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

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1   **Summary**

2   Conservation has long focused on preserving or restoring pristine ecosystems. However,

3   understanding and managing novel ecosystems has grown in importance as they outnumber

4   pristine ecosystems worldwide. While non-native species may be neutral or detrimental in

5   pristine ecosystems, it is possible that even notorious invaders could play beneficial or mixed

6   roles in novel ecosystems. We examined the effects of two long-established non-native species –

7   Philippine deer (*Rusa marianna*) and feral pigs (*Sus scrofa*) – in Guam, Micronesia, where

8   native vertebrate frugivores are functionally absent leaving forests devoid of seed dispersers. We

9   compared the roles of deer and pigs on seedling survival, seed dispersal, and plant community

10   structure in limestone karst forests. Deer, even at low abundances, had pronounced negative

11   impacts on forest communities by decreasing seedling and vine abundance. In contrast, pigs

12   showed no such relationship. Also, many viable seeds were found in pig scats whereas few were

13   found in deer scats, suggesting that pigs, but not deer, provide an ecosystem function – seed

14   dispersal – that has been lost from Guam. Our study presents a discrepancy between the roles of

15   two non-native species that are traditionally managed as a single entity, suggesting that

16   ecological function, rather than identity as a non-native, may be more important to consider in

17   managing novel systems.

18 **Introduction**

19   The extent of human influence is so pervasive that the earth today is comprised mostly of

20 novel ecosystems [1] – anthropogenically modified systems with species compositions and

21 relative abundances that have not been previously observed [2]. Species introductions create and

22 maintain novel ecosystems both by adding new species and by removing native ones [1]. Novel

23 ecosystems typically still harbour many native species [3]; however, effective management of

24 these systems is challenging due to the potentially new ecological roles of the remnant native and

25 introduced species that comprise them.

26   Although the negative impacts of introduced species are extensive, some may also play

27 beneficial roles [4]. Introduced species can be preferred candidates for restoring severely

28 degraded habitats [5]. For example, non-native trees have been used in abandoned pastures

29 where the native plants would not have originally facilitated the return of native plant

30 communities [6]. Some introduced species may provide desirable ecological functions such as

31 seed dispersal or food sources for native species [7]. The introduced Japanese white-eyes

32 (*Zosterops japonica*) in Hawaii are seed dispersers for native plants that previously relied on now

33 extinct or rare native birds [8]. Finally, invasive species may slow or reverse negative ecological

34 effects from other anthropogenic impacts. Cascading ecological effects from overfishing in Cape

35 Cod salt marshes are being reversed by green crabs (*Carcinas maenas*), which are normally

36 considered a harmful invasive [9].

37   The negative effects of introduced deer and pigs have been well documented in

38 ecosystems across the globe [10-13]. Deer alter forest structure by browsing on seedlings and

39 saplings, and suppressing forest regeneration [14]. Introduced deer in New Zealand had effects

40 on understory and forest composition that persisted even after control of deer (*Cervus elaphus*)

41 populations [15]. Similarly, pigs are known to affect regeneration and recruitment in a number of

42 forest systems. For example, feral pigs have a pronounced effect on regeneration in lowland

43 forests of Malaysia, by direct predation on seeds and by soil-rooting [16,17]. Rooting kills or

44 physically damages seedlings and alters soil properties [18,19].

45   The southernmost island of the Mariana Archipelago, Guam, as with many islands around

46 the world, has had a long history of species introductions [20], making its forests prime examples

47 of novel ecosystems, albeit with unique challenges. One of the world's most infamous invasive

48 species is the brown treesnake (*Boiga irregularis*), which was unintentionally introduced to

49 Guam on military cargo at the end of World War II [21]. It is responsible for the extinction of

50 most of Guam's native birds between 1945 and 1985 [22,23], functionally leaving the island

51 bereft of native vertebrate nectarivores, frugivores, or insectivores [20]. While snakes are a

52 relatively recent introduction, Philippine deer (*Rusa marianna*) (referred to as deer from here on)

53 and feral pigs (*Sus scrofa*) (referred to as pigs from here on) have been established for centuries

54 in Guam [24,25,26]. Deer were introduced to the wild in Guam in 1772 by Spanish Governor

55 Mariano Tobias as game [27], while pigs in the forests of Guam are descended from livestock

56 brought by Spanish colonizers in the 1660's, and subsequently mixed with other livestock

57 throughout the centuries [24]. We have no evidence that wild boar have ever been introduced to

58 Guam. The lone study estimating ungulate abundance on Guam used spotlight counts from

59 multiple vehicles along abandoned runways on the Air Force Base [29]. They estimated 1.83

60 deer per hectare (95% confidence interval = 1.44-2.21) and feral pig densities of 0.38 pigs per

61 hectare (95% confidence interval = 0.20-0.55), indicating that ungulates can reach high densities

62 on Guam, particularly in this area with limited access for hunting.

63   Like ungulates in other systems, both deer and pigs are thought to have negative effects

64 on plant communities in Guam [25,28,29]. Deer density in Guam has been correlated with

65 reduced seedling recruitment in some species of native trees [25,28]. Pigs in Guam, similar to

66 pigs in other systems, alter habitats by rooting and wallowing [24], which can disrupt forest

67 regeneration. However, the effects from deer and pigs are occurring within novel rather than

68 pristine ecosystems, therefore a more thorough examination of the role of each species within the

69 larger ecological context is needed to make appropriate management decisions.

70   We investigated the ecological role of non-native ungulates in the novel ecosystems of

71 Guam by examining the influence of non-native deer and pigs on seedling survival, seed

72 dispersal, and seedling abundance in limestone karst communities. First, we experimentally

73 tested whether deer and pigs affect seedling survival of a specific subset of native and non-native

74 plants. We also tested the capabilities of deer and pigs for dispersing seeds by germinating scats

75 collected in the wild. Finally, we compared plant community characteristics (e.g. native and non-

76 native seedling abundance, vine abundance) across a range of relative ungulate densities to

77 assess whether the effects of ungulates as herbivores or dispersers is evident in the forest.

78 **Methods**

79 *Study area*

80   Guam (13.5° N, 144.8° E; 544 km^2) is the largest and southernmost island of the Mariana

81 Island Archipelago in the Western Pacific. The dominant forest type of Guam is limestone karst

82 forest. Plant communities in these forests are growing on top of calcareous rock – the brittle,

83 fossilized remains of ancient marine organisms. This karst is extremely porous and easily

84 weathered by water, creating sharp features that hold very little topsoil [31,32]. It is extremely

85 rugged, with small crevasses and holes throughout. While a variety of karst types exist in

86   northern Guam, our seedling plot and transect sites all occurred on reef facies and detrital facies

87   of what is classified as Mariana Limestone – that is, Plio-Pleistocene reef and lagoon that

88   comprises 75% of Guam's karst formations [32].

89   Guam's karst forests were chosen as the focus of this study because they contain a larger

90   variety of native and endemic tree species relative to other habitats, such as savannah or ravine

91   forest [30,33]. We chose sites for this project that were considered native limestone karst forest

92   in order to maintain similarities between sites and maximize the likelihood of discerning

93   differences due to pig and deer abundance rather than other site characteristics like history of

94   disturbance or species composition. Native trees still dominate these sites. However, the relative

95   abundances of vegetation differ from early descriptions of Guam forests, suggesting that forests

96   have changed over time [33,34]. This, combined with the presence of non-native plants, insects,

97   and mammals [20] and the absence of birds provides an ideal setting for investigating roles of

98   non-native species in a novel ecosystem.

99   *Effect of ungulates on seedling survival*

100   To assess ungulate effects on seedling survival, we set up paired plots in eight selected

101   karst forest sites in northern Guam. At each site, we erected a 1.8-m tall chicken-wire fence

102   around one plot, and left the adjacent plot unfenced, allowing ungulate access. Each seedling plot

103   covered an area of about 3.5 m x 5.5 m. The fenced and unfenced plots were placed so that

104   individual pairs had similar canopy cover, rockiness, slope, and ground cover, as well as similar

105   adult tree composition, density, heights, and diameters. While species composition of adult trees

106   already present was almost impossible to match exactly, species composition often overlapped.

107   Using linear mixed effect models and the lsmeans package for posthoc comparisons, we

108   compared the fenced and unfenced treatments and found no significant differences in numbers of

109 adult trees (p=0.22), canopy cover (p=0.92), average diameter at breast height (p=0.78), and

110 average height of adult trees (p=0.85) between paired plots (See Supp Tables 1-3 and Supp

111 Figure 3). We avoided gaps, depressions in the substrate, or any other features that might have

112 caused a difference between the paired plots outside of our treatments.

113   We selected six species for this experiment encompassing a variety of common native

114 and one introduced tree that occur in Guam's karst forests: *Carica papaya*, *Morinda citrifolia*,

115 *Ochrosia oppositifolia* (synonym *Neisosperma oppositifolia*), *Aglaia mariannensis*, *Premna*

116 *serratifolia*, and *Psychotria mariana*. All are common components of Guam's limestone karst

117 forests, although the non-native *C. papaya* tends to favor edges, and *P. mariana* is less common

118 than the other species. For each species, we collected seeds from at least five trees and at least

119 four different sites to minimize maternal effects and effects of local adaptation. The date of seed

120 collection and subsequent out-planting was staggered by species due to differences in fruiting

121 phenology. Seeds were planted under 60% shadecloth at a nursery in Guam and allowed to grow

122 in these conditions until they had fully rooted and grown their first true leaves. At this point, the

123 seedlings were transported to the exclosure sites for out-planting.

124   Seedlings of each species were out-planted in the control and treatment areas at each site

125 on the same day. Seedlings were placed at least 0.3 m apart from each other, and at least 0.5 m

126 away from the fences in fenced treatments. Seedlings were haphazardly placed within the

127 seedling plot since they had to be planted around rocky karst structures and roots from

128 neighbouring trees. Fourteen seedlings of each species were planted in each treatment at each

129 site, except for *O. oppositifolia*, a tree with large fruits and seeds, which had only nine seedlings

130 planted per treatment. The seedlings planted during drier months (*C. papaya, M. citrifolia,* and

131 *O. oppositifolia*) were watered about every other day during the first few weeks following

132   transplanting to ensure they successfully established. Guam's "dry season" occurs roughly from

133   December to May annually. We monitored seedling mortality monthly, but final counts used in

134   analysis were recorded in July 2011, or 15 months after the first species was transplanted and

135   four months after the last.

136   Seedling survival was compared for each planted species between fenced and unfenced

137   plots, using generalized linear mixed effects models (lme4 package) in R [35]. Fencing was

138   considered a fixed effect, whereas site was considered a random effect. After determining that

139   the effect of the treatment (fenced or unfenced) was not dependent upon the duration of time

140   seedlings were growing (Table 1a), we analysed seedling survival for each species separately

141   (Table 1b). Factors were considered to have a significant effect on seedling survival if they

142   reduced Akaike Information Criterion, corrected for smaller sample sizes (AICc), scores by more

143   than 2 in the corresponding model [36].

144   *Germination from scats*

145   We collected scats from deer and pigs from limestone karst forest sites to determine if

146   either species dispersed viable seeds via endozoochory. We collected throughout the year,

147   through both rainy and dry seasons from four sites in northern Guam. Scats were layered on top

148   of a 50% perlite and 50% peat moss soil mix in germination trays. The trays were kept outdoors

149   at a nursery under shade cloth. Deer pellets were admixed at the surface, pig scats were broken

150   up and mixed at the surface. Trays were watered regularly before and after seedlings emerged

151   from scats. Seedlings were then identified and counted. Because the nursery was open air,

152   species that were known to be wind-dispersed and that germinated across all seedling trays,

153   including adjacent experiments at the nursery, were not counted. We then compared the

154   abundance of species germinating in scats to their natural abundances in nature, using our

155   vegetation transect data. Proportional abundance in nature (left hand panel, Figure 3) for each

156   species was calculated by dividing the total count of adults of that species across our fourteen

157   sites and dividing that by the total number of adult trees across all sites. (Total adult count of one

158   species / total adult count of all species counted on vegetation transects). We counted only adult

159   trees in calculations to represent potentially fruiting trees. We used a similar approach to

160   calculate the proportional abundance of seedling species found in pig and deer scats: the total

161   number of scats that has a given species of seedling germinating from it, divided by the total

162   number of either deer or pig scats that we had collected.

163   *Effects of ungulates on community composition*

164   We surveyed the community composition of karst forest sites by using 100-m by 1-m belt

165   transects at 14 different sites across northern Guam, where limestone karst dominates the forest

166   types. All plants within these transects were identified to species and categorized by growth form

167   (i.e. vines or trees) and as native or non-native. Plants were considered seedlings if they appeared

168   to be within their first year of growth – for woody species, they had no woody stem yet, or were

169   less than 0.5-m tall.

170   Scats from pigs and deer were counted along the vegetation transects described above. To

171   detect a range of scat abundances, we also surveyed a greater area at each site by including 2-m-

172   wide belt transects encircling the vegetation transects (see Figure 1). These were walked and

173   length estimated using GPS, with total area surveyed amounting to approximately 800 m^2.

174   However, since transect lengths used to count scats differed slightly from site to site, scat

175   abundances used in analysis were number of scats per 100 m^2. Actual ungulate densities in any

176   habitat in Guam is unknown and has rarely ever been attempted because common methods such

177   as spotlighting, visual counts on transects, and aerial counts are challenging in dense tropical

178 forests. Although they do not give exact population abundance, counts of scats can be used as an

179 index to compare abundance of ungulates among sites [37]. We used scat as an indicator of

180 ungulate abundance because other sign, such as animal tracks, are rarely visible in karst forest

181 terrain and the detectability of other sign such as trails and browsing sign varies widely even in

182 similar habitats [25].

183   We used linear regressions to determine whether ungulate scat abundance covaried with

184 forest characteristics measured on vegetation transects. Deer scat abundance and pig scat

185 abundance were considered as separate independent factors, although a model including both

186 provided qualitatively similar results (Supp. Tables 4-7). The forest characteristics included as

187 dependent variables were total seedling abundance, native seedling abundance, non-native

188 seedling abundance, and vine abundance. For each correlation, we report r^2 values.

189 *Permissions and licenses*

190   We applied for and received special use permits to conduct research on U.S. Fish and

191 Wildlife Service (Department of Interior) Wildlife Refuge property in 2010. This was

192 coordinated through Refuge Manager Joseph Schwagerl (Joseph_Schwagerl@fws.gov) and

193 Refuge Biologist Cari Eggleston (cari_eggleston@fws.gov). For study sites on Government of

194 Guam property, we received approval from Guam Department of Agriculture for use of the Anao

195 Conservation Area, and approval from the Chamorro Land Trust for use of Chamorro Land Trust

196 lands. In addition, surveys carried out on Department of Defense property were coordinated with

197 permission from U.S. Air Force, 36th Wing Civil Engineering Squadron, Environmental Flight.

198 **Results**

199 *Effects of ungulates on seedling survival*

200   Since planting dates were staggered for each species, we tested whether the effect of

201   treatment depended on the length of time a seedling was growing by comparing a model

202   including data from all species and a time by treatment interaction, with relevant submodels. The

203   best fit model did not include a time by treatment interaction (Table 1a), indicating that the

204   treatment effect did not vary depending on growing time, but it did include a species by

205   treatment interaction, indicating differences between species. Since we were interested primarily

206   in treatment effects on a species level, we then analyzed treatment effects separately for each

207   species.

208   For four species, *C. papaya*, *M. citrifolia*, *P. serratifolia*, and *P. mariana*, fencing

209   treatment contributed to the best-fit model explaining proportion alive (Table 1b, Figure 2), with

210   higher survival of seedlings when protected from ungulates. For *A. mariannensis* and *O.*

211   *oppositifolia*, AICc values were <2 between models including and not including treatment,

212   indicating that these two species did not benefit from protection from ungulates. Almost all

213   mortality observed in seedling plots was in the form of deer herbivory – evident by leaves and

214   stems being cut from the seedlings – instead of disturbed by uprooting by pigs.

215   *Germination from scats*

216   Only four of the 20 deer scats collected produced seedlings (20%), and only 13 seedlings

217   germinated, from four different species of non-native plants and two unknown species (Table 2,

218   Figure 3). Eight *Passiflora suberosa* seedlings germinated from one pellet group. In addition,

219   one *C. papaya*, one *Vitex parviflora,* and one *Mikania micrantha* seedling each emerged from

220   separate pellet groups. The *M. micrantha* may have been ingested by the deer accidentally, as

221   this species has wind-borne seeds lacking a fruit. The wind-dispersed species that were common

222   to many trays in the nursery, and were found separate from the scat samples within the planting

223   trays, were excluded from this count. The *M. micrantha* seedling, however, was only found in

224   one tray, sprouting directly from one of the deer pellets, and so was included.

225   Many more seedlings emerged from the 31 pig scats that we collected from four different

226   sites. Of these, 25 scats had seedlings (80.6%), with a total of 1658 seedlings germinating (Table

227   2). Eight species germinated from pig scats. They were the native trees *M. citrifolia* (in 20 out of

228   31 scats), and *Ficus prolixa* (in three scats); the non-native trees *C. papaya* (in 16 scats) and

229   *Leucaena leucocephala* (in one scat); the non-native vines *Passiflora* spp. (in three scats) and

230   *Coccinia grandis* (in three scats); and the non-native herb *Chromolaena odorata* (in one scat).

231   All of these except for *C. odorata* and *L. leucocephala* have edible, fleshy fruits.

232   We used data from our vegetation surveys to compare the most abundant species that

233   germinated from scats to the most abundant species found in nature (Figure 3). Proportional

234   abundances for species in nature reflected their proportion of all adult trees sampled in our

235   transects, with *Meigyne cylindrocarpa* being the most abundant. These abundances differed

236   dramatically from the proportional abundances in scat, suggesting some selection of these fruits

237   by pigs in nature. The species found in the highest proportion of scats for both deer and pigs did

238   not reflect the most abundant species in nature, suggesting some selection for certain species.

239   The most numerous seedlings germinating from scat were from many-seeded fleshy fruits like

240   *Carica papaya* and *Morinda citrifolia*, but their proportional abundances, which we calculated to

241   as the number of scats that they appeared in / total number of scats, were still very high (Figure

242   3). For example, *Carica papaya* seeds germinated in 16 out of 31 pig scats. Therefore, the

243   proportional abundance was 16 divided by 31, or it appeared in 0.52 of the scats. Full results are

244   in Figure 3. Because multiple species occurred in some single scats, the values for proportional

245   abundance in scats do not necessarily add up to 1.

246   *Effects of ungulates on community composition*

247   Strong negative loglinear relationships were detected between the following forest

248   community abundances and deer scat counts: total seedling abundance ($r^2 = 0.707$, P < 0.001),

249   native seedling abundance ($r^2 = 0.649$, P < 0.001), non-native seedling abundance ($r^2 = 0.792$, P

250   < 0.001), and vine abundance ($r^2 = 0.792$, P <0.001) (Figure 4). In contrast, no correlations were

251   detected between these metrics and pig scat counts.

252   The two species for which seedling survival was unaffected by the ungulate exclosure

253   treatment in the experiment above, *O. oppositifolia* and *A. marianennsis*, are also dominant in

254   nature. After *Meiogyne cylindrocarpa*, they comprise the top three most common tree species for

255   adults across all sites, accounting for over 30% of adult tree species surveyed for this study

256   (Figure 3, top panel). In addition, together, they accounted for over 60% of seedlings recorded in

257   our transects in Guam, and were present even in the areas with the high deer abundance.

258   **Discussion**

259   We found that two non-native species often managed as a single entity – ungulates –

260   differ in their effects at a species level. Deer selectively browse four of the six species tested

261   while avoiding the other two (Figure 2), and as a result, have potential to shape forest community

262   diversity through herbivory. When assessing seed dispersal, we found that deer dispersed very

263   few seeds, while pigs dispersed large numbers of predominantly native seeds. The negative

264   effects of deer were evident across the forest, as there were far more seedlings in areas with few

265   deer than in areas with moderate or high pellet counts from deer, whereas no such correlations

266   were detected with pig abundance (Figure 4). This, in combination with the observation that

267   most mortality in the exclosure study appeared to come from browsing rather than rooting,

268   indicates that deer have a greater impact on seedling mortality than do pigs. While the benefits of

269   pigs as seed dispersers were not evident in the seedling community, neither was a negative role

270   for pigs; herbivory by deer is likely to mask any benefits provided via dispersal by pigs. In a

271   novel ecosystem completely lacking native seed dispersers, the negative effects of non-native

272   deer on seedling presence and abundance and the potential for non-native pigs to fill a missing

273   ecological function provide support for a management approach based on functional roles rather

274   than native/non-native status.

275   Both native and non-native seeds germinated from pig scats. However, fruit traits and

276   ecological roles are more likely to determine how pigs affect ecosystems through dispersal. The

277   most abundant seedlings in pig scats were from species that produce fruit containing numerous

278   small seeds. The high number of small seeds in a given *M. citrifolia, Ficus* sp., or *C. papaya* fruit

279   means that there are many opportunities for germination once a single fruit is encountered by a

280   pig in the forest. *M. citrifolia* has an average of about 120, *Ficus prolixa* has about 190 and *C.*

281   *papaya* has about 700 seeds per fruit (unpub. data). Both *M. citrifolia* and *C. papaya* are known

282   to grow easily in disturbed or edge areas [38,39]. Although *C. papaya* is not a native plant, it is

283   naturalized and not considered invasive in the Marianas [34]. It is common in Guam in

284   previously disturbed areas and edges but not in deeper forests [30,34], indicating that it may be

285   important for primary or secondary succession and forest regrowth in disturbed areas. This,

286   coupled with the results of our seedling plots indicating that both *C. papaya* and *M. citrifolia* are

287   browsed by deer, suggests that while deer can inhibit regrowth in disturbed areas, pigs may be

288   one of the few vertebrate species that could move successional species into edges and gaps.

289   Plant traits may be useful for predicting how plant species were affected by either deer or

290   pigs. As mentioned above, *M. citrifolia, Ficus* sp., and *C. papaya* all contain a large number of

291   small seeds per fruit, contributing to the numbers we recorded germinating from pig scats. They

292 are also fleshy-fruited and sweet or pungent when ripe, suggesting appeal to pigs when

293 encountered in the forest. Evidence also points to small seed size being advantageous to dispersal

294 [40]. In terms of traits providing defense from herbivory, none of the seedling species that we

295 planted had obvious physical defences such as thorns or spikes. While species-specific studies

296 have rarely been done on the chemical traits of species planted in our seedling plots, studies on

297 other species of deer suggest their selective browsing depends on chemical composition of

298 different plants. For example, deer tended to avoid plants with high amounts of tannic acid

299 [41,42]. We do not have chemical composition studies on the two species that were consistently

300 avoided in seedling exclosures (*O. oppositifolia* and *A. mariannensis*). However, *O. oppositifolia*

301 has a thick, milky sap like other Apocynaceae, and other members of the *Aglaia* genus are

302 known to have high tannin content [43,44], potentially contributing to lower palatability by deer.

303 *M. citrifolia*, *P. serratifolia*, *C. papaya*, and other species of *Psychotria* have documented

304 medicinal uses [27,46-48], suggestive of potent chemical properties, but all were consumed by

305 deer in our open seedling plots indicating that these chemical defenses might not provide

306 adequate protection from deer herbivory.

307   Because deer and pigs are being managed within the context of novel ecosystems, these

308 functional differences suggest that different management strategies should apply to each species,

309 especially in limestone karst forests. Deer are not replacing a lost ecological function, but instead

310 have a strongly negative impact on forest communities by hindering forest regeneration (Figure

311 4). The two most common tree seedlings across all of our survey sites and two of the most

312 common adult species in the forests on Guam (after *Meiogyne cylindrocarpa*) are the two species

313 that survived just as well outside our seedling exclosures as they did inside – *O. oppositifolia* and

314 *A. mariannensis*. This suggests that browsing preferences have already been shaping the forest

315   species composition on Guam. Unfortunately, since both deer and pigs have been present for

316   centuries, we had no true "ungulate-free" control. To remedy this, we used exclosures and

317   gradients of abundance to tease apart what their effects are to plant communities. Our findings

318   are consistent with many studies on the detrimental effects of invasive deer, primarily through

319   selective browsing [10,11,14]. We anticipate that deer eradication or control to very low

320   abundance would prove beneficial on Guam, which has never had native mammalian herbivores.

321   In contrast to deer, we did not detect strong negative impacts from pigs in the native

322   limestone forest, and pigs are one of the last major vertebrate dispersers on an island that has lost

323   its native dispersers. We know that pigs are present in these forests, and their wallows are

324   abundant in ravine forests. However, unlike other forest types, the forest floor in a limestone

325   karst forest is rocky and rigid [29,31], which would be difficult for pigs to root and wallow in,

326   thereby limiting the extent of their damage to seedlings. In contrast, feral pigs in Hawaii and

327   Malaysia cause seedling mortality, increase erosion, affect biogeochemical cycling, and spread

328   invasive plants [17,49-51]. These impacts are unlikely to be as severe in the rocky substrates of

329   Guam's limestone karst forests. Rather, removing pigs from the limestone forests on Guam could

330   have detrimental effects to plant species that have been limited by the lack of dispersers. We

331   recognize pigs would likely have a greater impact in areas, such as secondary forest or volcanic

332   forest, with more soil. However, the role of non-native species must be evaluated on the basis of

333   each habitat and ecological situation, rather than on a species basis. We encourage more studies

334   into the distribution, abundance, and potential seed dispersal capabilities of pigs in Guam.

335   Invasive species are normally managed with the goal of control or eradication, but in

336   novel ecosystems with multiple species and factors contributing to ecological changes, a blanket

337   approach may not be wise. Feral ungulates are components of novel ecosystems around the

338   world, and although their negative effects are well-documented [52-54], there are a few

339   examples where they play beneficial roles [55,56] or have unexpectedly insignificant effects on

340   native flora [57,58]. While the novel ecosystems of Guam provide an important context in

341   determining the relative detriment or benefit of these ungulates, the natural limestone karst forest

342   features, which are easier for deer to traverse in, but more difficult for pigs to root and wallow in,

343   also played a large role in determining this. A similar study in the clay soils of Guam would

344   likely produce different results. Ungulate eradication is an important restoration tool, especially

345   in island environments where ungulates are considered destructive invasive species [59].

346   Although this may still be the preferred management tool for Guam's systems, there may be

347   unintended consequences. These include the release of invasive plant species [15,58] or reduced

348   seed dispersal [55]. Natural resource managers would be aided by discerning which non-native

349   species serve important functions and which species are especially destructive in a particular

350   habitat type, before implementing conservation actions in a novel ecosystem.

351   Most conservation goals emphasise reintroducing reduced or extirpated native species to

352   historical abundances, and efforts that have focused on removing invasive species and

353   reintroducing native species have yielded many positive results [60-62]. In the Marianas,

354   management plans are focused on eradicating ungulates, and pigs are frequently the targeted

355   ungulate species. However, removing invasive species could have negative consequences if these

356   species play important ecological roles otherwise missing from the novel system [63]. In

357   addition, while more research should be done on the importance of species traits in determining

358   relationships between the plants in these ecosystems and their potential herbivores and

359   dispersers, our results indicated that traits such as number of seeds per fruit, palatability, and

360   morphology (vine/tree/herb) were, indeed, more important than native status in determining

361 these relationships. If restoration of native species is a future possibility, non-native species may

362 act as a temporary placeholder until species reintroductions can occur. Restoring a functioning

363 ecosystem rather than the exact original complement of species, or considering restoration an

364 iterative process with strategic and temporary use of non-natives, may be more feasible for

365 highly degraded ecosystems [64].

366 **Ethics**

367 No animal or human subjects were used to carry out this study. This study was designed and

368 written solely by the authors listed. See Methods section for permissions for use of government

369 properties.

370 **Competing Interests**

371   We have no competing interests.

372 **Data Availability**

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

374 **Author's Contributions**

375   Ann Marie Gawel helped to design the study, set up the experiments, collect data, analyse

376 and draft the manuscript. Haldre Rogers helped design and coordinate the study, set up

377 experiments, and aided in analysis and drafting the manuscript. Alexander Kerr aided in

378 designing and coordinating the study, reviewing the analysis, and drafting and reviewing the

379 manuscript. Ross Miller aided in designing and coordinating the study and reviewing the

380 manuscript. All authors gave final approval for publication.

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