

# Functional robustness of seed dispersal by a remnant frugivore population on a defaunated tropical island

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## Abstract

We surveyed zoochorous seedlings at an urbanized site on Guam with a remnant population of frugivores, and an otherwise similar site lacking all frugivores. Both seedling richness and abundance were much higher at the site with frugivores, providing hope that small populations can retain or restore ecological function.

Abstract in *Fino'* CHamoru is available with online material.

## KEYWORDS

*Aplonis opaca*, frugivory, functional rescue, Guam, Mariana Islands, nucleation, restoration, zoochory

## 1 | INTRODUCTION

Anthropogenic defaunation, the human-mediated population decline, extirpation and extinction of animal species, is affecting ecosystems on a global scale. Defaunation has been accelerating in terrestrial systems worldwide due to overexploitation, habitat destruction, and the impacts of invasive species (Dirzo et al., 2014). The loss of wildlife populations has been documented to cause disruption of critical ecosystem services such as decomposition, nutrient cycling, and seed dispersal (Bueno et al., 2013; Rumeu et al., 2017). The loss of frugivores, particularly on islands where functional redundancy is low, may rapidly lead to the partial or total interruption of seed dispersal (Pérez-Méndez et al., 2016). Given that zoochory is the predominant mode of seed dispersal within tropical forests (Howe & Smallwood,

1982), the cascading effects of defaunation on plant populations are likely profound (Kurten, 2013; Stoner et al., 2007).

The loss of frugivores need not be complete for seed dispersal to be disrupted. Cryptic function loss, whereby an ecosystem function is lost before an animal population is extirpated (McConkey & O'Farrill, 2015), may be caused by a variety of context-specific mechanisms, such as density-dependent changes in foraging behavior (McConkey & Drake, 2006) or decreases in mean body size within populations (Costa-Pereira & Galetti, 2015). The apparent prevalence of cryptic function loss (McConkey & O'Farrill, 2015) motivates questions regarding the usefulness of conservation and restoration of species for their ecosystem roles. Should managers make efforts to sustain small animal populations for the ecological functions they provide? Should animal populations be

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restored in situations where historical abundances are unlikely to be achieved?

The corollaries to cryptic function loss are that small populations may play an appreciable role in sustaining ecosystem function, which we are terming “functional robustness,” to describe the maintenance of function by a remnant population, or “functional rescue,” to describe the recovery of function by a translocated or reestablishing population. The term “robustness” is borrowed from the resilience literature (Mumby et al., 2014) and signifies, in this context, that an ecological process can persist despite a significant decrease in the abundance of a species. “Functional rescue” implies that an ecological process has been lost through local extinction, but that it can be recovered through species reintroduction or ecological replacement. For example, translocated populations of frugivores such as tortoises (Griffiths et al., 2011) and agouti (Mittelman et al., 2020) have reversed the suppressed recruitment of rare tree species in their respective habitats. In defaunated ecosystems, ecological functions such as seed dispersal may be dependent on remnant animal populations. Therefore, it is crucial to document the extent to which small populations result in cryptic function loss, or alternatively demonstrate functional robustness or rescue. In this study, we do so in a highly modified and defaunated novel ecosystem retaining a remnant population of frugivorous birds.

The island of Guam, in the western Pacific Ocean (Figure S1), offers a globally unique scenario for studying the impacts of disperser loss and the potential for restoring seed dispersal through frugivore population recovery. The mid-twentieth century introduction of the brown treesnake (*Boiga irregularis*) brought about the near-total extinction of the island's vertebrate seed dispersers (Fritts & Rodda, 1998; Savidge, 1987). Moreover, extirpated native dispersers have not been replaced by functionally equivalent non-native species, making Guam the only known location to have experienced the functional loss of all vertebrate seed dispersal services (Rogers et al., 2017). The loss of seed dispersal has changed the spatial pattern of seed rain and likely reduced seedling recruitment for many fleshy-fruited plant species (Rogers et al., 2017), with implications for forest dynamics such as delayed regeneration in forest gaps (Wandrag et al., 2017). Loss of dispersal has also had detrimental social and economic impacts due to the disappearance of culturally valuable plant species, such as the wild chili pepper (*Capsicum frutescens*), from the landscape (Egerer et al., 2018). Seed rain from native forest to adjacent degraded forest has effectively ceased, potentially leading to altered successional pathways in regenerating areas (Caves et al., 2013). However, a remnant population of about 1400 birds of a single frugivorous species (Sâli or Micronesian starling, *Aplonis opaca*) persists in northern Guam, concentrated mainly within the urbanized landscape of a military installation. The Sâli's broad diet (Craig, 1996; Jenkins, 1983; Pollock et al., 2020) and frequent movements between habitat types (Rehm et al., 2018) make it a good candidate for restoring seed dispersal across the landscape.

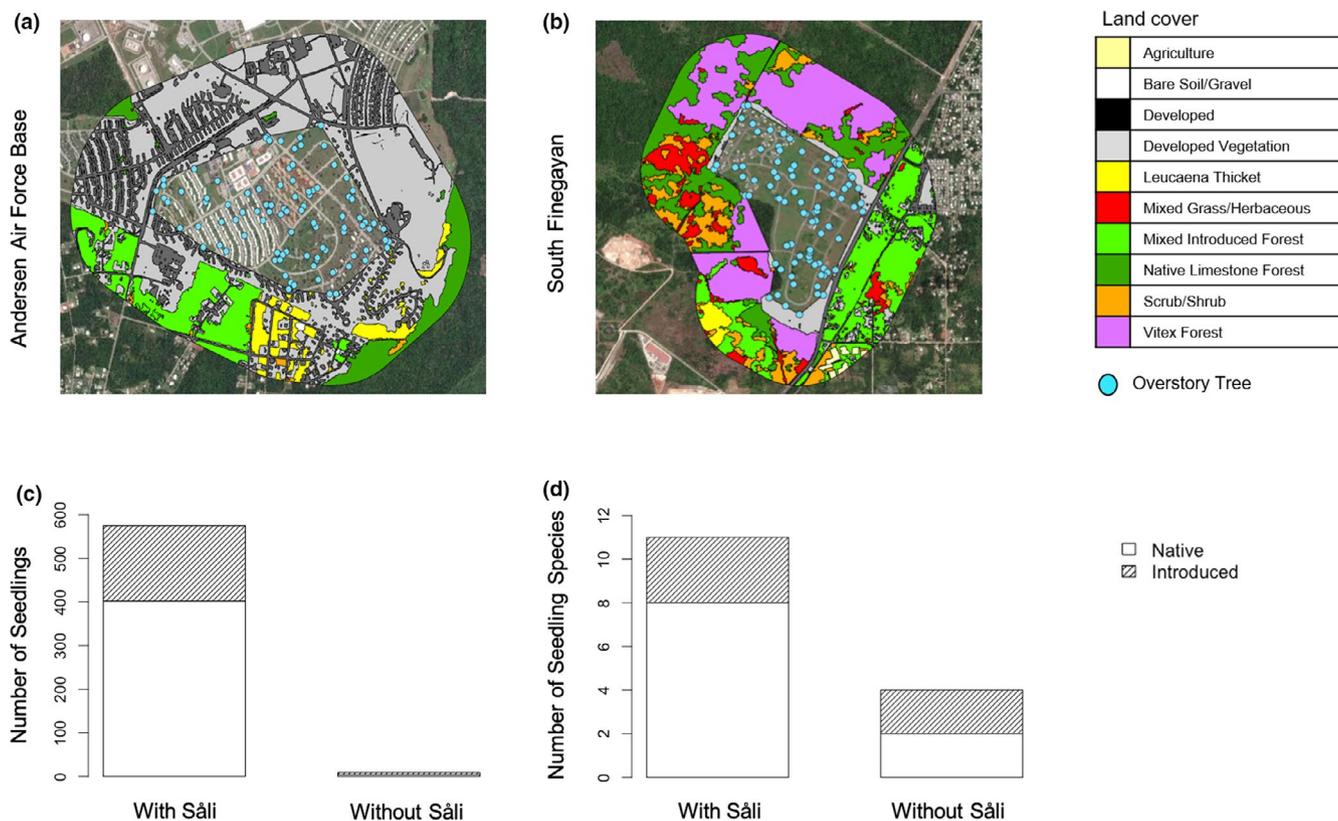
In this study, we compared seedling abundance and richness between a site encompassing the nesting and roosting range of the remnant Sâli population and a similar site lacking Sâli to assess the

species' impact on seed dispersal and its potential to contribute to regeneration of degraded areas. We predicted that seedling abundance and species richness would be higher where Sâli are present, providing evidence for functional robustness by the remnant population. No difference in the seedling community between sites with and without Sâli would provide support for cryptic function loss. We also assessed the presence of invasive vines to evaluate whether Sâli are facilitating their spread.

We surveyed seedling communities at two study sites on Guam during November–December 2017 (Figure S1). Both sites are located on U.S. military land in northern Guam and are situated adjacent to a combination of native and introduced forest types, which serve as a seed source (Figure 1; Table S1). Andersen Air Force Base (AAFB; 13°34'N, 144°55'E) is an 8,100-ha installation that harbors the majority (>90%) of the Sâli population on Guam. For comparison, we selected South Finegayan (SF; 13°33'N, 144°49'E), a 117-ha installation located 8 km from AAFB, because it was in close proximity to AAFB, similar in habitat, and lacked Sâli. We focused on housing areas at each site because Sâli roost and nest almost exclusively in the urbanized parts of AAFB and use the surrounding forest extensively for foraging, serving as mobile links between the forest and urbanized areas (*sensu* González-Varo et al., 2017). We used Google Earth© to delineate study areas of similar sizes (95 ha at AAFB and 88 ha at SF) comprised primarily of housing (i.e., open lawn interspersed with buildings and isolated trees) and adjacent landscaped regions.

Although both study sites are surrounded by ample forested habitat (Figure 1, Figure S1), foraging areas are more abundant near SF, the site without Sâli. We assessed forest cover within a 500 m buffer around each study area, which represents the area within which most Sâli are likely foraging. Native limestone forest comprises 7% of this buffer area at AAFB and 20% at SF (Figure 1, Table S1), and introduced forest types comprise 10% (all mixed introduced forest) of the buffer area at AAFB and 50% (20% mixed introduced and 30% *Vitex* forest) at SF. The dominant species in native limestone forest are, in descending order of commonness, *Meiogyne cylindrocarpa*, *Aglaiia mariannensis*, *Ficus prolixa*, *Premna serratifolia*, *Cycas micronesica*, *Ochrosia oppositifolia*, and *Ochrosia mariannensis*, and in mixed introduced forest are *Leucaena leucocephala*, *Talipariti tiliaceum*, *Vitex parviflora*, *Triphasia trifolia*, *Pandanus tectorius*, and *Meiogyne cylindrocarpa* (H.S.R. and E.C.F., unpublished data).

Our study sites at both bases experience similar intensive landscaping regimes. Virtually all seedlings in open areas are destroyed soon after establishment (M.K. and H.S.P., pers. obs.); however, the trunks and roots of large trees serve as refugia for seedling recruitment and so we limited our surveys of seedling communities to a 1-meter area around the base of such trees. In most cases, seedlings were so tightly clustered around the trunks of the overstory trees that they were unaffected by landscaping regimes (Figure S2). Therefore, we do not expect that the extent or timing of landscaping at either site relative to our surveys would have a substantial impact on our results.



**FIGURE 1** (a, b) Landcover maps showing habitat types within a 500 m buffer of sites with (Andersen Air Force Base; a) and without Sâli (South Finegayan; b). (c) Number of native and introduced seedlings recorded at the sites with and without Sâli. (d) Number of native and introduced seedling species recorded at the sites with and without Sâli. Unidentified seedlings are excluded from graphs c and d.

Guam's frugivore community is almost entirely defaunated, with five of six native avian frugivore species having become extirpated within a few decades of the establishment of the invasive brown treesnake on the island (Savidge, 1987; Wiles et al., 2003). The only extant native avian frugivore is the Sâli, with a population of approximately 1,400 individuals persisting on AAFB in northern Guam at an overall population density of 3–4 birds/ha (H.S.P. and M.K., unpublished data). An estimated 100 additional Sâli are present as individuals, in pairs and small groups scattered throughout other urbanized areas of the island (M.K. and H.S.P., pers. obs.). The size of the current Sâli population is an order of magnitude smaller than in the 1980 s, when it was estimated at 17,000 individuals, despite its range having already been largely constrained to northern Guam at that point (Engbring & Ramsey, 1984). A population of approximately 50 Mariana fruit bats (*Pteropus mariannus*) persists on and around AAFB in northern Guam, although they are generally restricted to undisturbed areas of karst forest and are unlikely to feed or roost in urbanized areas (Mildenstein, 2018). Feral pigs (*Sus scrofa*) disperse seeds of native and introduced tree species (Gawel et al., 2018), yet they remain primarily in forested and agricultural areas. Other non-native frugivores on Guam include three species of rat (*Rattus diardii*, *Rattus exulans*, and *Rattus norvegicus*; Wiewel et al., 2009) and Philippine collared-doves (*Streptopelia dussumieri*). Rats are not present in significant numbers at either study site and are predators

to all but the smallest seeds they consume (A. Gawel, pers. comm.). Philippine collared-doves are present in low densities at both sites but they are thought to be seed predators (Corlett, 1998; Loyn & French, 1991). Therefore, the species likely to be responsible for the vast majority of endozoochorous seed dispersal within our study sites is the Sâli.

To select overstory trees for sampling of seedling communities, we first assigned a unique number to all trees within each study area using Google Maps® imagery. We chose to exclude coconut palms (*Cocos nucifera*) because they have narrow bases where seedlings are more susceptible to mowing and bushcutting and, as a result, cannot support appreciable seedling communities (M.K. and H.S.P., pers. obs.). We then used the "sample" function in R version 3.3.3 (R Core Team, 2017) as a random number generator to select 100 trees at each site from the available pool of trees at AAFB ( $n = 896$  trees) and SF ( $n = 108$  trees). To ensure overstory trees were large enough to support seedling communities, we limited our study to trees that were >7 m in height and >20 cm diameter at breast height (dbh), giving a total of 97 trees from four species at AAFB and 95 trees from four species at SF (Figure S3). When there were overlapping canopies of multiple individual trees at a single sampling point, we randomly selected one individual as the overstory tree. Most trees in our study sites

**TABLE 1** The seedling species found under overstory trees at Andersen Air Force Base (with Sâli;  $n = 97$  trees) and South Finegayan (without Sâli;  $n = 95$  trees), including seedling abundance (i.e., total number of seedlings found) and seedling occurrence (i.e., percentage of overstory trees under which the seedling species was found).

Seedling species	Seedling abundance ( $n$ )		Seedling occurrence (%)	
	With Sâli	Without Sâli	With Sâli	Without Sâli
Tree species				
<i>Aglaia mariannensis</i>	1	0	1.0	0
<b><i>Carica papaya</i></b>	20	3	10.3	3.2
<i>Ficus</i> spp.	102	1	25.8	1.1
<i>Macaranga thompsonii</i>	53	0	8.2	0
<i>Melanolepis multiglandulosa</i>	55	3	18.6	3.2
<i>Morinda citrifolia</i>	145	0	40.2	0
<i>Phyllanthus mariannensis</i>	1	0	1.0	0
<i>Pipturus argenteus</i>	1	0	1.0	0
<i>Premna serratifolia</i>	46	0	14.4	0
<b><i>Schefflera actinophylla</i></b>	1	0	1.0	0
<i>Tabernaemontana rotensis</i>	1	0	1.0	0
<b><i>Vitex parviflora</i></b>	154	0	22.7	0
Shrub species				
<b><i>Triphasia trifolia</i></b>	1	2	1.0	1.1
UNID species				
Morphotype_4	1	0	1.0	0
Morphotype_9	6	0	6.1	0
Total	588	9		
Vine species				
<b><i>Coccinia grandis</i></b>			66.0	1.1
<b><i>Momordica charantia</i></b>			4.1	1.1
<b><i>Passiflora foetida</i></b>			11.3	0
<b><i>Passiflora suberosa</i></b>			87.6	65.3

Note: Data for the four vine species represent presence-absence rather than abundance. Introduced species are indicated in bold.

were isolated, and any clusters we encountered were of trees of the same species.

At each overstory tree, at least two observers counted and identified all zoochorous woody species growing within a 1-meter radius of the tree (or epiphytically on its trunk). We did not distinguish between life stages in the surveys and refer to all individuals as seedlings, given that they were the stage most frequently encountered (Figure S2). The only bird-dispersed overstory tree species was *Vitex parviflora*; for this species, we excluded conspecific seedlings to avoid artificially inflating recruitment estimates due to possible gravity dispersal. We were able to positively identify ~99% (590 of 597) of seedlings. The remaining seven unidentified individuals comprised two morpho-species, which we included in the analyses. We recorded the presence or absence of invasive vine species because we often encountered vine tangles in which we were unable to distinguish between multiple individuals of the same species. While we were surveying seedlings, we tallied the total number of Sâli present in the overstory tree as a crude metric of disperser presence.

All statistical analyses were conducted in R version 3.3.3 (R Core Team, 2017). To test for differences in seedling communities between our treatment site (AAFB: Sâli present) and control site (SF: Sâli absent), we ran generalized linear mixed effects models (GLMMs) with seedling abundance and richness as the response variables, respectively. We included overstory tree species as a random effect because (a) the community of overstory tree species differed significantly between sites ( $\chi^2 = 44.15$ ,  $df = 6$ ,  $p < 0.0001$ ; Figure S3) and (b) some overstory tree species may be associated with systematically positive or negative effects on seedling recruitment (e.g., allelopathy in *Casuarina*; Batish et al., 2001, Hata et al., 2010). We initially assumed a Poisson error distribution, but detected overdispersion (i.e.,  $\theta > 1.4$ ) in both models using the function *dispersion\_glm* in the package *blme* (Korner-Nievergelt et al., 2015). We therefore switched to negative binomial distributions for both models, which did not exhibit overdispersion and fit the data significantly better based on AIC model comparisons for both seedling abundance (negative binomial: 566.6; Poisson: 1352.0) and richness (negative binomial:

377.7; Poisson: 384.3). We ran our negative binomial mixed models for both seedling abundance and richness using the function *glmer.nb* in the package *lme4* (Bates et al., 2015), and assessed significance using *p*-values. We tested for the influence of tree size (i.e., overstory tree dbh) on seedling communities, because larger trees provide more available area for developing seedlings and may provide a more suitable microclimate (Zahawi & Augspurger, 2006). However, we found that neither seedling abundance nor richness was correlated with overstory tree dbh, so did not include it in the model. Furthermore, mean dbh of overstory trees was similar between AAFB (95% CI: 56.43–61.75 cm) and SF (95% CI: 50.52–58.29 cm), indicating that there were no systematic differences in tree size between sites. To test for differences in the presence of invasive vines between the sites, we ran a GLMM with a binomial error distribution (vines present or absent) that included site as a fixed effect and overstory tree species as a random effect.

Overall, we documented large differences in seedling communities between the two sites. Both seedling abundance ( $z = -8.97$ ,  $p < 0.0001$ ) and richness ( $z = -7.59$ ,  $p < 0.0001$ ) were significantly higher at AAFB, the site where *Sâli* are present. We did not detect any *Sâli* (0 of 95 trees) at SF and found only nine seedlings of four tree species (two native) present there (Figure 1). In contrast, we detected *Sâli* in 34 of 97 (35.1%) overstory trees at AAFB and found 588 seedlings from 15 tree and shrub species (eight native; Table 1, Figure 1) beneath 64 of 97 (66%) overstory trees. Seedlings of the four tree species found at SF were a nested subset of those present at AAFB (Table 1). Finally, we found that zoochorous invasive vines were significantly more abundant on AAFB than SF ( $z = -3.54$ ,  $p = 0.0004$ ), particularly *Coccinia grandis* and *Passiflora suberosa* (Table 1).

We took advantage of a unique situation, the near-total loss of seed dispersers on Guam, to explore the impact of a remnant frugivorous bird population on patterns of zoochorous seed dispersal and seedling establishment. We found marked differences in the abundance and richness of seedlings between study sites. There was a consistent presence of zoochorous seedlings under perch and roost trees at the site with *Sâli* present, whereas seedlings were very scarce at the site without *Sâli*. All 15 species of seedlings found at AAFB have been previously documented in the *Sâli*'s diet (Pollock et al., 2020), strengthening the evidence that they were the primary dispersers, and that they are dispersing at least some viable seeds. Overall, our findings demonstrate that disperser loss can effectively halt seed dispersal, but also that even a small frugivore population can provide functional robustness. Moreover, we underline the importance of avian seed dispersers and their habitat in promoting connectivity at the urban–forest interface in tropical ecosystems.

Our results offer insights into the ecological contexts in which populations may exhibit cryptic functional loss or functional robustness, and therefore, the contexts in which dispersers or their restoration may be most effective. We show that functional effects of *Sâli* are large in the context of dispersal below roost trees in urbanized areas, despite their small population size, likely because they have

relatively high local densities in these areas. Yet, the functional effects we are able to observe are confined to microsites below roost trees because of landscaping within these urbanized landscapes, and herbivory by introduced deer within the forest. Systems where disperser density is consistently decreased across the range or where reduced density influences disperser behavior (e.g., McConkey & Drake, 2006) may be more likely to exhibit cryptic function loss. The nature of the disturbance, the continued presence of other anthropogenic drivers, and efforts to restore dispersal can shape whether ecosystems exhibit function loss or functional robustness. We expect our results may be most applicable to other situations where seed dispersers are locally protected. This provides an argument in favor of reestablishing dispersal, even at small population sizes of dispersers, within local areas, because our results show that remnant populations can maintain important ecological functions despite a small overall population size.

We found seedlings below nearly 70% of the overstory trees at the site with *Sâli*, the majority of which were from native forest species (73% of species and 70% of total seedlings identified), demonstrating the potential for a small disperser population to positively impact forest regeneration. Indeed, we discovered a seedling of a federally-listed threatened tree species, *Tabernaemontana rotensis*, growing under a perch tree, highlighting *Sâli*'s ability to restore threatened components of the ecosystem. Moreover, we confirm that *Sâli* are filling an important restoration function by dispersing viable seeds, including those of pioneer species (such as *Melanolepis multiglandulosa*), from native forest to degraded sites (Rehm et al., 2018). However, we also note that *Sâli* dispersed seeds of *Vitex parviflora*, a non-native tree that dominates some disturbed forest stands on Guam (Stone, 1970). Furthermore, although invasive vines were present at both study sites, they were significantly more abundant at the site with *Sâli*, suggesting they are contributing to their spread (see Gleditsch & Carlo, 2011).

The pattern of seedling establishment observed, while greatly constrained by landscaping, follows the successional model of nucleation, whereby isolated trees on the landscape catalyze the growth of pockets of secondary forest (Schlawin & Zahawi, 2008; Yarranton & Morrison, 1974). According to the theory, seeds are deposited by dispersers attracted to isolated trees and establish in their shade, expanding the borders of the nuclei as they grow. Indeed, we observed many of what we termed “fruit islands” within our study site, where seedlings of fleshy-fruited trees likely dispersed by *Sâli* have established below their perch or roost trees (Figure S2). Harnessing this phenomenon for restoration has been proposed as an alternative to traditional plantation-design reforestation approaches (Corbin & Holl, 2012). Notable advantages of disperser-induced nucleation over plantation-based approaches are that the former method is substantially cheaper and can produce a more heterogeneous landscape (Holl et al., 2020). Furthermore, our results support evidence that generalist, omnivorous bird species, possibly due to their propensity to forage or roost in open habitat, may be ideal dispersers within applied nucleation scenarios (Carlo & Morales, 2016; González-Varo et al., 2017; Wunderle,

1997). Allowing experimental plots to naturally regenerate within our study areas, or in similar contexts, may yield insight into the potential for nucleation-induced restoration in urban, tropical areas, and the importance of seed dispersers in the process.

Recovery of the Sâli population on Guam, currently hampered by extremely low fledgling survival (Pollock et al., 2019), could be accelerated by a number of tools currently in development. Various predator control devices, such as traps, bait tubes and aerial bait delivery (Clark & Savarie, 2012; Clark et al., 2012), may soon allow snake suppression throughout parts of the landscape, and predator-resistant nest boxes have been deployed successfully within the species' range (Savidge et al., 2018). Therefore, conditions on the island are ripe for rewilding (*sensu* Seddon et al., 2014) through the restoration of seed dispersal by Sâli. Even a single effective seed disperser can support a large proportion of interactions within a tropical forest ecosystem (Kaiser-Bunbury et al., 2010), and Sâli have been recorded as dispersing at least 88% of zoochorous species found in forest plots on Guam (Pollock et al., 2020). However, to build resilience within this system it will be important to strive toward the reintroduction of a full complement of native dispersers (Fricke et al., 2018). In order to restore forests on Guam, it will be necessary to combine the recovery of seed dispersers with invasive deer control due to the suppressive effect of deer on recruitment of many tree species (Gawel et al., 2018; Nafus et al., 2018).

Our results point toward a critical role of animal seed dispersers in restoration efforts, particularly in tropical forests with a strong reliance on zoochory (Şekercioğlu, 2006; Wunderle, 1997). There is an increasing recognition that highly interactive species such as seed dispersers can be crucial in the restoration of ecological dynamics, and as such their recovery must be prioritized (Byers et al., 2006; Soulé et al., 2003). While low levels of redundancy within oceanic island ecosystems can make their mutualistic networks more vulnerable to disruption of ecosystem function than mainland systems (Hansen & Galetti, 2009; Kaiser-Bunbury et al., 2010; Rumeu et al., 2017), defaunation trends across the world necessitate restoration efforts focused on maintaining and recovering ecosystem function. Evidence presented here from Guam, and from defaunated systems elsewhere where seed dispersers have been restored, shows that even small populations of seed dispersers can be effective in promoting forest regeneration (Galetti et al., 2017). We encourage land managers and conservation practitioners to assess the potential ecological benefits that may accrue from the recovery and reestablishment seed-dispersing species.

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## CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

## AUTHOR CONTRIBUTION

M.K., H.S.P., and H.S.R. conceptualized the study. M.R.K. and H.S.P. collected the data. H.S.P. performed the formal analysis. M.R.K. and H.S.P. wrote the original draft. All authors involved in developing the methodology, review, and editing.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on GitHub at URL: [https://github.com/EBL-Marianas/Functional-rescue\\_Sali](https://github.com/EBL-Marianas/Functional-rescue_Sali).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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