

Balancing the Good and the Bad: Assessing the Positive and Negative Effects of Alien
Species on Native Plant Demography

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Biology in the Graduate School
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ABSTRACT

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Abstract

Alien species are considered one of the primary threats to native plant populations and their control is often prominent among proposed management actions. While negative alien effects are well documented, there are also many ways that alien species can have positive effects on native plant populations that may actually contribute to their persistence. Moreover, the effect of alien species on native plants can change in magnitude and direction over varying abiotic conditions. The success of native plant populations is determined by a mix of ecological and genetic factors. Alien (and native) species and abiotic conditions could also drive selection of plant traits. In order to understand the drivers of native plant population success in the face of changing climate and increasing prevalence of alien species, it is vital to understand the relationship between genotype, phenotype, and fitness of native plants.

In chapter one, I quantified the effects of neighboring alien and native plants on all demographic rates in a population of the Hawaiian endemic plant *Schiedea globosa*, performing biannual censuses for 4 years to encompass relatively harsh and as well as benign seasons and years. The effects of alien neighbors were mixed but most often positive across many demographic rates in both harsh and more benign abiotic conditions, suggesting that alien neighbors benefit *S. globosa* plants through multiple mechanisms, such as nurse plant effects and associational resistance. The effects of

heterospecific native neighbors were less often positive, indicating fundamentally different effects of native and alien neighbors on the demography of the focal native. These mixed effects highlight the need to consider potential benefits of alien species in the management of threatened native plants and that those benefits may be altered by changing abiotic conditions.

In chapter two, I constructed population models for multiple *Schiedea* species across populations and years, using demographic rate regressions driven by the effects of alien and native neighbors, integrating the mixed effects of alien and native species on demographic rates of populations to project the net effect on population growth of native populations. The effects of alien and heterospecific native plant neighbors were mixed but most often positive across many demographic rates in both harsh and more benign abiotic conditions, suggesting that alien and native neighbors benefit native plants through multiple mechanisms, such as nurse plant effects and associational resistance. The effect of alien and heterospecific native neighbors on population growth was generally positive-- the mixed, but largely positive, net effects of alien and native neighbors on population growth highlight the need to consider potential benefits of alien, as well as native, species in the management of at-risk native plant populations, and that those benefits may be altered by changing

abiotic conditions, as indicated by differing effects across (and within) years and populations.

In chapter 3, I used paternal half-sibship pairs to measure the heritability of morphological traits under field conditions of the critically endangered *Schiedea adamantis*, which were found to be heritable in prior studies in greenhouse conditions, in reintroduced populations. I also performed a selection analysis, regressing fitness components against traits of outplants that I hypothesized might influence response to climate and alien and native neighbors to study the relationship between genotype, phenotype, and fitness of plants in restoration outplantings and assessing potential for evolutionary rescue. I found no significant heritability of any of the morphological traits. I did find evidence of selection, as leaf shape, area, and whole plant morphology had significant effects on fitness components (growth, survival, and reproduction), and significant interaction effects showing traits influenced fitness components differently at different levels of shade. Together, these results suggest that while variation in traits benefit individual plants in differing field conditions, these outplantings may not have the ability to respond to selection through evolution.

Dedication

To Hawaii, the place I am home, yet am always inspired to explore, discover, and learn.

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Introduction

Statement of Problem

Invasive species are considered one of the greatest threats to biodiversity worldwide (Vitousek et al., 1997). However, alien species could simultaneously have negative and positive effects on native species. Effects of alien species on native plant species can be direct (e.g., through consumption or competition for abiotic resources) or indirect (e.g., supporting populations of pollinators or making natives less apparent to enemies (e.g., herbivores) or mutualists (e.g., pollinators)) (Figure 1).

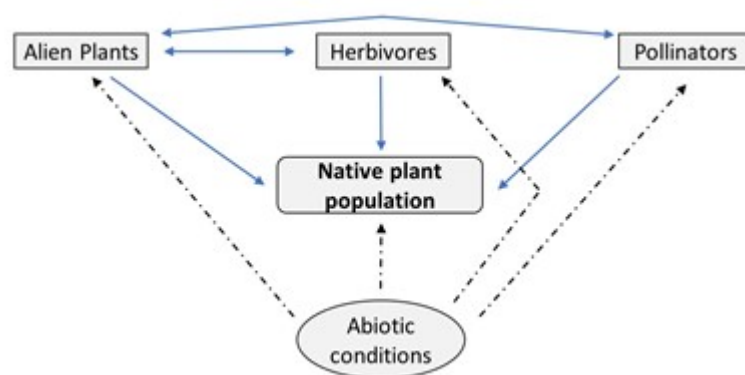


Figure 1: Species interaction diagram showing potential interactions likely to be important to focal native plant populations in ecosystems invaded by alien plants.

Indirect effects could be mediated through interactions with other invasives (e.g., non-native herbivores) or other native species. Furthermore, abiotic conditions, which are in flux due to ongoing climate change, could modify these indirect and direct effects, changing their magnitudes. While alien species are nearly universally considered in planning plant conservation and restoration, without tackling the complex ways that

invasive species may interact with each other and with multiple native species to determine the impact on focal natives, it is likely that control of invasive species will not be implemented in the most efficient and productive way. A better understanding of the positive and negative effects of invaders is of general importance in a world of greatly elevated anthropogenic species introductions. There are many anecdotal examples where alien species have not driven native species extinct. It is also possible that genetic variation in native plants produces sufficient phenotypic variation to allow native species to respond and persist under the pressure of alien species and changing climate (so-called "evolutionary rescue").

My research aims to help drive conservation decisions by developing a framework to determine if the net impacts of invaders are likely to be negative in order to direct limited management resources as efficiently as possible. I also seek to test whether genetic variation in native plants is sufficient to drive phenotypic variation in relevant traits to allow native populations to persist under changing climactic conditions and interacting with alien species. We need to identify traits that govern the balance of positive and negative effects of invaders on natives, so we can anticipate, without detailed study, which natives will be strongly impacted. **I aim to understand how alien species and climate directly and indirectly affect populations of native plants that differ in key traits and model how these interactions impact native plant populations**

into the future, and how genetic variation might drive phenotypic variation that drives response to alien species and climate.

Background

Invasive species have been traditionally viewed as detrimental and potentially disastrous for native plants (Simberloff, 1996), and there are many obvious ways invaders can have negative effects through competition for resources. However, there are several mechanisms by which alien species could also have positive effects on native plants. Alien plants could shelter natives from extreme abiotic conditions (Brooker et al., 2008), improve soil for native plants by fixing nitrogen or adding organic matter (Vitousek & Walker, 1989), or provide associational resistance against native or introduced herbivores (Parker & Hay, 2005). Alien herbivores could reduce native plant competition with native or alien neighboring plants (Hambäck et al., 2014). Alien plants could also increase pollinator visitation to native plants, by attracting them to areas with native plants (Masters & Emery, 2015) or by providing resources that increase pollinator populations (Tepedino et al., 2008). To understand the complete impact of invasive species on native plants, it is essential to consider these potentially beneficial interactions as well as any negative effects of invaders.

Neighboring plants are known to shelter plants from extreme abiotic conditions and there is no reason to discount the possibility that this could also be true when the neighbors are alien plants. The shifting balance between competitive and facilitative

interactions in co-occurring plants has been studied in depth. The most widely invoked prediction of this tradeoff is the stress gradient hypothesis, which predicts that co-occurring plants will serve as facilitative “nurse plants” in environments with high abiotic stress but will be competitors in more abiotically benign conditions (Callaway & Walker, 1997; Holmgren et al., 1997). Nevertheless, many exceptions to the simple stress gradient hypothesis have been observed, indicating that several mechanisms (including other biotic interactions and fine-scale variation in abiotic conditions) likely dictate when plants facilitate or compete with one another (Brooker et al., 2008; Holmgren & Scheffer, 2010; Maestre et al., 2009; Maestre et al., 2006). While invasive plants certainly have the potential to shelter natives from extreme abiotic conditions, such facilitation is likely modulated by variation in abiotic conditions or biotic interactions.

Alien plants can benefit native plants by improving the local environment. The primary mechanisms by which such facilitation can occur is through fixation of nitrogen or input of additional organic matter into the soil, processes invasive plants can be capable of doing at greater rates than native plants (Vitousek & Walker, 1989).

It cannot be assumed that invasive plants will always ultimately outcompete natives, cancelling any facilitative effects. In the majority of cases in which the competitive abilities of invasive and native plants have been compared, native species outperformed cooccurring invasive species under some conditions (Daehler, 2003).

Invaders don't always outcompete native species and abiotic, or biotic, conditions can tip the competitive balance between native and alien plants.

Alien plants can also benefit native plants by providing associational resistance against native or introduced herbivores. Neighboring plants affect interactions between a focal plant species and its herbivores, largely because plants vary in traits such as attractiveness and nutritional value to herbivores (Hambäck et al., 2014). The distribution and composition of neighboring plants can have an indirect, positive impact on native plants through reducing herbivory (Tahvanainen & Root, 1972). The interaction between herbivores, native plants, and invasive plants is context dependent (Lillian et al., 2018). Notably, increased density and diversity of neighboring plants can strongly reduce herbivory, especially by generalist herbivores (Castagneyrol et al., 2013), indicating that a plant surrounded by alien neighbors may be more resistant to herbivory than a plant with less dense or less diverse neighbors. However, other studies (Root, 1973) and plant apparency theory (Feeny, 1976) suggest that reduced herbivory with increased neighbors would be more likely with specialist herbivores, and novel interactions between native plants and alien herbivores could further complicate predictions of when neighboring plants are most likely to have beneficial effects. To evaluate when associational relationships with other plants will have beneficial (or negative) effects, it is necessary to consider many complex biotic and abiotic conditions, such as how climate influences population dynamics of herbivores and plants, density of

plant populations, variation in plant traits across the community, and whether herbivores are generalists or specialists (Underwood et al., 2014). However, beneficial effects clearly do occur and need to be considered to understand the net impact of invaders.

Alien herbivores can benefit native plants by reducing competition with neighboring native or alien neighbors. Herbivory has been found to reduce plant competition, dating back to Darwin's mowing experiment (Darwin, 1859), and subsequently in a variety of systems (Olf & Ritchie, 1998; Van Der Wal et al., 2000). While it is commonly predicted that generalist herbivores are more likely to prefer native species over invasive species, potentially due to lack of defensive traits (Blossey & Notzold, 1995), there is no consistent evidence that this is the case (Keane & Crawley, 2002). Invasive species are more likely to form dense, largely monotypic stands (Levine et al., 2003), potentially providing greater resources for herbivores than native plants, a potential benefit to native plants assuming they aren't completely excluded. If alien herbivores prefer invasive plants to natives, they could reduce competition.

Alien species can positively affect native plants by increasing visitation by pollinators. Many mechanisms have been proposed by which plant species compete with or facilitate one another for pollination (Mitchell et al., 2009). Invasive plants have been shown to have widely varying (including negative and positive) effects on biotic pollination of native plants due to variation in abiotic (primarily climate) and biotic

(density of both native and non-native plants) factors (Bartomeus et al., 2008; Bruckman & Campbell, 2014, 2016a, 2016b; Cariveau & Norton, 2009; Dietzsch et al., 2011; Lopezaraiza-Mikel et al., 2007; Masters & Emery, 2015). These pollination studies only assessed the effect of aliens on pollinator visitation to natives, so it is impossible to determine if the effect of alien plants on pollination was due to attraction of a constant pool of pollinators or increased populations of pollinators. There is some evidence that alien plants may sometimes increase pollinator visitation to native plants without increasing their reproductive success (Morales & Traveset, 2009), perhaps because reproductive success is not pollen limited, demonstrating the need to evaluate whether changes in pollinator visitation driven invasive by species actually impact reproduction and recruitment. Despite the prevalence of studies considering how invasive plants alter pollination of native plants, there is a lack of generalizable hypotheses for what might drive variable outcomes.

The breeding system of native plants is a trait likely to drive important differences in the effects of alien species and climate on population growth. Wind pollination of native plants rules out potential facilitative effects of alien species mediated through biotic pollination. Life history differences driven by evolution of separate sexes and pollination could modulate the effects of alien species on demographic rates. Breeding system could also make self-pollination less prevalent or impossible (through gynodioecy, dioecy, or self-incompatibility), making effects of

aliens on certain demographic rates more or less important to the net effect of alien species on population growth.

The fate of native plant populations is dictated by a combination of ecological and evolutionary factors (Lande, 1998). While native plant conservation and restoration frequently considers the genetic factors in planning, especially in reintroductions of rare plant populations (James, 2004; Maunder, 1992), the relative importance of genetics and demographic factors of population success are difficult to disentangle (Lande, 1988). A better understanding of the relationship between demographic rates, phenotype, and success of native plant populations would provide invaluable information to guide future conservation, especially when managing for alien species and climate change.

Even when acknowledging that invaders may have both positive and negative effects, most studies have focused on a single interaction or process, making it more likely that only positive or only negative effects will be found. Insufficient research has focused on the indirect effects of invasive species (White et al., 2006). Many of the ways invaders could impact native plants are not mutually exclusive, and it is clearly necessary to consider many ways invasive species can positively and negatively, directly and indirectly affect native species (Ricciardi et al., 2013). However, the impacts of alien species are often quantified in terms of their effects on coarse measures of communities such as native species richness (Parker et al., 1999). There are many mechanisms by which that alien species can positively affect native species. No studies have attempted

to quantify all these potential positive effects and integrate them with negative effects to comprehensively evaluate the effect of invasive species on native plant populations.

Significance of Research

As alien species have become ubiquitous worldwide, investigating the complex ways they impact native species will be essential to projecting the future of ecosystems. However, it is unlikely that the effects of alien species on native species are always negative. Integrating both positive and negative effects of alien species, and how they differ across native species varying in key traits, is essential to a better understanding of the fates of native species, particularly as humans increasingly introduce alien species and those species continue to spread. Using closely related congeners allows for comparison across breeding system and between populations experiencing different abiotic conditions. While there is strong evidence that many negative and positive, direct and indirect, effects of alien species drive native plant populations, no studies attempt to integrate the many effects of invaders in terms of native plant demography. Furthermore, no prior studies have attempted to select and compare traits (such as breeding system) of native plants that could predict the influence of interactions with suites of invaders. There is also no prior literature that uses the demographic impact of positive and negative effects of invaders to evaluate conservation management actions or reintroductions of rare and threatened native species.

In this dissertation, I have assessed the effects of alien species on native plant populations and the relationship between phenotype, genotype, and fitness in restoration outplantings.

In **Chapter 1**, I quantified the effects of neighboring alien and native plants on all demographic rates in a population of the Hawaiian endemic plant *Schiedea globosa*, performing biannual censuses for 3.5 years to encompass relatively harsh and benign seasons and years. By looking at effects of alien and native plants on demographic rates on a fine scale, both intra- and inter-annually, within a single population, I consider the potential mechanisms of effects of alien species on native plants.

In **Chapter 2**, I constructed population models for eight populations across four species and multiple years, using demographic rate regressions driven by the effects of alien and native neighbors. By using a structured population model to evaluate the outcomes of suites of interactions with alien species on native plant populations, I integrate the mixed effects of alien and native species on demographic rates of populations to project the net effect on population growth of native populations.

In **Chapter 3**, I used paternal half-sibship pairs to measure the heritability of morphological traits, which were found to be heritable in prior studies in greenhouse conditions, in reintroduced populations of a critically endangered native plant. I also performed a selection analysis, regressing fitness components against traits of outplants that I hypothesized might influence response to climate and alien and native neighbors

to study the relationship between genotype, phenotype, and fitness of plants in restoration outplantings and assessing potential for evolutionary rescue.

These chapters each address gaps in our understanding of invasion biology, population ecology, restoration ecology, evolution, and conservation biology. My research is an opportunity to compare alien plant effects within populations and species and among populations of native species varying in key traits. In addition to addressing important ecological questions, this research provides information that can be used directly in the conservation of native species, both through predicting the impact of management actions such as control of alien plants and herbivores and by providing evaluation of plant reintroductions, a key conservation tool.

Chapter 1: Positive effects outnumber negative effects of alien plants on an at-risk Hawaiian plant

1.1 Introduction

Invasive species are considered one of the greatest threats to biodiversity worldwide (Vitousek et al., 1997). Increasing anthropogenic disturbance and species introductions have made alien plants nearly ubiquitous (Office of Technology Assessment, 1993; Parker et al., 1999), and they are regularly assumed threaten the persistence and success of native plant populations (Byers et al., 2002; Wilcove et al., 1998). However, the effects of alien plants on native plants can be complex, for at least three reasons. First, aliens can have both negative and positive effects on native species (Ricciardi et al., 2013). Second, effects of invaders on natives can be direct (e.g., through competition for space or abiotic resources) or indirect (e.g., making natives less apparent to herbivores or mutualists). Third, abiotic conditions, which are in flux due to ongoing climate change, could modify the direct and indirect effects, changing their signs or magnitudes. While invasive species are nearly universally considered in planning plant conservation and restoration, without tackling the complex ways that alien species may interact with each other and with multiple native species to determine the impact on focal natives, management of invasive species is unlikely to be implemented in the most efficient and effective way.

While alien plants have been traditionally viewed as detrimental and potentially disastrous for native plants (Simberloff, 1996), there are several mechanisms by which

alien species could also have direct or indirect positive effects on native plants. Alien plants could shelter natives from extreme abiotic conditions (Brooker et al., 2008), improve soil for native plants by fixing nitrogen or adding organic matter (Vitousek & Walker, 1989), provide associational resistance against native or introduced herbivores (Parker & Hay, 2005), or facilitate the pollination of native plants (Bjerknes et al., 2007; Charlebois & Sargent, 2017; Schweiger et al., 2010). To understand the complete impact of invasive plants on native plants, considering these potentially beneficial interactions as well as any negative effects of invaders becomes essential.

The effects of alien plants on native plant populations can change in direction and magnitude through time and space with changing external environmental conditions. The Stress Gradient Hypothesis (SGH) (Bertness & Callaway, 1994) provides a framework to predict the conditions under which one species will have a positive or negative effect on another. The SGH predicts that: 1) when consumer pressure is low and abiotic conditions are benign, species will exert negative effects on one another through competition; 2) when consumer pressure is high, positive interspecific effects mediated through associational defense against consumers will become more likely; and 3) when abiotic conditions are harsh, species will be more likely to exert positive effects on one another by ameliorating the abiotic conditions. While predictions of the SGH sometimes fail (Holmgren & Scheffer, 2010; Lortie & Callaway, 2006; Maestre et al., 2009; Maestre et al., 2006; Malkinson & Tielbörger, 2010; Smit et al., 2009), the SGH provides a

starting point to predict changes in direction and magnitude of species interactions (He et al., 2013) that can easily be applied to the interaction between alien and native plants.

When applied to alien species, the SGH would predict that while aliens may have negative effects on natives under benign conditions, their effects may be positive under more stressful abiotic conditions or when consumers (either native or exotic) are abundant. If positive interactions occur during high stress or high disturbance conditions, suppressing alien plants could negatively affect native plants at the worst time. Ultimately, the balance of positive and negative effects of alien species will determine their long-term effect on native plant populations, and net positive effects would argue against control of aliens, even if their effects are sometimes negative.

While the SGH has been invoked largely to predict how the effects of species interactions will vary across spatial gradients in abiotic conditions (Armas et al., 2011; Louthan et al., 2018), it can also be applied to varying levels of abiotic stress across different seasons in a single year. In many tropical and sub-tropical areas, abiotically stressful hot, dry summers alternate with comparatively benign cool, wet winters, (in contrast with higher latitudes where stress is brought on by winter cold). This pattern provides an opportunity to study how changes in abiotic conditions can drive differences in the effect of alien plants on a native plant population. Furthermore, following a population through multiple years, when seasonal changes may be stronger

or weaker, can capture the wide variation in abiotic stress that native plants are likely to experience.

Understanding how the effect of alien species changes as abiotic conditions change is essential to effectively plan for the conservation of native plant biodiversity in the future, particularly considering ongoing climate change. As climatic conditions change, the mix of negative and positive effects of alien species on native plant populations could shift the net effect from negative to positive, or vice versa. If the conditions under which alien plants have positive effects became more frequent in the future, or negative effects became less frequent, control of alien plants could become less desirable. While it is still likely that management of alien plant species will be an essential component of the conservation of native plants, understanding when and how alien plants can have positive impacts on the vital rates of native plants will provide critical information on how to plan and implement conservation actions.

In this study, I investigated the impacts of alien plants and herbivores on a large population of the Hawaiian native plant *Schiedea globosa*, across wet and dry seasons over three and a half years. In the focal population, *Schiedea globosa* grows with a wide variety of neighbors, native and alien, including native and alien grasses, forbs, and woody shrubs. Alien generalist herbivores exist throughout the population, bringing about the potential for indirect effects of alien plant neighbors by modulating the effects of alien herbivores. I combined an observational study with experimental manipulation

of alien abundance to estimate the aliens' impact on all aspects of the demography of *Schiedea globosa*: survival, growth, reproduction, and recruitment. I use these data to address the following questions:

What are the negative and positive effects of alien and native neighbors on *Schiedea globosa*?

How strong are the direct and indirect effects of alien neighbors on demographic rates of the focal native plants and when are they negative or positive?

Do the net effects of alien neighbors vary seasonally?

How can likely future climate change be expected to change the net effects of alien plants on *Schiedea globosa*?

1.2 Methods

1.2.1 Study species

The genus *Schiedea* is an endemic Hawaii genus of 32 extant species representing remarkable diversity of breeding systems, habitats, and morphologies (Wagner et al., 1999; Wagner et al., 2005). Most of the species are rare, single-island endemics, with 23 federally listed as endangered (USFWS, 2010). *Schiedea globosa* is a subdioecious, suffruticose subshrub scattered in populations restricted to North and Northeast facing coastal cliffs and rocky slopes on the islands of Oahu, Molokai, Maui, and Hawaii. *S.*

globosa is one of the most widespread species in the genus and likely was able to disperse between islands via rare rafting across deep oceanic channels (Dixon et al., 2011; Wallace et al., 2009).

Despite being one of the more abundant species in the genus, *S. globosa* often occurs in areas adjacent to anthropogenic disturbance. It is threatened by fire promoted by alien grasses (Ellsworth et al., 2014) and other disturbance (such as human coastal development and trampling), leading to increased prevalence of alien plants, now ubiquitous throughout all habitat of *S. globosa*. While it is moderately abundant compared with the largely endangered native Hawaiian flora as a whole (Sakai et al., 2002), it is a species of conservation concern facing many of the same threats as species at even higher risk of extinction.

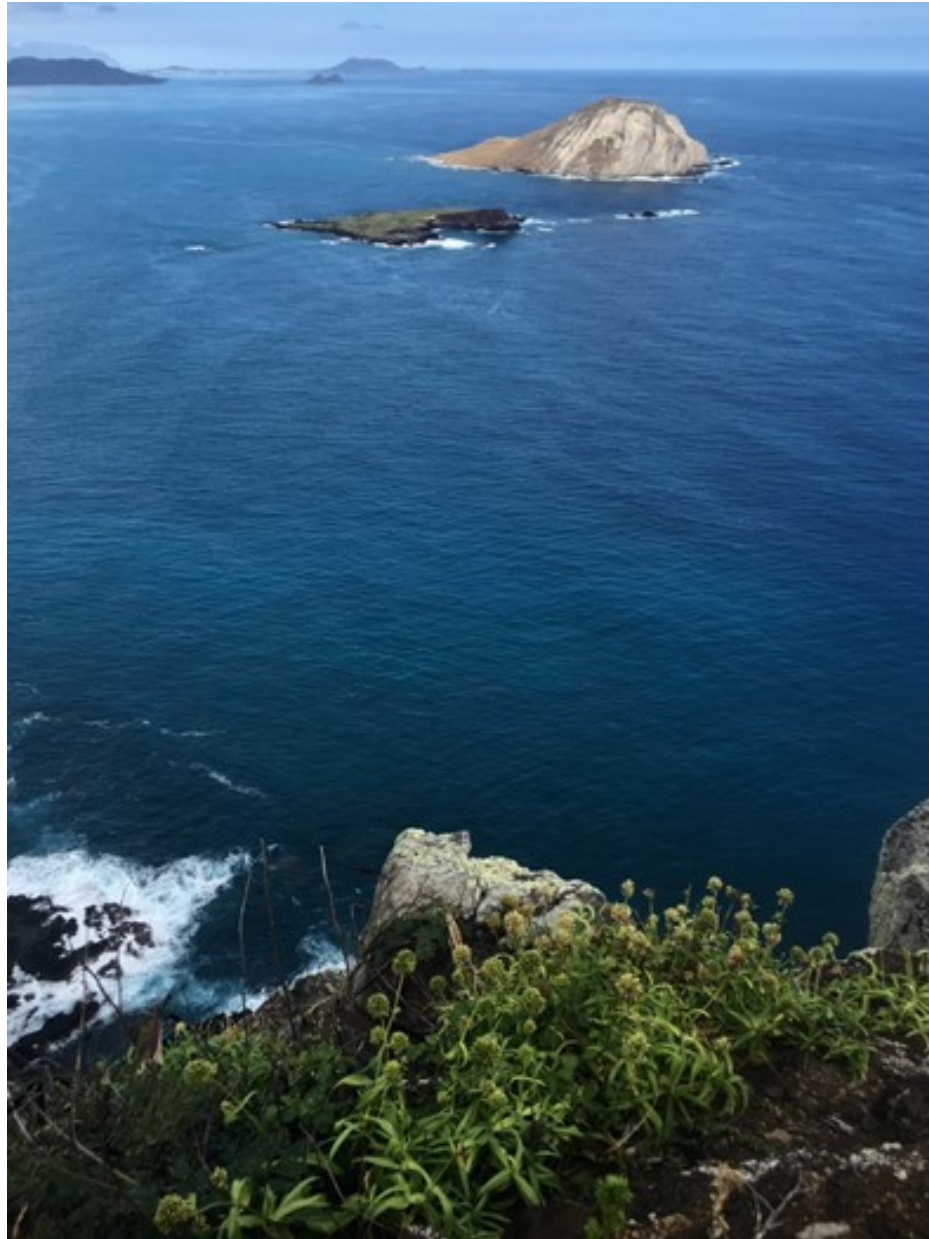


Figure 2: *Schiedea globosa* at Makapuu, showing cliff-edge habitat on north facing slopes and alien neighbors

1.2.2 Study population

I performed this study in the *S. globosa* population at Makapu'u (21. 308°, -157.51°), within the Kaiwi Coast State Park. This population covers the Northeast facing slopes and cliffs of Makapuu from approximately 60m to 170m above sea level (fig. 2). While the larger area of Makapuu is dominated by alien plants, on the relatively moist and shady slopes where *S. globosa* occurs, the plant community is a patchwork of native and alien grasses and shrubs, and small alien trees. The great majority of neighbors of *S. globosa* are heterospecific. Some *S. globosa* individuals occur with completely native or alien plant neighbors, many occur with both native and alien neighbors, and some occur on exposed rocky areas with no plant neighbors. The most common native plants are *Eragrostis variabilis*, *Sida fallax*, *Euphorbia degeneri*, *Lepidium bidentatum*, and *Lipochaeta integrifolia* and the most common native plants are *Chloris* spp., *Leucaena leucocephala*, *Casuarina equisetifolia*, *Schinus terebinthifolius*, *Emilia fosbergii*, and *Emilia fosbergii*. The primary herbivores found in the population are alien molluscs, Giant African Snails (*Lissachatina fulica*) and various slug species (*Veronicella leydigi*, *Vaginulus plebeia*, *Limax maximus*).

1.2.3 Demographic data collection

In summer 2017, I established demography transects throughout the core of the focal population ranging from 70-150m above sea level. Many plants are located on cliffs and are inaccessible, but ledges allow for walking access, allowing some plants on cliffs

to be included in transects (fig. 1b). I established 6 permanent transects ranging from 18-60 m in length depending on topography and extent of plants. All plants within 2 m on either side of the transect tape through the center of the transect were included in the study for a total of 383 unique focal plants across the four years. Each individual plant was tagged, and its unique location within the transect was recorded. From Summer 2017 to Summer 2020, the populations were visited twice a year, in July during the hot, dry season and in January, during the cooler, wet season (altogether, the data includes 1872 individual plant x half-year transitions). At each census, I measured survival, size (vegetative area), and fecundity (number of fruiting heads, only during the wet season censuses). *S. globosa* flowering begins in the fall and fruit are set in the winter, so a single census in January captures all reproductive output for the year.

A 4x1 m quadrat was randomly selected for every 10 m of each transect to record the number of recruits each census. Each wet season, all new recruits were tagged with a toothpick and counted, and surviving recruits from previous seasons were counted. Each summer, surviving recruits from the most recent winter and previous seasons were counted. Once the recruits exceeded 5 cm, the smallest size observed flowering in the population, they were designated adults and included in continuous size-based demography measurements.

1.2.4 Characterization of neighbors

For every plant in the transects, I characterized the neighbors using photographs taken during each census. I visually characterized the percentage cover of natives and aliens as well as the total neighbor cover within a 50cm radius of the focal plant. The same characterization was used to record the native, alien, and total cover within each recruitment plot. The sum of bare ground, native cover, and alien cover may exceed 100%, as native and alien cover often overlaps, including overtopping by shrubs and trees.

1.2.5 Demographic rate regressions

I performed all data processing, analysis, and visualization using R v. 4.0.1 (R Development Core Team, 2021). For all models, I tested all possible interactions between predictor variables including factors up to three-way interactions. I conducted model selection by dropping non-significant effects (using analysis of variance tables from the R-package 'car'(Fox et al., 2012)) from each model until only significant predictor variables remained in and the final models.

I modeled growth (linear) and survival (binomial) dependent on size using mixed effects regressions (using the R-package lme4) (Bates et al., 2011) with season (wet vs. dry) and year as fixed effects (factors), and transect as a random-intercept effect. Year and season were included as categorical variables. In the full growth model including

season as a predictor, season affected size in the second year through interactions with size in the first year, year, and alien cover. The different seasonal transitions represent growth under very different conditions, and abiotic conditions differ more between seasons in a single year than between the same season across years. Because of the ecological differences between seasons, and because I found an interaction between season and neighbor effects, I also fit separate growth regressions for the wet (growing) and dry(non-growing) seasons in order to interpret the season-specific neighbor effects. As there was no significant effect of season on survival, I did not fit separate models for growing and non-growing season survival.

I regressed number of fruiting heads (in the wet season) against size using a hurdle negative binomial mixed model (using the R-package 'glmmTMB')(Magnusson et al., 2017) with year as a fixed factorial effect and transect as a random-intercept effect. Fruiting only occurs once annually, so season was not included as a random-intercept effect. I modeled recruitment using a hurdle Poisson regression (using the R-package 'glmmTMB')(Magnusson et al., 2017), with year (factor) as a fixed effect and transect as a random-intercept effect and with fruiting heads per area each recruitment plot tested as a predictor variable for recruitment. Survival of recruits to the following year was modeled using a mixed effects binomial regression (using the R-package 'lme4')(Bates et al., 2011) with year as a fixed effect and transect as a random-intercept effect.

1.2.6 Manipulation of neighbors and water supplementation

In order to test if the effects of alien neighbors were spurious (e.g., *Schiedea* and aliens performing well in the same high-quality locations) and to increase the naturally occurring variation in alien neighbor cover, I performed an alien neighbor removal experiment. In 2018, I combined neighbor removal with a factorial water supplementation treatment to simulate the effects of an additional heavy summer precipitation event. I randomly assigned 50 plants within existing demography transects to be assigned to an alien neighbor removal group, 50 plants to a water supplementation group, 50 to receive both a water and alien removal treatment, and 50 to a control group. Treatments included a fairly equal distribution across plant sizes. For the neighbor removal treatment, in July of 2018, I cleared all alien plants from within a 50cm radius of focal *S. globosa* assigned to the alien neighbor removal treatment group, clipping all alien plants at the base to minimize soil disturbance. Plants assigned to the water supplementation treatment received 500ml of water at their base once in July of 2018. In 2019, I conducted a second neighbor removal experiment. I randomly assigned 70 plants within existing demography transects to an alien removal treatment group and 70 to a control group. When a random treatment assignment would affect adjacent demography plants, all plants affected were also assigned to that treatment. I collected demographic data on all experimental plants as part of the biannual censuses of the population.

To test if the effect of the alien neighbor removal was different than the effect of naturally occurring alien neighbor cover, I fit separate regressions for growth, survival, and fecundity with only size, alien cover, and neighbor removal treatment (removal vs control) as predictor variables, including testing for interaction effects between alien cover and neighbor removal treatment. There were no significant interactions between year or alien cover and the neighbor removal treatment in any models. As this indicates there was no difference between treatment and naturally occurring variation in alien neighbor cover, I removed the alien removal treatment as a predictor variable from all models.

1.2.7 Seed sowing experiment

To complement the observational study of recruitment, I performed a seed sowing experiment near the core of the demography population, sowing seeds in the early summer of 2017 and 2018. Seeds were collected from 40 individuals outside of demography transects throughout the population and pooled. One hundred seeds were evenly sown into each of 24 marked 15 cm x 15 cm plots each year, split evenly between two sites (~100 m apart, separated by a small ridge)—with three plots per site in each of four treatments: bare soil, 80-100% cover of native grass, 80-100% cover of alien grass, and 30-50% cover of native and alien grass (80-100% total cover). In addition, two unsown control plots of each cover type were marked at each site to monitor for ambient seed rain. I observed no seedlings in the unsown control plots, thus only raw numbers of

seedlings in seed sow plots were analyzed. Each year, three sown plots of each cover type were randomly selected to be watered with 500 mL of water when seeds were sown and again in July of Year 2. Starting the winter following sowing, plots were monitored for seedlings in January, March, May, and July for two years. Seedlings were counted, marked, measured, and followed over subsequent censuses.

As only a single new germinant was observed after the first census of the seedling plots, I considered the number of seedlings at the first census in January following sowing to be the total number of seedlings emerging for each plot. I performed three binomial regressions with cover type, sowing year, and watering treatment as categorical predictors of initial germination (total number of emerging seedlings out of 100 seeds sown), survival from first monitoring to final monitoring (surviving seedlings out of number of initially emerging seedlings), and surviving seedlings (number of surviving seedlings out of 100 seeds sown) at the final monitoring point, testing for differences between groups and interactions, treating year as a factor and site as a random effect.

1.3 Results

1.3.1 Growth

In the wet season, plants grew in size on average from the previous (dry) season and most individual plants grew (fig. 3). Alien neighbor cover had a small but significant positive effect on growth (fig. 3 $p < 0.001$), indicating that plants with more

alien neighbor cover had slightly higher growth, but there was no significant effect of native cover. There was a significant effect of year ($p < 0.001$) indicating that wet season growth varied between years, but there was no significant interaction between year and alien cover, suggesting that the effect of alien cover is consistent across wet seasons that varied in moisture (fig. 2).

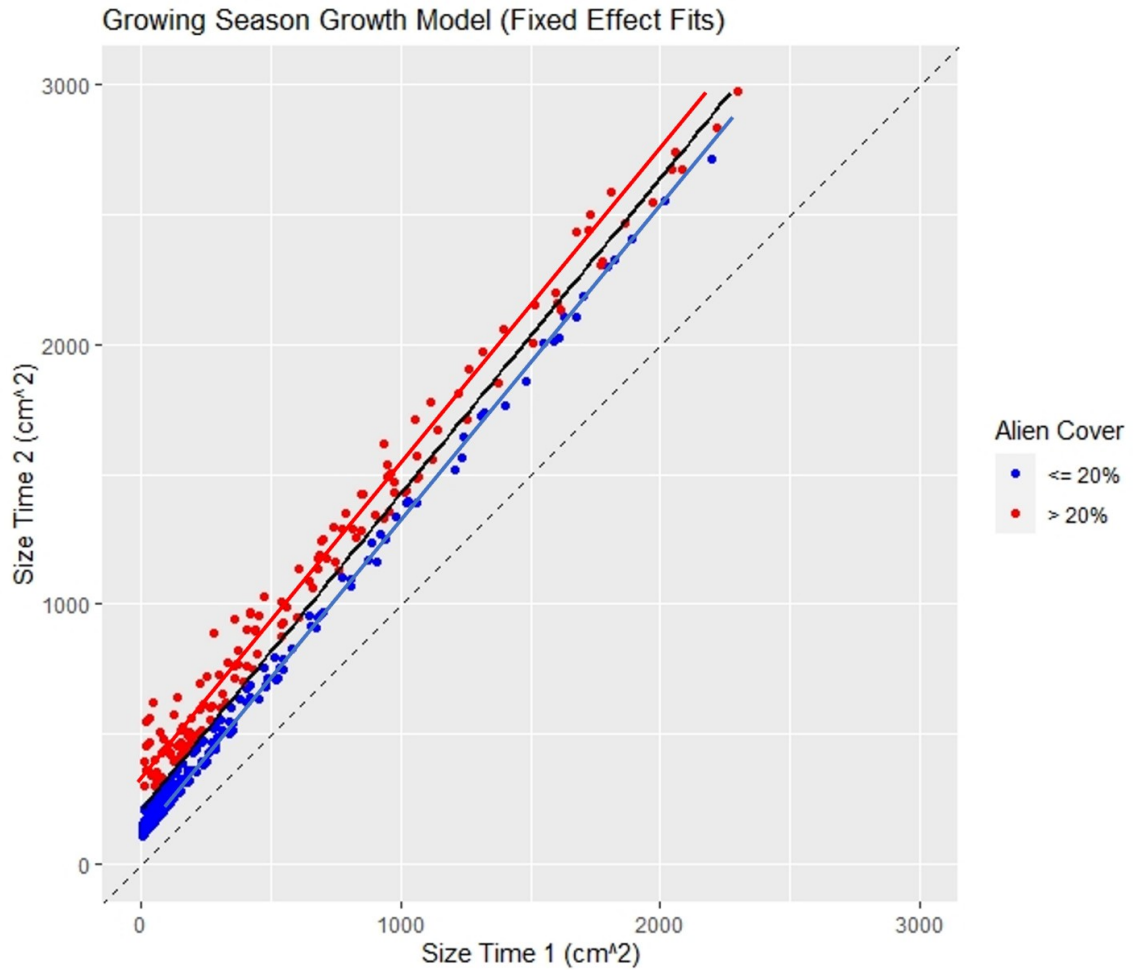


Figure 3: Wet season growth model: Model predictions (omitting random intercept effects) of changes between censuses by alien cover; plants above or below the 1:1 line (dashed) represents growth or retrogression, respectively. Fitted lines are shown for model predictions for all plants (black), and plants at the 25th (blue) and 75th (red) percentiles of alien cover. Plants grew on average and there was a slight but significant positive effect of alien cover on growth

In the dry season, plants retrogressed in size slightly on average from the previous (wet) season (fig. 4). The best regression model of size at the end of the dry season vs size at the start of the dry season included significant interactions between size and native neighbor cover (fig. 4c, $p < 0.001$), size and alien cover (fig. 4d, $p = 0.04$), and size and year ($p < 0.001$), and the main effects of alien neighbor cover (fig. 4a) and native neighbor cover (fig. 4b) were both negative. High cover of both alien (fig. 4c) and native (fig. 4d) neighboring plants led small individuals to retrogress even more but led large individuals to retrogress less.

However, there were significant interactions between size and native neighbor cover (fig. 4, $p < 0.001$), size and alien cover ($p = 0.04$), and size and year ($p < 0.001$). The interactive effects of size and cover of both alien and native plants show that alien and native neighbors (figs. 4c and 4d) suppress the growth of small individuals but enhance the growth of large individuals.

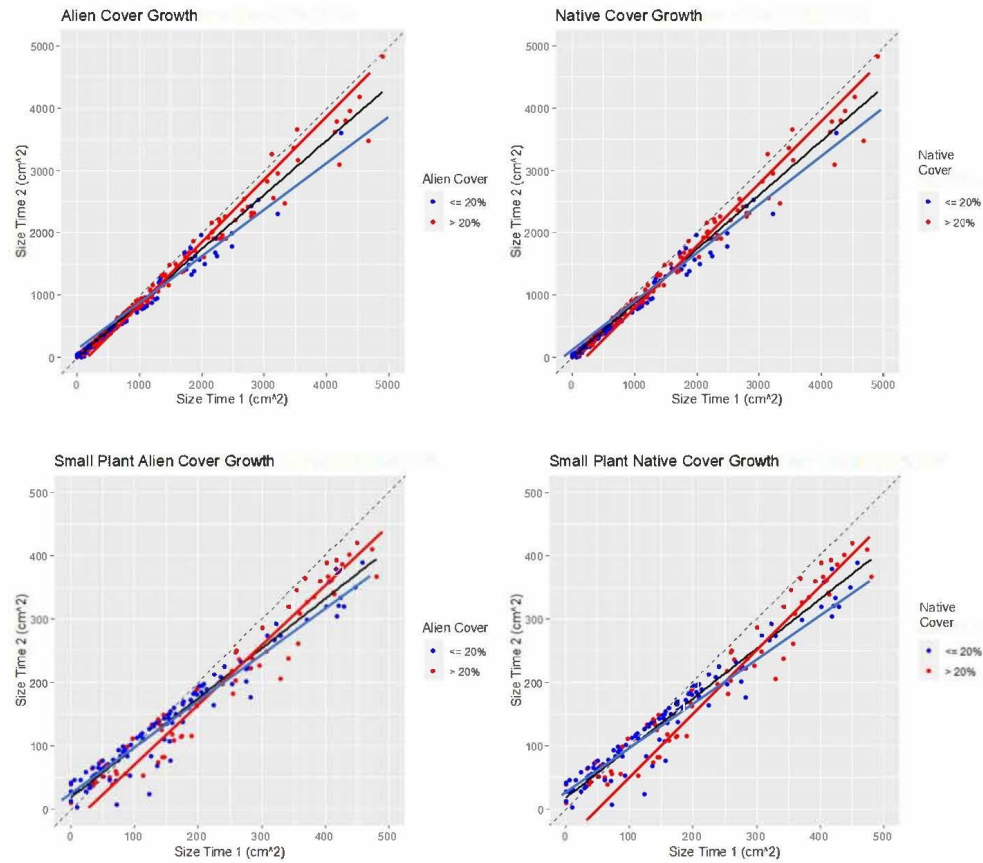


Figure 4: Dry season growth model: Model predictions (omitting random intercept effects) of changes between censuses by alien (panels a and c) and native (panels b and d) cover; plants above or below the 1:1 line (dotted) represents growth or retrogression, respectively. Fitted lines are shown for model predictions for all plants (black), and plants at the 25th (blue) and 75th (red) percentiles of alien cover percentage. Panels c and d show detail of plants < 500cm² to show size by cover interactions.

1.3.2 Survival

Size had a significant positive effect on survival ($p < 0.001$), but alien cover had no effect. While the positive main effect of native neighbor cover was not significant,

there was a significant ($p=0.03$) negative interaction between size and native neighbor cover-- a negative effect of native cover that was for large, but not small plants. Year was a significant predictor of survival ($p=0.02$). The year 2020 had far lower survival than all other years.

1.3.3 Fecundity (Fruiting)

Native cover had a positive effect (fig 5b, $p=0.03$) on the number of fruiting heads conditional on plants fruiting at all. There was a significant negative interaction between size and alien cover (fig 5a, $p<0.01$) in the conditional component of the model, indicating that larger fruiting plants with high alien cover had fewer fruiting heads. The interaction between cover and year had a significant positive effect in the probability of producing any fruit (the zero inflated portion of the model, $p<0.01$), indicating that plants with higher alien cover were more likely to produce fruiting heads in some years. Size had a positive, significant effect on the number of fruiting heads in both the conditional ($p<0.001$) and zero-inflated ($p<0.001$) components of the model. Year had a significant effect of fruiting in both the conditional ($p<0.001$) and zero-inflated ($p<0.001$) components of the model.

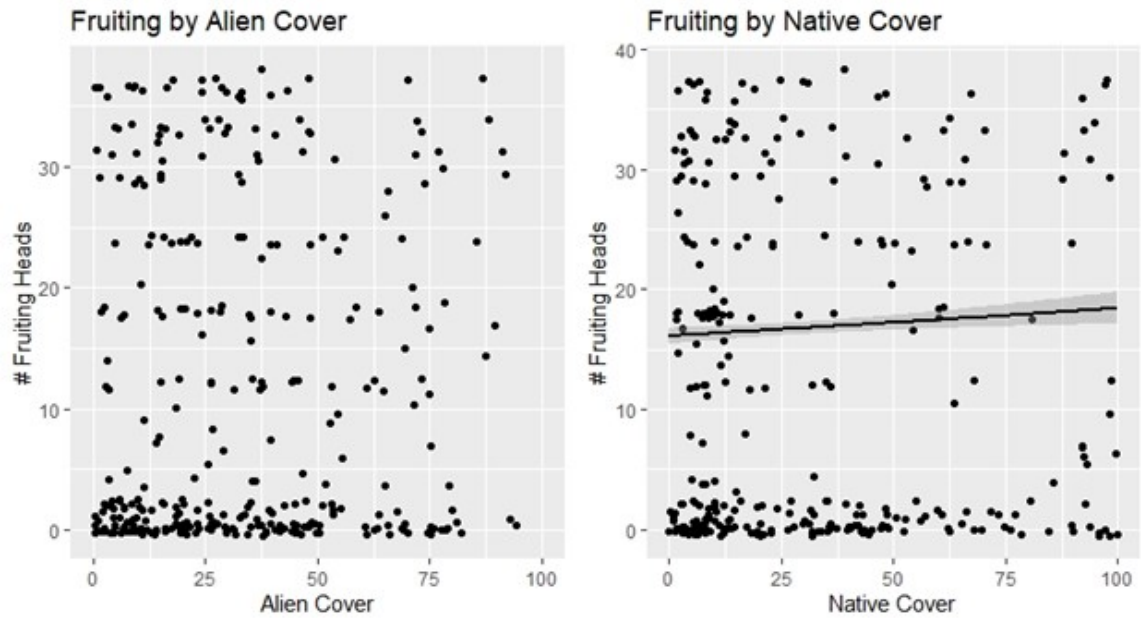


Figure 5: Fruiting by alien (a) and native (b) cover. Model line on b represents Poisson regression conditional on producing fruit

1.3.4 Field Recruitment and Recruit Survival

The number of new recruits did not differ by year and was not influenced by the number of fruiting heads in the areas with 5m of the recruitment plots, indicating seed rain is fairly uniform across the area, so I omitted fruiting heads per area from final models of recruitment. Recruitment was significantly higher in recruitment plots with higher native plant cover (fig. 6a, $p < 0.001$) and there was no significant effect of alien cover on number of recruits (fig. 6b).

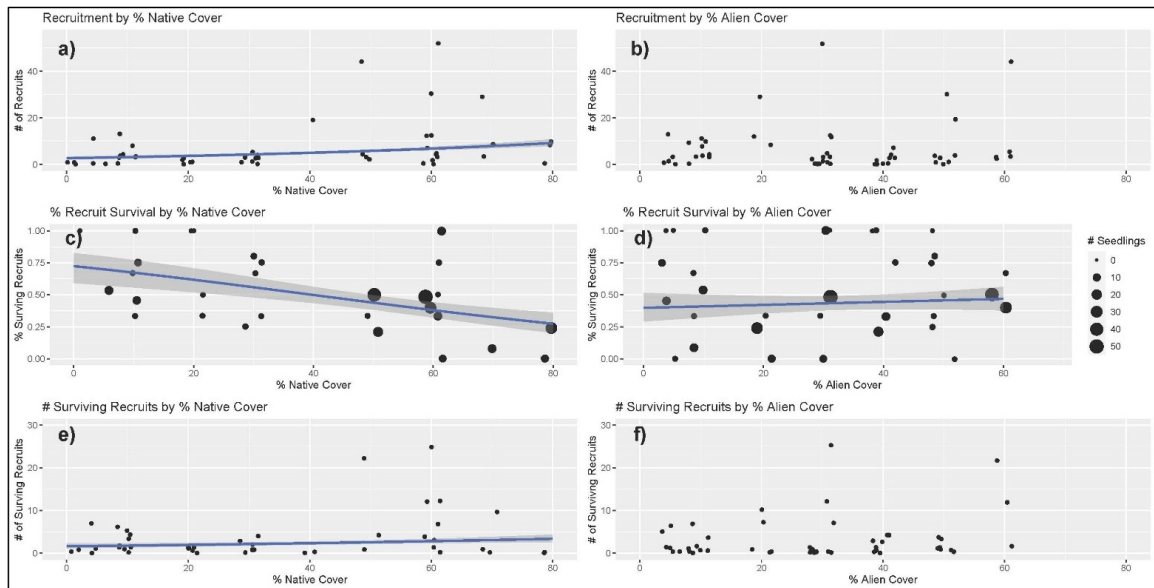


Figure 6: Recruitment, % recruit survival, and number of surviving recruits by native (a, c, e) and alien cover (b, d, f). Points in c and d are scaled by number of initial number of seedlings per plot (as show in a and b). Best fit model lines (omitting random effects) are shown for panels with a significant effect of cover (Poisson regression for a, e, binomial regression for c, d).

Recruit survival was significantly lower in recruitment plots with higher native cover (fig. 6c, $p < 0.001$) and significantly higher in recruitment plots with higher alien cover (fig. 6d, $p = 0.03$), but this effect was small-- as alien cover goes from 0% to 80%, recruit survival increased from just over .35 to nearly 0.5. Recruit survival varied significantly over years ($p = 0.04$), with survival from 2019 to 2020 higher than the other two years. The total number of surviving recruits was higher in plots with higher native cover (fig. 6e, $p = 0.02$) but not significantly higher with higher alien cover (fig. 6f).

1.3.5 Seed sowing experiment

Site had no effect on the number of emerging seedlings, the survival of seedlings, or the number of surviving seedlings, so it was removed from the models. Cover type had a significant effect on number of seedlings per plot (fig. 7a, $p < 0.001$). Bare ground plots had higher numbers of than seedlings of the 3 other cover types, followed by alien cover plots, then native and mixed cover plots. Plots sown in 2018 had significantly fewer seedlings ($p < 0.01$) and watered plots had a significantly higher number of seedlings than un-watered plots ($p < 0.01$). The interaction effect between cover type and year sown was negative with even fewer seedlings in bare ground plots in the lower seedling year. Watering treatments had a greater positive effect on total seedlings in 2018 than in 2017.

Cover type had a significant effect on seedlings survival ($p < 0.001$, fig. 7b), with bare ground having much lower survival than other cover types. Seedlings from the year 2018 had significantly greater survival than 2017 seedlings ($p = 0.02$). Interactions between year and cover ($p = 0.01$), cover and water treatment ($p = 0.02$), and cover, year, and water treatment ($p = 0.01$) had significant effects on seedling survival, indicating there is a complex relationship between cover and abiotic conditions (which vary by year and with treatment) and survival of seedlings.

Cover type had a significant effect on the number of seedlings surviving, but unlike initial seedlings ($p < 0.001$), bare ground had the fewest surviving seedlings (fig.

7c). The number of surviving seedlings was significantly less for plots sown in 2018 than 2017 ($p < 0.01$). The number of surviving seedlings did not significantly differ between unwatered and watered plots ($p < 0.01$). There was a significant interaction effect of cover type and 2018 sown plots and a significant 3-way interaction effect between cover type, 2018 sown seeds, and receiving the watering treatment.

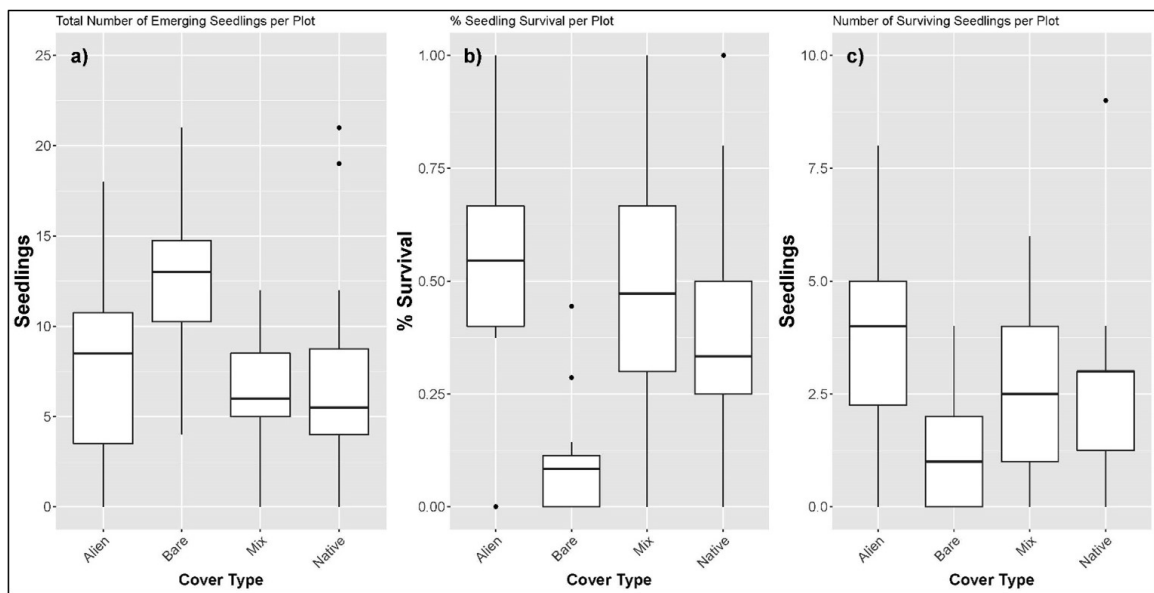


Figure 7: Boxplots of number of initial emerging seedlings, % survival of emerged seedlings, and number of surviving seedlings by cover type. Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

1.1 Discussion

I have shown that the effects of alien plant neighbors on a native plant vary in magnitude and direction at many levels: across vital rates, between wet and dry seasons, between good and bad years, and between small and large plants (Table 1). The effects

of heterospecific native plant neighbors also vary, sometimes mirroring the effects of aliens but often in differing in direction and magnitude, suggesting that there are functional differences between alien and native neighbors. However, there is no evidence that alien neighbors are fundamentally worse for the demography of this native plant population than native neighbors. In fact, many of the effects of alien neighbors were positive. Thus, in the short-term, it is likely that control of the “threat” of alien plants would have detrimental effects on this focal species. In the following paragraphs, I discuss: the possible mechanisms of positive effects of alien and native neighbors on *S. globosa* vital rates; how the results might generalize to other populations and sites; and the implications for the management of threatened species, especially in planning conservation of native plants in a changing climate.

Neighboring plants are known to shelter plants from extreme abiotic conditions, and this could be just as true when the neighbors are alien plants. The stress-gradient hypothesis (SGH) predicts that co-occurring plants will serve as facilitative “nurse plants” in environments with high abiotic stress but will be competitors in more abiotically benign conditions (Callaway & Walker, 1997; Holmgren et al., 1997), which appears to be the case for some of the vital rates I examined, such as growth and survival of small recruits, but not the case for others, such as fruiting and survival of mature individuals (Table 1). Many exceptions to the simple stress gradient hypothesis have been observed, indicating that several mechanisms (including biotic interactions

other than competition/facilitation) likely dictate when plants facilitate or compete with one another (Brooker et al., 2008; Holmgren & Scheffer, 2010; Maestre et al., 2009; Maestre et al., 2006), which appears to be the case in this population. While invasive plants certainly have the potential to shelter natives from extreme abiotic conditions, and likely do so in this population for some vital rates, such facilitation may be modulated by variation in abiotic conditions or biotic interactions in a way that is not consistent across demographic rates.

Table 1: Summary of model results for the effect of alien and native cover on all vital rates in this study. + indicates a positive effect, - a negative effect, and blank cells indicate no statistically significant effect ($p>0.05$).

Vital Rate	Alien Cover				Native Cover			
(Interactions)	Large Plants	Small Plants	Good Years	Bad Years	Large Plants	Small Plants	Good Years	Bad Years
<i>Growth (growing season)</i>	+		+					
<i>Growth (dry season)</i>	+	-			+	-	+	
<i>Survival</i>					-	-		
<i>Fruiting</i>		-			+			
<i>Total # Recruits in demography plots</i>					+			
<i>Recruit Survival % in demography plots</i>	+				-			
<i>Surviving # Recruits in demography plots</i>					+			
<i># of seedlings Emerging in seed sowing experiment</i>	-				-			
<i>Seed Sow Survival %</i>	+				+			
<i>Seed Sow # Surviving</i>	+				+			

While the effects of herbivores on demographic rates were not directly examined in this study, generalist alien herbivores (slugs and snails) are present and likely to impact vital rates of native plants. Alien herbivores can benefit native plants by reducing

competition with neighboring native or alien neighbors. Herbivory has been found to reduce plant competition in a variety of systems (Olf & Ritchie, 1998; Van Der Wal et al., 2000), but alien plants can also benefit native plants by providing associational resistance against native or introduced herbivores, a more plausible explanation for benefits of alien plants under the low to moderate levels of herbivory in this study system which lacks large herbivores. Neighboring plants affect interactions between a focal plant species and its herbivores, largely because plants vary in traits such as attractiveness and nutritional value to herbivores (Hambäck et al., 2014). The distribution and composition of neighboring plants can have an indirect, positive impact on focal plants through reducing herbivory (Tahvanainen & Root, 1972). While it is commonly predicted that generalist herbivores are more likely to prefer native species over invasive species, potentially due to lack of defensive traits (Blossey & Notzold, 1995), there is no consistent evidence that this is the case (Keane & Crawley, 2002). Alien species are more likely to form dense, monotypic stands (Levine et al., 2003), potentially providing greater resources for herbivores than native plants. As alien slugs and snails are present throughout the study population the direct and indirect effects of alien herbivores may explain some of the effects of alien and native neighbors observed in this study.

The overall effect of alien neighbors on growth of large plants was positive in both the harsh dry season and the abiotically benign wet season so it is unlikely that the

benefit is due to alien neighbors sheltering plants from harsh abiotic conditions. In fact, alien and native neighbors had a negative effect on the growth of small plants in the dry season — this suggests larger neighbors might outcompete small, shallow-rooted *S. globosa* for water in the dry season, while still benefitting larger plants (e.g., by partial shading). In the wet (i.e., abiotically benign) season, alien (but not native) neighbors had a positive effect on focal plants of all sizes. The stress gradient hypothesis predicts that positive effects in benign conditions are likely to be due to associational resistance to herbivores, suggesting that alien neighbors may possess traits that confer such a benefit that native plants do not. I detected a year by alien cover interaction in dry season growth. High alien cover more strongly enhanced the growth of focal plants in the wetter dry season, which parallels the differences between wet and dry seasons. Positive effects during wetter dry seasons may be particularly important as predictions of future climate in this area project potentially higher proportions of annual rainfall in intense events during the dry, summer months (Longman et al., 2021; Luo et al., 2020) even as overall average annual rainfall changes little, potentially resulting in less stressful dry seasons and more stressful growing seasons. While the water supplementation experiment did not significantly affect demographic rates measured in this study, the experiment only simulated the effects of a single dry-season rainfall event. With more frequent, intense, or widespread (i.e. affecting the entire native and alien plant

community broadly rather than focused on focal native individuals) events, responses in demographic rates would be more likely.

I found a weak negative effect of native, but not alien cover, on survival, suggesting that fatal direct competition is happening with native neighbors but not alien neighbors. While it is still possible that alien plants could replace native populations in the long term, I did not detect the replacement of native individuals with alien plants in the short term. Alien neighbor cover did have a negative effect on fruiting in small plants, possibly attributable to competition, but as alien neighbors had a positive effect on growth, small plants with more alien neighbors may be allocating more resources to growth instead of fruiting, not fruiting less because of negative interactions with alien neighbors. Furthermore, as the vast majority of fruit production can be attributed to large, fecund individuals, suppression of fruiting in small plants by alien neighbors is unlikely to have a large negative impact on overall reproduction in this population.

Alien neighbors did not have a positive impact on the number of recruits, either initially or on the number surviving after a year, indicating the observed positive effect of alien neighbors on recruit survival percentage did not result in more recruits ultimately joining the population. The positive effect of heterospecific native cover on the number of recruits surviving after a year shows that the negative effect of native cover on recruit survival was not strong enough to outweigh higher initial recruitment. In the seed sow experiment, any type of neighbor cover reduced initial germination

(relative to bare ground), but all cover types resulted in higher survival of seedlings and ultimately more surviving seedlings. While the net positive effect of native cover matches the effect observed in the field recruitment plots, the positive effect of alien cover was only observed in the seed sow experiment. However, cover was measured on a different scale in seed sow plots (0.0015m² plots nearly completely covered with native and/or alien plants or completely bare ground) compared to recruitment plots (4m² with a wide range of native and alien cover). The seed sow experiment showed a strong initial recruitment effect of bare ground, but the correlation between bare ground and native and alien cover in the larger recruitment plots indicates that differences in those plots were not due to effects of bare ground. Higher recruit survival in plots with high alien cover was thus not due to relatively lower amounts of bare ground, but likely due to habitat amelioration by alien neighbors occur on the scale of larger recruitment plots but not on the microscale of seed sow plots.

As the mixed and often positive effects of alien plants I found in this study highlights, it cannot be assumed that alien plants will always eventually outcompete natives, cancelling any facilitative effects. In the majority of cases in which the competitive abilities of invasive and native plants have been compared, native species outperformed cooccurring invasive species under some conditions (Daehler, 2003). Alien species don't always outcompete native species and abiotic, or biotic, conditions can tip the competitive balance between native and alien plants. To date, many studies have

quantified alien species effects in terms of coarse measures of communities such as native species richness (Parker et al., 1999). While such an approach may guide broad scale conservation policy, it does little to address the nuanced and complicated relationships between native plants and alien species in a way that can inform community- and species-level conservation decisions. Conservation plans continue to list alien species as threats to native plants (Wilcove et al., 1998), but there is a dearth of research investigating the temporal and spatial variation of that threat and whether it actually exists at all. As demonstrated in this study, it is possible that even if the broad scale, long-term effects of alien species are negative and potentially catastrophic for native ecosystems, alien species may have positive effects on some communities and populations of native plants.

As I have found that the effects of alien species shift with year to year variation in climate, it is possible that other populations of *S. globosa* would experience largely negative effects of alien species. While the effects of alien species were mostly (but not entirely) positive across the range of abiotic conditions I observed in this population, across a larger aridity gradient interaction with alien species could be negative—at wetter sites due to increased competition and at drier sites due to the increased risk of fire promoted by alien species, while this population exists at an intermediate moisture area where aliens have positive effects. *S. globosa* may already have become locally extinct in areas where alien species had overwhelmingly negative effects. However, as

conservation goals often require managing remnant populations, the positive effects of alien species I found in this population are still essential to consider.

While it is impossible to deny the potentially devastating effects of alien species on native ecosystems, I have shown the potential for benefits at the population level that must be considered in planning management of native plant species. The next step in understanding the impact of alien species is to integrate the demographic rates I have examined into a population model, which could be used to project the net effect of alien species on population growth into the future, potentially accounting for ongoing climate change. While it is impossible to conduct a detailed study on every species of conservation importance, I have demonstrated that it cannot be assumed that simply removing alien species will be a positive conservation action and managers need to be open to the possibility that such action will have detrimental effects on a population.

Chapter 2: Effects of alien and native neighbors on population growth vary, but are frequently positive, across related native species, populations, and years

2.1 Introduction

Alien species have long been considered to be one of the greatest threats to biodiversity across the world, (Vitousek et al., 1997) and they are regularly assumed to threaten the persistence and success of native plant populations (Byers et al., 2002; Wilcove et al., 1998). Species introductions, along with continued anthropogenic disturbances, have made alien plants prevalent worldwide (Office of Technology Assessment, 1993; Parker et al., 1999), creating the common assumption that they are always a threat to native plants, and often suggesting that alien species have and will continue to drive plant species to extinction (Bellard et al., 2016). However, while the risk of alien species to native biodiversity is real, some have questioned whether alien species really do drive population declines and extinction of native species (Gurevitch & Padilla, 2004; MacDougall & Turkington, 2005); promoted the value of ecosystems that include many alien species (Hobbs et al., 2006); and even argued that we should embrace non-native species in our ecosystems (Ewel & Putz, 2004; Schlaepfer et al., 2011). However, much of this argument is not backed up by data and may create a false dichotomy—aliens are not necessarily always good or always bad. A more practical set of questions for ecologists and those interested in the conservation of native plant

populations is when, where, why, and how are interactions with alien species good, bad, or neutral for native plant populations.

There are many situations in which alien species can have both negative and positive effects on native plants (Ricciardi et al., 2013). Effects of alien species could be direct or indirect and vary across different demographic rates through a variety of mechanisms. Only by integrating effects on different demographic rates into a measure of population growth using a demographic model is it possible to determine the net effect of alien species. Whether native populations are shrinking towards extinction or persisting in the presence of alien species depends on whether the population growth rate is less than or greater than 1, respectively.

The impact of alien species may vary between native species with fundamental differences, such as the breeding system and pollination syndrome of the species. Understanding if particular traits of native plants predict the impacts of alien species would be of great value to conservation efforts, guiding predictions and assumptions about which native species and populations might persist or go extinct in a future of increasing alien species.

The impact of aliens on native plants' demographic rates and thus population growth will likely differ between species with different breeding systems, which is an important component to better understanding the future impact of the combination of alien species and changing climate. Native plant breeding system is a trait that may

drive differences in the effects of alien species on native plant populations, primarily through pollination-related mechanisms. Species more reliant on biotic pollination are more likely to have their pollination facilitated by alien species (Sun et al., 2013). Wind-pollinated or highly selfing species likely wouldn't experience those beneficial interactions. If alien species also exert negative effects on natives (e.g., through resource competition), then the balance of positive and negative effects of aliens could differ between similar native species differing in breeding system. Anthropogenic disturbance, including invasion, is often predicted to drive native plants toward more self-pollination (Eckert et al., 2010) but if alien species facilitate pollination rather than interfere with it the opposite could be true. Understanding how the effect of interactions with aliens differ across breeding system will help predict the which native plant species might benefit from alien species. While there are many other traits of native plants, such as defensive traits (Keane & Crawley, 2002), that influence how invaders affect native plants, reproductive traits define the set of interactions with invaders to which a native plant could possibly be subjected. Beyond comparing biotic and abiotically pollinated species, other breeding system differences could influence the effects of alien species. Being surrounded by alien species could alter pollen deposition in wind pollinated species. This could have stronger effects on dioecious species, where self-pollination is impossible, than in gynodioecious species, where populations have some hermaphroditic individuals that can self if they don't receive outcrossed pollen. While

effects on gynodioecious compared to dioecious wind-pollinated species likely would not be as strong as in species relying on a biotic pollinator that is less consistent than wind, they could still drive important differences in demographic response to alien species. Finding trends in responses to alien species based on breeding system would help to predict effects of alien species and more efficiently make conservation decisions to avoid negative effects and promote potential benefits of alien species without extensive study of every species and population.

In Chapter 1, I demonstrated that the effects of alien and native species on the demographic rates of a focal native species, *Schiedea globosa*, are mixed and vary within a population across harsh and benign conditions, both intra- and inter-annually. Similarly, the effects of neighbors is likely to vary between populations that experience different abiotic conditions, as is the case with the populations in this study—each population experience different abiotic conditions and those conditions also vary between years within populations. The same mechanisms discussed in Chapter 1 would apply across populations, where variation of abiotic conditions is likely to be even greater than it is within a single population.

In this study, I investigated the impacts of alien species on eight wild populations distributed across four at-risk species in the Hawaiian native plant genus *Schiedea* differing in breeding system, one primarily insect-pollinated hermaphroditic species, and two gynodioecious and one dioecious primarily wind-pollinated species.

Hawaii's biodiverse but highly invaded terrestrial ecosystems provide an ideal system to study the interactions between native and alien species. In all the focal wild populations, *Schiedea* individuals grow with a wide variety of neighbors, native and alien, including native and alien grasses, forbs, and woody shrubs. Alien generalist herbivores exist in all populations, bringing about the potential for indirect effects of alien plant neighbors by modulating the effects of alien herbivores. I collected demographic data on focal populations across a two-year interval and conducted experimental manipulations of alien abundance to measure the effects of alien species on the survival, growth, reproduction, and recruitment of *Schiedea* populations. I used these data to construct integral projection models and used them to assess the net effect of alien species on focal native populations. Specifically, I address the following questions:

How do the effects of alien species on all demographic rates integrate into effects on the population growth rate of the four species of at-risk native plants?

How do the effects of alien species differ on closely related species of native plants that differ in breeding system and pollination syndrome?

How do the effects of alien species on native plant populations across sites with varying abiotic conditions differ and how will future climate change likely alter the net effects of alien plants on *Schiedea*?

What implications do the effects of native and alien species on *Schiedea* population growth have for conservation of these and other native plant species?

2.2 Methods

2.2.1 Study species and populations

I selected four species in the endemic Hawaiian genus *Schiedea* to conduct detailed demographic censuses. *Schiedea* (Caryophyllaceae), which consists of 34 species, evolved from a presumed single colonizing ancestor (Wagner et al., 1999), and represents a striking diversity of breeding systems, including species with separate sexes that are primarily wind pollinated and hermaphroditic species that are insect pollinated (Wagner et al., 2005). Most of the species in the genus are rare, single-island endemics, with 23 federally listed as endangered (USFWS, 2010) and all species at-risk and facing a multitude of threats.

Table 2: Characteristics of species included in this study. Habitat, breeding system, and pollination as listed in Wagner et. al, 2001.

Species	Breeding System	Pollination	Federal Status	Habitat	Island(s)
<i>S. globosa</i>	Dioecious	Wind	Not Listed	Coastal shrubland	Oahu, Maui, Molokai, Hawaii
<i>S. menziesii</i>	Hermaphroditic	Insect	Not Listed	Dry shrubland	Maui
<i>S. salicaria</i>	Gynodioecious	Wind	Endangered	Dry shrubland	Maui
<i>S. kealiae</i>	Gynodioecious	Wind	Endangered	Dry forest	Oahu

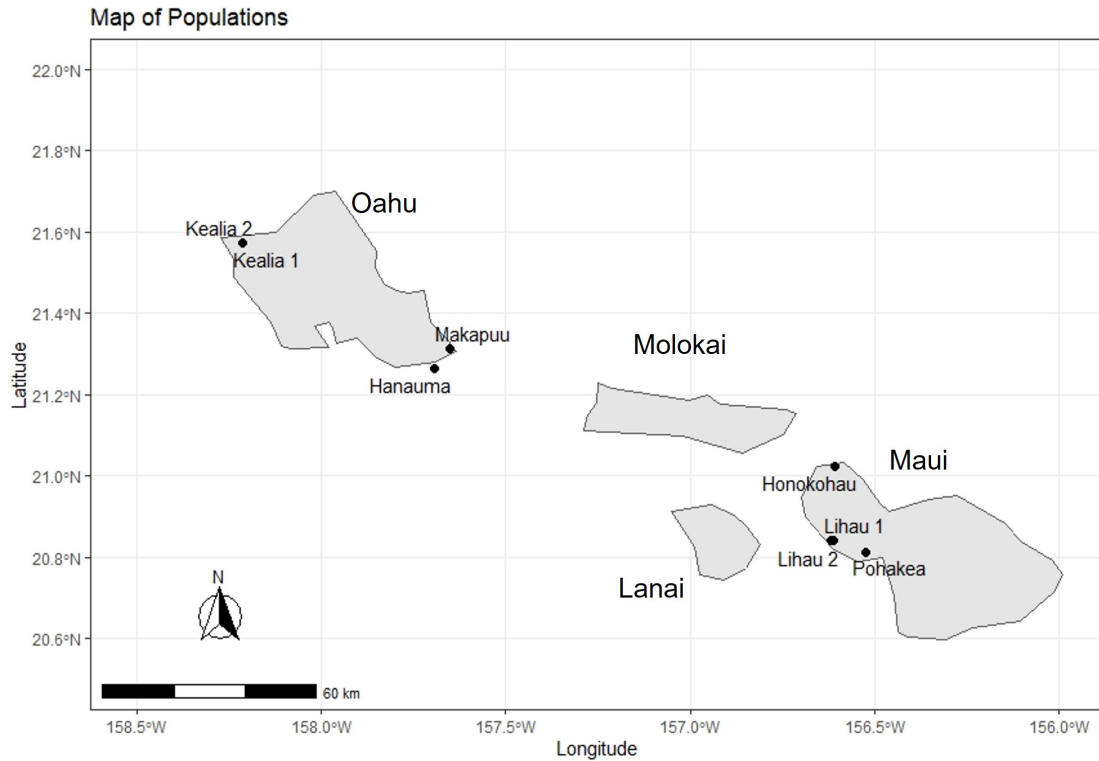


Figure 8: Map of study population locations on Oahu and Maui, approximated to protect sensitive resources

I studied 8 relatively large natural populations of 4 species (table 2). I selected populations that were large enough to collect sufficient demographic data, with a minimum of 150 reproductive plants that could be included in demography transects. As the majority of presumed biotically-pollinated species in the genus are critically rare, only one of the four species is insect pollinated (and hermaphroditic), with three primarily wind pollinated (two gynodioecious and one subdioecious) (table 2). Populations are located on the north, south, and east sides of the island of Oahu

(including the Waianae and Koolau volcanos) and on north, west, and south sides of West Maui (Mauna Kahalawai) (fig. 8), including coastal shrubland, dry shrubland, and dry forest habitats (table 2). All sites included a mix of native and alien plant species throughout the populations of focal *Schiedea* species. Populations ranged from 29m to 457m in elevation (table 3). Average annual rainfall ranged from 678mm to 1120mm (table 3) per the Hawaii Rainfall Atlas (Giambelluca et al., 2013).

Table 3: Characteristics of populations included in this study. Average annual rainfall from Hawaii Rainfall Atlas (Giambelluca et al., 2013) predicted by spatially interpolated data from rainfall gauges from 2005-2016.

Population	Species	Island	Coordinates	Elevation	Average Annual Rainfall	Census Time	# of Annual Transitions	Year of Initial Census	Recruitment Method	Manipulations
Makapuu	<i>S. globosa</i>	Oahu	21.3081°, 157.6529°	110m	678mm	Jan*	3	2017	Random plots	Alien Neigh., Water
Hanauma	<i>S. globosa</i>	Oahu	21.2651°, -157.6931°	59m	642mm	Feb	2	2017	Random plots	
Honokohau	<i>S. globosa</i>	Maui	21.0238°, -156.6093°	29m	1120mm	May	1	2018	Random plots	
Lihau 1	<i>S. menziesii</i>	Maui	20.8405°, -156.6131°	457m	878mm	May/June	2	2018	Entire transect	Alien Neigh.
Lihau 2	<i>S. menziesii</i>	Maui	20.8411°, -156.6178°	418m	737mm	May/June	1	2018	Entire transect	Alien Neigh.
Pohakea	<i>S. salicaria</i>	Maui	20.8143°, -156.5237°	347m	838mm	May/June	1	2018	Random Plots	
Kealia 1	<i>S. kealiae</i>	Oahu	21.5735°, -158.2123°	182m	921mm	March	2	2018	Random plots	Alien Neigh.
Kealia 2	<i>S. kealiae</i>	Oahu	21.5739°, -158.2129°	199m	945mm	March	2	2019	Random plots	Alien Neigh.

2.2.2 Demographic data collection

Beginning in the summer of 2017, I established demography transects throughout the core of each wild population. I continued to establish transects in additional populations through 2019 (see table 2 for initial year for each population). I established between four and nine transects per population, ranging from 10m to 65m in length depending on the extent of plants and topography of the population. Many of these transects are located in steep areas with inaccessible slopes or cliffs but transects included plants on ledges allowing for walking access to plants in steep areas. All plants within 2 m on either side of the transect tape were included in the study. Each individual plant was tagged with wire and metal tags or a toothpick, and its location within the plot was recorded. At each census, I measured survival, size (vegetative area), and fecundity (number of fruiting heads, only during the wet season censuses). Censuses of wild populations were performed annually in the peak reproductive season, winter or spring depending on the population (see table 1b), at a time of year that would capture all reproductive output for the year.

Recruitment was measured either by counting every recruit found within the transects (if few recruits) or by searching randomly selected areas within the transects if seedlings were more numerous (see table 1b). For populations in which random plots were used, a 4x1 m quadrat was randomly selected for every 10 m of each transect to record the number of recruits each census. Each census, all new recruits were tagged

with a toothpick or wire and a metal tag and counted and surviving recruits from previous seasons were counted. Once the recruits exceeded the smallest size observed flowering for that species, they were designated adults and included in continuous size-based demography measurements.

Due to the covid-19 pandemic travel restrictions, I was unable to visit two populations (Lihau 1 and 2) in 2020, but I collected the same demographic data across a two year period (2019 to 2021).

2.2.3 Characterization of neighbors

For each plant in demography plots, I characterized the neighbors at each census using photographs taken during each census. I visually characterized the percentage cover of heterospecific natives and aliens as well as the total neighbor cover within a 50cm radius of the focal plant. The same characterization was used to record the native, alien, and total cover within each recruitment plot. The sum of bare ground, native cover, and alien cover may exceed 100%, as native and alien cover often overlaps, but in no population did I observe greater than 70% of both types of cover around a single focal plant.

2.2.4 Statistical analysis of demographic rates

I performed all data processing, analysis, and visualization using R v. 4.0.1 (R Development Core Team, 2021). Alien and native cover was included as a predictor variable in every regression. For all models, I tested all possible interactions between

predictor variables including factors up to three-way interactions. I conducted model selection by dropping non-significant effects (using analysis of variance tables from the R-package 'car'(Fox et al., 2012)) from each model until only significant predictor variables remained in the final models, but including non-significant main effects if they were involved in significant interactions.

A separate regression was fit for all vital rates (growth, survival, probability of fruiting, amount of fruiting heads produced, and recruitment) for each annual transition in each population. I modeled growth (linear, size next year against size this year) and survival (binomial) using size dependent regressions using mixed effects models (lme4) (Bates et al., 2011) with interactive effects (up to three-way interactions), and transect as a random-intercept effect for each annual transition. I modeled the number of fruiting heads vs. size using a hurdle negative binomial regression (glmmTMB)(Magnusson et al., 2017) with plot as a random-intercept effect. Recruitment was modeled using a zero-inflated Poisson regression (glmmTMB)(Magnusson et al., 2017), with plot as a random-intercept effect and with fruiting heads per area of the larger demography plot tested as a predictor variable for recruitment. Survival of recruits to the following was modeled using a mixed effects binomial regression (lme4)(Bates et al., 2011) with plot as a random-intercept effect. For the two-year transitions at the Lihau populations, I fit all regressions on a two year interval to account for two years of each demographic rate.

Recruitment per fruit was estimated based on fruiting two years prior as there was no data available for the middle year.

2.2.5 Manipulation of neighbors and water supplementation

In order to test if the effects of alien neighbors were spurious (e.g., *Schiedea* and aliens performing well in the same high-quality locations) and to increase the naturally occurring variation in alien neighbor cover, I performed an alien neighbor removal experiment in some years in some populations (table 3). In populations and years that I applied treatments, I randomly assigned plants within existing demography transects to an alien neighbor removal group, a water supplementation group, a control group, and in one population, a water supplementation and alien removal group. Each treatment group included 50 to 70 individual plants and included a fairly equal distribution of plant sizes, equally representing size classes within treatments. For the neighbor removal treatment, I cleared all alien plants from within a 50cm radius of focal *Schiedea* assigned to the alien neighbor removal treatment group, clipping all alien plants at the base to minimize soil disturbance. Plants assigned to the water supplementation treatment received 500ml of water at their base once to simulate a single, large precipitation event, as projections of future climate in Hawaii predict higher proportions of annual rainfall in intense events during the dry, summer months (Longman et al., 2021; Luo et al., 2020). When a random treatment assignment would affect adjacent demography plants, all plants affected were also assigned to that treatment. I collected

demographic data on all experimental plants as part of the regular censuses of the population.

To test if the effect of the alien neighbor removal was different than the effect of naturally occurring alien neighbor cover, I fit separate regressions for growth, survival, and fecundity with only size, alien cover, and neighbor removal treatment (removal vs control) as predictor variables, including testing for interaction effects between alien cover and neighbor removal treatment. There were no significant main effects of removal treatment or interactions between alien cover and the neighbor removal treatment in any models. As this indicates there was no difference between treatment and naturally occurring variation in alien cover, ruling out spurious correlations of the effects of alien cover, I removed the alien removal treatment as a predictor variable from all models. Supplemental water treatment was included as a factor in populations it was applied but was also not significant in any regressions and thus was also removed as a predictor variable from all models.

2.2.6 Integral Projection Models

For each population transition year, I used the vital rate regressions to construct deterministic integral projection models of population growth, using size (always included for all demographic rate regressions except recruitment), alien cover, and native cover (when significant as a main effect or involved in significant interaction

effects) as covariates based on the model selection performed for each vital rate regression.

Each IPM spanned the size range from 90% of the size of the smallest individual to 110% of the size of the largest individual observed in each population. All IPMs were fit with 200 mesh points, enough for the predicted population growth rate to converge to a steady value. The sizes of new recruits followed a log-normal distribution parameterized from the mean and standard deviation of the log size of recruits in each population. I corrected for downward and upward eviction, dividing all size classes by the sum over all size classes to renormalize.

2.2.7 Analysis of population growth

As vital rate regressions included as drivers alien and native cover plus interactions between size and cover, I used the IPM to calculate the population growth rate λ across all combinations of alien and native cover, from 0-100% of each cover in intervals of 10%, obtaining λ at each of 121 combinations of the two cover values for each population x yearly transition. I used these values to generate heatmaps of λ for all potential combinations of alien and native cover. These combinations include values of drivers not observed in wild populations, including values unlikely to ever occur (e.g. 100% cover of both native and alien neighbors). However, these hypothetical combinations illustrate the direction and magnitude of effect of alien and native neighbors on native populations.

Additionally, I calculated the change in λ ($\Delta\lambda$) when each type of neighbor cover (alien and native) changed from zero to its median (30%), holding the other cover type at its median (30%) value. I also calculated the change in λ ($\Delta\lambda$) from zero cover to median cover of both alien and native neighbors to assess the effect of mixed alien and native neighbors.

I fit linear regressions and ANOVAs of the alien, native, and mixed $\Delta\lambda$ values against characteristics of site—elevation and average annual rainfall, and species characteristics—breeding system and presumed pollination syndrome (abiotic vs biotic). I also fit simple ANOVAs to test the effect of breeding system and presumed pollination syndrome on the alien, native, and mixed $\Delta\lambda$ values.

2.3 Results

2.3.1 Demographic rate regression effects

I found that alien and native cover had significant effects on many demographic rates, with 34 and 39 significant effects out of 70 possible, respectively (table 4). Overall, there were more positive than negative effects of both alien and native cover. The majority of significant effects were positive for both alien (26 out of 34) and native (34 out of 39) cover, including growth, survival, number of fruits, and recruitment. However, negative effects of both cover types were significant for some population \times year combinations for growth, survival, number of fruits, and recruitment. I did not find

significant effects of alien or native cover on whether plants fruited in any years in any populations.

Table 4: Number of significant ($p < 0.05$) positive (+) and negative (-) effects of alien cover (AC), native cover (NC), and interactions, for annual vital rate regressions, out of a maximum of 14 regressions (one per population x year combination) for each vital rate (70 regressions total). For regression coefficients, see Table 9 (Appendix B).

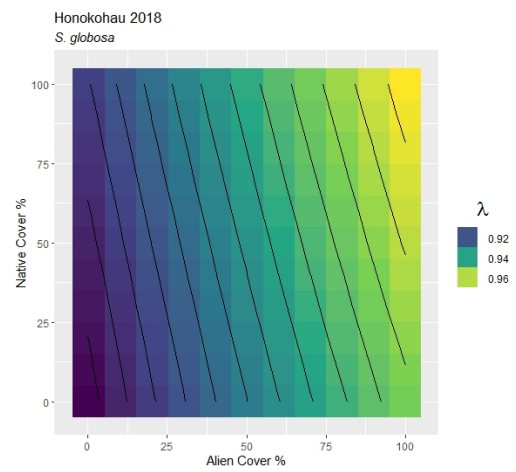
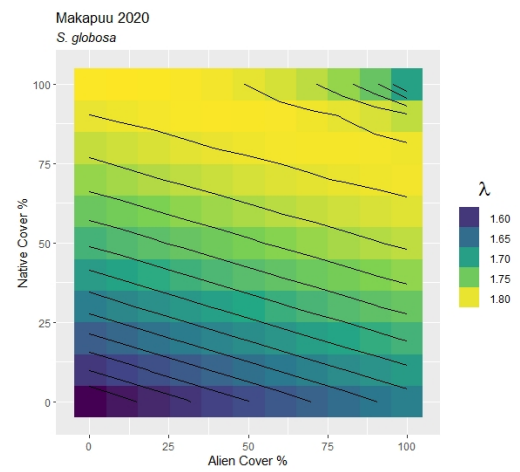
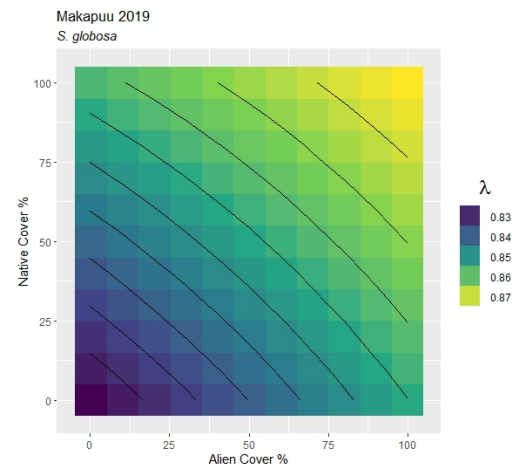
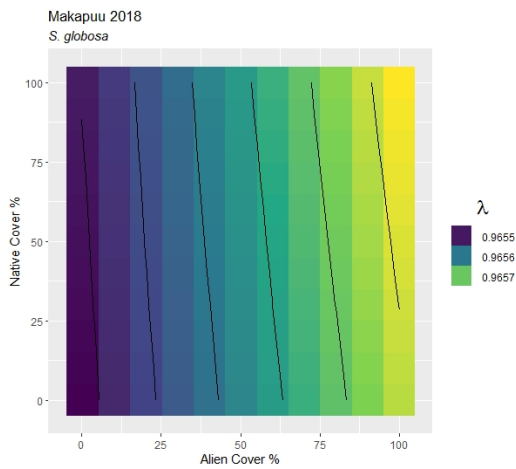
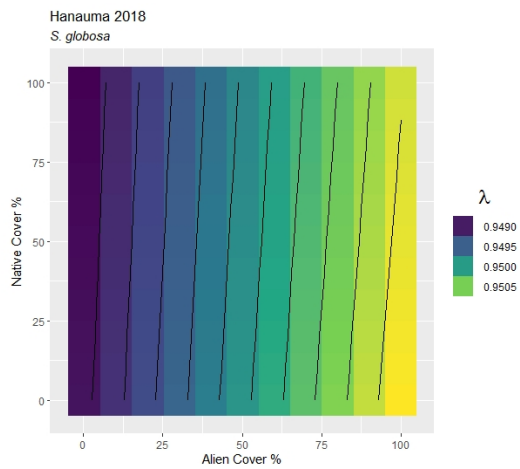
Vital Rate	AC	NC	AC*NC	AC*Size	NC*Size	AC*NC*Size
Growth	10+/2-	8+/4-	2+/3-	1+/3-	6+/2-	0/1-
Survival	3+/2-	8+/1-	0+/1-	0+/0-	0+/0-	0+/0-
Probability of fruiting	0+/0-	0+/0-	0+/0-	0+/0-	0+/0-	0+/0-
# of Fruits	6+/1-	5+/0-	0+/0-	0+/2-	0+/0-	0+/0-
Recruitment	7+/3-	13+/0-	0+/0-	0+/0-	0+/0-	0+/0-
Total	26+/8-	34+/5-	2+/4-	1+/5-	6+/2-	0+/1-

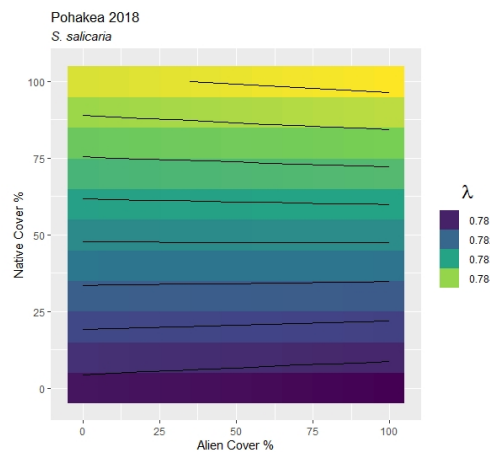
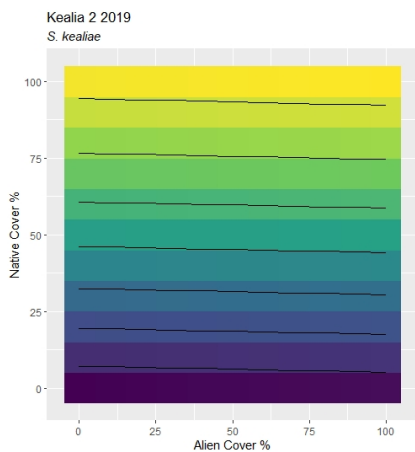
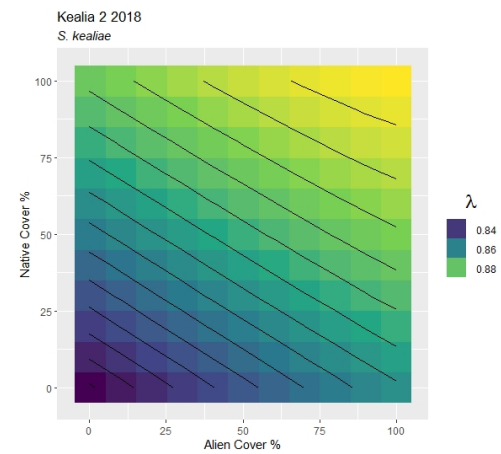
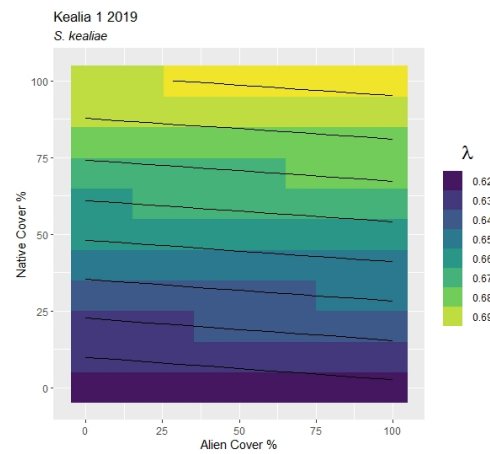
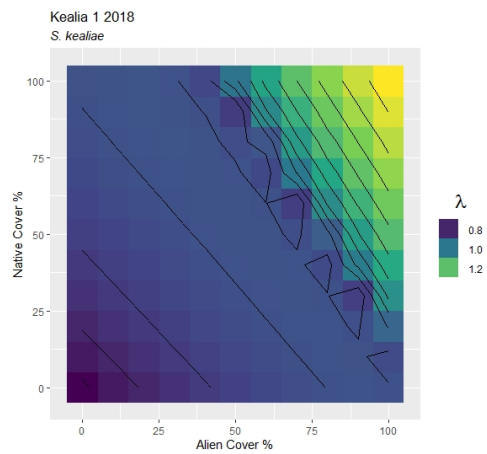
I found the greatest number of significant effects of alien and native cover on growth and recruitment, with the vast majority of annual transitions showing a significant effect of both native and alien cover. However, alien and native cover often did affect the number of fruits and survival as well. Interaction effects between size and cover were significant in some annual transitions but were not included in the majority of best-fit vital rate regressions.

2.3.2 Effects of alien and native cover on population growth

In all annual transitions in all populations, either alien or native cover, or both, had positive effects on the population growth rate λ predicted by the IPMs (fig. 9). In most transitions, λ was less than one across the entirety of driver space, but in some populations, λ crosses one, indicating that whether that population grows or not is determined by alien, native, or both types of cover. However, in populations in which both alien and native cover have a positive effect on λ , cover values that take λ above one exceed observed cover in the population (e.g. Kealia 1 2018).

In no population x year combinations does λ increase with decreasing cover of both alien and native neighbors (i.e., λ is never highest in the lower left corner of the heatmaps in fig 9). For some populations, λ does decrease slightly with increasing alien cover (e.g. Lihau 1 2018, Lihau 1 2019/2020, and Hanauma 2018) but the decrease in λ is almost entirely overwhelmed by the positive effect of native cover. In most populations with more than one year, the trend of the effects of alien and native cover on λ is largely consistent across years, even comparing years with relatively high and low λ (e.g. Makapuu), but this wasn't always the case—comparing the two Kealia populations, the effects of cover were more similar between population with year than between years within population.





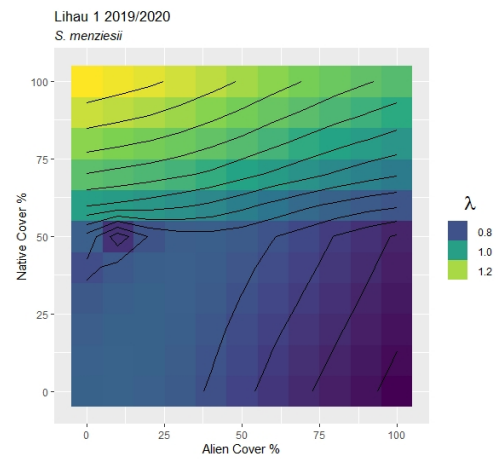
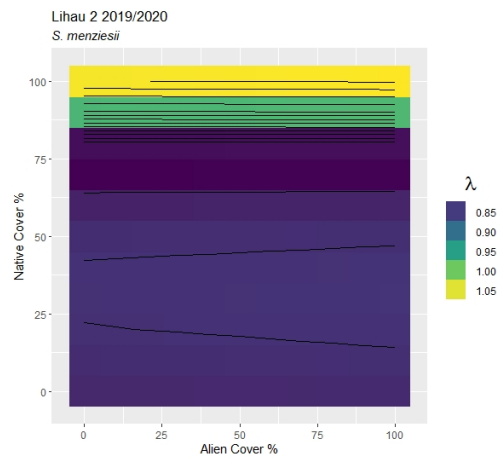
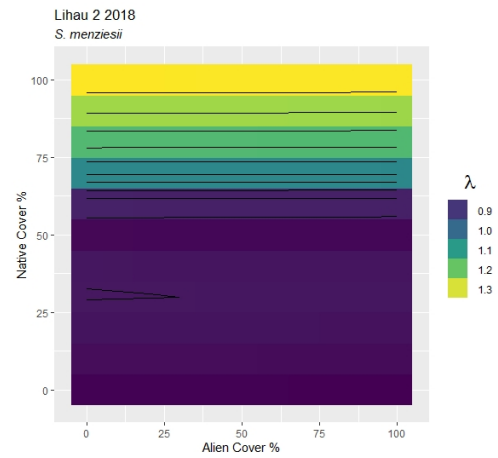
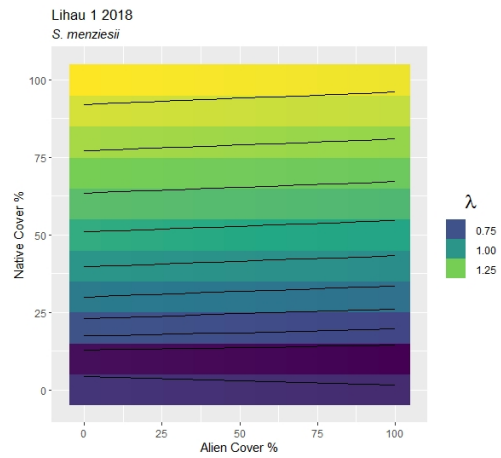


Figure 9: Heatmaps of population growth (λ) by alien cover and native cover for each population in each year. Scale for each heatmap is centered on median lambda for that population x year. Heatmaps include hypothetical levels of drivers not observed in the field (i.e. 100% cover of both alien and native numbers), but these levels are included to show the trends in λ at extreme driver values

Table 5: Change in λ from 0 to median alien neighbor cover (30%) for wild populations at median native cover (30%). * indicates $\Delta\lambda$ based on two year transition. Red $\Delta\lambda$ values indicate negative change in λ with increasing cover

Population	Year	Species	Pollination	Breeding System	Average Rainfall	Elevation	$\Delta\lambda$
Kealia 1	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	921mm	182m	0.04949
Kealia 1	2019	<i>S. kealiae</i>	Abiotic	Gynodioecious	921mm	182m	0.01035
Kealia 2	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	945mm	199m	0.01035
Kealia 2	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	945mm	199m	0.00168
Makapuu	2018	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.00008
Makapuu	2019	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.00801
Makapuu	2020	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.02649
Honokohau	2018	<i>S. globosa</i>	Abiotic	Dioecious	1120mm	29m	0.01707
Hanauma	2018	<i>S. globosa</i>	Abiotic	Dioecious	642mm	31m	0.00059
Lihau 1	2018	<i>S. menziesii</i>	Biotic	Hermaphroditic	878mm	457m	-0.0113
Lihau 1	2019/ 2020	<i>S. menziesii</i>	Biotic	Hermaphroditic	878mm	457m	*0.01707
Lihau 2	2018	<i>S. menziesii</i>	Biotic	Hermaphroditic	737mm	418m	-0.00045
Lihau 2	2019/ 2020	<i>S. menziesii</i>	Biotic	Hermaphroditic	737mm	418m	*0.000574
Pohakea	2018	<i>S. salicaria</i>	Abiotic	Gynodioecious	838mm	347m	-0.00002
							0.00858

Table 6: Change in λ from 0 to median native neighbor cover (30%) at median alien cover (30%). * indicates $\Delta\lambda$ based on two year transition.

Population	Year	Species	Pollination	Breeding System	Average Rainfall [‡]	Elevation	$\Delta\lambda$
Kealia 1	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	921mm	182m	0.04764
Kealia 1	2019	<i>S. kealiae</i>	Abiotic	Gynodioecious	921mm	182m	0.02345
Kealia 2	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	945mm	199m	0.01655
Kealia 2	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	945mm	199m	0.02409
Makapuu	2018	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.00001
Makapuu	2019	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.00916
Makapuu	2020	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.09587
Honokohau	2018	<i>S. globosa</i>	Abiotic	Dioecious	1120mm	29m	0.00350
Hanauma	2018	<i>S. globosa</i>	Abiotic	Dioecious	642mm	31m	-0.00003
Lihau 1	2018	<i>S. menziesii</i>	Biotic	Hermaphroditic	878mm	457m	0.25128
Lihau 1	2019/ 2020	<i>S. menziesii</i>	Biotic	Hermaphroditic	878mm	457m	0.01501*
Lihau 2	2018	<i>S. menziesii</i>	Biotic	Hermaphroditic	737mm	418m	0.02393
Lihau 2	2019/ 2020	<i>S. menziesii</i>	Biotic	Hermaphroditic	737mm	418m	0.00851*
Pohakea	2018	<i>S. salicaria</i>	Abiotic	Gynodioecious	838mm	347m	0.00106
MEAN							0.03714

Table 7: Change in λ from 0% alien and native cover to median alien and native neighbor cover (30% of each). * indicates $\Delta\lambda$ based on two year transition.

Population	Year	Species	Pollination	Breeding System	Average Rainfall [‡]	Elevation	$\Delta\lambda$
Kealia 1	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	921mm	182m	0.133733
Kealia 1	2019	<i>S. kealiae</i>	Abiotic	Gynodioecious	921mm	182m	0.025161
Kealia 2	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	945mm	199m	0.028291
Kealia 2	2018	<i>S. kealiae</i>	Abiotic	Gynodioecious	945mm	199m	0.024591
Makapuu	2018	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.00008
Makapuu	2019	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.018065
Makapuu	2020	<i>S. globosa</i>	Abiotic	Dioecious	678mm	110m	0.132064
Honokohau	2018	<i>S. globosa</i>	Abiotic	Dioecious	1120mm	29m	0.020175
Hanauma	2018	<i>S. globosa</i>	Abiotic	Dioecious	642mm	31m	0.000565
Lihau 1	2018	<i>S. menziesii</i>	Biotic	Hermaphroditic	878mm	457m	0.242051
Lihau 1	2019/ 2020	<i>S. menziesii</i>	Biotic	Hermaphroditic	878mm	457m	-0.00502*
Lihau 2	2018	<i>S. menziesii</i>	Biotic	Hermaphroditic	737mm	418m	0.023488
Lihau 2	2019/ 2020	<i>S. menziesii</i>	Biotic	Hermaphroditic	737mm	418m	*0.00917
Pohakea	2018	<i>S. salicaria</i>	Abiotic	Gynodioecious	838mm	347m	0.001008
MEAN							0.04667

Using the 14 annual transitions, I found no significant effects of elevation, average rainfall, breeding system, or presumed pollination syndrome on $\Delta\lambda$ from low to median alien cover, native cover, or mixed native and alien cover in the linear regression and ANOVA models I performed. In the great majority of annual transitions across populations and years, λ increased with increasing native cover and alien cover. In fact, λ increased with increasing alien cover in 11 out of 14 annual transitions (table 5), with increasing native cover in 13 out of 14 annual transitions (table 6), and with increasing both native and alien cover in 13 out of 14 annual transitions (table 7). The magnitude of change in λ varied across the annual transitions from less than 0.0001 to greater than 0.2. While there were no statistically significant effects of breeding system or pollination, two of the three decreases in λ with increasing alien cover occurred in populations of biotically pollinated species (out of only four biotically pollinated species annual transitions total).

2.4 Discussion

I have shown that the effects of both alien and heterospecific native neighboring plants differ in magnitude and direction across both the individual demographic rates (table 4) and, for the population growth rate, across populations and years (fig. 9) for native plant populations. While the mean effect of increasing alien cover on λ (0.00858, table 5) was less than the effects of increasing native cover (0.03714, table 6) or both native and alien cover (0.04667), that λ often increases with alien and native cover (fig. 9)

illustrates the necessity of considering potential net positive effects of alien neighbors on population growth of native species in addition to positive effects of heterospecific native neighbors.

The majority of significant effects of native and alien neighbors on individual vital rates (table 4) and the general trends in population growth (fig. 9) are positive, indicating that positive effects are more important than negative effects. In all populations, the effect of at least one of the types of cover is positive, with the other cover type usually either positive or having no effect on population growth. Even in the annual transition in which alien cover has a negative effect on population growth (Lihau 1 2019/20, fig. 9), that negative effect is weak, compared to the positive effect of native cover. While negative effects may still have an impact, reducing the positive effects of the other type of cover on other vital rates, positive effects are largely driving population growth.

While different mechanisms may be driving the positive effects of cover in different populations and years, it is clear that without considering positive effects, our understanding of the role of alien species will be incomplete. Applying hypotheses such as the stress gradient hypothesis (Bertness & Callaway, 1994), which predicts when interactions with neighbors might be negative or positive and through what mechanism, may provide a helpful framework to predict the mechanisms of positive interactions. The overall trends observed across the 14 annual transitions of this study, as well as the

effects on intra-annual demographic rates presented in Chapter 1, suggest that the SGH framework isn't likely to adequately predict when effects of neighbors will be on balance positive. It is likely that positive, facilitative effects such as nurse plant or habitat amelioration and positive, protective effects such as associational resistance are driving positive effects, both within and among populations and years. These two kinds of positive effects represent the extreme ends of the SGH, driven by high stress environments and high biotic interaction environments respectively, making it hard to place the net effects on the spectrum of predictions of the SGH.

The populations that show the greatest positive effect of heterospecific native neighbors with little to no positive effect of alien neighbors were the populations of *S. menziesii* at Lihau, the only biotically pollinated species included in this study. Despite the lack of a statistically significant relationship due to limited sample size (4 out of 14 annual transitions), the trend of increasing λ with increasing native, but not alien, neighbors suggests that native neighbors may be conferring a benefit to biotically pollinated *Schiedea* that doesn't exist for abiotically pollinated *Schiedea* species.

Although in the species of *Schiedea* in which an insect pollinator has been identified the moth pollinator is cryptic and its life history and ecology are unknown (Weller et al., 2017), heterospecific native neighbors could be critical to the success of these native pollinators (e.g., as food plants for the larvae, or as alternative nectar or pollen sources for the adults). Consequently, native neighbors could attract native pollinators to the

vicinity of a *Schiedea* individual. While some studies have found that alien plants can provide that same benefit (Sun et al., 2013), I did not detect positive effects that could be driven by facilitation of pollination by alien species in this study. The positive effects of native neighbors on λ of insect-pollinated populations highlight the need to consider the native plant community and its role in the ecology of pollinators in planning for the conservation of native plants.

While the observed positive effects of native neighbors on biotically pollinated species are only based on a single species, the benefits of native neighbors I detected bring up two important considerations. First, the reason only a single biotically pollinated species was included in this study is largely because the vast majority of biotically pollinated *Schiedea* populations are too small to collect adequate demographic data to build population models (Sakai et al., 2002; Wagner et al., 2005). This indicates that if heterospecific neighbors are important to supporting population growth of biotically pollinated native plants, the loss of native plant communities may have led to declines in populations to the point that they are critically threatened and lack sufficient numbers to study these interspecific plant effects. Second, the replacement of native plant communities by alien species may, by disrupting important plant-pollinator interactions, have already had negative effects on biotically pollinated native species that are greater than the positive effects of alien neighbors seen in other populations in this study.

It is important to acknowledge that the λ values I calculated for each annual transitions represent asymptotic values, assuming that the vital rates (and effects of alien and native neighbors) have remained constant for long enough for the population to reach its stable size distribution. The changes in λ and how λ is driven by neighbor cover I found clearly demonstrate that such constant conditions and demographic rates are unlikely to be the biological reality under variable abiotic (and biotic) conditions in the field, and level of variation between relatively good and bad years is likely to influence long term stochastic population growth. However, while deterministic λ for any one year will not project actual stochastic population growth into the future, it does demonstrate the integrated effects of alien and native neighbors on native populations, the components that would contribute to a long-term stochastic λ .

I did not detect patterns in changes in λ by elevation or average rainfall of each population. This study represents only a portion of the variation in elevation and precipitation that *Schiedea* and other native plant populations experience, but it was conducted in the relatively drier, relatively lower elevation areas in which alien species are most abundant. While trends might emerge if the study encompassed a wider range of elevation and precipitation, it is likely that the role of alien species on population growth is most important in these areas of high abundance, where alien species have replaced a higher proportion of the native plant community.

The largely positive effects of alien and heterospecific neighbors on population growth of native plants I found is of critical importance when planning current and future conservation of threatened and endangered native plants. While weed control, eliminating or thinning alien neighbor plants, is a common conservation action, the neutral or positive effects on λ of native populations (fig. 9) illustrate that investing limited conservation resources on such actions may be a waste of resources at best, and in some populations may actually have negative effects on the native plant populations they intend to benefit. Weed control can also have non-target effects that damage native populations, including trampling of small native plants and ground disturbance leading to erosion or displacement of seeds in the soil. The results of this study may also provide some evidence for other conservation actions, such as potentially implementing mixed native species outplantings along with focal threat(Weller et al., 2017)ened species, either into wild or reintroduced populations. There is little risk of negative effects of such mixed native outplantings, at least as indicated by the effects of heterospecific native neighbors on the species and populations studied here, with high potential benefits. This may particularly be the case for biotically pollinated species, when conspecific native neighbors may facilitate pollination by attracting or supporting the life cycle of the pollinators. Further investigation of which heterospecific native neighbors is challenging, as the ecology of the likely pollinators (crepuscular

microlepidoptera) is largely a black box (Weller et al., 2017), but would provide valuable insight into how best to promote facilitation of pollination of at-risk native species.

The large-scale negative effects of alien species on native Hawaiian ecosystems are impossible to deny. In many areas, alien species have replaced natives completely, or at least to the point where they are no longer considered viable habitat for any native plants. Alien plants have drastically altered fire regimes, allowing for the replacement of species rich communities of poorly fire adapted natives to be replaced by low diversity communities of fire adapted alien plants on a large scale. Conservation of native plants and ecosystems, however, largely focuses on the areas where remnant native plants exist, such as the populations included in this study. That both alien and heterospecific native neighbors drive increases in population growth of *Schiedea* species, as I found in this study, suggests that conservation should be implemented with an open mind towards positive effects of alien species, even if only to avoid wasting time on actions with limited benefit. However, I did not find any traits that predict generalizable patterns in the effects of alien or native species on native plants, suggesting that patterns might be more complex than expected. While the lack of a highly predictable trend in the effects of alien species is somewhat frustrating, I have demonstrated that an approach that attempts to balance the good and bad of alien species is warranted.

Chapter 3: Rare plant restoration genetics: the relationship between genotype, phenotype, and fitness in outplantings of a critically endangered species

3.1 Introduction

Predicting the factors driving population success or extinction is a critical question in biological conservation (Soule, 1986). Anthropogenic drivers of extinction are of particular concern, but they may have effects on either ecological or evolutionary processes, or both (Fugère & Hendry, 2018). In order to implement effective conservation of populations, investigating the interaction between demographic and genetic factors is crucial (Lande, 1988). If plant morphological traits affect fitness in different conditions, and those traits are heritable, plants can respond to selection. Understanding which traits might undergo selection in future conditions, such as changing moisture and changing abundances of neighboring alien and native species is essential to understanding the future fitness of native plant individuals and populations. Together, assessing the heritability of traits and selection on those traits in natural populations, in the context of anthropogenic threats to plant populations, provides important insight into the determinants of a species' long term success or extinction (Lande, 1998).

Reintroductions of rare and at-risk native plant species are an important conservation tool that has been in use for decades (Maunder, 1992). The ability to conserve plants ex situ and later reintroduce individuals into the wild provides the

backbone of much of the ongoing conservation of plant species (Cochrane et al., 2007). Understanding whether reintroductions are successful is difficult (Godefroid et al., 2011) and reintroductions can succeed or fail for many ecological and evolutionary reasons (Albrecht & Maschinski, 2012; Albrecht et al., 2019), but evaluating reintroduction efforts is critical to improving and implementing conservation efforts (Godefroid & Vanderborght, 2011).

It is likely that reintroductions will be even more important to the conservation of plants and terrestrial ecosystems in the face of ongoing climate change, presenting opportunities as well as risks (Maschinski & Haskins, 2012). There is doubt that many plant species will be able to track changes in climate (Corlett & Westcott, 2013), and managed translocation (i.e., outplanting populations of native species in areas suitable for their success under future climate conditions) has increasingly been suggested as a conservation response to changing climate (Zimmer et al., 2019). Managed translocation gives the opportunity to plant rare species in habitat believed to be ideal in the future, potentially decreasing detrimental effects of climate change, but also creates novel ecological and genetic factors determining success that are challenging to study prior to outplanting.

Planning outplantings to maximize their genetic diversity has often been the primary goal of many plant conservation efforts, especially for extremely rare species (Albrecht & Maschinski, 2012). Plant conservation efforts strive to reintroduce

populations with sufficient genetic diversity to persist, grow, and allow for future evolution (Cochrane et al., 2007; Falk et al., 1996; Maunder, 1992). However, many factors beyond genetic diversity determine the success of reintroductions (Albrecht et al., 2011; Albrecht et al., 2019) and populations succeed or fail for many ecological, genetic, and evolutionary reasons (Lande, 1988, 1998). Few previous studies have attempted to measure whether genetic diversity of outplants influence phenotypic diversity and whether phenotypic diversity drives the fitness of outplants, but theoretical predictions (Lande, 1988) and experimental evidence (Wootton & Pfister, 2013) suggest that demographic processes will drive small populations to extinction before genetic effects have major effects.

The balance between demographic and genetic considerations for the success of reintroductions is likely to be even more important for managed translocations—as populations are established outside the known range of a species, they will experience a novel abiotic and biotic environment and respond in a way not previously able to be observed. These conditions could drive differences in demography, affecting growth, survival, and reproduction directly or indirectly (by modulating biotic interactions), or they could drive evolution, imposing selection on traits that determine whether or not individuals survive and reproduce under new environmental conditions. While managed translocation is often proposed in the context of new abiotic conditions in response to climate change (Zimmer et al., 2019), biotic interactions, including with alien

species, are likely different in translocation sites in addition to differences in abiotic conditions, necessitating the consideration of the effect of interactions with alien species in planning conservation translocation as well. For example, translocation to a wetter location could lead to increased density of herbivores, or even interactions with new species of herbivores. The increased interest in planting native species in novel areas beyond their current or historic ranges brings with it an increased need for research into how native plants will respond to new conditions, including ecological responses to interactions with alien and native species and the relationship between genotype, phenotype, and fitness. To truly understand the success of reintroductions, particularly as populations are outplanted in areas where they experience new abiotic conditions, it is critical to investigate both the demographic and genetic drivers of population success.

In this study, I conducted outplantings of populations of the critically endangered Hawaiian endemic shrub *Schiedea adamantis* at the limit of and slightly beyond its known range, in areas largely dominated by alien plants around remnant native species. Outplantings included individuals from a set of paternal half-sibling families, generated by previous studies that quantified heritability of key morphological, ecophysiological and reproductive traits under greenhouse conditions (Campbell et al., 2011; Culley et al., 2006). I measured morphological and reproductive traits of the half-siblings in outplantings, to assess the heritability of traits under conditions in the field, where greater environmental variation is expected to increase plasticity of traits and

thus potentially decrease heritability. I also collected fitness data (survival, growth, reproduction) and measured plant traits in both outplantings, including the half-siblings as well as additional outplants, and I measured as well habitat characteristics that each plant experienced (shade and alien and native neighbor cover) to understand the relationship between fitness, traits, and habitat characteristics, indicating the potential for selection on those traits in outplantings and how selection varies with habitat. I also implemented experiments suppressing herbivores and supplementing water to increase the variation in conditions outplants experience. I used these data to answer the following questions:

Are morphological traits, some of which were found to be heritable under greenhouse conditions, heritable in outplanted populations of *Schiedea adamantis*, where higher environmental variation may increase plasticity?

How do measured morphological traits influence fitness components, leading to selection of phenotypes in populations outplanted in the field, especially under different abiotic and biotic conditions?

How should genetic, evolutionary, demographic, and ecological factors be considered in planning conservation translocation in the face of climate change and habitat modification by alien species?

3.2 Methods

3.2.1 Study species

The genus *Schiedea* is an endemic Hawaii genus of 32 extant species representing remarkable diversity of breeding systems, habitats, and morphologies (Wagner et al., 1999; Wagner et al., 2005). Most of the species are rare, single-island endemics, with 23 federally listed as endangered (USFWS, 2010). *Schiedea adamantis* is a gynodioecious, woody shrub scattered in populations restricted to two wild populations in low elevation areas in southern Koolau Mountains on the island of Oahu. *S. adamantis* is one of the rarest species in the genus and has been consistently declining in numbers, from over 250 flowering individuals observed in 1992 (Wagner et al., 2005) to only 10-20 wild individuals today. The remaining two wild populations of *S. adamantis* occur in areas of extreme anthropogenic disturbance and its likely past distribution is exclusively within urban east Honolulu. The species is threatened by fire promoted by alien grasses (Ellsworth et al., 2014) and other disturbances (such as human development and trampling), leading to increased prevalence of alien plants, now ubiquitous throughout all habitat of *S. adamantis*. *S. adamantis* was discovered first on the outer slopes of Leahi (Diamond Head Crater) and it was long believed to be only found in that area. However, in 2014, a second population was found at a higher elevation on a cliff in Kului gulch, confirming previous assumptions of a somewhat more expansive historic range. As of 2021 however, fewer than five wild individuals remain at Kului, with the

majority of the 10-20 extant wild individuals at the Leahi population. Leahi has been heavily developed and wetlands inside the crater were drained by the 1940s—it is likely that the entire crater, including the habitat of *S. adamantis*, was once wetter habitat than the dry, alien plant-dominated shrubland of present-day.

S. adamantis was the first species of *Schiedea* federally listed as endangered (in 1984) (USFWS, 2010) and has long been a target of conservation by the State of Hawaii Department of Land and Natural Resources Division of Forestry and Wildlife and the Oahu Plant Extinction Prevention Program (Sakai et al., 2017). Various large (100-300 individuals) outplantings have previously been attempted, adjacent to the wild site at Leahi crater. While a few individuals exist in nurseries, botanical gardens, and other gardens, but all previous wild outplanted populations failed, and no populations or individuals were extant in wild, natural areas prior to this study.

3.2.2 Paternal half-sibship families, seed source, study sites, and outplantings

Paternal half-sib families were produced for previous studies conducted at the University of California, Irvine (Culley et al., 2006; Weller et al., 2007). Plants originated from seeds and cuttings taken from the field and grown in the UC-Irvine glasshouse. A modified partial diallel crossing design (Meagher, 1992) was used, crossing each hermaphrodite with three unrelated females and crossing each female with three unrelated hermaphrodites, resulting in seeds representing 90 full sibships in 30 paternal

half sib families (Culley et al., 2006). One sire was randomly selected and crossed with multiple dams (Culley et al., 2006), using thirty unrelated hermaphrodites (sires) that were known to be heterozygous for the sex gene (Culley et al., 2006; Weller et al., 2007) and 30 females (dams). After depletion of seeds in previous studies and the failure of stored seeds from some families to germinate, I was able to outplant 18 paternal half-sib families in 2019, with a relatively equal distribution of the 268 individuals across families, at least three maternal plants per each family and ensuring all families were outplanted at both sites.

For this study, I prepared sites and outplanted two populations of *S.adamantis* in Kului Gulch (Lower Kului and Upper Kului). These populations are at 340m and 432m above sea level respectively. Both sites are wetter than the Leahi wild population (650mm annual rainfall), with the upper site wetter (1831mm annual rainfall) than the lower site (1393mm annual rainfall), according to the Rainfall Atlas of Hawaii (Giambelluca et al., 2013). The lower outplanting site receives similar levels of annual rainfall as the nearby wild population in Kului gulch (1313mm) but that population is extremely small (2-8 individuals) and it has not been represented in this study or any previous population genetic studies of the species.

Both outplanting sites are in areas largely dominated by alien trees; patches were cleared of these trees to create the outplanting areas. Remnant native trees and shrubs, including *Metrosideros polymorpha*, *Acacia koa*, *Pittosporum glabrum*, *Tetraplasandra lydgatei*,

and *Myrsine lessertiana*, among others, exist in the outplanting areas and adjacent areas. The lower outplanting site is dominated by the non-native *Psidium cattleianum* and *Schinus terebinthefolius* and the upper site is dominated by *Psidium cattleianum*. Various herbaceous and suffruticose shrubs, primarily alien species, have grown in cleared areas amongst outplants since the initial clearing and outplanting of *S. adamantis*. The primary herbivores found in both populations are alien slug species (*Veronicella leydigi*, *Vaginulus plebeia*, *Limax maximus*). Rat control was implemented in both populations to minimize potential impacts of introduced rodents.



Figure 10: *Schiedea adamantis* outplant (foreground) at Lower Kului population, showing cleared alien trees and various native shrubs in background

All seeds used to propagate outplants were taken from storage at the Lyon Arboretum Seed Bank in Honolulu, Hawaii. The paternal half-sibship family seeds were stored at the completion of the prior study, and additional seeds in storage came from collections in the late 1990s and early 2000s from the Leahi wild population and past outplantings (of Leahi sourced seeds) adjacent to the wild plants. Leahi-collected seeds were collected before the steep decline in that population over the past 15 years. Seeds were germinated and grown at various nursery facilities and outplanted from 4-inch round pots. In 2018, I outplanted 233 plants from non-paternal half sibship seeds at the

Lower Kului site. In 2019, I germinated and outplanted the paternal half-sibship families, 268 individuals split evenly between the Lower and Upper Kului Sites.

3.2.3 Collection of fitness and trait data and characterization of local environment

Each individual plant was tagged and its location within the plot was recorded. At each census, I measured survival, size (vegetative area), and fecundity (number of fruiting heads). Censuses were performed annually until 2022 in the peak reproductive season, February/March, a time of year that captures all reproductive output for the year for a total of three censuses of fitness and two annual measurements of traits of half sibling families.

I measured morphological traits in addition to the basic fitness data for all surviving individuals in both populations in the winter (December/January) of 2020/2021 and 2021/2022. As was done in the previous greenhouse study (Culley et al., 2006), I counted the number of stems and inflorescences of each individual plant. While size and reproduction are fitness components, the previous greenhouse study treated them as traits and I treated them as such when analyzing heritability (but not selection). I also measured the length and width (at widest point) of 5 leaves per plant from the second and/or third nodes from the top of stems, selecting leaves that were unshaded by other leaves of the same plant. Measurements of leaf length and width were used to calculate leaf area (as an ellipse) and the ratio of width to length, and I calculated the mean value of leaf length, width, area, and width to length ratio for each individual

plant. I calculated the ratios of stem number, plant width and length, and plant height, to size as further morphological traits indicating the general shape of each plant.

To characterize the microhabitat for each plant, I scored the level of shade on a scale of 0 to 5, with 0 in full sun throughout the day and 5 being completely shaded. In both populations, over 85% of the overstory is comprised of alien trees, primarily Strawberry guava (*Psidium cattalianum*) and Christmas berry (*Schinus terebenthifolius*), so shade scores are primarily due to the presence of these alien species.

For each plant in outplantings, I characterized the neighbors at each census using photographs taken during each census. I visually characterized the percentage cover of natives and aliens as well as the total neighbor cover within a 50cm radius of the focal plant. The same characterization was used to record the native, alien, and total cover within each recruitment plot. The sum of bare ground, native cover, and alien cover may exceed 100%, as native and alien cover often overlaps.

3.2.4 Watering supplementation and herbivore suppression experiments

At the lower Kului population, I performed a supplemental watering experiment to test if increased moisture affected selection on traits at the drier site. I randomly selected 85 plants to receive a watering treatment. Treatment plants received water directly at their base by drip irrigation for ten minutes, once per week. Watering treatment began in April 2018 and continued through November 2020. Watering treatment was included as a predictor variable in statistical models was included as a

predictor variable in statistical models of selection on traits, but I found no significant effects and dropped it from all final models.

At both populations, I implemented an herbivore suppression experiment targeting alien slugs, which are likely to be the primary herbivore affecting outplants (Joe & Daehler, 2008). I applied a molluscicide, Ferroxx® Slug & Snail Bait (Neudorff North America), to randomly selected blocks of each population (approximately 10m x 10m) approximately every two weeks from April 2018 through November 2020, per label instructions and common practice as a conservation tool in Hawaii (Adamski et al., 2020; Kawelo et al., 2012). I tracked the effect of the treatment using beer traps—4 jars filled with beer, buried so that the rim of each jar was 2cm above the surface of the soil with corrugated plastic cover to prevent organic matter from falling in 3cm above the top of jar, per treatment and control block. I counted the number of slugs in each trap monthly from January through August both years of molluscicide treatment. Herbivore suppression treatment was included as a predictor variable in statistical models of selection on traits. While beer traps indicated that treatment had a significant effect on number of slugs using a simple ANOVA ($p < 0.02$), I found no significant effects of herbivore suppression treatment on selection of traits, and thus dropped it as a predictor in all final models.

3.2.5 Analysis of heritability of traits

I performed all data processing, analysis, and visualization using R v. 4.0.1 (R Development Core Team, 2021). I estimated narrow-sense heritability (h^2) for all half-sibship individuals for all traits measured, adapting the methods used for analysis in the prior study that created the half-sib families and measured h^2 under greenhouse conditions (Culley et al., 2006). I used restricted maximum likelihood (to account for the unbalanced design of crosses that did not include all possible combinations of full-sibships) (Falconer & Mackay, 1996; Lynch & Walsh, 1998; R Development Core Team, 2021) from the package “lme4” (Bates et al., 2011), to estimate the variance caused by the random effects of paternal half-sibship for every trait. As the previous study found little sexual dimorphism in traits (Culley et al., 2006), I combined both sexes in the analysis and included sex as a fixed factor. I also included a fixed factor of shade score to account for the variation in microhabitat for each individual plant. No interaction term between paternal and maternal half-sibship could be included, as it is impossible to interpret such an interaction considering the missing cells from the crossing design (Searle et al., 2009). As is typical with this study design (Falconer & Mackay, 1996; Lynch & Walsh, 1998) and as was done in the previous study (Culley et al., 2006), I estimated additive genetic variance (V_A) as four times the variance among paternal-halfsibships. I calculated narrow-sense heritability for each trait as V_A divided by the total variance of each trait (V_P). I assessed the significance of the paternal half-sibship effects, which

would indicate significant additive genetic variance assuming the absence of additive epistasis (Lynch & Walsh, 1998), using a residual log-likelihood ratio test (Hothorn et al., 2015), comparing the full model with a model omitting the paternal effect and only including the maternal effect and residual error.

3.2.7 Selection analysis

I regressed the fitness components against values of traits to perform a selection analysis (Lande & Arnold, 1983). I modeled growth (linear) and survival (binomial) with mixed effects regression models (lme4) (Bates et al., 2011) with year, outplanting site, and size as fixed effects, interactions between fixed effects, and block (section of each outplanted population) as a random-intercept effect. For growth, proportional change in size (size.final minus size initial divided by size initial) was regressed against each trait. I modeled number of fruiting heads using size a quasipoisson regression using a mixed effects model (glmmTMB)(Magnusson et al., 2017) with year as a fixed effect and block as a random-intercept effect. I included plant size, year, and population as predictor variables, with up to three-way interaction terms between predictor variables.

Additionally, I included shade score, alien cover, and native cover as a predictor variables. I tested for interaction effects between trait, shade score, alien and native neighbor cover to test if shade and alien and native neighbors alter selection. I conducted model selection by dropping non-significant effects (using analysis of variance tables from the R-package 'car'(Fox et al., 2012)) from each model until only

significant predictor variables remained in the final models, but including non-significant main effects if they were involved in significant interaction effects. Alien and native neighbor cover was not significant in any models and thus was dropped from all final models.

3.3 Results

The upper Kului outplanting site had low survival rates (only 50% and 13% of outplants surviving after one and two years respectively), so the majority of data used to assess heritability of traits and relationship between traits and demographic rates is from the lower Kului site.

4.3.1 Variation of traits and heritability

I found no statistically significant narrow-sense heritability of any of the traits I measured (table 8). The h^2 values I found in the field were very low, ranging from 0 to 0.11 as compared the values above 0.4 in the greenhouse study (Culley et al., 2006), including statistically significant values greater than 0.47 for number of stems and number of infructescences for both female and hermaphroditic plants. Culley et al. also found significant heritability of other traits not measured in this study—stomatal conductance was found to be significantly heritable under greenhouse conditions for females but not hermaphrodites. Culley et al detected low paternal variance in other traits with no significant heritability.

Table 8: Narrow sense heritabilities (h^2) of outplanted half-sibships, using 18 paternal families, for morphological traits, from this study and for analogously assessed traits from prior greenhouse study (Culley et al., 2006), given for females and hermaphrodites respectively. *Culley et al assessed specific leaf area (area/mass), but did not report heritability of leaf area

Trait	h^2	P	h^2 (Culley et. al) Female/Herm.	P (Culley et. al) Female/Herm.
# stems	0.02	0.55	0.47, 0.50	0.012, 0.019
# stems : size	0.04	0.44	NA	NA
# stems : width	0	0.93	NA	NA
# stems : height	0.07	0.64	NA	NA
# infrct.	0.11	0.31	0.46, 0.21	0.014, 0.206
# infrct : size	0.02	0.97	NA	NA
# infrct : # stems	0.06	0.59	NA	NA
# infrt : height	0.01	0.73	NA	NA
# infrt : width	0	1	NA	NA
Leaf length	0	1	NA	NA
Leaf width	0.1	0.79	NA	NA
Leaf area	0.12	0.83	NA	NA
Leaf width: length	0.02	0.88	NA*	NA*

4.3.2 Selection analysis

Table 9: Summary of selection analysis, showing direction of significant effects of traits on fitness components. Blank cells denote no significant effect

Fitness Component	Leaf area	Leaf area x shade	Leaf shape (width: length)	Leaf shape x shade	# of Stalks	# Stalks x shade	Plant height to size ratio	Height: Size x shade
Growth (proportional size change)	+	+	+	+	+	+	+	
Survival			-	+	+			
Fruiting					+		+	+

I found several significant relationships between measured traits and fitness components (table 9). For growth (proportional change in size) as a fitness component, leaf area (fig. 11), leaf width to length ratio (fig. 12), number of stalks (fig. 13), and plant height to size ratio (fig 14), all had significant positive effects, as did shade. I also found significant positive interactions between shade score and leaf area, leaf width to length ratio, and number of stalks, showing a steeper slope for growth vs leaf area (fig. 11), relative leaf width (width:length) (fig. 12), and number of stalks (fig. 13), at higher levels of shade. There was no significant relationship between number of flowering/fruitlet heads (measured as a trait in Culley et al and treated as such as well as a fitness component in current study) and growth. I found no significant effects of any other measured traits on growth.

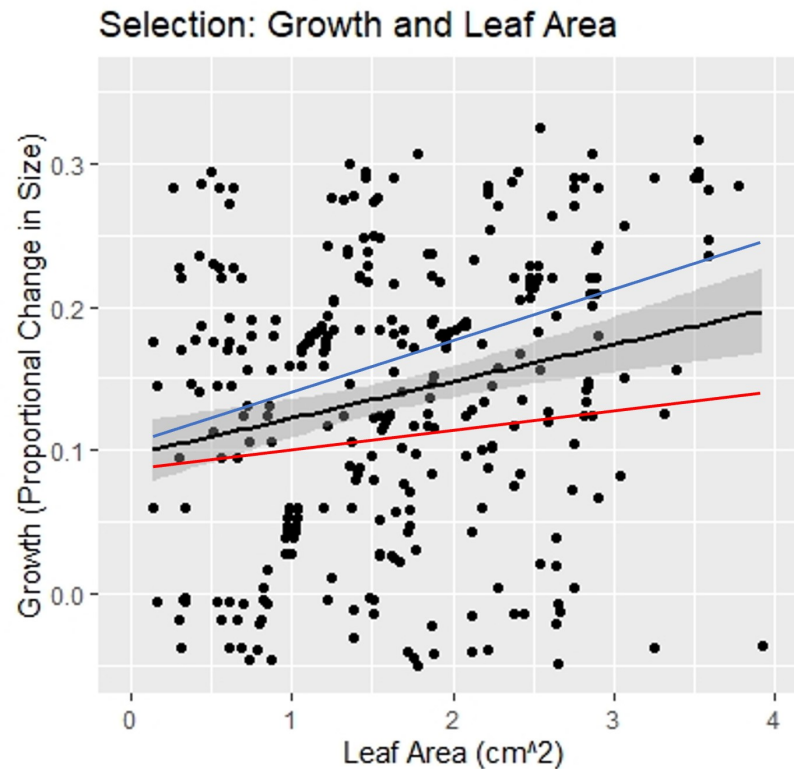


Figure 11: Selection analysis, showing relationship between leaf area (cm²) and growth (proportional change in size). Black line shows linear regression line, gray area shows standard error of model, while red and blue lines show model at moderately low (2 out of 5) and moderately high (4 out of 5) shade scores.

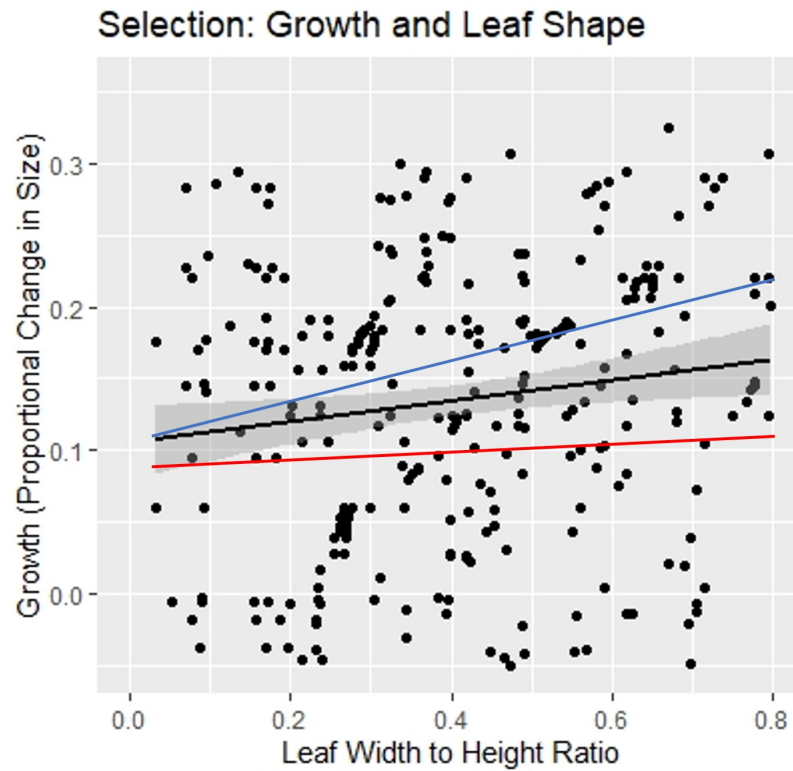


Figure 12: Selection analysis, showing relationship between leaf shape (width to length ratio) and growth (proportional change in size). Black line shows linear regression line, gray area shows standard error of model, while red and blue lines show model at moderately low (2 out of 5) and moderately high (4 out of 5) shade scores.

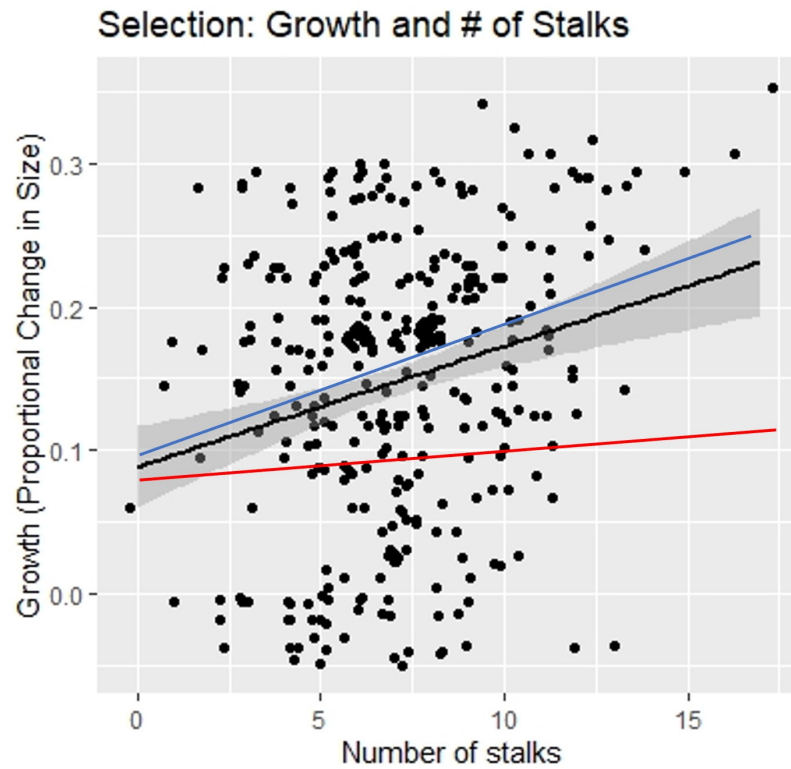


Figure 13: Selection analysis, showing relationship between number of stalks and growth (proportional change in size). Black line shows linear regression line, gray area shows standard error of model, while red and blue lines show model at moderately low (2 out of 5) and moderately high (4 out of 5) shade scores.

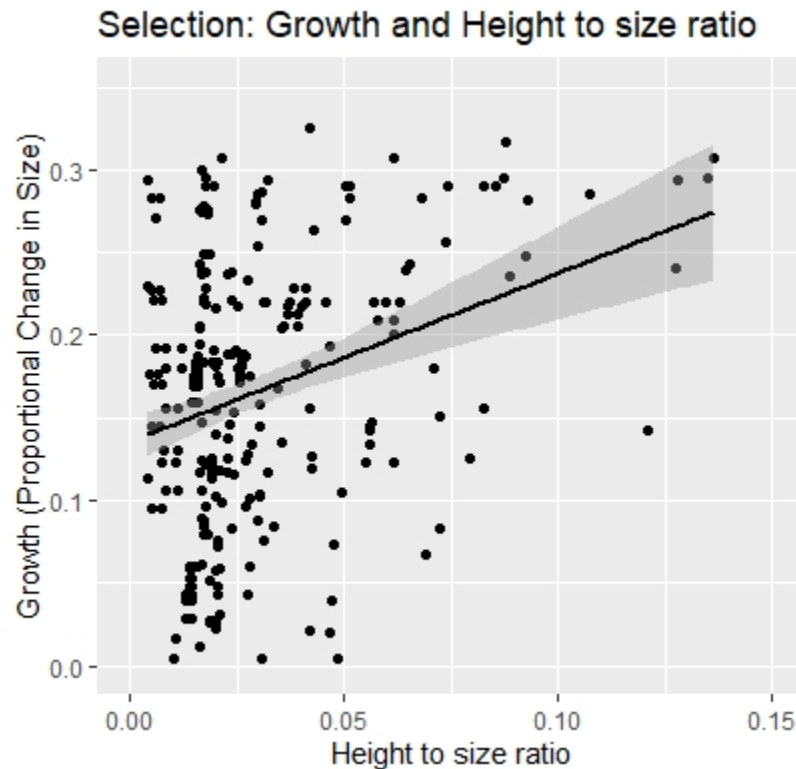


Figure 14: Selection analysis, showing relationship between total plant height to size ratio and growth (proportional change in size). Black line shows linear regression line and gray area shows standard error of model. There was no significant interaction effect on growth between height to size ratio and shade.

For survival, I found that number of stalks had a significant positive effect on survival, as did plant size and higher shade, while higher width to length ratio had a significant negative effect. I found a significant positive interaction between shade score and leaf width to length ratio, showing higher survival for plants with wider leaves when shade was greater despite the negative main effect. There was no significant relationship between leaf area, number of stalks, or number of flowering/fruiting heads and survival. There was no significant interaction between number of stalks and size,

highly correlated predictors, so the effect of number of stalks is likely attributable to larger size. I found no significant effects of any other measured traits on survival.

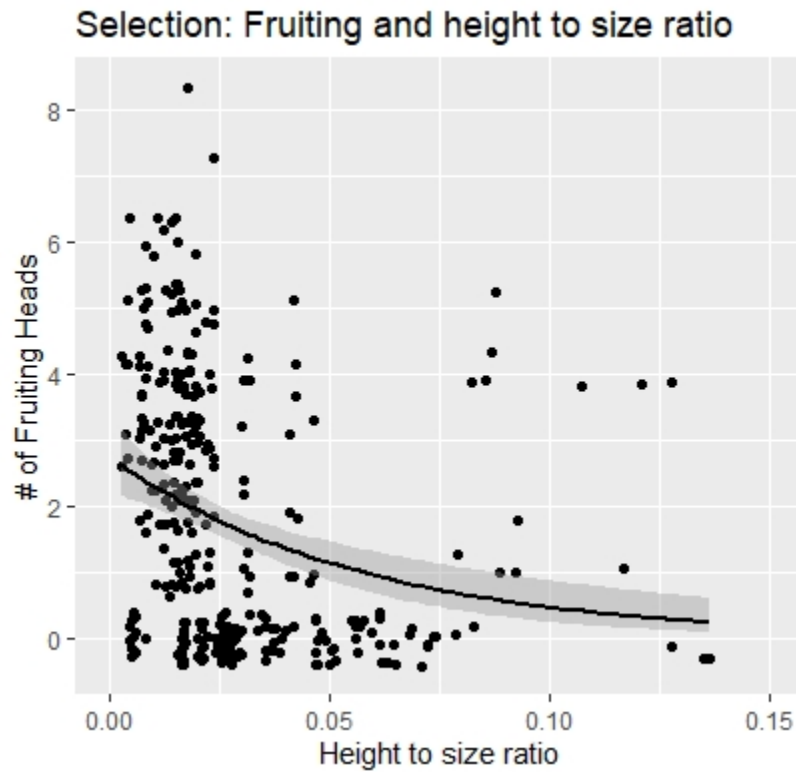


Figure 15: Selection analysis, showing relationship between total plant height to size ratio and number of fruiting heads produced. Black line shows quasipoisson regression line and gray area shows standard error of model. There was no significant interaction effect on fruiting between height to size ratio and shade.

For reproduction, I found that size to height ratio had a significant negative effect on the number of fruiting heads produced (fig. 15), while number of stalks had a significant positive effect, as did size. I found no significant interaction effect of shade score and number of stalks. I also found no significant interaction effect of size and number of stalks, so the effect of number of stalks is likely attributable to larger size

which is highly correlated with number of stalks. There was no significant relationship between leaf area or shape on fruiting. I found no significant effects of any other measured traits on growth.

4.4 Discussion

I have shown that despite some traits being heritable under greenhouse conditions, many morphological traits are not heritable in the field (table 8), even when accounting for variation in shade and moisture (through planting at sites with different amounts of rainfall and supplemental watering at the drier site). I did find that key traits had significant effects on the fitness components in outplanted populations, demonstrating that traits are under selection. These results suggest that while some of the morphological traits I measured are subject to selection under field conditions, the outplanted population is not predicted to evolve in response to that selection, given the lack of genetic variation.

The lack of statistically significant narrow-sense heritability detected in this study suggests that unlike phenotypic variation in the greenhouse in the previous study (Culley et al., 2006), morphological (and potentially ecophysiological) phenotypic variation in the field is not driven by genetic differences. While my study power was somewhat limited by a lower number of remaining families available compared to the greenhouse (18 rather than 30), the values of h^2 are so low that is unlikely that even the greater number of families used in the greenhouse study, would result in detection of

significant heritability under field conditions—all cases of h^2 greater than 0.28 were significant in that study, while the vast majority of h^2 I detected were less than 0.1 and the highest h^2 I detected was 0.11.

While I did not find that traits were heritable, I did detect many significant effects of traits on fitness components indicating that selection on those traits is likely occurring. As the goal of reintroductions is to establish populations with significant genetic diversity to allow for future evolution (Maunder, 1992), this suggests that these outplantings do not have the capacity to evolve in response to varying conditions, a particularly concerning finding as the outplantings in this study represent the high end of possible founder diversity for an extremely rare taxon. However, many reintroductions do not persist and grow to the point where evolution becomes possible, with lack of survival and recruitment dooming their long term persistence (Albrecht et al., 2011; Godefroid et al., 2011). Considering those frequent failures, conservation efforts might be justified to consider ecological and demographic factors, such the ability to grow, survive and reproduce under a changing climate and with anthropogenically altered biotic interactions before considering the potential for evolution. Without an ability to outplant individuals that survive and regenerate, attempting to outplant populations for future evolution is a futile task.

The relationship between shade score, traits, and fitness components illustrates the importance of morphological traits in the success of outplantings in heterogeneous

habitats. Higher shade increased growth and survival of outplants, and positive interaction terms between shade and leaf traits show that variability of those traits among individuals allow some to perform better in more or less shade while others lack traits to thrive. While none of the traits I measured show heritability in the field, the variation in these traits could be important to population success, even if the variation is not driven by genetic diversity, if conditions within an outplanted population (such as shade) are heterogeneous. In the populations in this study, the benefit of shade is conferred almost entirely by alien trees and shrubs (which comprise >85% of the overstory species in the successful, Lower Kului population and >95% of the overstory in the far less successful, Upper Kului population. As both outplanting sites were created by clearing patches in the largely alien overstory, it appears that the shade provided by the remaining alien trees around the edges of the patches are critical for the success of native outplantings. While a population could likely be planted in an area that has been restored to a predominantly native plant community, the efforts to create such a setting could be time consuming and costly. In a highly invaded and largely degraded place like the habitat of *Schiedea adamantis* and many other Hawaiian plants, relying on benefits of alien dominated systems is likely to be more efficient. The positive effects of shade, conferred largely by alien plants, I found here parallels the beneficial effects of alien species I found in chapters one and two.

The results of the selection analyses also show that there may be tradeoffs between fitness components for some traits. I found that plant height to size ratio had a positive effect on growth, but a negative effect on production of fruiting heads. This potential growth/reproduction tradeoff shows the downside of assessing selection based on fitness components and it may be prudent to integrate across fitness components to find the effect of traits on total fitness. One approach would be to use trait values to drive demographic rate regressions (analogous to the selection analyses in this study) that are fed into a population model, such as the integral projection models presented in chapter two. Even if not all demographic rates in such a model were dependent on trait values, deterministic population growth would be a measure of total fitness that shows net selection rather than simply selection on individual components of fitness. However, such a model requires a full range of plant sizes to accurately project population growth, and in outplanted populations of perennial plants, this requires more time for plants to grow to their largest size.

It is possible that while phenotypic plasticity under field conditions made it impossible to detect heritability of traits in this study, the underlying genetic diversity allowed for variation in traits that had significant effects on fitness components. Without extensive prior knowledge that certain founders have traits that are favored in conditions at certain outplanting sites (and that will continued to be favored under reasonable predictions of future conditions), there is certainly little downside in planting

a population with as many founders as possible, maximizing potential genetic diversity, as has been suggested in previous research on reintroductions (Albrecht & Maschinski, 2012; Albrecht et al., 2019). However, time and money spent on conservation efforts represent trade-offs, and the lack of heritability of traits does suggest that perhaps those limited resources would be better spent improving other aspects that contribute to the success of an outplanting, such as increasing the number of outplants regardless of genetic diversity (Albrecht et al., 2011; Albrecht & Maschinski, 2012), as compiling genetically diverse propagules can be difficult and time consuming. Once demographic factors determining success are better understood, an investment of resources into maximizing genetic diversity would be more warranted

There is a great deal of momentum towards managed translocation of rare species. While this tool will certainly benefit conservation of some species and ecosystems (Zimmer et al., 2019), this study demonstrates the limitations of such efforts, particularly in the context of limited ecological information about the determinants of a species' ability to persist and grow. While *Schiedea adamantis* seemed to succeed at the lower Kului outplanting site, it largely failed at the upper, wetter site. While both sites are wetter than the primary wild population and there is likely a benefit to increased moisture compared to that site, there appears to be a limit to that benefit. Like success of outplantings as a whole, this could be caused by demographic and ecological factors, including novel biotic interactions or physiological responses to different abiotic

conditions, by genetic constraints, lacking phenotypic diversity sufficient to survive in novel environmental conditions, or, most likely, by a combination of both ecological and genetic factors (Lande, 1998). Managed translocation is an appealing theory and a tool likely to be important in a changing climate, but it should be implemented based on the best possible ecological and evolutionary science that indicates that it may succeed.

While gaining knowledge into trait, fitness, and environment relationships is difficult, especially for rare species, the apparent inability to respond to selection in both outplantings and the failure of the wetter population highlight some important considerations in planning and implementing translocation. In the case of *Schiedea adamantis* in this study, it seems that past evolution in a dry habitat has led to dry-adapted traits that do not benefit the species in wetter areas. Even if its primary wild habitat has become too dry and it would benefit from being translocated to a somewhat wetter site, there are limits to the amount of moisture that will benefit *Schiedea adamantis* and populations will ultimately fail at sites that are too wet. The leaf traits I found to have significant effects on growth, survival, and reproduction directly play a role in how plants use moisture and light—wider and larger leaves increase photosynthesis in shady, light-limited areas. However, the positive effect of narrower leaf shape on survival could be a trait adapted to hot, dry conditions, and perhaps tradeoffs between selection on different fitness components are playing out on different traits. Further, the significant interactions between leaf traits and shade suggest that variation in those

traits drive the ability of individuals to survive, grow, and reproduce in wetter and drier, shadier and sunnier sites. The shape of whole plants (including height to size ratio and number of stalks) could indicate physiological responses to shade. As alien plants increase in density and alter shading of native plants, there could be additional benefits to these morphologic traits. The lack of detectable heritability of those traits suggests that variation may not be driven by genetic differences. Plasticity of those leaf traits, however, appears to allow for success in a wider range of habitats and may allow for successful translocation to novel conditions, even if there is a limit to the conditions under which *Schiedea adamantis* may ultimately succeed.

Perhaps more than anything else, my findings in this study have demonstrated the ecological and evolutionary complexity of plant conservation—the factors that determine success are messy, especially in real world, field conditions and with ongoing anthropogenic change altering biotic and abiotic interactions. This necessitates the implementation of conservation based on incomplete scientific information most of the time. However, despite these limitations, conservation should strive to use the best-available scientific basis for action and scientists should strive to provide information that has practical use to conservation. In this study, I have found that traits of a rare plant are under selection under field conditions and that selection is modulated by shade that is conferred almost exclusively by alien species. However, I have also not detected heritability of those traits, and while outplants may be able to persist for now,

there is little potential for evolutionary rescue. While this may have discouraging conservation implications, it does not necessarily doom these outplantings and this species—rather, it suggests that in order to best manage rare species, we must continue efforts to understand the relationship between genotype, phenotype, and fitness as part of ongoing conservation.

Appendix A: Chapter 1 Supporting Materials

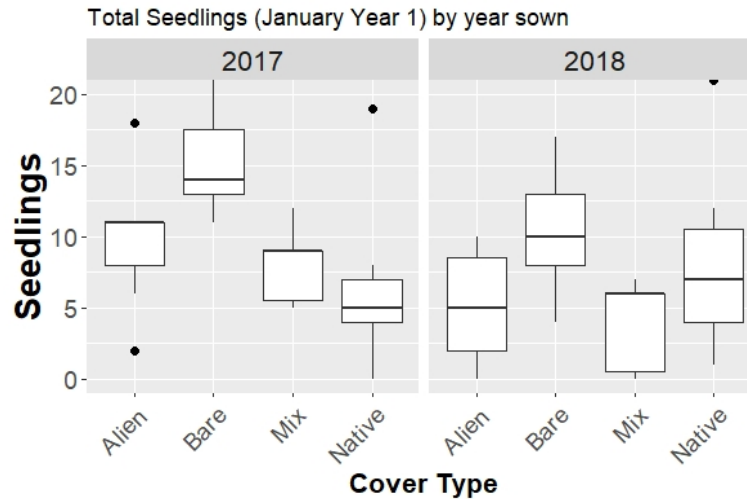


Figure A.1: Boxplot of number of initial emerging seedlings by cover type comparing years. Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

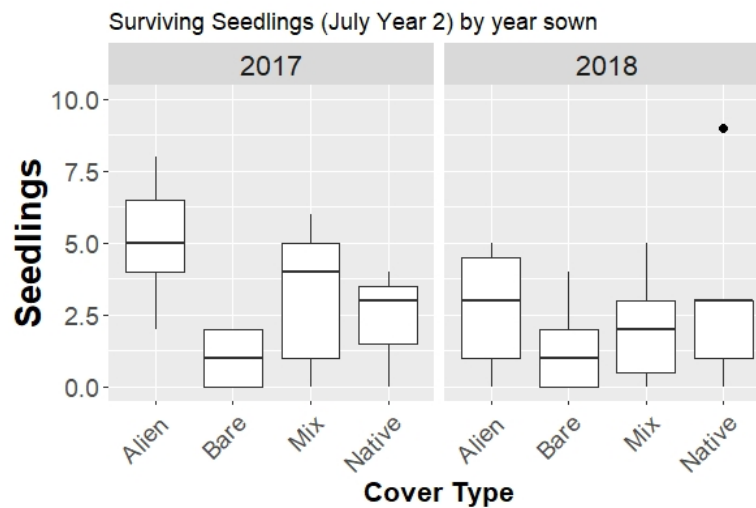


Figure A.2: Boxplot of number of surviving seedlings by cover type comparing years. Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

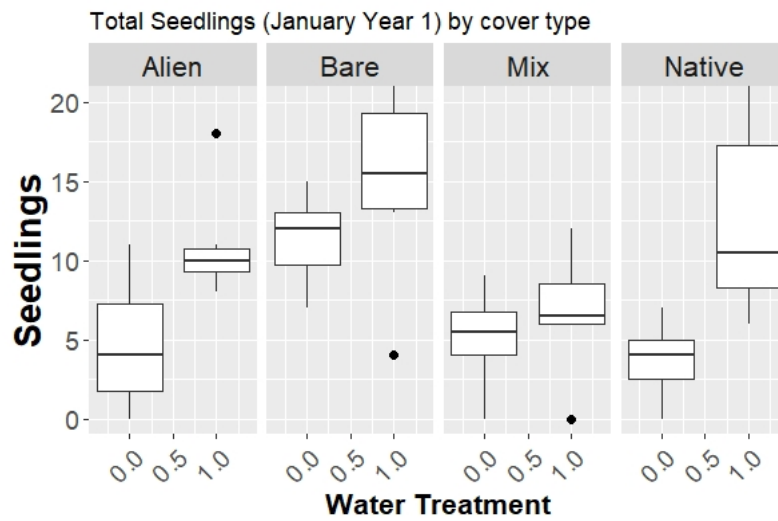


Figure A.3: Boxplot of number of initial emerging seedlings by cover type comparing water treatments (0 = control, 1 = treatment). Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

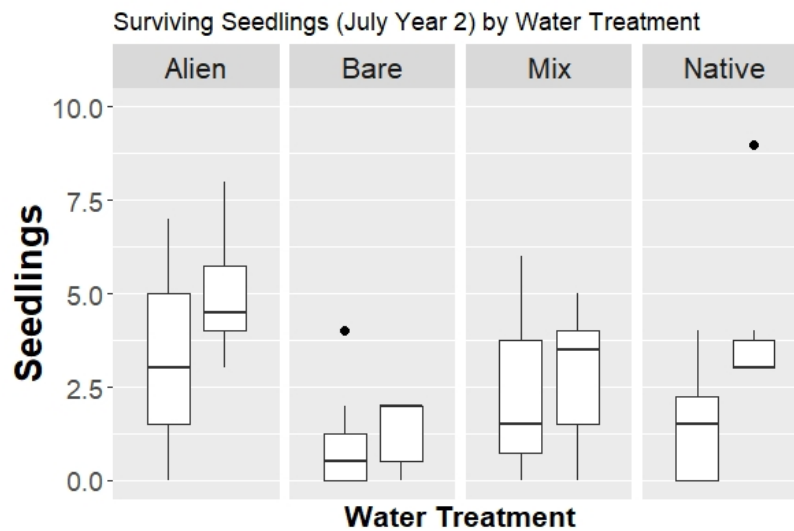


Figure A.4: Boxplot of number of surviving seedlings by cover type comparing water treatments (left box = control, right box = treatment). Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

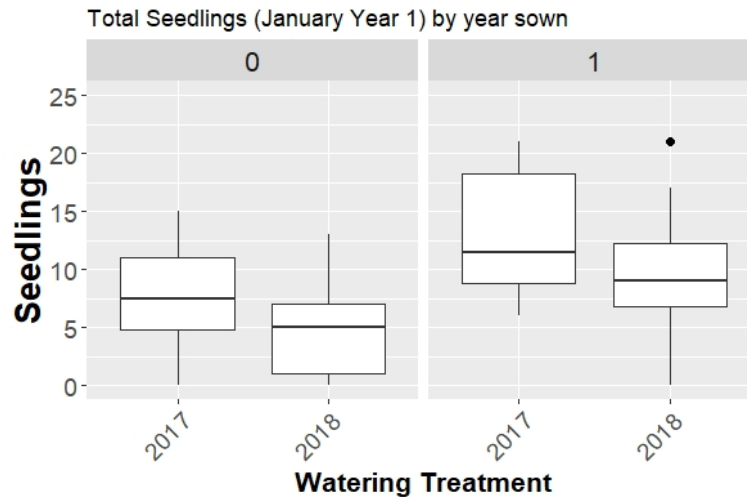


Figure A.5: Boxplot of number of initial emerging seedlings by year and water treatments (0 = control, 1 = treatment). Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

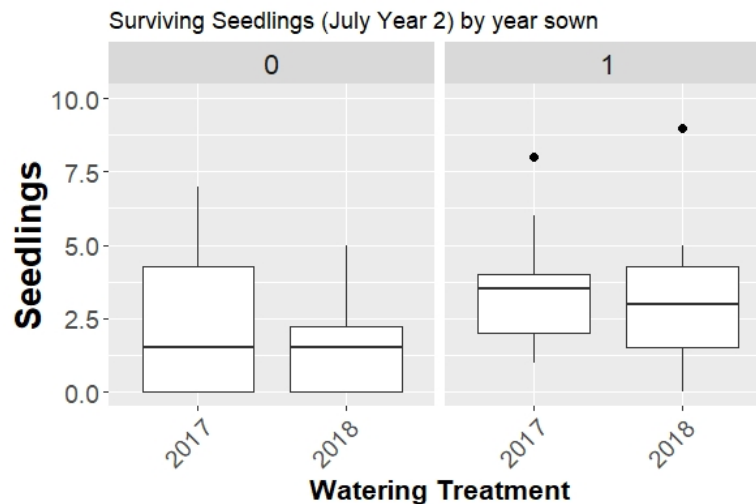


Figure A.6: Boxplot of number of initial emerging seedlings by cover type comparing water treatments (left box = control, right box = treatment). Lower and upper box limits represent 25th and 75th percentile respectively, dark line represent median for each group, and whiskers represent 1.5x the interquartile range. Dots represent outlying data points beyond 1.5x the interquartile range.

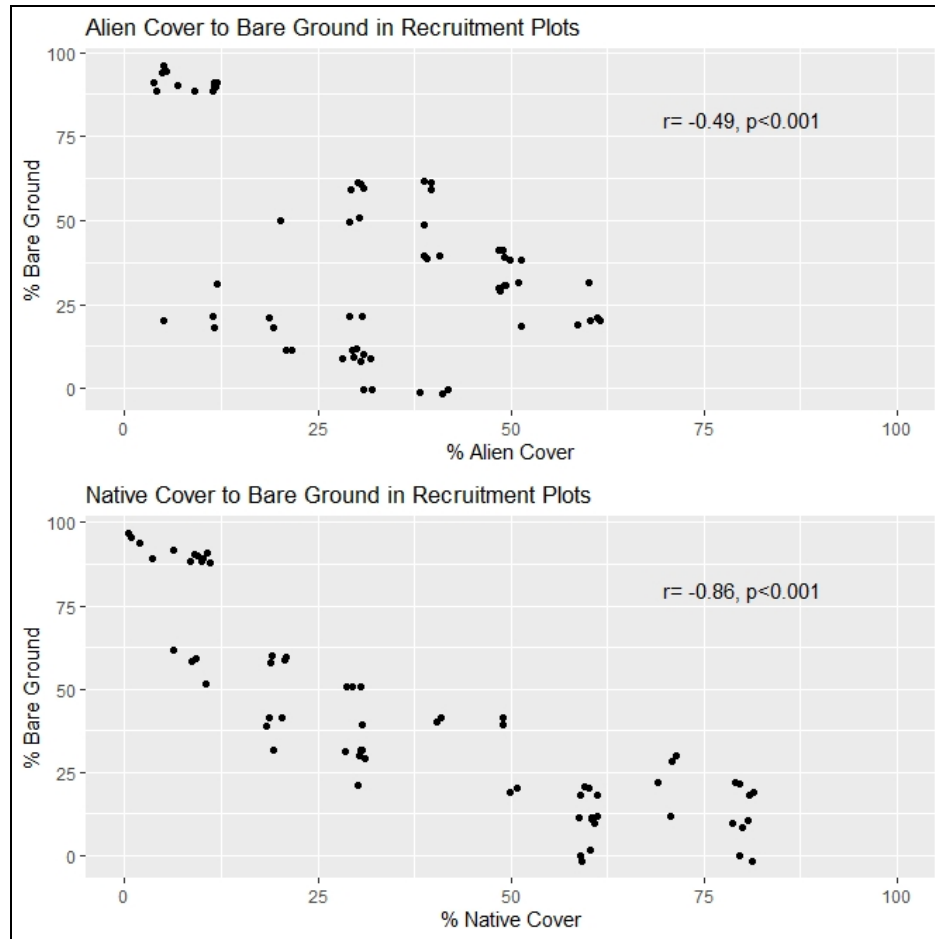


Figure A.7: Correlation between % Bare ground and % Alien and Native cover in recruitment plots

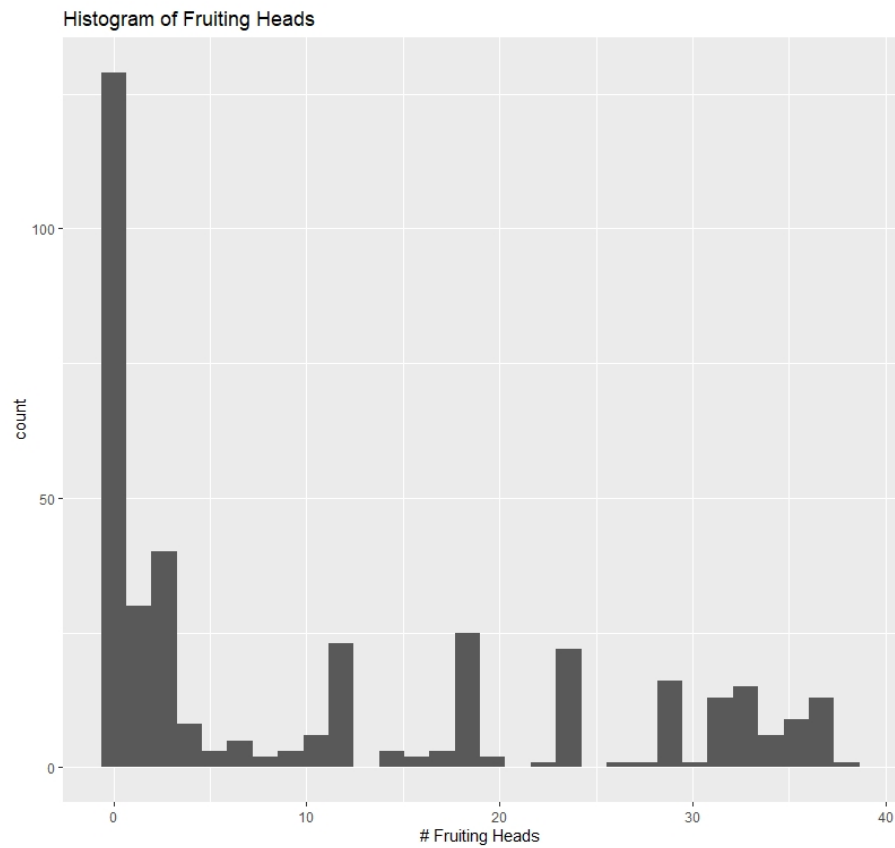


Figure A.8: Histogram of number of fruiting heads counted on reproductive size Makapuu individuals, showing prevalence of zeros

Appendix B: Chapter 2 Supporting Materials

Table B.1: Table of demographic rate coefficients used in integral projection models dependent on native and alien cover. Species denoted by 6 letter codes (Genspp)

Population	Year	Species	Demographic Rate	Intercept	Size	Alien Cover	Native Cover	AC * NC	S*AC	S*NC	S*AC*NC	Standard Deviation
Kealia 1	2018	schkea	growth	-54.0573	1.0467	2.3414	0.0396	0.0000	0.0000	0.0035	0.0000	1383.1413
Kealia 1	2018	schkea	surv	1.1822	0.0010	0.0000	-0.0177	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2018	schkea	didrep	0.5557	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2018	schkea	repro	4.4721	0.2115	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2018	schkea	recruit	-0.4027	0.0000	0.0312	0.0203	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	growth	-81.5713	1.0691	2.7236	-0.4784	0.0000	0.0000	0.0040	0.0000	1748.4970
Kealia 2	2018	schkea	surv	1.4524	0.0005	0.0000	0.0234	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	didrep	0.3563	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	repro	4.4721	0.2115	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	recruit	-0.3024	0.0000	0.0102	0.0040	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2019	schkea	growth	-67.3284	1.0691	2.7236	-0.3100	0.0000	0.0000	0.0021	0.0000	1748.4970
Kealia 1	2019	schkea	surv	1.0180	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2019	schkea	didrep	0.5557	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2019	schkea	repro	4.4721	0.2115	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 1	2019	schkea	recruit	-0.3800	0.0000	0.0002	0.0095	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	growth	-88.7430	1.0691	2.1000	0.3100	-0.0100	0.0000	0.0000	0.0000	1748.4970
Kealia 2	2018	schkea	surv	0.9918	0.0002	0.0000	0.0310	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	didrep	0.5557	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	repro	4.4721	0.2115	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Kealia 2	2018	schkea	recruit	-0.2000	0.0000	-0.0002	0.0095	0.0000	0.0000	0.0000	0.0000	NA
Makapuu	2018	schglo	growth	76.0143	1.0357	2.6218	0.0000	0.0000	0.0000	0.0000	0.0000	1342.4130
Makapuu	2018	schglo	surv	1.2249	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Makapuu	2018	schglo	didrep	-0.7523	-0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Makapuu	2018	schglo	repro	-0.1460	0.0005	0.0261	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Makapuu	2018	schglo	recruit	-0.3027	0.0000	0.0112	0.0103	0.0000	0.0000	0.0000	0.0000	NA
Makapuu	2019	schglo	growth	-35.6000	0.8940	-0.2820	-0.0446	0.0530	0.0033	0.0032	-0.0001	1384.5790
Makapuu	2019	schglo	surv	0.8679	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA

Lihau 1	2019/2020	schmen	repro	2.2600	0.3730	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Lihau 1	2019/2020	schmen	recruit	-0.0535	0.0000	-0.0013	0.0085	0.0000	0.0000	0.0000	0.0000	NA
Lihau 2	2019/2020	schmen	growth	43.8310	1.0914	1.2000	0.4300	0.0000	0.0000	0.0000	0.0000	1652.0000
Lihau 2	2019/2020	schmen	surv	0.9370	0.0005	0.0021	0.0110	0.0000	0.0000	0.0000	0.0000	NA
Lihau 2	2019/2020	schmen	didrep	0.5731	0.0019	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	NA
Lihau 2	2019/2020	schmen	repro	4.2700	0.4170	-0.0009	0.0096	0.0000	0.0000	0.0000	0.0000	NA
Lihau 2	2019/2020	schmen	recruit	-0.0700	0.0000	0.0000	0.0074	0.0000	0.0000	0.0000	0.0000	NA

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Biography

Alex Loomis attended Central Union Preschool and Punahou School in Honolulu, Hawaii, where he developed an interest and passion for the native flora and fauna of the Hawaiian Islands. He received a B.A. from the University of Colorado in Boulder, Colorado in 2013, majoring in Geography and Environmental Studies, Minor in Ecological and Evolutionary Biology, and receiving a certificate in Western American Studies. He has spent years working in conservation in Hawaii, and upon his graduation from CU-Boulder, he worked for the Oahu Army Natural Resources Program as part of the University of Hawaii's Pacific Cooperative Studies Unit, implementing stabilization plans for threatened and endangered species impacted by Army training on the island of Oahu. Alex's PhD research was supported by Duke Biology Departmental Fellowships and grants from Phipps Conservancy and the Duke Graduate School. His research has been published in journals including *Proceedings of the National Academy of Sciences*, *New Phytologist*, *Conservation Biology*, and *Ecosphere*.