



USER'S GUIDE

Restoring Seed Dispersal to Guam: A User's Guide

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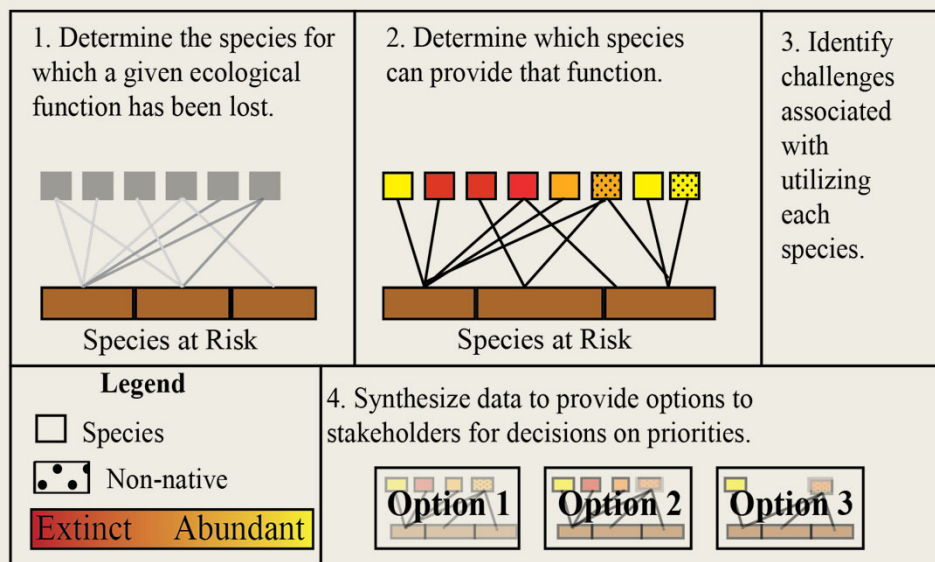


1. BACKGROUND

1.1 Rewilding to Restore Ecological Function

Species invasions threaten ecosystems worldwide. They not only simplify and change communities, creating novel ecosystems, but also threaten important ecological processes that maintain these systems. The Department of Defense (DoD) is responsible for management of extensive areas of land, much of which contain invasive species. Species invasions challenge DoD's mission to sustain the long-term ecological integrity of the resource base and the ecosystem services they provide. The return of highly degraded systems to their original state may not be feasible or even technically possible, but DoD is still mandated to maintain habitat for threatened and endangered species, regardless of the state of the system. In highly degraded systems, managers may need to work to recover function without attempting to replicate the original ecosystem, which requires a deep understanding of how these systems function.

The goal of our project was to assess the indirect impacts of an invasive species that has caused the loss of functionally important native species, and to determine if and how the lost ecological function could be recovered. Below, we present four steps to rewilding an ecosystem to restore ecological function below. Our project focuses on seed dispersal, but other relevant ecological functions may include other mutualisms (e.g., pollination), predation, or facilitation, or benefits of these interactions, like carbon storage or agricultural yield.



1.2 Introduction to Seed Dispersal

About half of the world's plants rely on animals for seed dispersal (Rogers et al. 2021). Plants may benefit from flesh removal and seed scarification during gut passage by frugivores, movement of seeds away from areas of high mortality underneath the parent tree, and movement to microsites suitable for germination (e.g., treefall gaps). Individual plant species that lose their dispersers may see a change in the spatial pattern of new recruits and a decline in abundance. In addition, vertebrate seed dispersal may affect forest structure by disrupting treefall gap dynamics and impact the pace and trajectory of plant community recovery from disturbance.

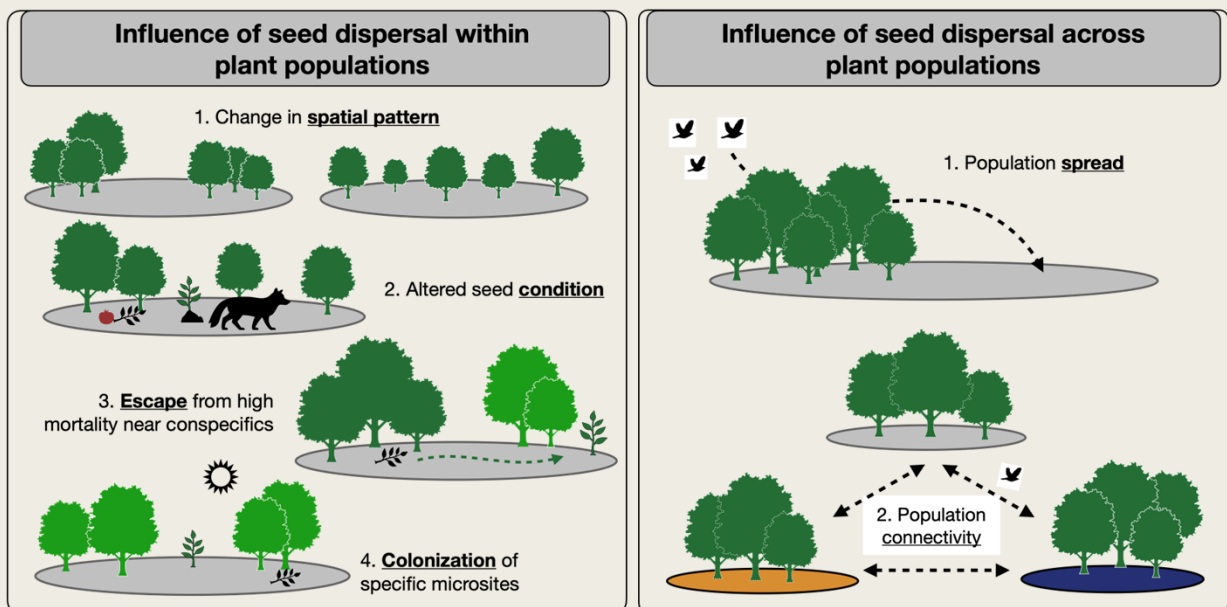


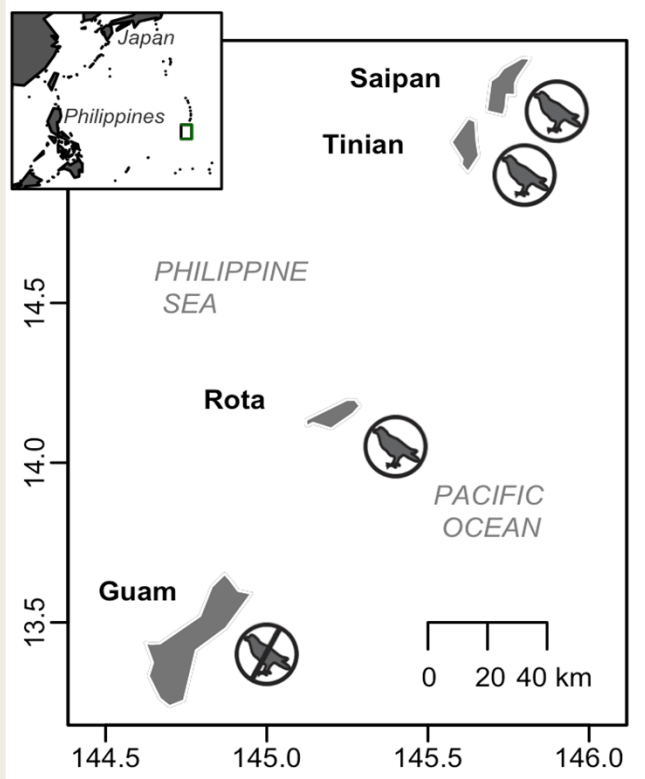
Image adjusted from Rogers et al. 2021

1.3 The Mariana Islands

The Mariana Island chain is in the Western Pacific and is composed of the US Territory of Guam and the Commonwealth of the Northern Mariana Islands. Guam is the southernmost major island and the largest (549 km²). Saipan is the second largest island in the Mariana Island chain (115.38 km²). Rota (85.39 km²) is smaller but has had fewer human impacts over the years than Guam or Saipan, and thus has a larger proportion of intact forest remaining.

Guam has functionally lost all native vertebrate frugivores except the Micronesian Starling, whose distribution is primarily limited to the built environment on Anderson Air Force Base (AAFB). Saipan's native bird fauna is largely intact, and the composition is similar to that that used to be on Guam. The majority of Mariana fruit bats in the inhabited southern Marianas occur on Rota, which has an estimated population of ~3,000 individuals.

Approximately 50-100 Mariana fruit bats remain on Guam. Non-native rats are present throughout the islands (Wiewel et al. 2009) and feral pigs can be found on Rota and Guam.



1.4 Limestone Forest

The primary forest type used by native, fruit-eating birds and bats in the Mariana Islands is limestone karst forest. The limestone forest canopy is relatively short, about 7-12 m, due to frequent typhoons. The islands experience a distinct wet and dry season, an average temperature of 27 °C, and an average annual rainfall of roughly 2000 mm (Lander and Guard 2003, Lander 2004).



1.5 Brown Treesnakes



The most famous and devastating species introduced to Guam is the brown tree snake (*Boiga irregularis*, BTS), which has caused the complete loss of 10 of 12 forest bird species and the functional extirpation of the other two (Savidge 1987, Wiles et al. 2003). This includes the loss of two nectarivorous, five frugivorous, and 10 insectivorous bird species (several species are in more than one category), disrupting plant-pollinator, fruit-frugivore, and predator-prey interactions in the forests. Additionally, BTS contributed to the decline of native fruit bats (*Pteropus mariannus*) on Guam (Allison et al. 2008), disrupting another set of fruit-frugivore interactions.

Island-wide eradication of BTS would allow restoration of many of these bird and bat species. Unfortunately, eradication is currently unlikely due to limitations in technology and funding.

2. THE IMPORTANCE OF SEED DISPERSAL TO GUAM'S FORESTS

2.1 Seed Dispersal of Limestone Forest Plants

About 90% of the tree species in limestone forest have fleshy fruits adapted for vertebrate dispersal. Below, we list the top 21 most abundant tree species in limestone forest on Saipan, Rota, and Guam, and their likely dispersal mode. These species account for about 85% of the stems in an average forest.

Rank abundance	Species	Likely dispersed by birds?	Likely dispersed by bats?	Likely dispersed by pigs/rats?
1	<i>Cynometra ramiflora</i> *	No	No	No
2	<i>Meiogyne mariannensis</i>	Yes	Yes	Yes
3	<i>Aglaia mariannensis</i>	Yes	Yes	Yes
4	<i>Eugenia reinwardtiana/palumbis</i>	Yes	Yes	Yes
5	<i>Ochrosia oppositifolia</i> **	No	Yes	Yes
6	<i>Psychotria mariana</i>	Yes	Yes	Yes
7	<i>Triphasia trifolia</i>	Yes	Yes	Yes
8	<i>Ochrosia mariannensis</i> **	No	Yes	Yes
9	<i>Ficus tinctoria</i>	Yes	Yes	Yes
10	<i>Carica papaya</i>	Yes	Yes	Yes
11	<i>Pandanus dubius/tectorius</i> **	No	Yes	Yes
12	<i>Mammea odorata</i> **	No	Yes	Yes
13	<i>Pisonia grandis</i> ***	Yes	Yes	Yes
14	<i>Aidia cochinchinensis</i>	Yes	Yes	Yes
15	<i>Ficus prolixa</i>	Yes	Yes	Yes
16	<i>Maytenus thompsonii</i>	Yes	Yes	Yes
17	<i>Premna serratifolia</i>	Yes	Yes	Yes
18	<i>Melanolepis multiglandulosa</i>	Yes	Yes	Yes
19	<i>Polyscias grandiflora</i>	Yes	Yes	Yes
20	<i>Dendrocnide latifolia</i>	Yes	Yes	Yes
21	<i>Morinda citrifolia</i>	Yes	Yes	Yes

* Abiotically-dispersed species.

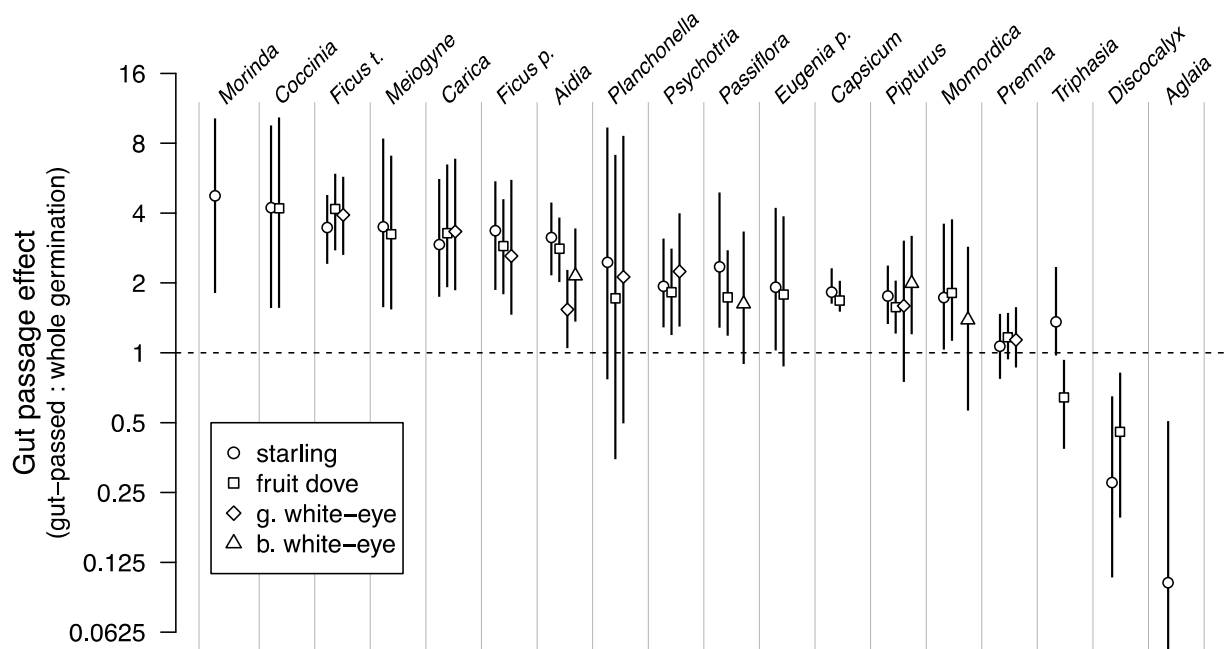
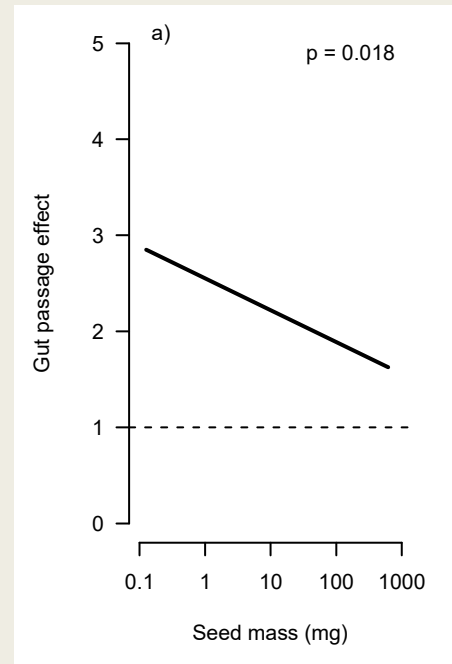
** Large-seeded species with husky seeds that are unlikely to be swallowed, thus dispersal is likely via carrying and dropping the seed.

*** Species has sticky seeds and is likely dispersed via ectozoochory.

2.2 Effect of Gut Passage on Germination

We quantified the impact of gut-passage on germination using feeding trial experiments. In these experiments, we fed seeds to captive birds, bats, pigs, and rats, collected their feces, and planted the seeds alongside seeds within whole fruit and seeds with the flesh manually removed.

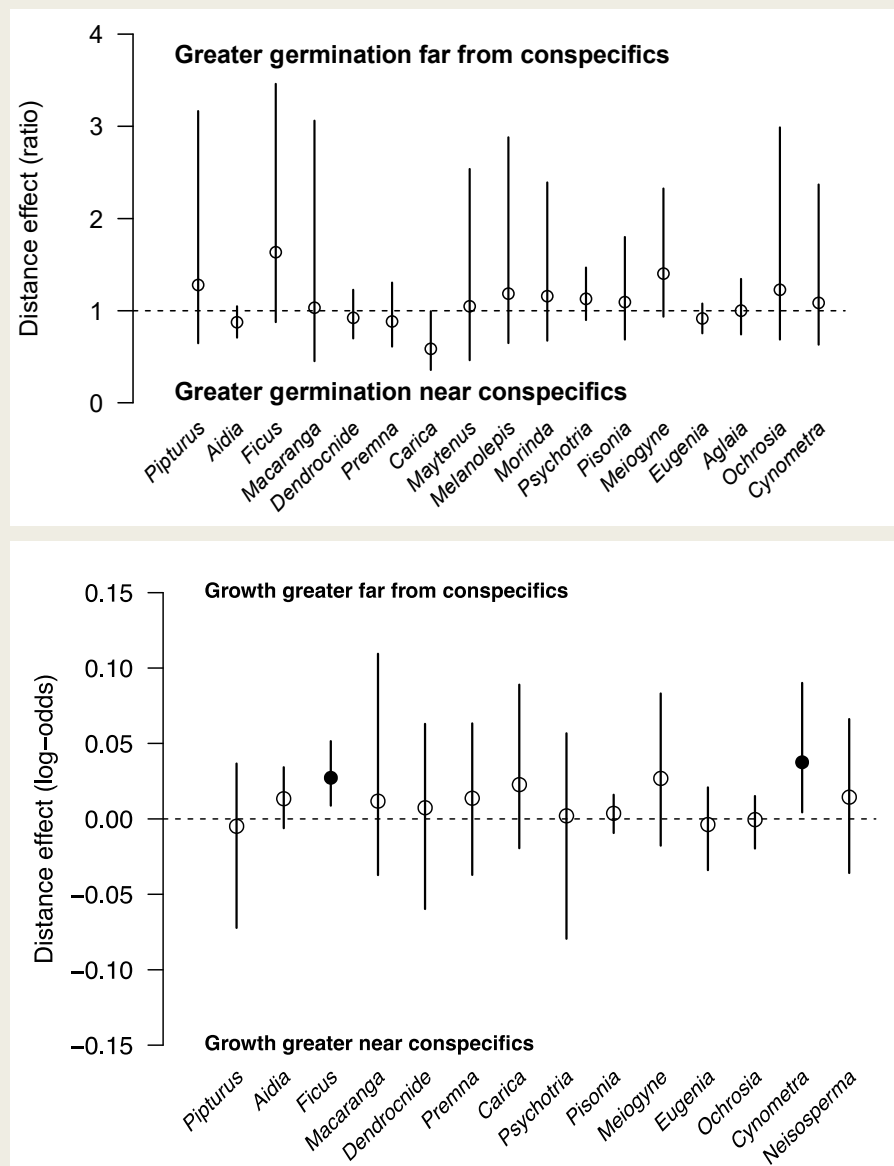
Results from bird feeding trials (below) show that most species benefit from gut passage, with higher germination of gut-passed seeds relative to seeds within whole fruit. However, no plant species required gut passage for germination; rather, some seeds from whole fruit germinated for all species. In addition, smaller-seeded species benefit more from gut passage than larger-seeded species (right). Results from the mammal feeding trials will be discussed in Section 3.



Results published in Fricke, Bender et al. 2019.

2.3 Effect of escape from mortality near conspecifics

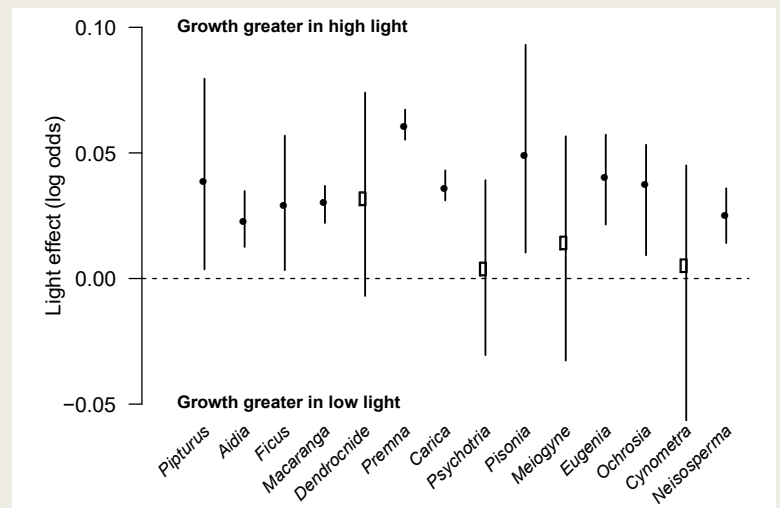
To understand how dispersal of seeds away from conspecific adults influences survival, we performed tests in the field with seeds and seedlings of plant species on Saipan. We added seeds and seedlings at locations near or far from adult conspecifics in the field and observed seed germination, seedling growth, and seedling survival. We found large variation across and within species, but surprisingly, distance to conspecifics typically had little to no effect on germination, growth, and survival.



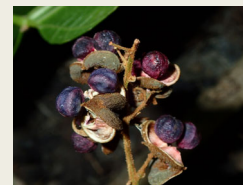
2.4 Benefits of colonization for gap-dependent plants

One of the most important microhabitats in forest are light gaps, often created by treefalls. These areas are spatially patchy and temporally fleeting, thus dispersers can be important for moving seeds to high light or spreading seeds broadly so that they can take advantage of high light conditions that might arise.

We estimated the benefit of reaching high-light areas for seedling germination, growth, and survival. While some species benefited from high light for germination and survival, nearly all species demonstrated greater growth in high light conditions (right).



We created treefall gaps on Saipan, Rota, and Guam, and monitored seedling regeneration within these gaps (Wandrag et al. 2017). Four pioneer species (below) were commonly found in gaps on islands with native dispersers and rarely found in gaps on Guam. This suggests a dependence on dispersal for reaching high-light areas.

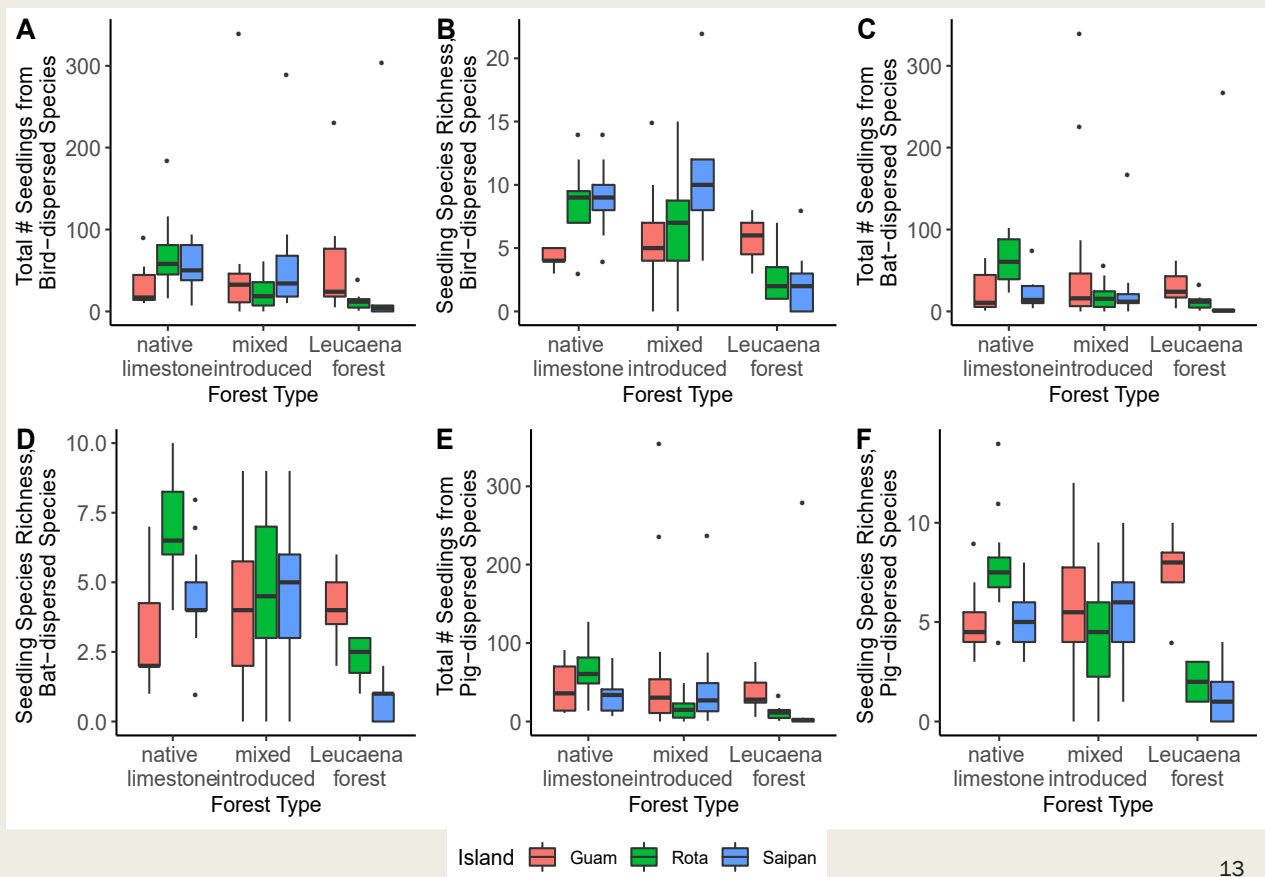


	<i>Pipturus argenteus</i>	<i>Psychotria mariana</i>	<i>Melanolepis multiglandulosa</i>	<i>Carica papaya</i>
Saipan & Rota	11 gaps 55%	11 gaps 55%	15 gaps 75%	19 gaps 95%
Guam	0 gaps 0%	0 gaps 0%	0 gaps 0%	4 gaps 20%

2.5 Restoration of degraded areas

Seed dispersal is an important process in restoration of degraded areas. We surveyed transects in native, mixed introduced, and *Leucaena* (a dominant non-native species in degraded areas) forest. We found that there are few seedlings in the limestone forest away from their conspecific adults on Guam, compared to other islands and that the disperser community present on each island is reflected in the native forest seedling community composition. This is problematic for future of native limestone forest on Guam, as the trajectory is likely to head towards lower diversity. Rota, which is the only island with a significant bat population, shows a clear signal of bats with increased richness and seedling abundance of bat-dispersed species in native limestone forest.

Interestingly, there are more dispersed seedlings in *Leucaena* forest on Guam than on nearby islands, likely due to the presence of pigs. However, many of these dispersed seedlings are from non-native species, foretelling a future forest dominated by non-natives.

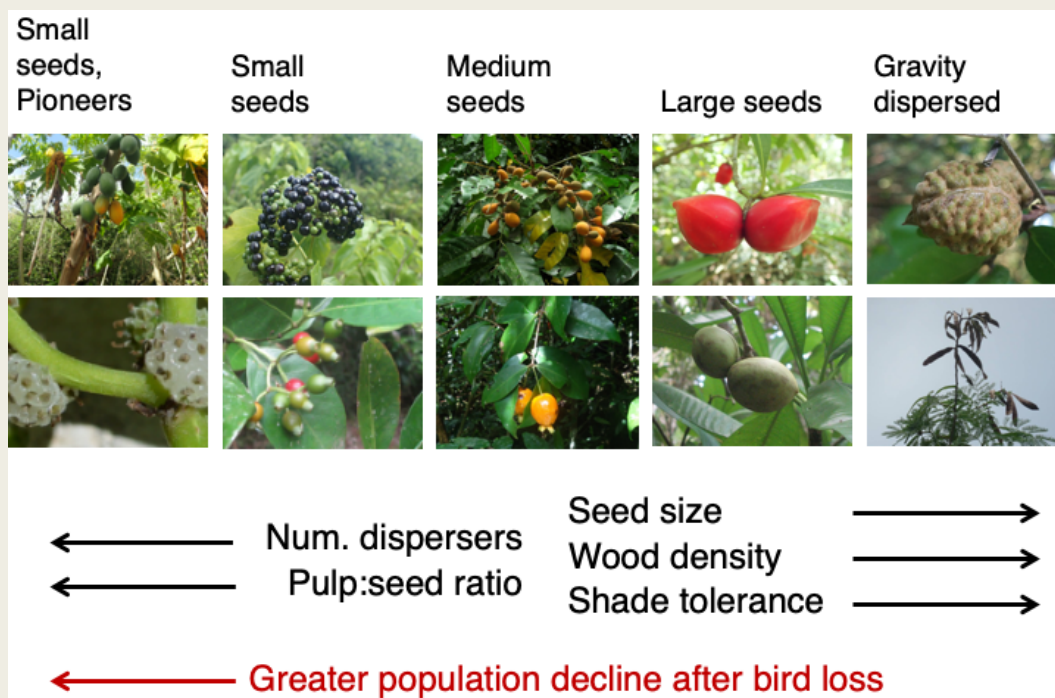


2.6 Summary

With the loss of seed dispersers, small seeded pioneer species are likely to experience the most negative impacts, largely due to an inability to reach the specific microsites required for germination and growth combined with a reduced probability of germination without gut passage. We found evidence for an decreasing dependence on dispersal with increasing seed size (below), suggesting a transition towards larger-seeded species in a forest without frugivores, as is the case on Guam.

With reduced colonization of gaps by quick-growing pioneer species in the absence of frugivores, gaps will close more slowly. Meanwhile, new gaps will continue to form, leading to a more open forest structure.

Patterns of regeneration reflect the disperser community, with evidence for bird dispersal in native forest on Saipan and Rota, pig dispersal in degraded forest on Guam, and a strong signal of bat dispersal on Rota.



3. REWILDING FRUGIVORES TO RESTORE DISPERSAL TO GUAM

3.1 Candidate Frugivores for Restoring Dispersal to Guam

Prior to the invasion of the brown treesnake, there were five native avian frugivore species on Guam: the white-throated ground-dove, Mariana fruit dove, bridled white-eye, Micronesian starling, and Mariana Crow. Of these, only the Micronesian Starling persists on Guam. We do not consider the Mariana crow as a candidate for rewilding because it is highly endangered in its entire range. We do, however, consider the golden white-eye, which is common on Saipan, but is not known to have existed on Guam.

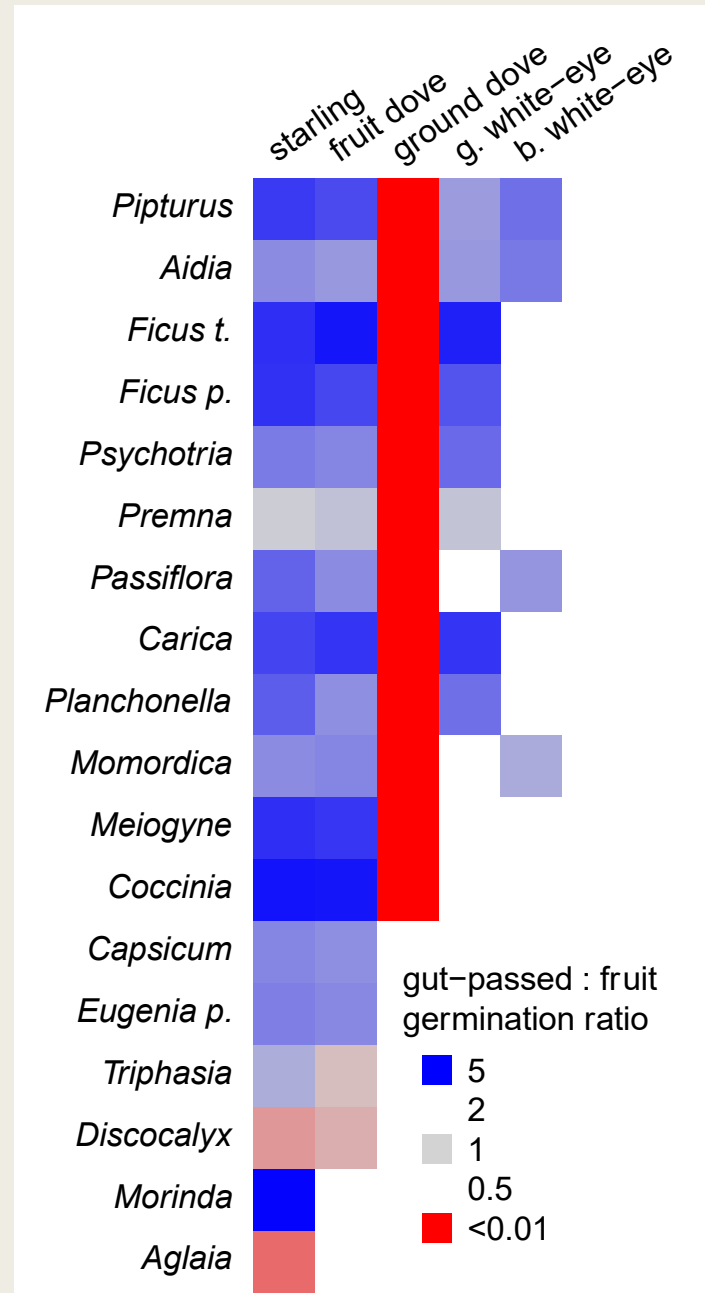
There is only one native mammalian frugivore species in the Marianas, the endangered Mariana fruit bat. Our two focal non-native mammalian frugivores are the feral pig and the ship/black rat. The feral pig has been present on Guam since the late 1700's (Conry 1988). The Asian house rat is present on all islands in the Southern Marianas, but in much lower densities on Guam due to brown treesnakes (Wiewel et al. 2009).

Group	Species (English, Chamoru, Latin)	Native status on Guam	Present on Guam?	Diet
Bird	Micronesian Starling, Sâli, <i>Aplonis opaca</i>	Native	Limited	insects, fruit, nectar
	Bridled White-eye, Nosa', <i>Zosterops conspicillatus</i>	Native	Extirpated	insects, fruit, nectar
	Mariana Fruit-Dove, Totot, <i>Ptilinopus roseicapilla</i>	Native	Extirpated	fruit
	White-throated Ground-Dove, Paluman Á'paka', <i>Pampusana xanthonura</i>	Native	Extirpated	fruit, insects
	Golden White-eye, Canario, <i>Cleptornis marchei</i>	Non-native	No	Insects, fruit, nectar
Mammal	Mariana Fruit Bat, Fanihi, <i>Pteropus mariannae</i>	Native	Limited	fruit
	Feral pig, <i>Sus scrofa</i>	Non-native	Yes	Omnivore
	Rat, <i>Rattus rattus</i>	Non-native	Yes	Omnivore

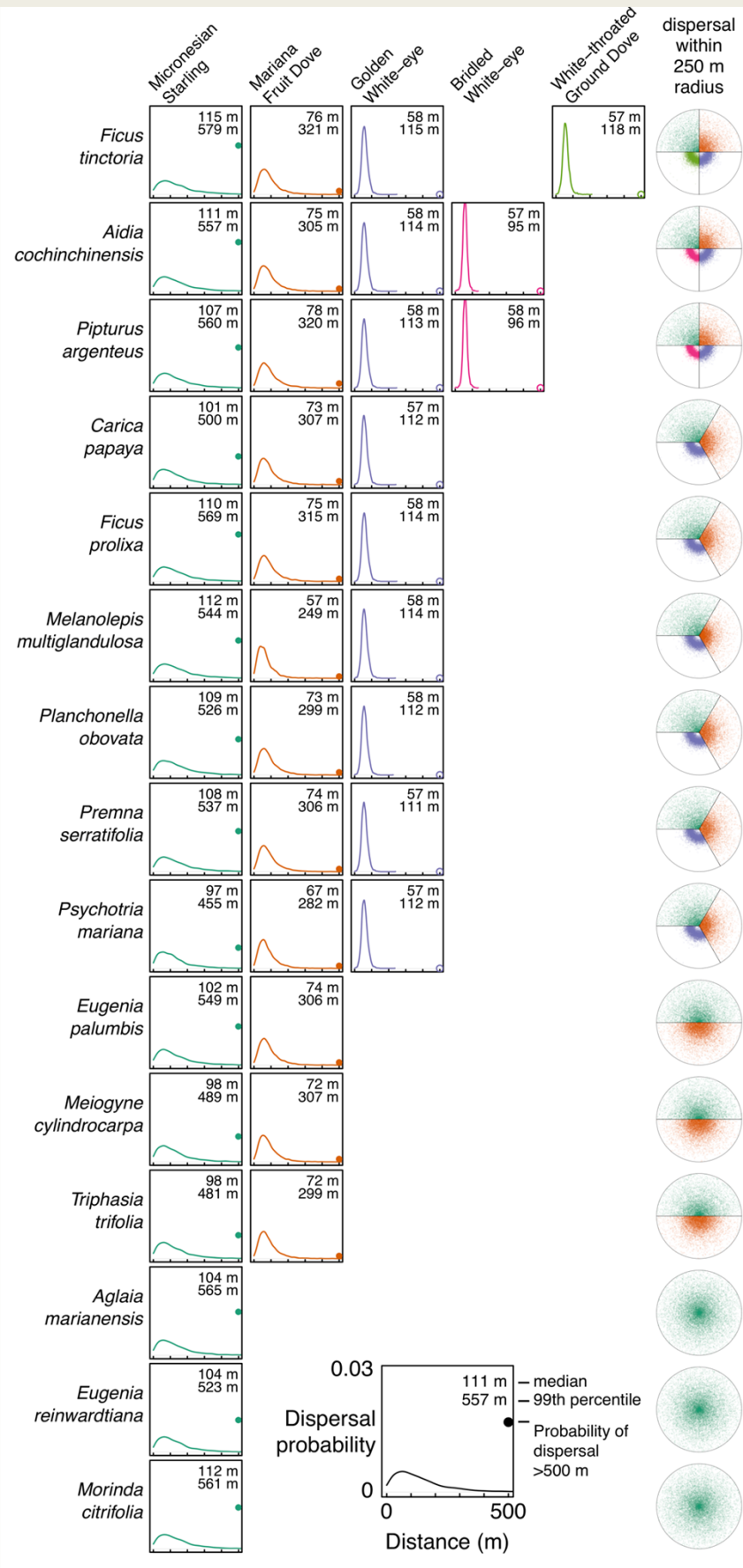
3.2 Birds—Gut Passage Effect

The results from our feeding trials with captive birds show the effects of gut passage on germination within the plant-frugivore network (right). The colors represent the ratio of the probability of germination of gut-passed seeds to the probability of germination of seeds within whole fruits, with red indicating negative impacts of gut passage and blue positive impacts. Bird-plant combinations that were not recorded in nature and were not tested are left blank.

Gut passage by birds led to up to five-fold increases in germination relative to seeds within whole fruit (Fricke et al. 2019). The key exception was the White-throated ground dove, which destroyed seeds during gut passage. Aside from the ground dove, the effects of gut passage on germination were similar between bird species.



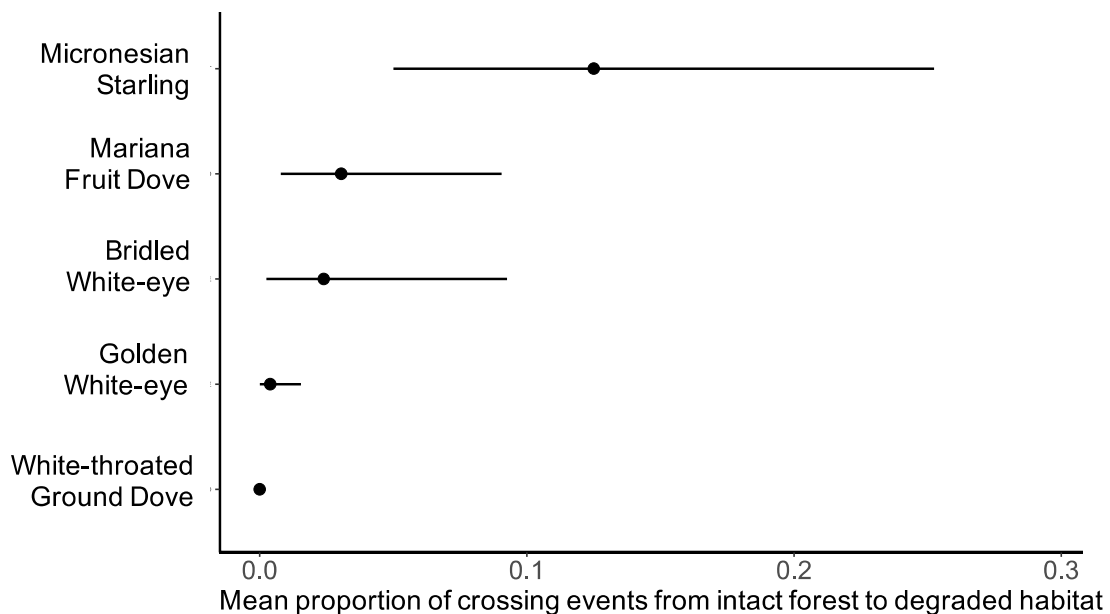
3.3 Birds—Dispersal Kernels



We modeled seed dispersal distances across the five frugivore species and 15 plant species by combining gut passage times and bird movement (Rehm et al. 2019). Differences in seed dispersal distance were largely driven by interspecific variation in bird movement rather than intraspecific variation in gut passage times. The median dispersal distance was at least 56 m for all species-specific combinations, indicating all species play a role in reducing high seed mortality under the parent tree. However, one species – the Micronesian Starling - performed 94% of dispersal events > 500 m, suggesting this species could be a key driver of long-distance dispersal services (e.g., linking populations, colonizing new areas).

3.4 Birds—Restoring Degraded Areas

To assess the propensity for bird species to move seeds to degraded areas and assist in forest regeneration, we compared habitat composition of bird start and end locations for movement intervals based on mean gut passage times (Rehm et al. 2017). The proportion of movement intervals that began in intact, native



3.5 Bats

During feeding trials, Mariana fruit bats consumed fruit differently than the native bird species, typically sucking the juices from the flesh and then dropping the flesh and seeds rather than swallowing them. As such, the majority of species and fruits were handled and then dropped, and only seeds from the smallest-seeded species (*Dendrocnide latifolia*, *Ficus spp.*, *Pipturus argenteus*, *Premna serratifolia*, and *Psychotria mariana*) were gut-passed. The effect of gut passage varied by species, but gut passage and bat-handled seeds tended to germinate at a similar rate as mechanically handled seeds, suggesting that the benefits of dispersal are largely due to pulp removal rather than scarification, and movement of the seeds to new locations.

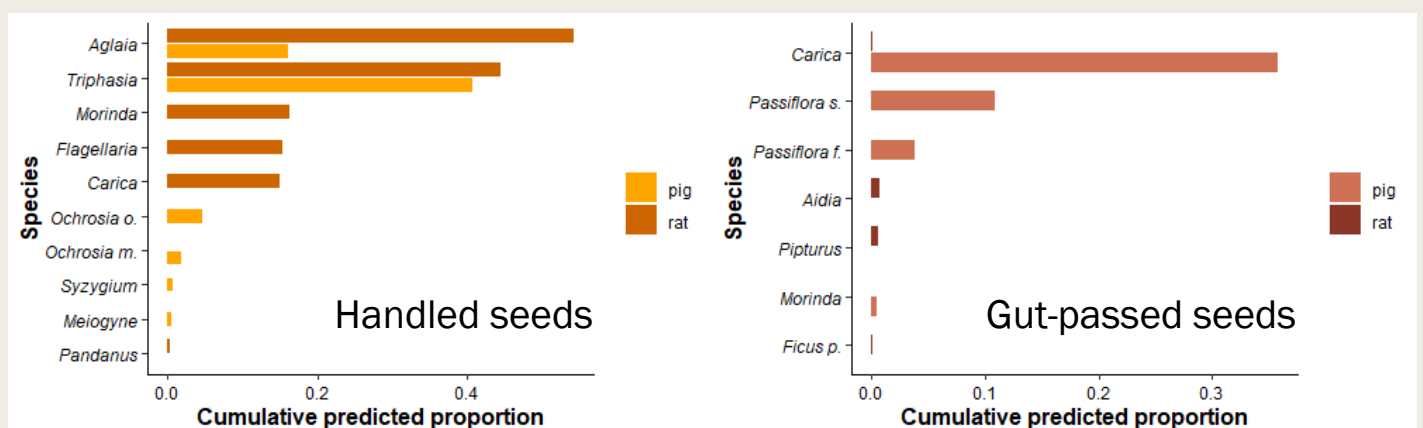
We tracked the movement of eight Mariana fruit bats on Rota using satellite tags for 1-26 days. Below, each color represents a different individual. The mean daily movement distance was 6.31 km (SD= 5.14 km). We predicted that bats would travel widely across the small island, however their movements were more constrained to a single region, likely near their roost.



3.6 Non-native mammals

We used feeding trials to test the role of non-native rats and pigs as seed dispersers. Their impacts depended on the plant species. Both rats and pigs interacted with, rather than ignored, most of the fruits they were presented, either handling (without ingesting) or ingesting over 80% of the seeds. However, rats and pigs destroyed 78% and 90%, respectively, of the seeds with which they interacted. For the seeds that were not destroyed, rat handling improved germination of the seeds compared to seeds within whole fruits, whereas pig handling reduced germination. The approximately 1.5% of seeds fed to rats that ended up surviving gut-passage did germinate in higher proportions than seeds planted in whole fruits, as did the 5% of seeds that passed intact through pigs.









Our results suggest that these invasive mammals will not act as substitutes for lost native frugivores, because although they do improve germination for a small number of seeds from a portion of the plant species fed to them, they destroy most seeds with which they interact.



Above: Cumulative effect of pigs and rats on germination of forest plant species, combining the likelihood of interacting with the species, the outcome of that interaction (destroyed or not), and the probability of germinating if not destroyed.

3.7 Summary

Our results elucidate which native species perform dispersal services for the plant species of the Marianas. Birds in the Mariana Islands handle fruit from a large proportion of the tree species in the native limestone forest. Fecal analyses, gut passage trials, and animal movement data show that Micronesian Starlings, Mariana Fruit Doves, and Golden White-eyes provide the majority of seed dispersal services on Saipan, and that Micronesian Starlings and Mariana Fruit Doves move seeds furthest. Starlings also have the largest home range and are most likely to move seeds from intact native forest to degraded areas. Bridled white-eyes disperse seeds from just a subset of tree species that are also dispersed by the other bird species, and White-throated Ground Doves are predators rather than dispersers. Bats likely complement the dispersal services of birds, as they move several large-seeded species that are too big for birds. Pigs and rats destroy most seeds fed to them, and thus are not effective surrogate species.

Green = native Orange= non-native to Guam	 Sali	 Totot	 Paluman	 Nosa'	 Fanihi	 Canario	 Pig	 Rat
# native plant species consumed	18	10	6	6	25	10	13	13
Effect of gut passage on germination	+	+	-	+	+/-	+	+/-	-
Median distance seeds moved (m)	115	76	57	57	Ongoing	58	No data, but likely far	No data
Proportion of native to degraded forest crossings	0.13	0.04	0	0.03	Ongoing	0.02	No data, but likely frequent	No data

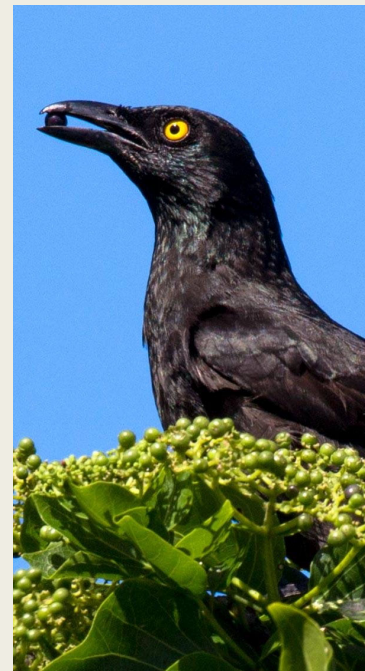
4. HOW TO RESTORE ECOLOGICAL FUNCTION TO GUAM

4.1 Rewilding Sali

Most of Guam's bird populations experienced rapid declines following the introduction of the brown treesnake (Wiles et al. 2003). However, the Micronesian starling has managed to persist in the presence of the snake although they are restricted in geographic range, with most of the population (~1500 individuals) residing in northern Guam on Andersen Air Force Base and scattered micro-populations of between 2-10 individuals in urban centers around the island (Pollock et al. 2020).

Breeding Micronesian Starling adults are constrained to nest in urban areas with lower snake abundance, and therefore have smaller home-ranges and use less forest habitat than juveniles. Dispersal simulations indicate that juveniles on Guam contribute more (~9x) to effective seed dispersal than breeding adults

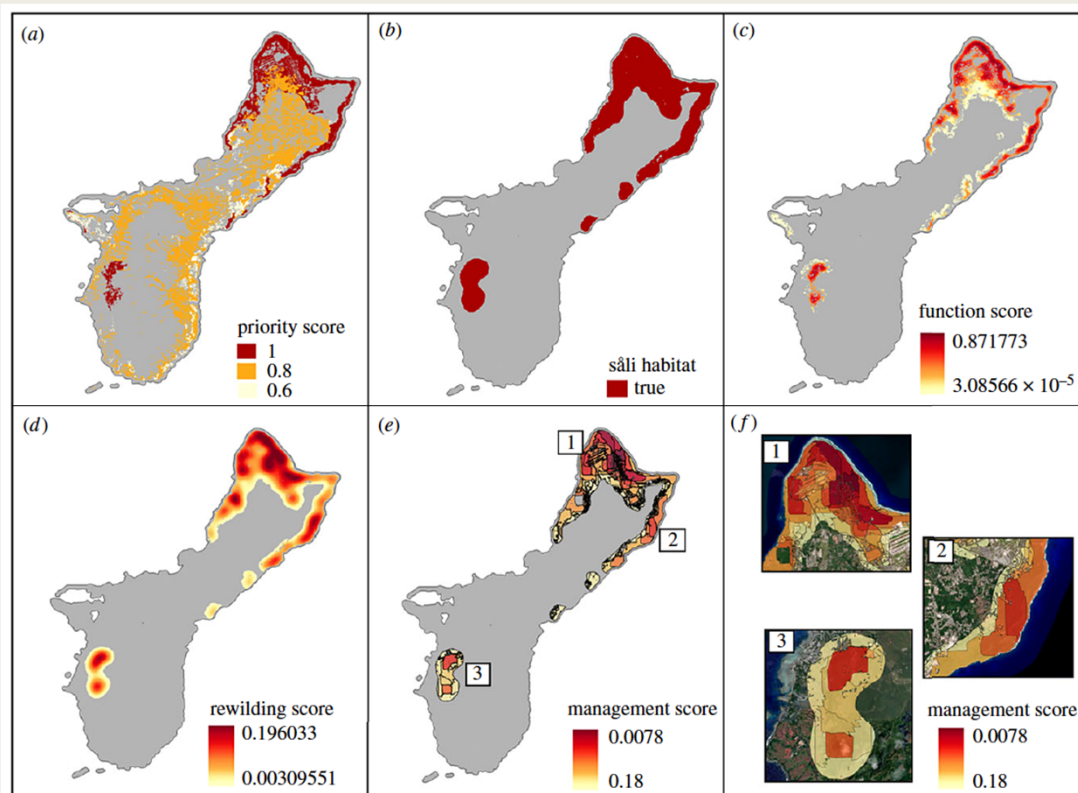
Micronesian Starlings consumed the majority of fleshy-fruited species in limestone forests in the Marianas; plant species observed to be dispersed by Sali comprised 88% of bird-dispersed adult stems and 54% of all adult stems in the forest monitoring plots. On Guam, Micronesian Starlings are highly frugivorous, suggesting they will still be a good seed disperser in the absence of other bird species.



4.2 Spatial Planning of Rewilding

The Spatial Planning of Rewilding Effort (SPORE) framework was developed to identify priority locations for rewilding by simultaneously considering habitat suitability and provisioning of ecological function (Thierry and Rogers 2020). While it can be applied for any ecological function, we used this to identify areas for rewilding Sâli to maximize the ecological benefit.

Below: The spatial distribution across Guam of (a) areas where ecological function is needed, (b) habitat suitable for Sâli, (c) areas where restoring seed dispersal by Sâli would be beneficial, (d) areas where Sâli rewilding is likely to be successful and beneficial, (e) areas that emerged as high priority for restoring dispersal, and (f) with (1) the northern part of the island, including Uranao, Finegayan, Litekyan and Tarague, (2) the Anao cliff line, and (3) Fena .



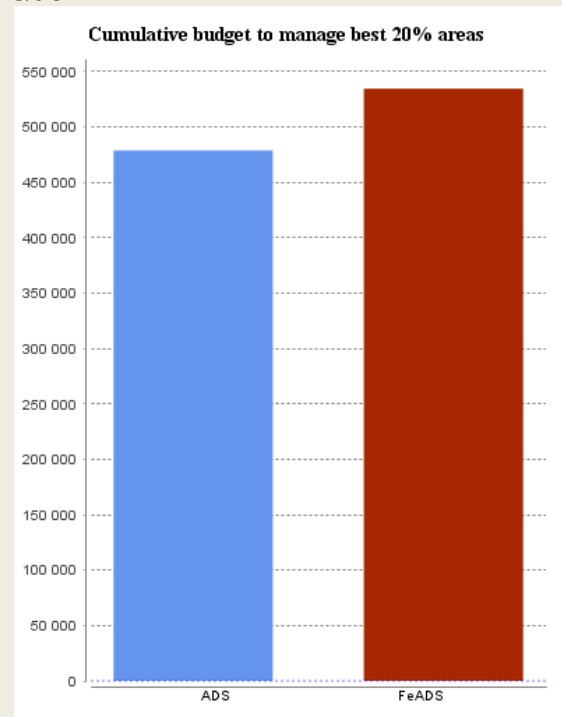
4.3 Cost of Snake Control for Rewilding

The Economic Costs of Management Scenarios (EcoCosMS) model is a tool for exploring the potential costs of brown treesnake management and selecting management areas according to ecological, landownership, or economic criteria. Users input a map of potential areas for snake control, with each area given a score based on priority. Users choose to select management units based on either a total budget over a set period of time or a given area. EcoCosMS produces a map with associated costs for each control method and combination of methods. The tool is setup for maximum flexibility, as users can adjust the cost of every aspect of each control method (e.g., the cost of mice, acetaminophen, helicopter usage, etc.). This allows users to identify areas for research and development that would reduce costs and have significant effects on conservation.

EcoCosMS outputs facilitate discussions between biologists, stakeholders, and decision-makers to help design effective rewilding and restoration projects. The example below demonstrates the cost of snake control for the top 20% of the areas selected by the SPORE model, which focuses on restoring birds to maximize restoration of seed dispersal on Guam.



The areas in green represent the highest priority areas for restoring seed dispersal, based on SPORE results.



The cost of snake control (in thousands of dollars) over 50 years in the areas shown in the map to the left using either the automated delivery system (ADS) or fencing plus ADS).

4.4 Limiting seed dispersal of invasive plants

Invasive trees and vines can outcompete native tree species during the reforestation process and thus impede the natural succession back to native forest. The vines, *Coccinia grandis* and *Passiflora* spp. (particularly *suberosa*), and the tree *Vitex parviflora* are common on Andersen Air Force Base and surrounding areas, likely due in part to seed dispersal by Sali and feral pigs. In addition, pigs disperse *Carica papaya*, *Passiflora suberosa* and *foetida*, *Triphasia trifolia*, and other non-native species throughout many degraded forest areas.

Any management project aiming at reintroducing native seed dispersers should be preceded by invasive plant control. Methods for controlling invasive plants include mechanical and manual removal, and the use of herbicides.



Passiflora suberosa



Vitex parviflora

4.5 Summary

The Micronesian Starling, or Sali, is a top candidate for restoring dispersal, as it is an effective disperser and is still present on Guam. The largest remnant population on Guam has been recorded dispersing a large variety of plant species, although it is constrained to the area on and adjacent to Andersen Air Force Base. Snakes and cats are the greatest threats to the Sali population.

Using the SPORE model, we identified three areas that would be the priority for rewilding to restore ecological function: (1) Uranao, Finegayan, Litekyan and Tarague in Northern Guam, (2) the Anao cliffline, and (3) Fena area. The EcoCosMS model can be used to estimate the cost for snake control in a given area.

In addition to snake control, invasive plant control should be a priority prior to rewilding, as dispersers will also move invasive plants around.

5. OVERALL SUMMARY

5.1 Overall Summary

Our studies on dispersal of plant species in the Marianas show that seed dispersers are important for many plant species and drive patterns of community composition and structure. In particular, we found that most plant species benefit from gut passage by birds and likely bats, as seeds germinate poorly if not de-pulped by their dispersers. This suggests that on Guam, where fruits simply fall from trees intact due to the lack of dispersers, plant regeneration rates are likely to be lower than on nearby islands with dispersers. We also found that a few species benefit from dispersal away from parent canopies, although this benefit was less widespread than expected. In addition, forests will become more open as gaps close slowly without the dispersal of pioneer species. Taken together, these large benefits of dispersal suggest negative consequences for the native limestone forest community on Guam in the absence of seed dispersers.

By systematically examining the role of five bird species, the Mariana fruit bat, and the non-native rat and pig, we determined that the most effective dispersers were the Micronesian Starling, Mariana Fruit Dove, and the Mariana Fruit Bat. The non-native rat and pig are primarily seed predators, not dispersers.

The Micronesian Starling population on Guam is the top candidate for restoring dispersal, but is limited by snake and cat predation of fledglings. The juveniles that do survive are excellent dispersers, as they move into the forest and spend all day foraging, then return to base during the night to roost, ostensibly due to lower snake predation. Nesting adults forage briefly in the forest before returning to the nest, making them less effective dispersers. The diet of the starlings on Guam includes the majority of native forest tree species, and appears to be roughly similar to the diet on Saipan, indicating they are still effective dispersers.

5.1 Overall Summary— continued

We developed a tool called Spatial Planning of Optimal Rewilding Effort, or SPORE, to identify and rank areas for restoring ecological function via rewilding. SPORE considers where ecological function is most needed and what areas are suitable habitat for function providers and combines these to create a rewilding score. Then, SPORE considers other factors such as land ownership and invasive species control methods to produce a map of ranked management units.

Snake control is required for bird recovery on Guam, but there are several control tools available that have varying costs. The Ecocosms is an economic decision-support tool for exploring the costs of snake control using each of the available control methods individually and in combination.

Our results have provided resource managers with DoD and other agencies on Guam important insight on the long-term consequences associated with the loss of seed dispersers, and guidance in the possible options for recovering ecological function in Guam's forests. Our modeling efforts inform decisions on where to strategically situate planned and anticipated snake fences. Although our research is directly applicable to the resource managers in the Mariana Islands, the strategy we took in this research can guide management of any highly degraded land, providing a roadmap for restoring ecological function in other novel ecosystems.

References cited

- Allison, A., Bonaccorso, F., Helgen, K. & James, R. (2008). *Pteropus mariannus*. iucnredlist.org.
- Conry, P.J. (1988). Management of feral and exotic game species on Guam. *Transactions of the Western Section of the Wildlife Society*, 24, 26–30.
- Gawel, A.M., Rogers, H.S., Miller, R.H. & Kerr, A.M. (2018). Contrasting ecological roles of non-native ungulates in a novel ecosystem. *R Soc Open Sci*, 5, 170151.
- Kastner, M., Pollock, H.S., Savidge, J.A., Fricke, E.C. & Rogers, H.S. (2021). Functional robustness of seed dispersal by a remnant frugivore population on a defaunated tropical island. *Biotropica*, 53, 359–366.
- Lander, M. (2004). *Rainfall Climatology for Saipan: Distribution, Return-periods, El Nino, Tropical Cyclones, and Long-term Variations*. Water and Environmental Research Institute of the Western Pacific, University of Guam, Mangilao, Guam.
- Lander, M. & Guard, C. (2003). *Creation of a 50-Year Rainfall Database, Annual Rainfall Climatology and Annual Rainfall Distribution Map for Guam*. University of Guam, Water and Environmental Research Institute of the Western Pacific, Mangilao, Guam.
- Pollock, H.S., Fricke, E.C., Rehm, E.M., Kastner, M., Suckow, N., Savidge, J.A., et al. (2020). Sáli (Micronesian starling – *Aplonis opaca*) as a key seed dispersal agent across a tropical archipelago. *Journal of Tropical Ecology*, 36, 56–64.
- Pollock, H.S., Kastner, M., Wiles, G.J., Thierry, H., Dueñas, L.B., Paxton, E.H., et al. (2021). Recent recovery and expansion of Guam's locally endangered Sáli (Micronesian Starling) *Aplonis opaca* population in the presence of the invasive brown treesnake. *Bird Conservation International*, 1–16.
- Rehm, E., Fricke, E., Bender, J., Savidge, J. & Rogers, H.S. (2019). Animal movement drives variation in seed dispersal distance in a plant–animal network. *Proc. Biol. Sci.*, 286, 20182007.
- Rehm, E.M., Chojnacki, J., Rogers, H.S. & Savidge, J.A. (2017). Differences among avian frugivores in seed dispersal to degraded habitats. *Restoration Ecology*, 67, 1.
- Rogers, H.S., Buhle, E.R., HilleRisLambers, J., Fricke, E.C., Miller, R.H. & Tewksbury, J.J. (2017). Effects of an invasive predator cascade to plants via mutualism disruption. *Nat Commun*, 8, 14557.
- Rogers, H.S., Cavazos, B.R., Gawel, A.M., Karnish, A., Ray, C.A., Rose, E., et al. (2021a). *Frugivore gut passage increases seed germination: an updated meta-analysis*.
- Rogers, H.S., Donoso, I., Traveset, A. & Fricke, E.C. (2021b). Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 52, 641–666.
- Savidge, J.A. (1987). Extinction of an island forest avifauna by an introduced snake. *Ecology*, 68, 660–668.
- Thierry, H. & Rogers, H. (2020). Where to rewild? A conceptual framework to spatially optimize ecological function. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20193017.
- Wandrag, E.M., Dunham, A.E., Duncan, R.P. & Rogers, H.S. (2017). Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. *PNAS*, 114, 10689–10694.
- Wiewel, A.S., Yackel Adams, A.A. & Rodda, G.H. (2009). Distribution, Density, and Biomass of Introduced Small Mammals in the Southern Mariana Islands¹. *Pacific Science*, 63, 205–222.
- Wiles, G.J., Bart, J., Beck Jr, R.E. & Aguon, C.F. (2003). Impacts of the Brown Tree Snake: Patterns of decline and species persistence in Guam's avifauna. *Conservation Biology*, 17, 1350–1360.