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 recover 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, fruit-eating birds and bats - 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) and existing non-native species. 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 identify candidate frugivore assemblages based upon the results from the studies described above, and then use conservation planning tools to identify spatially-explicit snake control strategies that would maximize the function provided by the disperser assemblage. .

BENEFITS: Our results will provide resource managers with DoD and other agencies on Guam important insight on the long-term consequences associated with the loss of seed dispersers, and guidance in the possible options for recovering ecological function in Guam's forests. Our modeling efforts will inform decisions on where to strategically situate planned and anticipated snake fences. 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, in particular, on islands, where invasive species can have particularly devastating effects. The capacity of DOD to maintain diverse and resilient ecosystems in the face of invasive species relies on an understanding of the impact of the invader on key species interactions within the invaded community, as well as a willingness to consider novel management techniques for management of these novel ecosystems.

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 recover ecological function. Our research will focus on a critical ecological process in tropical systems – animal mediated seed dispersal. It will be conducted on the island of Guam, where the invasive brown tree snake (*Boiga irregularis*) has functionally extirpated all native forest birds and the only native mammal, and in doing so, virtually eliminated all primary seed dispersal services. We will investigate the impacts of this island-wide ecological disruption using nearby islands with very similar forests and relatively intact frugivore communities to examine the ecological importance of native fruit-dispersing species. We will evaluate the challenges associated with using these species in system-wide restoration and consider the ecological role of non-native species currently present in the system. 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 understand which ecological functions have been disrupted, then identify the role native and non-native species could play in restoring ecological function despite the continued presence of invasive species. We will investigate the limitations of restoration options, and develop a "User's Guide" for managers so they may weigh the advantages and disadvantages of each approach.

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 and existing non-native species that may be used to restore ecological function?

Q3: What are the limitations or challenges associated with using native or existing non-native species 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 (Dunn et al. 2009, Colwell et al. 2012), reducing the capacity of the ecosystem to respond to change. Maintaining ecosystem services within a rapidly changing environment is a very real economic and ecological issue given recent and expected climate change (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".

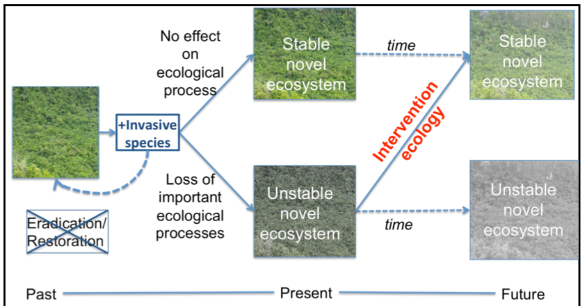


Fig.1: The use of "Intervention Ecology" to restore function in the face of invasive species

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 tree snake) is still present and its removal appears intractable, managers may need to utilize the strategy of "intervention ecology" (Fig.1; Hobbs et al. 2011), restoring function within these novel systems without attempting to restore the original ecosystem (Marris 2011).

When using an intervention ecology approach, restoration must 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, maintain diversity, and be able to recover from disturbance. 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.2). Although using native species to restore function is ideal, it may also be possible to include the use of key non-native species already present in the system. There are often alternate pathways for the restoration of function (Seastedt et al. 2008), so the feasibility and efficacy of each option must be explored, and the various options along with the benefits and drawbacks of each option presented to key stakeholders. Creating a 'functioning ecosystem' from a highly degraded system is often more practical and achievable 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).

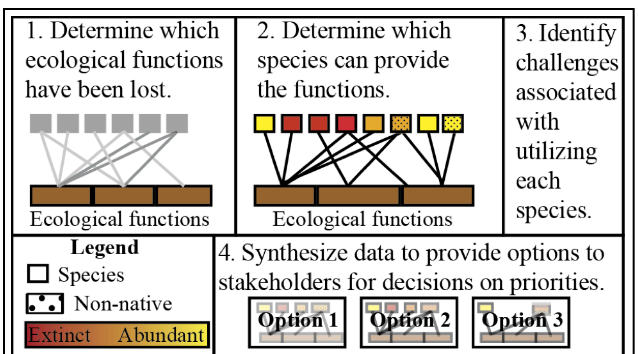


Fig.2: The steps for 're-wilding' to restore ecological function to a novel ecosystem.

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 tree snake (*Boiga irregularis,* BTS), which has caused the complete loss of 10 of 12 forest bird species and the functional extirpation of the other two (Savidge 1987, Wiles et al. 2003). This includes the loss of two nectarivarous, five frugivorous, and 10 insectivorous bird species (several species are in more than one category), disrupting plant-pollinator, fruit-frugivore, and predator-prey interactions in the forests. Additionally, BTS contributed to the decline of native fruit bats (*Pteropus mariannus*) on Guam (Allison et al. 2008), disrupting another set of fruit-frugivore interactions. Island-wide eradication of BTS would allow restoration of many of these bird and bat species, as only one species (Guam Flycatcher, *Myiagra freycineti*) is extinct. Unfortunately, eradication is currently unlikely, as existing control tools only reach a subset of the population.

Since island-wide restoration of T&E bird and bat species is unlikely in the near-term, we must shift our management goals towards 1) reducing the likelihood of secondary extinctions and 2) maintaining healthy habitat for the potential reintroduction of T&E species at some point in the future. The loss of functionally important species or interactions may trigger a cascade of extinctions (Colwell et al. 2012), thus it is important to restore critical ecosystem functions to prevent these secondary extinctions. In addition, the limestone forest on Guam DoD installations is or has been home to 1 ESA-listed plant species and 4 listed animal species (3 birds and the fruit bat), as well as several plant species that are candidates for listing. Snake reduction is possible within fenced areas, and future research may produce effective island-wide eradication methods, which would in turn allow the restoration of native bird and bat species in these areas; this will only be successful if the habitat in which they lived is still hospitable. We have evidence to suggest that a path of inaction would result in a highly degraded system potentially unable to support existing T&E bird and bat species. *We envision an end-state to our intervention ecology efforts where forest diversity and structure are stable or increasing, and forests recover from disturbance as they do on nearby islands. Healthy forests are more likely to support reintroduced populations of extirpated T&E species and less likely to necessitate additional species listings.*

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 models for studying the functioning of relatively intact systems, 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.2) 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. Step 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, in step 4, this information is 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 tree snake has impacted ecological function in Guam's forests and identify the consequences for long-term forest health.

The island of Guam is comprised of a flat limestone plateau in the north and a mountainous volcanic region in the south. Most of the native species affected by the BTS were limited to the limestone karst forest, therefore we focus our efforts on this ecosystem. 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 (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 (Fig.3). 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 after disturbance are affected by vertebrate loss. The EBL project has collected 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, we can fully characterize the ecological impacts of disperser loss.

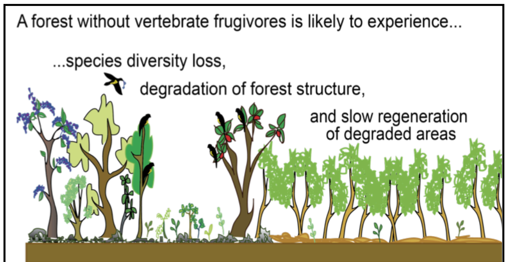


Fig. 3: The impact of vertebrate frugivores on ecological function.

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 other common vertebrate-dispersed tree 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 (Fricke et al. 2014). 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, the results of which will complement the proposed work. In this grant, we determine the demographic importance of reaching light gaps for 15 tree species, and we create experimental treefall gaps on islands with and without dispersers to determine whether dispersers affect gap regeneration rates or the pattern of succession within gaps (see Supplemental Material for a longer description).

Finally, disperser loss may deal a huge blow to forest regeneration after disturbance. 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 disperser 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. 2013). While mixed *Leucaena*-native forests are common on Saipan and the nearby island of Rota, they are rare on Guam. A lack of dispersers on Guam is likely slowing forest regeneration, however the process of regeneration is affected by many stochastic events, so a large sample size is needed to assess how regeneration is affected by disperser loss. We will examine how differences in the disperser community affect seed rain and regeneration of degraded forests across three islands- two with dispersers, and one without.

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), which holds the majority of the island's intact karst forest. 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) and existing non-native species 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. Because the use of taxon substitutes is highly controversial and is typically considered a last resort (Hansen 2010, Kaiser-Bunbury et al. 2010), we do not address this option in our proposal.

A thorough understanding of the ecological role of each candidate species is needed to prioritize management efforts. 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. 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: Four of the five native avian frugivore species (White-throated Ground-Dove (*Gallicolumba xanthonura*), Mariana Fruit-Dove (*Ptilinopus roseicapilla*), Bridled White-eye, and Micronesian Starling (*Aplonis opaca)* have potential for being used to restore ecological function to Guam (Table S1). We have omitted the fifth 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. In addition, we have omitted the only native mammalian frugivore, the endangered Mariana Fruit Bat (*Pteropus mariannus*), even though we believe it may be an important disperser, because hunting is a primary threat, thus a cultural shift would be needed to restore large populations of fruit bats on Guam. 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. 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). Invasive black rats (*Rattus rattus*) are both seed predators and dispersers in Hawaii: seeds smaller than 1.2 mm in length are typically dispersed, whereas seeds larger than 1.2 mm are usually predated (Shiels and Drake 2011). Pigs (*Sus scrofa*) are seed dispersers in many systems (Nogueira-Filho et al. 2009, O'Connor and Kelly 2012, Barrios-Garcia and Ballari 2012). In New Zealand, for example, feral pigs are important dispersers of the native matai tree (O'Connor and Kelly 2012), and in the Brazilian Pantanal, the feral pig is now the most important frugivore for maintaining stability of the fruit-frugivore network (Donatti 2011).

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 due to BTS predation (Conry 1988, Wiles et al. 2003). Historic observations on Guam and various studies on Saipan indicate this species is rarely found in forest interior (e.g. Perez 1970, Engbring et al. 1986); for example, zero Island Collared-Doves were seen consuming fruit in over 900 hours of observation of six tree species in intact forest on Saipan and Rota (Fricke, pers.comm.). Thus, we do not consider the Island Collared-Dove a key species for dispersing seeds in the karst forest on Guam; however, we do not rule out the possibility that it affects regeneration of non-native forest by dispersing native seeds in degraded forest/edge habitat. The feral pig (*Sus scrofa*) has been present on Guam since the late 1700's (Conry 1988). Preliminary research suggests pigs disperse seeds of at least two native tree species in the forests on Guam (Kerr 2012) and as they are one of the only dispersers left on Guam, they may currently be the most effective vertebrate seed disperser on the island. 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. While rats and pigs may play important roles as dispersers of some tree species in karst forest, we do not believe rats and pigs alone are sufficient to restore dispersal services, as both species are currently present on Guam yet many signs of dispersal limitation are evident (Fig. S3-S6).

We acknowledge that pigs (Nogueira-Filho et al. 2009, Barrios-Garcia and Ballari 2012) and rats (Towns et al. 2006, Jones et al. 2008) 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 and rats could provide valuable seed dispersal services, and thus a functioning ecosystem on Guam may have a role for select non-native species. Since the potential beneficial aspects of pigs and rats must be weighed against their detrimental impacts, we explore the negative impacts of feral pigs and rats in Obj. 3 (Schlaepfer et al. 2011, Davis et al. 2011).

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

Once the potential role of individual species has been determined, we can begin to address the challenges in using native or non-native species to restore ecological function to Guam's forests. A good disperser must be able to exist on Guam, and must not cause more harm through disturbance, predation, or dispersal of non-native species than the benefits it might provide as a disperser.

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.

Micronesian Starlings are the only remaining **native avian frugivore** on Guam and show promise for being part of the solution. It is largely confined to AAFB (about 200 birds; D. Vice, personal communication), and 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. By understanding its survival strategies on Guam, we might be able to develop ways to expand its population, and thus the ecological functions it provides. By comparing diet and movement of Micronesian Starlings between Saipan and Guam, we can gain valuable information on the functions they are 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** 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 rats or pigs for restoring seed dispersal to the forests of Guam.

The negative effects of feral pigs are caused by the direct consumption of native seedlings, physical disturbance from rooting and trampling, dispersal of invasive species, increased soil erosion, and disruption of biogeochemical cycles (Drake and Pratt 2001, Nogueira-Filho et al. 2009, Krull et al. 2013, Murphy et al. 2014). Feral pigs have been studied extensively in Hawaii, and shown to strongly reduce the density of woody plants in mineral soil (Cole et al. 2012), and to have a particularly detrimental impact on tree ferns (Murphy et al 2014). The karst rock substrate and lack of standing or flowing water in the forests of northern Guam may limit the detrimental effects of pigs caused by rooting and soil erosion. Preliminary research in the Marianas did not show a relationship between the abundance of pig scat and the diversity or density of native or invasive seedlings (Gawel, pers.comm.), although there was a clear link between diversity and deer abundance. In addition, pig scat may not be an adequate proxy for pig abundance (Engeman et al. 2013). In summary, Guam's forests have characteristics that may make them more resilient to pig damage than Hawaiian forests, yet pigs have a long track record as destructive invaders, so more research is needed to determine the full suite of negative impacts in the Mariana Islands.

In addition to likely being seed dispersers, invasive rats are known seed and egg predators around the world (Towns et al. 2006). The black rat, a close relation to the rat commonly found in the karst forest of the Marianas, consumes a wide diversity of seeds, predates animals from seabirds to bats to lizards, and consumes many invertebrates (Shiels et al. 2014). In the Marianas, the strength of predation by rats on seeds of 6 tree species depended on plant species (Mattos et al. n.d.). The density of rats on Guam is already much lower than on Saipan, Tinian and Rota due to BTS predation (Wiewel et al. 2009), though rats quickly increased after snake removal from a fenced area (Reed, pers.comm.) suggesting any efforts to control the snake in order to reintroduce birds will be accompanied by an increase in rats. More research is needed to determine the effect of rats on seeds of forest species in relation to rat density.

We will thoroughly examine the potential negative impacts associated with utilizing each of these species, and incorporate results into the FORMIND model described in Obj 1.3 and Obj 4.

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 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 will be to develop a spatially-explicit restoration plan for the bases; 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 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 protected areas. 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 "User's Guide" for 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. These species may be dispersed primarily by birds, bats, or both. 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 4 years of the project.

Objective 1: Determine how the invasive brown tree snake 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 affects germination rates (as in Bartuszevige and Gorchov 2006, Linnebjerg et al. 2009). We will capture 5-15 of each native bird focal species from the wild. 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 (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 generalized mixed models (binomial errors), 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 the strength of distance-dependent mortality between islands, and Saipan does not require extensive fencing to exclude invasive ungulates, as do Rota and Guam. We will gather ripe seeds from the 16 focal species not previously tested 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 mixed model (binomial errors) 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 frugivore presence affects the regeneration of native forest, we will use a generalized linear mixed effects model with proportion native trees as the response and frugivore presence 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 an individual-based, spatially-explicit, three-dimensional tree growth model that can incorporate recruitment, disturbance, and seed dispersal processes. Details about the application of this model are described well in the appendix of Groeneveld et al. (2009). We will initially develop the model for forests in the Mariana Islands as part of the NSF grant to PI Rogers, in which we use the model to determine how changes in gap dynamics may affect forest structure and abundance of tree species dependent on gaps. With the data collected in Obj 1.1, we will be able to integrate species-specific germination and survival data 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 diversity, 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. We will parameterize the model using data from forest plots on AAFB, which will allow 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). The results of this modeling effort will show the likely future for forests on AAAFB with and without frugivores, and will be delivered in a report to AAFB environmental personnel. Finally, in Obj. 4, we will use the FORMIND model, in conjunction with a spatially-explicit conservation planning program such as ZONATION, to assess the effectiveness of potential restoration efforts.

Objective 2. Determine the ecological roles of frugivorous species, including native species (both extant and extirpated) and existing non-native species 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. 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.

2.1: Ecological roles of native birds

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 feeding 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 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 obtain a minimum of 50 hours of video and visual observations of fruiting branches for each focal species to quantify the proportion of fruits removed by each frugivore species. We completed frugivory monitoring for six focal species in summer 2013. We anticipate that some species are primarily dispersed by bats, of which there are few on Saipan, therefore we will cease observations if no fruit are removed in the first 25 hours; these species may be strongly affected by disperser loss but are unlikely to benefit from reintroduction of native birds. Because rates of frugivory may relate to fruit availability, we will include fruit abundance from phenology monitoring in our analysis. During visual observations, we will 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 on Saipan and obtain fecal droppings. Net position will be adjusted to capture birds utilizing various forest strata. Some species will be harder to catch then others, but we will aim for 20-30 birds of each species within the fruiting season and off-season. 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 identified using a reference collection. Seeds will be quantified by tree species, seeds per sample, and seed size.

Using data collected above, we will create a seed dispersal interaction network where links between frugivores and trees (Fig.S8) are weighted by frugivory rates 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. Tree species with fewer links are at greater risk than species dispersed by multiple frugivores, and frugivores with many links or unique links may be more important. Information regarding the dependence of trees on each frugivore is crucial for comparing restoration options (Obj. 4.1).

2.1b: Telemetry to determine movement patterns: Using telemetry, we will determine movement patterns for each of the native bird species 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 ranges (to be used in Obj. 3 and 4). A subset of birds caught by our mist nets used for diet studies (above) will be fitted with transmitters. Our nets will be placed both within limestone and degraded forest to catch and track birds that may be using both habitats. Tracking will be done during two main fruiting seasons as well as during one off-season to see how dispersal services provided by each species may change seasonally. We plan to track a minimum of 15-20 birds of each of the four species on Saipan. Transmitters for the birds can be expected to last from 1-2 weeks (white-eyes) to several months for the larger bird species. Much of the forest is unsuitable for determining bird location by homing due to the difficulty of walking in rough karst and dense forest. Thus, we will use triangulation of simultaneous bearings by three observers communicating with two-way radios to determine bird locations and following suggestions in White and Garrott (1990). Antennae will be Precision Direction Finding arrays of from 3-5 elements and will be elevated above the relatively low forest canopy on mobile tripods outfitted with extensions for best line-of-site bird locations. For potential dispersal distances, we will take bearings every 10-15 minutes during a tracking session. A tracking session will generally last 2-3 hours, with morning and afternoon sessions.

Bird locations will be estimated using the program LOAS (Ecological Software Solutions), and locations will then be imported into ArcMap (ArcINfo, ESRI) to measure distances moved between points. 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 (Obj. 1) to estimate median dispersal distances for seeds by each species (Weir and Corlett 2007) and each season. For birds utilizing both limestone and degraded forest, we will be able to calculate the amount of time in these respective habitats. 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.

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

As with native frugivores, we will use a combination of feeding trials with germination experiments and fecal analyses to investigate whether feral pigs and Asian house rats are effective seed dispersers.

2.2a: Feral Pigs- We will determine the effect of ingestion on germination using feeding trials with captive animals (as in O'Connor and Kelly 2012). 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 (Kerr 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. In addition, to determine whether pigs disperse seeds from intact to degraded forest, we will collect pig scat from degraded forest and determine whether pigs are depositing seeds in degraded forest that are typically found in intact forest.

2.2b: 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.

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

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?

For successful re-establishment or expansion of bird populations on Guam, birds must have adequate and safe habitat for foraging, roosting, and nesting. Thus, areas with reduced or no snakes are likely necessary, and birds must have behaviors that allow them to benefit from these areas.

3.1a: Diet and habitat requirements of native birds: Our diet and telemetry research in Obj. 2.1 will provide data on habitat utilization by native bird species. While monitoring movements of native birds on Saipan, we will obtain data on night roost utilization. Characterization of roost sites will include nightly location, substrate, and when applicable, various characteristics of the nesting tree and canopy cover. We expect that a bird that returns to the same area to nest on Saipan is more likely to return to the confines of protected areas on Guam. In addition, we can ensure protected areas on Guam have adequate roost sites. 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 peak and off-fruiting seasons.

3.1b: Differences in ecology between Guam and Saipan: Native Micronesian Starlings have shown their ability to withstand some level of BTS presence, but information is needed on what ecological function they provide on Guam and on their survival strategies if their ranges are to be expanded. Thus, we will study what fruits this species consumes 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. Mist nets will be placed to maximize starling capture, which will be along the ecotone between AAFB housing and adjacent forest. We will also record characteristics of roost sites used 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 nesting success on Guam: To evaluate the possibility of expanding starling populations on Guam, we must know where this species is nesting and how nesting success relates to BTS abundance. Because of a reduced population, finding active nests will be challenging, but we will attempt to locate and monitor at least 20-30 nests, most 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. Starlings use cavities for nesting, so we expect to find nests associated with human structures as well as in trees; we 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 will either be on urban structures or in trees isolated from contiguous forest, further from forest, and in areas with reduced BTS densities. In addition, a better understanding of starling nesting requirements could inform the development of snake-proof nest boxes, thus providing a low-cost tool for expanding the range of the starling.

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

Feral pigs and rats have had large detrimental effects around the world and may be having negative impacts on Guam. We have identified the most likely impacts, and designed experiments to assess these effects in the karst forests of Guam.

3.2a: Negative impacts of pigs: On Guam, pigs could be affecting native plant diversity and abundance through seed predation, browsing, trampling, and rooting. To identify the relationship between pig density and seed predation rates, we will place seeds of species known to be predated by pigs along transects in karst forest with varying pig densities and record the rate of removal. Along these same transects, we will assess native seedling diversity and abundance (similar methods to Gawel et al. in prep). Simultaneously, we will use camera traps to estimate pig density (as in Engeman et al. 2013) rather than scat, as in Gawel et al (in prep). Pigs may also affect regeneration in treefall gaps if they preferentially seek out gaps for browsing or rooting. We will also place camera traps in recent treefall gaps (in addition to cameras used above) to determine whether pigs are more likely to root in gaps than in the closed canopy forest.

3.2b: *Negative impacts of rats*: The most harmful impacts of rats on Guam are likely through bird, egg, and seed predation. Since there are far fewer rodents on Guam than on nearby islands with birds, we do not expect predation of eggs or chicks to limit bird populations on Guam, although rat predation should be closely monitored if/when birds are reintroduced to Guam. We will focus instead on the role of rats as seed predators. 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 (as in Shiels and Drake 2011). 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. n.d.). The experiment will include trays that only allow insect access and trays that allow access to all possible predators. We will place camera traps next to the seed trays to confirm that rodents are removing the seeds.

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 and assessment of candidate frugivores assemblages: We will examine all possible combinations of the 6 candidate frugivores under study in Obj. 2 and Obj. 3, using a community-focused network approach (as in Mello et al. 2011). Our criteria for assessing subsets of these 6 consumers will include assemblage sufficiency (the proportion of dispersal services that would be potentially restored to each tree species on Guam), assemblage efficiency (the number of different disperser species required), assemblage risk (the reliance of each assemblage on rats and pigs, each of which present significant risks to the ecology of Guam), complementary specialization (the degree of overlap in the identity of plant species dispersed by each disperser) and robustness (the impact on the plant community associated with the failure to establish each species in the frugivore assemblage). This procedure will use all of the data gathered on the impact of each native and non-native member of each potential restoration assemblage (from Obj. 2 and Obj. 3).

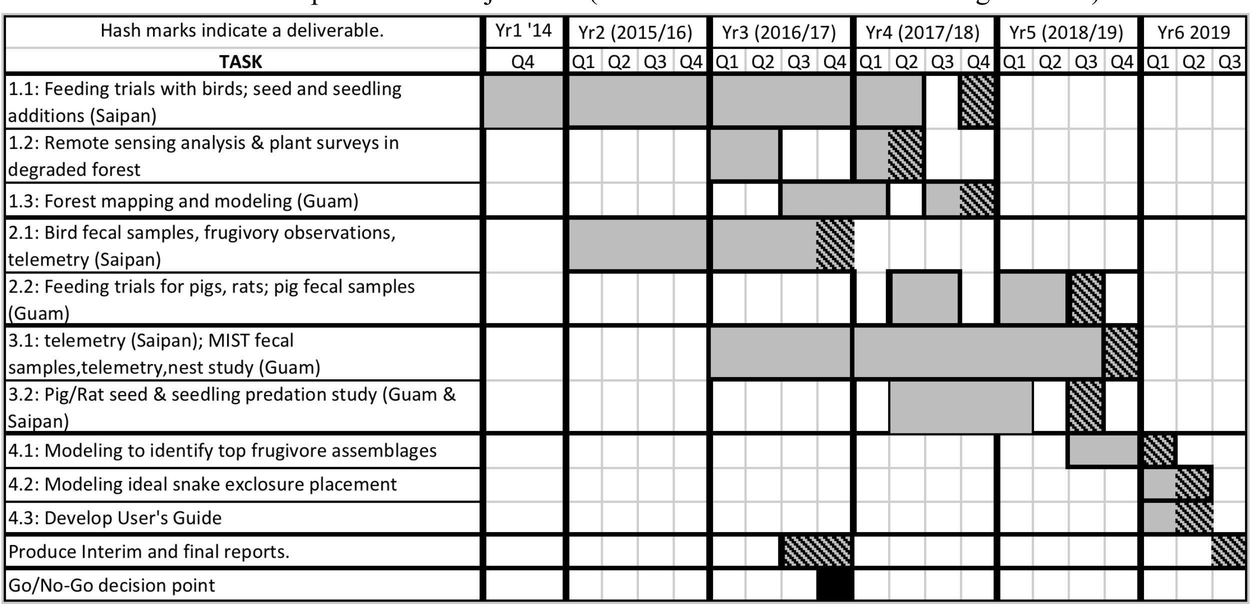
4.2: Optimal snake fence placement:

Once the top frugivore subsets are identified, the next steps will be to define the needs of species within the selected frugivore community, focusing on the importance and optimal spatial arrangement of snake-free areas to create zone where introduced birds can maintain viable populations. These areas could range in size from a single protected tree or nest box to large fenced areas (currently two 55-ha snake fences exist on Guam). Optimizing the location of snake fences will be an iterative process using a combination

of tools, because the frequency, size, and placement of such fences will depend on 1) the identity of frugivore species within candidate frugivore assemblages and their habitats, 2) the sufficiency and spatial extent of the candidate frugivore assemblage, 3) the distribution of target tree species for which frugivore intervention will be most important, and 4) the spatial distribution of land use and ownership that will influence fence-placement feasibility. We will use complementary, linked approaches to this problem. To evaluate all possible locations for snake-fence placement, we will modify and use the ZONATION conservation planning software (Moilanen et al. 2005). ZONATION uses iterative removal of least optimal sites to produce hierarchical prioritization landscape maps, and has the flexibility to integrate spatial information on the distributions of target tree species. It can be modified to incorporate a species-specific spatial restoration function associated with the frugivore assemblage used for restoration and the decay in effectiveness moving outwards from snake exclusion areas. ZONATION will thus be used to evaluate a range of optimal fence placements, using land-use/land-cover maps, frugivore-specific seed dispersal kernels based on gut passage time, movement, and home range of dispersers, and frugivore habitat requirements as model inputs. The output will produce optimum locations and sizes of snake exclosures, given the cost of creating and maintaining these areas and the relative effectiveness for target tree species. These will be course-grained analyses, given the number of parameters under consideration, and thus we will use the more data-intensive FORMIND model to assess forest health 20, 50, and 100 years into the future based on the top models produced through the ZONATION process.
4.3: User's Guide: We will deliver a User's Guide of management options for restoring ecological function to Guam's forests. This will summarize the ecological role of each disperser species (Obj. 2 & 3) and describe the level to which each of the top 3-5 candidate frugivore assemblages maintains species diversity, forest structure, and an ability to recover from disturbance (Obj. 4.1). In addition, this User's Guide will present options for snake fence placement to maximize the utility of frugivores (Obj. 4.2).

C.3: MILESTONES AND DELIVERABLES

Time frames for completing significant events and tasks are outlined in the Gantt chart below. Completion of research components is indicated by a hash mark; these demonstrate when we expect to finish deliverables. Deliverables include yearly In-Progress Reviews, an Interim Report at the end of Year 3, a Final Report in September 2019, a User's Guide (as discussed above) in July 2019, and papers suitable for submission to peer-reviewed journals (between the end of Year 3 through Year 6).



In conjunction with our Interim Report and the completion of most of Obj.1 and all of Obj.2.1, we will have a Go/No-Go decision point. A "Go" decision for the remainder of the project is justified if at least one of the bird species is seen taking fruits of at least two native tree species (2.1) and in doing so, either increases seed germination through seed handling (1.1), increases survival through movement of seeds away from the parent tree or to treefall gaps (1.1), or disperses seeds to native and/or degraded forest (2.1b). A "Go" decision for the Micronesian Starling research on Guam (3.1b and 3.1c) is justified if the starling is found to perform the above dispersal services for at least one native tree species.

D. RESEARCH TEAM

Haldre Rogers (PI) is currently a Huxley Fellow in the Ecology and Evolutionary Biology Department at Rice University. Her research focuses on the ecological importance of vertebrates in forested systems. She has been working in the Mariana Islands since 2002, initially focused on BTS interdiction and more recently on the ecology of bird loss. 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. Dr. Rogers will take primary responsibility for overseeing the field research associated with plants, pigs and rodents. She will supervise two post-doctoral researchers and one graduate student. One post-doc will focus on the plant-centric research (Obj. 1), a second post-doc will focus on landscape-level modeling (Obj. 4) and synthesize the results for effective transfer to the DoD. A MS student will conduct the research on feral pig and rat dispersal (Obj. 2 & 3). Dr. Rogers will spend 3-6 person-months/year on the project. Salary is requested for thirteen months.

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 and the nest success of forest birds in native and non-native forest on Saipan. In collaboration with USGS, Dr. Savidge has led research on control and biology of the invasive brown tree snake on Guam for more than 15 years. She will take primary responsibility for overseeing field research with birds and will provide expertise on the snake fence modeling component of the research. Dr. Savidge will commit 2-3 person-months per year to the project, which will include supervising 2 postdoctoral research associates (one associated with birds on Saipan and the other studying Micronesian Starlings on Guam).

Joshua Tewksbury (co-PI) is the director of the Luc Hoffmann Institute at the World Wildlife Fund and a Professor at the University of Washington. He has extensive experience with nest searching, feeding trials, and conservation planning at local and global levels. He is the advisor of Evan Fricke, a graduate student working in the Mariana Islands who has been and will continue to be involved in the project. Dr. Tewksbury will commit an average of 1 person-month per year on the project. No salary is requested.

Key co-performers: 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. Creighton Litton (University of Hawaii-Manoa) is an expert on the ecological impacts of feral pigs in Hawaii; he will provide guidance on feral pig research. **Key end-users and collaborators:** Ruben Guieb and Leanne Obra (AAFB, letter attached), Earl Campbell (USFWS, letter attached), Paul Radley (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.

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, Creighton Litton, Paul Radley, and Ran Nathan will be in-kind contributions. No other agency will be contributing funds to the project.

F. TRANSITION PLAN

Transitioning our results to end-users is an important component of our proposal. Our key end-users include those responsible for managing DoD and other lands 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. We will transfer our results in the following ways:

1. We will produce a report predicting the impact of disperser loss on karst forest of AAFB, based on the results of the plant-related research from Obj. 1, and present it to AAFB resource managers.
2. We will create a User's Guide of potential management options for restoring ecological function as described in Obj.4.3. We will disseminate our User's Guide to DoD resource managers and other key agencies in the Mariana Islands through a workshop on Guam at the end of our project.
3. Throughout our project, we will work closely with regional DoD resource managers at AAFB and NAVFACMARIANAS, and other key agencies to identify ways to incorporate their interests and concerns. We have been in contact with natural resource staff from DoD while developing this proposal. In addition, we will provide annual updates at the yearly BTS meeting.
4. Although our research will be directly applicable to the resource managers in the Mariana Islands, the strategy we take in this research will provide a roadmap for possible restoration of ecosystem function to other highly degraded systems. We will present our results at the National Military Fish and Wildlife Association meeting at the end of our project to reach a wider audience.
5. We will establish a web page where all results, models, and datasets are presented, and all data will 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

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. M., S. B. Jennings, J. HilleRisLambers, J. J. Tewksbury, and H. S. Rogers. 2013. Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. PLoS ONE 8:e65618.
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.
Cole, R. J., C. M. Litton, M. J. Koontz, and R. K. Loh. 2012. Vegetation Recovery 16 Years after Feral Pig Removal from a Wet Hawaiian Forest. Biotropica 44:463–471.
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.
Donatti, C. I. 2011, December 5. Ecological Studies on Seed Dispersal Networks: Insights From a Diverse Tropical Ecosystem.
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.
Engbring, J., F. L. Ramsey, and V. J. Wildman. 1986. Micronesian forest bird survey, 1982:

Saipan, Tinian, Agiguan, and Rota.
Engeman, R. M., G. Massei, M. Sage, and M. N. Gentle. 2013. Monitoring wild pig populations: a review of methods. Environmental Science and Pollution Research 20:8077–8091.
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.
Fricke, E. C., J. J. Tewksbury, and H. S. Rogers. 2014. Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. Ecology Letters.
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: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.
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.

Kerr, A. (Ed.). 2012, June 20. The Ecology of Invasive Ungulates in Limestone Forests of the Mariana Islands. University of Guam.

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.

Krull, C. R., D. Choquenot, B. R. Burns, and M. C. Stanley. 2013. Feral pigs in a temperate rainforest ecosystem: disturbance and ecological impacts. Biological Invasions 15:2193–2204.

Linnebjerg, J. F., D. M. Hansen, and J. M. Olesen. 2009. 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.

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.

Murphy, M. J., F. Inman-Narahari, R. Ostertag, and C. M. Litton. 2014. Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. Biological Invasions 16:63–71.

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.

Perez, G. 1970. Ecological Features of Philippine Turtle Doves on Guam. Trans. IX Internat. Congr. Game Biologists.

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.

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. B., W. C. Pitt, R. T. Sugihara, and G. W. Witmer. 2014. Biology and Impacts of Pacific Island Invasive Species. 11. Rattus rattus,the Black Rat (Rodentia: Muridae). Pacific Science 68:145–184.

Shiels, A., and D. Drake. 2011. Are introduced rats (Rattus rattus) both seed predators and dispersers in Hawaii? Biological Invasions 13:883–894.

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.

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.

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.

d. Supporting Technical Data

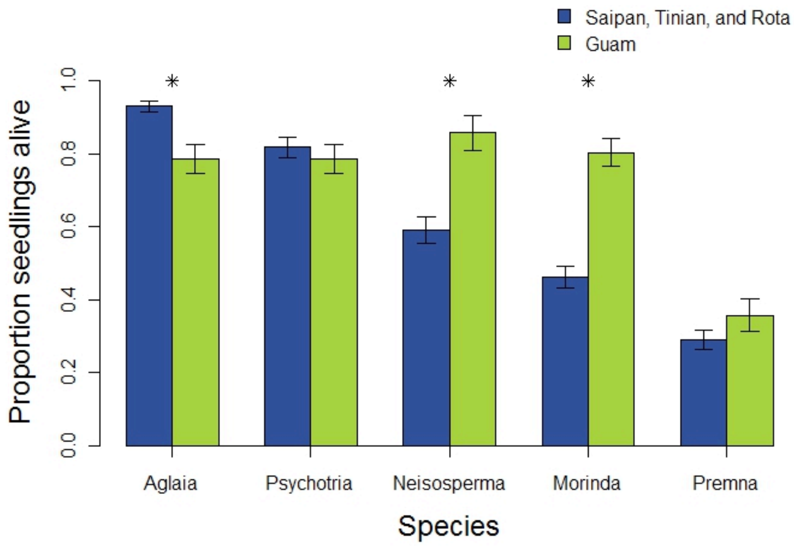


Fig. S1: Comparisons of seedling survival between forests without birds (Guam) and forests with birds (Saipan, Tinian and Rota) for five fleshy-fruited tree species. One species, *Aglaia mariannensis* had higher survival with birds, but the other four species either survived better on Guam (without birds) 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.

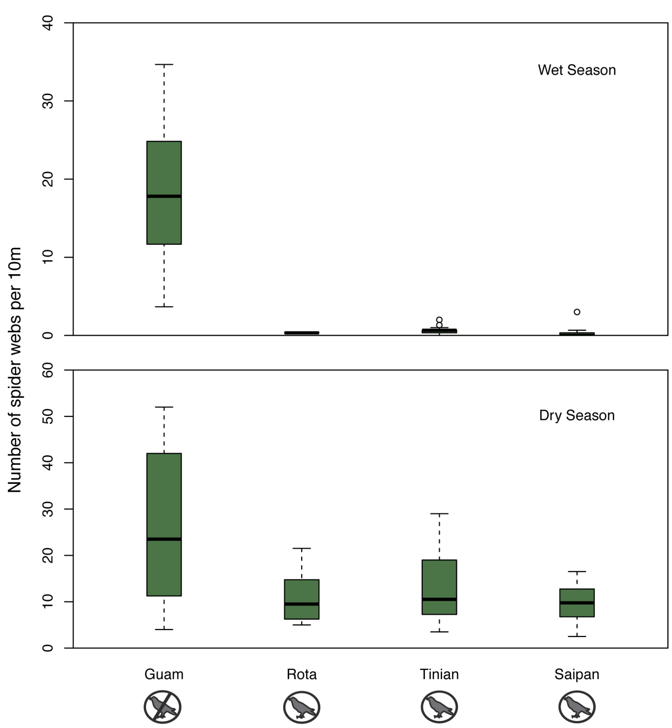


Fig. S2: Comparison of spider web abundance between Guam (no birds in forests) and nearby islands (with birds) during the wet season (top) and dry season (bottom). There were twice as many spiderwebs per 10m on Guam in the dry season and 40 times more spider webs in the wet season. This increase in spider 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.

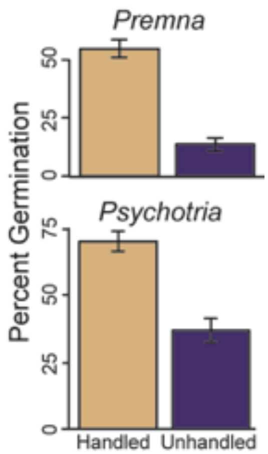


Fig. S3: Germination of seeds handled by birds versus whole fruits.

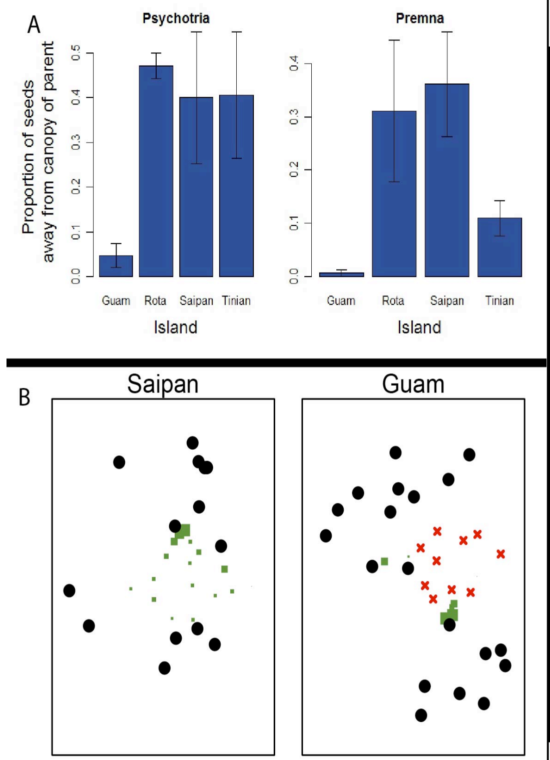


Fig. S4: A) Very few seeds landed in seed traps placed away from parent trees on Guam, as compared to Saipan, Tinian and Rota. B) In many cases, as demonstrated here for one site on Guam and one on Saipan, no seeds fell in traps over a 9 month seed trapping period. The black circles represent trees, 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.

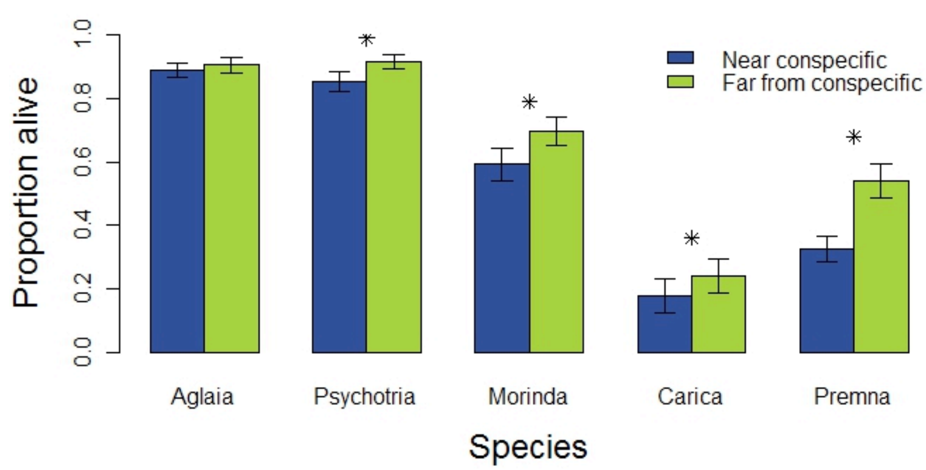


Fig. S5: Difference in survival for five forest tree species between seedlings planted near and those planted ‘far’ (~7+m) from conspecific trees. A star (*) indicates significant effect of distance in linear mixed effects models. Species are ordered by the strength of distance dependence, from no effect 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.

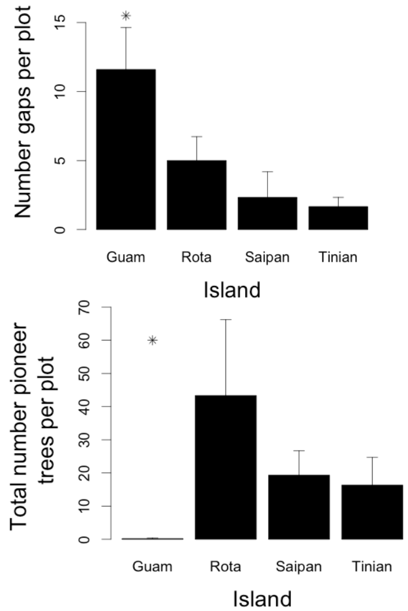


Fig. S6: Forest plots (60x60m) on Guam, an island without vertebrate dispersers, have a) more gaps, and b) fewer pioneer trees than plots on nearby islands with vertebrate dispersers.

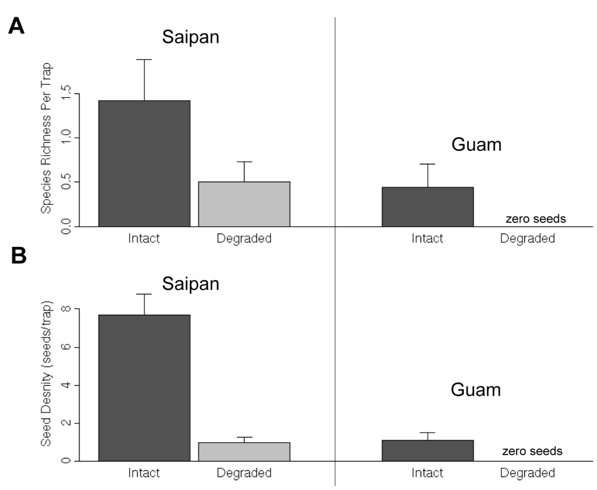


Fig. S7: Richness (A) and density (B) of seed rain from native forest species in traps placed in intact and degraded (*Leucaena leucocephala*) forest on Saipan (with birds) and Guam (without birds). Without birds, seed rain in intact forest is less diverse, and no native seeds reach degraded forest.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

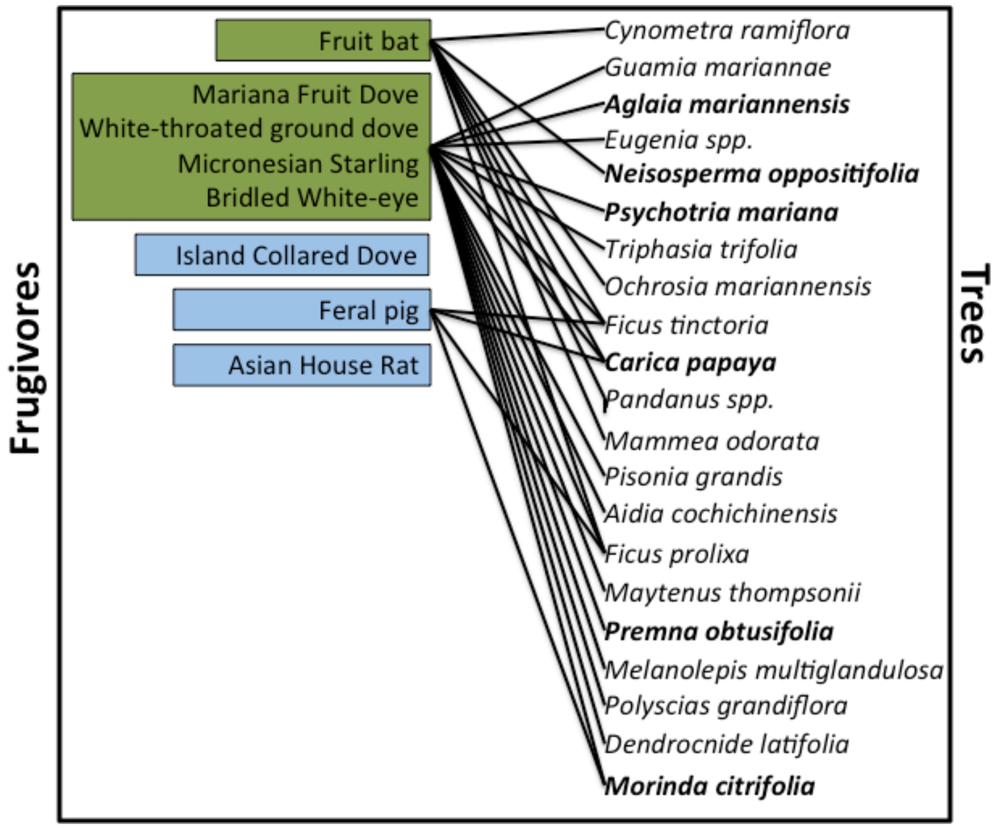


Fig.S8: Hypothetical seed dispersal network in the Mariana Islands. Green boxes indicate native frugivores, whereas blue boxes indicate non-native frugivores currently on Guam, and red indicates non-native frugivores that could be introduced to Guam. The tree species listed are (in order from top) the 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 the frugivores that could be used to restore dispersal services to Guam, 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	Uncertain
Feral pig	Non-native	Yes	Omnivore	Unknown
Rat	Non-native	Yes	Omnivore	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.