ABIOTIC AND BIOTIC FACTORS ASSOCIATED WITH CURRENT AND LONG-TERM NATIVE AND NON-NATIVE PLANT COVER ACROSS AN INVADED HAWAIIAN LANDSCAPE

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BY

Joshua Hibit

Dissertation Committee:

Curtis C. Daehler, Chairperson

David C. Duffy

Donald R. Drake

Mark D. Merlin

Travis W. Idol, University Representative

Keywords: Island forest communities, native species, invasive species, abiotic conditions, diversity measures, long-term impacts

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Abstract

Extended periods of disturbance and the introduction of non-native species pose major threats to native Hawaiian forests, many of which exist today as remnant patches, harboring native plant species that are on the brink of extinction. When native Hawaiian plant species are faced with competition from biogeographically cosmopolitan non-native species they are often at a disadvantage, especially in easily accessible areas and where high resource availability fuels the growth of invasive species, which can displace existing natives. However, relatively few datasets exist which can give insight into the long-term impacts of anthropogenic disturbance and species introductions on indigenous and endemic Hawaiian plant species across the myriad of abiotic site conditions that exist in the Hawaiian Islands. In addition, the importance of plant functional diversity, phylogenetic diversity, and biogeographical diversity for determining native resilience in invaded oceanic island forests has not been well established. To address this gap in knowledge I established fifty 400 m^2 forest plots in the Waiʻanae and Koʻolau mountain ranges on Oʻahu, Hawaiʻi, and assessed current native and non-native plant cover trends in relation to measures of diversity and trait-mediated interactions of the constituent species in each plot. Thirty-two of these plots had also been previously surveyed, which allowed for an assessment of trends in endemic, indigenous, and non-native plant cover over time, and how these trends vary across abiotic gradients from dry to wet forest.

The results of this study indicate that native Hawaiian forests may not be successfully regenerating and are being invaded by non-natives. Native and non-native plant cover values were determined by their respective diversity measures, as well as competition for light. invasion success was not related to overall trait dissimilarity, but there are likely additional traits which were not measured in this dissertation that influence competitive outcomes and/or niche filling between natives and non-natives. Non-natives exhibited a variety of successional strategies, reflecting the introduction history of tree species into the Hawaiian Islands for forestry purposes, as well as the intentional or accidental introduction histories of other herbaceous and woody species, and the diverse biogeographical origins from which these species arrived. Long-term trends showed that, as non-native plant richness and abundance has increased over time, native species in aggregate have concomitantly declined. However, this was largely the result of the loss of endemic species richness and cover, which were more susceptible than indigenous species to decline in the face of invasion, even where ungulates were excluded. Endemic species were more dependent on site conditions than indigenous species, which increased in overall cover over time, indicating that generalizations about natives as a single group may be misleading. Some of the indigenous species which increased in cover the most were early successional species, and may thus reflect disturbed or degraded conditions, rather than a trend toward recovery of natural native forests. These results suggest that an upscaling of active management efforts is needed to avoid further decline of native species, particularly endemics, and to stymie the tide of forest invasion by non-native species.

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AIC: Aikake Information Criterion

BA: Basal area

BD: Biogeographical diversity

FD: Functional diversity

FDdiv: Functional divergence

FDe: Functional evenness

FDr: Functional richness

HI: Hawaiian Islands

Hmax: Maximum height

IV: Importance values

KV: Kahana Valley

MFR: Mokulēʻia Forest Reserve

PCA: Principal components analysis

PCoA: Principal coordinates analysis

PD: Phylogenetic diversity

PNAR: Pahole Natural Area Reserve

RD: Relative density

RF: Relative frequency

SDM: Seed dry mass

SLA: Specific leaf area

SSD: Specific stem density

ULA: Understory light availability

Chapter 1: Introduction

The native flora of the Hawaiian Islands (HI) is a unique assemblage comprised of species that were able to naturally disperse great distances across the Pacific, as well as their descendants. There are approximately 1190 native vascular plant species (1,029 angiosperms and 161 pteridophytes) currently known to reside in the HI, and as the most isolated island archipelago on the planet, natural colonization events occur with extreme infrequency (Harrington & Ewel, 1997; Palmer, 2003; Wagner et al., 1999). For example, there have been ~259 known successful colonizations of angiosperms in the HI, which suggests that the average establishment rate for angiosperms is one successful colonization per every 116,000 years; pteridophytes have ~114 known colonization events in the HI, which suggests that the average successful establishment rate for ferns and fern allies is roughly one per every 265,000 years (Price & Wagner, 2018; Ziegler, 2002). As a result, there is a high proportion of endemic species in the Hawaiian flora (~90% for angiosperms, and 74% for ferns and lycophytes), and the native flora is decidedly lacking in particular aspects of diversity, with certain plant functional groups (e.g., large seeded species, pyrophytic grasses) missing or underrepresented when compared with continental flora (Ostertag et al., 2015; Sakai et al., 2002; Selmants et al., 2017; Vernon & Ranker, 2013). Unfortunately, the unique species which have evolved in the HI are currently under threat as a result of human activity.

The arrival of humans to the HI has led to drastic changes in the structure and distribution of native plant communities, beginning with the introduction of the Polynesian rat (*Rattus exulans*), and later with the clearing of lowland forests and grasslands for agriculture by early Polynesian colonists (Athens, 2009; Woodcock, 2003). Contact with Europeans brought the addition of many non-native plant and animal species, as well as new anthropogenic stressors on native forests, with further clearing of forests for the sandalwood and whaling trades, as well as for sugar cane and pineapple production (Woodcock, 2003; Ziegler, 2002). The introduction of feral ungulates has proven to be an especially destructive force in Hawaiian plant communities

(Cabin et al., 2000; Cole & Litton, 2014; Merlin & Juvik, 1992). Ungulate browsing removes native vegetation, which is not adapted to herbivory by large mammals, and disperses seeds of non-native species (e.g., *Psidium cattleyanum*) (Merlin & Juvik, 1992). Fire frequency has also increased with the arrival of humans in the HI, removing native vegetation and increasing resource availability for incoming species (e.g., light or nutrients deposited from ash following fire) (Cuddihy & Stone, 1990; Smith & Tunison, 1992). In addition, fragmentation of native dominated habitats in highly disturbed areas (e.g., agricultural fields) impedes the dispersal of natives that typically rely on animal or wind vectors, limiting native colonization ability (Buckley & Catford, 2016; Denslow et al., 2006).

Regeneration of natives, which are generally not adapted to frequent disturbance, is slow, and when coupled with increased dispersal limitation and habitat fragmentation, landscapes may often remain in a degraded state following disturbance (Woodcock, 2003). Early botanists assigned the task of revegetating denuded areas in the HI, such as Harold Lyon, thought that native species were better adapted for primary succession on lava flows, and that in well-developed soils natives are quite unable to regenerate once perturbed (Woodcock, 2003). As a result, these early botanists sought the help of non-native plant species which could rapidly grow and restore watershed functioning in degraded landscapes (Woodcock, 2003). Thousands of non-native plant species from cosmopolitan biogeographic origins have been introduced for reforestation or horticultural purposes, with millions of individuals planted (Woodcock, 2003). Today the number of naturalized plant species exceeds that of native species, and that number is increasing as more species are introduced at the rate of about 40 per year over the last two centuries, vastly exceeding the natural rate of plant colonization in the HI (Imada, 2012; Mac et al., 1998).

Some of the non-native plants introduced into the HI have become invasive pests (Staples, 2000), encroaching into native dominated areas over time and displacing them (Woodcock, 2003). Invasion is often precipitated by disturbance, where once natives are removed they may not be able to compete with some of their more vigorous non-native counterparts (Catford et al., 2012; Willis & Birks, 2006). Some of the non-natives which have already established can further increase susceptibility to invasion by other species (e.g., N-fixing species in N-limited habitats), directly impact native survival, growth and reproductive output, and alter disturbance regimes (Catford et al., 2012; Ellsworth et al., 2013; Selmants et al., 2017). Even relatively intact native forest communities may still be susceptible to invasion by shade tolerant species. For example, Foster Huenneke & Vitousek (1990) found that animal dispersal of *P. cattleyanum* allowed it to invade undisturbed areas in the HI, and its clonal growth contributed to its ability to eventually dominate once established.

Non-native plant invasion impacts are further exacerbated by the introduction of non-native frugivores, which may preferentially feed on and disperse the fruits of alien plant species, while introduced seed predators may kill native plant seeds (e.g., rats feeding on *Pritchardia* fruits) (Foster & Robinson, 2007; Merlin & Juvik, 1992; Shiels, 2011). At the same time, the extinction of native Hawaiian co-evolved or symbiotic species due to human agency, such as pollinators and dispersal agents, may virtually eliminate some plant species which relied on their services (e.g., *Brighamia insignis*). Decreasing availability of resources for native pollinators and seed dispersers due to declines in native plant diversity and abundance can additionally feedback to decrease the likelihood of pollination or dispersal for remaining native plant species (Chimera & Drake, 2011; Drake, 1998). Furthermore, the lack of pests and pathogens normally present in an invader's native range may also allow it to grow relatively unimpeded (i.e., 'enemy release') when compared with native species, which are vulnerable to the pests and pathogens already present in Hawaiʻi (e.g., *Clidemia hirta*, DeWalt, Denslow, & Ickes, 2004). Native species are additionally subjected to novel pests and pathogens (e.g., Rapid ʻŌhiʻa Death) as the result of anthropogenic activities, leading to yet further decline (Fortini et al., 2019).

The combined effects of these ecosystem alterations have resulted in the large-scale decline of native plant species in the HI. At present, land cover of native dominated areas (> 50% native cover) across all islands amount to only 31% of vegetated areas (Selmants et al., 2017). This varies from island to island, with the island of Hawaiʻi having the greatest proportion of vegetated areas dominated by natives (58%), and the island of Kahoʻolawe having the lowest (1%); the most populated island, Oʻahu, only has 16% of its vegetated areas dominated by natives (Selmants et al., 2017). The situation is even more dire when considering the viability of native populations, with 9% of the native angiosperms already listed as extinct, and about 52.5% of the native Hawaiian flowering plants at risk of extinction (approximately 9% extinct in the wild, 25% endangered, and 18.6% vulnerable or rare), and this risk has been found to be greater for endemic species, which have narrower distributions than indigenous species (Sakai et al., 2002).

Despite these enormous pressures, intact native forests may still be resistant to invasion in some cases where anthropogenic disturbance is largely absent, and some native species may even be able to reestablish in non-native dominated areas (Aplet & Vitousek, 1994; Harrington & Ewel, 1997; Wirawan, 1974). However, there are large gaps in the scientific understanding of circumstances and mechanisms which would favor native persistence or prevalence in the face of invasion. For example, few studies have investigated long-term native plant cover trends in areas which have experienced invasion in the HI. In addition, while disturbance and availability of resources has been shown to affect the relative performance of native and non-native plants (Chardon et al., 2019; Daehler, 2003; Merlin & Juvik, 1992), the influence of abiotic site conditions on long-term native persistence in invaded Hawaiian forests, and how these persistence trends may differ between indigenous and endemic Hawaiian plant species, has not been investigated.

Plant functional traits may also play a role in determining which species may be able to invade and compete with native species, either through niche differentiation or habitat filtering processes (Maire et al., 2012). A greater diversity of traits (i.e., functional diversity) or evolutionary histories (i.e., phylogenetic diversity) amongst native species in a given community can theoretically increase niche overlap, thereby excluding similar species (MacArthur & Levins, 1967; Mouchet et al., 2010). However, the influence of functional and phylogenetic diversity on invasion resistance in native Hawaiian forest communities has not been well established. Invasibility may also be influenced by the diversity of invaders (Gallien & Carboni, 2017); the non-native flora of the HI come from disparate biogeographic origins (Palmer, 2003; Wagner et al., 1999), which may also be related to their diversity and thus influence the potential impact of these species on native plant communities (Buckley & Catford, 2016; Cavender-Bares et al., 2016). However, this has not been investigated as a potential explanatory factor for invasion success in Hawaiian forests.

In an effort to address these gaps in knowledge, I revisited seven remnant dry forest patches that were previously surveyed in 1950 and 1970 in the Mokulēʻia Forest Reserve on Oʻahu, Hawaiʻi in order to assess long-term native persistence (Chapter 2). I also revisited 25 plots established in mesic and wet forests on the island of Oʻahu, Hawaiʻi (initially established in 1973-74 in Kahana Valley and 1990-91 in the Pahole NAR) to document indigenous and endemic Hawaiian plant species' cover change over time across gradients of slope, elevation, precipitation, and understory light availability (Chapter 3). I then surveyed the cover of native and non-native species in an additional 19 plots, for a total of 50 plots on the island of Oʻahu, Hawaiʻi to determine how native cover in mixed native/non-native communities relates to differences in the values of four performance-related plant functional traits in the resident species (Specific leaf area, stem specific density, seed dry mass, and maximum height), as well the dominant growth form of each species. I assessed whether native and non-native plant cover was related to measures of functional and phylogenetic diversity, and whether greater diversity of biogeographic origins in resident non-native species influenced the ability of non-natives to dominate in areas where they had invaded (Chapter 4). By answering these questions, it my hope that this dissertation will be useful for guiding future conservation efforts in Hawaiian plant communities which have been impacted by anthropogenic activities and species introductions.

Chapter 2: Long-term decline of native tropical dry forest remnants in an invaded Hawaiian landscape

Citation:

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Abstract

Tropical dry forests are among the most threatened vegetation types as a result of human activities, yet relatively few datasets exist which can give insight into the long-term impacts of anthropogenic disturbance and species introductions in these diverse biomes, especially in insular systems. In this study I revisited remnant dry forest patches that were previously surveyed in 1950 and 1970 in the Mokulēʻia Forest Reserve on Oʻahu, Hawaiʻi in order to assess long-term native persistence. I tested the hypothesis proposed by Hatheway (1952), suggesting that where disturbances were absent and natives were in sufficient abundance, native forests can maintain themselves, suppress non-native invasion, and even expand within a broadly invaded landscape. My resurvey of the seven original remnants occurred between June 2016 and May 2017, and found that natives declined in basal area in every plot except one, and maintained basal area dominance over non-natives in only three of seven plots. Pooled across all plots, there was a dramatic decline in the richness of native woody species in 2017 (10 species), when compared with observations in 1950 (27 species) and 1970 (32 species). Natives experienced substantial declines in densities, and the greatest reductions in terms of native basal area and species richness occurred in formerly well-developed native forest plots, which previously had the highest native diversity. Only the most common native species were able to maintain their populations, and they are aging. At the same time, non-native woody species richness across all 7 plots increased from 1950 (3 species) to 1970 (7 species) to 2017 (13 species), such that non-native richness exceeded native richness in 2017. Non-native relative basal area pooled across plots also increased substantially from 1950 (9%) and 1970 (5%), to where it nearly equals native basal area currently (49%). These results indicate that despite there being no change in disturbance levels since these areas were last surveyed, native Hawaiian dry forest remnants are being invaded by nearby non-natives, and will likely continue to decline if not supported by active management.

Keywords: *Hawaiʻi, native plants, invasive species, dry forest, succession, long-term impacts*

Introduction

Tropical dry forest is one of the planet's most diverse biomes and once constituted nearly half of the Earth's tropical and subtropical land area (Janzen, 1988; Murphy & Lugo, 1986). However, these forests are also among the most threatened vegetation types as a result of human activities, and have substantially decreased in size globally (Gillespie et al., 2011; Janzen, 1988). Anthropogenic disturbances and species introductions often result in systems with biotic and abiotic components that have been altered to the point where they may not naturally return to historical conditions (i.e., novel ecosystems), yet relatively little is known about the long-term trends in native community persistence and recovery in tropical dry forests (Cabin et al., 2000; Gillespie et al., 2011; Hobbs et al., 2013; Janzen, 1988; Miles et al., 2006). Island biotas are especially susceptible to anthropogenic disturbances because they are typically disharmonic, have high levels of endemism, and small populations (Emery, 2007; Hobbs et al., 2013; Zimmerman et al., 2008). This is especially notable in the Pacific, where tropical dry forests have been reduced to less than 5% of their original extent (Gillespie et al., 2011; Janzen, 1988). Pacific islands have experienced the most rapid increase in naturalized species per land area, which has resulted in dramatic changes in many Pacific island plant communities (Graham et al., 2017; Hobbs et al., 2013). Such is the case in Hawaiian Islands (HI), where the highly endemic flora (~89%) has been heavily impacted by non-native species introductions (Carlquist, 1965; Degener, 1930; Wirawan, 1974;

Woodcock, 2003; Zimmerman et al., 2008). The tropical dry forests found in Hawaiʻi may thus serve as a model system for understanding the future of insular tropical dry forests that have a history of anthropogenic disturbance and species introductions.

Dry forests are considered to historically have been more speciose than rainforests in the HI (Chimera & Drake, 2010; Rock, 1913; Sandquist & Cordell, 2007). However, dry forests are particularly susceptible to fire and feral ungulate grazing, and have less potential to recover quickly from such disturbances (Janzen, 1988; Murphy & Lugo, 1986). As a result, native dry forests in the HI have been reduced to the point that only a few small, scattered remnant native patches remain (Chimera & Drake, 2010; Denslow et al., 2006; Sandquist & Cordell, 2007; Selmants et al., 2017; Woodcock, 2003). It has been argued that native Hawaiian plants are unable to naturally recolonize degraded habitats when faced with competition from more vigorous non-native invaders, and may be on track to extinction (Carlquist, 1965; Degener, 1930; Wirawan, 1974; Woodcock, 2003). This view is supported when considering that 52.5% of the native Hawaiian flowering plants are at risk of extinction (9% extinct in the wild, 25% endangered, and 18.6% vulnerable or rare) (Sakai et al., 2002); 25% of the endangered Hawaiian flora come from dry forests, and 45% of Hawaiian dry forest flora are threatened (Cabin et al., 2000; Pau et al., 2009). However, Egler (1942) held that native Hawaiian woody species may eventually outlast and replace non-native pioneer species in later successional stages following disturbance. In order to test Egler's hypothesis, Hatheway (1952) examined remnant native dry forest patches in the Mokulēʻia Forest Reserve (MFR) on the Island of Oʻahu, Hawaiʻi. His study found little evidence that rare Hawaiian endemics in remnant native forest patches were being replaced by non-native invaders. He additionally agreed with Egler that non-native pioneer species such as *Leucaena leucocephala, Psidium* spp., and *Lantana camara*, which are frequently found in disturbed dry and mesic areas, represent an earlier seral stage than intact native seasonally dry forest. Thus, he came to the conclusion that native forests may be able to recover under "certain conditions" (e.g., under the shade of nurse crops which can reduce palatable forage for grazing and browsing animals), and that well-developed native forests could perpetuate in the absence of disturbance.

Wirawan (1974) conducted a follow up survey of Hatheway's plots to determine whether native dry forest was indeed persisting or even spreading beyond the original remnants after 20 years. He found that almost all native species recorded by Hatheway could still be found in their respective plots and that most of the dominant native plant species were maintaining their populations in five out of seven plots. However, he also found that new non-native plant species invaded almost all of the plots, while new native species were recruiting only in plots where natives were already present in higher abundances, closer to propagule sources, and where cattle had not been present. Wirawan agreed that where disturbances by grazing or fire were not significant and natives were in sufficient abundance, native dry forests can maintain themselves.

Neither Hatheway (1952) nor Wirawan (1974) specifically mentioned feral pigs or goats as threats to native forest, despite the fact that they have been common elements of the Hawaiian landscape since the 1700's, and their grazing behaviors have been shown to be quite destructive to native forests (Chynoweth et al., 2010; Denslow et al., 2006; Foster Huenneke & Vitousek, 1990; Hobbs et al., 2013; Howarth et al., 1985). Wirawan (1974) did note the presence of pigs and goats in these plots, and they can still be observed in the landscape (Hibit, personal observation). Thus, despite the constant presence of grazing disturbance which precludes the original hypothesis put forth by Hatheway (1952) and Wirawan (1974), native woody species were able to persist or even expand within a landscape that has been broadly invaded by non-native plants and animals.

Since no additional disturbances by fire or storm damage have been recorded in the vicinity of the plots, it may be said that there has been no documented change in disturbance regime or intensity since that time (Hawaii Wildfire Management Organization, 2013; National Oceanic and Atmospheric Administration). In addition, many areas throughout the HI have experienced a continuing influx of new non-native plant species and pests (Howarth et al., 1985; Sax et al., 2002). It would thus be very interesting to determine whether native Hawaiian dry forest patches were able to persist despite these constant pressures in the forty-seven years that have elapsed since Wirawan (1974) last surveyed these remnant dry forest patches. The objective of this study was to resurvey these dry forest remnants to determine whether native dry forest patches were still persisting in the long-term, given a similar disturbance regime and intensity to that which would have been found in the previous surveys. If the conclusions of Hatheway (1952) and Wirawan (1974) hold true, I expect that: **1)** There should be no decline in native species richness, densities, or basal areas, and their populations should be stable or growing. **2)** There should be no increase in non-native species richness, densities, or basal areas, and their populations should not be perpetuating themselves.

Methods

Site description

The Mokulēʻia Forest Reserve (MFR), which is situated in the Waiʻanae Range on Oʻahu, Hawaiʻi contains many steep gulches and narrow ridges that are more or less parallel to each other. The local topography creates barriers to dispersal and has been cited by Hatheway (1952) as a catalyst for local endemism, and thus unique community compositions may be found from gulch to gulch. The study area has a warm subtropical climate, with mean January and July temperatures at 20°C and 23°C, respectively (Giambelluca et al., 2014). The rainy season occurs from November to April, followed by the dry season until late October (Hatheway, 1952; Wirawan, 1974). The sample plots are frost-free, have annual precipitation ranging between 500 and 2,000 mm, and a dry season lasting >4 months, and thus fall under the classification of tropical dry forest (Giambelluca et al., 2013; Murphy & Lugo, 1986; Pau et al., 2009). Plots 1-5 were located in areas that were historically used for cattle ranching until 1918, when the area was set aside as a forest reserve, but cattle still roamed the forest reserve until about 1922

(Coulter, 1931; Hatheway, 1952; Wirawan, 1974). Cattle were able to re-enter the forest reserve briefly during World War II, when animals from ranches were not well controlled, but the cattle were subsequently removed by 1947 (Wirawan, 1974). However, efforts to exclude feral pigs and goats by fencing and trapping/hunting have proven cost prohibitive to utilize extensively, and have not eliminated goats and pigs from the MFR (Stone, 1985).

Plot attributes

Hatheway (1952) identified remnant native forest patches in the MFR (Figure 1.1) and surveyed seven plots ranging in size from 30 to 1000 m^2 (Table 1.1). He noted that steep slopes of gulches and slopes covered with boulders had a relatively high proportion of native species as compared to valley bottoms or wind-swept ridges. He attributed this to the possibility that the steep slopes are less accessible to feral grazing animals which may disturb native vegetation and create opportunities for non-native plant species to invade. He established plots 4, 5, 6, and 7 (Table 1.1) in these steeply sloped areas to assess native species composition in relatively intact remnant stands, which will hereafter be collectively referred to as 'well-developed native forest plots'. Plots 1-3 (Table 1.1) were established by Hatheway as examples of seral stands that contained immature native trees. They were established to determine whether natives can invade and replace introduced vegetation (Hatheway, 1952; Wirawan, 1974). Random site selection was deemed to be inappropriate due to the patchiness, rarity, and small area of remnant native stands separated by topographic barriers (Hatheway, 1952).

Study design

The sites used by Hatheway and Wirawan were located using coordinates provided in each study, correcting for changes in map projections. These coordinates did not always exactly match site descriptions, so they were compared with site pictures, slopes, elevations, and plant community compositions to obtain the best fit for where each site originally existed. In some cases remnant markers left by Wirawan were discovered allowing definitive confirmation of original plot locations, but none of the plots had been defined with permanent markers. For the present study, once the general area of each plot was located, a plot was laid out using PVC pipe to permanently mark plot corners. Plot midpoint coordinates may be found in appendix A. Plots were established to maximize inclusion of native vegetation, thus any declines discovered in native vegetation are not likely to be due to choice of plot placement. Hatheway (1952) and Wirawan (1974) utilized variable plot sizes both within their own analyses, and between their respective studies (Table 1.1). For consistency, this study utilized a standardized plot size of 20x20m (400m^2). These plots were square, rather than the circular plots which had been utilized by Wirawan (1974). Due to variability in plot sizes in 1970, plots 4-7 were larger in 1970 than 2017 (Table 1.1). However, a walkthrough of a 10m wide belt surrounding each plot was used to determine species richness at sites where original plots were >400m^2, yielding 1600m^2 total area that was assessed for species richness (larger than all previous plot sizes, ensuring that any observed decline in richness is not due to differences in size of survey area).

In the original study conducted by Hatheway (1952), the number of native and non-native woody individuals larger than 2.5 cm diameter at breast height (DBH) were recorded and grouped into diameter classes. In order to develop a greater understanding of the maintenance trends of native and non-native woody populations, Wirawan expanded this analysis to include the measurement of all woody individuals, including seedlings and juveniles. He used diameter classes similar to those used by Hatheway, except that all individuals <2m in height were grouped into height classes. These classes also differed in size between plots, presumably due to differences in average size of individuals in each plot, and the number of individuals that occurred on average in each size class (Table 1.2). This study utilized the same diameter and height classes created by Hatheway (1952) and later modified by Wirawan (1974) with a further modification: individuals <10cm in height were excluded from the analysis, as the presence or absence of a flush of small seedlings may simply reflect the timing of the survey rather than a long-term temporal trend in population.

In the present study, sampling occurred between June 2016 and May 2017. Individuals were measured from their stem base, and those individuals >2m in height had their DBH measured using a diameter tape at 1.4m from the stem base (Powell, 2005). Native and non-native basal area (BA) were compared across all three time periods (1950, 1970, and 2017). BA comparisons with the datasets of Hatheway (1952) and Wirawan (1974) were only possible for individuals >2.5cm DBH, while relative species density (RD) was calculated using all individuals >10cm. BA could not be compared with 1950 data in plot 2 because Hatheway (1952) did not report those values. Species importance values (IV) were calculated using RD, relative dominance (based on BA), and relative frequency (RF) across all plots, utilizing a scale from 0-3. Comparison of height or diameter class distributions and RD was only possible between data collected in 1970 (Wirawan 1974) and 2017 due to the more limited amount data collected by Hatheway (1952).

Assessing changes in size and height class distributions

Due to mortality patterns, the population size class structure of self-perpetuating or growing plant populations characteristically assumes an inverse J-shaped distribution, whereby the greatest number of individuals occurs at the smallest size and the number of surviving individuals typically found decreases as size/age increases (Wirawan 1974; Leak 2002). By contrast, a species which is not successfully regenerating may have a higher proportion of individuals of greater size/age due to limited recruitment and high juvenile mortality, shifting its population size/height distribution to the right. A change in size distribution from left-weighted to right-weighted over time (suggesting population decline, which is also supported by BA/density ratios) is illustrated in figure 1.2. Changes in the diameter/height class distribution of individuals of each woody species were assessed using the Kruskal-

Wallis Test in R (v3.3.2) package 'Coin' (R Core Team, 2013). This tests for a shift in the central mass of the size distribution (either left or right along the x-axis), which may be used to infer a trend towards population growth, stability, or decline.

Results

Species richness

Pooled across all plots, there was a dramatic decline in the richness of native woody species in 2017 (10 species), when compared with observations in 1950 (27 species) and 1970 (32 species); no new native species were found in a 10m radius surrounding each plot, indicating the observed declines in native richness were not due to plot size differences in 2017. The decline in native richness largely reflected the loss of most of the rare native woody species recorded by Hatheway and Wirawan in the well-developed forest plots 4, 6, and 7. Even some of the more common native species (e.g., *Metrosideros polymorpha*) could no longer be found in these plots. No native species were found in 2017 which had not been previously documented in the plots (Table 1.3).

Non-native woody species richness across all 7 plots increased from 1950 (3 species) to 1970 (7 species) to 2017 (13 species), such that non-native richness exceeded native richness in 2017. New non-natives found in 2017 were *Spathodea campanulata* (Plot 5), *Fraxinus udhei* (Plots 6 and 7), *Casuarina equisetifolia* (Plot 2), *Ficus microcarpa* (Plot 5), *Broussonetia papyrifera* (Plot 6), and *Carica papaya* (Plot 1). These new invaders were mainly represented by small populations constituting a small proportion of the total absolute BA (Table 1.4).

Density

Summed across all plots, native absolute densities (n/ha) decreased for every species, with the exception of *Diospyros hillebrandii*, which increased in one of the two plots it was found in. This trend was less clear for non-natives which could be found in both 1970 and 2017, with four species seeing a decline (*Leucaena leucocephala, Schinus terebinthifolius, Syzygium cumini,* and *Psidium guajava*), and three species increasing in density (*Grevillea robusta, Psidium cattleyanum,* and *Aleurites moluccanus*). Both natives and non-natives saw a decline in overall absolute density for all species across all plots, with non-natives experiencing the greatest decline (native Δ = -85%; non-native Δ = -98%). The non-native *Leucaena s*aw the largest decline as a result of the large number of individuals (1970 n= 822,767; 2017 n = 5450) reported by Wirawan (1974). However, when *Leucaena* is excluded from consideration, non-native decline becomes less than that of natives (69%) (Table 1.5).

Considering only those species found in 2017, native RD decreased in four out of seven plots (Figure 1.4). Where this occurred, the top four native species in terms of importance values accounted for the majority of the loss of native RD in these plots (*Sapindus* in plot 1, *Erythrina sandwicensis* in plot 3, *Diospyros sandwicensis* and *Psydrax* in plots 6 and 7). This was accompanied by an increase in the density of some non-natives, in addition to new invaders which were able to gain a foothold. In plots where native RD increased, this was primarily due to large decreases in current non-native *Leucaena* density compared to that recorded by Wirawan, rather than increases in native densities. Including *Leucaena*, there is a dramatic increase in overall native RD by 2017 due to a decline in *Leucaena* densities (1970 native RD = 0.134; 2017 native RD = 0.583). However, excluding *Leucaena* reverses this trend both overall (1970 native RD = 0.82; 2017 RD = 0.688), and in each plot where native RD increased (Table 1.5).

Basal Area

Total BA of natives declined in five out of seven plots (3, 4, 5, 6, and 7) compared to higher observed values in in 1950 or 1970. Natives maintained BA dominance over non-natives in only three of seven plots in 2017, and the relative native BA (Ratio of native to non-native BA) decreased in six of seven plots, with the greatest decline in native BA occurring in the well-developed native forest plots (Figure 1.3). Overall, absolute native BA (cm^2/ha) decreased from 1950 to 1970 and from 1970 to 2017, and every native species except for *Psydrax odorata, Polyscias sandwicensis,* and *Diospyros hillebrandii* decreased in absolute BA since 1970. At the same time, non-native absolute BA increased in 2017 compared to either 1950 or 1970 values, and every non-native species except for *Leucaena leucocephala* increased in absolute BA since 1970. In contrast to the general trend of native BA decline in 2017, native BA was stable in plot 1. This was a seral plot identified by Hatheway which had become dominated by native *Sapindus* in 1970, and this species retained a similar degree of dominance in 2017.

Population structure trends

Among nine native populations which had five or more individuals >2.5cm DBH present in both 1970 and 2017, five populations (56%) shifted right, while four populations showed no significant change. The pattern was similar for non-natives, where five populations shifted right and three populations showed no significant change. The distribution of native individuals <2m in height shifted to the right in populations of the native *Sapindus oahuensis* (Plots 1 and 5) and *Diospyros sandwicensis* (Plot 7), left shifts were observed in populations of *Psydrax odorata* and *Diospyros sandwicensis* (both plot 6), and three populations had no significant change. Among non-natives <2m in height, shifts to the left were observed in populations of *Psidium cattleyanum* (plot 6) and *Leucaena leucocephala* (plot 3), while six populations (67%) had no significant change (Table 1.6).

Discussion

Whereas Wirawan (1974) and Hatheway (1952) believed native dry forest tree populations would be able to perpetuate themselves, I found that native populations had declined overall, and that many rare natives had completely disappeared over the past 47 years. Density and absolute BA of those natives which remain have also declined substantially overall, with the top four natives in terms of importance values (*Sapindus oahuensis*, *Diospyros sandwicensis*, *Psydrax odorata*, and *Erythrina* *sandwicensis*) accounting for the majority of the decrease. In addition, decreases in richness and percent BA were most significant in the well-developed native forest plots which previously had the highest native dominance and diversity, indicating that a simplification of woody forest species composition is occurring, where only the most common natives may be found in these areas currently. As these stands have matured, the average BA/stem of all native and non-native species with individuals >2.5cm DBH in both 1970 and 2017 increased by 2017 (With the exception of the native *Diospyros hillebrandii* and *Colubrina oppositifolia*). This decrease in density and increase in BA/stem, combined with significant shifts in diameter and height class distributions, indicates that populations of both natives and non-natives are aging, and that fewer juveniles are establishing under or around their canopies.

A reduction in natural regeneration of natives has been widely documented in Hawaiian dry forests, and in tropical dry forests worldwide (Cabin et al., 2000; Chimera & Drake, 2011; Janzen, 1988). This may be especially true for rare natives which have since disappeared from these plots. Hatheway (1952) stressed that many of the rare native plants he found in the plots may be highly localized due to topographic barriers to migration, and loss of rare natives from some areas may mean their local extirpation due to the patchy occurrence of propagule sources. In addition, 76% of native trees in Hawaiian dry forests are adapted for zoochorous dispersal (Chimera & Drake, 2011). Where propagule sources occur, natives may fail to disperse away from parent trees in the absence of native avian seed dispersers, which have been largely replaced by introduced species that preferentially feed on and disperse non-native fruits and seeds. Native fruits and seeds are thus left to fall under parent trees, where they are vulnerable to predation from introduced rodents and arthropods (Chimera & Drake, 2010, 2011; Shiels, 2011).

Pests may also attack native propagules before they are able to disperse. For example, Wirawan (1974) frequently observed larvae of the introduced Objurgatella Moth (*Alucita objurgatella*) feeding on the fruits and seeds of *Psydrax odorata*, which he suggests may be a reason for the decline of its population in plot 2. The native tree *Erythrina sandwicensis* has also been under threat due to the accidental introduction of the seed-predating beetle *Specularius impressithorax* to Hawaiʻi in 2001 (Medeiros et al., 2008), and the Erythrina gall wasp (*Quadrastichus erythrinae*) in 2005 (Rubinoff et al., 2010). In addition, despite the fact that pigs and goats were also present at the time of Hatheway (1952) and Wirawan's (1974) surveys, their persistent long-term activity may have played a role in further facilitating the displacement of rare natives over time. Pigs and goats may preferentially feed upon island endemics, which often lack defense mechanisms against herbivory (e.g., thorns, poisons), and have also both been shown to be effective dispersal agents for non-native plants, further contributing to non-native species proliferation (Cabin et al., 2000; Foster Huenneke & Vitousek, 1990).

Even where natives still remained dominant in the canopy, shade-tolerant non-natives were able to establish in the understory, as evidenced by the prevalence of *Psidium cattleyanum* in the well-developed native forest plot 7. Where non-natives occur in sufficient density, shade intolerant native seedlings may be excluded altogether and thus prevent regeneration of native stands. For example, *Erythrina sandwicensis* seedlings were excluded from dense growth of the non-native grass *Melinis minutiflora* in plot 3 in 1970 (Wirawan, 1974), which has since been replaced by the invasive non-native grass *Megathyrsus maximus*, and now covers >90% of the area in plots 2 and 3 (Hibit, unpublished data). As a result, the number of *Erythrina* individuals has decreased substantially (Table 1.5), and all individuals in 2017 were mature, with no juveniles observed and multiple dead trees present. Thus, it seems likely that *Erythrina* will continue to decline.

Where natives have declined, non-natives have gradually been able to increase their foothold. Based on a weed risk assessment protocol adapted for Pacific Islands by (Daehler et al., 2004), ten of the thirteen non-native woody species found in 2017 have been documented as invasive, likely to be invasive, or in need of further evaluation On a per-species basis, the success of each species was mixed and varied between plots. Some non-natives had declined in density and could no longer be found in some plots, while invading and increasing in density in other plots. Other new invaders were only represented by small populations of mature individuals with very few juveniles, indicating that they may have been able to become established initially, but have failed to recruit in subsequent years, or they may undergo episodic recruitment. However, taken together non-natives outperformed natives and were able to increase in richness and absolute BA. The exception was Le*ucaena leucocephala,* which is generally seen as an early successional species (Egler, 1942; Hatheway, 1952; Mueller-Dombois, 1992), and may have benefited from previous dispersal and disturbance associated with cattle.

Conclusions

Egler (1942) believed that many of the rare indigenous tree species in the HI are climax species which are "highly tolerant", and will eventually replace many of the weedy scrub species found on dry steep slopes on Oʻahu in the absence of disturbance. However, this was only found to be the case in a single *Leucaena leucocephala* dominated plot which has become dominated by native *Sapindus oahuensis* (Plot 1). Furthermore, those plots where natives were still dominant in 2017 in terms of BA only contained one or two common native species. The simplification of the previously diverse well-developed native forest remnants may be the result of altered site conditions in concert with species introductions. Despite declines in native diversity, the continued presence of the more common native species indicates that they may be able persist in mixed communities with non-native invaders. But even these native populations are becoming aged, and their juveniles are occurring in substantially reduced densities from those found in previous surveys. Thus, in the absence of active management to exclude feral ungulates, remove invasive plants, and outplant native species, it is unlikely that native dry forest communities can re-establish or persist over the long-term, even to the patchy extent observed by Hatheway (1952).

Given the ease with which many datasets may be obtained for forest plots throughout the world, the case can be made that resurveys of legacy plots such as these may be quite useful for determining long-term trends in forest communities without having to wait a substantial amount of time. This can also be useful for conservation purposes, where selecting species for out-planting which are similar to those that were previously documented in an area, especially those which have had the most success in the long-term (e.g., *Sapindus oahuensis*, *Psydrax odorata*, and *Diospyros* spp. in the Mokulēʻia Forest Reserve), may increase the chances of successful establishment.

Table 1.1 Size, elevation, and slope of plots as used by Hatheway (1952), Wirawan (1974), and the present study (2017)

			Size (m2)			Elevation (m)				
Plot	**Vegetation type**	**Location**	**1950**	**1970**	**2017**	**1950**	**1970**	**2017**	**Slope**	**Precititation (mm/yr)**
1	Seral stand	Keālia trail	30	100	400	78	84	86	36°	896
2	Seral stand	Keālia trail	1000	400	400	306	300-323	313	12°	895
3	Seral stand	Keālia trail	200	400	400	279	282	298	43°	895
4	Semi-deciduous forest	Kapuna gulch	400	600	400	354	354	353	45°	1204
5	Semi-deciduous forest	Kawaihāpai	1000	1200	400	90	96-126	117	36°	946
6	Semi-deciduous forest	Makaleha valley	400	600	400	384	405	391	45°	1647
7	Evergreen forest	Makaleha valley	1000	1000	400	546	510-546	555	51°	1681

Precipitation data is from Giambelluca et al (2013)

Table 1.2 Ranges (cm) of height and diameter classes as specified by Wirawan (1974)

Class	Plots 1, 3, 5	Plots 2, 4, 6, 7
Height classes (Plants <2m in height)		
1	0-10	0-10
2	10-30	10-25
3	30-100	25-50
4	100-200	50-100
5		100-150
6		150-200
Diameter classes (Plants >2m in height)		
1	0-3.8	0-1.3
2	3.8-6.3	1.3-3.8
3	6.3-8.8	3.8-6.3
4	8.8-11.3	6.3-8.8
5	11.3-17.5	8.8-11.3
6	17.5-22.5	11.3-13.8
7	22.5-27.5	13.8-16.3
8	27.5-32.5	16.3-18.8
9	32.5-37.5	18.8-21.3
10	37.5-42.5	21.3-23.8
11	42.5-47.5	23.8-26.3
12	47.5-52.5	26.3-28.8
13	52.5-57.5	28.8-31.3
14	57.5-62.5	31.3-33.8
15	62.5-67.5	33.8-36.3
16	67.5+	36.3+

Table 1.3 Absolute basal area (cm^2/ha) for native woody species >2.5 cm DBH found from 1950 to 2017, ranked by 2017 BA values. Blank spaces indicate that a species was not present during this time period

Native species	1950	1970	2017
Sapindus oahuensis	18.41	20.44	13.87
Erythrina sandwicensis	42.88	16.25	12.32
Diospyros sandwicensis	7.32	9.54	6.81
Polyscias sandwicensis	2.47	1.66	1.78
Psydrax odorata	1.31	0.72	1.42
Diospyros hillebrandii	1.08	0.21	1.20
Nestegis sandwicensis	2.64	1.55	0.56
Colubrina oppositifolia	1.62	3.29	0.08
Psychotria hathewayi	2.93	0.80	*
Dodonaea viscosa	0.05	0.14	*
Metrosideros polymorpha	6.95	11.97	
Syzygium sandwicense		6.00	
Pisonia umbellifera	2.91	4.20	
Bobea hookeri		1.38	
Dracaena aurea	2.93	0.96	
Pouteria sandwicensis	0.75	0.59	
Santalum freycinetianum	0.58	0.52	
Rauvolfia sandwicensis	0.04	0.43	
Bobea elatior	0.42	0.41	
Myrsine lessertiana	0.68	0.35	
Polyscias oahuensis	0.68	0.32	
Myoporum sandwicense		0.31	
Streblus pendulinus		0.20	
Mezoneuron kavaiensis	0.48	0.18	
Antidesma pulvinatum		0.18	
Pelea wawreana	0.04	0.13	
Elaeocarpus bifidus		0.09	
Eugenia reinwardtiana	0.42	0.06	
Wikstroemia oahuensis		0.03	
Pittosporum sulcatum		0.02	
Psychotria mariniana		0.02	
Charpentiera obovata	0.09	0.00	
Ochrosia sandwicensis	0.40		
Xylosma Hawaiiensis	0.15		
Neraudia angulata	0.10		
Nototrichium viride	0.05		
Total native BA/ha	98.35	82.93	38.03

* No individuals >2.5cm DBH present

Table 1.4 Absolute basal area (cm^2/ha) for non-native species >2.5cm DBH found from 1950 to 2017, ranked by 2017 BA values. Blank spaces indicate that a species was not present in during this time period

Non-native species	**1950**	**1970**	**2017**
Grevillea robusta		*	11.06
Schinus terebinthifolius		0.16	7.30
Syzygium cumini	1.01	1.02	5.73
Aleurites molucanna		0.13	5.07
Spathodea campanulata			2.90
Leucaena leucocephala	8.35	3.27	2.09
Psidium cattleianum		0.04	1.38
Casuarina equisetifolia			0.56
Fraxinus udhei			0.32
Ficus microcarpa			0.07
Psidium guajava	†	0.01	0.06
Broussonetia papyrifera			*
Carica papaya			*
Total non-native BA/ha	9.36	4.63	36.54

* No individuals >2.5cm DBH present

† No basal area data available

Table 1.5 Relative density (RD) of woody species found in each plot in 2017 compared to 1972 (exlcuding height class 1), ranked by importance value (IV, 0-3 scale) of species found in 2017

		Seral plots						**Well-developed native forest plots**							
		Plot 1		**Plot 2**		**Plot 3**		**Plot 4**		**Plot 5**		**Plot 6**		**Plot 7**	
	Year	**1972**	**2017**	**1972**	**2017**	**1972**	**2017**	**1972**	**2017**	**1972**	**2017**	**1972**	**2017**	**1972**	**2017**
IV (0-3)	**Native species**														
0.626	*Sapindus oahuensis*	0.94	0.66					0.07	0.12	0.79	0.83	0.02	0.01		
0.319	*Diospyros sandwicensis*							0.02	0.42			0.73	0.33	0.45	0.42
0.172	*Psydrax odorata*			0.01	0.33	0.01	0.04	0.01	0.08			0.13	0.10	0.45	0.03
0.145	*Erythrina sandwicensis*			0.00	0.02	0.10	0.06								
0.057	*Polyscias sandwicensis*									†	0.01	0.01	†		
0.049	*Nestegis sandwicensis*											0.04	0.01	0.01	0.02
0.039	*Diospyros hillebrandii*											†	0.08		
0.023	*Dodonaea viscosa*			†	0.09										
0.021	*Psychotria hathewayi*													0.01	0.01
0.020	*Colubrina oppositifolia*											0.02	†		
	Non-native species														
0.290	*Leucaena leucocephala*	0.06	0.33	0.99	0.16	0.02	0.63	0.89	0.05	0.20	0.13				
0.267	*Schinus terebinthifolius*					0.86	0.17	0.01	0.12			†	0.05	0.01	0.19
0.251	*Grevillea robusta*			0.00	0.09	0.00	0.08	0.00	0.03‡					†	†
0.243	*Syzygium cumini*					0.02	0.02	†	0.12	0.01	0.01	0.01	0.09	0.02	†
0.173	*Psidium cattleianum*			†	0.21							0.03	0.16	0.05	0.29
0.083	*Aleurites molucanna*							0.00	0.03‡	†	0.01				
0.072	*Fraxinus udhei*											0.00	0.12‡	0.00	0.04‡
0.032	*Spathodea campanulata*									0.00	†‡				
0.029	*Broussonetia papyrifera*											0.00	0.05‡		
0.026	*Casuarina equisetifolia*			0.00	0.11										
0.022	*Psidium guajava*							0.00	0.03‡						
0.021	*Ficus microcarpa*									0.00	0.01‡				
0.020	*Carica papaya*	0.00	0.01												
	Total native RD	**0.94**	**0.66**	**0.01**	**0.44**	**0.11**	**0.10**	**0.10**	**0.62**	**0.79**	**0.84**	**0.96**	**0.53**	**0.92**	**0.48**
	Total non-native RD	**0.06**	**0.34**	**0.99**	**0.56**	**0.89**	**0.90**	**0.90**	**0.38**	**0.21**	**0.16**	**0.04**	**0.47**	**0.08**	**0.52**

† Relative density <0.01

‡ New arrival (2017)

Table 1.6 Woody species found in both 1974 and 2017 in each plot. A significant shift in the height and diameter class distribution of each species is indicated when the shift is to the right (R), and to the left (L). Species that did not significantly shift their distributions are denoted (ns).

	Seral plots						Well-developed native forest plots							
	Plot 1		Plot 2		Plot 3		Plot 4		Plot 5		Plot 6		Plot 7	
Native species	height	DBH	height	DBH	height	DBH	height	DBH	height	DBH	height	DBH	height	DBH
Colubrina oppositifolia												††		
Diospyros hillebrandii												†		
Diospyros sandwicensis							ns	†††			L***	R***	R**	R***
Dodonaea viscosa			ns											
Erythrina sandwicensis						R***								
Nestegis sandwicensis												††	†††	††
Polyscias sandwicensis										†††		††		
Psychotria hathewayi													††	
Psydrax odorata			††	R***		††		ns			L**	ns	ns	††
Sapindus oahuensis	R***	ns					†	R*	R***	ns		†††		
Non-native species														
Aleurites moluccana														
Leucaena leucocephala	ns	R***	††	††	L**	†	ns		ns	R*				
Psidium cattleianum			††								L*	††	ns	ns
Schinus terebinthifolius					ns	R**	†	R*			†		ns	ns
Syzygium cumini								R*				ns	††	

***** P < 0.05

****** P < 0.01

******* P < 0.001

† < 5 individuals present in this category in 1972

†† < 5 individuals present in this category in 2017

††† < 5 individuals present in this category during either sampling period

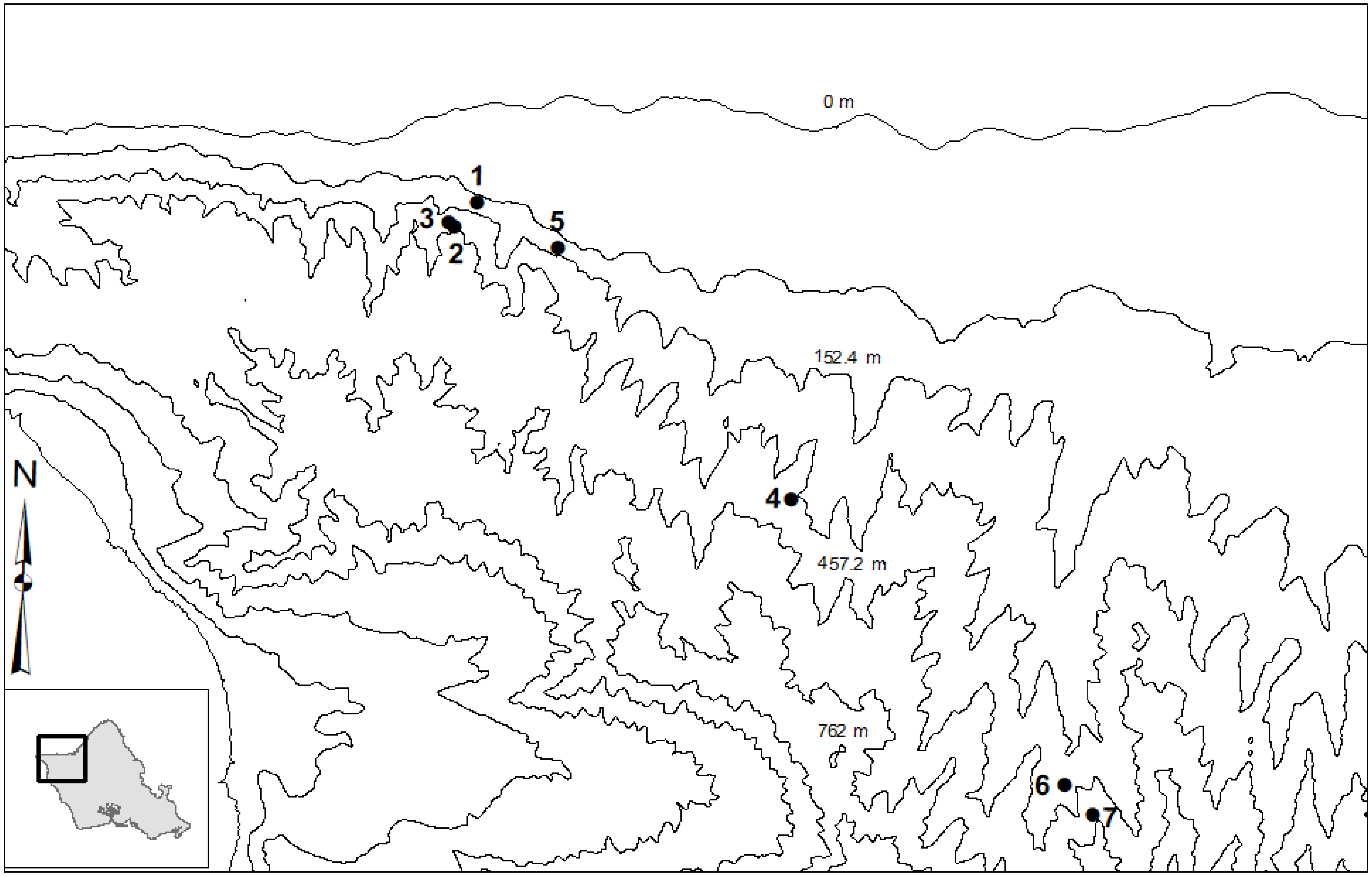

Figure 1.1 Topo map of the Mokulēʻia Forest Reserve with plot locations

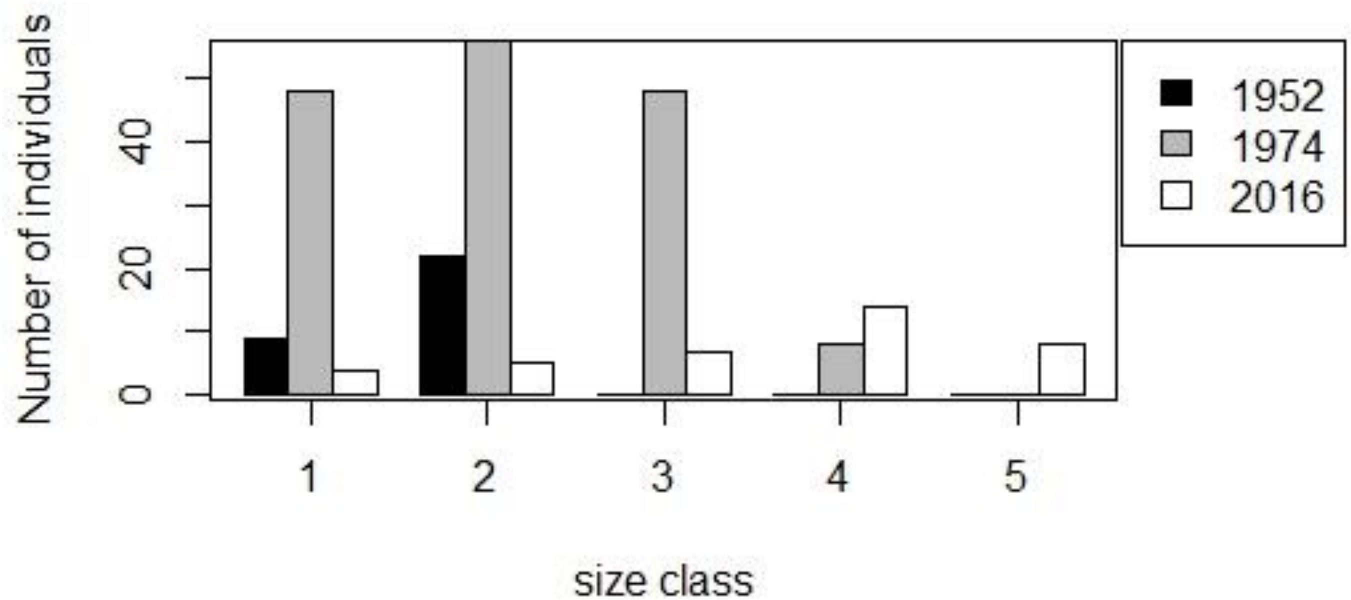

Figure 1.2 Example of a shift in size class distribution towards the right over time in the *L. leucocephala* population in plot 1. Individuals were found spanning five size classes, ranging up to 17.5cm DBH 2017 (Hatheway 1952, Wirawan 1974)

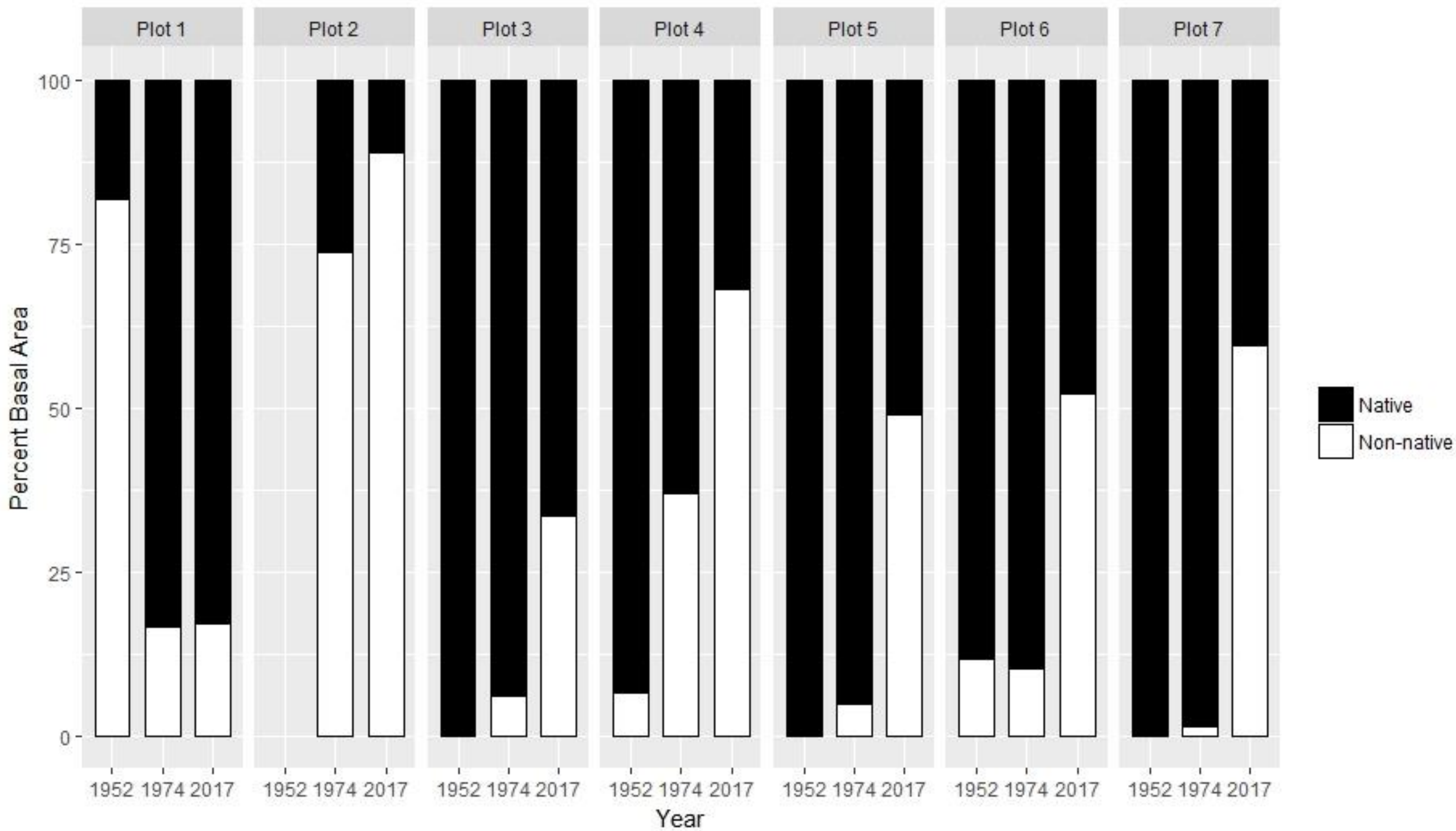

Figure 1.3 Relative native and alien basal area (BA) of individuals >2.5cm DBH for 1950, 1970, and 2017 (Hatheway 1952, Wirawan 1974)

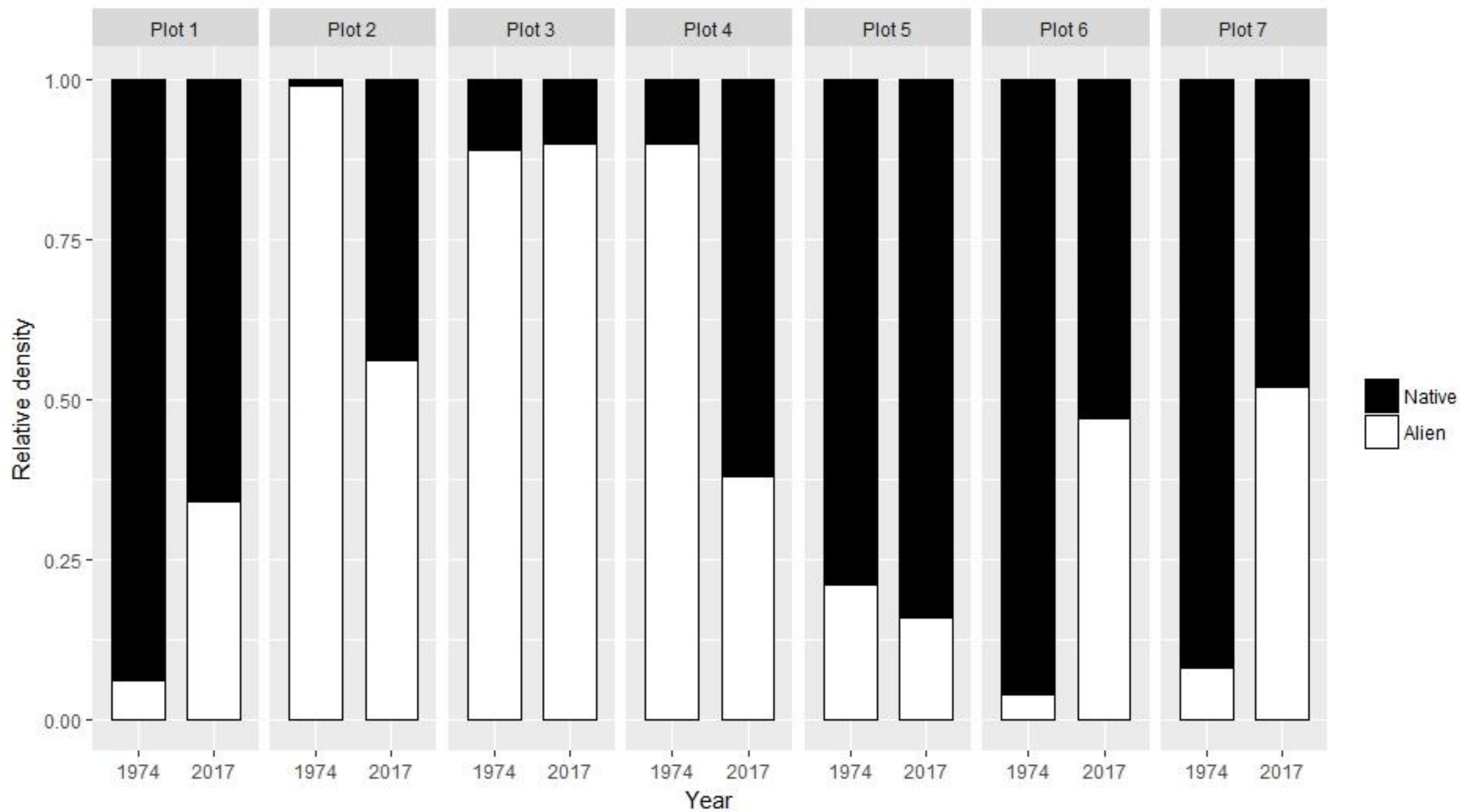

Figure 1.4 Relative density of species found in 2017 compared to 1970 (Wirawan 1974)

Chapter 3: Differential change in indigenous and endemic plant cover over time across abiotic gradients in an invaded Hawaiian landscape

Abstract

I revisited 25 previously established plots (400 m^2 each) in the Pahole Natural Area Reserve and Kahana Valley on the island of Oʻahu, Hawaiʻi, USA across gradients of slope, elevation, precipitation, and understory light availability to document indigenous and endemic Hawaiian plant species' cover change, and how those changes relate to abiotic site conditions. I analyzed the effect of these abiotic factors on the previous, current, and delta (current minus previous) values for absolute cover of endemic and indigenous Hawaiian plants, as well as that of non-native species. Endemic species had a net loss of cover since the previous surveys, while indigenous species had a net gain, as did non-natives. Endemic species cover was associated with higher elevations and in some cases with steeper plot slopes. Change in endemic species cover was negatively correlated with precipitation, but other relationships found between endemic and indigenous species and resource availability may be been driven by idiosyncrasies of particular species and plots surveyed. These results indicate that site accessibility (as determined by slope and elevation) and availability of precipitation were more important determinants of endemic cover than indigenous cover, and endemic species are more susceptible than indigenous species to decline in the face of invasion and disturbance. Even in some plots where ungulates were excluded, endemic cover declined while non-native cover increased. In addition, those indigenous and endemic species which increased in cover are generally recognized as being associated with habitat degradation. Thus, more comprehensive planning and active efforts may be required to maintain native Hawaiian forest communities and prevent further invasion, with focus particularly on conservation of endemic species, which seem to be more vulnerable to decline. Furthermore, although endemic species cover decreased over time, indigenous cover increased, indicating that generalizations about natives as a single group may be misleading.

Keywords: *Hawaiʻi, island forest communities, native species, endemic, indigenous, invasive species, abiotic conditions, slope, elevation, precipitation, light availability*

Introduction

Endemic island floras are often vulnerable to anthropogenic impacts and introduction of invasive non-native plant species (Adsersen, 1989; Jäger et al., 2009; Sakai et al., 2002). Islands typically have high proportions of endemic species due to their geographic isolation, and as the most isolated archipelago on the planet, the Hawaiian Islands (HI) have a particularly high degree of endemism (~90% for angiosperms, and 74% for ferns and lycophytes) (Kier et al., 2009; Sakai et al., 2002; Vernon & Ranker, 2013). Similar to other isolated island archipelagoes, the Hawaiian endemic flora is disharmonic, having evolved in the absence of large mammalian herbivores, and its species often have low population densities, restricted geographical ranges, and specific environmental requirements (Graham et al., 2017; Sakai et al., 2002; Zimmerman et al., 2008). On the other hand, indigenous species are components of native floras that have broader geographic distributions. Species with broader geographic ranges might have greater tolerance of shifts in environmental conditions or community composition, and less reliance on specific pollination or dispersal mutualisms (Buckley & Catford, 2016), which theoretically could lend to greater resilience for indigenous native species when compared to endemic native species. Altogether, native plant species have experienced substantial declines since humans arrived in the HI, with 52.5% of native Hawaiian angiosperms now considered to be at risk of extinction (Sakai et al., 2002). However, it is relatively unknown to what degree indigenous and endemic Hawaiian plant species are differentially affected by anthropogenic disturbance and species invasions in the long-term. In addition, while abiotic site conditions have been shown to influence the invasion process (Gallien & Carboni, 2017; Strayer et al., 2006), the relative importance of resource availability and site accessibility by feral pigs (*Sus scrofa*) and humans for the maintenance of endemic and indigenous plant species cover and diversity in the HI has not been investigated.

Where previous surveys have been conducted, resurveying becomes a powerful approach to understand long-term trends in forest communities (Condit, 1995). It was therefore the objective of this study to revisit plots previously established by Wirawan (1978) and Welton (1993) to document if/how indigenous and endemic Hawaiian plant species' respective cover values have changed, and how those changes are related to abiotic conditions in these plots. My expectations were as follows: **1)** Previous and current availability of resources (understory light availability and precipitation) will be negatively correlated with both endemic and indigenous plant cover, as greater resource availability may create opportunity for invasion followed by competitive displacement of native species (Blumenthal, 2006; Daehler, 2003). **2)** Elevation and slope will be positively correlated with endemic and indigenous plant cover, as areas of greater slope and elevation will be less accessible to feral pigs and have a reduced likelihood of anthropogenic disturbance (Chardon et al., 2019; Chynoweth et al., 2010; Merlin & Juvik, 1992). **3)** The aforementioned abiotic conditions will be also associated with losses or gains of native species cover over time. **4)** Endemic species will tend to be more vulnerable to decline than indigenous species (Sakai et al., 2002).

Study design and analyses

Study sites

Wirawan's (1978) doctoral work established sixty-four plots in Kahana Valley, Oʻahu (Figure 2.1). Kahana valley is located on the windward side of Oʻahu, extending about 7 km from the crest of the Koʻolau mountains (~780 m elv.) to the mouth of Kahana Bay, at sea level (Wirawan, 1978). The mean temperature in Kahana Valley is 22.3˚C, and ranges from 20.7˚C in January to 23.9˚C in August (Giambelluca et al., 2014). These plots ranged from mesic to wet forest (1787 – 6101 mm mean annual precipitation, appendix A) (Gagne & Cuddihy, 1990; Giambelluca et al., 2013).

Welton's (1993) thesis work established twenty-five plots in the Pahole Natural Area Reserve (NAR) (Figure 2.2), a mesic forest (1358 - 1597 mm mean annual precipitation, appendix A) in the Waianae Mountains on the island of Oʻahu, Hawaiʻi (Gagne & Cuddihy, 1990; Giambelluca et al., 2013). The Pahole NAR is located in the Waiʻanae mountains on Oʻahu, and ranges from ~341 m up to the ridge crest of the Waiʻanae range at 790 m in elevation. The mean temperature in the Pahole NAR is 19.3˚C, and ranges from 17.3˚C in February to 21.3˚C in August (Giambelluca et al., 2014).

No disturbances as a result of fire or major storm damage are known to have occurred in the vicinity of these plots in either location since the previous surveys (Hawaii Wildfire Management Organization, 2013; National Oceanic and Atmospheric Administration). Plots were identified on topographical maps of Kahana Valley (Figure 2.1) and the Pahole NAR (Figure 2.2), created by the authors of the previous surveys. I overlaid these maps onto a digital map layer and used ArcGIS software to determine GPS coordinates for each plot. For some of the plots in the Pahole NAR, rebar markers that identified original plots were relocated, allowing precise placement of the plot to be resurveyed. For other plot locations where permanent markers had not been placed or could not be located, coordinates were matched with site descriptions, slopes, aspects, elevations, and general plant community compositions to identify the best fit for where each plot originally existed. A subset of the original plots at each study site was sampled to ensure spatial dispersion and avoid sampling closely spaced plots. In some cases, trails had deteriorated to the point that certain plots were unreachable. This resurvey was thus limited to a total of 25 plots (12 from the Pahole NAR and 13 from Kahana Valley) for this study. A list of midpoint coordinates for each resurveyed plot in 2018 can be found in appendix A.

Vegetation surveys

A resurvey of each plot was conducted from May to October of 2018. Similar to the methods described by Wirawan (1978), either 20 x 20 m or 10 x 40 m plots ($400m^2$) were re-established at Kahana Valley, depending on the previous layout, which itself was dependent on topographical position (e.g., narrow ridgelines were not conducive for establishment of square plots). Welton (1993) used $400m^2$ circular plots, which were also used in the present study in the Pahole NAR (appendix B). Similar to methods used by Wirawan (1978), all vascular plant species in each plot were recorded and the cover values of each were estimated using the Domin-Krajina cover abundance scale, as described by Mueller-Dombois & Ellenberg (1974). This is a finer scale measurement of abundance than the Braun-Blanquet cover abundance scale used by Welton (1993), and comparison with previous estimates made in that study was facilitated by converting each cover abundance category from both scales into the midpoint of their corresponding percent cover value ranges. The previous studies also examined cover at multiple canopy height categories. However, for the purposes of this study I was interested in obtaining a single estimate of overall two-dimensional coverage for each species in a plot. I therefore used the single highest cover value previously recorded as the estimate of previous cover values for each species and compared it to the single cover value recorded in the present resurvey. This method is thus able to provide a conservative estimate of previous cover, so as not to overestimate previous cover and create false indications of decline in native cover. All scores from each survey were combined additively to obtain the total estimated percent coverage (absolute cover) of all species in each plot. When the cover of each species in a plot was combined, it was possible to exceed 100% coverage due to overlap among species.

Abiotic factors

Plot midpoint coordinates and elevation were recorded within a 10 m accuracy using the Polaris GPS smartphone application. Slope was measured using a Haglöf electronic clinometer. Precipitation values were obtained using annual mean values as reported in the online rainfall atlas of Hawaiʻi (Giambelluca et al. 2013). Understory light availability was measured using a Spectrum Technologies Light Scout 6 sensor quantum light bar with a Spectrum Technologies Field Scout sensor reader. Measurements of photosynthetically active radiation ($\mu mol\ m^{-2}\ s^{-1}$) were taken at five locations in each plot; one at the plot midpoint, and four placed at roughly 90˚ angles to each other within 9 m of the midpoint. Measurements were taken at ground-level, or just above any ground cover, where no understory vegetation would interfere with readings. Light measurements were averaged across all five points and compared to readings taken shortly before or afterwards from a neighboring point with no canopy coverage to calculate the proportion of available light in the understory (Hereafter referred to as ULA, appendix C). Previous canopy cover values (defined as cover of woody tree species) were used to approximate canopy light transmittance for the determination of ULA for previous surveys, as well as the change in ULA between the original survey and the current resurvey (current minus previous ULA).

Analyses

Delta values (current cover minus previous cover) were calculated for all species in each plot. Previous indigenous, current indigenous, and current endemic cover values were all normalized using the Tukey's Ladder of Powers to determine the optimal lambda value for transformation prior to analysis (rcompanion package, transformTukey function); previous endemic cover did not require transformation. The relationships between precipitation, slope, elevation, ULA, and the indigenous and endemic plant cover values in current and previous surveys, as well as the delta values (current minus previous cover), were then determined using a multiple regression analysis in R v3.5.3, function lm(). I created a single model for each analysis which included every explanatory variable and subsequently removed variables in additional models to assess different combinations of variables and reduce complexity. Model selection was performed using the Aikake Information Criterion (AIC), using the function AICctab(). The difference between current and previous indigenous and endemic species cover (delta values) was tested for significance using a two-sample independent t-test (R Core Team, 2013).

Results

Temporal changes in cover

Averaged across all plots, there was an overall decrease in the ratio of endemic to indigenous species (Table 2.1), and the means of indigenous and endemic cover delta values were significantly different from each other (Figure 2.3, $P < 0.01$), as predicted. Endemic species cover decreased in 19 out of 25 plots, with an overall net decrease in cover (-45%) across all plots between surveys, while indigenous species increased in cover in 15 out of 25 plots and had a net increase in cover (+29%) across all plots since the previous survey (Table 2.1). The three native species which experienced the greatest net gain in cover were indigenous, while the top four native species that experienced the greatest net loss of cover were endemic (Table 2.2).

Because indigenous species were found to have increased overall in cover, I followed up my analysis by summing the cover estimates from every canopy height category for each species in each plot in the previous surveys, rather than taking the single highest cover estimate, to produce a maximum possible estimate of previous cover and ensure that the finding of an increase in cover was not the result of underestimating previous cover. I found that indigenous species still increased in cover overall, albeit to a lesser degree (+16% using the maximum cover estimate compared to +29% using the single highest cover estimate), leading to the conclusion that the finding of an increase in indigenous cover was not the result of underestimating previous indigenous cover.

Endemic cover loss was greater in Kahana Valley, where the endemic proportion of native cover (33%) is currently much lower than in the Pahole NAR (76%). By contrast, Kahana Valley plots had a greater overall increase in the cover of indigenous species than those in the Pahole NAR, although the percentage of increase was greater in the Pahole NAR (+73%) than in Kahana Valley (+20%) given its lower previous indigenous cover values. Sites also differed in terms of change in non-native cover; there was a net decrease in non-native cover (-47%) in Kahana Valley, and an increase in the ratio of native to non-native species. However, the Pahole NAR had a large increase (+73%) in non-native cover, and a decrease in the ratio of native to non-native species, leading to a slight net gain (~1%) of non-native cover across all plots when considering the Pahole NAR and Kahana Valley plots together (Table 2.1). The non-natives which declined the most in Kahana Valley were *Spathoglottis plicata* (-97%) and *Clidemia hirta* (-92%). The non-natives which increased the most in the Pahole NAR were *Psidium cattleyanum* (+546%) and *Oplismenus hirtellus* (+185%). All of these species, with the exception of *O. hirtellus*, were amongst the non-natives which experienced the largest changes in cover across all plots since previous surveys (Table 2.2).

Abiotic correlates

Contrary to my expectation that increased resource availability (ULA and precipitation) would be associated with lower native cover, there was no significant correlation between ULA and either endemic or indigenous cover in these plots, and precipitation was positively correlated with previous endemic cover ($P < 0.05$). There was a negative correlation with precipitation and the change in endemic cover between surveys ($P < 0.05$), as predicted, although this pattern was driven by the Kahana Valley site, since plots at the Pahole NAR site had little variation in precipitation (Figure 2.4). Elevation was positively correlated with both previous ($P < 0.01$) and current ($P < 0.01$) endemic cover as expected (Figure 2.5); however, contrary to expectations, elevation was negatively correlated with previous indigenous cover ($P < 0.001$). As predicted, slope was positively correlated with previous endemic cover (Figure 2.6, $P < 0.05$), but was negatively correlated with the change in endemic cover over time ($P < 0.05$), which was not expected; slope was not significantly correlated with indigenous cover or indigenous cover delta values.

Discussion

While it has been shown that native Hawaiian plants in aggregate may actually have greater ecological ranges than non-natives in terms of environmental tolerances (Kitayama & Mueller-Dombois, 1995), this may not be true for all native species. For example, Sakai et al. (2002) ascribed the greater vulnerability of Hawaiian endemic plant species to extinction to the fact that the majority of these species are habitat specialists. Similarly, this study found differences between indigenous and endemic Hawaiian plant species in terms of abiotic site condition associations and persistence trends over time. While these findings conformed somewhat to my expectations, the results of this study also brought to light certain site and abiotic factor-specific idiosyncrasies which were not expected.

Differences between sampling sites

There are some differences between the two sampling sites in terms of historical land use and current conservation practices. Kahana valley was the site of a Polynesian fishing and farming settlement prior to European contact, and later was used by the United States military in World War 2 for jungle warfare training, and so the valley was subject to extensive disturbance in low-lying areas (Mueller-Dombois & Wirawan, 2005). This area has since rewilded, with no further largescale anthropogenic disturbance evident since plots were initially established in the 1970s. However, there is little in the way of conservation work occurring in this area. On the other hand, while the selected Pahole NAR plots had no observable evidence of conservation activities having had occurred within them since the previous survey, other areas of the Pahole NAR are actively managed to eliminate feral ungulates and invasive plants, in addition to native species outplanting. The Pahole NAR also has an ungulate exclusion fence (constructed from 1995-96), while Kahana Valley does not. Ungulate fences have proven to be an effective tool for slowing or even reversing native plant decline as a result of ungulate disturbance at other sites in the HI (Cabin et al., 2000; Cole & Litton, 2014; Weller et al., 2018). There is also a roughly 17-year difference in lapsed time between the previous surveys in the Kahana Valley (1973-74) and Pahole NAR (1990-91) sites. However, despite the apparent advantages afforded indigenous and endemic plant species in the Pahole NAR site over the more historically degraded Kahana Valley site in terms of less elapsed time since the previous survey and both active and passive management, I did not find any statistically significant differences between sampling sites in the means of endemic or indigenous delta values, and endemic cover declined in both sites. While more sampling may need to be done in the Pahole NAR to better assess the long-term effectiveness of current conservation measures, the decline of endemic species in the resurveyed Pahole NAR plots highlights the difficulty that Hawaiian endemic species may face in invaded habitats, even after fencing and control of feral ungulates.

Indigenous species identities differed somewhat between sites and may help to explain the greater increase in indigenous cover found in Kahana Valley. For example, two of the top three natives in terms of net cover gain (*Dicranopteris linearis* and *Pandanus tectorius*, Table 2.2), both of which are indigenous, were only found in plots located in Kahana Valley (*D. linearis* can be found in the Pahole NAR, but was not present in my plots). Together, these two species accounted for ~81% of the increase in indigenous cover across all plots (appendix D). Both of these species are also associated with regrowth following anthropogenic burning in Polynesian settlements (i.e., pyrophytic), reflecting past land use history (Kirch, 1996). *D. linearis* (Uluhe), an indigenous fern, had the largest increase in cover of all natives in these plots (Table 2.2, appendix D). This species is frequently found colonizing secondary successional sites following disturbance (Russell et al., 1998), and thus increases in the cover of Uluhe may indicate recent or past disturbance in the Kahana Valley plots. Similarly, the endemic species which saw the greatest increase in cover since the previous survey, *Metrosideros polymorpha* (ʻŌhiʻa), a keystone Hawaiian tree species which accounted for ~24% of the total increase in the cover of all endemics in these plots, only increased in cover in Kahana Valley (appendix D). Given that this species is adapted to areas with thin or low nutrient soils (Zimmerman et al., 2008), the increase in cover that ʻŌhiʻa experienced in this area may reflect the potential erosion of soil resulting from feral pig activity in Kahana Valley (Nogueira-Filho et al., 2009). Thus, while it may seem promising to see an increase in cover for some native plants, these increases may be symptomatic of the degraded state of the plots where they occurred.

Understory light availability

Greater availability of light has been shown to confer an advantage to invaders, especially in early successional stages (Daehler, 2003; Mao et al., 2014), leading me to believe that this would be negatively associated with native cover. However, I did not find any association between ULA and endemic or indigenous cover. Even more surprisingly, further testing of non-native cover showed that ULA was negatively correlated with non-native cover in both the previous ($P < 0.01$) and current ($P < 0.001$) surveys. However, when data from the two sampling sites were analyzed separately, I found that indigenous cover in the Kahana Valley plots was positively correlated with ULA in the current resurvey ($P < 0.05$). This may be related to the change in cover of Uluhe, which saw the largest increase in cover of all natives (Table 2.2). When Uluhe is removed from consideration, ULA was not significantly correlated with indigenous cover in Kahana Valley. Uluhe has a low growth habit, and it tended to dominate in areas that lacked overhead tree cover at Kahana Valley. The dominance of Uluhe in some plots may also help to explain the negative association between non-native cover and ULA, and thus provide an encouraging example of native species preventing invasion of non-native species following disturbance, although Uluhe dominance can also lead to an arrested successional state (Russell et al., 1998).

Precipitation

Non-native species have also been shown to have an advantage over native species where water is not limiting (Daehler, 2003; Ibanez et al., 2019; Valliere et al., 2019). In addition, areas of higher rainfall are subject to more frequent landslides, especially with increasing slope, creating opportunity for invasion following disturbance (Deb & El-Kadi, 2009). My finding that the delta values of endemic species cover were negatively correlated with precipitation likely reflects the long-term changes in native composition associated with disturbance and subsequent competition with non-native invaders that are better able to take advantage of available precipitation. However, it was surprising to find that precipitation was positively correlated with previous endemic cover. This finding may have been driven by site differences, as there was much greater variation in precipitation in Kahana Valley than in the Pahole NAR. In Kahana Valley, the most remote areas, closest to the back of the valley, were also the areas with the highest precipitation values. The previously higher endemic cover in these areas may thus reflect the decreased amount of anthropogenic disturbance in these remote areas which are rarely accessed by people. Forest canopy cover also tends to be positively associated with precipitation to a point (Asner, Elmore, Hughes, Warner, & Vitousek, 2005), which may indicate that while endemic cover was higher previously in less accessible areas with greater precipitation, declines in endemic cover in these areas may have resulted from accumulated impacts of disturbance and invasion over time.

Elevation

Although feral ungulates can be found from low to high elevations in the HI (Stone, 1985), areas of higher elevation are generally less accessible and consequently subject to fewer instances of human disturbance (Chardon et al., 2019). I therefore expected that there would be a positive association between elevation and both endemic and indigenous cover, which was found to be true for both previous and current endemic cover. Given that both the previous and current endemic cover values were greater in the higher elevation Pahole NAR plots than in the Kahana Valley plots (Table 2.1), I tested both locations separately to determine whether this finding was driven by elevation differences between sampling sites. When this was done, there was a positive relationship between previous endemic cover and elevation in Kahana Valley ($P < 0.01$), indicative that this pattern can be observed in the lower elevation plots in Kahana Valley as well, and thus confirming that there is indeed a positive relationship between elevation and Hawaiian endemic plant cover in my study plots.

I observed the opposite trend with elevation for previous indigenous cover (negative correlation), although this was likely due to the much lower indigenous cover in the higher elevation Pahole NAR plots than in the Kahana Valley plots in the previous surveys. When both locations were tested separately, neither site had a significant relationship between previous indigenous cover and elevation. In fact, no other abiotic factor which I examined in this study was significantly correlated with indigenous cover (with the exception of ULA in Kahana Valley), indicating that indigenous species in these plots may not necessarily be constrained by the abiotic site conditions measured in this study in the same way that endemic species were.

Slope

I inferred that slope would be a determinant of site accessibility since areas with steep slopes are difficult to access by humans, and preferentially avoided by feral pigs (Baber & Coblentz, 1986; Hone, 1995). I therefore expected native species cover to be generally higher where slope was steeper as these areas can be assumed to be subject to fewer instances of mammalian disturbance. This was the case for previous endemic cover. However, slope was negatively correlated with change in endemic cover over time. This correlation was largely driven by substantial declines in endemic cover in four plots which had steep slopes. In Kahana Valley, the plot with the greatest decrease in endemic cover lost cover of both natives and non-natives and had a large increase in the cover of Uluhe (+386%), indicating that disturbance likely occurred in this plot. Evidence of disturbance in the form of landslides was visible near this plot. However, in the Pahole NAR there was no evidence of disturbance in the three plots which had the largest decrease in endemic cover. Rather, there were large increases in cover of the shade-tolerant invader, *Psidium cattleyanum* (+306%, +620%, and +1580% in Pahole NAR plots 10, 12, and 19, respectively), which can establish under the shade of native canopies, reproduce clonally, and form dense thickets, thus preventing recruitment of natives (Foster Huenneke & Vitousek, 1990). Evidence of widespread invasion by *P. cattleyanum* can be found throughout the Pahole NAR, and this invader is likely to pose a significant conservation challenge for some time to come, possibly leading to monotypic stands in the absence of continued efforts to remove this problematic species.

Biotic-mediated species turnover

While several endemic plants did increase in cover for some plots (appendix D), Hawaiian endemics continue to face novel threats, such as Rapid ʻŌhiʻa Death (*Ceratocystis* spp.), which was discovered on Oʻahu soon after these surveys were conducted and leads to large scale dieback of ʻŌhiʻa (Fortini et al., 2019). Die back stands are often rapidly colonized by non-native pioneer species which can then prevent reestablishment of native species (Catford et al., 2012; Mueller-Dombois, 1985), and as non-native populations increase, so too does non-native propagule pressure (Daehler, 2003). This may be further exacerbated by the replacement of extinct native frugivorous avifauna on the island of Oʻahu with non-native frugivores, which has led to the creation of novel dispersal networks that favor the dispersal of non-native plants (Vizentin-Bugoni et al., 2019). Endemic island plants are also often more susceptible to herbivory as they frequently lack defenses which can deter feral ungulates (Cabin et al., 2000; Foster Huenneke & Vitousek, 1990; Merlin & Juvik, 1992). Moreover, rooting by feral ungulates also provides ideal microsites for establishment of non-native propagules, which are sometimes simultaneously deposited via droppings (Nogueira-Filho et al., 2009). Thus, the interplay of native plant dieback, disturbance, and herbivory with increasing non-native propagule pressure is likely to continue to positively feedback to the detriment of the remaining endemic populations in the HI in the absence of more extensive conservation measures.

Conclusions

My resurvey of previously established forest plots allowed me to assess vegetation trends, focusing on whether native plant cover has declined in conservation areas and whether trends are related to abiotic factors. I found that patterns differed between Hawaiian endemic and indigenous plants, with endemic plants having generally declined over time and indigenous plants having maintained or increased their cover. Thus, generalizations of endemic and indigenous species together under the umbrella term of “native” could be misleading, and future studies may be more informative if a distinction is made between these two groups of natives.

Endemic species cover was associated with higher elevations and in some cases with steeper plot slopes, matching expectations, assuming higher elevations and steeper slopes are less accessible and better protected from anthropogenic and feral ungulate disturbance. Resource availability (rainfall and understory light availability) was correlated with total endemic and total indigenous cover in different ways that may be been driven by characteristics of particular species and plots surveyed. My findings suggest that Hawaiian endemic plant species are indeed more dependent on specific habitat conditions than indigenous species and are thus more susceptible than indigenous species to decline in the face of invasion and disturbance.

Increases in the cover of some indigenous and endemic species may be the result of historical and recent disturbance or soil degradation, possibly due to ungulate activity, and suggests that areas where their cover increased may be in a degraded state. However, even where ungulates were excluded, endemic cover still declined over time, while cover of non-native species has increased. Thus, more comprehensive planning and active efforts may be required to maintain existing native Hawaiian forest communities and prevent further invasion, with focus particularly on conservation of the endemic species, which seem to be more vulnerable to decline. Similar challenges may exist in many island ecosystems where anthropogenic impacts have led to endemic plant species' decline (e.g., Adsersen, 1989; Jäger et al., 2009), and the results of this study may help inform conservation efforts and strategies in other invaded island forest communities worldwide.

Table 2.1 Endemic/indigenous and native/non-native proportions and delta values between percent cover values from both survey periods in each plot

	% Endemic		% Native			% Cover delta values			
Plot	**Prior**	**2018**	**Prior**	**2018**		**Endemic**	**Indigenous**	**Total native**	**Non-native**
Kahana Valley									
KV8	50.0	21.6	100.0	41.2		0.0	47.5	47.5	119
KV12	57.4	61.9	21.1	42.8		-4.0	-7.5	-11.5	-170
KV4	52.8	83.6	42.1	38.1		-15.0	-49.0	-64.0	-52
KV10	68.1	39.8	38.4	40.1		-59.5	16.0	-43.5	14
KV18	78.6	8.1	98.3	75.8		-69.0	69.5	0.5	31
KV23	87.0	33.3	99.2	92.1		-75.5	71.0	-4.5	11
KV35	25.0	66.7	25.9	5.2		-23.5	-85.5	-109.0	-106
KV46	36.9	32.4	25.4	24.2		-18.0	-26.5	-44.5	-71
KV50	1.9	34.5	36.7	60.9		24.0	-28.5	-4.5	-129.5
KV61	53.9	4.9	22.9	79.1		-49.5	69.5	20.0	-147.5
KV37	42.5	20.1	41.8	43.9		-19.5	15.5	-4.0	12.5
KV21	59.8	22.5	48.0	88.6		-150.0	-23.0	-173.0	-144
KV42	76.1	3.6	26.5	34.6		-56.0	62.5	6.5	99.5
Avg.	**53.1**	**33.3**	**48.2**	**51.3**	**Sum**	**-515.5**	**131.5**	**-384.0**	**-533.0**
Pahole Natural Area Reserve									
PNAR1	40.0	61.1	18.4	10.1		6	-0.5	5.5	78.5
PNAR2	91.2	90.4	74.1	67.9		56	6.5	62.5	17.5
PNAR21	70.6	53.5	37.9	42.1		-81	-20	-101.0	-47.5
PNAR23	94.4	80.0	62.6	57.6		-10	17	7.0	26
PNAR11	96.9	93.7	67.2	39.6		-19.5	2	-17.5	83
PNAR10	97.1	85.7	32.1	17.1		-131.5	-1.5	-133.0	54
PNAR20	75.6	73.8	83.8	70.7		46.5	18.5	65.0	35.5
PNAR7	86.9	46.9	39.2	42.2		2.5	45	47.5	52.5
PNAR19	92.7	69.7	19.6	9.8		-90	-3	-93.0	71.5
PNAR6	97.3	94.0	59.5	44.0		-22	2.5	-19.5	56
PNAR9	97.5	91.0	72.5	52.1		-1.5	10	8.5	85
PNAR12	94.1	71.9	55.7	47.3		-121.5	15	-106.5	42.5
Avg.	**86.2**	**76.0**	**51.9**	**41.7**	**Sum**	**-366.0**	**91.5**	**-274.5**	**554.5**
Total Avg.	**69.6**	**54.6**	**50.0**	**46.5**	**Total Sum**	**-881.5**	**223.0**	**-658.5**	**21.5**

Table 2.2 Top five native and non-native species in terms of net increase and decrease in absolute cover (m2), summed across all plots, and their respective percent increase or decrease in cover since previous surveys

Native species	Δ ABS cover	% Δ	Non-native species	Δ ABS cover	% Δ
		Increase			
Dicranopteris linearis	340	282	*Psidium cattleianum*	504.5	369.6
Microlepia strigosa	75.5	50	*Ardisia elliptica*	243.5	†
Pandanus tectorius	73	387	*Phlebodium aureum*	110	†
*Metrosideros polymorpha**	41	13.9	*Falcataria molucanna*	99	†
*Planchonella sandwicensis**	40.5	66.4	*Schefflera actinophylla*	97.5	121.9
		Decrease			
*Wikstroemia oahuensis**	-221	-93.2	*Paspalum conjugatum*	-200	-97.1
*Scaevola gaudichaudiana**	-132.5	-98.9	*Spathoglottis plicata*	-185	-97.4
*Coprosma foliosa**	-108.5	-77.2	*Clidemia hirta*	-97	-54.5
*Cibotium chamissoi**	-95	-42.8	*Cordyline fruticosa*	-86.5	-91.1
Ophioderma pendulum subsp. Falcatum	-58.5	-99.2	*Passiflora suberosa*	-86.5	-97.7

* endemic species

† not recorded in previous surveys

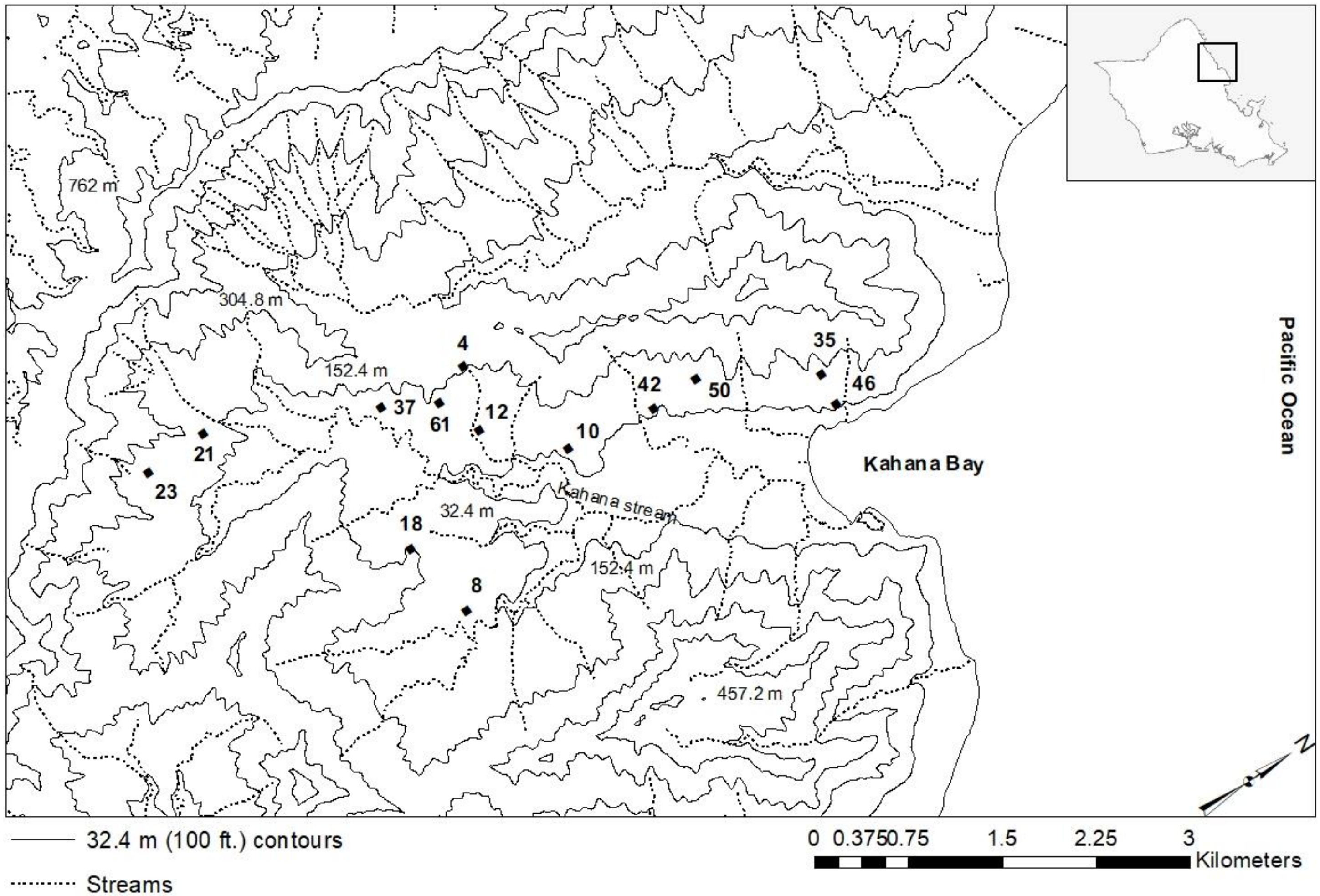

Figure 2.1 Topographical map of Kahana Valley with plot locations

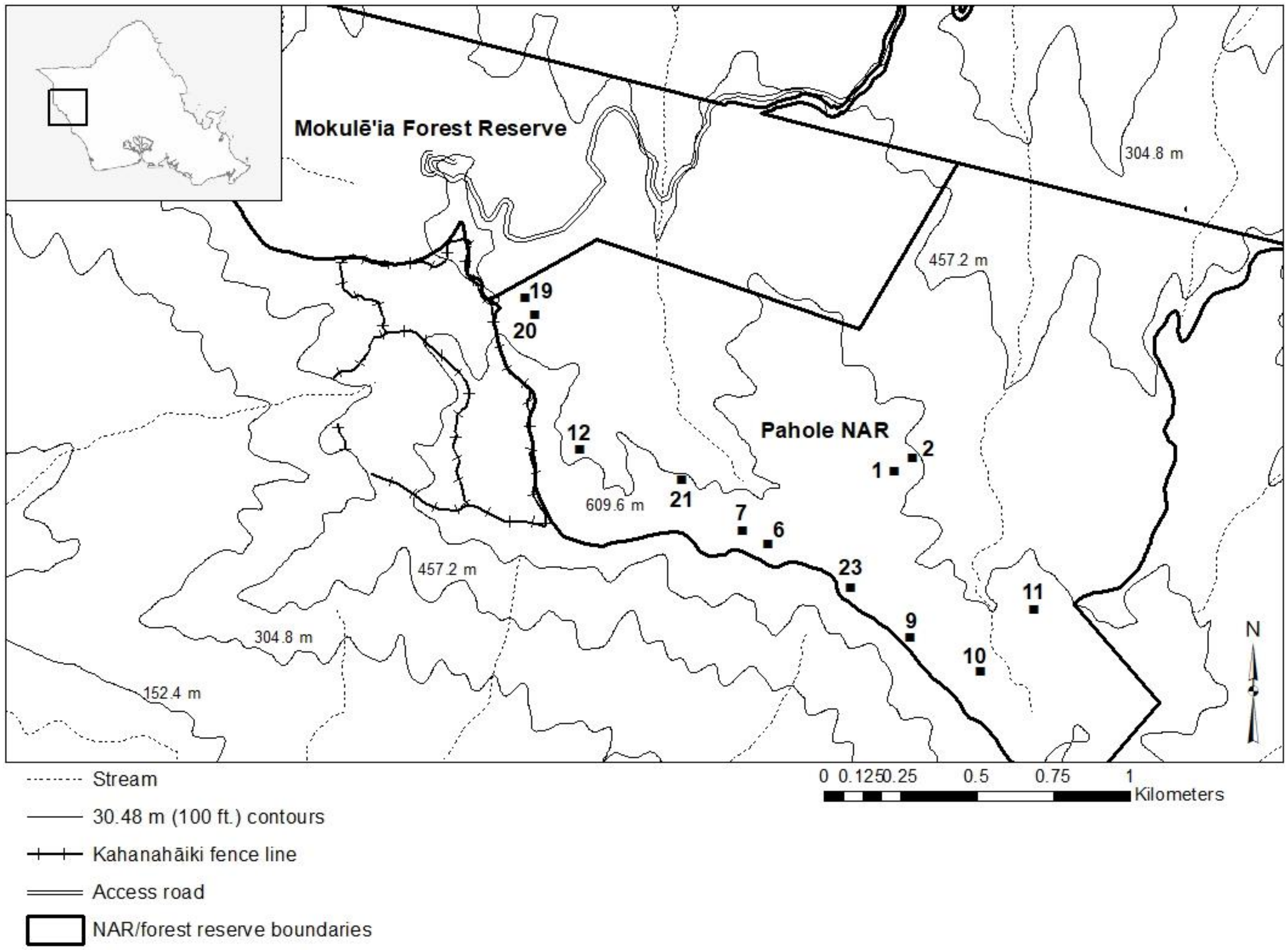

Figure 2.2 Topographical map of the Pahole Natural Area Reserve (NAR) with plot locations

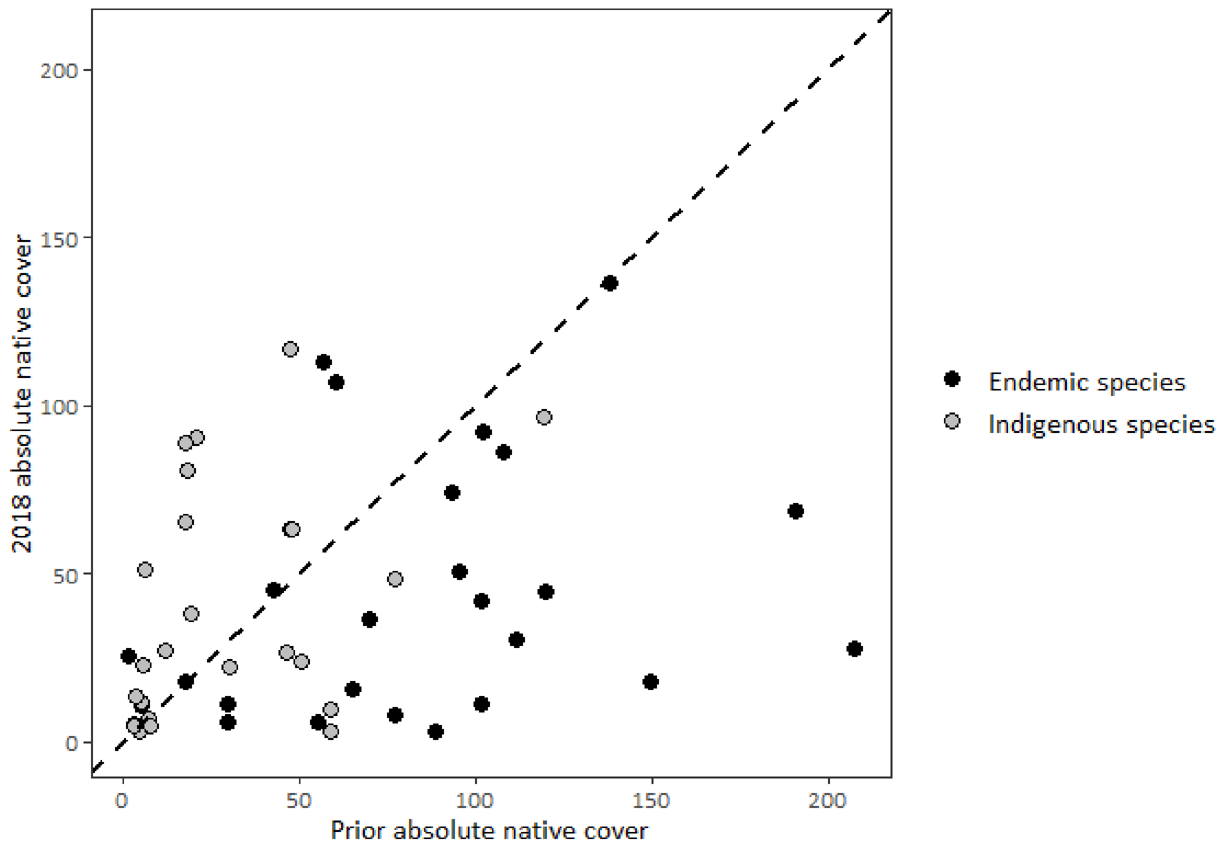

Figure 2.3 Total sum of indigenous and endemic species absolute cover across all plots in 2018 versus in the previous surveys. For endemic species, most points fall below the 1:1 line, (dashed line) indicating decline in 2018. For indigenous species, most points fall above the 1:1 line, indicating increase

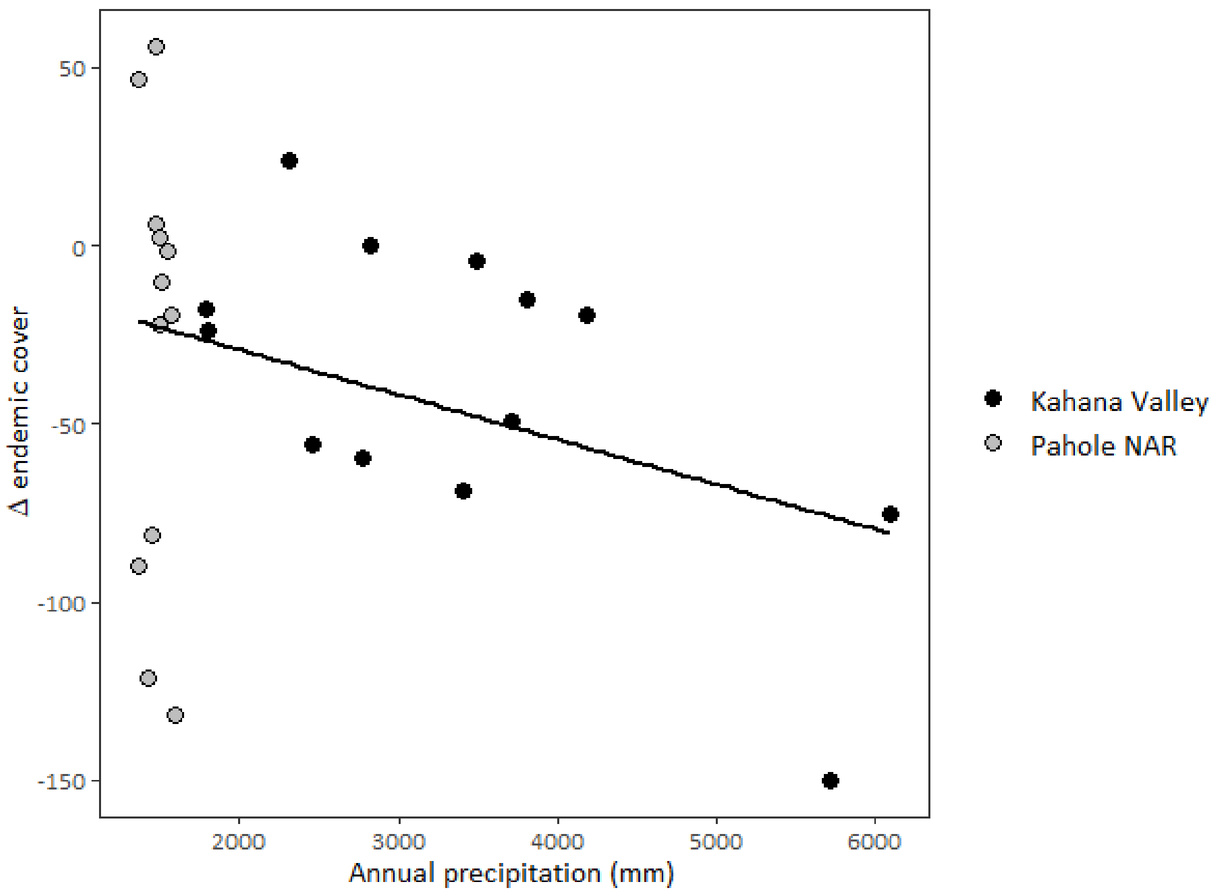

Figure 2.4 Negative relationship between annual mean precipitation and the change in total sum of endemic species' absolute cover ($P < 0.01$) in each plot

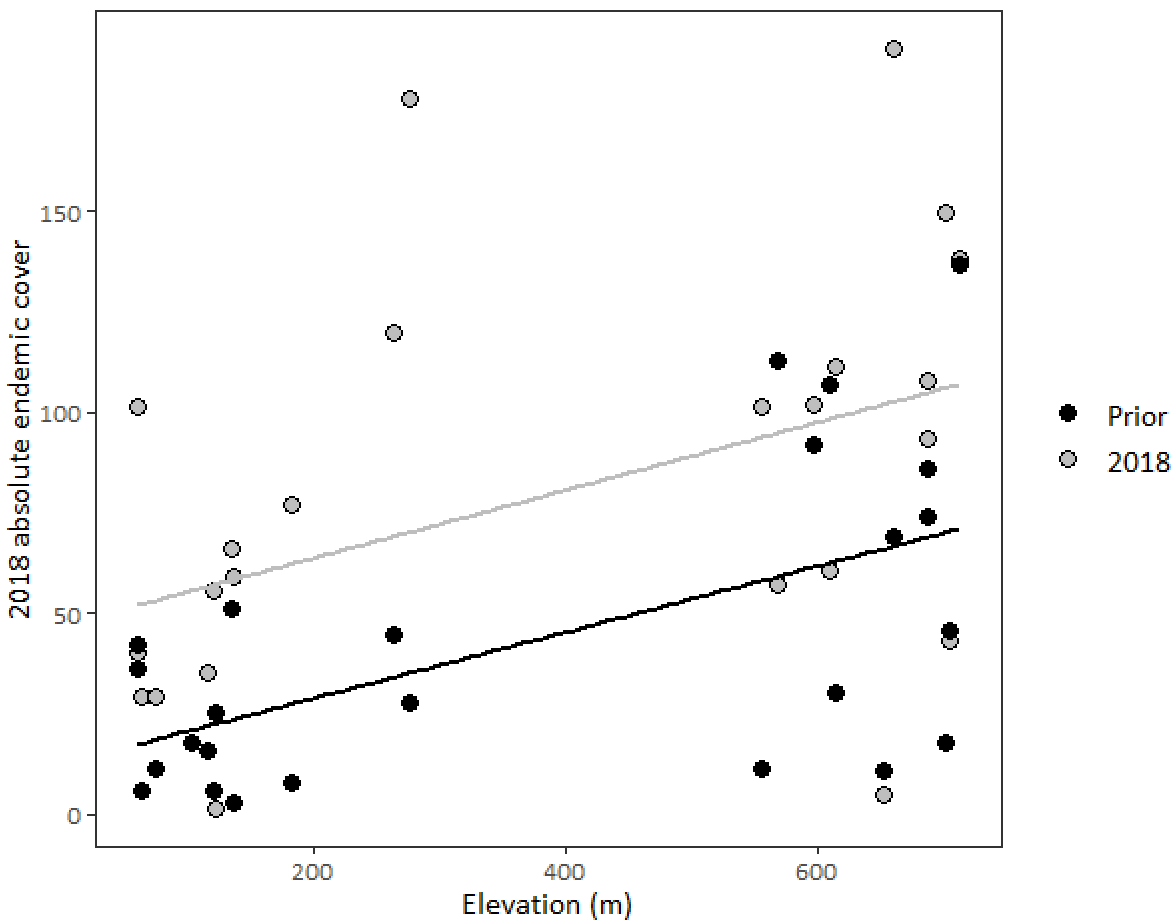

Figure 2.5 Positive relationship between elevation and the previous and current (2018) total sum of endemic species' absolute cover in each plot (P < 0.01 for both)

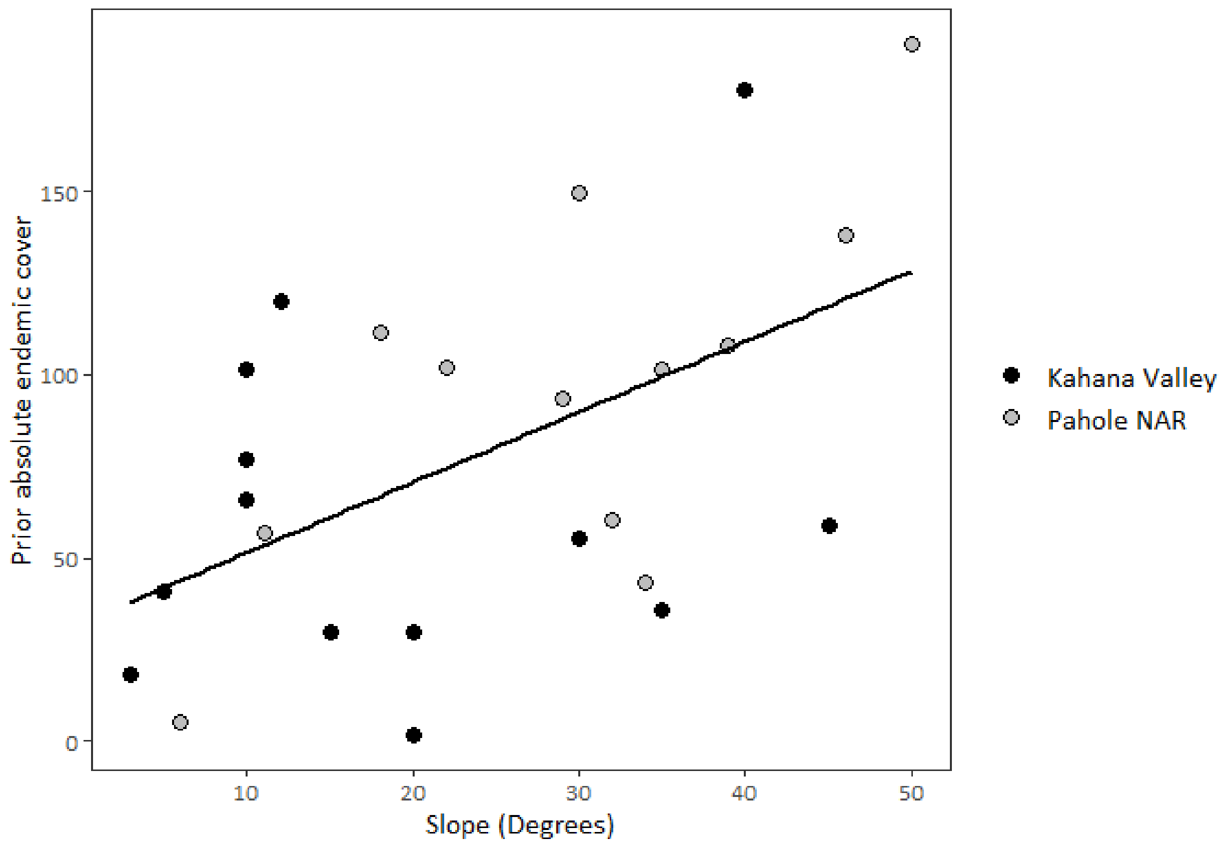

Figure 2.6 Positive relationship between slope and the previous total sum of endemic species' absolute cover in each plot (P < 0.05)

Chapter 4: Plant functional, biogeographical and phylogenetic diversity are related to native and non-native plant abundance in invaded Hawaiian forests

Abstract

Numerous introduced species from cosmopolitan biogeographic origins have naturalized in the Hawaiian Islands and are spreading while native plant cover has concomitantly declined. Phylogenetic, functional, and biogeographical diversity have been shown to influence invasion success, but the importance of these diversity measures for determining native plant abundance in invaded oceanic island forests has not been well established. I surveyed the cover of native and non-native plant species in 50 plots located on the island of Oʻahu, Hawaiʻi. I measured four performance-related functional traits in the resident species (specific leaf area, stem specific density, seed dry mass, and maximum plant height), and determined the growth form of each species. Measures of diversity were assessed using phylogenetic distances, trait and species abundance data, and the biogeographical areas of origin for each non-native species. I calculated the differences between native and non-native community weighted mean trait values and determined the effect of these differences and diversity measures on native and non-native cover. Average trait values were significantly higher for maximum height in natives, and significantly higher for specific leaf area and stem specific density in non-natives. The difference in maximum height of natives and non-natives was negatively correlated with non-native cover. Functional diversity (as measured by functional divergence) and phylogenetic diversity of natives were positively correlated with native cover. Functional evenness, divergence, and richness of non-natives was correlated with non-native cover. Biogeographical diversity was not significantly correlated with non-native cover but had indirect effects via its significant correlation with non-native phylogenetic diversity, which was positively correlated with non-native cover. Non-native cover, in turn, was strongly negatively correlated with native cover. These findings suggest that diversity and competition for light (as evidenced through maximum plant height), but not overall trait dissimilarity, may be important

determinants for the cover of native and non-native species. However, there are likely additional traits which were not measured that influenced competitive outcomes and/or niche filling between natives and non-natives.

Keywords: *functional diversity, biogeographical diversity, phylogenetic diversity, native, non-native, Hawaiʻi, plant invasion, functional traits*

Introduction

Introduction of non-native invasive plant species has become a global ecological issue of concern. Invasive plant species are especially problematic in island communities, where depauperate and disharmonic floras are relatively lacking in functional diversity compared with their continental counterparts (Essl et al., 2019; Hobbs et al., 2013; Zimmerman et al., 2008). The flora of the Hawaiian Islands (HI), located on the most isolated island chain on the planet, is particularly lacking in diversity and missing certain plant functional groups (e.g., large seeded species) (Ostertag, Warman, Cordell, & Vitousek, 2015; Zimmerman et al., 2008). The highly endemic flora in the HI (~90% for angiosperms, and 74% for ferns and lycophytes) is especially susceptible to anthropogenic and feral ungulate disturbances, which greatly exceed natural disturbance frequencies and intensities in the HI (Ostertag et al., 2015; Vernon & Ranker, 2013; Woodcock, 2003). Where disturbance occurs, native propagules from increasingly smaller and fragmented remnant patches are often rare, and seedlings face competition from a multitude of non-native plants (Daehler, 2003). In addition, many of the tree species introduced to the HI for reforestation were intentionally selected for characteristics which would allow them to rapidly revegetate areas where native regeneration was considered to be too slow (Woodcock, 2003). While the impact of these species introductions on native plant communities was not a primary concern at the time, the same characteristics which made many of these species desirable for forestry purposes have likely contributed to their invasive potential.

As concerns over the long-term impacts of invasive species on native plant communities have grown, plant functional traits have gained increasing attention as an explanatory mechanism governing competitive interactions among native and non-native species in invaded communities. Functional traits are physiological attributes of an organism that influence its fitness or performance (Pérez-Harguindeguy et al., 2013), and can capture tradeoffs with regard to resource acquisition, longevity, size, reproductive capacity, growth rates, or other important physiological characteristics and strategies employed by a given plant (Moles, 2018; Rees, 2001; Westoby et al., 2002). Among the multitude of functional traits which have been discussed in the literature, four performance-related plant traits have been examined extensively: Stem specific density, specific leaf area, maximum height, and seed dry mass.

Stem specific density (SSD, or when limited to woody species, 'Wood density') can serve as an indicator of a tradeoff between relative growth rate (RGR) and mechanical strength. SSD is negatively correlated with growth rate, but positively correlated with tolerance of competition for resources (i.e., 'exploitative competition'); it is also positively correlated with tolerance to drought in some circumstances (Kunstler et al., 2016; O'Brien et al., 2017; Pérez-Harguindeguy et al., 2013). Specific leaf area (SLA, or its inverse, leaf mass per area) is associated with a tradeoff between leaf construction costs and longevity, where SLA is positively correlated with growth rate and photosynthesis, but negatively correlated with longevity (Kunstler et al., 2016; Mao et al., 2014; Westoby et al., 2002). Maximum height (Hmax) is associated with a tradeoff between rapid reproduction and increased access to light, as well as avoidance of competition (Carboni et al., 2018; Kunstler et al., 2016). Plant height tends to be positively correlated with canopy size and leaf area, as well as seed dispersal distance; it is also negatively correlated with disturbance, and generally increases with successional age in tree species (Letcher et al., 2015; Moles, 2018). Seed dry mass (SDM) and fecundity have been found to be negatively correlated, indicating a tradeoff between resource investment in individual seeds, which can affect their chance of successful seedling establishment, and number of propagules (Westoby et al., 2002; Zhang et al., 2015).

Generally speaking, invasive plant species have been found to exhibit mean trait values associated with rapid growth, resource acquisition, and high reproductive capacity more so than native and non-invasive non-native species (van Kleunen et al., 2010). Where disturbance exceeds natural frequencies, non-native pioneer species adapted for rapid dispersal and growth are often able to establish in microsites first, occur in high abundances, and can exclude natives via priority effects (Catford et al., 2012). The more non-native species that are able to disperse into a community, the higher the potential functional diversity, and thus the higher the likelihood that a species with high performance traits values will be present (Buckley & Catford, 2016). The potential for a sampling effect may also exist when considering the biogeographical realms of origin and phylogenetic diversity for constituent non-native species in a community; as the number of distinct biogeographical realms of origin represented among propagules increases, so does the probability that non-natives will be represented by a wider array of distinct evolutionary histories (i.e., greater phylogenetic diversity), or exhibit traits which are not well represented in the recipient community (i.e., 'novel functional groups'), and thus be more likely to be able to establish and compete with existing natives (Catford et al., 2012; Cavender-Bares, Ackerly, Hobbie, & Townsend, 2016; Ostertag et al., 2015). Thousands of non-native species have already been introduced to the HI from diverse biogeographical origins, to the point where naturalized species now outnumber native species, and more species are becoming naturalized every year (Sax et al., 2002; Wagner et al., 1999; Woodcock, 2003). It is therefore plausible that the diversity of origins for non-native species may be an important determinant of the collective ability of non-natives to invade and negatively impact native plant communities. However, diversity of origins has received little attention as a possible factor explaining the degree of overall dominance by invaders in a community.

The continued proliferation and spread of non-native species in the HI has coincided with large-scale declines of native forest communities (Hibit & Daehler, 2019; Sax et al., 2002). However, some native plant assemblages may be less susceptible to invasion than others. For example, more functionally and phylogenetically diverse native communities may have greater niche overlap with potential invaders and thus exclude them where disturbance does not exceed natural frequencies (Buckley & Catford, 2016; Galland et al., 2019; Maron & Marler, 2007). Indeed, the success of non-natives in forest communities has been shown to vary in the HI, and some natives are still able to persist in the face of invasion in some areas (Hibit & Daehler, 2019; Zimmerman et al., 2008). However, while some studies have investigated the relationship between functional diversity and invasion resistance in restored Hawaiian plant communities (e.g., Ostertag et al., 2015), little is known about how native and non-native trait dissimilarity, functional diversity, or phylogenetic diversity influences invasibility in oceanic island forests which have not undergone restoration. Conservation efforts in the HI and similarly invaded island habitats may therefore benefit from better understanding the circumstances under which natives in island plant communities are more likely to be able to resist invasion.

Here I attempted to address this gap in understanding by assessing plots in Hawaiian forests containing varied proportions of native and non-native plant species in order to determine the relative importance of these factors for predicting the cover of native and non-native species in invaded island habitats. I asked: **1)** How do natives and non-natives differ in terms of values for performance traits related to growth, resource acquisition, and fecundity (in this study SLA, SSD, Hmax, and SDM)? **2)** Is dissimilarity in trait values between natives and non-natives correlated with non-native cover? **3)** Is the biogeographical diversity of non-natives correlated with non-native functional and phylogenetic diversity? **4)** Is the functional and phylogenetic diversity of native and non-native species in a community correlated with their respective cover values?

Methods

Site description

From February of 2018 to February of 2019, I sampled fifty 400 m^2 plots from seven locations across the island Oʻahu, Hawaiʻi, USA. Twenty-five plots were sampled from the Mokulēʻia Forest Reserve, the Pahole Natural Area Reserve, and the Waiʻanae Kai Forest Reserve, situated in the Waiʻanae Mountain Range; the remaining twenty-five plots came from Kahana Valley, Mount Tantalus, Waʻahila Ridge, and Hawaiʻi Loa, situated in the Koʻolau Mountain range. All selected plots had a minimum of three native and three non-native plant species in order to create a convex hull volume (i.e., two-dimensional trait space) by which functional diversity could be determined. Plots ranged from 60 to 815 m in elevation, and from dry to wet forest, with a yearly mean precipitation across all plots from around 895 to 6100 mm (Giambelluca et al., 2013). Temperatures in the plots ranged from an average minimum of 18.7˚C to an average maximum of 22.3˚C, with a yearly average temperature 20.4˚C (Giambelluca et al., 2014). A list of coordinates and attributes for each plot can be found in appendix A.

Vegetation surveys

The vascular plants in each plot were identified to species and their cover values were estimated using the Domin-Krajina cover abundance scale (Ellenberg & Mueller-Dombois, 1974). The midpoint value of each cover-abundance category was then used as the estimate of percent coverage for each species, and the cover of each species in a plot was combined separately for natives and non-natives to obtain the total coverage of each. Each species was assessed as a single estimate of its two-dimensional coverage (i.e., canopy layers were not considered separately). Due to overlap of plant cover among species in the three-dimensional canopy, total coverage summed across all species in each plot may exceed 100%.

Trait measurement

Whenever possible, trait data was obtained from databases (TRY and DRYAD) (Kattge et al., 2011). Growth form and Hmax (m) data were obtained from Palmer (2003) for pteridophytes, and Wagner et al (1999) for angiosperms; data for species not found in those sources were obtained from additional literature sources (See data sources section and appendix F). If data could not be found in the literature, measurements were made from field-collected plant material. SSD (g/cm^3), SLA (cm^2/g), and SDM (g) were measured using the protocols set forth in Pérez-Harguindeguy et al. (2013). Leaf area for SLA was measured using a laser leaf area meter (CID, Inc. CI-203, Camas, WA USA) for simple leaves, and compound leaves were measured via image analysis using image j software (Schneider et al., 2012). SSD was determined using the water displacement method (Pérez-Harguindeguy et al., 2013). Even with extensive data mining and field sampling, I was not able to obtain trait data for some rare or endangered species, or was unable to obtain a sufficient number of samples to meet with the standards laid out in Pérez-Harguindeguy et al. (2013). Additionally, some species did not possess certain traits: Pteridophytes were not included in measurement of SDM; Rosette forming species or those with only rhizomes were not included in the measurement of SSD; Species lacking true leaves (e.g., *Psilotum* spp.) were not included in the measurement of SLA; Vines and lianas, which may grow at length either horizontally or vertically, were omitted from the measurement of Hmax. Excluding those species where certain trait measurements were not applicable due to their physiology, 12% of the species were missing one of more trait measurements. To ensure the accuracy of functional diversity indices, I imputed values for missing trait measurements using multivariate imputation by chained equations (MICE) in the 'mice' package in R v3.2.2, which uses predictive mean matching to impute values (Azur et al., 2011; Májeková et al., 2016; Taugourdeau et al., 2014; R Core Team, 2013). The complete list of species and traits can be found in appendix E. All new trait measurements made for this study will be added to the TRY database.

Functional diversity analysis

I used the FD package in R v3.2.2 to determine the community weighted means (i.e., trait values weighted by abundances of constituent species in each plot) and functional evenness (FDe), richness (FDr), and divergence (FDdiv) of native and non-native species in each plot (Muscarella & Uriarte, 2016; R Core Team, 2013). These are measures of the relative abundance of given trait values in trait space, the amount of trait space occupied, and the degree of trait value separation in trait space, respectively (Mason et al., 2005). The FD package can take the heterogeneity in scale of measurement for each trait, as well as data types (e.g., categorical and qualitative) into account. It utilizes a dissimilarity version of Gower's formula (Gower 1971, modified by Podani 1999) to estimate a distance matrix. This formula allows for a mixture of variable types, as well as missing data values. A Principal Coordinates Analysis (PCoA) is then used to represent the distribution of species in a multidimensional trait space. Using the Euclidean distances from the PCoA, the values for FDe, FDr, and FDdiv were then determined using the methods described by Villéger, Mason, & Mouillot (2008).

Biogeographic diversity analysis

The native range of non-native plant species in each plot was identified from the descriptions in Palmer (2003) and Wagner et al. (1999); where this was unclear, native range was determined using additional literature sources (CABI, IFAS, and Missouri Botanical Garden, see data sources section). The biogeographic realm for each species' native range was then determined using the definitions of Olson et al. (2001). Non-natives in these plots had native ranges from six of the eight defined biogeographic realms (Afrotropic, Australasia, Indo-Malay, Nearctic, Neotropic, Palearctic); those species with ranges not contained within only one of the defined biogeographic realms were categorized as 'Widespread'. Amongst those widespread species were those found within a seventh biogeographical realm, 'Oceania' (appendix G). The richness of biogeographical realms in each plot (BD) was determined as the number of different realms represented and patterns were analyzed using the FD package in R v3.2.2 (R Core Team, 2013).

Phylogenetic analyses

I reconciled my species list with the classifications found in the NCBI database (Benson et al., 2009; Sayers et al., 2009) using the classifications() function in the R v3.2.2 'Taxize' package. A phylogenetic tree was then constructed using the class2tree() function, and the 'phylo' class tree was then extracted. I used this tree in combination with abundance data to calculate phylogenetic diversity (PD), defined as the sum of branch lengths on a phylogenetic tree for a group of selected species (Faith, 1992), using the PD() function in the 'picante' package (R Core Team, 2013).

Statistical models and trait comparison

I tested for differences in community weighted means of numerical trait values (SSD, SLA, Hmax, and SDM) between natives and non-natives; trait dissimilarity was calculated as the absolute value of the difference between community weighted mean values for each native and non-native numerical trait. I tested whether there was a relationship between dissimilarity for each trait and non-native cover. The relationship between non-native BD and non-native diversity measures (FDe, FDr, FDdiv, and PD) was also assessed, as well as the relationship between each native and non-native diversity measure and their respective cover values. For each analysis, I started with a single model which included all explanatory variables and removed variables in subsequent models to reduce complexity and test different combinations of variables. Model selection was then performed using the Aikake Information Criterion (AIC), using the function AICctab() in package 'bbmle' in R v3.2.2 (R Core Team, 2013).

Results

The average species richness of natives and non-natives was roughly the same across all plots; non-natives had higher richness in 27 out of 50 plots (Table 1). The community weighted mean values in each plot showed that trees were the dominant growth form for both natives (30 out of 50 plots), and non-natives (36 out of 50 plots). Independent two-sample T-tests determined that community weighted mean trait values across all plots were significantly different between natives and non-natives for Hmax, SLA, and SSD ($P < 0.001$ for each). These values were higher for SDM (non-significant) and Hmax in natives, and higher for SLA and SSD in non-natives (Table 1). Multiple regression analyses found that trait dissimilarity for the community weighted mean values of Hmax was negatively correlated with non-native cover ($P < 0.001$); no other differences in trait community weighted mean values were found to be significantly correlated with non-native cover (Figure 3.1).

The mean values for functional diversity measures were all higher for natives than non-natives, while the mean non-native PD was greater than that of natives (Table 1); independent two-sample t-tests did not find that any of these diversity measures were significantly different between natives and non-natives. Using, multiple regression analyses, I found that the only diversity measures which significantly predicted native cover were native FDdiv and PD ($P < 0.05$ for both), both positive correlations (Figures 3.2 and 3.3). The number of different biogeographical realms represented by non-natives in each plot ranged from 1-6, but the community weighted mean values indicate that the Neotropics contributed the most species in the majority (33 out of 50) of the plots. Non-native BD was found to be positively correlated with both non-native FDr ($P < 0.05$, figure 3.4) and PD ($P < 0.001$, figure 3.5), and non-native cover was negatively correlated with non-native FDe ($P < 0.001$, figure 3.6), and positively correlated with non-native FDr ($P < 0.05$, figure 3.7) and FDdiv ($P < 0.01$, figure 3.8).

Discussion

Trait differences

While invaders commonly have life history strategies adapted to early successional stages (Catford et al., 2012; Rees, 2001; van Kleunen et al., 2010), non-native species in this study were represented by a variety of trait syndromes. For example, the finding of significantly higher community weighted mean SLA and lower community weighted mean SDM values (although not significantly different for SDM) for non-natives corroborate findings both in and outside of the HI (Daehler, 2003; Ordonez et al., 2010), and reflect the early successional strategies often exhibited by non-native pioneer species adapted for rapid dispersal and growth following disturbance (Rees, 2001; Suda, Meyerson, Leitch, & Pyšek, 2015). However, I found that trees were the dominant growth form amongst non-natives, and that non-natives exhibited significantly higher community weighted mean values of SSD. This suggests that the most dominant non-natives in these plots employed strategies consistent with later successional and shade-tolerant species (Falster & Westoby, 2005; Rees, 2001), likely reflecting the extensive introduction history of non-native trees for varying revegetation and forestry purposes throughout the HI (Woodcock, 2003). At the same time, native community weighted mean Hmax of both woody and herbaceous species was greater than that of non-natives. This result is surprising since non-natives in other locations have been found to generally exhibit greater Hmax values than natives (Divíšek et al., 2018; Suda et al., 2015; Wang et al., 2018), and most native Hawaiian trees are relatively short statured (although *Acacia koa* and *Metrosideros polymorpha*, the most common native forest trees, are notable exceptions) (Little & Skolmen, 1989).

The difference in community weighted mean Hmax values between natives and non-natives was the only trait disparity which was associated with non-native cover (negative correlation), suggesting the importance of competition for light between natives and non-natives as a determinant of native abundance in invaded Hawaiian forests, similar to findings elsewhere (Levine et al., 2003). However, not all non-natives encountered in this study were limited by light. Follow up analyses found a positive correlation between the native tree growth form community weighted means and non-native cover ($P < 0.01$), indicating that some non-natives are thriving in the understory of native canopies. Indeed, shade tolerant species have been found to exhibit shorter statures on average (Poorter et al., 2003), and shade tolerant trees such as *Psidium cattleyanum* and *Ardisia elliptica* were found to be some of the most prolific invaders in these plots, consistent with numerous reports both within and outside of the HI (Florens, Baider, Seegoolam, Zmanay, & Strasberg, 2017; Foster Huenneke & Vitousek, 1990; Meyer, 2000). These species are dispersed by feral pigs and non-native birds, and are able to establish under native canopies and become dominant even in the absence of disturbance (Catford et al., 2012; Foster Huenneke & Vitousek, 1990; Vizentin-Bugoni et al., 2019). Some non-native invaders also have a high degree of phenotypic plasticity, allowing them to vary their niche between their native and introduced ranges (Pattison et al., 1998). For example, *Clidemia hirta* is an invasive woody shrub in the HI which can be frequently found in Hawaiian forest understories, including the plots in this study. This species does not occur in forest understory in its native range, and is apparently more shade tolerant in its introduced range (DeWalt 2004). Thus, the success of non-natives in aggregate in the HI may be due to their ability to fill niche space in their introduced range which they do not normally occupy in their native range, as well as the varied successional and competitive strategies they collectively employ.

Diversity measures

Various studies have found conflicting results with regard to the relationship between FD and resistance to invasion in plant communities. Some research suggests that higher FD in recipient communities actually increased susceptibility to invasion, possibly as a result of increased availability of niche space between more functionally divergent native species (Galland et al., 2019; Loiola et al., 2018). By contrast, a comprehensive review conducted by Gallien & Carboni (2017) found evidence that native diversity confers greater resistance to invasion. Their review also highlighted the disagreement that exists as to the association between community PD and resistance to invasion. While it is important to note that this study was limited to observation, without the means to determine causality between plant cover and traits or measures of diversity in order to infer invasion resistance, the observed correlation between measures of functional and phylogenetic diversity of natives and non-natives with their respective cover values suggest that they may play a role, and at the very least are associated with the relative abundance of native and non-native plants in island forest communities which have already been invaded. However, it is possible that other factors (e.g., disturbance by feral ungulates, or lack thereof) may have had an influence on native and non-native abundances as well.

The postulated relationship between FD and invasion resistance hinges on the idea that functionally similar species are competitively excluded by species already established in a community (i.e., 'Limiting similarity') (MacArthur & Levins, 1967; Mouchet et al., 2010). By the same convention, functionally dissimilar species may have a greater chance of occupying available niche space in a given community. With some exceptions (e.g., Loiola et al., 2018; Price & Pärtel, 2013), there is strong evidence that invaders which are functionally dissimilar from species in recipient communities have a greater likelihood of successful establishment (Gallien & Carboni, 2017; Ordonez et al., 2010). However, there was no evidence to support this in my study plots. In fact, the only significant correlation with trait dissimilarity between native and non-native species (Hmax) was negative for non-native species. At the same time, both native and non-native Hmax values were positively correlated with their respective cover values ($P < 0.001$ and $P < 0.01$, respectively), suggesting an importance of competition for light, but not niche filling in these plots for determining which non-natives are able to invade and exist in tandem with native species, at least with regard to the functional traits I measured in this dissertation.

The availability of niche space in a recipient community is also related to the degree of (dis)similarity between species in said community, which is analogous to FDdiv (Mason et al., 2005). In their study examining native diversity and invasion, Loiola et al. (2018) found that invaders may be successful when they are able to fill niches within existing trait space, rather than occupying areas outside of such a trait space. However, this study does not support this finding. In fact, FDdiv was the only measure of native functional diversity that was significantly correlated with native cover (positive correlation), and follow up tests found that native FDdiv was positively correlated with native Hmax ($P < 0.01$). This suggests that greater native dissimilarity increased the chances that natives will be represented by tall species which can compete for light with non-natives. However, native PD in these plots was not correlated with native FDdiv or Hmax; PD can be used as a proxy for unmeasured traits (Galland et al., 2019), and as such suggests that there are likely traits which were not measured in this study that influenced the higher observed native cover in plots with higher native PD. For example, flowering phenology, clonality, root biomass allocation, and nutrient use efficiency have all been associated with invasiveness in plants (Pyšek & Richardson, 2008; van Kleunen et al., 2010). It is thus possible that traits other than those I had measured in this study may influence native and non-native coexistence via niche processes similar to findings in other studies (e.g., Gallien & Carboni, 2017; Ordonez et al., 2010).

Biogeographic origins have also been shown to be useful predictors of a species' ability to impact native plant communities (Buckley & Catford, 2016). A review by Cavender-Bares et al. (2016) suggested that BD should be related to measures of FD. The finding that non-native BD was positively correlated with non-native FDr and PD supports their hypothesis. Non-native cover, in turn, was negatively correlated with native cover ($P < 0.001$), suggesting that measures of non-native diversity have an indirect effect on native cover through their influence on non-native cover. Interestingly, the strongest correlation between non-native diversity measures and non-native cover was a negative correlation with FDe, which may actually reflect the strong dominance exhibited by certain invasive tree species found in these plots and throughout the HI (e.g., *Psidium cattleyanum* and *Ardisia elliptica*), given that they are represented by a specific suite of traits. Thus, where monotypic dominance of certain non-natives is not present, native cover may be expected to be higher.

Conservation implications

Given my findings, when making species selections for restoration purposes, choosing natives with higher Hmax values (e.g., *Metrosideros polymorpha* and *Acacia koa* for woody species in the HI) may confer a competitive advantage to natives. It is additionally advisable to select species with trait values or evolutionary histories that diverge from those already found in the native community. Ostertag et al. (2015) discussed methodology for doing this using a principal components analysis (PCA) to determine where trait space in a community remains open, and which native or non-invasive non-native species may be able to occupy the greatest amount of functional space and thereby exclude non-native invaders. While this technique abandons the goal of returning to a completely native historical baseline, it did show a measure of success in the short-term (Ostertag et al., 2015), and may be able to prevent monotypic dominance of non-native invaders that can displace existing natives in the long-term. A PCA of traits measured in the plots surveyed in this study showed that native and non-native species in these plots largely overlap in trait space where SDM, SSD, and Hmax are concerned, but non-natives occupied much more trait space at the high end of the SLA spectrum than did natives (Figure 3.9). While disparity in community weighted mean SLA values was not found to be significantly correlated with non-native cover in these plots, it was nearly so ($P = 0.06$), and may be an important consideration nonetheless when making outplanting decisions.

Conclusions

My findings in this study suggest that the determinants of native abundance in invaded Hawaiian forests are multifaceted. While I was unable to identify definite causes of invasion resistance or invasibility due to the observational nature of this study, diversity and competition for light seemed to be important determinants for the cover of both native and non-native species. I did not find support for greater dissimilarity between natives or between natives and non-natives promoting non-native cover (i.e., more heavily invaded communities), but the finding of a positive correlation between native PD and native cover, and a lack of correlation between native FD measures and PD, suggest that there are traits which were not measured in this study that are important determinants of competitive outcomes and/or niche filling between natives and non-natives. In addition, a wider representation of biogeographical realms amongst non-natives in plant communities was found to positively influence non-native diversity (FDr and PD), and thus has downstream effects on their ability to impact a given habitat. The non-natives I encountered in my plots exhibited a variety of successional strategies, reflecting the introduction history of tree species into the HI for forestry purposes. It may thus be expected that non-native species in general will be able to be found across successional gradients in Hawaiian forests, even in the absence of unnatural disturbances.

While some natives are able to coexist in these novel forests, native plants are being displaced over time throughout the HI (Hibit & Daehler, 2019; Zimmerman et al., 2008), and may continue to be negatively impacted as a result of species invasions and unnatural disturbances in the absence of active conservation efforts which can help to increase native diversity and invasion resistance. The negative impact of invasive species on native plant communities in the HI is similar to impacts documented on numerous other tropical islands (Essl et al., 2019; Pyšek et al., 2012), and some of the same invaders that can be found in the HI have also had similar detrimental effects on native plant communities of other island archipelagoes (e.g., *Psidium cattleyanum* in Mauritius, Florens et al., 2017). The findings of this study may thus be useful for guiding conservation actions in similarly invaded island habitats outside of the HI as well.

Table 3.1 Percent cover values, diversity measures, and community weighted means of trait values averaged across all plots

	Native	**Non-native**
Avg. % cover value	72	85
Diversity measures		
Functional richness	0.14	0.12
Functional evenness	0.59	0.55
Functional divergence	0.82	0.78
Phylogenetic diversity	253.92	291.42
Species richness	10.62	10.76
Community weighted mean trait values		
Seed dry mass (g)	0.22	0.14
Maximum height (m)	19.28	8.33
Stem specific density (g/cm^3)	0.62	0.72
Specific leaf area (cm^2/g)	97.04	126.62

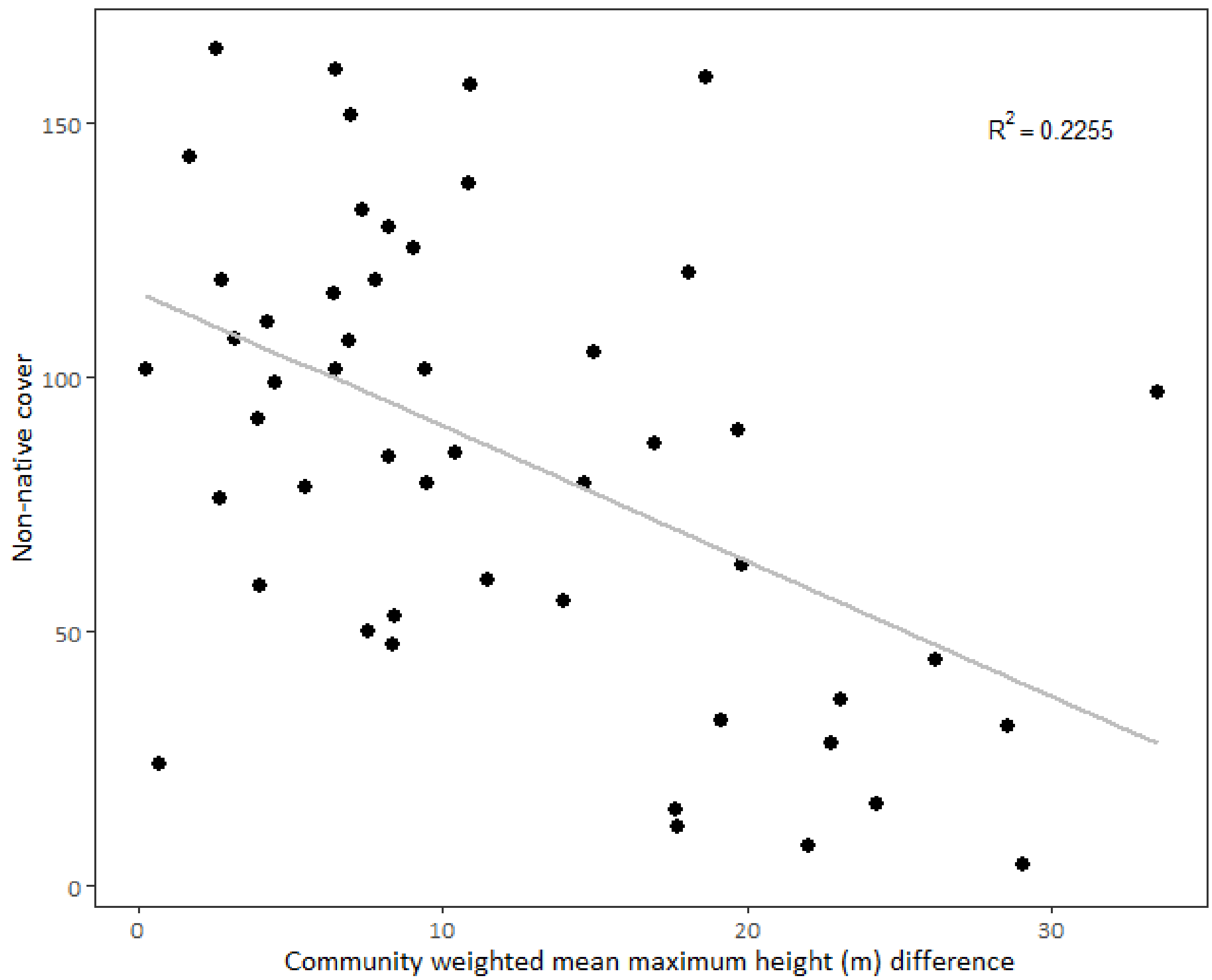

Figure 3.1 Relationship between the difference of community weighted mean maximum height values (m) and non-native cover (P < 0.01)

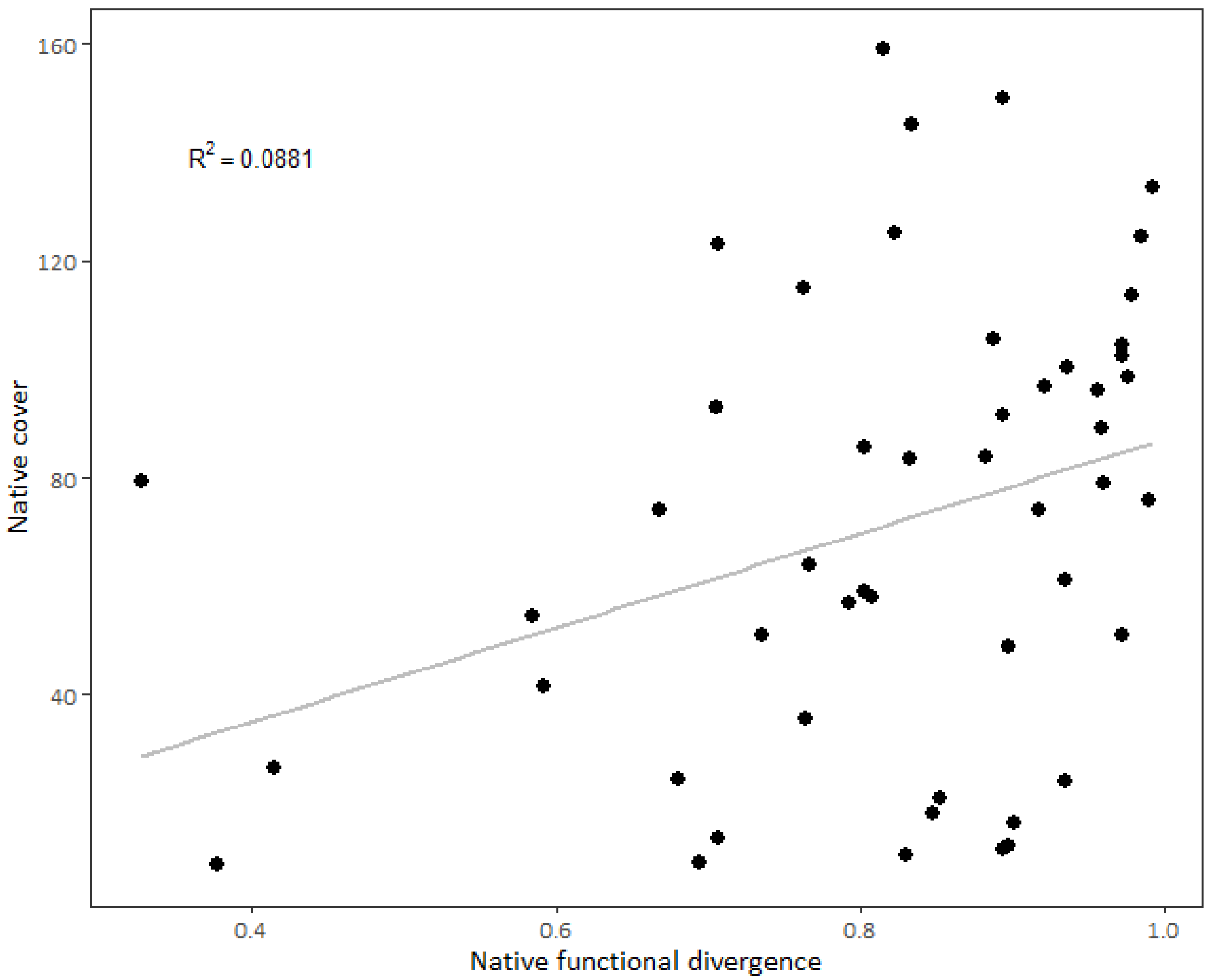

Figure 3.2 Relationship between functional divergence in native plant communities and native cover ($P < 0.01$)

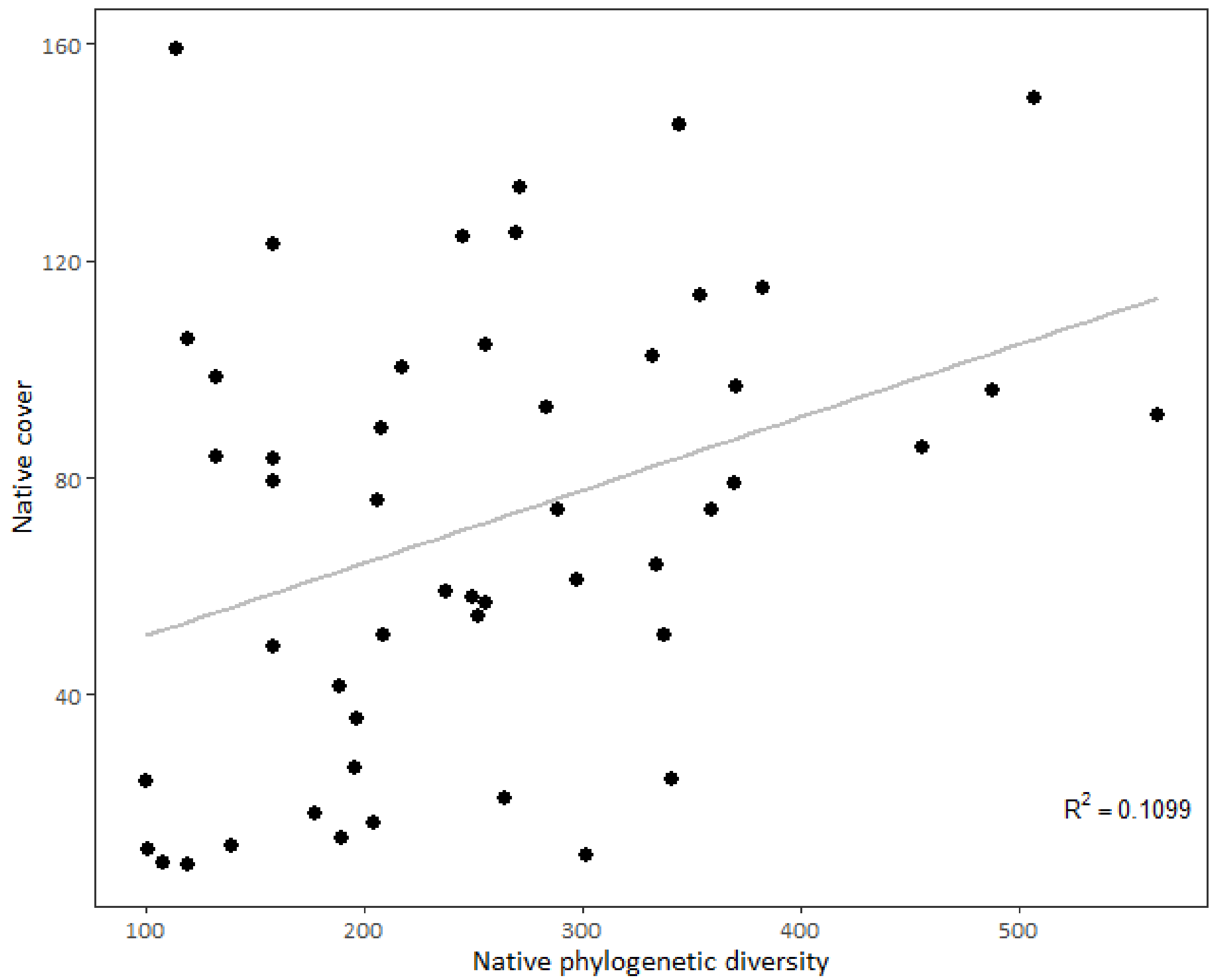

Figure 3.3 Relationship between phylogenetic diversity in native plant communities and native cover ($P < 0.05$)

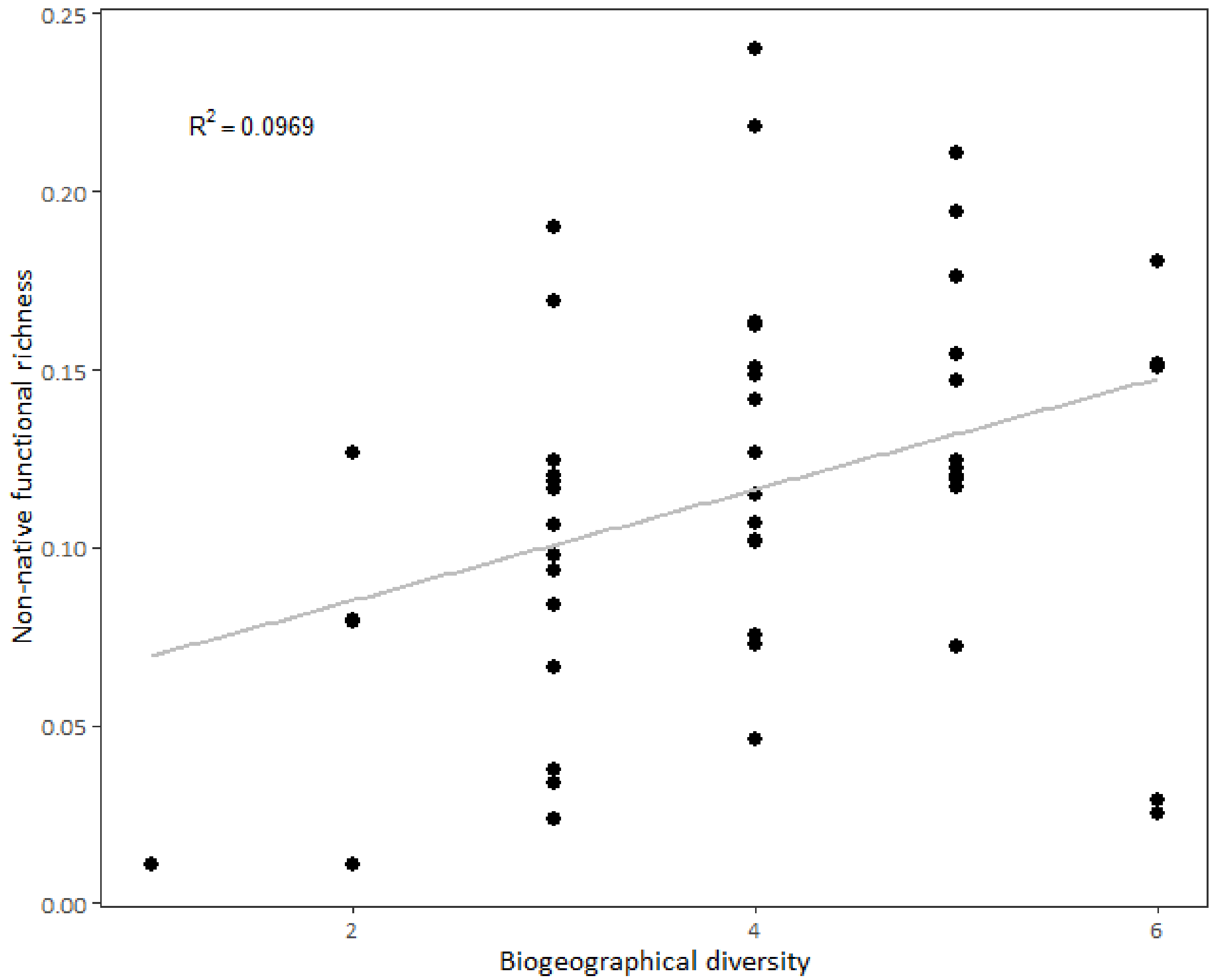

Figure 3.4 Relationship between biogeographical diversity and functional richness of non-natives ($P < 0.05$)

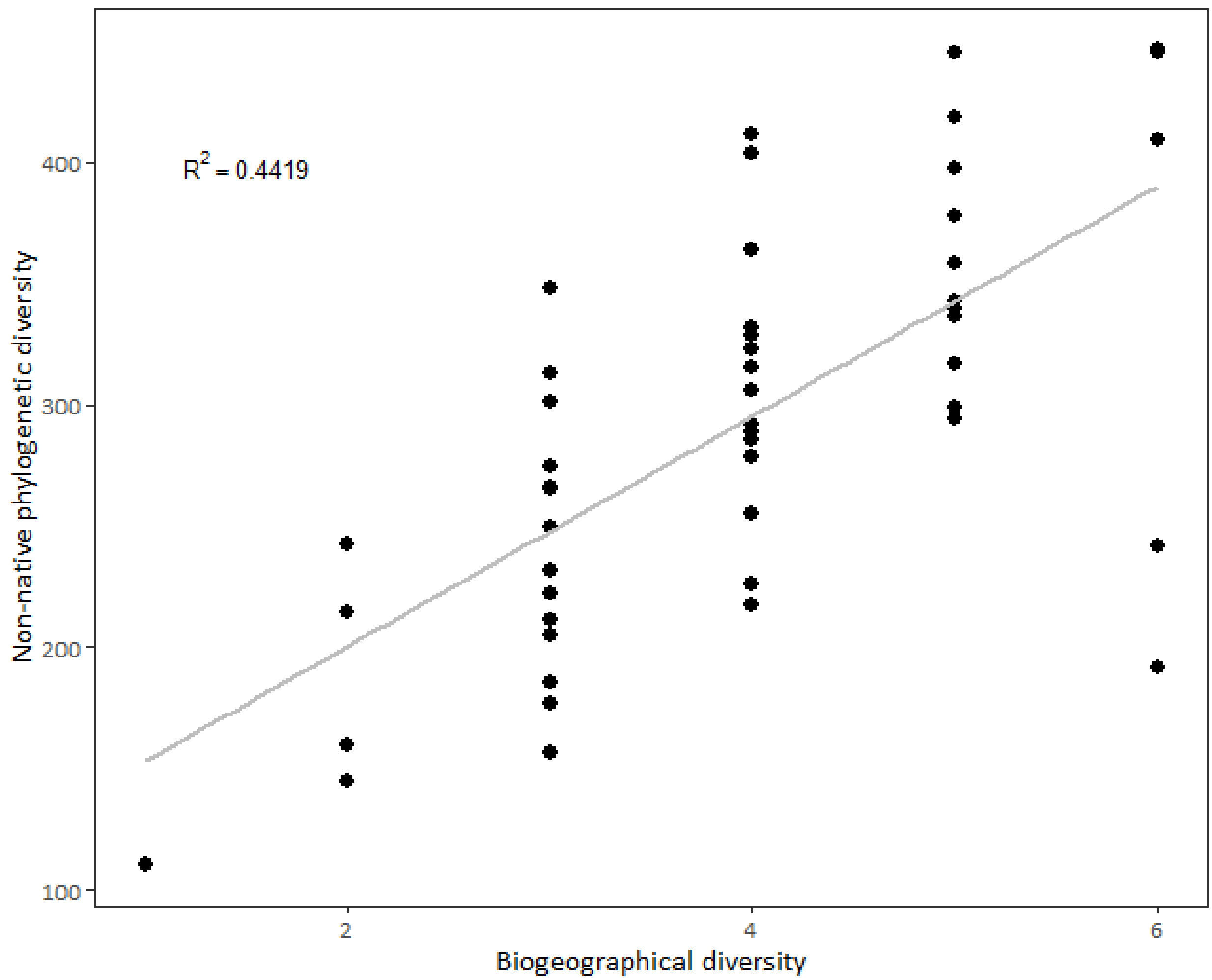

Figure 3.5 Relationship between biogeographical diversity and phylogenetic diversity of non-natives ($P < 0.001$)

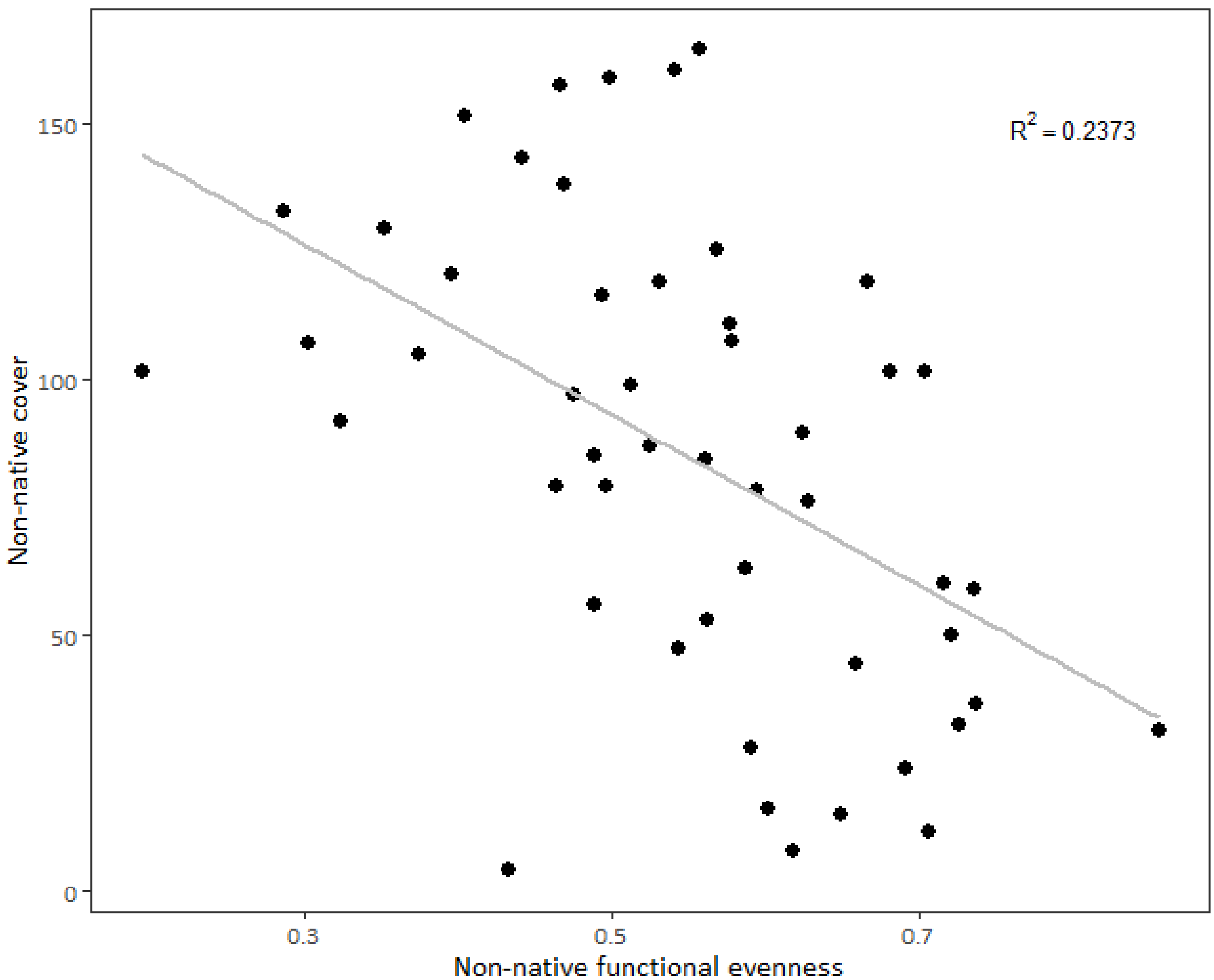

Figure 3.6 Relationship between functional evenness in non-native plant communities and non-native cover (P < 0.001)

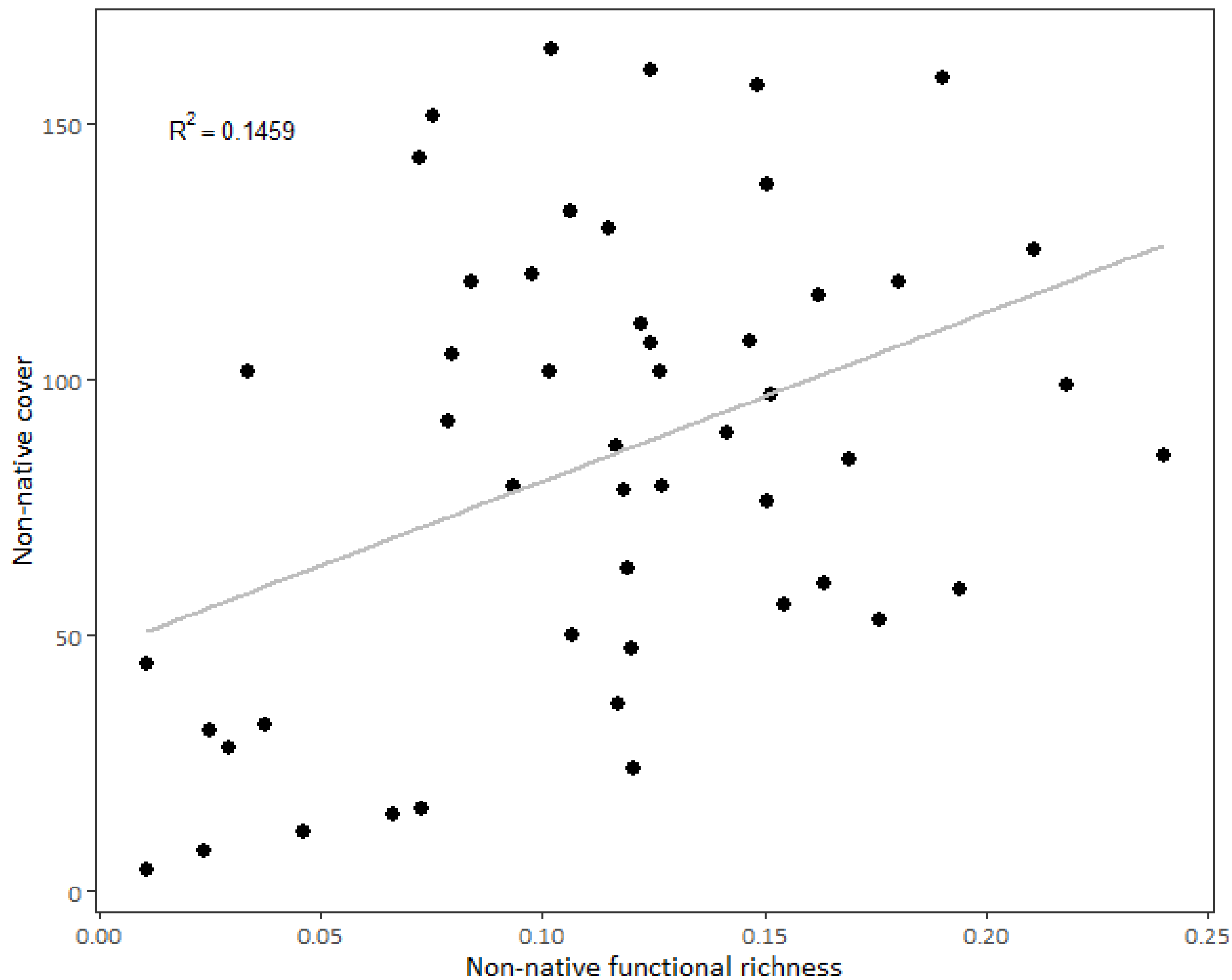

Figure 3.7 Relationship between functional richness in non-native plant communities and non-native cover (P < 0.05)

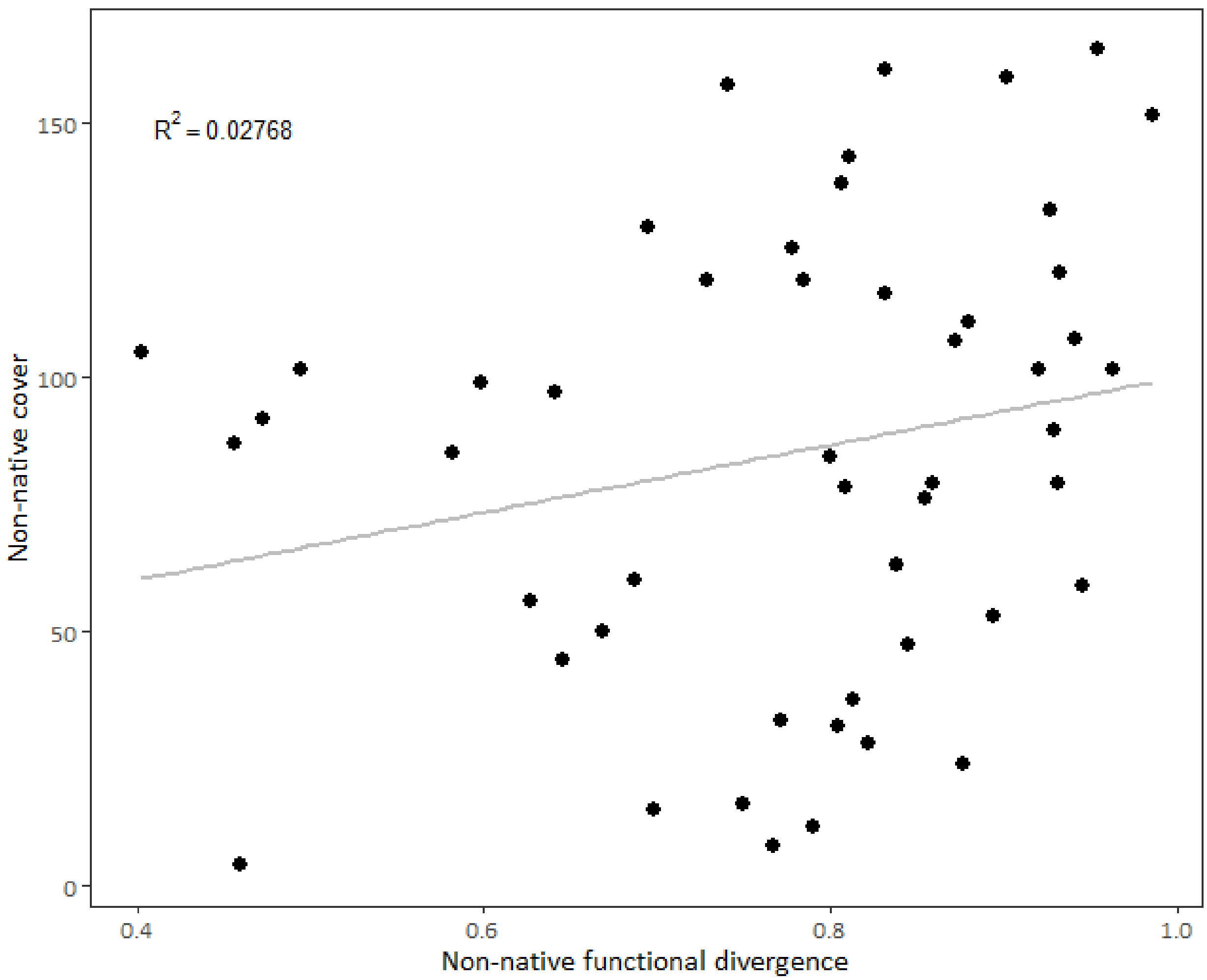

Figure 3.8 Relationship between functional divergence in non-native plant communities and non-native cover (P < 0.01)

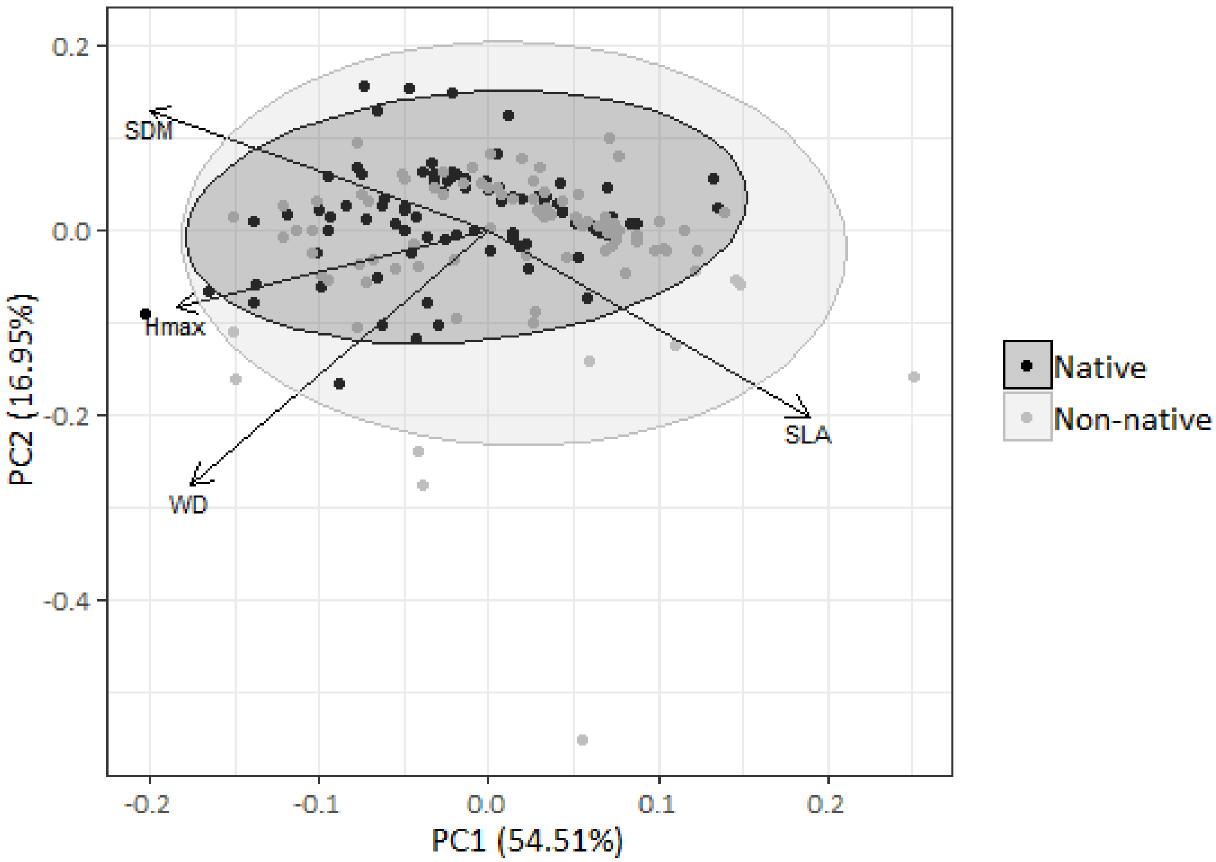

Figure 3.9 Principal components analysis (PCA) of native and non-native community weighted mean stem specific density (SSD), specific leaf area (SLA), maximum height (Hmax), and seed dry mass (SDM) values, plotted in trait space. Percentages in brackets represent the amount of variance explained by the principal component axis

Chapter 5: Synthesis

Summary of findings

In this dissertation, I examined current and long-term cover and abundance of endemic and indigenous Hawaiian plant species in invaded habitats, and how these trends are related to measures of native and non-native diversity as well as abiotic site conditions. In chapter 2, I show that native species in well-established dry forest plots are experiencing decline in the absence of large-scale disturbance, and that native forests are aging and not successfully replacing themselves. However, I found that some common native species may be able to coexist with non-native species in the long-term, and even replace non-native species in a limited capacity, as was found to be the case where *Sapindus oahuensis* replaced *Leucaena leucocephala* in the Mokulēʻia Forest Reserve. In chapter 3, I show that rates of decline/increase in native cover may differ between indigenous and endemic species, where endemic species, which are generally more restricted in range and environmental tolerances (Sakai et al., 2002), are more susceptible to decline in invaded Hawaiian forests. The prevalence of endemic species in particular appears to be more dependent on site conditions than indigenous species, where endemic species cover was associated with higher elevations and steeper slopes. The finding of differential rates of cover change between the two native categories also highlights the problem associated with lumping indigenous and endemic species into a single "native" category, as this may ultimately be misleading. However, this may be context dependent, such as in the case where some studies examining diversity-dependent interactions (e.g., chapter 4) take overall native diversity into account.

In chapter 4, I show that functional divergence (FDdiv) and phylogenetic diversity (PD) of natives in aggregate are associated with native resilience in the face of invasion. In addition, the observation that the maximum height of natives and non-natives was positively correlated with their respective cover values, and that the difference in maximum height values between natives and non-natives was negatively correlated with non-native cover, was used to infer that competition for light was likely an important determinant of relative native and non-native cover in these plots. However, the prevalence of shade tolerant species (e.g., *Psidium cattleyanum* and *Ardisia elliptica*) in the introduced flora of the Hawaiian Islands (HI) highlights the variety of strategies employed by non-natives in Hawaiian forests. This variety also applies to successional strategies exhibited by non-native species in the HI, as the greatest proportion of non-natives encountered were actually mid or later successional species (e.g., trees), reflecting the historical introduction of tree species into the HI for forestry purposes. There is also an extensive array of biogeographical realms represented in the introduced flora (Palmer, 2003; Wagner et al., 1999), and the biogeographical diversity (BD) of distinct native ranges of non-native species represented in my research plots was correlated with non-native functional richness (FDr) and PD. At the same time, measures of non-native diversity were correlated with non-native cover, which itself was negatively correlated with native cover, indicative of downstream impacts that introduction histories and diversity of non-native propagules may have on native cover.

While diversity measures (chapter 4) could not be used to asses potential links with rates of invasion over time, because 19 of the plots I surveyed had not been surveyed previously, 31 of the plots in that study were previously surveyed, and natives were declining over time when measured across all of those plots, while non-native cover concomitantly increased (Chapters 2 and 3). This is likely due not only to competitive displacement by non-natives which are able to invade, but also to disturbance which exceeds historical frequency. Disturbance was evident in some plots, and although no large-scale removal of vegetation has occurred in these plots since they were initially established, the presence of feral ungulates could sometimes be discerned. Even where ungulates were excluded (e.g., in the Pahole NAR), natives were declining, although this was primarily the result of loss of endemic cover.

Conservation implications

If the trends observed in endemic vs. indigenous species are representative of the overall trends that exist throughout the HI, and are allowed to continue unchecked, then it seems likely that there will be a shift in native species compositions of Hawaiian forest communities over time as an increasingly larger pool of indigenous propagules is available for recruitment, while the pool of endemic propagules becomes increasingly smaller. Such a shift could see rare endemic species become increasingly in danger of extinction. In addition, new threats to Hawaiian species continue to arise, such as Rapid ʻŌhiʻa Death (*Ceratocystis* spp.), which leads to large-scale dieback of the keystone endemic Hawaiian forest tree, *Metrosideros polymorpha* (Fortini et al., 2019). Thus, the trend of endemic cover decline and resultant reduction in overall native species richness, combined with the increase in non-native richness and cover over time that was observed in my study plots will likely continue if no additional conservation efforts are made to stymie the invasion of non-native species into remnant Hawaiian forests.

Even though some of the indigenous species which increased most in cover are associated with regrowth following disturbance, the finding of an overall increase in indigenous species cover (chapter 3) suggests that complete displacement of native species by non-natives in the long-term is unlikely. Furthermore, despite declines in overall endemic cover and diversity over time, the persistence of certain endemic species in the study plots suggests that some of them may be able to coexist to a limited degree with non-native species, even in degraded habitats. However, this appears to be more limited to areas which are less easily accessed by humans and feral ungulates (high elevation and steep slopes), especially where rare endemics are concerned. Given that complete eradication of feral ungulates from the entirety of the HI is doubtful, their sustained activity will likely continue to remove native vegetation, alter habitats, and spread seeds of non-native invaders. Fencing to exclude feral ungulates, while effective (Cabin et al., 2000; Cole & Litton, 2014; Weller et al., 2018), is costly and difficult to implement on a large-scale basis, and may still not be enough to prevent decline of endemic species in areas subject to invasion by shade tolerant species such as *Psidium cattleyanum* (as observed in chapter 3). It is equally unlikely that non-native plant species can be entirely eradicated at the whole island scale once they are naturalized, given the ease with which some species disperse, the persistence of their seed banks, the propensity for some species to resprout from underground structures, and the difficulty associated with reaching some of their populations in rugged and remote areas of the HI. Furthermore, the legacy of alien plant introductions can also continue to exert an influence even after eradication due to delayed decomposition of belowground structures and alteration of soil structure and nutrients. (Hobbs et al., 2013; Reynolds et al., 2017) Thus, conservation efforts are generally limited to the preservation of remnant native habitat patches, such as fenced natural area reserves (NARs).

While restoration of degraded landscapes may be possible given sufficient management inputs (Medeiros et al., 2014), many plant communities in the HI have been sufficiently altered in structure and function by human agency to the point where they may never naturally return to a historical baseline (i.e., 'Novel ecosystems', Hobbs et al., 2013). Where this occurs, it may be beneficial to focus conservation efforts on the mitigation of invasive impacts in these novel ecosystems by selecting species which can fill niche space, as done in Hawaiian lowland wet forest plots by Ostertag, Warman, & Cordell (2015), discussed in chapter 4. Ostertag et al. utilized both native species and non-invasive non-native species in order to achieve invasion resistance, with some success in the short-term. Adapting this methodology, the findings in chapter 4 indicate that focusing on the selection of species for outplanting that have traits differing from those species already found in the native community (i.e., increase FD), have high values for specific leaf area (SLA) and maximum height (Hmax), and diverse evolutionary origins (i.e., increase PD), could increase chances of establishing or increasing native cover in invaded Hawaiian forests. Amongst the natives found in my plots, the species with the highest Hmax values were *Acacia koa*, *Metrosideros* spp., and *Polyscias sandwicensis*. Natives with the highest SLA values were *Peperomia* spp. for herbaceous species, *Hibiscus arnottianus* for tree species, and *Diplazium* *sandwicianum* or *Microlepia strigosa* for fern species (appendix E). Vines and lianas are also underrepresented in the native Hawaiian flora, and the native vine *Alyxia stellata* can fill that niche in restoration areas. All of these species were amongst some of the more common natives found in my plots (appendix D), supporting the idea that the selection of native species which can fill performance-related trait space can increase native cover and resilience, and hints at the utility of these species for restoration purposes. Land managers should also take historical species assemblages into account, as they may be indicative of which species are best adapted for a given environment, especially focusing on those natives which have been shown to be able to coexist with non-native species in the same area (e.g., *Sapindus oahuensis* in dry Hawaiian forests, chapter 2). In addition, given that persistence of endemic species seems to be greatest in areas of greater elevation and steeper slopes, it may be more effective to limit outplanting of endemic species to those areas, while using indigenous species for outplanting in areas which are more accessible to humans or feral ungulates.

Final thoughts

The widespread introduction of species as a result of human activity has led to unprecedented mixing of species globally, the repercussions of which are only beginning to become understood. In island archipelagoes such as the HI these impacts are especially severe given the susceptibility of the highly depauperate and endemic flora to anthropogenic disturbances and invasion (Hobbs et al., 2013; Zimmerman et al., 2008). Given the finding of native (mainly endemic) plant decline along with the proliferation of naturalized non-native species, even where ongoing management efforts are underway, it is apparent that a novel condition in Hawaiian forests is inevitable. In order to avoid a perpetual cycle of outplanting native plants and removing non-natives, it should be the goal of conservationists in the HI to restore native populations to the point where they are able to naturally recruit and spread. Implementing more extensive conservation measures at broader scales with particular focus on the site-specific preservation of endemic species' habitat may be able to reverse declines for some native Hawaiian plants. However, the natural conditions under which many rare and endangered endemic Hawaiian plants once naturally maintained their populations may no longer exist in the HI. The artificial maintenance of these species' populations in the wild may thus be nothing more than a necessary exercise in futility. On the other hand, it should be expected that with time a novel equilibrium will be reached within forest communities of the HI, which will contain those natives and non-natives which are best able to compete within their respective niches and tolerate increased disturbance frequencies. Thus, a more realistic and obtainable objective for conservationists may be to encourage a natural balance by which the maximum number of native Hawaiian plant species populations are able to be naturally sustained in equilibrium with non-native species, utilizing directed management informed by ecological considerations brought to light by this and other studies, with the intention of eventually removing the need to intervene in the community assembly process.

Appendix A. Plot attributes and midpoint coordinates

Plot	Coordinates (Decimal degrees)		Elevation (m)	Slope°	Dates sampled*
MFR1	21.5739	-158.2083	86	36	2/23/2018
MFR2	21.5718	-158.2104	313	12	4/4/2018
MFR3	21.5721	-158.2109	298	43	4/4/2018
MFR4	21.5496	-158.1800	353	45	2/24/2018
MFR5	21.5702	-158.2011	117	36	2/1/2018
MFR6	21.5263	-158.1553	391	45	3/10/2018
MFR7	21.5238	-158.1528	555	51	3/9/2018
KV4	21.5393	-157.8957	135	10	9/10/2018
KV8	21.5296	-157.8799	103	3	9/24/2018
KV10	21.5423	-157.8859	60	10	6/19/2018
KV12	21.5377	-157.8909	60	5	9/7/2018
KV18	21.5288	-157.8863	182	10	9/24/2018
KV21	21.5210	-157.9026	276	40	10/5/2018
KV23	21.5162	-157.9025	263	12	10/5/2018
KV35	21.5604	-157.8797	64	15	7/17/2018
KV37	21.5327	-157.8966	116	35	9/19/2018
KV42	21.5490	-157.8848	137	45	7/19/2018
KV46	21.5601	-157.8772	75	20	7/13/2018
KV50	21.5527	-157.8848	122	20	7/19/2018
KV61	21.5364	-157.8944	121	30	9/10/2018
PNAR1	21.5368	-158.1809	652	6	9/26/2018
PNAR2	21.5372	-158.1803	568	11	8/29/2018
PNAR6	21.5347	-158.1849	687	39	7/23/2018
PNAR7	21.5351	-158.1857	704	34	7/23/2018
PNAR9	21.5319	-158.1804	713	46	10/15/2018
PNAR10	21.5309	-158.1782	701	30	10/15/2018
PNAR11	21.5327	-158.1765	687	29	8/29/2018
PNAR12	21.5375	-158.1908	660	50	7/25/2018
PNAR19	21.5420	-158.1925	556	35	5/7/2018
PNAR20	21.5415	-158.1922	610	32	5/7/2018
PNAR21	21.5366	-158.1876	614	18	9/26/2018
PNAR23	21.5334	-158.1823	596	22	7/24/2018
WR1	21.3306	-157.7840	584	0	11/16/2018
WR2	21.3250	-157.7875	505	8	11/16/2018
WR3	21.3216	-157.7884	496	8	1/22/2019
WR4	21.3192	-157.7892	488	21	1/22/2019
WK1	21.5004	-158.1573	683	20	11/2/2018
WK2	21.5020	-158.1565	815	37	11/2/2018
WK3	21.5028	-158.1614	793	13	11/2/2018

Appendix A. (Continued) Plot attributes and midpoint coordinates

Plot	Coordinates (Decimal degrees)		Elevation (m)	Slope°	Dates sampled*
WK4	21.5028	-158.1596	784	15	11/5/2018
WK5	21.5020	-158.1632	787	37	11/6/2018
WK6	21.5018	-158.1631	748	40	11/6/2018
WK7	21.5013	-158.1622	755	30	11/6/2018
HL1	21.3166	-157.7429	474	10	1/29/2019
HL2	21.3134	-157.7435	455	37	1/29/2019
HL3	21.3124	-157.7446	468	24	2/5/2019
HL4	21.3032	-157.7450	369	33	2/5/2019
HL5	21.2997	-157.7456	379	20	2/5/2019
T1	21.3454	-157.8032	651	12.5	2/12/2019
T2	21.3451	-157.8051	577	25	2/12/2019

- **Sampling dates refer to Domin-Krajina cover abundance scale measurements**

Appendix B. Plot descriptions

Plot	notes
MFR1	20x20m square plot near bottom of Keālia trail, bounded on two sides by the trait. Steep slope. Dominated by *Leucaena* and *Sapindus.*
MFR2	20x20m square plot next to trail and pavilion at top of Keālia trail. Guinea grass dominated with *Erythrina* trees.
MFR3	20x20m plot below Keālia trail near top.
MFR4	20x20m square plot on slope above gulch adjacent to access road to Peacock flats.
MFR5	20x20m square plot, mid slope.
MFR6	20x20m square plot, mid slope. Mixed forest. *Diospyros* dominated.
MFR7	20x20m square plot, mid slope. Mixed closed canopy forest. Rocky substrate with large boulders.
KV4	20x20m square plot. Muddy with pools of water and evidence of pig activity.
KV8	20x20m square plot. Close to trail. Dominated by *Koa, Albizia, Pandanus* in canopy; *Ardisia elliptica* dominated in understory. ʻŌhiʻa nearby.
KV10	20x20m square plot. *Ardisia elliptica* dominated.
KV12	20x20m square plot on ridge.
KV18	40x10m rectangular ridge plot. Uluhe dominated.
KV21	40x10m rectangular plot along ridge. Fairly open canopy. Dominated by ʻŌhiʻa and *P. cattleyanum.*
KV23	20x20m square plot to the E of trail. Mostly open. ʻŌhiʻa and Uluhe dominated.
KV35	20x20m square plot. Mid slope below ridge trail.
KV37	20x20m square plot near to ridge. Plot has small drainage down center. Slope and aspect varied throughout but was found to be +/- 110 degreed aspect, 35 degree slope.
KV42	20x20m square plot on small slope below ridge and above gulch.
KV46	20x20m square plot near *Casuarina* stand.
KV50	20x20m square plot on flat area of ridge.
KV61	40x10m rectangular plot. Open, Uluhe dominated.
PNAR1	400m2 circular plot near trail. No post found. *P. cattleyanum* and *Schinus* dominated.
PNAR2	400m2 circular plot. Post found. Rocky substrate, steep drop-off below plot. *Diospyros* dominated.
PNAR6	400m2 circular plot. Post found.
PNAR7	400m2 circular plot. Post found.
PNAR9	400m2 circular plot.
PNAR10	400m2 circular plot. *P*. *cattleyanum* and *Schinus* dominated.
PNAR11	400m2 circular plot. Post found.
PNAR12	400m2 circular plot. Post found.
PNAR19	400m2 circular plot. Post found.
PNAR20	400m2 circular plot. Post found.
PNAR21	400m2 circular plot. No post found.
PNAR23	400m2 circular plot. Post found.
WR1	40x10m rectangular ridge trail. Undulating ground, but relatively flat. ʻŌhiʻa/Uluhe dominated.

Appendix B. (Continued) Plot descriptions

Plot	notes
WR2	40x10m rectangular plot on either side of ridge trail. Undulating slope. Mixed novel forest, dominated by *P. cattleyanum*
WR3	40x10m rectangular plot along either side of ridge trail (predominantly to E). Mixed novel mesic forest.
WR4	400m2 circular plot to E of ridge trail. Uluhe dominated.
WK1	400m2 circular plot to E of trail. Uluhe, ʻŌhiʻa, *Koa* dominated; very few non-natives.
WK2	400m2 circular plot. Trail to SE, fence to NW. *P. cattleyanum* dominated.
WK3	40x10m rectangular plot on ridge, along trail on either side. Native dominated.
WK4	40x10m rectangular plot on ridge, along trail and adjacent to fence. Native dominated overstory, non-native dominated understory.
WK5	400m2 circular plot below ridge, to the NE of trail leading down from the ridge. Open understory.
WK6	400m2 circular plot to the NE of trail. *P. cattleyanum* dominated. Small drainage to the NE edge of plot.
WK7	400m2 circular plot to the NE of trail. Plot center is in the middle of small drainage.
HL1	400m2 circular plot to E of trail, upper slope. Becomes mostly native past this point.
HL2	400m2 circular plot to E of trail. *Santalum* in center of plot.
HL3	400m2 circular plot to NW below trail. Dieback clearing with *P. cattleyanum* canopy and ferns in understory. Dropoff steep to NW edge of plot.
HL4	400m2 circular plot to SE of trail. Mixed scrub vegetation. Rocky substrate. Hill overlooks trail and descends down ridge. Slope variable in plot, 33 degrees to SE (aspect) from highest point in plot.
HL5	400m2 circular plot. Center point next to large boulder to NE side of trail; trail runs right through the middle of the plot, and plot runs up/downslope on either side. Rocky substrate with scrub vegetation and encroaching *Casuarina* trees.
T1	10x40m rectangular plot along ridge on Pauoa Flats trail. Undulating slope, midpoint in middle of dip.
T2	400m2 circular plot in hump-shaped area bounded along half of its circumference by adjacent Pauoa Flats trail. Uluhe dominated. Slope calculated from prevailing aspect direction.

Appendix C. Understory light availability measurements in the Pahole Natural Area Reserve and Kahana Valley plots

Plot	% Understory Light availability (µmol m^{-2} s^{-1})
KV4	7.3
KV8	21.6
KV10	0.9
KV12	7
KV18	90.1
KV21	88.2
KV23	81.1
KV35	3.1
KV37	0.01
KV42	48.6
KV46	56.6
KV50	53.3
KV61	57.9
PNAR1	10.3
PNAR2	2.6
PNAR6	4
PNAR7	5.5
PNAR9	15.8
PNAR10	11.3
PNAR11	5.9
PNAR12	3.1
PNAR19	1.6
PNAR20	1
PNAR21	4.1
PNAR23	11.7

Appendix D. Site specific per species absolute (m^2) cover change, in descending order of cover delta values. Blank spaces indicate that a species was not present at a given time/location

Species	PNAR prev	PNAR 2018	KV prev	KV 2018	Total prev	2018 total	Total Δ
Native							
Dicranopteris linearis			120.5	460.5	120.5	460.5	340
Microlepia strigosa	19.5	95			19.5	95	75.5
Pandanus tectorius			146	219	146	219	73
Metrosideros polymorpha	263.5	248.5	31.5	87.5	295	336	41
Planchonella sandwicensis	61	101.5			61	101.5	40.5
Alyxia stellata	41.5	73.5		1	41.5	74.5	33
Diospyros hillebrandii	35	52			35	52	17
Diospyros sandwicensis	4	46.5	29.5	1	33.5	47.5	14
Diploterygium pinnatum			0.5	8	0.5	8	7.5
Metrosideros tremuloides			1	8	1	8	7
Lepisorus thunbergianus	1.5	4.5		1.5	1.5	6	4.5
Dryopteris sandwicensis		3.5				3.5	3.5
Elaphoglossum aemulum		3				3	3
Melicope oahuensis		3				3	3
Carex meyenii	1	4			1	4	3
Hibiscus tiliaceus				3		3	3
Ilex anomola	1	3.5		0.5	1	4	3
Leptecophylla tameiameia	0.5	0.5	0.5	3	1	3.5	2.5
Asplenium kaulfussii	2	4			2	4	2
Asplenium contiguum		1.5				1.5	1.5
Cuscuta sandwicensis				1		1	1
Elaphoglossum alatum	0.5	1.5			0.5	1.5	1
Dryopteris fusco-atra	0.5	1			0.5	1	0.5
Dryopteris glabra		0.5				0.5	0.5
Hymenophyllum lanceolatum				0.5		0.5	0.5
Peperomia membranacea		0.5				0.5	0.5
Dianella sandwicensis	0.5	1			0.5	1	0.5
Huperzia sp.				0.5		0.5	0.5
Carex wahuensis	1	1			1	1	
Dodonaea viscosa	0.5	0.5			0.5	0.5	
Streblus pendulinus	0.5	0.5			0.5	0.5	
Peperomia tetraphylla	1.5	1			1.5	1	-0.5
Adenophorus tamariscinus var. tamariscinus	1			0.5	1	0.5	-0.5
Athyrium microphyllum	1	0.5			1	0.5	-0.5
Elaeocarpus bifidus	5.5	5			5.5	5	-0.5
Psydrax odorata	61.5	60.5			61.5	60.5	-1

Appendix D. (Continued) Site specific per species absolute (m^2) cover change, in descending order of cover delta values. Blank spaces indicate that a species was not present at a given time/location

Species	PNAR prev	PNAR 2018	KV prev	KV 2018	Total prev	2018 total	Total Δ
Asplenium macraei	2.5	1.5			2.5	1.5	-1
Diellia falcata	1.5	0.5			1.5	0.5	-1
Doodia kunthiana	9.5	8.5			9.5	8.5	-1
Pipturus albidus	1.5	0.5			1.5	0.5	-1
Trichomanes davalloides	1.5	0.5			1.5	0.5	-1
Kadua acuminata	2.5	1			2.5	1	-1.5
Myrsine lessertiana	3	1.5			3	1.5	-1.5
Asplenium nidus	4.5	2.5			4.5	2.5	-2
Melicope cornuta var. decurrens	2.5	0.5			2.5	0.5	-2
Viola chamissonia	2.5	0.5			2.5	0.5	-2
Chrysopogon aciculatus			3	0.5	3	0.5	-2.5
Cocculus orbiculatus	5.5	2.5			5.5	2.5	-3
Freycinetia arborea	5.5	29	29.5	3	35	32	-3
Pisonia brunoniana	8	4.5			8	4.5	-3.5
Nephrolepis exaltata	50.5	46.5			50.5	46.5	-4
Psychotria mariniana	22.5	18.5			22.5	18.5	-4
Xylosma hawaiiensis	11	6.5			11	6.5	-4.5
Bidens torta	6.5	1			6.5	1	-5.5
Antidesma platyphyllum	49	36			49	36	-13
Osteomeles anthyllidifolia			18	3	18	3	-15
Diplazium sandwicianum	21.5	6			21.5	6	-15.5
Acacia koa	0.5	3	83.5	63.5	84	66.5	-17.5
Nestegis sandwicensis	37	19.5			37	19.5	-17.5
Psychotria hathewayi	18.5	1			18.5	1	-17.5
Charpentiera obovata	22	1.5			22	1.5	-20.5
Kadua affinis	48	24			48	24	-24
Pittosporum glabrum	31	6			31	6	-25
Psilotum nudum	1	1.5	29.5	1	30.5	2.5	-28
Machaerina angustifolia			29.5	0.5	29.5	0.5	-29
Euphorbia multiformis	33.5	2			33.5	2	-31.5
Sphenomeris chinensis	6	6.5	106.5	73	112.5	79.5	-33
Hibiscus arnottianus	56	11.5		0.5	56	12	-44
Polyscias oahuensis	2.5	0.5	42		44.5	0.5	-44
Psychotria hexandra			59	1	59	1	-58
Ophioglossum pendulum subsp. Falcatum			59	0.5	59	0.5	-58.5
Cibotium chamissoi	75	14	147	113	222	127	-95
Coprosma foliosa	140.5	32			140.5	32	-108.5

Appendix D. (Continued) Site specific per species absolute (m^2) cover change, in descending order of cover delta values. Blank spaces indicate that a species was not present at a given time/location

Species	PNAR prev	PNAR 2018	KV prev	KV 2018	Total prev	2018 total	Total Δ
Scaevola gaudichaudiana	0.5	0.5	133.5	1	134	1.5	-132.5
Wikstroemia oahuensis	0.5	1.5	236.5	14.5	237	16	-221
Non-native							
Psidium cattleyanum	77.5	500.5	59	140.5	136.5	641	504.5
Ardisia elliptica				243.5		243.5	243.5
Phlebodium aureum		2.5		107.5		110	110
Falcataria molucanna				99		99	99
Schefflera actinophylla			80	177.5	80	177.5	97.5
Oplismenus hirtellus	45.5	129.5	36	12	81.5	141.5	60
Grevillea robusta	20	69		0.5	20	69.5	49.5
Aleurites molucannus	40.5	65.5	0.5	3	41	68.5	27.5
Andropogon virginicus			30	53	30	53	23
Causuarina equisetifolia				21		21	21
Rhyncospora caduca				21		21	21
Passiflora edulis	3	0.5		22	3	22.5	19.5
Mangifera indica				18		18	18
Passiflora laurifolia				11		11	11
Christella parasitica	6	9		7.5	6	16.5	10.5
Sacciolepis indica				10.5		10.5	10.5
Arundina graminifolia				6.5		6.5	6.5
Heterotis rotundifolia				3.5		3.5	3.5
Cenchrus ciliatus				3		3	3
Megathyrsus maximus		3				3	3
Melaleuca quinquinerva				3		3	3
Pterolepis glomerata				3		3	3
Adiantum hispidulum	0.5	2			0.5	2	1.5
Lindsaea ensifolia				1.5		1.5	1.5
Ardisia crenata				1		1	1
Polystachya concreta				1		1	1
Toona ciliata		1				1	1
Adenathera microsperma				0.5		0.5	0.5
Ageratina riparia	0.5	1			0.5	1	0.5
Ageratum adenophora	0.5	1			0.5	1	0.5
Fraxinus uhdei		0.5				0.5	0.5
Neurolaena lobata				0.5		0.5	0.5
Rivina humilis		0.5				0.5	0.5
Spathodea campanulata		0.5				0.5	0.5

Appendix D. (Continued) Site specific per species absolute (m^2) cover change, in descending order of cover delta values. Blank spaces indicate that a species was not present at a given time/location

Species	PNAR prev	PNAR 2018	KV prev	KV 2018	Total prev	2018 total	Total Δ
Stachytarpheta cayennensis				0.5		0.5	0.5
Triumfetta semitriloba		0.5				0.5	0.5
Buddleia asiatica	0.5	0.5			0.5	0.5	
Cyrtomium falcatum	0.5	0.5			0.5	0.5	
Zingiber zerumet			0.5	0.5	0.5	0.5	
Youngia japonica	2.5	1			2.5	1	-1.5
Oxalis corniculata	3.5	1.5			3.5	1.5	-2
Schinus terebinthifolius	280	336	59	0.5	339	336.5	-2.5
Melinis minutiflora	5.5	0.5			5.5	0.5	-5
Rubus rosifolius	5	11.5	29.5		34.5	11.5	-23
Chamaechrista nicitans			29.5	1.5	29.5	1.5	-28
Paspalum scrobiculatum			30.5	0.5	30.5	0.5	-30
Christella dentata	2.5	1	29.5		32	1	-31
Syzygium cumini	5.5	3	89.5	58	95	61	-34
Emilia sonchifolia	0.5		42	0.5	42.5	0.5	-42
Morinda citrifolia	3.5		42	0.5	45.5	0.5	-45
Blechnum appendiculatum	126	79		0.5	126	79.5	-46.5
Stachytarpheta australis	2		72.5	1	74.5	1	-73.5
Lantana camara	9.5	4.5	71.5	0.5	81	5	-76
Psidium guajava	30.5	10.5	59.5	3.5	90	14	-76
Nephrolepis brownii		3	147.5	59.5	147.5	62.5	-85
Cordyline fruticosa	3.5	1.5	91.5	7	95	8.5	-86.5
Passiflora suberosa		1.5	88.5	0.5	88.5	2	-86.5
Clidemia hirta		66	178	15	178	81	-97
Spathoglottis plicata	0.5		189.5	5	190	5	-185
Paspalum conjugatum	58.5	2.5	147.5	3.5	206	6	-200

Appendix E. Trait values of species found across all plots. Blank spaces indicate missing trait values, NAs represent trait values which were not physiologically relevant for a given species

Species	Growth form	seed mass (g)	max height (m)	SSD (g/cm3)	SLA (cm2/g)
Acacia confusa	tree	0.026	15	0.712908	79.11
Acacia koa	tree	0.061	43	0.7387	51.83967
Adenanthera microsperma	tree	0.0495	15	0.64	
Adenophorus tamariscinus var. tamariscinus	fern	NA	0.2	NA	53.595213
Adiantum hispidulum	fern	NA	0.52	NA	87.173414
Ageratina adenophora	herb	0.000074	1.5	0.3276308	155.5
Ageratina riparia	herb	0.00007	0.8	0.401	220.118
Ageratum conyzoides	herb	0.00014	1.5	0.199	276.356
Aleurites moluccanus	tree	2.857	15.24	0.368508	111.11
Alyxia stellata	vine	0.5291	NA	0.59	125.307
Andropogon virginicus	grass/sedge	0.000292	0.4318	NA	184.72727
Antidesma platyphyllum	tree	0.0841	15	0.4215773	176.03542
Ardisia crenata	shrub	0.0361	1.5	0.5112917	108.62261
Ardisia elliptica	tree	0.04	4	0.62	56.85
Arundina graminifolia	herb	NA	2.5	0.31	124.66
Asparagus densiflorus	herb	0.048	0.6	0.4108827	NA
Asplenium contiguum	fern	NA	0.8	NA	152.78252
Asplenium kaulfussii	fern	NA	0.85	NA	
Asplenium macraei	fern	NA	0.4	NA	
Asplenium nidus	fern	NA	2	NA	122.86671
Athyrium microphyllum	fern	NA	0.9	NA	
Bidens pilosa	herb	0.00036	1.8	0.4534326	170
Bidens torta	herb	0.0016	2.5	0.225957	214.36881
Bischofia javanica	tree	0.0106	18.7	0.59	98
Blechnum appendiculatum	fern	NA	0.6	NA	154.21556
Broussonetia papyrifera	shrub	0.0022	20	0.29	185.465
Buddleja asiatica	shrub/tree	0.00065	7	0.28	253.81
Caesalpinia bonduc	sprawling shrub	2.108	NA	0.3408521	192.56498
Carex meyenii	grass/sedge	0.0008	0.7	NA	105.571
Carex wahuensis	grass/sedge	0.00088	1	NA	123.24
Casuarina equisetifolia	tree	0.003	35	0.75768	NA
Cenchrus ciliarus	grass/sedge	0.0012	0.9144	NA	118.34
Centella asiatica	herb	0.001501	0.2	NA	186.99
Chamaecrista nictitans	herb	0.00443	2	0.325037	108.61986
Charpentiera obovata	tree	0.00085	6	0.48	
Christella dentata	fern	NA	1	NA	252.45576

Appendix E. (Continued) Trait values of species found across all plots. Blank spaces indicate missing trait values, NAs represent trait values which were not physiologically relevant for a given species

Species	Growth form	seed mass (g)	max height (m)	SSD (g/cm3)	SLA (cm2/g)
Christella parasitica	fern	NA	0.9	NA	221.48217
Chrysopogon aciculatus	grass/sedge	0.00012	0.25	NA	167.33641
Cibotium chamissoi	fern	NA	7.0104	NA	182.8
Cinnamomum burmannii	tree	0.02936	20	0.43	89.05
Citharexylum spinosum	tree	0.13563	11.8872	0.7	99.028153
Clidemia hirta	shrub	0.00003	3	0.5943214	246.333
Coccinia grandis	vine	0.01246	NA	0.1238358	412.46472
Cocculus orbiculatus	vine	0.06597	NA	0.4954155	202.54334
Coffea arabica	tree	0.1323	4	0.6000554	178.77449
Colubrina oppositifolia	tree	0.038	13	0.7	NA
Coprosma foliosa	shrub	0.03258	8	0.5884041	153.89327
Cordyline fruticosa	shrub	0.00815	3.048	0.3266947	165.1586
Crotalaria pallida	herb	0.00969	2	0.3626614	95.333717
Cuphea carthagenensis	herb	0.0007	0.05		
Cuscuta sandwicensis	vine	0.0009733	NA	0.752	NA
Cyperus hypochlorus	grass/sedge	0.0003	1.3	NA	105.152
Cyperus meyenianus	grass/sedge	0.002	0.5	NA	205.2387
Cyperus sp.	grass/sedge	0.0002	0.97	NA	103.367
Cyrtomium falcatum	fern	NA	0.6	NA	
Deparia petersenii	fern	NA	0.6	NA	278.10276
Desmodium incanum	herb	0.0074	3.048	1.067	270.43942
Dianella sandwicensis	herb	0.0093	2	NA	63.301392
Dicranopteris linearis	fern	NA	NA	NA	112
Diellia falcata	fern	NA	0.95	NA	NA
Diospyros hillebrandii	tree	0.2032	10	0.626	89.66
Diospyros sandwicensis	tree	0.19	15	0.713	16.398
Diplazium sandwicianum	fern	NA	1.5	NA	227
Diplopterygium pinnatum	fern	NA	NA	NA	62.951381
Dodonaea viscosa	shrub	0.0059	5	0.84	93.197
Doodia kunthiana	fern	NA	0.65	NA	130.61436
Dracaena halaapepe	tree	0.30004	10	0.3548027	64.419528
Dryopteris fusco-atra	fern	NA	0.8	NA	
Dryopteris glabra	fern	NA	1	NA	
Dryopteris sandwicensis	fern	NA	1.25	NA	
Elaeocarpus bifidus	tree	0.95	10	0.48	101.94
Elaphoglossum aemulum	fern	NA	0.45	NA	61.539143
Elaphoglossum alatum	fern	NA	0.6	NA	95
Emilia sonchifolia	herb	0.0001571	1	0.2351619	238.139

Appendix E. (Continued) Trait values of species found across all plots. Blank spaces indicate missing trait values, NAs represent trait values which were not physiologically relevant for a given species

Species	Growth form	seed mass (g)	max height (m)	SSD (g/cm3)	SLA (cm2/g)
Epidendrum x obrieniatum	herb	NA	1.3	NA	76.302648
Erigeron bonariensis	herb	0.000002	1.5	0.3077823	187.94499
Erythrina sandwicensis	tree	0.54304	9.144	0.19	148.528
Euphorbia multiformis	shrub	0.00096	3	0.4729664	145.94565
Falcataria moluccana	tree	0.022	40	0.28413	108.6
Ficus microcarpa	tree	0.00034	20	0.52	67.3
Fraxinus uhdei	tree	0.02749	28	0.52	66.38
Freycinetia arborea	climber	NA	NA	0.2303147	74.532518
Gahnia beecheyi	grass/sedge	0.0058	1.2	NA	60.355689
Grevillea robusta	tree	0.00649	30.48	0.538	98
Heterotis rotundifolia	herb	0.00032	0.2	0.63	165.59
Hibiscus arnottianus	tree	0.0159272	10	0.4262	231.37
Hibiscus tiliaceus	tree	0.0156	5	0.43	100.736
Hymenophyllum lanceolatum	fern	NA	0.16	NA	102.38821
Hyptis pectinata	herb	0.00006	2.5		
Ilex anomola	tree	0.00832	12	0.48	143.50702
Kadua acuminata	shrub	8.1667E-05	4		152.91
Kadua affinis	shrub	0.016	5	0.4185777	132.3933
Korthalsella taenioides f. taenio ides	Parasitic epiphyte	0.00068	NA	0.4207642	NA
Lantana camara	shrub	0.009	4	0.6936	190.198
Lepisorus thunbergianus	fern	NA	0.35	NA	103.70773
Leptecophylla tameiameia	shrub	0.00534	5	0.74	155.84335
Leucaena leucocephala	tree	0.0339	10.0584	0.7	133.73
Lindsaea ensifolia	fern	NA	0.17	NA	100.63014
Lycopodium venustulum	fern ally	NA	NA		NA
Macadamia integrifolia	tree	4.27665	18	0.58	84.407117
Machaerina angustifolia	grass/sedge	0.0002	1.3	NA	82.236923
Machaerina mariscoides	grass/sedge	0.0022	0.9	NA	63.006116
Mangifera indica	tree	4.5	30	0.543291	83.133
Megathyrsus maximus	grass/sedge	0.000759	3	NA	128.38482
Melaleuca quinquenervia	tree	0.0003125	30	0.6145734	78.792622
Melicope cornuta var. decurrens	shrub	0.01	7	0.4546	71.429
Melicope oahuensis	shrub	0.01	7	0.5523573	78.909411
Melinis minutiflora	grass/sedge	0.00011	1	NA	256
Metrosideros polymorpha	tree	0.000012	30	0.7614	63.095734
Metrosideros tremuloides	tree	3.5922E-05	30	0.72	111.23

Appendix E. (Continued) Trait values of species found across all plots. Blank spaces indicate missing trait values, NAs represent trait values which were not physiologically relevant for a given species

Species	Growth form	seed mass (g)	max height (m)	SSD (g/cm3)	SLA (cm2/g)
Microlepia strigosa	fern	NA	1	NA	205.6585
Mirabilis jalapa	herb	0.0571	1.5	0.0904803	308.58421
Morinda citrifolia	tree	0.015	6.096	0.56	166.67
Myrsine lessertiana	tree	0.067	8	0.53	64.565423
Nephrolepis brownii	fern	NA	1	NA	124.59061
Nephrolepis exaltata	fern	NA	1	NA	97.578676
Nestegis sandwicensis	tree	0.511	25	0.6924844	122.38151
Neurolaena lobata	shrub	0.001	4	0.329	260.74
Odontosoria chinensis	fern	NA	0.8	NA	123.31003
Ophioglossum pendulum subsp. *Falcatum*	fern	NA	0.4	NA	170.37
Oplismenus hirtellus	grass/sedge	0.00128	0.25	NA	203.4
Osteomeles anthyllidifolia	sprawling shrub	0.13321	3.6576	0.659	65.485
Oxalis corniculata var. debilis	herb	0.00001	0.2	1.3189286	524.95504
Pandanus tectorius	tree	0.61	10	0.3309	40
Paspalum conjugatum	grass/sedge	0.00055	0.6	NA	194.6425
Paspalum scrobiculatum	grass/sedge	0.0019	1.2	NA	168.2869
Paspalum urvillei	grass/sedge	0.0004	2.5	NA	166.60485
Passiflora edulis	vine	0.01546	NA	0.2636113	255.29084
Passiflora suberosa	vine	0.003	NA	0.935	244.534
Peperomia membranacea	herb	0.000055	0.8	0.1153269	275.74353
Peperomia tetraphylla	succulent	0.0001111	0.4	0.069	261.74303
Phlebodium aureum	fern	NA	1	NA	111.73
Phlegmarius phyllanthus	fern ally	NA	0.35	0.2823273	NA
Phymatosorus grossus	fern	NA	0.75	NA	96.825759
Pipturus albidus	tree	0.00002	6	0.3	78.082299
Pisonia brunoniana	tree	0.3767	6	0.3014	70.9
Pittosporum glabrum	tree	0.03125	8	0.57	
Pityrogramma calomelanos var. austroamericana	fern	NA	0.9	NA	52.25884
Planchonella sandwicensis	tree	1.606	24.384	0.5145418	113.76585
Polyscias oahuensis	tree		10	0.41	
Polyscias sandwicensis	tree	0.00301	30	0.41	221.20985
Polystachya concreta	herb	5.64E-07	0.04	NA	
Psidium cattleyanum	tree	0.0923	8	1.12	79.153
Psidium guajava	tree	0.01262	7.62	0.67	106.764
Psilotum complanatum	fern ally	NA	0.65	0.3512774	NA

Appendix E. (Continued) Trait values of species found across all plots. Blank spaces indicate missing trait values, NAs represent trait values which were not physiologically relevant for a given species

Species	Growth form	seed mass (g)	max height (m)	SSD (g/cm3)	SLA (cm2/g)
Psilotum nudum	fern ally	NA	0.6	0.2865777	NA
Psychotria hathewayi	shrub	0.0313	8	0.5245205	110.6563
Psychotria hexandra	tree	0.00977	6	0.52	
Psychotria kaduana	tree	0.05328	8	0.5509481	101.03399
Psychotria mariniana	tree	0.0975	20	0.4399203	80.906248
Psydrax odorata	tree	0.0551	15	0.86961	54.328334
Pteridium aquilinum var. decompositum	fern	NA	2	NA	167.0856
Pterolepis glomerata	herb	0.00004	0.5	0.0568556	653.37726
Rhyncospora caduca	grass/sedge	0.0004489	1.2	NA	189.73
Rivina humilis	shrub	0.0038	1.2	0.386	441.958
Rubus argutus	shrub	0.002779	3	0.479	187.4
Rubus rosifolius	shrub	0.0006	1	0.1830482	164.32828
Sacciolepis indica	grass/sedge	0.00032	0.5	NA	81.35
Santalum freycinetianum	tree	0.02777	13	0.7594	82.3
Sapindus oahuensis	tree	0.803	15	0.566	105.71511
Scaevola gaudichaudiana	shrub	0.01569	3	0.333	130.15508
scaevola mollis	shrub	0.024	2.5	0.500	106.04
Schefflera actinophylla	tree	0.006719	15	0.41328	48.72
Schinus terebinthifolius	tree	0.0181	13	0.411	78.431
Setaria palmifolia	grass/sedge	0.0006	2	NA	230.68434
Setaria parviflora	grass/sedge	0.00044	1.2	NA	343.41332
Sida fallax	herb	0.002233	3	0.483	168.336
Smilax melastomifolia	vine	0.0536432	NA	0.3887888	136.97538
Spathodea campanulata	tree	0.00515	25	0.31	354.8
Spathoglottis plicata	herb	NA	1.5	NA	154.18049
Stachytarpheta cayennensis	herb	0.00099	2	0.3509181	202.47173
Streblus pendulinus	tree	0.015175	8	0.7114	
Syzygium cumini	tree	0.1132	18.288	0.65436	70.035014
Toona ciliata	tree	0.00567	30	0.43	128.0407
Trichomanes cyrtotheca	fern	NA	0.37	NA	168.25273
Trichomanes davalloides	fern	NA	0.45	NA	
Triumfetta semitriloba	shrub	0.0383	2		
Viola chamissoniana	shrub	0.00174	0.9	NA	NA
Waltheria indica	herb	0.00169	1.3	0.4951833	132.77551
Wikstroemia oahuensis	shrub	0.0238363	6	0.441	94.45
Xylosma hawaiiensis	tree	0.045073	9	0.593	90.5
Youngia japonica	herb	0.0001037	0.9	NA	367.55065

Appendix E. (Continued) Trait values of species found across all plots. Blank spaces indicate missing trait values, NAs represent trait values which were not physiologically relevant for a given species

Species	Growth form	seed mass (g)	max height (m)	SSD (g/cm3)	SLA (cm2/g)
Zingiber zerumet	herb		2	NA	353.00282

Appendix F. Literature and database sources for trait data

Species	Notes
Acacia confusa	SSD = TRY; Hmax = Wagner (1999); SLA = Penuelas et al (2010)
Acacia koa	SDM and Hmax = TRY; SSD = Asner and Goldstein (1997)
Adenanthera microsperma	SDM and SSD = TRY; Hmax = Orwa et al (2009)
Adenophorus tamariscinus var. tamariscinus	Hmax = Palmer (2003)
Adiantum hispidulum	Hmax = Palmer (2003)
Ageratina adenophora	SDM = TRY; SLA = Feng (2008); Hmax = Wagner (1999)
Ageratina riparia	SDM = Murray and Philips (2010); height = DB
Ageratum conyzoides	seed = DB; height = Wagner
Aleurites moluccanus	seed, height, WD = DB; SLA = Ostertag et. Al (2016) SERDP Project
Alyxia stellata	seed = Bakutis thesis (2005); height =
Andropogon virginicus	all DB
Antidesma platyphyllum	seed = Bakutis thesis (2005); height = Wagner
Ardisia crenata	height = Wagner
Ardisia elliptica	SLA = DB; height = Wagner; seed = Munoz and Ackerman (2011); WD = FIA
Arundina graminifolia	height = Wagner
Asparagus densiflorus	height = Gilman (1999)
Asplenium contiguum	height = Palmer
Asplenium kaulfussii	height = Palmer
Asplenium macraei	height = Palmer
Asplenium nidus	height = Palmer
Athyrium microphyllum	height = Palmer
Bidens pilosa	height = wagner; SLA = Vaieretti et al (2005)
Bidens torta	seed = Bakutis thesis (2005); height = wagner
Bischofia javanica	
Blechnum appendiculatum	height = palmer
Broussonetia papyrifera	all DB
Buddleja asiatica	height and WD = DB; seed = Bakutis (2005); SLA = Penuelas et al (2010)
Caesalpinia bonduc	seed = DB
Carex meyenii	height = wagner
Carex wahuensis	height = wagner; SLA = Chau et al (2013)
Casuarina equisetifolia	height and WD = DB
Cenchrus ciliarus	seed and height = DB; SLA = Chandra and Dubey (2009)
Centella asiatica	seed and height = DB; SLA = Devkota and Jha (2009)
Chamaecrista nictitans	height = Wagner; 10 seeds measured at Bishop
Charpentiera obovata	seed = Bakutis (2005); height = wagner; WD = FIA

Appendix F. (Continued) Literature and database sources for trait data

Species	Notes
Christella dentata	height = Palmer
Christella parasitica	height = Palmer
Chrysopogon aciculatus	height = Wagner
Cibotium chamissoi	height and SLA = DB
Cinnamomum burmannii	WD = brown 1997; height = Wuu-Kuang (2011); SLA = Penuelas et al (2010); 10 seeds measured at Bishop
Citharexylum spinosum	seed, height, and WD = DB
Clidemia hirta	seed and SLA = DB; height = Wagner
Coccinia grandis	seed = DB
Cocculus orbiculatus	seed and height = DB
Coffea arabica	seed and height = DB
Colubrina oppositifolia	WD = FIA; height = Wagner; 11 seeds weighed at Bishop
Coprosma foliosa	height = Wagner; 10 seeds weighed at Bishop
Cordyline fruticosa	seed and height = DB
Crotalaria pallida	seed = DB; height = Wagner
Cuphea carthagenensis	seed = DB; height = Wagner
Cuscuta sandwicensis	15 seeds weighed at Bishop
Cyperus hypochlorus	height = Wagner; 10 seeds measured at Bishop
Cyperus meyenianus	height = Wagner
Cyperus sp.	
Cyrtomium falcatum	height = Palmer
Deparia petersenii	height = Palmer
Desmodium incanum	seed and height = DB
Dianella sandwicensis	height = Wagner; 10 seeds measured at Bishop
Dicranopteris linearis	growth indeterminate; SLA = Allison and Vitousek (2004)
Diellia falcata	Critically endangered; height = Palmer
Diospyros hillebrandii	height = Wagner; 11 seeds measured at Bishop
Diospyros sandwicensis	height = Wagner; seed = Ostertag et. Al (2016) SERDP Project
Diplazium sandwicianum	height = Palmer; SLA = Allison and Vitousek (2004)
Diplopterygium pinnatum	growth indeterminate
Dodonaea viscosa	height, WD, and SLA = DB
Doodia kunthiana	height = Palmer
Dracaena halaapepe	height = Wagner; 10 seeds measured at Bishop
Dryopteris fusco-atra	height = Palmer
Dryopteris glabra	height = Palmer
Dryopteris sandwicensis	height = Palmer

Appendix F. (Continued) Literature and database sources for trait data

Species	Notes
Elaeocarpus bifidus	WD = FIA; height = Wagner; SLA = Penuelas et al (2010)
Elaphoglossum aemulum	height = Palmer
Elaphoglossum alatum	height = palmer; SLA = Allison and Vitousek (2004)
Emilia sonchifolia	height = Wagner; 28 seeds weighed at Bishop
Epidendrum x obrieniatum	height = Wagner
Erigeron bonariensis	height = Wagner; 50 seeds weighed at Bishop
Erythrina sandwicensis	seed and height = DB
Euphorbia multiformis	height = Wagner; 15 seeds weighed at Bishop
Falcataria moluccana	seed and WD = DB; height = Wagner; SLA = Asner et al (2008)
Ficus microcarpa	seed = DB; WD = FIA; height = Little and Skolmen (1989); SLA = avg. of two values given in Asner et al (2008)
Fraxinus uhdei	seed = DB; WD = FIA; height = Wagner; SLA = avg. of two values given in Asner et al (2008)
Freycinetia arborea	seeds too small to extract from fruit
Gahnia beecheyi	height = Wagner
Grevillea robusta	all = DB
Heterotis rotundifolia	seed = DB; height = Wagner
Hibiscus arnottianus	WD = FIA; height = Wagner; SLA = Chau et al (2012); 11 seeds weighed at Bishop
Hibiscus tiliaceus	all = DB
Hymenophyllum lanceolatum	height = Palmer
Hyptis pectinata	seed = DB; height = Wagner
Ilex anomola	WD = FIA; height = Wagner; Seed and SLA = Medeiros et al (2018) from DRYAD
Kadua acuminata	height = Wagner; SLA = Penuelas et al (2010); 60 seeds weighed at Bishop
Kadua affinis	height = wagner
Korthalsella taenioides f. taenioides	parasitic leafless epiphyte
Lantana camara	all = DB
Lepisorus thunbergianus	height = Palmer
Leptecophylla tameiameia	height = Wagner; SLA = Medeiros et al (2018) from DRYAD; 10 seeds measured at Bishop
Leucaena leucocephala	all = DB
Lindsaea ensifolia	height = palmer
Lycopodium venustulum	Horizontal stems
Macadamia integrifolia	WD = FIA; height = Orwa et al (2009); 12 seeds weighed at Bishop
Machaerina angustifolia	height = wagner; seed = Loh and Daehler (2007)

Appendix F. (Continued) Literature and database sources for trait data

Species	Notes
Mangifera indica	all = DB
Megathyrsus maximus	seed = DB; height = Wagner
Melaleuca quinquenervia	seed, height = DB
Melicope cornuta var. decurrens	endangered; WD = FIA (spp.); height = wagner; seed and SLA (spp.) = Ostertag et. Al (2016) SERDP Project
Melicope oahuensis	height = wagner; seed (spp.) = Ostertag et. Al (2016) SERDP Project
Melinis minutiflora	seed = DB; height = Wagner; SLA = Baruch and Goldstein (1999)
Metrosideros polymorpha	SLA and height = DB; WD = Asner and Goldstein 1997; seed = Bakutis (2005)
Metrosideros tremuloides	WD = FIA; height = Rock (1913) for genus only; SLA = Penuelas et al (2010); 103 seeds weighed at Bishop
Microlepia strigosa	height = Palmer
Mirabilis jalapa	seed and height = DB
Morinda citrifolia	seed, height, and WD = DB; SLA = Ostertag et. Al (2016) SERDP Project
Myrsine lessertiana	SLA = DB; WD = FIA; height = wagner
Nephrolepis brownii	height = Palmer
Nephrolepis exaltata	height = Palmer
Nestegis sandwicensis	height = Wagner; 10 seeds weighed at Bishop
Neurolaena lobata	formerly *Pluchea symphytifolia*; seed = DB; height = wagner
Odontosoria chinensis	formerly *sphenomeris;* height = palmer
Ophioglossum pendulum subsp. *Falcatum*	height = palmer
Oplismenus hirtellus	all = DB
Osteomeles anthyllidifolia	seed and height = DB
Oxalis corniculata var. debilis	height = DB; 10 seeds weighed at Bishop
Pandanus tectorius	WD = FIA; height = wagner; seed and SLA = Ostertag et. Al (2016) SERDP Project
Paspalum conjugatum	seed = DB; height = Wagner
Paspalum scrobiculatum	seed = DB; height = wagner
Paspalum urvillei	height = wagner
Passiflora edulis	seed = DB
Passiflora suberosa	
Peperomia membranacea	height = wagner; 60 seeds weighed at Bishop
Peperomia tetraphylla	height = wagner; SLA = Feng and Fu (2008); 27 seeds weighed at Bishop
Phlebodium aureum	height = palmer; SLA = Xiong et al (2018)
Phlegmarius phyllanthus	height = palmer

Appendix F. (Continued) Literature and database sources for trait data

Species	Notes
Pipturus albidus	seed = Bakutis (2005); WD = FIA; height = wagner; SLA = Medeiros et al (2018) from DRYAD
Pisonia brunoniana	seed = Bakutis (2005); WD = FIA; height = wagner; SLA = Asner et al (2008)
Pittosporum glabrum	WD = FIA; height = wagner
Pityrogramma calomelanos var. austroamericana	height = Palmer
Planchonella sandwicensis	seed and height = DB
Polyscias oahuensis	WD = FIA (spp.); height = wagner; Seeds not separable from fruit in pressed specimens
Polyscias sandwicensis	WD = FIA; height = wagner; 10 seeds sampled at Bishop
Polystachya concreta	height = JSTOR global plants; seed = Lallana et al (2019)
Psidium cattleyanum	height and WD = DB; seed = Bakutis (2005)
Psidium guajava	all = DB
Psilotum complanatum	height = palmer
Psilotum nudum	height = palmer
Psychotria hathewayi	height = wagner; 10 seeds weighed at Bishop
Psychotria hexandra	WD = FIA; height = wagner; 10 seeds sampled at Bishop
Psychotria kaduana	height = wagner; 10 seeds weighed at Bishop
Psychotria mariniana	seed = Bakutis (2005); height = wagner
Psydrax odorata	WD = DB; seed = Bakutis (2005)
Pteridium aquilinum var. decompositum	all = DB
Pterolepis glomerata	seed = DB; height = Wagner
Rhyncospora caduca	height = wagner; 19 seeds weighed at Bishop
Rivina humilis	
Rubus argutus	height = wagner; SLA = Baruch and Goldstein (1999); 30 seeds weighed at Bishop
Rubus rosifolius	seed, height, and SLA = DB
Sacciolepis indica	height = wagner; 20 seeds weighed at Bishop
Santalum freycinetianum	WD = FIA; height = wagner; SLA = Penuelas et al (2010); 10 seeds weighed at Bishop
Sapindus oahuensis	height = wagner
Scaevola gaudichaudiana	height = Wagner; 10 seeds measured at Bishop
Scaevola mollis	WD = FIA (spp.); height = wagner; SLA = McKown et al (2016)
Schefflera actinophylla	seed and WD = DB; height = Wagner; SLA = Asner et al (2008)
Schinus terebinthifolius	all = DB
Setaria palmifolia	height = wagner

Appendix F. (Continued) Literature and database sources for trait data

Species	Notes
Sida fallax	WD = FIA; height = wagner; Seed and SLA = Medeiros et al (2019) from DRYAD
Smilax melastomifolia	10 seeds weighed at Bishop
Spathodea campanulata	seed and WD = DB; SLA = Ostertag et al (2008)
Spathoglottis plicata	height = wagner
Stachytarpheta cayennensis	height - wagner; Barreto et. Al. (2016)
Streblus pendulinus	seed = DB; WD = FIA; height = wagner
Syzygium cumini	seed, height, and WD = DB
Toona ciliata	seed, WD, and SLA = DB; height = wagner
Trichomanes cyrtotheca	height = palmer
Trichomanes davalloides	height = palmer
Triumfetta semitriloba	height = Wagner; 10 seeds measured at Bishop
Viola chamissoniana	height = FWS report; Critically endangered; 10 seeds collected at Bishop
Waltheria indica	
Wikstroemia oahuensis	height = Wagner; 11 seeds measured at Bishop
Xylosma hawaiiensis	WD = FIA; height = wagner; SLA = average of plots from Austin and Vitousek (1998); 15 seeds measured at Bishop
Youngia japonica	height = wagner; 27 seeds measured at Bishop
Zingiber zerumet	height = wagner; unable to obtain any seeds at Bishop or in field

Appendix G. Non-native biogeographical realms of origin

Species	Area of origin	Notes
Acacia confusa	Indo-malay	
Adenanthera microsperma	Indo-malay	Source = CABI
Adiantum hispidulum	Australasia	Widespread, but center of diversity thought to be Australia (Source = CABI)
Ageratina adenophora	Neotropic	
Ageratina riparia	Neotropic	
Ageratum conyzoides	Neotropic	
Aleurites moluccanus	Indo-malay	
Andropogon virginicus	Nearctic	
Ardisia crenata	Indo-malay	
Ardisia elliptica	Indo-malay	
Arundina graminifolia	Indo-malay	Source = Missouri Botanical Garden
Asparagus densiflorus	Afrotropic	
Bidens pilosa	Neotropic	
Bischofia javanica	Indo-malay	
Blechnum appendiculatum	Neotropic	
Broussonetia papyrifera	Palearctic	
Buddleja asiatica	Indo-malay	
Casuarina equisetifolia	Australasia	
Cenchrus ciliarus	Widespread	
Centella asiatica	Palearctic	
Chamaecrista nictitans	Neotropic	
Christella dentata	Widespread	
Christella parasitica	Widespread	
Cinnamomum burmannii	Indo-malay	
Citharexylum spinosum	Neotropic	Source = IFAS
Clidemia hirta	Neotropic	
Coccinia grandis	Afrotropic	
Coffea arabica	Afrotropic	
Cordyline fruticosa	Australasia	
Crotalaria pallida	Afrotropic	
Cuphea carthagenensis	Neotropic	
Cyperus meyenianus	Neotropic	
Cyrtomium falcatum	Palearctic	Source = CABI
Deparia petersenii	Widespread	
Desmodium incanum	Neotropic	Source = CABI
Emilia sonchifolia	Neotropic	Source = CABI
Erigeron bonariensis	Neotropic	
Falcataria moluccana	Indo-malay	
Ficus microcarpa	Widespread	

Appendix G. (Continued) Non-native biogeographical realms of origin

Species	Area of origin	Notes
Fraxinus uhdei	Neotropic	
Grevillea robusta	Australasia	
Heterotis rotundifolia	Afrotropic	
Hyptis pectinata	Neotropic	
Lantana camara	Neotropic	
Leucaena leucocephala	Neotropic	
Lindsaea ensifolia	Widespread	
Macadamia integrifolia	Australasia	Source = Missouri Botanical Garden
Mangifera indica	Indo-malay	Source = CABI
Megathyrsus maximus	Afrotropic	
Melaleuca quinquenervia	Australasia	
Melinis minutiflora	Afrotropic	
Mirabilis jalapa	Neotropic	
Morinda citrifolia	Widespread	
Nephrolepis brownii	Indo-malay	
Neurolaena lobata	Neotropic	
Oplismenus hirtellus	Widespread	
Oxalis corniculata var. debilis	Widespread	
Paspalum conjugatum	Neotropic	
Paspalum scrobiculatum	Widespread	
Paspalum urvillei	Neotropic	Source = CABI
Passiflora edulis	Neotropic	
Passiflora suberosa	Neotropic	
Phlebodium aureum	Neotropic	
Phymatosorus grossus	Widespread	
Pityrogramma calomelanos var. austroamericana	Neotropic	
Psidium cattleyanum	Neotropic	
Psidium guajava	Neotropic	
Pterolepis glomerata	Neotropic	
Rhyncospora caduca	Nearctic	
Rivina humilis	Widespread	
Rubus argutus	Nearctic	
Rubus rosifolius	Widespread	
Sacciolepis indica	Widespread	
Schefflera actinophylla	Australasia	
Schinus terebinthifolius	Neotropic	
Setaria palmifolia	Indo-malay	

Appendix G. (Continued) Non-native biogeographical realms of origin

Species	Area of origin	Notes
Spathodea campanulata	Afrotropic	
Spathoglottis plicata	Widespread	
Stachytarpheta cayennensis	Neotropic	Source = CABI
Syzygium cumini	Indo-malay	
Toona ciliata	Widespread	
Triumfetta semitriloba	Neotropic	
Youngia japonica	Indo-malay	
Zingiber zerumet	Indo-malay	

References

Adsersen, H. (1989). The rare plants of the Galápagos Islands and their conservation. *Biological Conservation*, *47*(1), 49–77.

Aplet, G. H., & Vitousek, P. M. (1994). An Age—Altitude Matrix Analysis of Hawaiian Rain-Forest Succession An age altitude matrix analysis of Hawaiian rain-forest succession. *Source Journal of Ecology*, *82*(1), 137–147.

Asner, G., Elmore, A., Flinthughes, R., Warner, A., & Vitousek, P. (2005). Ecosystem structure along bioclimatic gradients in Hawai'i from imaging spectroscopy. *Remote Sensing of Environment*, *96*(3–4), 497–508.

Athens, J. S. (2009). Rattus exulans and the catastrophic disappearance of Hawai'i's native lowland forest. *Biological Invasions*, *11*(7), 1489.

Azur, M. J., Stuart, E. A., Frangakis, C., & Leaf, P. J. (2011). Multiple imputation by chained equations: What is it and how does it work? *International Journal of Methods in Psychiatric Research*, *20*(1), 40–49.

Baber, D. W., & Coblentz, B. E. (1986). Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. *Journal of Mammalogy*, *67*(3), 512–525.

Benson, D. A., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., & Sayers, E. W. (2009). GenBank. *Nucleic Acids Research*, *37*(Database issue), D26-31.

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, *9*(7), 887–895.

Buckley, Y. M., & Catford, J. (2016). Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *Journal of Ecology*, *104*(1), 4–17.

Cabin, R. J., Weller, S. G., Lorence, D. H., Flynn, T. W., Sakai, A. K., Sandquist, D., & Hadway, L. J. (2000). Effects Alien of Ungulate on Exclusion and Recent Species of Control the Preservation Tropical Dry Restoration a Hawaiian. *Conservation Biology*, *14*(2), 439–453.

Carboni, M., Calderon-Sanou, I., Pollock, L., Violle, C., Thuiller, W., & Thuiller, W. (2018). Functional traits modulate the response of alien plants along abiotic and biotic gradients. *Global Ecology and Biogeography*, *27*(10), 1173–1185.

Carlquist, S. (1965). *Island Life: A Natural History of the Islands of the World*. Natural History Press.

Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., Rejmánek, M., Bellingham, P. J., Pergl, J., Horvitz, C. C., & Hulme, P. E. (2012). The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*(3), 231–241.

Cavender-Bares, J., Ackerly, D. D., Hobbie, S. E., & Townsend, P. A. (2016). Evolutionary legacy effects on ecosystems: Biogeographic origins, plant traits, and implications for management in the era of global change. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 433–462.

Chardon, N. I., Rixen, C., Wipf, S., & Doak, D. F. (2019). Human trampling disturbance exerts different ecological effects at contrasting elevational range limits. *Journal of Applied Ecology*, *56*(6), 1389–1399.

Chimera, C. G., & Drake, D. R. (2010). Patterns of seed dispersal and dispersal failure in a hawaiian dry forest having only introduced birds. *Biotropica*, *42*(4), 493–502.

Chimera, C. G., & Drake, D. R. (2011). Could poor seed dispersal contribute to predation by introduced rodents in a Hawaiian dry forest? *Biological Invasions*, *13*(4), 1029–1042.

Chynoweth, M., Lepczyk, C. A., Litton, C. M., & Cordell, S. (2010). Feral Goats in the Hawaiian Islands: Understanding the Behavioral Ecology of Nonnative Ungulates with GPS and Remote Sensing Technology. *24th Vertebrate Pest Conference*, 41–45.

Cole, R. J., & Litton, C. M. (2014). Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. *Biological Invasions*, *16*(1), 125–140.

Condit, R. (1995). Research in large, long-term tropical forest plots. *Trends in Ecology & Evolution*, *10*(1), 18–22.

Coulter, J. (1931). *Population and Utilization of Land and Sea in Hawaii, 1853* (Vol. 88, p. 33). Bernice P. Bishop Museum.

Cuddihy, L. W., & Stone, C. P. (1990). Alteration of native Hawaiian vegetation. *University of Hawaii Cooperative National Park Study Unit*.

Daehler, C. C. (2003). Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 183–211.

Daehler, C. C., Denslow, J. S., Ansari, S., & Kuo, H. C. (2004). A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology*, *18*(2), 360–368.

Deb, S. K., & El-Kadi, A. I. (2009). Susceptibility assessment of shallow landslides on Oahu, Hawaii, under extreme-rainfall events. *Geomorphology*, *108*(3–4), 219–233.

Degener, O. (1930). *Illustrated guide to the more common or noteworthy ferns and flowering plants of Hawaii National Park: With descriptions of ancient Hawaiian customs and an introduction to the geologic history of the islands*.

Denslow, J. S., Uowolo, A. L., & Flint Hughes, R. (2006). Limitations to seedling establishment in a mesic Hawaiian forest. *Oecologia*, *148*(1), 118–128.

DeWalt, S. J., Denslow, J. S., & Ickes, K. (2004). Natural-Enemy Release Facilitates Habitat Expansion of the Invasive Tropical Shrub Clidemia Hirta. *Ecology*, *85*(2), 471–483.

Dieter Mueller-Dombois, & Dieter Ellenberg. (1974). *Aims Methods of Vegetation Ecology*.

Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N. J., Lososová, Z., Pyšek, P., Richardson, D. M., & Molofsky, J. (2018). Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nature Communications*, *9*(1), 4631–4631.

Drake, D. R. (1998). Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science*, *9*(1), 103–112.

Egler, F. E. (1942). Indigene Versus Alien in the Development of Arid Hawaiian Vegetation. *Ecology*, *23*(1), 14–23.

Ellenberg, D., & Mueller-Dombois, D. (1974). *Aims and methods of vegetation ecology*. Wiley New York.

Ellsworth, L. M., Litton, C. M., Taylor, A. D., & Kauffman, J. B. (2013). Spatial and temporal variability of guinea grass (Megathyrsus maximus) fuel loads and moisture on Oahu, Hawaii. *International Journal of Wildland Fire*, *22*(8), 1083–1092.

Emery, S. M. (2007). Limiting similarity between invaders and dominant species in herbaceous plant communities? *Journal of Ecology*, *95*(5), 1027–1035.

Essl, F., Dawson, W., Kreft, H., Pergl, J., Pyšek, P., Van Kleunen, M., Weigelt, P., Mang, T., Dullinger, S., Lenzner, B., Moser, D., Maurel, N., Seebens, H., Stein, A., Weber, E., Chatelain, C., Inderjit, Genovesi, P., Kartesz, J., … Winter, M. (2019). Drivers of the relative richness of naturalized and invasive plant species on Earth. *AoB PLANTS*, *11*(5).

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*(1), 1–10.

Falster, D. S., & Westoby, M. (2005). Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, *93*(3), 521–535.

Florens, F. B. V., Baider, C., Seegoolam, N. B., Zmanay, Z., & Strasberg, D. (2017). Long-term declines of native trees in an oceanic island’s tropical forests invaded by alien plants. *Applied Vegetation Science*, *20*(1), 94–105.

Fortini, L. B., Kaiser, L. R., Keith, L. M., Price, J., Hughes, R. F., Jacobi, J. D., & Friday, J. B. (2019). The evolving threat of Rapid ʻŌhi ʻa Death (ROD) to Hawai ʻi's native ecosystems and rare plant species. *Forest Ecology and Management*, *448*, 376–385.

Foster Huenneke, L., & Vitousek, P. M. (1990). Seedling and clonal recruitment of the invasive tree Psidium *cattleyanum*: Implications for management of native Hawaiian forests. *Biological Conservation*, *53*(3), 199–211.

Foster, J. T., & Robinson, S. K. (2007). Introduced Birds and the Fate of Hawaiian Rainforests. *Conservation Biology*, *21*(5), 1248–1257.

Gagne, W. C., & Cuddihy, L. W. (1990). *Vegetation. Manual of the flowering plants of Hawaii*. University of Hawaii Press, Honolulu.

Galland, T., Adeux, G., Dvořáková, H., E-Vojtkó, A., Orbán, I., Lussu, M., Puy, J., Blažek, P., Lanta, V., Lepš, J., Bello, F. de, Carmona, C. P., Valencia, E., & Götzenberger, L. (2019). Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology*, *107*(5), 2090–2104.

Gallien, L., & Carboni, M. (2017). The community ecology of invasive species: Where are we and what's next? *Ecography*, *40*(2), 335–352.

George W. Staples. (2000). *Survey of invasive or potentially invasive cultivated plants in Hawaiʻi*. Bishop Museum Press.

Giambelluca, Thomas W., Chen, Q., Frazier, A. G., Price, J. P., Chen, Y. L., Chu, P. S., Eischeid, J. K., & Delparte, D. M. (2013a). Online rainfall atlas of Hawai'i. *Bulletin of the American Meteorological Society*, *94*(3), 313–316.

Giambelluca, T.W., Shuai, X., Barnes, M. L., Alliss, R. J., Longman, R. J., Miura, T., Chen, Q., Frazier, A. G., Mudd, R. G., Cuo, L., & Businger, A. D. (2014a). *Evapotranspiration of Hawaiʻi. Final report* *submitted to the U.S. Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawaiʻi*.

Gillespie, T. W., Keppel, G., Pau, S., Price, J. P., Jaffré, T., Meyer, J.-Y., & O'Neill, K. (2011). Floristic Composition and Natural History Characteristics of Dry Forests in the Pacific. *Pacific Science*, *65*(2), 127–141.

Gower, J. C. (1971). A General Coefficient of Similarity and Some of Its Properties. *Biometrics*, *27*(4), 857.

Graham, N. R., Gruner, D. S., Lim, J. Y., & Gillespie, R. G. (2017). Island ecology and evolution: Challenges in the Anthropocene. *Environmental Conservation*, *44*(4), 323–335.

Hall, W. L. (1904). *The forests of the Hawaiian Islands*. US Dept. of Agriculture, Bureau of Forestry.

Harrington, R. R. A., & Ewel, J. J. J. (1997). Invasibility of tree plantations by native and non-indigenous plant species in Hawaii. *Forest Ecology and Management*, *99*(1–2), 153–162.

Hatheway, W. (1952). Composition of certain native dry forests: Mokuleia, Oahu, TH. *Ecological Monographs*, *22*(2), 153–168.

Hawaii Wildfire Management Organization. (2013). *Hawaii State Wildfire History Data Set*.

Hibit, J., & Daehler, C. C. (2019). Long-term decline of native tropical dry forest remnants in an invaded Hawaiian landscape. *Biodiversity and Conservation*, *28*(7), 1699–1716.

Hobbs, R. J., Higgs, E. S., & Hall, C. (2013). *Novel Ecosystems: Intervening in the New Ecological World Order*. John Wiley & Sons, Incorporated.

Hone, J. (1995). Spatial and temporal aspects of vertebrate pest damage with emphasis on feral pigs. *Journal of Applied Ecology*, 311–319.

Howarth, F. G., Stone, C. P., & Scott, J. M. (1985). Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. *Hawaiis Terrestrial Ecosystems Preservation and Management*, 149–179.

Ibanez, T., Hart, P., Ainsworth, A., Gross, J., & Monello, R. (2019). Factors associated with alien plant richness, cover and composition differ in tropical island forests. *Diversity and Distributions*, *25*(12), 1910–1923.

Imada, C. T. (2012). Hawaiian native and naturalized vascular plants checklist. *Honolulu: Hawaii Biological Survey, Bishop Museum*.

Jäger, H., Kowarik, I., & Tye, A. (2009). Destruction without extinction: Long-term impacts of an invasive tree species on Galápagos highland vegetation. *Journal of Ecology*, *97*(6), 1252–1263.

Janzen, D. H. (1988). Management of Habitat Fragments in a Tropical Dry Forest: Growth. *Annals of the Missouri Botanical Garden*, *75*(1), 105.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Bodegom, P. M. V., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., … Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, *17*(9), 2905–2935.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, *106*(23), 9322–9327.

Kirch, P. V. (1996). Late Holocene human-induced modifications to a central Polynesian island ecosystem. *Proceedings of the National Academy of Sciences*, *93*(11), 5296–5300.

Kitayama, K., & Mueller-Dombois, D. (1995). Biological invasion on an oceanic island mountain: Do alien plant species have wider ecological ranges than native species? *Journal of Vegetation Science*, *6*(5), 667–674.

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., … Westoby, M. (2016).

Plant functional traits have globally consistent effects on competition. *Nature*, *529*(7585), 204–207.

Letcher, S. G., Lasky, J. R., Chazdon, R. L., Norden, N., Wright, S. J., Meave, J. A., Pérez-García, E. A., Muñoz, R., Romero-Pérez, E., Andrade, A., Andrade, J. L., Balvanera, P., Becknell, J. M., Bentos, T. V., Bhaskar, R., Bongers, F., Boukili, V., Brancalion, P. H. S., César, R. G., … Williamson, G. B. (2015). Environmental gradients and the evolution of successional habitat specialization: A test case with 14 Neotropical forest sites. *Journal of Ecology*, *103*(5), 1276–1290.

Levine, J. M., Vilà, M., D’Antonio, C. M., Dukes, J. S., Grigulis, K., & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1517), 775–781.

Little, E., & Skolmen, R. (1989). *Common forest trees of Hawaii*.

Loiola, P. P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C. P., Pyšek, P., & Lososová, Z. (2018). Invaders among locals: Alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *Journal of Ecology*, *106*(6), 2230–2241.

Mac, M. J., Opler, P. A., Haecker, C. E. P., Doran, P. D., & Geological Survey. (1998). *Status and trends of the nation’s biological resources*. US Dept of the Interior, US Geological Survey.

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, *101*(921), 377–385.

Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F., & Louault, F. (2012). Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist*, *196*(2), 497–509.

Májeková, M., Paal, T., Plowman, N. S., Bryndová, M., Kasari, L., Norberg, A., Weiss, M., Bishop, T. R., Luke, S. H., Sam, K., Bagousse-Pinguet, Y. L., Lepš, J., Götzenberger, L., & Bello, F. de. (2016). Evaluating Functional Diversity: Missing Trait Data and the Importance of Species Abundance Structure and Data Transformation. *PLOS ONE*, *11*(2).

Mao, P., Zang, R., Shao, H., & Yu, J. (2014). Functional Trait Trade-Offs for the Tropical Montane Rain Forest Species Responding to Light from Simulating Experiments. *The Scientific World Journal*.

Maron, J., & Marler, M. (2007). Native plant diversity resists invasion at both low and high resource levels. *Ecology*, *88*(10), 2651–2661.

Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, *111*(1), 112–118.

Medeiros, A. C., Allmen, E. I. von, & Chimera, C. G. (2014). Dry Forest Restoration and Unassisted Native Tree Seedling Recruitment at Auwahi, Maui. *Pacific Science*, *68*(1), 33–45.

Medeiros, A. C., Vonallmen, E., Fukada, M., Samuelson, A., & Lau, T. (2008). Impact of the newly arrived seed-predating beetle Specularius impressithorax (Coleoptera: Chrysomelidae: Bruchinae) in Hawai'i. *Pacific Conservation Biology*, *14*(1–2), 7–12.

Merlin, M. D., & Juvik, J. O. (1992). Relationships among native and alien plants on Pacific islands with and without significant human disturbance and feral ungulates. *Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research*, 597–624.

Meyer, J.-Y. (2000). Preliminary review of the invasive plants in the Pacific islands (SPREP Member Countries). *Invasive Species in the Pacific: A Technical Review and Draft Regional Strategy*, 85.

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., Kapos, V., & Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*, 491–505.

Moles, A. T. (2018). Being John Harper: Using evolutionary ideas to improve understanding of global patterns in plant traits. *Journal of Ecology*, *106*(1), 1–18.

Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), 867–876.

Mueller-Dombois, D. (1985). *'Ohi'a dieback in Hawaii: 1984 synthesis and evaluation*.

Mueller-Dombois, D. (1992). Distributional dynamics in the Hawaiian vegetation. *Pacific Science*, *46*(2), 221–231.

Mueller-Dombois, D., & Wirawan, N. (2005). The Kahana Valley ahupua 'a, a PABITRA study site on O 'ahu, Hawaiian Islands. *Pacific Science*, *59*(2), 293–315.

Murphy, P., & Lugo, A. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*, 57.

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827).

National Oceanic and Atmospheric Administration, C. P. H. C. (n.d.). *Climatology of Tropical Cyclones in the Central Pacific Basin*.

Nogueira-Filho, S. L. G., Nogueira, S. S. C., & Fragoso, J. M. V. (2009). Ecological impacts of feral pigs in the Hawaiian Islands. *Biodiversity and Conservation*, *18*(14), 3677.

O'Brien, M. J., Engelbrecht, B. M. J., Joswig, J., Pereyra, G., Schuldt, B., Jansen, S., Kattge, J., Landhäusser, S. M., Levick, S. R., Preisler, Y., Väänänen, P., & Macinnis-Ng, C. (2017). A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones. *Journal of Applied Ecology*, *54*(6), 1669–1686.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience*, *51*(11), 933.

Ordonez, A., Wright, I. J., & Olff, H. (2010). Functional differences between native and alien species: A global-scale comparison. *Functional Ecology*, *24*(6), 1353–1361.

Ostertag, Rebecca, Warman, L., Cordell, S., & Vitousek, P. M. (2015). Using plant functional traits to restore Hawaiian rainforest. *Journal of Applied Ecology. 52 (4): 805-809*, *52*(4), 805–809.

Palmer, D. D. (2003). *Hawai'i's ferns and fern allies*. University of Hawaii Press.

Pattison, R. R., Goldstein, G., & Ares, A. (1998). Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia*, *117*(4), 449–459.

Pau, S., Gillespie, T. W., & Price, J. P. (2009). Natural history, biogeography, and endangerment of Hawaiian dry forest trees. *Biodiversity and Conservation*, *18*(12), 3167–3182.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167.

Podani, J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *TAXON*, *48*(2), 331–340.

Poorter, L., Bongers, F., Sterck, F. J., & Wöll, H. (2003). ARCHITECTURE OF 53 RAIN FOREST TREE SPECIES DIFFERING IN ADULT STATURE AND SHADE TOLERANCE. *Ecology*, *84*(3), 602–608.

Powell, D. C. (2005). *How To Measure a Big Tree*. United States Department of Agriculture, Forest Service.

Price, J. N., & Pärtel, M. (2013). Can limiting similarity increase invasion resistance? A meta-analysis of experimental studies. *Oikos*, *122*(5), 649–656.

Price, J. P., & Wagner, W. L. (2018). Origins of the Hawaiian flora: Phylogenies and biogeography reveal patterns of long-distance dispersal. *Journal of Systematics and Evolution*, *56*(6), 600–620.

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725–1737.

Pyšek, P., & Richardson, D. M. (2008). Traits associated with invasiveness in alien plants: Where do we stand? In *Biological invasions* (pp. 97–125).

Rees, M. (2001). Long-Term Studies of Vegetation Dynamics. *Science*, *293*(5530), 650–655.

Reynolds, P. L., Glanz, J., Yang, S., Hann, C., Couture, J., & Grosholz, E. (2017). Ghost of invasion past: Legacy effects on community disassembly following eradication of an invasive ecosystem engineer. *Ecosphere*, *8*(3).

Rock, J. F. C. (1913). *The indigenous trees of the Hawaiian Islands.*

Rubinoff, D., Holland, B. S., Shibata, A., Messing, R. H., & Wright, M. G. (2010). Rapid Invasion Despite Lack of Genetic Variation in the Erythrina Gall Wasp (Quadrastichus erythrinae Kim). *Pacific Science*, *64*(1), 23–31.

Russell, A. E., Raich, J. W., & Vitousek, P. M. (1998). The ecology of the climbing fern Dicranopteris linearis on windward Mauna Loa, Hawaii. *Journal of Ecology*, *86*(5), 765–779.

Sakai, A. K., Wagner, W. L., & Mehrhoff, L. A. (2002). Patterns of endangerment in the Hawaiian flora. *Systematic Biology*, *51*(2), 276–302.

Sandquist, D. R., & Cordell, S. (2007). Functional diversity of carbon-gain, water-use, and leaf-allocation traits in trees of a threatened lowland dry forest in Hawaii. *American Journal of Botany*, *94*(9), 1459–1469.

Sax, D. F., Gaines, S. D., & Brown, J. H. (2002). Species Invasions Exceed Extinctions on Islands Worldwide: A Comparative Study of Plants and Birds. *The American Naturalist*, *160*(6), 766–783.

Sayers, E. W., Barrett, T., Benson, D. A., Bryant, S. H., Canese, K., Chetvernin, V., Church, D. M., DiCuccio, M., Edgar, R., Federhen, S., Feolo, M., Geer, L. Y., Helmberg, W., Kapustin, Y., Landsman, D., Lipman, D. J., Madden, T. L., Maglott, D. R., Miller, V., … Ye, J. (2009). Database resources of the National Center for Biotechnology Information. *Nucleic Acids Research*, *37*(Database issue), D5-15.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671.

Selmants, P., Giardina, C., Jacobi, J. D., & Zhu, Z. (2017). Baseline and projected future carbon storage and carbon fluxes in ecosystems of Hawai‘i. In *U.S. Geological Survey Professional Paper* (Vol. 1834).

Shiels, A. B. (2011). Frugivory by introduced black rats (Rattus rattus) promotes dispersal of invasive plant seeds. *Biological Invasions*, *13*(3), 781–792.

Smith, C. W., & Tunison, J. T. (1992). Fire and alien plants in Hawaii: Research and management implications for native ecosystems. *Alien Plant Invasions in Native Ecosystems of Hawaii: Management and Research. Cooperative National Park Resources Studies Unit, Honolulu*, 394–408.

Stone, C. P. (1985). Alien animals in Hawai’i’s native ecosystems: Toward controlling the adverse effects of introduced vertebrates. *Hawaii’s Terrestrial Ecosystems: Preservation and Management Proceedings of a Symposium Held June 5-6, 1984 at Hawaii Volcanoes National Park*, 251–2197.

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, *21*(11), 645–651.

Suda, Jan, Meyerson, L. A., Leitch, I. J., & Pyšek, P. (2015). The hidden side of plant invasions: The role of genome size. *New Phytologist*, *205*(3), 994–1007.

Taugourdeau, S., Villerd, J., Plantureux, S., Huguenin-Elie, O., & Amiaud, B. (2014). Filling the gap in functional trait databases: Use of ecological hypotheses to replace missing data. *Ecology and Evolution*, *4*(7), 944–958.

R Core Team (2013). *R: A language and environment for statistical computing*.

Valliere, J. M., Escobedo, E. B., Bucciarelli, G. M., Sharifi, M. R., & Rundel, P. W. (2019). Invasive annuals respond more negatively to drought than native species. *New Phytologist*, *223*(3), 1647–1656.

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*(2), 235–245.

Vernon, A. L., & Ranker, T. A. (2013). Current Status of the Ferns and Lycophytes of the Hawaiian Islands. *American Fern Journal*, *103*(2), 59–111.

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301.

Vizentin-Bugoni, J., Tarwater, C. E., Foster, J. T., Drake, D. R., Gleditsch, J. M., Hruska, A. M., Kelley, J. P., & Sperry, J. H. (2019). Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawaiʻi. *Science*, *364*(6435), 78–82.

Wagner, W. L., Herbst, D. R., & Sohmer, S. H. (1999). Manual of the flowering plants of Hawai'i–Revised Edition. *Bishop Museum Special Publication*, *97*, 988.

Wang, C., Zhou, J., Liu, J., Xiao, H., & Wang, L. (2018). Differences in functional traits and reproductive allocations between native and invasive plants. *Journal of Central South University*, *25*(3), 516–525.

Weller, S. G., Sakai, A. K., Clark, M., Lorence, D. H., Flynn, T., Kishida, W., Tangalin, N., & Wood, K. (2018). The effects of introduced ungulates on native and alien plant species in an island ecosystem:

Implications for change in a diverse mesic forest in the Hawaiian Islands. *Forest Ecology and Management*, *409*, 518–526.

Welton, P. (1993). *Community organization and population structures of a lowland mesic forest in Pahole Natural Area Reserve, Oahu (Hawaii).* [Masters thesis]. University of Hawaii at Manoa.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant Ecological Strategies: Some Leading Dimensions of Variation between Species. *Annual Review of Ecology and Systematics*, *33*, 125–159.

Willis, K. J., & Birks, H. J. B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, *314*(5803), 1261–1265.

Wirawan, N. (1974). *Floristic and structural development of native dry forest stands at Mokuleia, NW Oahu* [Masters thesis]. University of Hawaii at Manoa.

Wirawan, N. (1978). *Vegetation and soil-water regimes in a tropical rain forest valley on Oahu, Hawaiian Islands* [PhD Thesis]. University of Hawaii at Manoa.

Woodcock, D. (2003). To Restore the Watersheds: Early Twentieth-Century Tree Planting in Hawai‘i. *Annals of the Association of American Geographers*, *93*(3), 624–635.

Zhang, H., Qi, W., John, R., Wang, W., Song, F., & Zhou, S. (2015). Using functional trait diversity to evaluate the contribution of multiple ecological processes to community assembly during succession. *Ecography*, *38*(12), 1176–1186.

Ziegler, A. C. (2002). *Hawaiian natural history, ecology, and evolution*. University of Hawaii Press.

Zimmerman, N., Hughes, R. F., Cordell, S., Hart, P., Chang, H. K., Perez, D., Like, R. K., & Ostertag, R. (2008). Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai’i. *Biotropica*, *40*(3), 277–284.

Data sources

Allison, S. D., & Vitousek, P. M. (2004). Rapid nutrient cycling in leaf litter from invasive plants in Hawaiʻi. *Oecologia*, *141*(4), 612–619. doi: 10.1007/s00442-004-1679-z

Arundina graminifolia, Missouri Botanical Garden Plant Finder, http://www.missouribotanicalgarden.org/plantfinder/plantfindersearch.aspx, Accessed September 1, 2019

Asner, G. P., Jones, M. O., Martin, R. E., Knapp, D. E., & Hughes, R. F. (2008). Remote sensing of native and invasive species in Hawaiian forests. *Remote Sensing of Environment*, *112*(5), 1912–1926. doi: 10.1016/j.rse.2007.02.043

Asner, G. P., & Goldstein, G. (1997). Correlating Stem Biomechanical Properties of Hawaiian Canopy Trees with Hurricane Wind Damage. *Biotropica*, *29*(2), 145–150.

Aubin, I., Messier, C., Gachet, S., Lawrence, K., McKenney, D., Arseneault, A., … Ricard, J. P. (2012). TOPIC–traits of plants in Canada. *Natural Resources Canada, Canadian Forest Service, Sault Ste. Marie, Ontario.*

Austin, A. T., & Vitousek, P. M. (1998). Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia*, *113*(4), 519–529. doi: 10.1007/s004420050405

Bakutis, A. C. (2005). *Investigating seed dispersal and seed bank dynamics in Hawaiian mesic forest communities* (PhD Thesis).

Barreto, L. C., Santos, F. M. G., & Garcia, Q. S. (2016). Seed dormancy in Stachytarpheta species (Verbenaceae) from high-altitude sites in south-eastern Brazil. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *225*, 37–44. doi: 10.1016/j.flora.2016.09.009

Baruch, Z., & Goldstein, G. (1999). Leaf construction cost, nutrient concentration, and net CO 2 assimilation of native and invasive species in Hawaii. *Oecologia*, *121*(2), 183–192. doi: 10.1007/s004420050920

Brown, S., & Nations, F. and A. O. of the U. (1997). *Estimating Biomass and Biomass Change of Tropical Forests: A Primer*. Food & Agriculture Org.

CABI, 2019. Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Chandra, A., & Dubey, A. (2009). Assessment of ploidy level on stress tolerance of Cenchrus species based on leaf photosynthetic characteristics. *Acta Physiologiae Plantarum*, *31*(5), 1003–1013. doi: 10.1007/s11738-009-0317-0

Chau, M. M., Walker, L. R., & Mehltreter, K. (2013). An invasive tree fern alters soil and plant nutrient dynamics in Hawaii. *Biological Invasions*, *15*(2), 355–370. doi: 10.1007/s10530-012-0291-0

Devkota, A., & Jha, P. K. (2009). Variation in growth of Centella asiatica along different soil composition. *Botany Research International*, *2*(1), 55–60.

Edward F. Gilman, R. W. K. (2019, February 14). Asparagus densiflorus “Myers” Myers Asparagus Fern. Retrieved May 8, 2019, from https://edis.ifas.ufl.edu/fp052

Feng, Y.-L. (2008). Photosynthesis, nitrogen allocation and specific leaf area in invasive Eupatorium adenophorum and native Eupatorium japonicum grown at different irradiances. *Physiologia Plantarum*, *133*(2), 318–326. doi: 10.1111/j.1399-3054.2008.01072.x

Feng, Y.-L., & Fu, G.-L. (2008). Nitrogen allocation, partitioning and use efficiency in three invasive plant species in comparison with their native congeners. *Biological Invasions*, *10*(6), 891–902.

FIA Inventory Data. PNW Research Station. USDA Forest Service. (n.d.). Retrieved September 1, 2019, from https://www.fs.fed.us/pnw/rma/fia-topics/inventory-data/

Gilman, E. F., Watson, D. G., Klein, R. W., Koeser, A. K., Hilbert, D. R., McLean, D. C. (2017). *Citharexylum spinosum*: Fiddlewood (FPS130). Gainesville: University of Florida Institute of Food and Agricultural Sciences.

Green, W. (2009). *USDA PLANTS Compilation, version 1, 09-02-02*. (http://bricol.net/downloads/data/PLANTSdatabase/) NRCS: The PLANTS Database (http://plants.usda.gov, 1 Feb 2009). National Plant Data Center: Baton Rouge, LA 70874-74490 USA.

Kattge, Jens, Knorr, W., Raddatz, T., & Wirth, C. (2009). Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, *15*(4), 976–991.

Lallana, V. H., Michel, A., & García, L. F. (2019). Flowering, fructification and seed production in plants of Polystachya concreta (Jacq.) Garay y HR Sweet (Orquidaceae). *Investigación Agraria*, *21*(1), 65–72.

Little, E. L., & Skolmen, R. G. (1989). *Common Forest Trees of Hawaii: Native and Introduced. USDA Forest Service Agriculture Handbook No. 679*.

Loh, R. K., & Daehler, C. C. (2007). Influence of Invasive Tree Kill Rates on Native and Invasive Plant Establishment in a Hawaiian Forest. *Restoration Ecology*, *15*(2), 199–211. doi: 10.1111/j.1526-100X.2007.00204.x

Macadamia integrifolia, Missouri Botanical Garden Plant Finder, http://www.missouribotanicalgarden.org/plantfinder/plantfindersearch.aspx, Accessed September 1, 2019

McKown, A. D., Akamine, M. E., & Sack, L. (2016). Trait convergence and diversification arising from a complex evolutionary history in Hawaiian species of Scaevola. *Oecologia*, *181*(4), 1083–1100. doi: 10.1007/s00442-016-3640-3

Medeiros, Camila D et al. (2018), Data from: An extensive suite of functional traits distinguishes wet and dry Hawaiian forests and enables prediction of species vital rates, Dryad, Dataset, https://doi.org/10.5061/dryad.cq47n7s

Munoz, M. C., & Ackerman, J. D. (2011). Spatial distribution and performance of native and invasive Ardisia (Myrsinaceae) species in Puerto Rico: the anatomy of an invasion. *Biological Invasions*, *13*(7), 1543–1558.

Murray, B. R., & Phillips, M. L. (2010). Investment in seed dispersal structures is linked to invasiveness in exotic plant species of south-eastern Australia. *Biological Invasions*, *12*(7), 2265–2275. doi: 10.1007/s10530-009-9637-7

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., & Simons, A. (2009). Agroforestree Database: a tree reference and selection guide. Version 4.

Ostertag, Rebecca, Fung, B., Pante, P., Tate, R., Vizzone, A., Rayome, D., … Vitousek, P. (2016). *SERDP Project RC-2117*.

Ostertag, Rebecca, Giardina, C. P., & Cordell, S. (2008). Understory colonization of Eucalyptus plantations in Hawaii in relation to light and nutrient levels. *Restoration Ecology*, *16*(3), 475–485.

Penuelas, J., Sardans, J., Llusià, J., Owen, S. M., Carnicer, J., Giambelluca, T. W., … Niinemets, Ü. (2010). Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology*, *16*(8), 2171–2185. doi: 10.1111/j.1365-2486.2009.02054.x

Polystachya concreta in Global Plants on JSTOR. (n.d.). Retrieved October 23, 2019, from https://plants.jstor.org/compilation/polystachya.concreta

Vaieretti, M. V., Harguindeguy, N. P., Gurvich, D. E., Cingolani, A. M., & Cabido, M. (2005). Decomposition Dynamics and Physico-chemical Leaf Quality of Abundant Species in a Montane Woodland in Central Argentina. *Plant and Soil*, *278*(1–2), 223–234. doi: 10.1007/s11104-005-8432-1

Vergutz, L., Manzoni, S., Porporato, A., Novais, R. F., & Jackson, R. B. (2012). A global database of carbon and nutrient concentrations of green and senesced leaves. *ORNL DAAC*.

Vergutz, Leonardus, Manzoni, S., Porporato, A., Novais, R. F., & Jackson, R. B. (2012). Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*, *82*(2), 205–220.

Wirth, C., & Lichstein, J. W. (2009). carboni. In *Old-growth forests* (pp. 81–113). Springer.

Wuu-Kuang, S. (2011). Taxonomic revision of Cinnamomum (Lauraceae) in Borneo. *Blumea-Biodiversity, Evolution and Biogeography of Plants*, *56*(3), 241–264.

Xiong, D., Douthe, C., & Flexas, J. (2018). Differential coordination of stomatal conductance, mesophyll conductance, and leaf hydraulic conductance in response to changing light across species: Coordination of CO_2 diffusion and H_2O transport inside leaves. *Plant, Cell & Environment*, *41*(2), 436–450. doi: 10.1111/pce.13111