ABSTRACT: RESTORING ECOLOGICAL FUNCTION TO A NOVEL ECOSYSTEM IN THE PRESENCE OF ONE OF THE WORLD'S MOST DESTRUCTIVE INVASIVE SPECIES

OBJECTIVE: Species invasions are threatening ecosystems worldwide. They not only simplify and change communities, creating novel ecosystems, but also threaten important ecological processes that maintain these systems. Island ecosystems are at particular risk of losing ecological function due to invasive species because of their isolated evolutionary history. The Department of Defense (DoD) is responsible for management of extensive areas of land, including land on Pacific islands; unstable novel ecosystems caused by 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 financially feasible or even technically possible, but these ecosystems still have tremendous value. Managing them to maximize that value requires an understanding of how these systems function, and how they can serve the DoD mission. DoD is mandated to maintain habitat for threatened and endangered species, regardless of the state of the system. **In highly degraded systems, such as the island of Guam where virtually all native birds have been extirpated and the cause of species loss and species endangerment (the brown treesnake) is still present, managers may need to work to restore function without attempting to replicate the original ecosystem.**

Our research will focus on a critical ecological process in tropical systems, and likely the furthest reaching ecological casualty of the invasion – animal mediated seed dispersal. The **objective of our research is to assess if and how seed dispersal could be returned to Guam's forests.** We aim to first understand how dispersal services have been disrupted, then identify the role that native and non-native species could play in restoring seed dispersal despite the continued presence of invasive brown treesnakes. We will investigate the limitations of different restoration options, and develop a "User's Guide" for managers so they may weigh the advantages and disadvantages of each approach.

TECHNICAL APPROACH: The proposed research will be conducted in karst limestone forest - the primary forest type used by native forest birds and bats (frugivores) - and in degraded forest on Guam, as well as on the nearby islands of Saipan and Rota, which have relatively intact frugivore communities. We have identified four steps to the process of restoring function to Guam's forests. Initially, we will determine how loss of frugivores has impacted ecological function in Guam's forests and identify the consequences for long-term forest health. To do this, we will investigate the impact of disperser loss on the 21 most common fleshy-fruited forest tree species and on forest regeneration in degraded habitat, followed by modeling what these forests may look like in the future. Next, we will determine the ecological role of frugivorous species that may be used to restore ecological function, including native species (both extant and extirpated from Guam), existing non-native species, and potential taxon substitutes – non-native species introduced specifically to restore lost ecological interactions. We will use foraging observations and fecal analyses on Saipan and Guam to determine which tree species are dispersed by which frugivore and, along with germination trials, the relative importance of each frugivore species. Using telemetry, we will determine movement patterns for the various species to predict the area over which an individual could potentially provide dispersal services, and whether species move seeds to degraded forest. Third, we will address challenges that might be faced when attempting to re-establish avian frugivores or expand the range of existing frugivores on Guam and evaluate the benefits and dangers of using non-native species to restore ecological function. Lastly, we will use decision support and modeling tools to develop strategies for develop strategies for restoring ecological function to Guam's forests utilizing various frugivore assemblages.

BENEFITS: Our results will provide resource managers with DoD and other agencies on Guam important insight on the long-term consequences associated with the removal of dispersers, and guidance in the possible options for restoring ecological function to Guam's forests. Although our research will be directly applicable to the resource managers in the Mariana Islands, **the strategy we take in this research will be a useful guide for management of any highly degraded land, providing a roadmap for restoring ecological function in other novel ecosystems.**

TECHNICAL SECTION

RESTORING ECOLOGICAL FUNCTION TO A NOVEL ECOSYSTEM IN THE PRESENCE OF ONE OF THE WORLD'S MOST DESTRUCTIVE INVASIVE SPECIES

A. SERDP RELEVANCE

While supporting the military mission, Department of Defense (DoD) installations must also work to ensure the long-term sustainability of natural resources on their land. Executive Order 13112 directs agencies, including DoD, to "minimize the economic, ecological, and human health impacts that invasive species cause." Additionally, DoD Instruction Number 4715.03 states that DoD protect and enhance resources for maintenance of ecosystem services. The spread of invasive species throughout installations worldwide have made these very tall orders. Invasive species can have particularly devastating effects on island ecosystems, and the capacity of DOD to minimize impacts and maintain ecosystem services in these areas will depend on our understanding of relationships within ecosystems and their capacity to sustain ecosystem services.

The FY2014 Statement of Need (SON; *RCSON-14-01*) is in response to the challenges of invasive species in the Pacific Islands. Our proposal responds to both key objectives articulated in the SON: 1) understanding how key ecological processes have been altered by invasive species, and 2) learning how to restore these processes in order to restore ecological function. Our research will focus on a critical ecological process in tropical systems – animal mediated seed dispersal - and will be conducted on the island of Guam, where primary seed dispersal services have been virtually eliminated by the invasive brown treesnake, which has functionally extirpated all native forest birds and the only native mammal. We will investigate the impacts of this island-wide ecological disruption, and we will use nearby islands with very similar forests and intact frugivore communities to examine the ecological importance of fruit-dispersing species and the challenges associated with using these species in system-wide restoration. Our results will provide resource managers the first look at the long-term consequences associated with the removal of dispersers, and guidance in the possible options for restoring ecological function to Guam's forests.

B. TECHNICAL OBJECTIVE

The goal of this project is to assess if and how ecological function could be returned to a highly degraded novel ecosystem. We aim to first understand which ecological functions have been disrupted, then identify the role that native and non-native species could play in restoring ecological function despite the continued presence of invasive species. We will investigate the limitations of various restoration options, and develop a "User's Guide" for managers so they may weigh the advantages and disadvantages of different restoration approaches.

Q1: How have invasive species impacted ecological function on the island of Guam and what are the consequences for long-term forest health?

Q2: What are the ecological roles of potential native seed-dispersing species, existing non-native species, and possible taxon substitutes that may be used to restore ecological function?

Q3: What are the limitations or challenges associated with using native, existing non-native species, or taxon substitutes to restore ecological function?

Q4: Synthesis- what are the feasible options for restoration of ecological function on Guam?

C. TECHNICAL APPROACH

C.1: BACKGROUND

Species invasions, extinctions, and climate change have produced ecosystems with combinations of species never before found on earth (Hobbs et al. 2006, Seastedt et al. 2008). In some cases, these novel ecosystems are in a relatively stable state, where the system is still able to maintain species diversity and structure and recover from disturbance. However, if important species are lost –mutualists, top predators, keystone species, ecosystem engineers- the ecosystem may degrade, losing diversity, structure, and resilience, reducing the capacity of the ecosystem to respond to change. Maintaining ecosystem services in the face of change has moved from a theoretical construct to a very real economic and ecological issue with the rapid advance of climate disruption (Chapin et al. 1997, Hooper et al. 2005). DoD is responsible for management of extensive areas of land, and even in the absence of a rapidly changing climate, unstable novel ecosystems caused by species invasions challenge DoD's mission to "sustain the long-term ecological integrity of the resource base and the ecosystem services they provide".

Novel ecosystems are causing land managers to re-calibrate their restoration goals and rethink their restoration toolkit. The return of such systems to their original state may not be financially feasible or even technically possible due to extinctions, invasive species, or climate change, but these ecosystems still have tremendous value (Hobbs et al. 2011), and managing them to maximize that value requires us to understand how these systems function, and how they can serve the DoD mission. For example, DoD is mandated to maintain habitat for threatened and endangered (T&E) species, regardless of the state of the system. In places such as Guam, where the cause of species loss and species endangerment (the brown treesnake) is still present and its removal appears intractable, managers may need to utilize the strategy of "intervention ecology" (Hobbs et al. 2011), restoring function within these novel systems without attempting to restore the original ecosystem (Marris 2011). This approach calls on managers to first assess which functions have been lost, and then to determine the ability of various species to restore those functions (Fig.1). Although using native species to restore function is ideal, additional options include the use of key non-native species already present in the system as well as introductions of taxon substitutes, exotic species introduced to replace extinct native species (Hansen 2010, Kaiser-Bunbury et al. 2010). The feasibility and efficacy of each option must be explored, and the various options presented to key stakeholders, as there are often alternate options for the restoration of function (Seastedt et al. 2008). The goal is not to recreate an ecosystem that is identical to the original, but instead to use a strong understanding of the natural history and ecology of the component species to build a novel ecosystem that will support T&E species. The goal of creating a 'functioning ecosystem' is often more practical and achievable in highly degraded systems than re-creating an earlier ecosystem. However, this approach remains primarily theoretical (Donlan 2005, Donlan et al. 2006, Kaiser-Bunbury et al. 2010), with only a few notable exceptions, including a recent SERDP-funded project focused on manually creating novel plant communities composed of native and non-native species (Ostertag 2011, proposal RC-2117).

The island of Guam provides a unique and high profile opportunity to employ the concept of intervention ecology and demonstrate that restoration of ecological function may be the most appropriate strategy in highly degraded areas. The island is a textbook example of a novel ecosystem (Hobbs et al. 2009) because it has been severely impacted by multiple invasive species (Fritts and Rodda 1998). The most famous and devastating species introduced to Guam is the brown treesnake (*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 nectarivarous, five frugivorous, and 10 insectivorous bird species (several species are in more than one category). Additionally, BTS contributed to the decline of native fruit bats (*Pteropus mariannus*) on Guam (Allison et al. 2008). Island-wide eradication of BTS is currently deemed unlikely. However, eradication may be possible within fenced areas, and future research may produce effective eradication methods, further emphasizing the importance of restoring function to Guam's forests now.

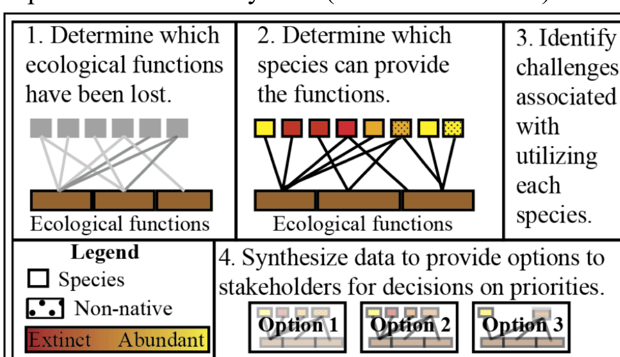


Fig.1: The steps for 're-wilding' to restore ecological function to a novel ecosystem.

Guam has two key characteristics that make it a good candidate for a project to restore ecological function to a novel ecosystem. First, the nearby islands of Saipan and Rota have forest ecosystems that can serve as a model for studying the functioning of an intact system, and they have populations of the bird and bat species that have been extirpated from Guam, providing a potential source for re-introductions. Second, DoD controls approximately 28% of Guam's total land area, including some of the most undisturbed native forest on the island, and has the ability to efficiently spearhead forest restoration on the island. The pathway we propose for resource management on Guam could serve as a model for restoration of novel ecosystems around the world.

We have identified four steps to the planning process of restoring function to a degraded ecosystem (Fig.1) and these correspond to the four objectives of our research project. The first step is to understand which functions have been disrupted and the impacts of these disruptions on species and communities; typically this necessitates fieldwork focused on ecological interactions and a strong understanding of the system's natural history. Steps 2 assesses which species may be able to provide the desired function, while step 3 explores the factors limiting the ability of native species to provide that function, along with the dangers associated with using non-native species. Finally, this information must be synthesized and presented to land managers and decision makers, who are then responsible for implementation. We propose research into each of these steps.

Objective 1: Determine how the invasive brown treesnake has impacted ecological function in Guam's forests and identify the consequences for long-term forest health.

While the BTS is responsible for the functional or complete extirpation of all 12 native forest bird species and is partly responsible for the functional extirpation of the Mariana Fruit Bat, as well as declines in skink and gecko populations, current evidence suggests that the loss of frugivorous birds and bats may have the greatest cascading effects on the ecosystem. Generally, the loss of mutualists, predators, keystone species and ecosystem engineers will have the largest ecosystem-wide impacts (Dunn et al. 2009, Estes et al. 2011, Colwell et al. 2012), and birds and bats play several of these roles. PI's Rogers and Tewksbury started the Ecology of Bird Loss Project (EBL) in 2006 to investigate the impact of bird loss on ecological function; our research shows that the loss of insectivorous birds appears to have had a relatively minor impact on the forest (Fig.S1), potentially due to the presence of a resilient food web with alternate invertebrate predators (e.g., spiders, Fig.S2) (Rogers et al. 2012). Additionally, less than 10% of forest trees on Guam were bird pollinated, and nearly all species are setting seed adequately without birds (A. Brooke, pers. comm., but see Mortensen et al. 2008). However, approximately 80% of forest tree species have fleshy fruits adapted for vertebrate dispersal; seed dispersal influences the spatial pattern and abundance of tree species as well as regeneration of degraded forest areas (Wunderle 1997, McConkey et al. 2012). Our research on birds thus far and research in other systems on fruit bats shows a strong impact of disperser loss on forest species and entire forest ecosystems. Thus, this proposal will focus on how BTS have disrupted the ecological function of seed dispersal provided by frugivorous vertebrates.

Fleshy-fruited tree species may rely on frugivorous birds and bats for seed scarification through consumption (Fig.S3), movement of seeds away from high mortality underneath the parent tree (Figs.S4,S5), movement to microsites suitable for germination (e.g., treefall gaps; Fig.S6), and colonization of new areas (e.g., degraded habitats; Fig.S7). Without vertebrate frugivores, these processes are disrupted. We propose a series of projects to determine which tree species are at greatest risk from the loss of dispersers, and to understand how forest structure and regeneration are affected by vertebrate loss. The EBL project has collected dramatic preliminary data quantifying impacts on several of these processes on a subset of tree species (e.g., Fig.S3-5). With targeted studies using our established protocols across a broad set of species on more islands, we can fully characterize the ecological impacts of disperser loss across tree species.

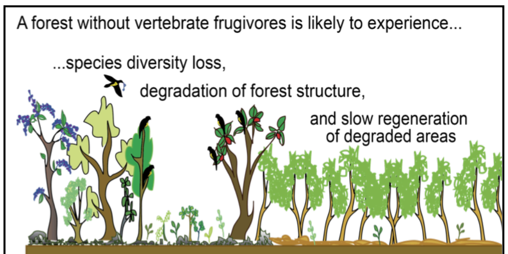


Fig. 2: The impact of vertebrate frugivores on ecological function.

Individual tree species may experience population declines as a result of disperser loss, but the strength of disperser loss impacts vary by species (Markl et al. 2012). A key goal of this proposal is to predict the severity of population declines that result from disperser loss across species. In previous research, we used a series of field experiments to show that five vertebrate-dispersed forest tree species were negatively – but differentially – affected by the loss of seed dispersers (Figs.S5,S7). Yet there are many more reasonably common bird-dispersed species in the community (Fig.S8); our preliminary work indicates effects vary across species, and different species are impacted at different life history stages through different processes. To attain a broad understanding of disperser loss across Guam's forest species, we must examine the effect of vertebrate frugivores on germination and survival of a larger set of species (Fig.S8), by considering both spatial impacts (near vs far from parent trees) and non-spatial impacts (seed scarification).

Disperser loss may also impact forest structure. If dispersers are critical in moving pioneer seeds into gaps, where they can germinate and initiate gap colonization, then the lack of dispersers should impede succession in gaps, slowing gap closure rates. Our observational data support this hypothesis, as Guam has more than twice as many gaps as nearby islands with birds (Fig.S6). A concurrent grant to PI Rogers from the National Science Foundation explores this hypothesis (see Supplemental Material for a description), the results of which will complement the proposed work.

Finally, disperser loss may deal a huge blow to restoration. Due to forest clearing during WWII and since, large portions of forest on the Mariana Islands exist in a degraded state, dominated by the non-native leguminous tree, *Leucaena leucocephala*. We hypothesize that native forest trees on islands with intact dispersal communities will naturally recolonize these degraded forests, gradually restoring native biodiversity and ecosystem function. Our previous research has shown that on the island of Saipan, which has a healthy frugivore community, a significant number of seeds from intact forests are dispersed into degraded forest, whereas seed rain in degraded forests on Guam comes completely from trees found within the degraded forest (Fig.S6; Caves et al. unpub). While mixed *Leucaena*-native forests are common on Saipan, they are rare on Guam. A lack of dispersers on Guam is likely slowing forest regeneration dramatically, but we know little about the relative importance of different parts of the frugivore community (addressed in Obj. 2.1). Rota has the largest fruit bat population in the Southern Marianas, but it also has much lower abundances of some bird species (e.g., Bridled White-eye, *Zosterops conspicillatus*). We will examine how this large-scale shift in the disperser community affects seed rain and regeneration of degraded forests, and compare that to rates of regeneration on Saipan and Guam.

Critical from a management perspective, we will bring all of these pieces together to predict the impact of disperser loss on species diversity, forest structure, and regeneration of degraded forest on Anderson Air Force Base (AAFB). We will focus on the impact of vertebrate loss on key aspects of critical habitat for endangered species- will the forests be able to support these endangered species in 50 years?

Objective 2: Determine the ecological role of frugivorous species, including native species (both extant and extirpated), existing non-native species, and potential taxon substitutes that may be used to restore ecological function.

Once the impact of disperser loss is quantified, both on an individual and community scale, we can begin to determine the potential of different dispersers (extant or extirpated, native or non-native) to restore function to species and communities. The most effective way to fully restore ecological function to a novel ecosystem might be to reintroduce all missing native species (Garcia and Martinez 2012); however, that is often not feasible (Seastedt et al. 2008). Additional options include facilitating the spread of existing native and non-native species that perform key ecological functions or introducing taxon substitutes (i.e., non-native analogues of extirpated species) that might be better adapted to the novel ecosystem. A thorough understanding of the ecological role of each candidate species is needed to prioritize management efforts. There is relatively little known about the ecological role of each native and non-native seed disperser in the Mariana Islands, so targeted research is important to determine which species can perform the necessary functions.

Native species: Five of the six known native bird and bat frugivore species (White-throated Ground-Dove

(*Gallicolumba xanthonura*), Mariana Fruit-Dove (*Ptilinopus roseicapilla*), Bridled White-eye, Micronesian Starling (*Aplonis opaca)*, and Mariana Fruit Bat (*Pteropus mariannus*) have potential for being used to restore ecological function to Guam (Table S1). We have omitted the sixth species, the Mariana Crow (*Corvus kubaryi*), as a candidate because it is highly endangered in its entire range and unlikely to be used in restoration. Despite being formally listed as threatened, we have included the Mariana Fruit Bat in our study. The primary threat to its population outside of Guam is hunting, and thus the population could potentially recover and persist on Guam, given lower hunting pressure. The effectiveness of each frugivore species for restoring ecosystem function is unknown, including how they treat seeds they disperse (e.g., does handling by these animals enhance seed germination – Obj. 1.1), the distances they disperse seeds, and where they disperse seeds (e.g., which species are helping restore degraded forest). This project will provide valuable data on the ecological roles of these native species.

Non-native species already present in a novel ecosystem may perform valuable ecological functions, although results are mixed. Some studies have found non-native birds to have similar diets to native species or to be effective dispersers (Kawakami et al. 2009, Burns 2012), however, other research has found non-native birds largely ineffective (Chimera and Drake 2010, Spotswood et al. 2012). Although invasive mammals are usually known for their negative effects in island ecosystems, they may also provide benefits. In New Zealand, non-native birds and rats are now key pollinators for three forest plant species (Pattemore and Wilcove 2012). Rats may be both seed predators and dispersers in Hawaii (Shiels and Drake 2011), and pigs are known to disperse seeds (Nogueira-Filho et al. 2009, O'Connor and Kelly 2012, Barrios-Garcia and Ballari 2012).

Several non-native species known to consume fruit are present on Guam and could potentially play an important role in restoring lost seed dispersal services (Schlaepfer et al. 2011). The only non-native avian frugivore on Guam is the Island Collared-Dove (*Streptopelia bitorquata*), which has been present since the late 1700's, although their population is currently reduced and uncommon in the forests due to BTS predation (Conry 1988, Wiles et al. 2003). As is true for the native frugivores, no quantitative studies have been conducted on the location and condition of seeds dispersed by collared-doves in the Mariana Islands. The Asian House Rat (*Rattus diardii;* precise taxonomic status and common name is debated) is present on all islands in the Southern Marianas, but in much lower densities on Guam due to BTS (Wiewel et al. 2009). It is unknown whether rats act as dispersers in the Mariana Islands; if they do, a low rodent population may have benefits that outweigh well-known costs. The feral pig (*Sus scrofa*) has been present on Guam since the late 1700's (Conry 1988), and preliminary research suggests pigs disperse seeds of at least two native tree species in the forests on Guam (Gawel 2012). If they are dispersing large numbers of seeds, they may currently be the most effective vertebrate seed disperser on Guam.

We acknowledge that invasive birds (Yap and Sodhi 2004), rats (Towns et al. 2006, Jones et al. 2008), and pigs (Nogueira-Filho et al. 2009, Barrios-Garcia and Ballari 2012) can have severe negative impacts on islands, particularly when they are at high densities, as pigs are on Guam. One of the planned restoration activities on AAFB is an ungulate fence, which is *necessary* for reducing the destruction caused by extraordinarily high densities of pigs. However, it is possible that low-densities of pigs, rats, or non-native birds could provide valuable seed dispersal services, and thus a functioning ecosystem on Guam may have a role for select non-native species. We explore the negative impacts of these species in Obj. 3, because they must be balanced against the positive (Schlaepfer et al. 2011, Davis et al. 2011).

Taxon substitution is a new and controversial tool in conservation (Griffiths and Harris 2010); intentional introduction of non-native species to replace extinct species may be able to prevent secondary extinctions. The poster child for this method is the reintroduction of a giant tortoise to the Mascarene Islands; the tortoise successfully restored dispersal services and increased seedling recruitment for a canopy tree species (Griffiths et al. 2011). Guam is a prime location to consider for taxon substitution, given that nearly all native forest birds have been extirpated from the island and cannot be reintroduced without extensive snake control. However, the taxon substitute must be able to provide the desired ecological functions and withstand high snake predation pressure to be a viable possibility for introduction. Here we explore the potential ecological role a taxon substitute could fill. We acknowledge the dangers of intentional introductions and address them in Obj. 3.3.

Objective 3. Identify the limitations associated with using native, existing non-native species, or taxon substitutes to restore ecological function.

Once the potential role of individual species has been determined, we can begin to address the challenges in using native, nonnative, or taxon substitutes to restore ecological function to Guam's forests.

Reintroduction of native birds currently extirpated from Guam will need to occur in either snake-free or snake-reduced areas (such as areas protected by barrier fencing). Understanding factors that could influence bird use of these areas will be critical to success; for instance, we need to know if these areas will provide adequate food and habitat, and if foraging behavior will take birds regularly outside the protected area. Movement outside is desirable for extended ecosystem services, as long as birds return to protected locations for night roosting (when BTS are foraging and apt to predate a bird). The technical limitations associated with the translocation and reintroduction process are outside the scope of this grant, but our research in Obj. 2 will contribute to a better understanding of diet and habitat utilization by these species, two factors that could limit their use of protected areas on Guam.

Existing avian frugivores on Guam show promise for being part of the solution, but their survival strategies have not been studied. Micronesian Starlings are the only native frugivore still on Guam and are largely confined to AAFB (about 200 birds; D. Vice, personal communication). Presumably this species remains because of its ability to utilize urban and suburban environments and its capacity to persist in areas under snake control. However, little is known about the Guam population (and Micronesian Starlings in general), including nest success, nest and roost locations, or what snake densities have allowed them to survive. Largely a cavity nester, their population could potentially be expanded using protected nest structures. Non-native Island Collared-Doves are rarely found in forested areas on Guam but could be capable of dispersing many forest tree species. By understanding the factors limiting the range of both of these species on Guam, we might be able to develop strategies to expand their populations, and thus the ecological functions they provide. By comparing the diets and movements of these species on Saipan and Guam, we can gain valuable information on the functions these species are currently performing on Guam and how their diet and capacity to disperse seeds may have changed due to the lack of competitors and/or high snake predation pressure.

The use of **non-native species or taxon substitutes** for 'restoration' is controversial; therefore a thorough examination of the negative effects of each species is necessary to weigh against the benefits it might provide. We are exploring the possibility of using pigs, rats, Island Collared-Doves, and taxon substitutes for restoring seed dispersal to the forests of Guam. The negative effects of pigs are due primarily to direct consumption of native species, physical disturbance, and dispersal of invasive species (Drake and Pratt 2001, Nogueira-Filho et al. 2009), however most studies have been done in locations with extremely high pig densities where their effects are magnified, and research from the Mariana Islands is limited. Invasive rats are known seed and egg predators in other locations (Towns et al. 2006), yet their impact on seeds in the Marianas depends on species (Mattos et al. unpub), and their density on Guam is already much lower than on Saipan, Tinian and Rota due to BTS predation (Wiewel et al. 2009). How would a low density of rats affect trees and birds? Introducing a taxon substitute might affect the success of future native species reintroduction efforts or have unintended side effects (Chimera and Drake 2010). To date, taxon substitutes have used a closely related species to replace an extinct species, in which case there are likely few negative effects; however the situation on Guam is more complicated. We will thoroughly examine the potential negative impacts associated with utilizing each of these species so that we can assess the full costs and compare them to the expected benefits.

Objective 4: Synthesize data on the lost functions (Obj. 1), ecological roles (Obj. 2) and limitations (Obj. 3) of each frugivore species to determine the feasible options for restoration of ecological function.

Once we understand which ecological functions are missing on Guam (Obj. 1), and we understand which species can provide those functions (Obj. 2), and what limitations are associated with each species and strategy (Obj. 3), we can develop strategies for restoring ecological function to Guam's forests. We will need to balance the positive benefits provided by each species with the likelihood for successful reintroduction to Guam (for native species and taxon substitutes) and the possible negative side effects (for non-native species). We divide this project into two steps.

The first step is to identify which combinations of frugivores would provide the desired ecological functions. We will take a network analysis approach to this problem, by testing for complementarity and redundancy in dispersal services (as in Mello et al. 2011). The next step would be to develop a spatially-explicit restoration plan for the bases and for the entire island; since the likelihood of eradicating BTS island-wide is low, our working model would be based on the strategy that has been promoted by the DoD and the USFWS – the creation of areas with low snake density or even snake-free areas, to which frugivores susceptible to snakes could be reintroduced. Currently, there are three snake-proof fences (two on DoD land) and two areas where large-scale snake population reduction has occurred. These areas are primarily proof-of-concept areas or designed for research, rather than for restoration. There has been no spatial modeling done (of which we are aware) to show whether and how a network of snake-free zones might be used for conservation purposes, nor any consideration of connectivity between these zones.

If the goal of creating areas with reduced snake density is to restore ecological function to the surrounding forest, then the areas serviced will depend heavily upon the species used. Terrestrial frugivores will be unable to move outside of fenced areas. Volant frugivores have varied home range sizes and foraging behavior that may or may not keep them within the protected area. We propose to use data we obtain from our studies along with principles of reserve design to develop an optimal network of snake-free zones (or zones of reduced snake density), and resulting areas of seed dispersal outside of the fences, given possible combinations of frugivores.

Finally, all data and results from this research will be compiled into a final synthetic report with a "User's Guide" for use by end-users such as AAFB and Naval Base Guam.

C.2: METHODS

Study area: The proposed research will be conducted in karst limestone forest - the primary forest type used by native forest birds and bats- and in degraded forest dominated by the non-native tree, *Leucaena leucocephala*. Research sites will be on AAFB and in similar forest surrounding the base on Guam, as well as on the nearby islands of Saipan and Rota; both islands have similar forest to Guam. On all three islands, the EBL project has established permanent forest plots (3 each on Rota and Saipan, 5 on Guam) that will be used for much of this research. We will focus on the 21 most common fleshy-fruited tree species, which comprises about 85% of an average forest. Most of these species fruit from April-August, although some fruit outside that time period. Since multiple sections of our proposal require data on the fruiting status of each tree species, and this can vary slightly between islands and by year, we will monitor phenology of marked trees within permanent forest plots throughout the first 3.5 years of the project.

Objective 1: Determine how the invasive brown treesnake has impacted ecological function in Guam's forests and identify the consequences for long-term forest health.

We outline three approaches to understand the impact of disperser loss on Guam's forests. The first assesses how fruit consumption and movement away from parent trees increases survival of seeds and seedlings. The second addresses impacts on degraded forest regeneration. The last models impacts of different disperser loss scenarios on forest composition and diversity over space and time. A concurrent National Science Foundation grant will focus on the impact of vertebrate disperser loss on treefall gap dynamics and forest structure, the results of which will inform this objective. See the description of this grant in the supplemental materials for more details.

1.1: Impact of disperser loss on individual forest tree species

1.1a) Effect of vertebrates on seed germination: For each of our 21 focal tree species, we will conduct germination experiments to determine how ingestion by birds and fruit bats affects germination rates (as in Bartuszevige and Gorchov 2006, Linnebjerg et al. 2007). We will capture 5-15 of each native bird focal species from the wild, and we will use 4 captive fruit bats at the Guam National Wildlife Refuge. We will hold animals in appropriately-sized wire cages with a solid bottom covered by plastic, so we can collect droppings. Only water (no food) will be offered during an initial acclimation period (1-4 hours, depending on species). We will collect ripe fruits from at least 10 fruiting trees and randomly divide them into these categories: whole fruit, fruit from which seeds will be mechanically separated from pulp, and fruits to be fed to each frugivore species. We will then feed 10 fruits to each animal, and collect the fecal matter over the next 8 hours, recording gut passage time (for use in Obj. 2.1b). We will maintain animals on an appropriate diet (no seeds) between trials (see Holbrook and Smith 2000, and Tewksbury et al. 2008 for general methods). Once the fecal samples are obtained from all birds for an individual species, we will place seeds in moistened Petri dishes (as in (Spiegel and Nathan 2007)), and compare germination across treatments (whole fruit, seeds mechanically removed from fruits, and seeds passed though the guts of dispersers). We will analyze results using a generalized linear mixed effects model (binomial error structure), to obtain the predicted impact of each species on germination rates

1.1b) Seed and seedling addition experiments: We will use seed and seedling addition experiments near and far from con-specific trees to determine if dispersal away from the parent tree increases germination and growth, as is predicted when trees experience strong density- or distance-dependent mortality (Swamy and Terborgh 2010, Metz et al. 2010, Terborgh 2012). These experiments will be done on Saipan only, as earlier experiments on 5 species (indicated in Fig.S8) showed no difference in results between islands, and Saipan does not require extensive fencing to exclude invasive ungulates, as do Rota and Guam. We will gather ripe seeds from trees for all focal species to be used for both seed and seedling additions. Seedlings will be grown for two months in a nursery before being added. We will select four locations under the canopies of conspecific trees and four locations more than 7 meters away from the canopy of conspecific trees at each of three forest sites. At each location, we will establish three plots – one for seed additions, one for seedling plantings, and one control (no seeds or seedlings added). In the seed addition plot, we will add between 20 and 100 seeds (depending on seed size), and in the seedling addition plot, we will plant 10 seedlings. The other plot will serve as a control to estimate natural seedling emergence and survival rates. We will monitor plots for seed germination and seedling survival weekly for the first 4 months, then every two months for the next 2 years. For each species, we will use a generalized linear mixed-effect model with a binomial distribution to assess whether dispersal enhances germination or survival, with distance as the main effect and site as a random effect.

1.2: Impact of disperser loss on forest regeneration in degraded habitat

1.2a) Surveys in degraded forest: To determine whether limited seed rain into degraded forests leads to long-term differences in regeneration, and thus whether successional processes differ in the presence of native dispersers, we will compare regeneration on Guam to that on Rota and Saipan. We will use historical satellite imagery and aerial photographs from the Marianas to identify plots of land cleared in the 1970's, 1980's, 1990's and 2000's on Guam, Saipan, and Rota (a partial list of available imagery is in Kottermair 2012). We will select at least 6 areas per island per time point (x 4 time points = 24 clearings/island), with areas separated by >300 meters. To confirm the land use history of the area, we will visit each cleared area and talk with local landowners. At each site, we will survey adult and juvenile trees using modified Whittaker plots (Stohlgren et al. 1995). We will randomly select a 20m x 50m ($1000m^2$) plot of formerly cleared forest with one edge abutting undisturbed forest and establish nested subplots of three sizes ($1m^2$, $10m^2$, and $100m^2$). We will survey seedlings, saplings and adults in small, medium, and large subplots, respectively. To determine whether bird or bat abundance affects the regeneration of native forest, we will use a generalized linear mixed effects model with proportion native trees as the response and island as the predictor, with length of time since clearing and intact forest diversity as covariates, and site as a random effect.

1.3: Cumulative impact of disperser loss on forest diversity, structure and regeneration

Over the last 20 years, there have been large advances in modeling tropical forest dynamics due to the advent of individual-based, spatially-explicit stochastic cellular automata models like SORTIE (Pacala et al. 1996), DivGame (Alonso and Sole 2000), TROLL (Chave 1999), and FORMIND (Köhler and Huth 1998). These models are based on grids, can be parameterized using field-collected data, and allow users to explicitly incorporate ecological processes into the modeling framework. Simulations using these forest models have explored the impact of fragmentation on diversity and forest structure (Köhler et al. 2003, Huth et al. 2005, Pütz et al. 2011), but they have not explored the impact of disperser loss, although it is well within the capabilities of the models.

We have chosen the FORMIND model to model the impacts of disperser loss on Guam's forests. The model is a three-dimensional tree growth model that includes recruitment, disturbance, and seed dispersal processes. Details about the application of this model are described well in the appendix of Groeneveld et al. (2009). The model will allow us to integrate species-specific germination and survival data collected in Obj. 1.1 with species-specific seed dispersal kernels parameterized from previously collected seed rain data, to predict the demographic impact of seed disperser loss on all 21 focal tree species. In addition, we will extend the model to estimate biomass (as in Groeneveld et al. 2009) and forest structure (number of gaps on the landscape) at 20, 50 and 100 years in the future. The model will be parameterized with data from forest plots on AAFB, allowing us to evaluate the future impact of *not* restoring seed dispersal on AAFB on the quality of critical habitat for endangered species (e.g., Mariana Fruit Bat, Mariana Crow, Micronesian Kingfisher).

Objective 2. Determine the ecological roles of frugivorous species, including native species (both extant and extirpated), existing non-native species, and potential taxon substitutes that may be used to restore ecological function.

Prioritization of management actions for restoring dispersal services must be based on knowledge of the dispersal ecology of individual frugivore species. The ideal frugivore would effectively disperse seeds from many species of trees (i.e., consume large quantities of seeds of all sizes, increase germination through handling, move seeds away from the parent if necessary), move seeds of pioneer species to gaps, and frequently travel to/across degraded forest areas. However, this suite of dispersal services can likely only be achieved with multiple, complementary dispersers. We propose a series of studies to examine the diet and movement of native and non-native species that exist or have existed on Guam, along with research to develop a list of appropriate taxon substitutes.

2.1: Ecological roles of native birds and bats

2.1a: Foraging observations and fecal analyses to link frugivores to tree species: We will use foraging observations and fecal analyses on Saipan and Rota to determine which tree species are dispersed by which frugivore and, with germination trials (Obj. 1.1), determine the relative importance of each frugivore species to tree species. Foraging observations will allow us to record which tree species birds and bats are visiting, get removal rate by species, and observe fruit handling. Fecal analyses will tell us the relative importance of various trees for the different bird species, about foraging strategies, and allow us to detect seeds for tree species not included in our foraging observations. Both will be done during the primary fruiting season and the off-season to ensure we fully characterize the seed dispersal network.

For our foraging observations of bird species, we will quantify rates of frugivory by each bird species on our focal tree species on Saipan. We will also include tree species that are less common but often found in the fecal analyses. We will use video observations of fruiting branches of 20 individual trees per species to quantify the portion of fruits that each bird species removes per time period. Because rates of frugivory may relate to fruit availability, we will include fruit abundance from phenology monitoring in our analysis. We will supplement video observations with human observations to characterize the manner of fruit handling by each species (how each bird species handles seeds of each tree species to assess if they are an effective disperser or simply consume pulp without moving seeds away from the parent).

For fecal analyses of birds, we will employ mist nets to capture birds and obtain fecal droppings. Net position will be adjusted to capture birds utilizing various forest strata. We anticipate operating 10-12 nets and capturing a minimum of 20-30 birds of each species within each season and year. We may need to adjust number of nets and frequency of deployment to reach these numbers. Captured birds will be held in plastic boxes for 5-10 minutes to obtain fecal samples (Blake and Loiselle 1992). Samples will be preserved in alcohol and seeds later identified using a reference collection. Seeds will be quantified by tree species, seeds per sample, and seed size. For fecal analysis of bats, bat feces will be collected non-invasively under trees used by bats while foraging. We will dissect fecal samples to identify the species of seeds and other plant parts found in the feces. From the fecal sample observations, we will develop a comprehensive list of fruiting tree species used by bats on Rota.

Using the data collected above, we will create a seed dispersal interaction network where links between birds, bats, and trees (Fig.S8) are weighted by rates of frugivory and impact of frugivory on germination and survival. Our analysis will identify which frugivores are most important for maintaining dispersal services across the tree community, and will allow us to assess how sets of dispersers can restore dispersal services on Guam. Tree species with fewer links are at greater risk than are species dispersed by multiple frugivores, and frugivores with many links or unique links may be more important; information regarding the dependence of trees on particular frugivores is crucial for comparing restoration options.

2.1b: Telemetry to determine movement patterns: Using telemetry, we will determine movement patterns for each of the native bird species and the Mariana Fruit Bat to predict the area over which an individual could potentially provide dispersal services, and whether species move seeds to degraded forest. We will also estimate home range using these same methods (to be used in Obj. 4). A subset of birds caught by our mist nets used for diet studies (above) will be fitted with transmitters. Bats will be captured in mist nets while flying to fruiting trees, to avoid disturbing colonies, and fitted with a GPS satellite transmitter. Tracking will be done during the main fruiting season over 2-3 years as well as during one off-season to see how dispersal services provided by each species may change seasonally. We will aim to track a minimum of 20 birds of each of the four species on Saipan and 15 bats on Rota. Transmitters for the birds can be expected to last from 1-2 weeks (white-eyes) to several months for the larger bird species. Using handheld Yagi antennas and receivers, we will use triangulation of simultaneous bearings from tracking stations to determine bird locations. For potential dispersal distances, we will take bearings every 15 minutes during a tracking session. We will continuously track a subset of individual birds to determine actual time spent in degraded forest. Tracking sessions will generally last 2-4 hours and will include both morning and afternoon sessions. We will aim for 30-50 locations for estimating kernel home range for each species (White and Garrott 1990, Millspaugh and Marzluff 2001). Bird location will be estimated using the program LOAS (Ecological Software Solutions), and locations will then be imported into ArcMap (ArcINfo, ESRI) to measure distances. The bat transmitters will be programmed to record locations every 10 minutes, and the movement data will be downloaded daily while the bats are roosting. Home ranges will be estimated in the Animal Movement Extension (Hooge and Eichenlaub 2000) in ArcView GIS (ESRI Inc); both the 95% kernel (the area in which the animal occurs 95% of the time; Worton 1989) and 50% kernel will be calculated along with habitat composition of these kernels. Displacements over time from a starting point (which represents a potential fruiting tree) will be combined with gut passage times found with the captive birds and bats (Obj. 1) to estimate median dispersal distances for seeds by each species (Weir and Corlett 2007). Using methods similar to those outlined in Murray (1988) and Holbrook and Smith (2000), the probability of seed deposition in forest and degraded forest will be calculated for animals whose home ranges overlap both habitat types.

2.2: What is the ecological role of select non-native fruit-eating species currently present on Guam?

As with native frugivores (Obj. 2.1), we will use a combination of feeding trials with germination experiments, fecal analyses, and/or movement data to investigate whether non-native Island Collared-Doves, feral pigs, and Asian house rats are effective seed dispersers.

2.2a: Island Collared-Dove – We will determine the effect of seed ingestion on germination using feeding trials with captive animals on Saipan following methods and analyses outlined in Obj. 1.1. We will use similar methods as described in Obj. 2.1 (fruiting tree observations, fecal analyses, telemetry) to link collared-doves to tree species and understand movement patterns.

2.2b: Feral Pigs- We will determine the effect of ingestion on germination using feeding trials with captive animals (as in O'Connor and Kelly 2012). For this experiment, we will utilize four pigs that were born in the wild, but have been kept in captivity since they were juveniles. At each session, 100 ripe fruits of a single species will be fed to each pig. We will record if pigs avoid, ingest, or handle and spit out the seeds. All seeds that were handled and spit out will be collected for germination trials. Pig feces will then be collected for the next 3 consecutive days and sifted to recover seeds; gut passage time will be recorded. Any recovered seeds will be planted alongside the un-ingested but handled fruits, with whole fruits and manually de-pulped fruits serving as controls. This process will be repeated for each of the focal tree species. Results will be analyzed as in previous germination experiments (Obj. 1.1).

To determine which fruits are commonly consumed and pass through the gut in the wild, we will collect pig scat from limestone forest and allow seeds from feces to germinate in a nursery (Gawel 2012). We will collect fresh scats from existing permanent forest plots on Guam and spread each scat over potting soil. Planted scats will be watered and monitored for 3 months; all seedlings that germinate from scats will be identified and removed to avoid recounting. We will collect scats 4 times throughout the year to ensure we capture the fruiting season of all focal tree species.

To determine whether pigs disperse seeds from intact to degraded forest, and to estimate the area a single pig may service as a disperser, we will track pigs using GPS collars. We will use baited cage traps to capture 20 feral pigs, each separated by at least 500 meters. Each pig will be anesthetized, tagged, measured, weighed, photographed, and collared before being released. We will estimate home ranges from GPS location data as in Obj. 2.1.

2.2c: Asian house rats- To determine the effect of seed consumption by rats on germination, we will conduct feeding trials with captive animals following methods used by Shiels and Drake (2011). We will capture 20 adult Asian house rats from limestone karst forest on Saipan, where rats are far more abundant than on Guam due to predation by BTS. We will house rats in metal mesh cages and allow them to acclimate on a standard diet for at least 1 week before trials begin. For each trial, we will place fruits of a single species in each cage and leave them there for 24-48 hours. After 24 hours, we will examine the fruit offered to each rat and record whether the fruit was left untouched, some flesh was consumed, or the entire fruit was ingested. For fruits that were not ingested, we will estimate the proportion of the fruit consumed. For all fruits, we will measure the remaining fruit mass and seed mass. Ingested and non-ingested will be placed in a moistened Petri dish, alongside seeds from fresh fruit and seeds with the flesh removed by hand, and allowed to germinate. The germination rate of seeds consumed by rats will be compared to those still in fleshy fruit and those with their fleshy fruit manually removed as in Obj. 1.1.

2.3: What are the potential ecological roles that could be filled by candidate taxon substitutes?

A taxon substitute must fill an ecological role of a now-extirpated species. We will compile a list of key morphological (e.g., gape width), behavioral (e.g., habitat use, home range), physiological (climatic niche), and diet characteristics a taxon substitute must possess, based on existing and field collected data from frugivores on Saipan and Rota (Obj. 2.1) to perform the ecological functions currently missing on Guam. We will utilize existing databases of frugivorous vertebrates and discussions with experts in the field to develop a comprehensive list of species that fit our criteria. Once we have this comprehensive list, we will perform a literature review to narrow the list. We will again contact experts who have studied the species or closely related species to determine whether each would likely provide the desired ecological function. The next step of the research is evaluating the potential negative impacts of each species, described in Obj. 3.2.

Objective 3. Identify the limitations associated with using native, existing non-native species, or taxon substitutes to restore ecological function.

With knowledge of the potential role of various frugivores, we can begin to address conditions necessary for their success along with challenges in using these species. Here we present methods for investigating challenges related to the reintroduction of native species, expanding the range of existing species on Guam, and use of non-natives.

3.1: What challenges might be faced when attempting to re-establish avian frugivores or expand the range of existing frugivores on Guam?

3.1a: Diet and habitat requirements of native birds: Our diet and telemetry research in Obj. 2.1 will contribute to a better understanding of habitat utilization and requirements by native bird species. While monitoring movements of native birds on Saipan, we will also obtain data on night roost utilization, which could inform the likelihood of individuals returning to the confines of protected areas. Characterization of roost sites will include nightly location, substrate, and when applicable, various characteristics of the nesting tree and canopy cover. To see if birds employ different roosting strategies when fruit is less abundant (e.g., individuals are less likely to return to the same or nearby roost location because of greater movements in search of food), we will assess if roosting strategies change between the peak fruiting season versus when fruit is less available.

3.1b: Differences in ecology between Guam and Saipan: The two avian species that remain on Guam, native Micronesian Starlings and nonnative Island Collared-Doves, have shown their ability to withstand some level of BTS presence, but information is needed on what ecological function they are able to provide on Guam and on their survival strategies if their ranges are to be expanded. Thus, we will study what fruits these species are consuming and what habitat they utilize on Guam. We will employ mist nets to obtain fecal samples for diet analyses and radio telemetry for home range and movements, as described for our work on Saipan (Obj. 2.1). Our study sites will be primarily AAFB for starlings, along with nearby habitat for collared-doves. Mist nets will be placed to maximize starling capture, which will be along the ecotone between AAFB housing and adjacent forest and along forest edge for collared-doves. We will also record characteristics of roost sites used by these species on Guam but will include distance to forest (if roost locations are on urban structures), and an estimate of BTS abundance, which will be based on known trapping efforts or data from island-wide visual surveys (S. Siers, unpublished data).

3.1c: Keys for starling and dove nesting success on Guam: To evaluate the possibility of expanding starling and dove populations on Guam, we must know where these species are nesting and how nesting success relates to BTS abundance. Because of reduced populations of these species, finding active nests will be challenging, but we will attempt to locate and monitor at least 20-30 nests of each species, many of which we expect to find on AAFB. Nests will be checked every 2-4 days until they fail or fledge young and the number of successful fledglings recorded. We expect to find nests associated with human structures as well as in trees, and will characterize nest site attributes and general BTS abundance similar to that done for roost sites discussed above. The nest survival model in Program MARK (White and Burnham 1999) will be used to estimate daily survival probabilities, which will be modeled as a function of the various covariates (including year and season). We predict successful nests to be on urban structures or in trees isolated from contiguous forest, further from forest, and in areas with reduced BTS densities.

3.1d: Enhancing starling populations using nest boxes: For possible use in facilitating range expansion, we will test whether Micronesian Starlings will utilize predator-proofed nest boxes. Initially we will employ 25-30 artificial nest boxes in various locations on AAFB to see if starlings will utilize these structures (nest box specifications for other starling species are readily available). If birds accept and nest in these structures, we will monitor nesting success as done for other nests. Additionally, we will begin testing various designs (e.g., use of a conical metal shield below the nest box) under a controlled laboratory setting to see if BTS can be excluded from the prototypes. Once an acceptable design is obtained, we will retrofit existing boxes (if possible) and deploy an additional 25 boxes in the field at AAFB. We will work with resource managers on AAFB to develop a nest-monitoring program for these structures.

3.2: What are the dangers of using non-native species to restore ecological function?

We propose to explore the use of pigs, rats, Island Collared-Doves, and taxon substitutes for restoring seed dispersal to the forests of Guam, however we recognize that some of these species have caused major problems on Guam and elsewhere.

3.2a: Negative impacts of pigs and rats: We will conduct an exhaustive literature survey and conduct interviews with pig and rodent experts in the Marianas, Hawaii, and other tropical island systems to assess the negative impacts associated with pigs and rodents. If there are adequate data on the effects of pigs and rats associated with estimates of their densities, we will perform a meta-analysis to develop a relationship between density and impact. Among the most harmful impacts are bird and egg predation (rats), physical disturbance (pigs), and seed predation (primarily rats). To test how varying densities of rodents may affect tree species through seed predation, we will conduct a seed removal experiment for all of the focal species predated by rats during feeding trials in Obj. 2.2. We will set out trays of seeds in areas of varying rodent density on Guam and Saipan and record removal rates (Shiels and Drake 2011, Wiewel et al. 2009, Mattos et al. unpub). Finally, we will produce a report detailing the tradeoffs associated with using pigs and rats as part of the solution.

3.2b: Risk assessment for taxon substitutes: An appropriate taxon substitute must have a range of characteristics to be seriously considered as a restoration option. They must provide the desired service, persist with some level of snake predation, not impact native bird species currently present on the island or potentially reintroduced to the island, and not spread to other islands and affect species or processes there. The negative effects of taxon substitutes are more difficult to estimate than those of known non-native species, because it is less likely there are studies documenting their negative effects. However, for every species that reaches the short list (Obj. 2.3), we will explore the potential side effects of introduction. We will develop a risk assessment process similar to that used for Weed Risk Assessment around the world (Pheloung et al. 1999, Gordon et al. 2008). This will score each species based on a suite of characteristics associated with risk for causing ecological or economic harm (Kolar and Lodge 2001, Sol et al. 2002). We will develop this list of characteristics using information on the impact of intentional introductions of birds around the world, as well as input from all interested parties in the Mariana Islands and expert opinion from tropical ornithologists. Any species with a particularly high risk of causing ecologic or economic harm will be dropped from the list.

Objective 4: Synthesize data on the lost functions (Obj. 1), ecological roles (Obj. 2) and limitations (Obj. 3) of each frugivore species to determine the feasible options for restoration of ecological function.

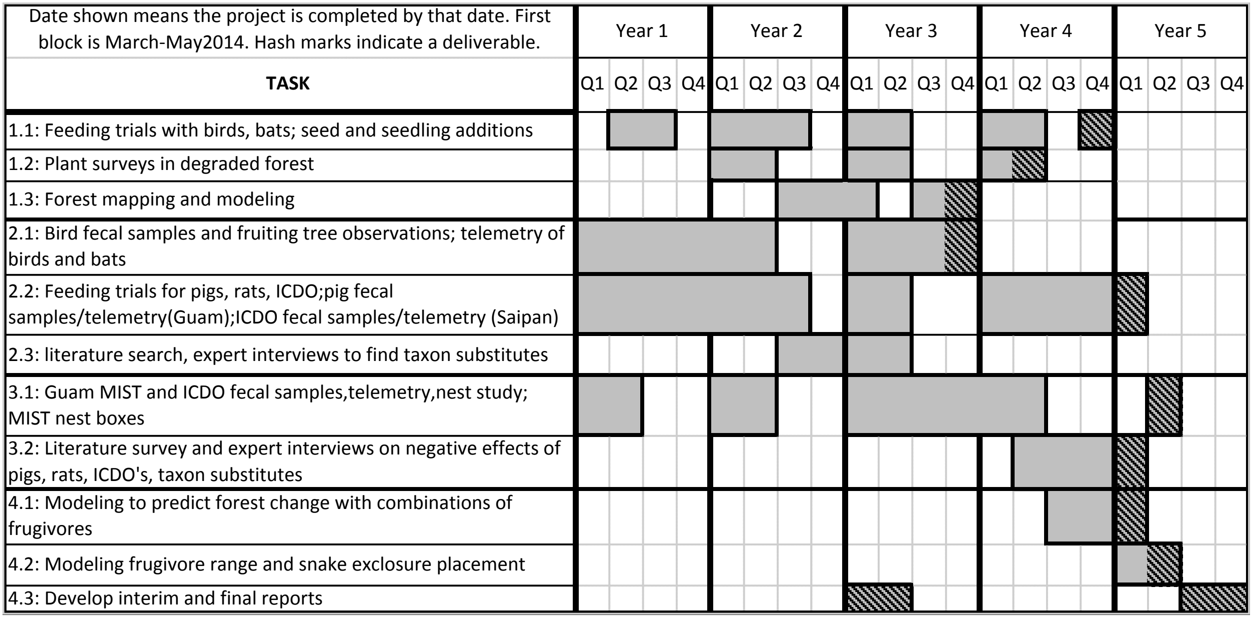
4.1: Development of candidate frugivores assemblages: Using a network approach that links frugivores to the tree species they disperse (as in Mello et al. 2011), with links weighted by the effectiveness of each disperser-tree combination (based on Schupp et al. 2010 Seed Dispersal Effectiveness framework), we will develop a portfolio of options for frugivore assemblages. We will first omit any species where the negative impacts clearly outweigh the positive effects. Next we will use network theory to determine which combinations of frugivores maximize dispersal of the majority of tree species (Mello et al. 2011). It is unlikely that any single frugivore can provide all seed dispersal services, however, it is improbable that we would utilize all frugivores (native and non-native); we aim to provide several options along with a description of the benefits and potential drawbacks associated with each option.

4.2: Optimal snake fence placement: After developing our frugivore assemblages, we will use a decision support tool for conservation planning such as Zonation (Moilanen et al. 2005) to identify the ideal placement of snake reduction areas (fences or toxicant/trapping areas), if such areas are needed for the given assemblage of frugivores. We will use a recent land-use/land-cover map, frugivores-specific seed dispersal kernels based on gut passage time, movement, and home range of dispersers, and frugivore habitat requirements as model inputs, and optimize locations and sizes of snake exclosures, given the cost of creating and maintaining these areas.

4.3: Final report: We will deliver a final report summarizing our results from Obj. 1-3; this report will include a "User's Guide" of management options for restoring ecological function to Guam's forests.

C.3: MILESTONES

Time frames for completing significant events and tasks are outlined in the Gantt chart below. Completion of research components is indicated by hash marks; these demonstrate when we expect to finish analyses and prepare reports on them, suitable for submission to peer-reviewed journals.



D. RESEARCH TEAM

Haldre Rogers (co-PI) is currently a Huxley Faculty Fellow in the Ecology and Evolutionary Biology Department at Rice University. Her research focuses on the ecological importance of vertebrates in forested and agricultural systems, as well as the consequences of losing vertebrate species from these systems. She has used a combination of experimental and comparative studies to assess the effects of bird loss caused by the BTS on pollination, seed dispersal, and pest control/food web dynamics, and has ongoing research on the effects of rodents and ungulates (pigs/deer) on seed and seedling survival in the system. Dr. Rogers will take primary responsibility for overseeing the field research associated with plants, bats, pigs and rodents, and will work with Dr. Savidge to write all reports. Dr. Rogers will supervise three post-doctoral researchers and two graduate students. One post-doc will focus on the plant-centric research (primarily Obj. 1) in Years 1-3, a second post-doc will focus on fruit bats in Years 1-3, and a third postdoc will manage the research team in the final field season (Year 4) and synthesize the results for effective transfer to the DoD. A PhD student will conduct the research on feral pig movement and seed dispersal (Obj. 2 & 3) and a Masters student will conduct research on regeneration of degraded forest (Obj. 1.2). Dr. Rogers will spend roughly 15 person-months on the project. Salary is requested for a total of five summer months for Dr. Rogers.

Julie Savidge (co-PI) is a Professor of Conservation Biology at Colorado State University. Her primary research concentrates on the impacts and management of exotic species and factors affecting habitat selection and reproductive success of sensitive species. She has conducted research on a variety of taxa, including invasive snakes, rats, overabundant deer, and various avian species. Dr. Savidge has worked in the Mariana Islands for 25 years, including the original research on why the birds on Guam were declining, nest success of forest birds in native and non-native forest on Saipan, and, in collaboration with USGS, management of the invasive brown treesnake on Guam. She will take primary responsibility for overseeing field research with birds. Dr. Savidge will commit 2-3 person-months per year to the project which will include supervising 2 postdoctoral research associates (one associated with bird work on Saipan for 3 years and the other studying Island Collared-Doves on Guam for 16 months; the latter post-doc will also do Saipan-Guam comparisons), and a PhD student (studying aspects of Micronesian Starlings on Guam). She will collaborate with Dr. Rogers in project coordination, data analyses, and products.

Key co-performers: Josh Tewksbury (Hoffmann Institute, WWF/University of Washington) has extensive experience with nest searching, feeding trials, and conservation planning; Tammy Mildenstein

(University of Montana) has been conducting research on the ecology of fruit bats, including the Mariana Fruit Bat, for more than 13 years; Peter Luscombe (Pacific Bird Conservation) and Herb Roberts (Curator, Memphis Zoo) have spearheaded several translocations of birds from Saipan to other islands or zoos- they will assist with mist netting and feeding trials.

Key end-users and collaborators: Ruben Guieb and Leanne Obra (AAFB, letter attached), Earl Campbell (USFWS, letter attached), Paul Radley and Russ Benford (CNMI Division of Fish and Wildlife, letter attached)

Research advisory team: Ran Nathan (Hebrew University of Jerusalem) is an expert in movement ecology and will provide advice on the latest technology in tracking. Joe Fragoso (Stanford University) has extensive experience researching the ecological impacts of feral pigs in Hawaii and of other ungulates in South America; he will provide advice on feral pig research.

E. COOPERATIVE DEVELOPMENT

PI Rogers has received funding from the National Science Foundation to investigate the role of vertebrate dispersers on gap dynamics and forest structure. The results from the NSF grant are directly applicable to this project, and will be incorporated into the forest model in Obj. 1.3 and the final synthesis (Obj. 4). Time contributed by Josh Tewksbury, Peter Luscombe, Herb Roberts, Paul Radley, Russ Benford, Ran Nathan, and Joe Fragoso will be in-kind contributions to the project. No other agency will be contributing funds to the project.

F. TRANSITION PLAN

Transitioning our results to potential end-users is an important component of our proposal. Our key end-users include those directly responsible for managing DoD and other public and private lands on Guam and in the Mariana Islands, including AAFB, Naval Base Guam, the Guam Division of Aquatic and Wildlife Resources, the CNMI Division of Fish and Wildlife, and the Guam National Wildlife Refuge. As part of our objectives, we will provide a final report including a model projecting the state of Guam's forests in the distant future under different scenarios including a scenario where frugivores are not reintroduced. We will also create a user's guide of potential management options for restoring ecological function. Additionally, based on our results of home ranges and movements of various important frugivores, we will illustrate what a possible network of snake-free zones might look like on Guam. Although our research will be directly applicable to the resource managers in the Mariana Islands, the strategy we take in this research will be a useful guide for management of any highly degraded land and will help provide a roadmap for possible restoration of ecosystem function. We will transfer our results in the following ways:

1. Throughout our project, we will work closely with regional DoD resource managers at AAFB (Ruben Guieb and Leanne Obra) and Naval Base Guam/NAVFACMARIANAS (Anne Brooke), and other key agencies to identify ways to incorporate their interests and concerns. We have been contact with natural resource representatives and biologists from these agencies while developing this proposal.
2. We will provide annual updates at the yearly BTS meeting (held on Guam, Saipan, or Hawaii) and to DoD resource managers through individual meetings. We will disseminate our final report and findings to DoD resource managers and other key agencies through a workshop on Guam at the end of our project.
3. We will establish a web page where all results, models, and datasets are presented. All data will also be archived at Dryad, a publicly accessible data archive, within 1 year of publication.

a. List of Acronyms

AAFB	Anderson Air Force Base
BTS	Brown Treesnake (*Boiga irregularis*)
CNMI	Commonwealth of the Northern Mariana Islands
DoD	Department of Defense
EBL	Ecology of Bird Loss Project
GPS	Global positioning system
n.d.	No date (for a publication)
NSF	National Science Foundation
PI	Principal Investigator
SON	Statement of Need
T&E	Threatened and Endangered
USGS	United States Geological Survey
USFWS	United States Fish and Wildlife Service
WWF	World Wildlife Fund

c. Literature citations

Allison, A., F. Bonaccorso, K. Helgen, and R. James. 2008, accessed January 7. Pteropus mariannus. www.iucredlist.org.

Alonso, D., and R. V. Sole. 2000. The DivGame simulator: a stochastic cellular automata model of rainforest dynamics. Ecological Modelling 133:131–141.

Barrios-Garcia, M. N., and S. A. Ballari. 2012. Impact of wild boar (Sus scrofa) in its introduced and native range: a review. Biological Invasions 14:2283–2300.

Bartuszevige, A. M., and D. L. Gorchov. 2006. Avian Seed Dispersal of an Invasive Shrub. Biological Invasions 8:1013–1022.

Blake, J. G., and B. A. Loiselle. 1992. Fruits in the diets of Neotropical migrant birds in Costa Rica. Biotropica:200–210.

Burns, K. C. 2012. Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (Turdus merula). New Zealand Journal of Ecology 36:171.

Caves, E., S. Jennings, J. Hille Ris Lambers, J. J. Tewksbury, and H. S. Rogers. (n.d.). Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500–504.

Chave, J. 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. Ecological Modelling 124:233–254.

Chimera, C. G., and D. R. Drake. 2010. Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. Biotropica 42:493–502.

Colwell, R. K., R. R. Dunn, and N. C. Harris. 2012. Coextinction and Extinction Cascadees. Annual Review of Ecology, Evolution, and Systematics 43.

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.

Davis, M. A., M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. A. Pickett, J. C. Stromberg, P. Del Tredici, K. N. Suding, J. G. Ehrenfeld, J. P. Grime, J. Mascaro, and J. C. Briggs. 2011. Don't judge species on their origins. Nature 474:153–154.

Donlan, C. J., J. Berger, C. E. Bock, J. H. Bock, D. A. Burney, J. A. Estes, D. Foreman, P. S. Martin, G. W. Roemer, F. A. Smith, M. E. Soulé, and H. W. Greene. 2006. Pleistocene Rewilding: An Optimistic Agenda for Twenty‐First Century Conservation. The American Naturalist 168:660–681.

Donlan, J. 2005. Re-wilding North America. Nature 436:913–914.

Drake, D. R., and L. W. Pratt. 2001. Seedling mortality in Hawaiian rain forest: The role of small-scale physical disturbance. Biotropica 33:319–323.

Dunn, R. R., N. C. Harris, R. K. Colwell, L. P. Koh, and N. S. Sodhi. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proceedings. Biological sciences / The Royal Society 276:3037–3045.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. SHURIN, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Fritts, T. H., and G. H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: A case history of Guam. Annual Review of Ecology and Systematics 29:113–140.

Garcia, D., and D. Martinez. 2012. Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. Proceedings of the Royal Society B: Biological Sciences 279:3106–3113.

Gawel, A. M. 2012, June 20. The Ecology of Invasive Ungulates in Limestone Forests of the Mariana Islands. University of Guam.
Gordon, D. R., D. A. Onderdonk, A. M. Fox, R. K. Stocker, and C. Gantz. 2008. Predicting Invasive Plants in Florida Using the Australian Weed Risk Assessment. Invasive Plant Science and Management 1:178–195.
Griffiths, C. J., and S. Harris. 2010. Prevention of secondary extinctions through taxon substitution. Conserv Biol 24:645–646.
Griffiths, C. J., D. M. Hansen, C. G. Jones, N. Zuël, and S. Harris. 2011. Resurrecting extinct interactions with extant substitutes. Current Biology 21:762–765.
Groeneveld, J., L. F. Alves, L. C. Bernacci, E. Catharino, C. Knogge, J. P. Metzger, S. Pütz, and A. Huth. 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. Ecological Modelling 220:2450–2459.
Hansen, D. M. 2010. On the use of taxon substitutes in rewilding projects on islands. Islands and Evolution.
Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology & Evolution 24:599–605.
Hobbs, R. J., L. M. Hallett, P. R. Ehrlich, and H. A. Mooney. 2011. Intervention Ecology: Applying Ecological Science in the Twenty-first Century. BioScience 61:442–450.
Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P. R. Epstein, J. J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, D. M. Richardson, E. W. Sanderson, F. Valladares, M. Vila, R. Zamora, and M. Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.
Holbrook, K. M., and T. B. Smith. 2000. Seed dispersal and movement patterns in two species of Ceratogymna hornbills in a West African tropical lowland forest. Oecologia 125:249–257.
Hooge, P. N., and W. M. Eichenlaub. 2000. Animal Movement extension to
ArcView. ver. 2.0. US Geological Survey, Anchorage, AK.
Hooper, D. U., F. S. Chapin Iii, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, and S. Naeem. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.
Huth, A., M. Drechsler, and P. Köhler. 2005. Using multicriteria decision analysis and a forest growth model to assess impacts of tree harvesting in Dipterocarp lowland rain forests. Forest Ecology and Management 207:215–232.
Jones, H. P., B. R. Tershy, E. S. Zavaleta, D. A. Croll, B. S. Keitt, M. E. Finkelstein, and G. R. Howald. 2008. Severity of the effects of invasive rats on seabirds: a global review. Conserv Biol 22:16–26.
Kaiser-Bunbury, C. N., A. Traveset, and D. M. Hansen. 2010. Conservation and restoration of plant–animal mutualisms on oceanic islands. Perspectives in Plant Ecol, Evol and Systematics 12:131–143.
Kawakami, K., L. Mizusawa, and H. Higuchi. 2009. Re-established mutualism in a seed-dispersal system consisting of native and introduced birds and plants on the Bonin Islands, Japan. Ecological Research 24:741–748.
Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16:199–204.
Kottermair, M. 2012. Microsoft Word - TechReport_113_mkotterm_revised_120214_p11:1–104.
Köhler, P., and A. Huth. 1998. The effects of tree species grouping in tropical rainforest modelling: Simulations with the individual-based model FORMIND. Ecological Modelling 109:301–321.
Köhler, P., J. Chave, B. Riera, and A. Huth. 2003. Simulating the Long-term Response of Tropical Wet Forests to Fragmentation. Ecosystems 6:114–128.
Linnebjerg, J. F., D. M. Hansen, and J. M. Olesen. 2007. Gut passage effect of the introduced red-whiskered bulbul (Pycnonotus jocosus) on germination of invasive plant species in Mauritius. Austral Ecology 34:272–277.

Markl, J. S., M. Schleuning, P.-M. Forget, P. Jordano, J. E. Lambert, A. Traveset, S. J. Wright, and K. Bohning-Gaese. 2012. Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. Conservation Biology 26:1072–1081.
Marris, E. 2011. Rambunctious Garden: Saving Nature in a Post-Wild World. Bloomsbury Publishing USA.
Mattos, K., C. Adams, J. Tewksbury, J. HilleRisLambers, and H. S. Rogers. (n.d.). Interactions between invasive species affect predation of native forest seeds on two Pacific islands.
McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaría. 2012. Seed dispersal in changing landscapes. Biological Conservation.
Mello, M. A. R., F. M. D. Marquitti, P. R. Guimarães, E. K. V. Kalko, P. Jordano, and M. A. M. de Aguiar. 2011. The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. PLoS ONE 6:e17395.
Metz, M. R., W. P. Sousa, and R. Valencia. 2010. Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. Ecology 91:3675–3685.
Millspaugh, J., and J. M. Marzluff. 2001. Radio Tracking and Animal Populations. Academic Press Ltd.
Moilanen, A., A. M. A. Franco, R. I. Early, R. Fox, B. Wintle, and C. D. Thomas. 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings. Biological sciences / The Royal Society 272:1885–1891.
Mortensen, H. S., Y. L. Dupont, and J. M. Olesen. 2008. A snake in paradise: Disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. Biological Conservation 141:2146–2154.
Murray, K. G. 1988. Avian Seed Dispersal of 3 Neotropical Gap-Dependent Plants. Ecological Monographs 58:271–298.
Nogueira-Filho, S. L. G., S. S. C. Nogueira, and J. M. V. Fragoso. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. Biodiversity and Conservation 18:3685–3686.
O'Connor, S.-J., and D. Kelly. 2012. Seed dispersal of matai (Prumnopitys taxifolia) by feral pigs (Sus scrofa). New Zealand Journal of Ecology 36:228.
Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander Jr, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66:1–43.
Pattemore, D. E., and D. S. Wilcove. 2012. Invasive rats and recent colonist birds partially compensate for the loss of endemic New Zealand pollinators. Proceedings of the Royal Society B: Biological Sciences 279:1597–1605.
Pheloung, P. C., P. A. Williams, and S. R. Halloy. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Biological Conservation 57:239–251.
Pütz, S., J. Groeneveld, L. F. Alves, J. P. Metzger, and A. Huth. 2011. Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. Ecological Modelling.
Rogers, H., J. Hille Ris Lambers, R. Miller, and J. J. Tewksbury. 2012. "Natural experiment" demonstrates top-down control of spiders by birds on a landscape level. PLoS ONE 7:e43446.
Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68:660–668.
Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The Potential Conservation Value of Non-Native Species. Conservation Biology 25:428–437.
Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333–353.
Seastedt, T. R., R. J. Hobbs, and K. N. Suding. 2008. Management of novel ecosystems: are novel approaches required? Frontiers in Ecology and the Environment 6:547–553.
Shiels, A., and D. Drake. 2011. Are introduced rats (Rattus rattus) both seed predators and dispersers in Hawaii? Biological Invasions 13:883–894.

Sol, D., S. Timmermans, and L. Lefebvre. 2002. Behavioural flexibility and invasion success in birds. Trends in Ecology & Evolution 63:495–502.
Spiegel, O., and R. Nathan. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. Ecol Lett 10:718–728.
Spotswood, E. N., J.-Y. Meyer, and J. W. Bartolome. 2012. An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. Journal of Biogeography 39:2007–2020.
Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A Modified-Whittaker nested vegetation sampling method. Plant Ecology 117:113–121.
Swamy, V., and J. W. Terborgh. 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. The Journal of Ecology 98:1096–1107.
Terborgh, J. 2012. Enemies Maintain Hyperdiverse Tropical Forests. The American Naturalist 179:303–314.
Tewksbury, J. J., D. J. Levey, M. Huizinga, D. C. Haak, and A. Traveset. 2008. Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chilies. Ecology 89:107–117.
Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.
Weir, J. E., and R. T. Corlett. 2007. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? Landscape Ecology 22:131–140.
White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.
White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio tracking data.
Wiewel, A. S., A. A. Yackel Adams, and G. H. Rodda. 2009. Distribution, Density, and Biomass of Introduced Small Mammals in the Southern Mariana Islands1. Pacific Science 63:205–222.
Wiles, G. J., J. Bart, R. E. Beck Jr, and C. F. Aguon. 2003. Impacts of the Brown Tree Snake: Patterns of decline and species persistence in Guam's avifauna. Conservation Biology 17:1350–1360.
Worton, B. J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecology 70:164–168.
Wunderle, J. M., Jr. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223–235.
Yap, C. A. M., and N. S. Sodhi. 2004. Southeast Asian invasive birds: ecology, impact and management. Ornithological Science 3:57–67.

d. Supporting Technical Data

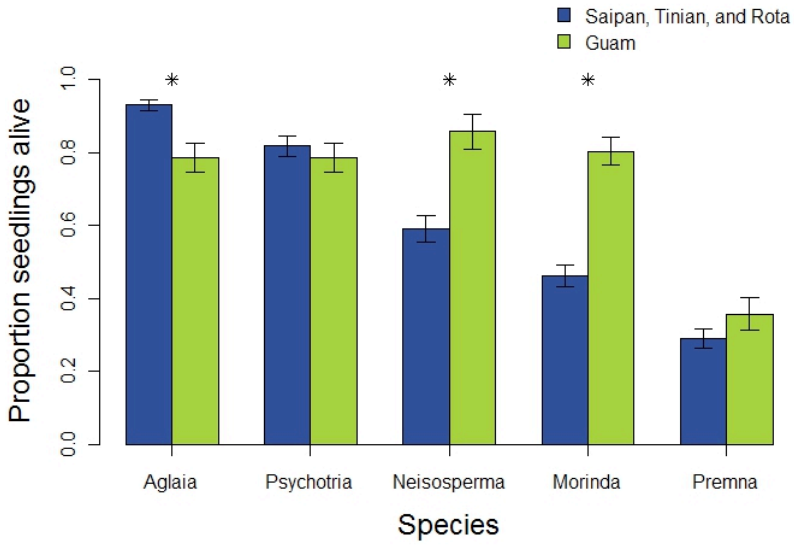


Fig. S1: Comparisons of seedling survival between forests without birds (Guam) and forests with birds (Saipan, Tinian and Rota) for five fleshy-fruited tree species. One species, *Aglaia mariannensis* had higher survival with birds, but the other four species either survived better on Guam (without birds) or showed no difference between islands. This, when combined with our pilot study showing no difference in adult leaf herbivory between islands, suggests that the loss of invertebrate-feeding birds has not initiated a strong trophic cascade down to the plant level.

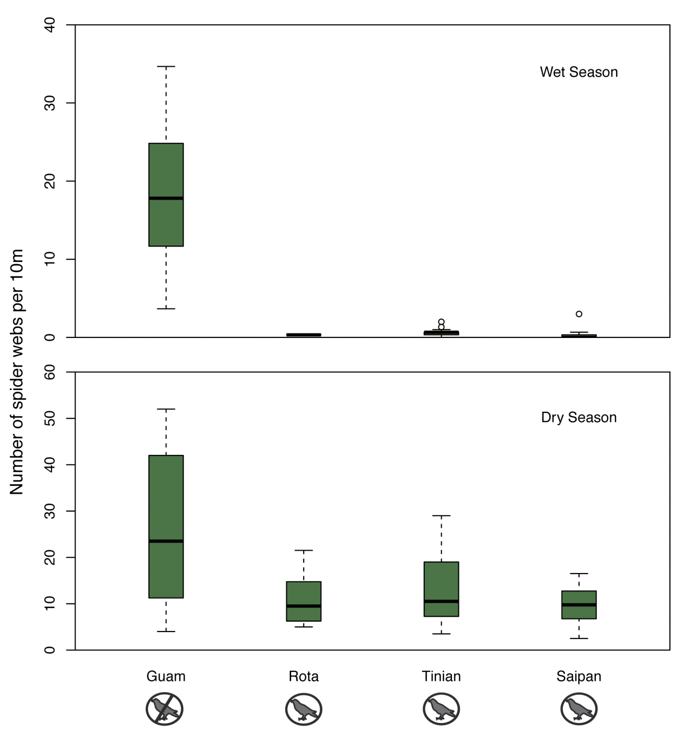


Fig. S2: Comparison of spider web abundance between Guam (no birds in forests) and nearby islands (with birds) during the wet season (top) and dry season (bottom). There were twice as many spiderwebs per 10m on Guam in the dry season and 40 times more spider webs in the wet season. This increase in spider webs may account for the lack of effect of bird loss on seedling survival (Fig. S1), as spiders may compensate for the loss of birds to some extent.

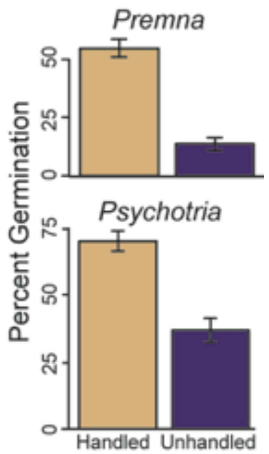


Fig. S3: Germination of seeds handled by birds versus whole fruits.

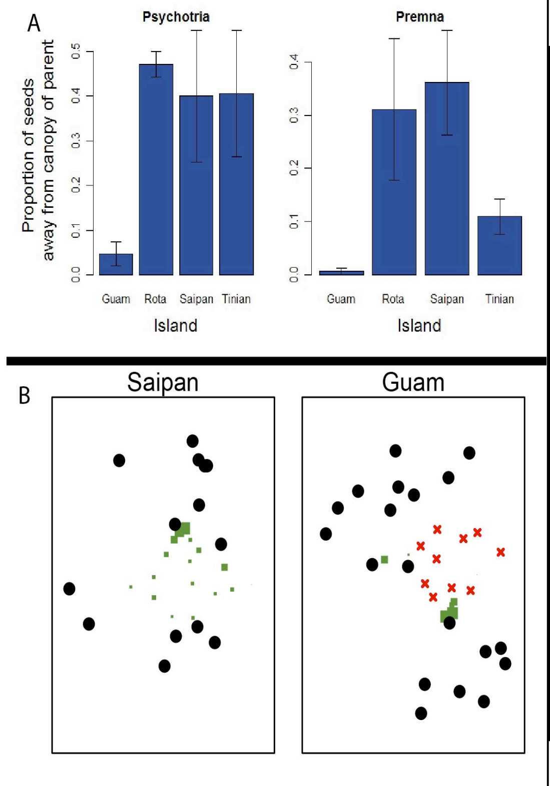


Fig. S4: A) Very few seeds landed in seed traps placed away from parent trees on Guam, as compared to Saipan, Tinian and Rota. B) In many cases, as demonstrated here for one site on Guam and one on Saipan, no seeds fell in traps over a 9 month seed trapping period. The black circles represent trees, green squares represent seed traps scaled to the abundance of seeds they received, and the red squares show traps that did not receive any seeds.

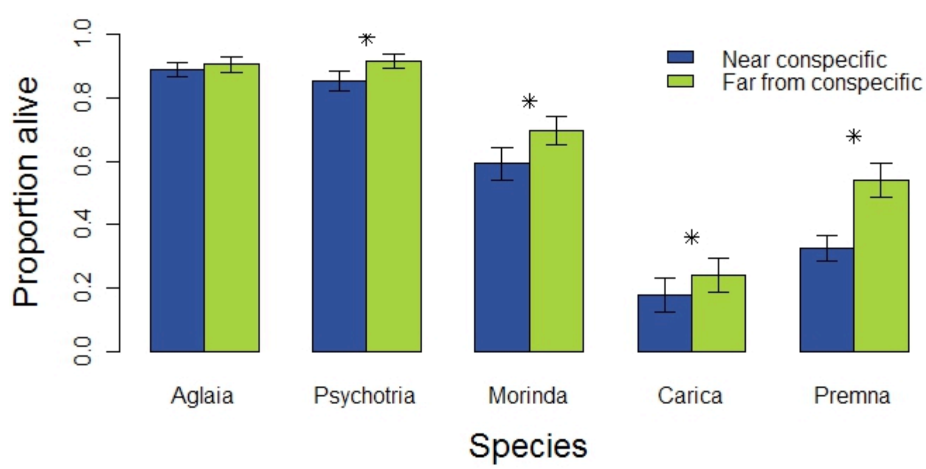


Fig. S5: Difference in survival for five forest tree species between seedlings planted near and those planted 'far' (~7+m) from conspecific trees. A star (*) indicates significant effect of distance in linear mixed effects models. Species are ordered by the strength of distance dependence, from no effect of distance on the left to a strong effect on the right, given the range of canopy openness values present in the forest. For four out of five species, dispersal away from the parent tree increases seedling survival, suggesting that disperser loss is likely to have a negative demographic effect on these species.

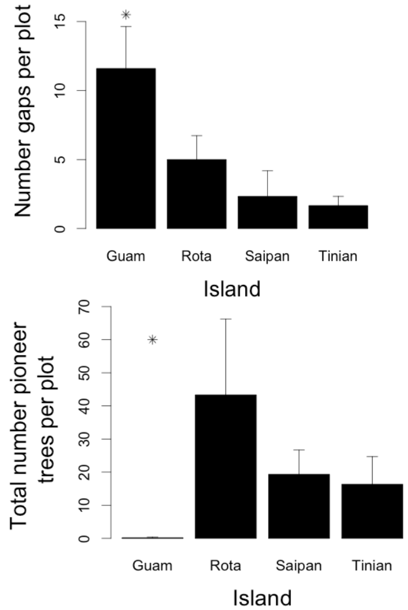


Fig. S6: Forest plots (60x60m) on Guam, an island without vertebrate dispersers, have a) more gaps, and b) fewer pioneer trees than plots on nearby islands with vertebrate dispersers.

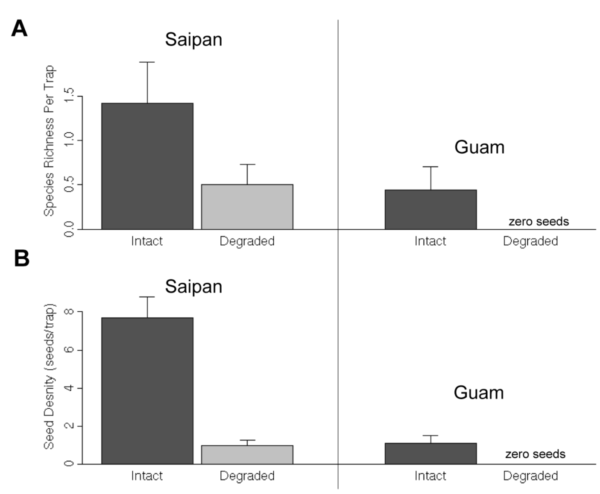


Fig. S7: Richness (A) and density (B) of seed rain from native forest species in traps placed in intact and degraded (*Leucaena leucocephala*) forest on Saipan (with birds) and Guam (without birds). Without birds, seed rain in intact forest is less diverse, and no native seeds reach degraded forest. Regeneration is expected to proceed extremely slowly without seed rain from the native forest.

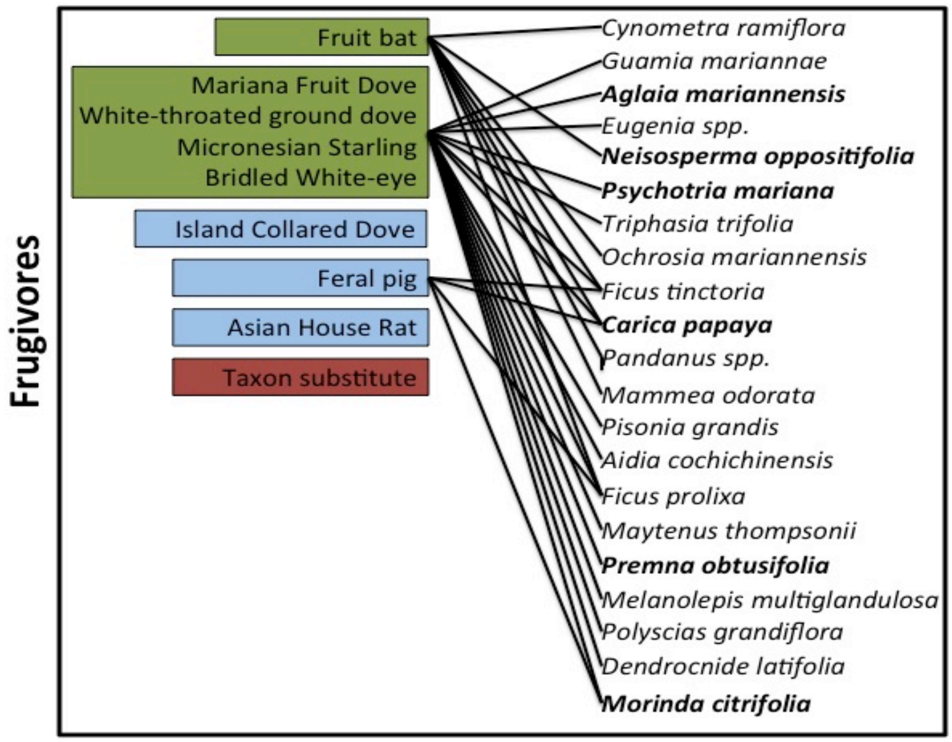


Fig.S8: Hypothetical seed dispersal network in the Mariana Islands. The frugivores include only those that are the focus of this proposal. Three additional frugivores (Coconut crabs and the Mariana Crow) may provide additional seed dispersal but were omitted from consideration from this proposal. Green boxes indicate native frugivores, whereas blue boxes indicate non-native frugivores currently on Guam, and red indicates non-native frugivores that could be introduced to Guam. The tree species listed are (in order from top) the 21 most abundant species based on 14 vegetation plots across Guam, Rota, Tinian and Saipan. Species in bold have been the focus of previous research by PI Rogers. Links between tree species and frugivores indicate likely seed dispersal relationships, based on personal observation and published data. In this proposal, we aim to use feeding trials, fruiting tree observations and fecal analyses to determine which fruiting trees are linked to each frugivore, and to weight the links based on quantity and quality of seed dispersal service provided by each frugivore.

Table S1: Candidate species for use in restoring ecological function to Guam

Species	**Native status**	**Present on Guam?**	**Ecological role**	**Useful for restoration?**
Micronesian Starling	**Native**	Yes	Omnivore, tendency toward frugivory	Yes
Bridled White-eye	**Native**	Extirpated	Insectivore; also fruit, nectar	Yes
Mariana Fruit-Dove	**Native**	Extirpated	Frugivore	Yes
White-throated Ground-Dove	**Native**	Extirpated	Frugivore	Yes
Mariana Crow	**Native**	Extirpated	Omnivore	No?*
Mariana Fruit Bat	**Native**	Limited	Frugivore	Unlikely?**
Island Collared-Dove	Non-native	Yes	Frugivore	Yes
Feral pig	Non-native	Yes	Omnivore	Unknown
Rat	Non-native	Yes	Omnivore	Unknown
Taxon substitute	Non-native	No	Frugivore	Unknown

* Unlikely, as remaining population is highly endangered on island of Rota.
** Endangered status, but populations on Rota and Northern Islands, and tiny population coexists with snake on Guam today; reducing human hunting pressure and snake predation (on Guam) are key challenges.

f. Existing Support

Rogers is also the PI on a proposal to the National Science Foundation that was recently funded (June 2013-May 2017; $600K). This grant focuses on one of the three ecological functions provided by frugivorous vertebrates, as described in Question 1; it complements, but does not overlap, the research proposed in Q1.1 and 1.2. In the NSF-funded research, we aim to investigate whether vertebrate frugivores in tropical forests influence gap community composition and maintain forests as closed canopy landscapes. We have observed that forests on Guam have at least twice as many gaps and very few pioneer species when compared to nearby islands. We hypothesize that seeds from quick-growing, light-dependent species are not likely to reach treefall gaps without vertebrate dispersers, causing gap closure rates to slow, ultimately leading to more gaps on the landscape at a given time. Using a combination of models and field experiments, we will experimentally determine whether vertebrate frugivore loss from the island of Guam has altered tropical forest gap dynamics. We will use experimental gaps on all four islands to test whether vertebrates impact seedling community composition in gaps and gap closure rates. To explore how vertebrate dispersers affect the frequency of gaps across a landscape, we will parameterize a spatially explicit gap dynamics model from field data on gap creation rates and seed dispersal distances with and without vertebrate dispersers. We will compare experimental results of simulated vertebrate loss to actual results on the island of Guam, evaluating whether experimental results scale up to the landscape level and ultimately testing our capacity to predict the ecosystem-wide impacts of frugivore declines on the structure of tropical forests.