits.

Because very few seedlings emerged from deer faeces, the selectivity analysis was focused only on seedlings from pig faeces. Amongst seedlings emerging from pig faecal groups collected during the dry season, Manly's Selectivity Index indicated a slight selection for non-native species, with a value of  $0.62 \pm 0.04$  for non-native ( $0.38 \pm 0.07$  for native) (Figure 2). During the rainy season, Manly's Selectivity Index indicated strong selection for native species, with a value of 0.93 (0.07 for non-native) (Figure 2).

#### *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 ( $r^2 = 0.710$ ,  $P < 0.001$ ), native seedling abundance ( $r^2 = 0.648$ ,  $P < 0.001$ ), exotic seedling abundance ( $r^2 = 0.770$ ,  $P < 0.001$ ), and vine abundance ( $r^2 = 0.751$ ,  $P < 0.001$ ) (Figure 3). No correlations were detected between these community characteristics and deer abundance in Rota, and no associations were detected between these characteristics and pig abundance in either island.

## **Discussion**

Most conservation goals emphasise reintroducing reduced or extirpated native species to historical abundances – efforts that have focused on removing invasive species and reintroducing

native species have yielded many positive results (34-35). However, removing invasive species could have negative consequences if these species play important ecological roles otherwise missing from the novel system (36). Likewise, reintroducing reduced or extirpated native species may prove unsuccessful or detrimental if persistent threats and current conditions are poorly understood (37-38). Restoring a functioning ecosystem rather than the original complement of species may be more feasible for highly degraded ecosystems (37).

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, 13). In addition, deer dispersed very few seeds, while pigs dispersed large numbers of mostly 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 seed dispersal services that pigs provide.

Since 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. 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 provide seed dispersal services, which is a function that has been lost from the forests in the island of Guam (39) due to the absence of native forest birds and bats. 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. Therefore, we recommend focusing control efforts on deer and strongly discourage landscape-level control of pigs until solutions can be found to address the lack of seed dispersal in Guam's forests.

We also observed unexpected differences between Guam and Rota in community composition results and seedling plot survival. While we observed strong responses from the forest community to deer abundance in Guam, we did not detect similar patterns in Rota. We believe that a combination of small sample size (seven transect sites in Rota compared to 14 transect sites in Guam) and smaller range and maximum value of deer abundances in Rota (deer faecal groups per 100m<sup>2</sup> ranged between 0 and 5.7 for Rota and between 0 and 23.2 in Guam) contributed to our inability to detect similar patterns in that island. Results in each island also differed in our seedling plots. While mortality was greater in ungulate-accessible plots for four out of the six species, overall mortality was greater in Rota than in Guam, and island, more so than ungulate access, was important in determining mortality for two out of the six species. This suggests that another factor was contributing to mortality of seedlings in Rota, both inside and outside of ungulate exclosures. Veronicellid slugs are of particular concern in Rota, where they maintain unusually large aggregations, and where they have already taken a toll on crop species (40-41). Indeed, we observed levels of slug infestations at sites Rota that were greater than at sites in Guam, leading us to believe that slug herbivory contributed to interisland differences in

seedling mortality. We strongly encourage expanding future studies in Rota to capture more varied abundances of deer, to consider invertebrate herbivores, and to investigate ungulate seed dispersal as was done in Guam.

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 (42-43), there are a few examples where they play beneficial roles (44-45) or have unexpectedly insignificant effects on native flora (46). Ungulate eradication is an important restoration tool, especially in island environments where ungulates are considered destructive invasive species (47-48). While 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 (14, 49) or reduced seed dispersal (50). Natural resource managers would be aided by discerning which non-native species serve important functions, 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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### **Literature Cited**

1. Seastedt, T.R., R.J. Hobbs, and K.N. Suding. 2008. Management of novel ecosystems: are novel approaches required? *Front Ecol Environ* 6: 547-553. [doi: 10.1890/070046](https://doi.org/10.1890/070046)
2. Hobbs, R.J., E. Higgs, and J.A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* **24**, 599-605. ([doi: 10.1016/j.tree.2009.05.012](https://doi.org/10.1016/j.tree.2009.05.012))

3. Schlaepfer, M.A., D.F. Sax, J.D. Olden. 2011. The potential conservation value of non-native species. *Cons. Bio.* **20**, 428-437. ([doi: 10.1111/j.1523-1739.2010.01646.x](https://doi.org/10.1111/j.1523-1739.2010.01646.x))
4. Ewel, J.J. and F.E. Putz. 2004. A place for alien species in ecosystem restoration. *Front Ecol Environ.* **2**, 354-360. ([doi: 10.1890/1540-9295\(2004\)002\[0354:apfasi\]2.0.co;2](https://doi.org/10.1890/1540-9295(2004)002[0354:apfasi]2.0.co;2))
5. Lugo, A.E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *Forest Ecol. Manag.* **99**, 9-19. ([doi: 10.1016/s0378-1127\(97\)00191-6](https://doi.org/10.1016/s0378-1127(97)00191-6))
6. Goodenough, A.E. Are the ecological impacts of alien species misrepresented? A review of the “native good, alien bad” philosophy. *Community Ecol.* **11**, 13-21. ([doi: 10.1556/comec.11.2010.1.3](https://doi.org/10.1556/comec.11.2010.1.3))
7. Foster, J.T. and S.K. Robinson. 2007 Introduced birds and the fate of Hawaiian rainforests. *Conserv. Biol.* **5**, 1248 – 1257. ([doi: 10.1111/j.1523-1739.2007.00781.x](https://doi.org/10.1111/j.1523-1739.2007.00781.x))
8. Bertness, M.D. and T.C. Coverdale. 2013. An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. *Ecology* **94**, 1937-1943. ([doi: 10.1890/12-2150.1](https://doi.org/10.1890/12-2150.1))
9. Courchamp F., J.L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. *Biol. Rev.* **78**, 347–83. ([doi: 10.1017/s1464793102006061](https://doi.org/10.1017/s1464793102006061))
10. Allombert, S., S. Stockton, and J. Martin. 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. *Conserv. Biol.* **19**, 1917-1929. ([doi: 10.1111/j.1523-1739.2005.00280.x](https://doi.org/10.1111/j.1523-1739.2005.00280.x))
11. Takatsuki, S. 2009. Effects of Sika deer on vegetation in Japan: A review. *Biol. Conserv.* **142**, 1922-1929. ([doi: 10.1007/978-4-431-09429-6](https://doi.org/10.1007/978-4-431-09429-6))
12. Murphy, M.J., F. Inman-Narahari, R. Ostertag, and C.M. Litton. 2014. Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. *Biol. Invasions.* **16**, 63-71. ([doi: 10.1007/s10530-013-0503-2](https://doi.org/10.1007/s10530-013-0503-2))
13. Alverson, W.S., D.M. Waller, and S.L. Solheim. 1988. Forests too deer: edge effects in Northern Wisconsin. *Conserv. Biol.* **2**, 348-358. ([doi: 10.1111/j.1523-1739.1988.tb00199.x](https://doi.org/10.1111/j.1523-1739.1988.tb00199.x))
14. Coomes, D.A., R.B. Allen, D.M. Fosyth, and W.G. Lee. 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conserv. Biol.* **17**, 450-459. ([doi: 10.1046/j.1523-1739.2003.15099.x](https://doi.org/10.1046/j.1523-1739.2003.15099.x))
15. Ickes, K., S. J. Dewalt, and S. Appanah. 2001. Effects of native pigs (*Sus scrofa*) on woody understory vegetation in a Malaysian lowland rain forest. *J. Trop. Ecol.* **17**, 191-206. ([doi: 10.1017/s0266467401001134](https://doi.org/10.1017/s0266467401001134))
16. Singer, F.J., W.T. Swank, and E.E.C. Clebsh. 1984. Effects of wild pig rooting in a deciduous forest. *J. Wildlife. Manage.* **48**, 464-473. ([doi: 10.2307/3801179](https://doi.org/10.2307/3801179))
17. Schreiner, I.H. 1997. Demography and recruitment of selected trees in the limestone forest of Guam in relation to introduced ungulates. *Micronesica* **30**, 169-181.
18. Wiles, G.J., D.W. Buden, and D.J. Worthington. 1999. History of introduction, population status, and management of Philippine deer (*Cervus mariannus*) on Micronesian Islands. *Mammalia* **63**, 193-215. ([doi: 10.1515/mamm.1999.63.2.193](https://doi.org/10.1515/mamm.1999.63.2.193))

19. Fritts, T.H., and G.H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu. Rev. Ecol. Syst.* **29**, 113-140. (doi: [10.1146/annurev.ecolsys.29.1.113](https://doi.org/10.1146/annurev.ecolsys.29.1.113))
20. Rodda, G.H., T.H. Fritts, and P.J. Conry. 1992. Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. *Pac. Sci.* **46**, 46-57.
21. Savidge, J. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology*. **68**, 660-668. (doi: [10.2307/1938471](https://doi.org/10.2307/1938471))
22. Wiles, G.J., J. Bart, R.E. Beck Jr, and C.F. Aguon. 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. *Conserv. Biol.* **17**, 1350-1360. (doi: [10.1046/j.1523-1739.2003.01526.x](https://doi.org/10.1046/j.1523-1739.2003.01526.x))
23. Falanruw, M.C., T.G. Cole, and A.H. Ambacher. 1989. Vegetation survey of Rota, Tinian, Saipan, Commonwealth of the Northern Mariana Islands. Resource Bulletin PSW-RB-27, USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkley, CA
24. Safford, W.E. 1905. Useful Plants of Guam (Facsimile Edition Reprint).p. 76. Guam: Jillette Leon Guerrero / Guamology Publishing. (doi: [10.5962/bhl.title.55033](https://doi.org/10.5962/bhl.title.55033))
25. Conry, P. 1989. Ecology of the wild (feral) pig (*Sus scrofa*) on Guam. Technical Report 7. Division of Aquatic and Wildlife Resources, Department of Agriculture, Guam.
26. Wheeler, M.E. 1979. The biology of the Guam deer. Technical Report 3. Aquatic and Wildlife Resources Division, Department of Agriculture, Guam.
27. Fosberg, W. 1960. The Vegetation of Micronesia, 1: General Descriptions, the Vegetation of the Mariana Islands, and a Detailed Consideration of the Vegetation of Guam. *B. Am Mus. Nat. Hist.* **119**, 53-75.
28. Raulerson, R. and A. Rinehart. 1991. Trees and Shrubs of the Northern Mariana Islands. Coastal Resources Management, Saipan, Northern Mariana Islands. 120 pp.
29. Engeman, R.M., G. Massei, and M.N. Gentle. 2013. Monitoring wild pig populations: a review of methods. *Environ. Sci. Pollut. R.* **20**, 8077-8091. (doi: [10.1007/s11356-013-2002-5](https://doi.org/10.1007/s11356-013-2002-5))
30. R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
31. Burnham, K. P. and D.R. Anderson. 2004. [Multimodel inference: understanding AIC and BIC in Model Selection](#). *Sociol. Method. Res.* **33**, 261-304. (doi: [10.1177/0049124104268644](https://doi.org/10.1177/0049124104268644))
32. Manly BFJ, L.L. McDonald, D.L. Thomas. 1993. Resource selection by animals. Chapman & Hall, London. 221 pp. (doi: [10.1007/978-94-011-1558-2](https://doi.org/10.1007/978-94-011-1558-2))
33. Tryon, R.M. Jr. 1970. Development and evolution of fern floras of oceanic islands. *Biotropica* **2**, 76-84. (doi: [10.2307/2989765](https://doi.org/10.2307/2989765))
34. Campbell, K., and C. Donlan. 2005. Feral goat eradication on islands. *Conserv. Biol.* **19**, 1362-1374. (doi: [10.1111/j.1523-1739.2005.00228.x](https://doi.org/10.1111/j.1523-1739.2005.00228.x))



35. Allwood, A.J., E. T. Vueti, L. Leblanc, and R. Bull. 2002. Eradication of introduced Bactrocera species (Diptera: Tephritidae) in Nauru using male annihilation and protein bait application techniques. Pages 19-25 In Veitch, C. R. and Clout, M. N. (eds.). Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.
36. Zavaleta, E.S., R.J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* **16**, 454-459. ([doi: 10.1016/s0169-5347\(01\)02194-2](https://doi.org/10.1016/s0169-5347(01)02194-2))
37. Hobbs, R.J., L.M. Hallett, P.R. Ehrlich, and H.A. Mooney. 2011. Intervention ecology: applying ecological science in the twenty-first century. *BioScience* 61: 442-450. [doi: 10.1525/bio.2011.61.6.6](https://doi.org/10.1525/bio.2011.61.6.6)
38. Godefroid, S. et al., 2011. How successful are plant species reintroductions? *Biol. Conserv.* **144**, 672-682. [doi: 10.1016/j.biocon.2010.10.003](https://doi.org/10.1016/j.biocon.2010.10.003)
39. Wiles GJ, Bart J, Beck Jr RE, Aguon CF (2003) Impacts of the Brown Tree Snake: patterns of decline and species persistence in Guam's avifauna. *Conserv. Biol.* **17**, 1350–1360. ([doi: 10.1046/j.1523-1739.2003.01526.x](https://doi.org/10.1046/j.1523-1739.2003.01526.x))
40. Badilles, A.E., J. Manglona, N.I. Paeda, B. Richards, and E. Depalog. 2010. Suppression to Cuban Slug (*Veronicella cubensis*) (Pfleffer) using selected practices. Paper presented at the Pest Identification Workshop 2010, Saipan, CNMI.
41. Robinson, D.G. and R.G. Hollingsworth. 2004. Survey of slug and snail pests on subsistence and garden crops in the islands of the American Pacific: Guam, and the Northern Mariana Islands; The Federated States of Micronesia; and American Samoa, with special Reference to Samoa. Technical Report, USDA.
42. Nogueira-Filho, S.L.G., Nogueira, S.S.C., and Fragoso, J.M.V. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. *Biodivers. Conserv.* **18**, 3677-3683. ([doi: 10.1007/s10531-009-9697-0](https://doi.org/10.1007/s10531-009-9697-0))
43. Kotanen, P.M. 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. *Ecography* **18**, 190-199. ([doi: 10.1111/j.1600-0587.1995.tb00340.x](https://doi.org/10.1111/j.1600-0587.1995.tb00340.x))
44. Desbiez, A.L.J.; Keuroghlian, A.; Piovezan, U.; Bodmer R.E. 2011, Invasive species and bushmeat hunting contributing to wildlife conservation: the case of feral pigs in a Neotropical wetland., *Oryx* **45**, 78-83. [doi: 10.1017/s0030605310001304](https://doi.org/10.1017/s0030605310001304)
45. Klinger, R.C., P. Schuyler, and J.D. Sterner. 1994. Vegetation response to the removal of feral sheep from Santa Cruz Island. In Halvorson, W.K. and Maender, G.J. (eds.). The fourth California Islands symposium: update on the status of resources, pp. 341-350. Santa Barbara Museum of Natural History, Santa Barbara, CA.
46. De Garine-Wichatitsky, M., P. Duncan, A. Labbé, B. Suprin, P. Chardonnet, and D. Maillard. 2003. A review of the diet of rusa deer *Cervus timorensis russa* in New Caledonia: Are the endemic plants defenceless against this introduced, eruptive, ruminant? *Pacific Conserv. Biol.* **9**, 136-145. ([doi: 10.1071/pc030136](https://doi.org/10.1071/pc030136))
47. Kessler, C.C. 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. In Veitch, C.R. and

- 466 Clout, M.N. (eds.). Turning the tide: eradication of invasive species. IUCN SSC Invasive  
467 Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.
- 468 48. Spear, D. and S.L. Chown. 2009. Non-indigenous ungulates as a threat to biodiversity. *J.*  
469 *Zool.* **279**, 1-17. ([doi: 10.1111/j.1469-7998.2009.00604.x](https://doi.org/10.1111/j.1469-7998.2009.00604.x) )
- 470 49. Cabin, R.J., S.G. Weller, D.H. Lorence, T.W. Flynn, A.K. Sakai, D. Sandquist, and L.J.  
471 Hadway. 2000. Effects of long-term ungulate exclusion and recent alien species control  
472 on the preservation and restoration of a Hawaiian tropical dry forest. *Conserv. Biol.* **14**,  
473 439-453. ([doi: 10.1046/j.1523-1739.2000.99006.x](https://doi.org/10.1046/j.1523-1739.2000.99006.x))
- 474 50. O'Connor, S. and D. Kelly. 2012. Seed dispersal of matai (*Prumnopitys taxifolia*) by feral  
475 pigs (*Sus scrofa*). *New Zeal. J. Ecol.* **36**, 228-231.