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Conservation of Hawaii's dry forest: An application of habitat suitability modeling, GIS, and field methods

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Geography

by

Corey Marie Rovzar

2016

ABSTRACT OF THE DISSERTATION

Conservation of Hawaii’s dry forest: An application of habitat suitability modeling, GIS, and field methods

by

Corey Marie Rovzar

Doctor of Philosophy in Geography

University of California, Los Angeles, 2016

Professor Thomas Welch Gillespie, Chair

Tropical dry forests in Hawaii are among the most endangered forest types in the world with half of all plant species listed as federally threatened or endangered. Although there have been some efforts to protect remaining dry forest fragments, conservation of this ecosystem has proven difficult due to a poor understanding of the current distribution of native species, environmental factors influencing their distributions, potential sites for species reintroductions, and of how the dry forest has changed over the past 30 years. This dissertation addresses the question: How can field-based methods, habitat suitability modeling (HSM), geographic information systems (GIS), and remote sensing improve conservation and restoration efforts in Hawaii’s dry forest? To answer this question, habitat suitability modeling is used to assess factors influencing species distributions and identify potential sites for endangered species restoration. Secondly, a field-based case study is conducted to evaluate the environmental variables affecting restoration success of an endangered plant. Finally, GIS and remote sensing are used to assess changes in dry forest dynamics over the past decade across the Hawaiian Islands. Results from habitat suitability modeling suggest that topography and soil variables may be a key driver in the distribution of endangered dry forest species and that current protected areas may not capture the best habitat for reintroductions. Furthermore, results from the restoration study suggest that sites with low soil moisture and high exposure to sunlight may be the most suitable reintroduction sites for endangered dry forest species like, *Hibiscus brackenridgei*. The methodology and findings from this dissertation will provide a framework for conservation management of endangered dry forest fragments in Hawaii as well as other oceanic islands

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This dissertation is dedicated to Mom, Dad, Annie, Kelly, and Mikey

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CHAPTER 1

1. Introduction

1.1 Background

Globally, tropical dry forests are one of the most endangered and least-studied forest types (Aide et al., 2013; Gillespie et al., 2012; Janzen, 1988; Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). This is especially true for Hawaiian dry forest which has 45% of its endemic trees and shrubs listed as federally threatened or endangered (Pau et al., 2009). Historically, Hawaiian dry forest ecosystems contained high species richness and endemism (Rock, 1913), however, destruction of over 90% of the dry forest has resulted in widespread species loss (Bruegmann, 1996; Cabin et al., 2000; Sakai et al., 2002). Today, native dry forest habitat occurs in fragmented patches containing only a few rare and endangered individuals (Cabin et al., 2000). Major threats to Hawaii's dry forest include deforestation, land development, degradation by pigs, fire, invasive species, and non-native ungulate grazing (Blackmore & Vitousek 2000; Bruegmann 1996; Cabin et al. 2000; Cuddihy & Stone 1990; Stone et al. 1992). Although much of Hawaii's dry forest has been lost, preservation of remaining fragments is both biologically and culturally significant, due to the high degree of endemic and rare species as well as the importance of many of these endangered species to native Hawaiian culture (Anderson-Fung and Maly, 2002). Despite the pressing need for conservation of this ecosystem, management is greatly hindered by a lack of knowledge regarding species' biology, the historical and current distributions of Hawaiian dry forest species, and potential sites for reintroduction (Caujapé-Castells et al., 2010; Pau et al., 2009).

In general, conservation planning is not systematic and reserves tend to occur in places which do not effectively capture a habitat's biodiversity (Margules and Pressey, 2000). A systematic conservation plan involves six stages: measuring and mapping biodiversity, identifying conservation goals, reviewing existing reserves and selecting new ones, implementing conservation on the ground, and finally, managing and monitoring reserves (Margules and Pressey, 2000). In order to effectively address these stages, it is necessary to approach conservation management using a variety of methods.

Native species reintroduction is one widely used method to help preserve populations of endangered species and involves the release of wild or captive-bred individuals into novel or historical habitats (Armstrong and Seddon, 2008, 2008; Lipsey et al., 2007; Seddon et al., 2007). Although habitat restoration without the use of introduced individuals is the preferred method for species recovery (Menges, 2008), often times spontaneous recovery of a native population is hindered by a species' transient seed banks (Thompson, 1997) as well as dispersal limitations (Clark et al., 2007). The resulting deficiency in naturally occurring propagules necessitates species reintroduction as a means to increase the likelihood of species survival (Luijten et al., 2002; Pavlik, 1996; Van Groenendael et al., 1998). Despite its widespread use, reintroduction success rates are overall low due to the difficulty in identifying suitable habitat for restoration (Drayton and Primack, 2012; Godefroid et al., 2011; Questad et al., 2014). Thus, there is a need for methods which can identify suitable habitat for conducting endangered species reintroductions and evaluate the environmental factors influencing their distributions.

In the past decade, habitat suitability modeling (HSM) for rare and endangered species has rapidly progressed and become an informative tool for identifying key areas for restoration and habitat conservation (Butler, 2009; Gallardo and Aldridge, 2013; Gogol-Prokurat, 2011; Guisan et al., 2006; Loiselle et al., 2003; Pearson et al., 2007; Thompson, 2004; Wilson et al., 2013). HSMs, also referred to as ecological niche models or species distribution models, are statistical models which predict the potential geographic distribution (or habitat suitability) of a species by measuring the relationship between a species' spatial distribution and select environmental variables (Franklin, 2009). In order to identify and prioritize conservation areas, maps identifying habitat suitability are essential (Elith and Leathwick, 2009; Franklin, 2009a).

Another area which has grown rapidly in the past decade is remote sensing of protected areas using satellite imagery to assess land cover change and monitor biodiversity within individual protected areas (Fraser et al., 2009; Gillespie et al., 2014; Secades et al., 2014). Protected areas are widely regarded as one of the most successful measures implemented for the conservation of biodiversity, drawing upon traditional and community-based approaches, governance regimes, scientific and traditional knowledge, and contemporary practices of governments and conservation agencies (IUCN, 2013). Given the limited resources available for conservation efforts, it is critical that reserves are strategically planned to ensure the most effective protection of biodiversity and the most efficient use of land (Kupfer, 2012; Nagendra et al., 2013). However, the science has not been able to keep pace with the rapid accumulation of useful remote sensing data, the environmental changes that are occurring around the world, and real world information needs of natural resource managers, the conservation community, and the public in the over 100,000 decreed protected areas (UNEP and IUCN, 2009). Furthermore, the applications of spatial analysis tools and spaceborne remote sensing for protected areas has not been fully realized to date (Secades et al., 2014). Thus, there is a need to explore and test the utility of spaceborne sensors for conservation and management of protected areas and to develop standard and repeatable GIS and remote sensing methods, protocols, and products that can be used across all protected areas (Gaveau et al., 2009; Laurance et al., 2012; Nagendra et al., 2013).

This dissertation addresses the question: How can field-based methods, habitat suitability modeling, geographic information systems (GIS), and remote sensing improve conservation and restoration efforts in Hawaii's dry forest? To answer this question, habitat suitability modeling is used to assess factors influencing species distributions and identify potential sites for endangered species restoration. Secondly, a field-based case study is conducted to evaluate the environmental variables affecting restoration success of an endangered plant. Finally, GIS and remote sensing are used to assess the current extent, composition, and changes in dry forest dynamics over the past decade across the Hawaiian Islands. The methodology and findings from this dissertation will provide a framework for conservation management of endangered dry forest fragments in Hawaii as well as other oceanic islands.

1.2 Dissertation Structure

The overall aim of this research is to provide an understanding of how we can better inform restoration efforts for endangered plants in Hawaii's dry forest. The results from this dissertation provide the first-ever habitat suitability maps for plant species in Hawaii which will inform current and future conservation management and provide a template for modeling other species of conservation concern in Hawaii and other oceanic islands. All chapters excluding the introduction and conclusion are written as peer-reviewed publications for a scientific journal.

Chapter 3 has been published in *Forest Ecology and Management*. Chapter 2 will be submitted as a review article and chapters 4 and 5 will be submitted as primary research articles.

This first chapter provides context and organization for the remaining work. Chapter 2 reviews previous research on the historical and current state of Hawaii's dry forest and on threats which have led to its current endangerment. Overall, this chapter seeks to highlight seminal studies concerning Hawaii's dry forest as well as indicate areas which could benefit from additional research. Chapter 3 seeks to answer three primary questions relating to modeling rare species distributions on islands with rugged topography, such as Hawaii. First, does model accuracy significantly vary between a landscape, local, and site scale model? Second, what combination of variables and spatial scale yields the best result for modeling rare and endangered plants on islands with diverse topography and for the purposes of reintroduction site selection? Lastly, does the total number of species with overlapping suitable habitat (niche overlap) vary between spatial scales? Chapter 4 is a reintroduction study with three primary questions. First, can an endangered plant be successfully reintroduced with minimal management into a degraded habitat? Second, which environmental factors are correlated with survival and growth of endangered *Hibiscus brackenridgei mokuleinus* in Oahu's dry forest? Lastly, how effective is a habitat suitability model in identifying potential reintroduction sites? Chapter 5 uses two remotely sensed products to analyze the composition, extent, and changes to Hawaii's dry forest between the year 2000 and 2014. The goals of this chapter are to quantify the extent and composition of remaining dry forest fragments on six of the main Hawaiian Islands, assess change between 2000 and 2014, and evaluate the effectiveness of reserves in protecting dry forest habitat.

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CHAPTER 2

2.0 Past degradation and current threats to Hawaii’s dry forest

2.1 Abstract

Globally, tropical dry forests are one of the most endangered and least studied forest types. This is especially true on Hawaii where it is estimated that over 90% of the dry forest has been destroyed. Despite its conservation importance, little is known concerning the history and current state of Hawaii’s dry forest. Furthermore, there have been no review papers concerning Hawaii’s dry forest to date. This paper provides a much-needed review of research related to the degradation of Hawaii’s dry forest, both past and present, in order to identify gaps in the literature. The aim of this review is to provide an overview of the historical and current state of Hawaii’s dry forest and assess threats which have led to its current endangerment. Overall, this paper seeks to highlight seminal studies concerning Hawaii’s dry forest as well as indicate areas which could benefit from additional research.

2.2. Introduction

Tropical dry forests in Hawaii are among the most endangered forest types in the world with 45% of endemic trees and shrubs on the federal threatened and endangered species list (Pau et al., 2009). Hawaii’s dry forest and dry scrub ecosystems contain over 25% of all endangered plant species in Hawaii, which accounts for 38% of all endangered and threatened plant species in the United States (Cabin et al., 2000; Sakai et al., 2002). In the past, Hawaiian dry forest ecosystems occurred between 0-1,500 m elevation on the rain shadow side of the islands (Cuddihy et al., 1989; Cuddihy and Stone, 1990; Stone et al., 1992) and contained high species richness and endemism compared with other habitats in Hawaii (Rock, 1913). However, today, over 90% of the dry forest area has been destroyed resulting in widespread species loss (Bruegmann, 1996; Cabin et al., 2000; Sakai et al., 2002). Currently native dry forest habitat occurs in fragmented patches containing only a few rare and endangered individuals. Although much of Hawaii's dry forest has been lost, preservation of remaining fragments is both biologically and culturally significant, due to the high degree of endemic and rare species as well as the importance of many of these endangered species to native Hawaiians.

This research provides a review of the degradation of the Hawaiian dry forest, both past and present, to highlight research which has expanded our understanding of this issue as well as identify areas which could benefit from additional research. For the purposes of this paper, degradation is defined as a loss of natural productivity, biodiversity, and ecosystem services as well as the creation or shift of risk ecology (Robbins, 2004). In this paper, land degradation in Hawaii is evaluated as it relates to the destruction of the dry forest which continues to be degraded both directly and indirectly by humans. To prioritize research and optimize conservation efforts, it is important to evaluate the history of dry forest degradation, current threats to the ecosystem, and conservation and restoration efforts which have been implemented.

2.3 Past Degradation

2.3.1 Polynesian Period

The first instances of human degradation of Hawaiian dry forests were during the Polynesian period when dry forested areas were cleared for agriculture (Pau et al., 2009; B Rolett and Diamond, 2004). The dry forest regions were the first to be inhabited and utilized for resources due to the favorable climate which reduced the chance of contracting potential diseases, as well as the fertile soil which was more suitable for agriculture (Allen, 2000). The Polynesians first arrived around AD 800 and primarily used burning as a means of clearing forest for slash-and-burn or shifting cultivation (Kirch, 1982; Pau et al., 2012). Pollen and charcoal analysis from a sediment core taken on Flat Top Bog in Maui suggests that there was limited activity at high elevation regions during the Polynesian era, followed by an increase in grass fires and introduced species after European contact (Burney et al., 1995). A similar study was conducted in a lowland site in Kauai and argued that in the past, the site contained vegetation which is now only found in highland regions (Burney et al., 2001). This suggests that these species are currently restricted to highland areas due to the difficult topography and climate which has deterred humans from colonizing these regions.

In addition to forest clearance for agriculture, the Polynesians were able to indirectly impact the forest due to the introduction of the Polynesian rat, *Rattus exulans* (Athens et al., 2002). In a study conducted on the ‘Ewa Plain, a lowland limestone reef in Oahu, pollen and charcoal analysis as well as radiocarbon dating were used to determine the role of humans in the destruction of the forest and the resultant avifaunal extinctions (Athens et al., 2002). The pollen and charcoal analyses indicated that the forest declined prior to Polynesian colonization of the area. Furthermore, radiocarbon dating of the rat bones suggested that the Polynesian rat was the primary cause of forest decline through seed, plant material, and fruit predation (Athens et al., 2002; Cuddihy and Stone, 1990). Although more recent research supports the view that introduced rats are plant predators (Athens, 2009; Campbell and Atkinson, 2002; Howald et al., 2007; Towns et al., 2006; Traveset et al., 2009), Shiels and Drake (2009) argue that rats can also facilitate seed dispersal through fruit and seed transport based on field and laboratory experiments measuring the relative likelihood of seed predation and dispersal by the black rat. These findings suggest that although rats may have contributed to dry forest decline, they may have also influenced species dispersal and forest composition. Despite the value of paleoecological records in providing evidence for Polynesian impact, there have been relatively few studies mainly conducted at low elevation sites and often at a coarse temporal resolution (Athens et al., 2002, 1992; Athens and Ward, 1993; Burney et al., 2001, 1995; Burney and Burney, 2003; Hotchkiss and Juvik, 1999; Pau et al., 2012).

2.3.2 Ancient Hawaiian Perceptions of the Land

Although the Polynesian colonizers degraded areas of lowland forest to support their growing population through agriculture, their perceptions of the land suggests they had some type of conservation ethic. In ancient Hawaiian society, vegetation regions were valued beyond their ecological significance as they also housed their gods and were places to feel the vitality of the Hawaiian universe flow through them (Anderson-Fung and Maly, 2002). The Hawaiians' belief that "ola" (life) was found in all aspects of nature including rocks, trees, and water formed the basis of the ideal that Hawaiian people were part of the universe and not a product of it. Furthermore, the Hawaiians viewed themselves as the newest members to the extended family they considered nature, and as such, had a responsibility to nurture their universe while never considering it expendable. The Hawaiians also valued learning about their environment and developed extensive scientific knowledge through observation, identifying and classifying species, as well as experimenting (Anderson-Fung and Maly, 2002). In particular, the forests were perceived as highly spiritual places in which an individual would not take from them without asking for permission. Although lowland forest clearance did occur following

Polynesian colonization, ultimately, their damage was minimal compared with the European era and modern times (Anderson-Fung and Maly, 2002).

In terms of land ownership, land and natural resources were under the authority of the high chiefs who allotted the land to the native people (Maly & Wilcox 2000). Land was divided into boundaries based on watersheds (ahupua'a) and those living within each boundary were responsible for sustainable use of the resources. Regarding resource use, the mantra for Polynesian culture was “care for the land, and the land, in turn, shall care for you” (Maly & Wilcox 2000). The arrival of the Europeans in 1778 exposed the Polynesians to a new perspective of the land, one centered on extraction and export of resources.

2.3.3 European Period

Human impact on the dry forest continued with European arrival which brought large-scale ranching and commercial agriculture to the region (Pau et al., 2012). During the early 20th century, forestry practices involved the widespread planting of non-native tree species in order to stabilize watersheds necessary for agriculture (Woodcock, 2003). Studies using pollen and charcoal analyses as well as radiocarbon dating have shown the emergence of non-native taxa, the decline of native species, as well as fossil remains of livestock at the onset of European arrival (Burney et al., 2001, 1995). Using high temporal resolution palynological, charcoal, and sedimentological analysis for a lowland catchment lake in Maui, Pau et al. (2012) compared the impacts of the early Polynesians (around 800 AD) with those of the Europeans (after 1778) on the dry forest, and concluded that European destruction was much more widespread whereas Polynesian impacts were largely confined to the lowlands. Furthermore, historical accounts from European explorers have provided evidence of the extent of Polynesian impact on the dry forest as well as the impacts of Europeans including agricultural practices, grazing of livestock, and the introduction of exotic plants and animals (Cuddihy & Stone 1990; Pau et al. 2012).

In addition, rodents were also introduced by the Europeans, including the black rat, the Norway rat, and the house mouse (Tomich 1986; Shiels & Drake 2011). Similar to the Polynesian rat, the black rat preys upon the plant material of native dry forest species (Athens et al. 2002; Pérez et al. 2008) as well as endangered birds (VanderWerf, 2001). Today, the black rat is the most common rodent in Hawaii forests found up to 3,000 m in elevation (Amarasekare 1994; Meyer and Shiels 2009).

In 1778, European settlers introduced goats, followed soon after by cattle, to the Hawaiian islands for grazing purposes (Smith et al., 1983). After receiving numerous grazers as gifts from the Europeans, King Kamehameha, the ruling monarch at the time, placed a taboo against killing the animals. With no natural predators, the introduced grazers proliferated and by 1830, 20,000 cattle were estimated on the island of Hawaii alone (CITE). As the number of grazers increased, both European settlers and Polynesians began to observe the environmental impacts. Around 1856, European naturalists began to write and warn about the potential consequences of continued forest degradation, including increasing invasive species as well as climatic changes, associated with commercial grazing. Furthermore, during the 1820s, King Kamehameha's successor, King Liholiho, commissioned hunting in order to help preserve the native forests and their gardens (Smith et al., 1983).

Although modern science has enhanced our awareness of the endangerment of Hawaii's dry forest, local environmental knowledge of both the Polynesians and Europeans suggest a level of awareness for the need to conserve the dry forest. For example, after the introduction of grazers, the Polynesians observed the destructive effects to both their gardens and the native forest (Smith et al., 1983). As a result, around 1820, King Liholiho commissioned hunting and exported the hides and tallow in order to reduce the number of grazers. Our understanding of the past degradation of Hawaii's dry forest primarily stems from palynology which has enabled us to reconstruct vegetation of the past. Continued work in this field will further our understanding of the magnitude of destruction that occurred both during the Polynesian and European eras.

2.4 Current Threats

Currently, major threats to Hawaii's dry forest include deforestation, land development, degradation by pigs, fire, invasive species, and non-native ungulate grazing (Blackmore & Vitousek 2000; Bruegmann 1996; Cabin et al. 2000; Cuddihy & Stone 1990; Stone et al. 1992). These threats have resulted in a an inability for canopy-tree regeneration within the remaining dry forest fragments in the Hawaiian Islands (Bruegmann, 1996). While deforestation and land development have degraded the dry forest, ultimately grazing and foraging by pigs, fire, invasive species, and grazing by cattle represent ongoing threats which continuously degrade the dry forest, however, have the potential to be mitigated.

2.4.1 Pigs

Pigs (*Sus scrofa*) were first introduced to the Hawaiian Islands by the early Polynesian colonizers as a source of food, followed by the introduction of the European pig by early Europeans (Tomich, 1986). Before European arrival, pig populations were kept low by frequent hunting which resulted in minimal forest degradation by pigs (Barret and Stone, 1983; Stone, 1985). In addition, minimal sources of animal protein further limited pig populations during the Polynesian era (Barret and Stone, 1983). However, the introduction of earthworms by the early

Europeans provided a source of protein and thus, enabled the widespread population expansion of the pigs (Giffin, 1978). Furthermore, land clearance for pastures as well as the introduction of the dung beetle to decompose cattle feces contributed to an increased habitat and provided another protein source for the pigs, respectively (Howarth, 1985; Nogueira-Filho et al., 2009). The dung beetle (Scarabaeid family) has also been found to enhance soil nutrient cycling (Howarth, 1985), which would benefit earthworm population growth and thus, enable pig population expansion (Nogueira-Filho et al., 2009). Today, feral pigs are found on all of the main Hawaiian Islands except for Lanai, where they have been eradicated. Furthermore, pigs are restricted to dense rainforests and private ranches on Kauai, Oahu, and Maui, while they are more widespread on the Island of Hawaii.

Research has utilized exclosure studies to assess the impacts of pigs on native vegetation as well as the potential for native plant recovery (Nogueira-Filho et al., 2009). These studies involve building pig-proof exclosures and then sampling the vegetation inside the exclosure as well as outside. Typically, vegetation will be sampled annually for up to 5 years after the exclosure is created (Loope and Scowcroft, 1985). Results from exclosure studies suggest that the removal of feral pigs will result in native vegetation recovery, with little impact on non-native species distribution (Aplet et al., 1991; Jacobi, 1976; Katahira, 1980; Stone, 1991; Stone et al., 1992). Although pigs have degraded the Hawaiian dry forest, complete eradication may be difficult due to the cultural and religious significance of the pig (Stone, 1985).

Feral pigs threaten the native Hawaiian dry forest predominantly due to direct consumption of native plant species (Nogueira-Filho et al., 2009). Foraging and trampling also contributes to plant uprooting, soil erosion, and degradation of watersheds (Cuddihy and Stone, 1990). Pigs have been found to damage native species through trampling and also by increasing soil fertility (Stone, 1985). Because most native species are adapted to poor soils, increased soil fertility due to pig rooting results in difficulties for native species reestablishment while promoting the colonization of invasive species (Stone, 1985). Indirectly, feral pigs have significant ecological consequences by altering native species population dynamics as well as contributing to the spread and establishment of non-native species. Overall, these impacts result in changes in the composition and structure of dry forest communities.

2.4.2 Fire

Naturally ignited fires resulting from volcanism and lightning have occurred throughout Hawaii's disturbance history (Ainsworth and Kauffman, 2009). Previous research using pollen and charcoal analysis of sediment cores taken from bogs suggest that wildfires were prevalent in Hawaii before the arrival of Europeans (Burney et al., 1995; Mueller-Dombois, 1981; Smith and Tunison, 1992). Although fire disturbance is part of Hawaii's natural history, it occurred at very low frequencies in the past (Smith and Tunison, 1992). Fires generated from volcanic eruptions are highly localized and thus, do not have a widespread impact on the native vegetation (Smith and Tunison, 1992). As a result, the native vegetation has evolved under low fire conditions resulting in low flammability as well as difficulty regenerating after fire disturbance (Smith and Tunison, 1992). In modern times, fires have increased in frequency due to climate change, nonnative species invasions, and greater sources of human ignition. Field studies of native Hawaiian dry woodland post-fire response suggest that the rapid increase in grass invasions have increased the frequency and size of fires. The expansion of grasses acting as fuel together with dry and windy conditions perpetuates the grass/fire cycle (Ainsworth and Kauffman, 2009;

D'Antonio and Vitousek, 1992; Freifelder et al., 1998; Hughes et al., 1991). The grass/fire cycle in Hawaii involves a positive feedback loop which begins with the establishment of invasive grasses after a fire. The invasive grasses increases the frequency of fire, and the cycle continues with an expansion of the grasses which typically regrow faster compared with woody species (D'Antonio and Vitousek, 1992; Freifelder et al., 1998; Hughes et al., 1991).

As a result of increased fire, dry woodlands dominated by native species have been converted to non-native grasslands and shrublands (Ainsworth and Kauffman, 2009). Continued conversion of dry forest to grassland accelerates the loss of dry forest as well as the frequency and intensity of fire (Janzen, 1988). In addition to the perpetuation of the grass/fire cycle, studies in moist evergreen forests have found that conversion from forest to grassland results in microclimate changes from humid to drier and hotter conditions which favor higher fire frequencies and intensities (Nepstad, 1989; Nepstad et al., 1991; Uhl and Buschbacher, 1985; Uhl and Kauffman, 1990). However, it is unknown whether the patterns would be the same for open dry forest habitat (Freifelder et al., 1998).

Fire modeling and remote sensing have provided further understanding of the fire potential among dry forests which are dominated by invasive grasses. Research using fire modeling for a Hawaiian dry forest site has found that under similar synoptic conditions, fires originating in grasslands will spread much faster than those ignited in woodland (Freifelder et al., 1998). The modeling revealed that wind speed was significantly greater among grassland compared with woodlands and the most important driver of differences in the modeled spread of fire between grassland and woodlands. Wind speed in woodlands tends to be lower than open grasslands due to the aerodynamic drag created below the canopy. Furthermore, wind may increase evaporation and directly perpetuate the spread of fire (Freifelder et al., 1998). Although fire models are useful for estimating grass-fuel extent, biomass, and moisture content at a regional scale, they often rely on environmental data layers such as elevation, albedo, rainfall, temperature, and evapotranspiration which may not be available from field or remote sensing measurements (Varga and Asner, 2008). As an alternative to fire models, Varga and Vitousek (2008) proposed the use of airborne hyperspectral and light detection and ranging (LiDAR) measurements in order to quantify the extent of invasive grasses acting as fuels as well as the potential for fire to spread. This technology represents a quicker approach due to the ability for fully automated data analysis and thus, is very useful for continuous monitoring and management of fuel loads.

2.4.3 Invasive Plant Species

Compared with the impacts of anthropogenic induced climate change and greenhouse gas emissions, biological invasions have caused greater species extinctions, globally (D'Antonio and Vitousek, 1992). The Hawaiian islands are highly susceptible to plant invasions due to the geographically isolated conditions in which native species evolved as well as factors which prevent them from competing with non-native species, such as dispersal limitations and slow growth (Denslow, 2003; Fordham and Brook, 2010). Invasions result when species are moved from one place to another, both accidentally and purposefully (D'Antonio and Vitousek, 1992). Although not a direct form of forest degradation, invasive species have profoundly impacted Hawaii's dry forest by outcompeting native species for light, nutrients, and water, and changing ecosystem functioning (Blackmore and Vitousek, 2000; Cordell et al., 2002; Cordell and Sandquist, 2008; D'Antonio et al., 2000; Litton et al., 2008; Mack and D'Antonio, 2003;

Vitousek, 1990; Weller et al., 2011). The presence and spread of invasive grasses has increased both the frequency and intensity of fires throughout Hawaii. Studies using radiocarbon dating of fossil charcoal collected from bog sediment cores suggest that wildfire occurred throughout Hawaii's geologic history due to lightening and volcanic eruptions (Ainsworth and Kauffman, 2009; Mueller-Dombois and Goldammer, 1990). However, these fires tended to be infrequent and localized near the source of ignition. Many of the invasive grasses present in Hawaii evolved in fire-prone regions which enables them to survive and recover quickly after fire (Christensen, 1985). Although native Hawaiian plants are also fire-adapted, their slow growth inhibits them from establishing post-fire (Ainsworth and Kauffman, 2009; Mueller-Dombois and Goldammer, 1990). As a result, grass invasion can promote a grass/fire cycle in which the spread of invasive grasses facilitates fire, and subsequently, further expansion of invasive grasses and the decline of natives (D'Antonio and Vitousek, 1992; Hughes et al., 1991). One grass-fueled fire can lead to the destruction of most native trees and shrubs in an area. For example, the invasion of C4 grasses (*Schizachyrium condensatum, Melinis minutiflora*) in a seasonal sub-montane woodland has caused an increase in both the frequency of fire and the total burned area in Hawaii Volcanoes National Park (Hughes et al., 1991). Before invasion and over a 48 year period, there were 27 fires with an average of 4 hectares burned per fire. Twenty years after invasion, there were 58 fires with an average of 205 hectares burned per fire. In this ecosystem, the invasion by grasses creates a positive feedback cycle through which non-flammable, mostly native vegetation converts to an invasive dominated grassland with low diversity (Hughes et al., 1991). Land clearance for agriculture or cattle ranching allows exotic grasses to pervade the forest and then spread after fire disturbance. Furthermore, interconnected fuel loads are formed when invasive grasses colonize cleared land by volcanic eruptions resulting in a greater potential for widespread impacts by fire (Adkins et al., 2011; Hughes et al., 1991; Williams and Black, 1994).

The introduction of non-native perennial grasses, coupled with extensive deforestation of dry and mesic forests, occurred in the mid-1800s by Europeans to facilitate large-scale ranching in Hawaii (Cuddihy and Stone, 1983). Introduced grasses, primarily African in origin, dominate much of the dry forest habitat in Hawaii and were brought by early Europeans in order to support cattle grazing (D’Antonio and Vitousek, 1992; Smith and Tunison, 1992). Feral goats, also brought over by the colonists, contributed to the spread of invasive species throughout Hawaii’s forest. Although the introduction of grasses to the island has been fairly recent in geologic time, nearly all fragments of dry forest have been invaded (Freifelder et al., 1998). In contrast to native species, most of the invasive grasses have evolved within habitats highly susceptible to fire and thus, have traits which favor post-fire regeneration (Adkins et al., 2011; Vogl, 1975). In general, invasive plant species tend to have a high tolerance to disturbance (Bryson and Carter, 2004) and produce widely dispersed seeds in large quantities (D'Antonio and Vitousek 1992) which are long-lived (Lonsdale et al., 1988), lack dormancy, and do not have special germination requirements (Adkins et al., 2011; Rejmanek, 1995). Due to their high growth rates and competitive advantage over native species for limiting resources, invasive grasses are ultimately able to displace native ecosystems (D’Antonio and Vitousek, 1992). Furthermore, grass invasions are particularly destructive to the Hawaiian dry forest because they are actively spread by humans, effectively compete with native species, alter nutrient cycling and regional microclimates, and can withstand as well as propagate fire (D’Antonio and Vitousek, 1992).

Today, some of the most common invasive grasses present in Hawaii include *Paspalum, Pennisetum, Melinus miutiflora, Hyparrhenia rufa, Cenchrus ciliarus,* and *Digitaria decumbens* originally from Africa, and *Andropogon virginicus* and *Schizachyrium condensatum*, two North American bunch grasses (D'Antonio and Vitousek, 1992).

In order to understand the impacts of invasive species on native dry forest vegetation, studies have evaluated species-specific germination characteristics of invasive grasses. Generally, the most destructive invasive plants in Hawaii are tropical and subtropical C4 grasses, which dominate large areas within dry and seasonally dry ecosystems (Hughes et al., 1991). Using field and laboratory experiments, Adkins et al. (2011) tested the influence of light and fire on the germination of fountain grass, a C4 bunchgrass introduced to Hawaii during the early 20th century (Adkins et al., 2011; Wagner et al., 1999). The study concluded that the invasiveness of the species relates to its ability to germinate in the absence of light as well as from depths of 5 cm which enable seeds to escape exposure to fire. However, fire was found to kill fountain grass seeds, which ultimately requires the species to resprout immediately following fire in order to establish. Other research on the impacts of fountain grass have found that the species negatively influences the ability for native tree species to attain below-ground resources such as water availability (Cordell and Sandquist, 2008).

Invasive trees have also impacted native dry forest species in Hawaii. Using measurements of photosynthetic gas exchange, nitrogen and water use efficiency, leaf water potential, and seasonal patterns of leaf production for native and invasive Hawaiian dry forest species, Stratton and Goldstein (2001) found that the high phenotypic plasticity of the invasive species enabled it to more effectively utilize resources than the native species. The phenotypic plasticity observed by the invasive species included high water and carbon dioxide uptake during the rainy season coupled with high leaf water potential during the dry season, thus, reducing water loss (Stratton and Goldstein, 2001). These studies demonstrate the potential for invasive species to cause widespread destruction of the Hawaiian dry forest. As a result, active management either through prescribed fires or invasive species extirpation will be needed in order to control their spread (Adkins et al., 2011; Cordell and Sandquist, 2008).

In addition to fire, invasive grasses in Hawaii also outcompete native species for resources and subsequently, alter ecosystem functioning. Generally, forest loss due to competition with invasive species tends to occur much slower than other more immediate processes, such as fire and grazing, but impacts native species over longer time spans (Cordell and Sandquist, 2008). In a study evaluating nutrient dynamics in an invaded Hawaiian woodland, invasive grasses were found to reduce growth and lower tissue nitrogen in seedlings of native shrubs when grown together after a wildfire (D'Antonio and Vitousek, 1992). Studies involving the removal of invasive grasses from native dry forest ecosystems corroborate these findings and suggest that native plants have greater access to soil nitrogen and sunlight as well as increased seedling recruitment after grass removal (Cabin et al., 2000; D'Antonio et al., 1998). Furthermore, in their study analyzing stable oxygen isotope oxygen ratios to assess the impacts of an invasive grass on native tree water-use efficiency, Cordell and Sandquist (2008) found that trees growing in the absence of the invasive grasses obtained a greater proportion of water from shallow soil sources and retained higher mid-day water potentials, particularly during drier months, suggesting greater water accessibility for native plants (Cordell and Sandquist, 2008). In order to evaluate the impact of invasive grasses on soil nitrogen (N) dynamics within a

Hawaiian dry woodland, Mack and D'Antonio (2003) measured net and gross N mineralization as well as nitrification in three vegetation plots with varying levels of grass invasion. The study found that changes in forest composition from native abundant to grass dominated influenced the timing and amount of N available for plant uptake by changing the local microclimate and soil organic matter composition. Other research has evaluated the impact of non-native grasses on aboveground and belowground carbon pools in Hawaiian dry forest (Litton et al., 2008, 2006). Comparing biomass estimates between native, invaded, and converted land cover, Litton et al. (2006) evaluated the differences in population structure and aboveground carbon pools. The study concluded that native forests had both higher species abundance as well as leaf biomass which prevented the intrusion of invasive grasses due to limited light availability. Furthermore, once forests were converted to grasslands, there was a reduction in the carbon sink strength in aboveground biomass. In a study quantifying the impact of invasive grasses on soil C pools and fluxes, grass invasion was found to increase the flux of carbon both into and out of soils without altering short-term C pools as long as the native forest canopy remained intact (Litton et al., 2008). These results suggest that as long as the forest is not completely converted to grassland, soil carbon stocks may be maintained. Additionally, conversion of dry forest to grasslands can also lower below-ground soil carbon storage due to the higher propensity for grazing, and subsequently, release of sequestered soil carbon to the atmosphere (Elmore and Asner, 2006). Overall, the impacts of invasive species go beyond losses in biodiversity and could result in consequences for ecological functioning.

2.4.4 Grazing

Although it was introduced by the early Europeans, grazing continues to be a major threat to the dry forest. In1983, the state of Hawaii contained about 800 ranches and beef was the third largest agricultural export (Smith et al., 1983). However, between 1970 and 1999, Hawaii's share of the beef market dramatically declined from 30% to about 10%, and the number of ranches decreased as well (Cox and Bredhoff, 2003). The continuing decline in Hawaii's beef economy results from the high cost of shipping livestock to the continental United States. Despite the decline in commercial beef production, grazers continue to threaten the Hawaiian dry forest by consuming tree seedlings and saplings which prevents forest regeneration (Scowcroft, 1983; Stone, 1985). In addition to aboveground biomass, grazing has also been found to reduce belowground carbon storage. In a study using hyperspectral remote sensing and soil organic carbon (SOC) measurements, Elmore and Asner (2006) evaluated the impact of forest to pasture conversion on SOC. Long-term grazing was found to lower SOC, more so than changes associated with elevation, due to a decrease in overall vegetation cover, increased erosion in grazed areas, and changes in species composition.

Despite the threats to the dry forest, grazing acts as a double-edged sword after the initial grazing disturbance enables the establishment of invasive grasses (Blackmore and Vitousek, 2000). Continued grazing contributes to a steady, but slow decline in forest cover. However, if grazing stops, grass biomass accumulates rapidly and increases the potential for frequent and more intense fires. Using classified air photos from 1954 to 1994 and fire modeling, Blackmore and Vitousek (2000) assessed the impacts of grazing on a dry forest in North Kona. The modeling concluded that under fire enhancing conditions such as increased wind and dryness, there was a low chance of fire in grazed grasses. Grazing was also found to reduce fire risk by limiting the spread of more flammable grass species. Furthermore, the fire model results indicated that wind exposure was critical, and that widespread fires could only result under high wind speeds at ground level with sparse tree cover and high grass abundance (Blackmore and Vitousek, 2000; Freifelder et al., 1998). While grazing thins the forest canopy and exposes fuels to wind, its removal increases the risk of fire due to the mass accumulation of fuel. As a result, a balance must be found between the positive and negative impacts of grazing on the dry forest.

Although cattle grazing can have negative impacts on the dry forest ecosystem, other threats including fire, invasive species, and pigs may be of more concern due to the continued decline of commercial ranching. However, preservation of the forest may economically benefit commercial ranchers who rely on tourists to pay premium prices for beef (Cox and Bredhoff, 2003). Furthermore, ranchers with pastures near threatened and endangered species may be forced to move their herds elsewhere (Erdman et al., 2000). As a result, ranches are contributing to conservation efforts through projects including seed propagation, fencing, controlled grazing techniques, weed management, and community outreach. Through their efforts, the ranchers hope to demonstrate how tightly controlled grazing can help manage invasive species and protect native species, so that they can continue to use their pastures. Another potential economic benefit for the ranchers would be tours of native forest habitat, which is often found within their privately owned land (Medeiros et al., 2014). Overall, coordination between conservation managers and ranchers will be important to ensure a balance of grazing among different patches of the dry forest.

2.5 Restoration Effort

2.5.1 Pigs

Current techniques to manage pig populations in Hawaii include fencing, cage or corral traps, snares, aerial shooting, ground shooting, and hunting with dogs (Littauer 1993, 2007, Campbell and Long 2009). Although fences are effective and help define management areas, they are often expensive and only act as a short-term solution. Cages are useful in that they can catch multiple animals at once as well as animals who know how to avoid the other techniques. However, cages are not very effective in areas with abundant food sources, require frequent checks, and are bulky to move and transport. While snares are the least expensive method, they may potentially harm other animals, can be broken by larger pigs, and can only catch one pig at a time. Aerial shooting has the benefits of only removing the target animal, quickly and with reduced ecological damage, but is costly and can be dangerous in rugged topography. Similarly, ground shooting is a highly selective technique which can also be done during the night. However, requires much time and effort with low success rates when population densities are low. Lastly, hunting with dogs has proven successful for targeting pigs which have evaded other methods, removing pigs in a short amount of time, and providing public access to hunting resources, but is limited due to potential dog injuries and deaths, labor intensive dog training, potential for harming other wildlife, and potential heat stress to the dogs. Overall, effective management will incorporate multiple techniques which are suitable to the managed area (Campbell and Long, 2009).

2.5.2 Fire and Invasive Grasses

In order to limit fires in dry forests, it is necessary to reduce the abundance of exotic grasses. In a 21 month long study, Cabin et al. (2002) evaluated the effects of microsite, water, weeding, and direct seeding on native and exotic species reestablishment. The study concluded that water was a primary limiting factor for both native and exotic species; however, native species were much more vulnerable to water stress. In addition, weeding was found to not effectively improve the performance of native flora. Overall, these findings suggest that exotic grasses highly influence native species establishment, and when controlled, will not deter restoration efforts for at least a few years. In addition, in-situ direct seeding is a viable and cost-effective method to facilitate Hawaiian dry forest species regeneration. In another study, seed rain and seedling and juvenile dynamics were monitored over 3 years to assess the effects of previous restoration treatments on natural forest regeneration compared with vegetation with no prior restoration (Thaxton et al. 2010). The results corroborated those of Cabin et al. (2000) finding that seedlings were much more successful in areas with prior restoration than without. This suggests that a long-term approach is necessary for Hawaiian dry forest restoration and that continuous invasive grass removal is needed to allow for native species to successfully regenerate.

2.5.3 Grazing

Although grazing has been found to be crucial for limiting the spread of invasive grasses, other research suggests that prescribed burns and the use of chemicals may be more effective for dry forest restoration (Castillo et al. 2007). Another method for eradicating feral ungulates in managed areas is to use fences. In a study evaluating the effects of ungulate grazing, Cabin et al. (2000) compared dry forest flora within a preserve with adjacent flora which has undergone continuous grazing since a fence was installed 40 years prior. The study found that the fenced area had much more diverse vegetation with greater native overstory and understory species. However, the widespread abundance of invasive fountain grass along with predation by introduced rodents suppressed the regeneration of native species until they were recently removed. The exclusion of ungulates was found to be a necessary and critical initial step for native forest regeneration, however, would not be sufficient enough to maintain the remaining dry forest patches. Furthermore, the use of fences was found to both regenerate native species and enable the establishment and potential invasion of exotic plant species. Despite these findings, other research suggests that controlled grazing may be an essential component to balancing the positive benefits of invasive species suppression with the negative impacts of native species loss (Blackmore and Vitousek 2000).

2.5.4 Restoring Native Species

Deciding the best places to implement native species restoration has posed challenges for researchers due to a dearth in knowledge surrounding the life history characteristics and environmental requirements for dry forest species. In order to determine optimal areas for restoration, research has compared the physiological performance differences between exotic and native species by measuring maximum rates of CO_2 assimilation, water use efficiency, daily carbon gain, and leaf morphology (Cordell et al. 2002). The study found a strong, positive correlation between physiological traits which are species-specific and species aboveground biomass, which allows for an estimation of individual species boundaries at different light exposures and subsequently, identification of potential restoration sites. Outplanting has been one technique used by conservation managers and involves transplanting endangered, native individuals grown in nurseries to protected areas (Allen 2000). However, this is often done without an understanding of how the dry forest functions as well as species composition and functioning prior to degradation due to a lack of research (Rovzar, 2013). A lack of understanding regarding the past state of the Hawaiian dry forest makes it difficult for researchers to know the model that dry forest restoration should follow (Questad et al., 2014; Rovzar et al., 2016). Supporting this conclusion, another study found that although the outplanting of dry forest species into a Hawaiian dry forest preserve increased the population of many endangered species, overall, there was high mortality of common and important species (Cordell et al. 2008). This suggests a need for outplanting programs to consider ecosystem functioning, not just species success, when assessing the success of management.

Broadcast seeding has also been used and involves broadcasting seeds pretreated to enhance germination followed by applying herbicide to reduce invasive species in the area (Brooks et al. 2009). In a two year study comparing treatments including broadcast seeding, herbicide, and broadcast seeding combined with herbicide, Brooks et al. (2009) found that broadcast seeding combined with herbicide was most effective in increasing native seed germination and survival due to an increase in seeds as well as the creation of a favorable microclimate resulting from invasive grass removal. When combined with other restoration techniques, broadcast seeding is a viable option for restoring large areas with limited accessibility (Arnup et al. 1988).

2.6 Conclusion

Although research has enhanced our understanding of dry forest degradation, there needs to be greater efforts towards quantifying the impacts posed by different threats in order to understand which factor is most important to manage. In addition, threats should be assessed annually to evaluate the rate at which a threat can cause changes in dry forest ecosystems. While previous research has shown the aboveground forest degradation caused by different threats, greater research should evaluate the impacts on belowground process such as nutrient cycling, which influences aboveground dynamics. Additionally, much research has been directed towards understanding the impact of invasive grasses and fire on Hawaii's dry forest while fewer studies have examined the impacts of pigs and livestock grazing. An ISI Web of Knowledge search using the key words "Hawaii" "invasive" and "grass" generates 60 results while using "Hawaii" "invasive" and "pig" results in only 14 articles. One possible reason for this discrepancy could be the magnitude of risk associated with each, which would cause scientists to divert more attention to the one posing a greater risk. Due to the grass fire cycle and the ability for a single fire to destroy large fragments of dry forest, invasive grasses may be perceived by scientists as a much greater conservation risk, and thus, more likely to garner attention.

In regards to restoration, research needs to identify the ecological factors influencing the distribution of different species. Remote sensing and GIS are powerful tools which will allow for an understanding of how environmental variables impact both native and non-native distribution. Furthermore, these tools can be used to quantify the extent of impacts on a large scale. Overall, grazing and uprooting by feral ungulates, fire, and invasive species can have significant and often times compounding impacts on Hawaiian dry forest. In order to determine the best management techniques, it will be necessary to identify how these factors influence the dry forest ecosystems, both on their own and when they interact.

2.7 Figures

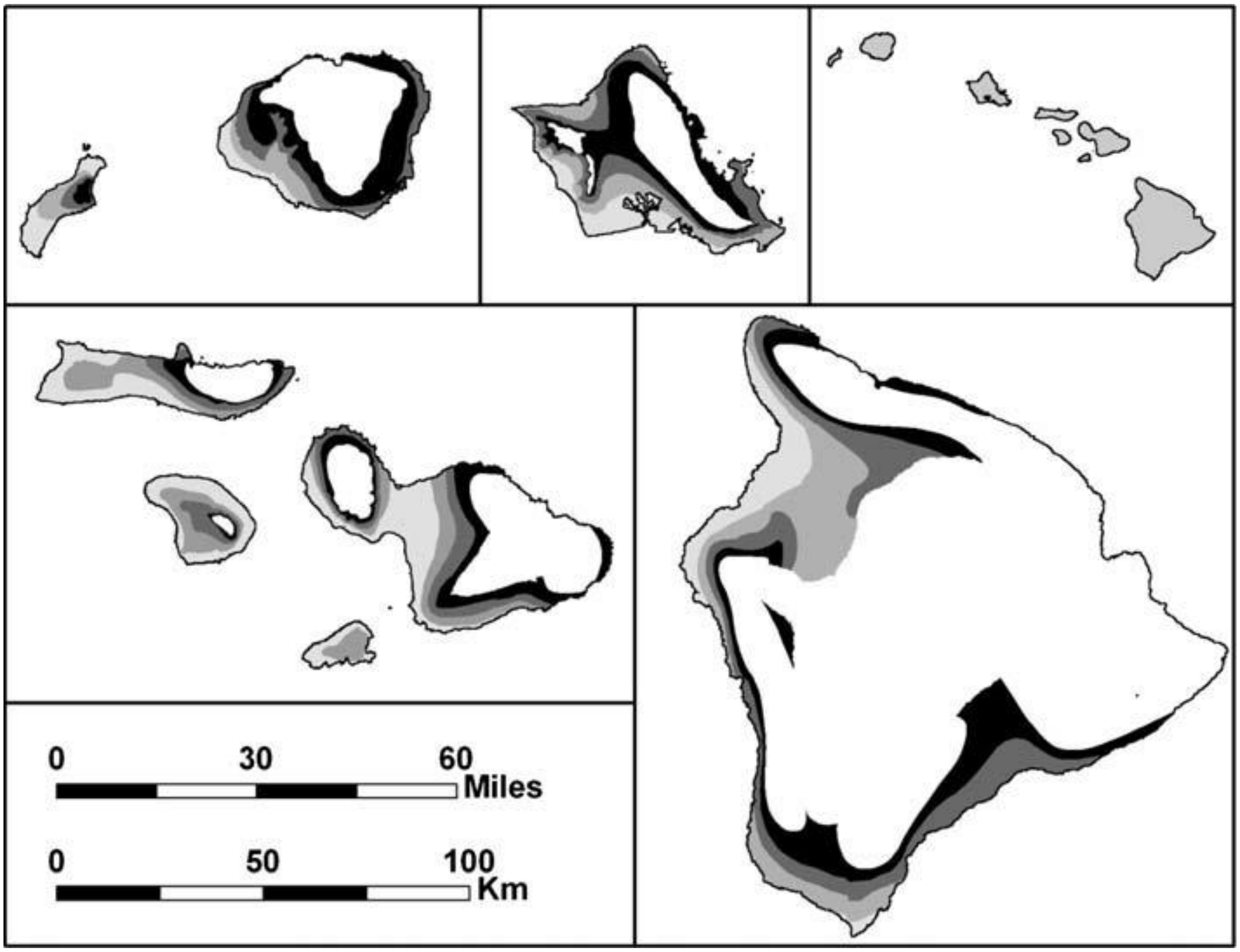
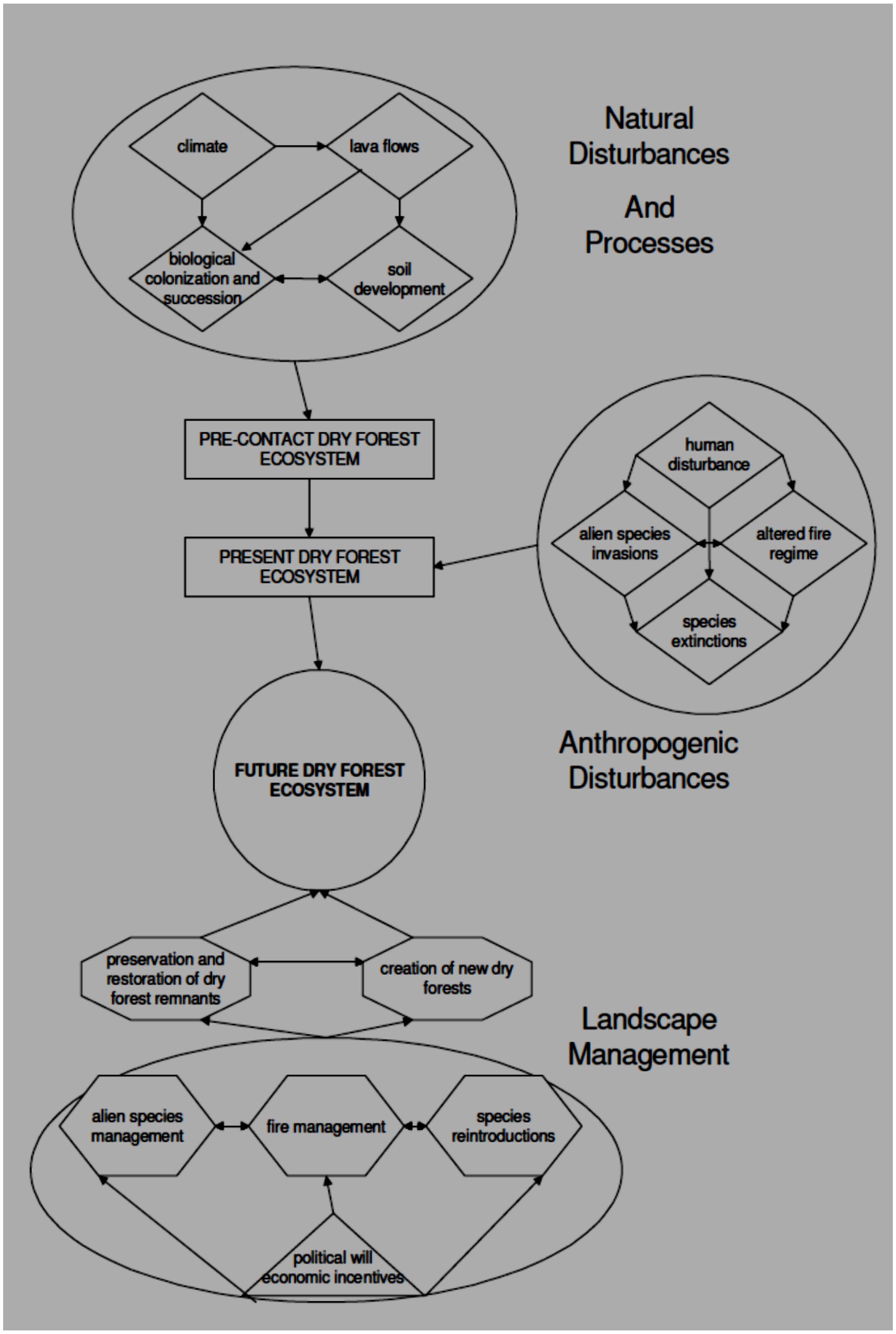


Figure 1: The map above illustrates the potential extent of the dry forest region based on climate regimes ranging from arid (light gray) to seasonally mesic (black). In reality, these regions contain highly degraded dry forest at best. All white areas are non-dry forest. Adapted from Price et al. (2008).



Natural Disturbances And Processes
climate
lava flows
biological colonization and succession
soil development
PRE-CONTACT DRY FOREST ECOSYSTEM
PRESENT DRY FOREST ECOSYSTEM
human disturbance
alien species invasions
altered fire regime
species extinctions
Anthropogenic Disturbances
FUTURE DRY FOREST ECOSYSTEM
preservation and restoration of dry forest remnants
creation of new dry forests
Landscape Management
alien species management
fire management
species reintroductions
political will
economic incentives

Figure 2: The flowchart above depicts the impact of different threats to Hawaii's dry forest before human arrival, at present, and potentially in the future from Cabin et al. (2004).

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CHAPTER 3

3. Landscape to site variations in species distribution models for endangered plants

3.1 Abstract

Present global plant extinction rates are 100 to 1000 times greater than pre-human levels and this is especially true on oceanic islands. There is a great need to model the distributions of endangered plants for reintroduction on oceanic islands, however, there are still questions concerning what is the most appropriate spatial scale and which environmental metrics should be included in order to guide restoration efforts. We examine the impact of spatial scale (1 km, 250 m, 10 m), environmental metrics (climate, topography, soils), and species overlap for 11 rare and endangered species in the dry forest of Oahu, Hawaii, which is one of the world's most endangered ecosystems, and contains some of the highest resolution data on species locations and environmental metrics for an oceanic island. At all spatial scales, the species distribution models reliably differentiated between occupied habitat and background for all 11 species (AUC ≥ 0.92). The relative importance of the environmental metrics did not vary across spatial scales with soil great group contributing most to the models followed by elevation, and mean precipitation of the driest quarter. The percent of the total island area with niche overlap for two or more species did not show any pattern with grain size, however, the 10 m model contained the largest areas of niche overlap for two or more species. There were 1,292 10 m pixels on Oahu where models predict niche overlap for eight endangered species, however, only 1.2% of the total area is currently in protected areas. Results suggests that species distribution models are useful for predicting habitat suitability at all scales (1 km, 250 m, 10 m), environmental metrics

do not change across scales but high resolution data on soils, topography, and precipitation are needed, and 10 m resolution data are the best for informing restoration decisions for the endangered species on Hawaii and other oceanic islands.

3.2 Introduction

Present global plant extinction rates are 100 to 1000 times greater than pre-human levels and could increase 10-fold by next century (Pimm et al., 1995; Ricketts et al., 2005a). This is especially true for plants on oceanic islands that are extremely deforested and degraded and experiencing some of the highest extinction rates on the planet (Caujapé-Castells et al., 2010; Barry Rolett and Diamond, 2004; Triantis et al., 2010). Native species reintroduction is one widely used method applied to conserving endangered species, which often face population growth challenges due to dispersal limitations and transient seed banks (Clark et al., 2007b; Thompson, 1997b). Despite its widespread use, reintroduction success rates are overall low due to the difficulty in identifying suitable habitat for restoration (Drayton and Primack, 2012; Godefroid et al., 2011; Questad et al., 2014). Thus, there is a need for methods that can identify suitable habitat for conducting endangered species reintroductions and evaluate the environmental factors influencing their distributions.

In Hawaii, almost half of all tropical dry forest tree and shrub species are listed as federally threatened or endangered (Pau et al., 2009). Historically, Hawaiian dry forest ecosystems contained high species richness and endemism (Rock, 1913), however, destruction of over 90% of the dry forest has resulted in widespread species loss (Bruegmann, 1996; Cabin et al., 2000; Sakai et al., 2002). Despite the pressing need for conservation of this ecosystem, management is greatly hindered by a lack of knowledge regarding the current distributions of

Hawaiian dry forest species as well as potential sites for reintroduction (Pau et al., 2009). Although previous research has used GIS spatial analyses to map Hawaiian plant ranges (Price et al., 2012), none have used a predictive modeling approach to target sites for endangered species reintroduction.

In the past decade, species distribution modeling (SDM) for rare and endangered species has rapidly progressed and become an informative tool for identifying key areas for reintroduction and habitat conservation (Butler, 2009; Gallardo and Aldridge, 2013; Gogol-Prokurat, 2011; Guisan et al., 2006; Loiselle et al., 2003; Pearson et al., 2007; Thompson, 2004; Wilson et al., 2013). SDMs, also referred to as ecological niche models or habitat suitability models, are statistical models which predict the potential geographic distribution (or habitat suitability) of a species by measuring the relationship between a species' spatial distribution and select environmental variables (Franklin, 2009b). In order to identify and prioritize conservation areas, maps identifying habitat suitability are essential for oceanic islands like Hawaii (Elith and Leathwick, 2009; Franklin, 2009b).

Recently, there has been debate regarding the appropriate scale for SDMs, which are often constrained by coarse-resolution climate data (Austin and Van Niel, 2011; Franklin et al., 2013; Guisan et al., 2007; Niamir et al., 2011; Potter et al., 2013). In general, ecological modeling has been applied mainly for evaluating broad-scale species distributions, with few studies applying multi-scale techniques for an hierarchical assessment of potentially suitable habitat (Cabeza et al., 2010; Fernández et al., 2003; Razgour et al., 2011). On average, the pixel size used in SDMs for plants tend to be ca. 1,000 times larger than the species being modeled, resulting in an inability for modeled distributions to capture the micro-environment in which a species lives (Potter et al., 2013). Accounting for microclimates is particularly important for oceanic islands with rugged terrain which often results in topographically controlled climate variation, only detected at 10-100 m scale (Caujapé-Castells et al., 2010; Franklin et al., 2013). Previous studies have successfully modeled potential distributions for rare plant species at fine-scale resolutions (25-250 m) (Engler et al., 2004; Gogol-Prokurat, 2011; Guisan et al., 2006; Marage et al., 2008; Williams et al., 2009); however, even scales of this resolution may not be fine enough. To be useful for local conservation planning, SDMs for rare and endangered species with low mobility and patchy distributions should identify suitable habitat at a similar scale to patch size (Trani, 2002). Thus, identifying the best spatial scale of SDM's for endangered species is of wide importance.

Variable choice has been another area of debate within the SDM community with some arguing that climate alone can be used in SDMs at coarse resolutions to broadly identify species distributions (Araújo and Peterson, 2012; Pearson and Dawson, 2003), whereas others suggest that SDMs based solely on coarse-scale climate data may not capture micro-environments determined by local topography (Ashcroft et al., 2009; Austin and Van Niel, 2011; Dobrowski, 2011; Franklin et al., 2013). While some studies have examined the contribution of variables to SDMs across spatial scales, few have compared variable contributions between even finer spatial resolutions. This is partly due to the lack of high-resolution spatial data for oceanic islands. Currently, globally comparative environmental metrics for oceanic islands are available at a1 km resolution for climate and up to 30 m resolution for elevation and topography. Furthermore, comparative geologic and soils data are limited. Despite the increased use of species distribution modeling for conservation planning, few studies have compared model predictions and variable importance for SDMs at different fine-scale resolutions: landscape (1 km), local (250 m), and site (10 m) levels for rare and endangered species on oceanic islands. This could identify the best environmental metrics and spatial resolution that should be used on other oceanic islands and other threatened ecosystems.

This research seeks to answer three primary questions relating to modeling rare and endangered species distributions on oceanic islands, such as Hawaii. First, does model accuracy significantly vary between a landscape, local, and site scale model? It is expected that coarser spatial scales will have lower model accuracies and higher predicted areas. Second, what combination of environmental metrics and spatial scale yields the best result for modeling rare and endangered plants on oceanic islands? In particular, we identify association among environmental metrics and identify if predictors of species distribution change across spatial scales. Third, does the total number of species with overlapping suitable habitat (niche overlap) vary between spatial scales?

3.3 Materials and methods

3.3.1 Study area

We created SDMs for rare and endangered plant species found in the seasonally dry forest on Oahu, Hawaii. Oahu is approximately 3.7 million years old and covers an area of 1,546 km^2 with a maximum elevation of 1229 m (Macdonald et al., 1983). Two mountain ranges, the Wai'anae and Ko'olau, contribute to variation in temperature and precipitation across the island. Mean annual precipitation is highly variable (50 cm to 715 cm) with the rainy season occurring from November to March and the dry season persisting from April through October (Walker, 1990). Mean temperature ranges from 15.7°C to 23.8°C (Giambelluca et al., 2013). Historically, native tropical dry forests, scrublands, and grasslands occurred at low elevations and on the rainshadow or dry sides of the Wai’anae and Ko’olau mountain ranges (Cuddihy et al., 1989) . On Oahu, there are 33 federally threatened and endangered dry forest plant species, many of which are on the brink of extinction (Pau et al., 2009).

3.3.2 Species and environmental data

Location data for 10 federally threatened and endangered plant species and one endemic dry forest plant species, that has experienced a recent decline in population size, were obtained from the Oahu Army Natural Resources Program (Gramling, 2005; Oahu Army Natural Resources Program, 2010), and are the only known living occurrences on Oahu (Table 1). These data are highly, spatially accurate due to precise GPS records of plants in the field, continuous monitoring, and searches conducted by botanists to find new individuals (Oahu Army Natural Resources Program, 2010). Only presence data were used for this study due to a lack of knowledge regarding the species historical distributions.

Climate, topography, and soil great group variables were used for creating SDMs at a landscape (1 km), local (250 m) and site (10 m) scale on Oahu, Hawaii. Mean monthly temperature and precipitation grids at a 250 m resolution were provided by T. Giambelluca (Giambelluca et al., 2013). Widely used bioclimatic variables at a 1 km (30 arc second) resolution were downloaded from WorldClim version 1.4 (Hijmans et al., 2005). Using the 250 m climate grids, 19 bioclimatic variables representing biologically meaningful variables for characterizing a species’ realized niche were calculated using ArcGIS 10.0. These variables are similar to the widely used WorldClim bioclimatic variables, but are at a finer resolution (250 m) and are based upon measurements from an increased number of weather stations. For the 10 m resolution SDMs, the bioclimatic variables were statistically downscaled using bilinear interpolation. This process involves averaging the four nearest grid cells to the target cell after each is weighted based on its distance to the target cell (Newbold et al., 2009).

Elevation data were downloaded from the U.S. Geological Survey National Elevation Dataset (NED) at a 10 m and 250 m resolution (U.S. Geological Survey, 2015). Slope, aspect, and curvature were calculated as continuous variables using ArcGIS 10.0. Additionally, soil great group (30 categories) representing subdivisions of suborders was downloaded at a 10 m resolution and included in the models as categorical variables (Hawaii Statewide Planning and GIS Program, 2016). Soil great group was resampled to a 250 m and 1 km resolution using nearest neighbor statistics.

3.3.3 Data analysis

SDMs were created at 10 m, 250 m, and 1 km spatial scales for 11 rare and endangered species. Presence data for rare and endangered species are often limited due to low population size and/or difficulty in finding new individuals. As a result, SDMs for rare species are often created using the MaxEnt (maximum-entropy) algorithm which has been found to produce robust results with limited and spatially biased presence data (Anderson et al., 2006; Loiselle et al., 2008; Pearson et al., 2007). Additionally, Maxent has the benefit of assessing variable importance by measuring the contribution of each variable to the predicted distribution (Kumar and Stohlgren, 2009; Ortega-Huerta and Peterson, 2008). Maxent version 3.3.3k was used to model habitat suitability for 11 species on Oahu using default parameters and 10,000 random background points (Elith et al., 2006; Phillips et al., 2006a). Due to limited presence data, all species' occurrences were used in both model training and testing.

Assessing the predictive success of SDMs often involves dividing occurrence data into training and testing groups. However, this method is inappropriate for this study due to the small sample sizes for each species (Pearson et al., 2007). As an alternative, 10 bootstrap iterations were conducted to assess model performance. With bootstrapping, occurrence data points are randomly selected with replacement. The mean and range from the bootstrap samples are then used to validate the model (Pearson et al., 2007). The averages of the ten replicate SDMs for each species were validated using the threshold-independent metric, Area under the Receiver Operating Curve (AUC). The AUC value ranges between 0 and 1.0 and represents the probability that the model ranks a random presence location higher than a random background site (Phillips et al., 2006a; Phillips and Dudík, 2008). Overall, the AUC metric provides an assessment of how accurately the model predicts the probability of occurrence for a species within a given area. Models with AUC values greater than 0.75 may be useful for identifying the potential distribution of a species (Elith et al., 2011). A non-parametric Wilcoxon-rank sum test was performed to assess if the AUC significantly differed from random prediction (0.5).

Principal component analysis (PCA) was performed on all the variables using a correlation matrix to assess variable correlations for models at all three spatial resolutions. Variables with correlations over 0.75 were removed so that only one of the correlated variables was used in the model. Final variable choice was decided by running separate models using only one of the correlated variables and assessing model AUC values. The final variable set was reduced to include elevation, slope, aspect, curvature, soil great group, and precipitation of the driest quarter. Precipitation of the driest quarter was chosen over other precipitation metrics because it produced the highest model AUC value compared with models run with the other correlated precipitation variables. Models for all species at all resolutions were re-run using the reduced variable set. Model validation was conducted for both the full and reduced variable models.

Binary maps of presence/absence were created using a minimum training presence threshold (MTP). This threshold was applied because the species' locations are precise and highly accurate. Use of the MTP threshold results in areas identified as suitable to be as least as suitable as the species' presence locations (Pearson et al., 2007). Many SDMs evaluate models based on the minimization of errors of omission and commission. However, for modeling aimed at identifying sites for reintroduction, commission (predicted presences in unoccupied locations) is the research interest rather than a source of error (Araújo and Peterson, 2012). As a result, models generated for reintroduction purposes should focus on minimizing predicted absences in occupied locations, referred to as omission errors (Peterson et al., 2008). A one-tailed, independent t-test was performed to assess if the MTP varied significantly between scales for all species.

The total percent of area predicted suitable based on the binary models was calculated for each species at all spatial resolutions. A one-tailed, independent t-test was performed to evaluate if the area predicted suitable varied significantly between scales for all species. Additionally, the spatial congruence index for each species was calculated by evaluating the spatial overlap of suitable habitat for models at each scale (Franklin et al., 2013). This index is based on a Dice Sorensen similarity measure: 2a/ (2a + b + c), where a is the overlap of suitable area at both scales, b is the area predicted suitable at only the coarser resolution, and c is the is the area predicted suitable at only the finer resolution. A higher index corresponds to a higher degree of spatial congruence (Legendre and Legendre, 1998). Lastly, niche overlap was calculated for all species at each spatial scale to evaluate potential sites for multi-species reintroduction. GIS data on land ownerships and protected areas were overlaid on locations of overlap for two or more species to identify areas where ecosystem-level reintroduction could occur (Hawaii Statewide Planning and GIS Program, 2016).

3.4 Results

3.4.1 Model predictions and agreement across scales

At all spatial scales, the SDMs reliably differentiated between occupied habitat and background for all 11 species ($AUC \geq 0.92$). Compared to random prediction (0.5), the AUC scores for all SDMs were highly statistically significant ($AUC \geq 0.92$, $p < 0.001$, degrees of freedom = 10, $t = 4.297$, one-tailed Wilcoxon rank sum test of AUC; Fig. 1). There was no significant variation between AUC values at different spatial scales for each species. However, the total area predicted suitable, based on the MTP threshold, varied by scale for each species (Fig. 2). Area predicted suitable was greatest for five species at a 10 m, two species at a 250 m, and four species at a 1 km spatial resolution. However, the differences in area predicted suitable between the scales for each species was not statistically significant ($t = 0.7649$, degrees of freedom = 10, $p = 0.13$). The MTP threshold was higher at a 1 km spatial resolution for nine species. The MTP threshold was lowest at a 10 m spatial resolution for eight of the species. The MTP threshold values were significantly different between the 10 m and 250 m models and the 10 m and 1 km models ($t = 2.764$, degrees of freedom =10, $p < 0.01$).

3.4.2 Environmental metrics

The relative importance of the variables did not vary across spatial scales. On average and for each species at all spatial resolutions, soil great group contributed most to the models followed by elevation, mean precipitation of the driest quarter, slope, aspect, and curvature (Table 2). The percent contribution to the predicted distribution was not significantly different among species (one-tailed t-test , $t = 1.98$, degrees of freedom = 10, $p < 0.01$). PCA analysis showed high correlations (>0.75) between all temperature metrics with all precipitation metrics and all of the temperature metrics were also highly correlated with elevation. As a result, elevation was used as a proxy for temperature, and no other temperature metrics were included in the model. At a 1 km spatial scale, elevation was highly correlated with mean annual temperature, maximum, minimum, and mean seasonal temperatures, and all precipitation metrics. Elevation was found to be highly correlated with the same temperature metrics but not precipitation metrics at 250 m and 10 m spatial resolutions. At all spatial scales, very low correlations were found between elevation, slope, aspect, curvature, soil great group, and precipitation variables.

3.4.3 Spatial niche overlap

The highest spatial congruence (overlap) was between the 10 m and 250 m models for 91% of all species (Fig. 3). Increasing grain size from 250 m to 1 km reduced the spatial congruence with SDMs at a 10 m spatial scale from an average of 29% to 22%, respectively. The total number of species with overlapping suitable habitat increased from eight species for the 10 m and 250 m models, to ten species for the 1 km models (Fig. 4). The percent of the total island area with niche overlap for two or more species was highest for 10 m models (36%), followed by 1 km models (13%) and 250 m models (12%). There are 1,292 10 m by 10 m areas on Oahu where the models predict niche overlap for eight endangered species. Of these areas, 1.3% of the total is on private land while 98.7% is on public land, and only 1.2% of the total area occurs in currently protected areas.

3.5 Discussion

3.5.1 Spatial scale and environmental metrics

The AUC values were found to be highly statistically significant at all spatial scales and with little variation between the values at different resolutions. This suggests that the models using high resolution location data are potentially useful for predicting habitat suitability and informing conservation for the modeled species. However, the inability for the AUC to determine the most appropriate model corroborates other research findings that the AUC may not be the best indicator of model performance (Lobo et al., 2008; Pearson et al., 2006).

Soil great group is the most important variable for predicting the distribution of endangered, endemic dry forest Hawaiian plants at landscape, local, and site-specific levels. In particular, Tropohumults-Dystrandepts and Oxic Rhodustalfs are the underlying soil great groups for the area predicted suitable for *A. sandwicense*. Other species with varying soil great groups include *H. brackenridgei* which was predicted to be found on Orthoxic-Tropohumults and *E. sandwicense* which was predicted to be found on Oxic rhodustalfs and Tropohumults-Dystrandepts. Overall, most species were predicted to occur in areas with Tropohumults-Dystrandepts including *A. micrococcus, E. koolauensis, E. kaenana*, *E. herbstii*, *P. forbesii*, *P. kaalae, P. macrocarpa*, *F. neowawrae*. Tropohumults-Dystrandepts is a soil association comprised of tropohumults, dystrandepts, and histosols. These soils tend to be highly acidic, well-drained soils containing reddish brown clay and are found in areas of Oahu with deep, V-shaped drainage ways and narrow ridges (Soil Survey Staff, 2016). Previous research has found guinea grass to occur on this soil great group type (Ellsworth et al., 2014). This finding supports results from previous studies on continental areas which have found soil variables to be important variables in predicting species' distributions (Austin and Van Niel, 2011; Beauregard and de Blois, 2014; Dubuis et al., 2013). These results stress that soil variables will be needed for modeling habitat suitability for rare and endangered species found on oceanic islands with rugged topography. Previous studies suggest that many SDMs are constrained by coarse resolution climate data, and as a result, do not account for microclimates (Austin and Van Niel, 2011; Potter et al., 2013; Suggitt et al., 2011; Varner and Dearing, 2014). Our result showing that soil and topographic variables are most important for predicting habitat suitability across all species suggests that high resolution topography data may be a better option than relying solely on coarse climate grids, especially when models are used to inform endangered plant reintroductions on small tropical islands. In conjunction with high resolution topography, and for tropical islands with rugged topography, the only climate variable which may be necessary for modeling the potential distribution of a rare species is precipitation. In tropical dry forests, a distinct dry season is one of the primary characteristics, which differentiate it from wetter ecosystems. Thus, dry season precipitation was of importance due to its relevance within dry forest ecosystems. Understanding how precipitation influences the species being modeled will allow for a decision concerning which precipitation variable to choose when precipitation metrics are all highly correlated. In our study, precipitation was found to correlate with elevation at the 1 km scale. However, at the 250 m and 10 m spatial scales, elevation was not found to be highly correlated with precipitation. This finding elucidates the importance of accounting for differences in topography which can drive micro-climates.

Our study suggests that freely available elevation data (e.g. USGS NED) can be used to map habitat suitability on Oahu, and at fine spatial scales, can be used as a proxy for temperature. For regions lacking reliable climate data due to limited weather stations, high-resolution elevation data (e.g. ASTER 30 m) may be a potential substitute for insufficient temperature data on oceanic islands. Recent studies have identified airborne lidar imagery as an appropriate variable for species distribution modeling due to its ability to capture micro-topography at fine spatial resolutions (Bradley and Fleishman, 2008; Buermann et al., 2008; Farrell et al., 2013; van Ewijk et al., 2014). Although lidar data are costly and not yet globally available, there appears to be a great need for lidar data on topography for all oceanic islands.

3.5.2 Spatial congruence

The AUC values were found to be highly statistically significant at all spatial scales and with little variation between the values at different resolutions. Despite similar AUC values, the spatial congruence between the finest and coarser scale resolutions for all but one of the species (*Abutilon sandwicenses*) decreased with coarser grain size, suggesting less similarity between models with greater differences in scale. This discrepancy in spatial congruence suggests that coarser resolution in environmental variables may lead to increased generalization errors (Franklin et al., 2013). Surprisingly, percent area predicted suitable was highest for most species at the finest scale model (10 m), suggesting that similarities in micro-topography and soil within a region are better detected at finer scales. While previous research has found that the area predicted suitable tends to decrease with finer grain size (Franklin et al., 2013; Gogol-Prokurat, 2011), our study suggests that this trend may only be evident at certain spatial scales. Alternatively, coarse scale models may not detect as much variation in topography compared with fine scale models resulting in the ability for the models to discern topographic similarities within the landscape. Both the differences in spatial congruence and percent area predicted suitable suggest that SDMs for each species vary by spatial scale. However, the high AUC values indicate that models at all spatial scales may be useful for conservation.

Observed differences in the models between species may best be attributed to varying numbers of occurrences used to generate the SDMs which is directly related to the endangered state of the species. The species with the lowest number of occurrences, *E. herbstii*, has the smallest area predicted suitable at each scale as well as the lowest spatial congruence between each scale. In contrast, the species with the most point locations, *A. macrococcus*, does not have a varying area predicted suitable, however, the spatial congruence between each spatial scale is greater relative to the other species. A likely explanation for these observations is that SDMs for extremely rare species may under predict the total area predicted suitable for reintroduction regardless of spatial scale due to limited information regarding the species preferred niche (Hernandez et al., 2008). Although limited occurrence data are not preferred to a more robust dataset, many studies have shown that SDM can be used to reliably predict distributions for rare species, especially using MaxEnt (Elith et al., 2006; Hernandez et al., 2008; Loiselle et al., 2008; Pearson et al., 2007). The high spatial congruence observed for the species with the most occurrence data is unsurprising and further supports that the more species' localities, the more accurate the predicted distributions, and the greater the agreement between models of different scales. Although under prediction is not ideal, results from SDM from very rare species still provide valuable information and can reliably be used to inform reintroduction.

3.5.3 Management implications and conclusions

This study shows that modeling habitat suitability at multiple scales provides insight into the appropriate scale and variables that should be used in studies utilizing SDM in Hawaii and other rare ecosystems with complex environments such as alpine habitats (Dubuis et al., 2013; Guisan et al., 1995; Guisan and Theurillat, 2000; Randin et al., 2009) and estuaries (Valle et al., 2011; Vasconcelos et al., 2015). At all spatial resolutions, variables related to soil and topography contributed most to the predicted habitat suitability. Coarse scale SDMs suggesting high contributions from topographical or edaphic variables, especially in regions with diverse topography, indicate the need to model habitat suitability at a finer spatial scale which can best capture landscape level differences in these variables (Bean et al., 2014).

It is important to note that like many other studies utilizing SDM, there are inherent issues that may arise due to selecting background points from too large an area resulting in an inflated AUC (Lobo et al., 2008; Pearson et al., 2006), a mismatch between sample location accuracy and a 10 m resolution (Jarnevich et al., 2015; Kumar et al., 2014), as well as issues related to downscaling climate (Franklin et al., 2013; Seo et al., 2009). Furthermore, there is growing support for the use of ensemble models for rare species (Bean et al., 2014; Grenouillet et al., 2011; Marmion et al., 2009). Although ensemble models can capture variability between model outputs, there remains uncertainty regarding interpretation of model differences and their causes (Buisson et al., 2010; Elith and Graham, 2009).

Little is known about the biology, geographic distribution, and habitat requirements for endangered plant species in Hawaii due to their limited population sizes (Pau et al., 2009). Although there is a pressing need for insights into potential sites for conservation management, there have only been a few studies using GIS, remote sensing, or predictive modeling to assess potential reintroduction sites for endangered plants in Hawaii (Price et al., 2012; Questad et al., 2014; Rovzar et al., 2013). Our study suggests that high resolution (<10 m) habitat data for all endangered plants are still needed for Hawaii. Once compiled, environmental data and methods used in our study can be applied to all endangered species and this should provide new insights for protection and reintroduction site selection, which are often conducted without any knowledge of the species historical or potential range.

Previous outplanting projects in Hawaii have increased the population of federally endangered dry forest species, and have identified potential field methods for increasing the overall survivorship of reintroduced individuals (Ammondt et al., 2013; Cabin et al., 2002; Cordell et al., 2008; Thaxton et al., 2012). Although it may not be possible to return Hawaiian ecosystems to their original composition and extent (Brooks et al., 2009; Cabin et al., 2002b; Cordell et al., 2007; Ostertag et al., 2015), planting dry forest species in different areas we identify may provide insight into potential habitat for threatened species reintroduction. Implementing a multi-species approach for endangered species reintroduction can be more cost-effective, enhance the probability of long-term success, and conserve time, money, and management effort, which are often in limited supply (Franklin 2013). Previous outplanting projects in Hawaii have successfully increased the population of federally endangered dry forest species, however, experienced low overall survivorship (Cordell et al., 2008; Jarrod M Thaxton et al., 2012)

Protected areas are often established in locations less likely to be developed for commercial or subsistence use (Davis and Stoms, 1996; Pressey et al., 2002, 2000). Conservation gap analysis is one method to evaluate the effectiveness of reserves in protecting biologically rich areas or habitat which may be best suited for outplanting (Dudley and Parish, 2006; Langhammer, 2007; Vimal et al., 2011). Results from spatial niche overlap identify 1, 292 10 m by 10 m areas on Oahu where the model predicts niche overlap for eight species, which represent areas where ecosystem-level reintroduction could occur. Of these areas, 1.3% of the total is on private land while 98.7% is on public land. For the regions of high niche overlap found on public land, 36% is under federal, 47.4% is under state, and 15.3% is under Honolulu county ownership, and only 1.2% of the total area occurs in currently protected areas. Although only a small percentage of the area predicted suitable for dry forest species' reintroductions is currently protected, there is high potential for increased development of protected areas due to the majority of the predicted suitable areas found on both state and federally owned land. If dry forest restoration becomes a priority, most of the areas predicted suitable for reintroduction will fall under its jurisdiction, allowing for these areas to become protected.

3.6 Acknowledgements

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3.7 Figures

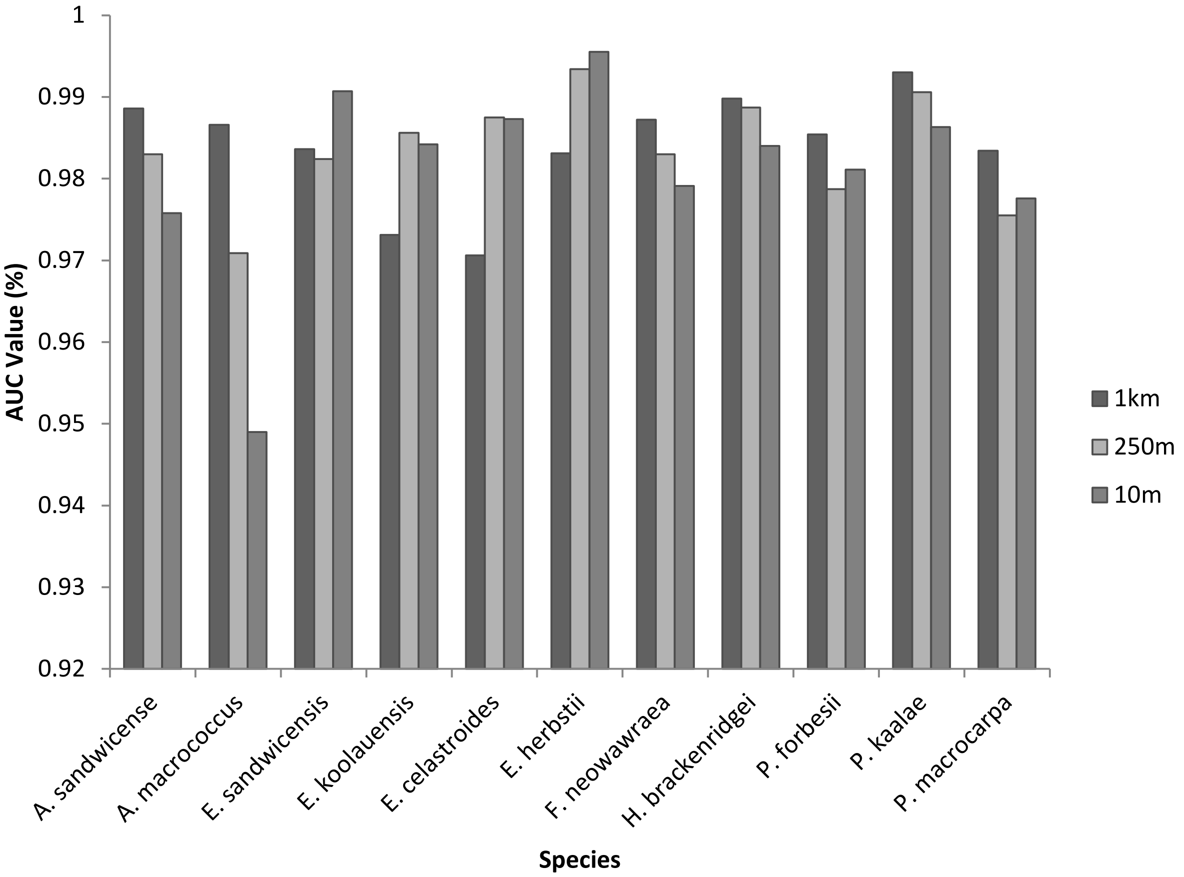

Figure 1: AUC values generated for 11 species at a 1 km, 250 m, and 10 m spatial resolution. All AUC values are significantly high (one-tailed t-test, t = 4.297, p < 0.001, degrees of freedom = 10), suggesting models for all species at all resolutions are reliable.

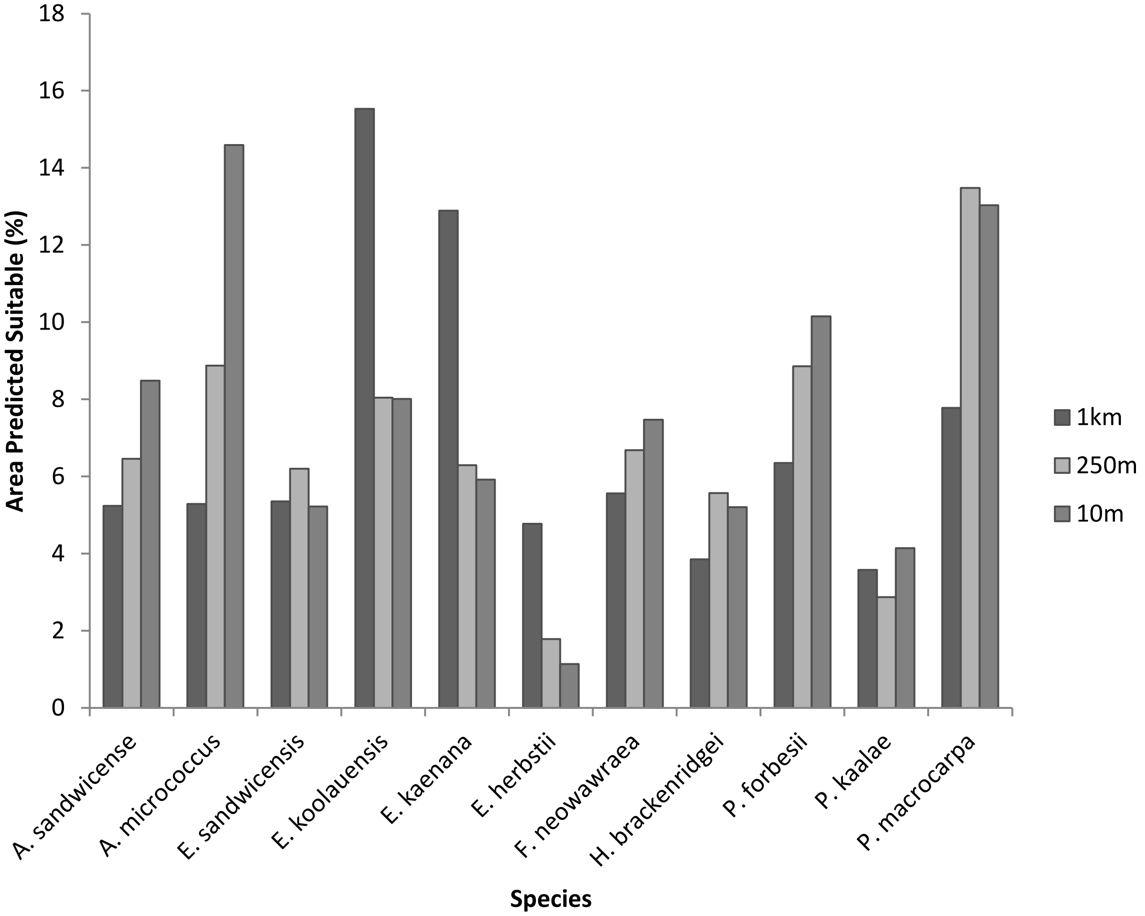

Figure 2: Total percent of area predicted suitable for each species at a 1 km, 250 m, and 10 m spatial resolution.

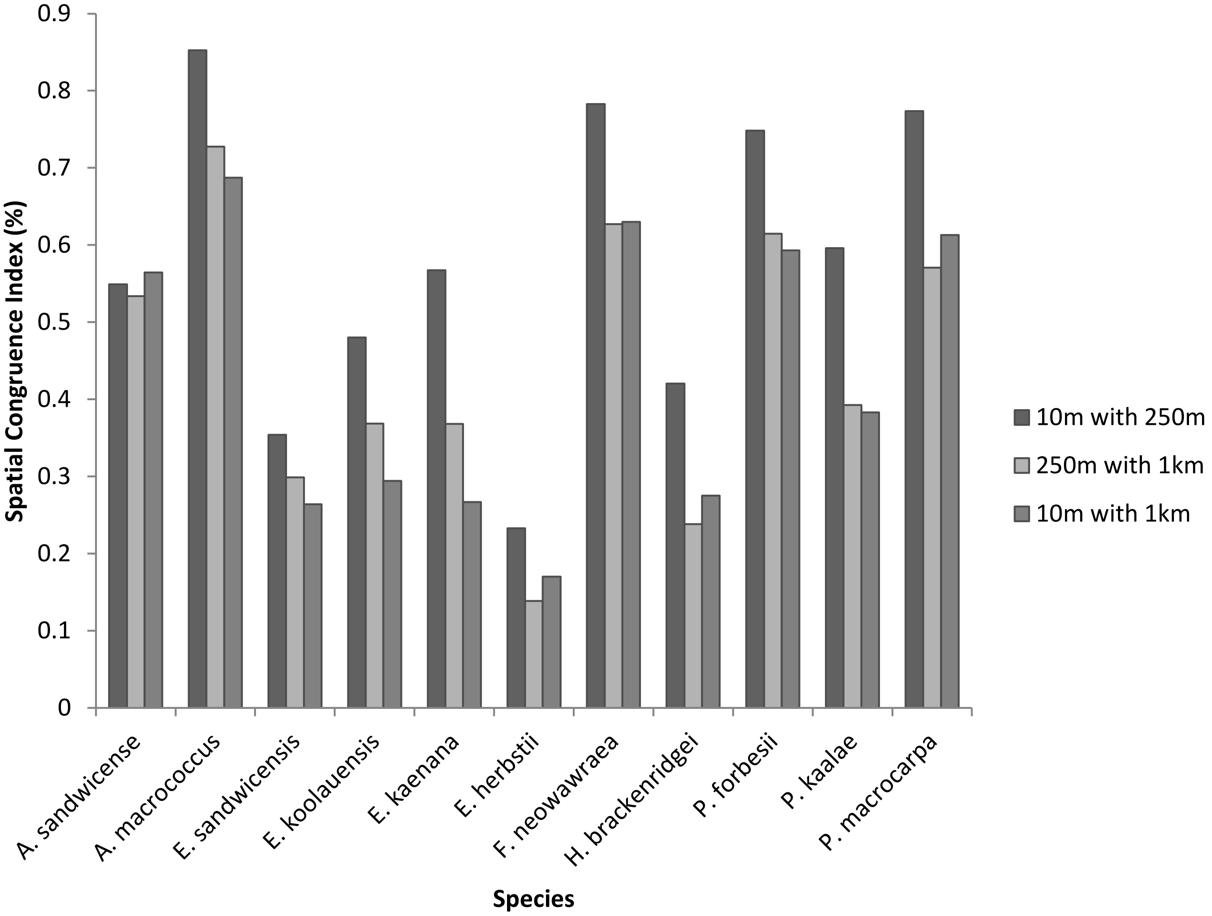

Figure 3: The spatial congruence between the 10 m and 250 m models, 250 m and 1 km models, and 10 m and 1 km models. Spatial congruence represents the similarity between the two models calculated using the Dice Sorenson similarity measure. High values of the index indicate higher degrees of spatial congruence.

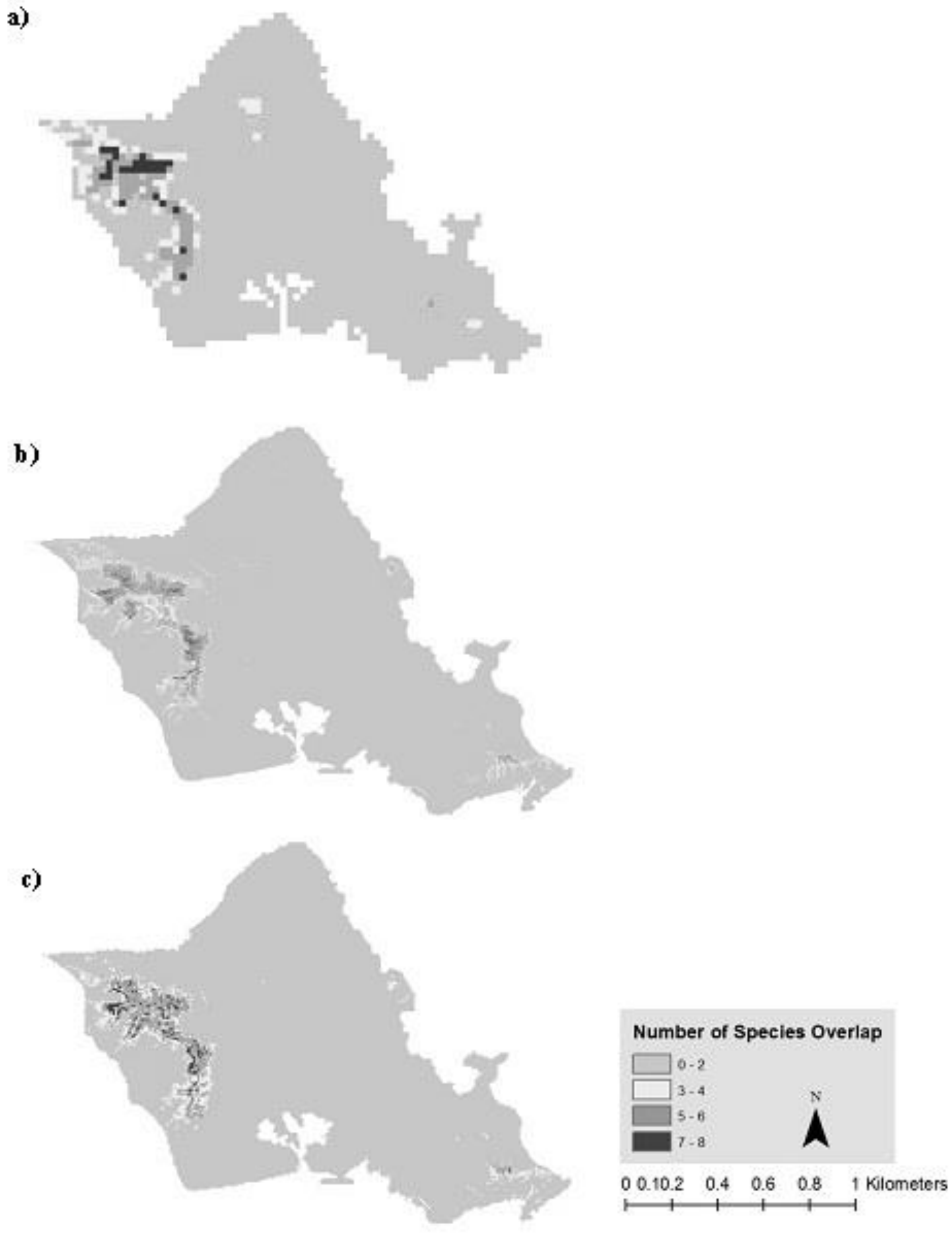

Fig. 4. Niche overlap between all species from lowest number of species overlap (gray) to highest number of species overlap (red) at a) 1 km, b) 250 m and c) 10 m spatial scales.

3.8 Tables

Scientific Name	**10 m**	**250 m**	**1 km**	**Federal**
Abutilon sandwicense	72	43	19	E
Alectryon macrococcus micrococcus	204	101	39	E
Erythrina sandwicensis	21	12	7	NL
Eugenia koolauensis	53	19	13	E
Euphorbia celastroides kaenana	32	19	13	E
Euphorbia herbstii	15	9	5	E
Flueggea neowawraea	60	46	26	E
Hibiscus brackenridgei mokuleianas	49	20	12	E
Pleomele forbesii	38	37	26	C
Pritachardia kaalae	45	27	14	C
Pteralyxia macrocarpa	53	46	28	C

Table 1: Study species with occurrence numbers used for model testing over different spatial resolutions. Federal listings: E = Endangered, C = Critically Endangered, NL = Not Listed.

Variable	**1 km**	**250 m**	**10 m**
Soil great group	34.85	35.85	33.22
Elevation	23.24	25.95	26.20
Mean precipitation of the driest quarter	13.50	18.40	17.88
Slope	11.09	13.51	15.64
Aspect	15.60	5.23	4.27
Curvature	1.60	1.06	0.86

Table 2: Percent contribution of variables across three spatial scales (average for all species).

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3.10 Supporting Information

AUC Value, MTP Threshold, Standard Deviation, Minimum Predicted Presence Area across spatial scales (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Appendix S1: AUC Value, MTP Threshold, Standard Deviation, Minimum Predicted Presence Area across spatial scales.

Table S1: 10m Model

Species Name	AUC Value	MTP Threshold	Standard Deviation	Minimum Predicted Presence Area
Abutilon sandwicense	0.9758	0.1398	0.001	0.0848
Alectryon macrococcus macrococcus	0.949	0.0698	0.001	0.1459
Erythrina sandwicensis	0.9907	0.1939	0.002	0.0522
Eugenia koolauensis	0.9842	0.0697	0.001	0.0801
Euphorbia celastroides kaenana	0.9873	0.146	0.002	0.0592
Euphorbia herbstii	0.9955	0.4641	0	0.0114
Flueggea neowawraea	0.9791	0.1323	0.001	0.0747
Hibiscus brackenridgei mokuleianas	0.984	0.2064	0	0.052
Pleomele forbesii	0.9811	0.1118	0.002	0.1015
Pritachardia kaalae	0.9863	0.1903	0.001	0.0414
Pteralyxia macrocarpa	0.9776	0.0556	0.002	0.1303

Table S2: 250 m Model

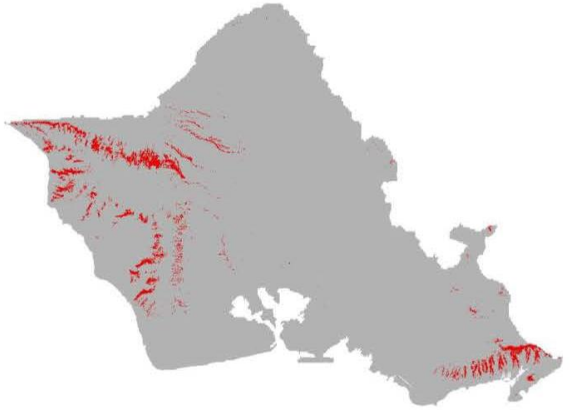
Species Name	AUC Value	MTP Threshold	Standard Deviation	Minimum Predicted Presence Area
Abutilon sandwicense	0.983	0.199	0.001	0.0646
Alectryon macrococcus macrococcus	0.9709	0.098	0.001	0.0887
Erythrina sandwicensis	0.9824	0.3557	0.005	0.062
Eugenia koolauensis	0.9856	0.1474	0.005	0.0804
Euphorbia celastroides kaenana	0.9875	0.1972	0.002	0.0629
Euphorbia herbstii	0.9934	0.462	0.002	0.0178
Flueggea neowawraea	0.983	0.1218	0.002	0.0668
Hibiscus brackenridgei mokuleianas	0.9887	0.2245	0.001	0.0557
Pleomele forbesii	0.9787	0.1519	0.003	0.0886
Pritachardia kaalae	0.9906	0.2398	0.001	0.0287
Pteralyxia macrocarpa	0.9755	0.0567	0.003	0.1348

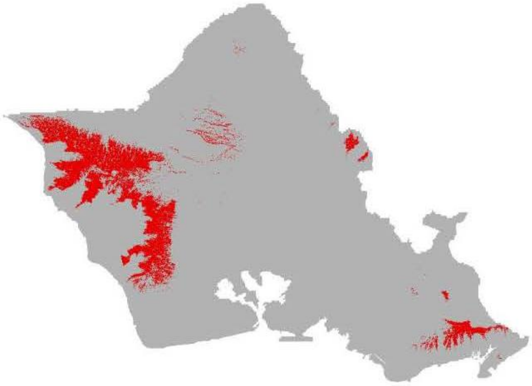
Table S3: 1 km Model

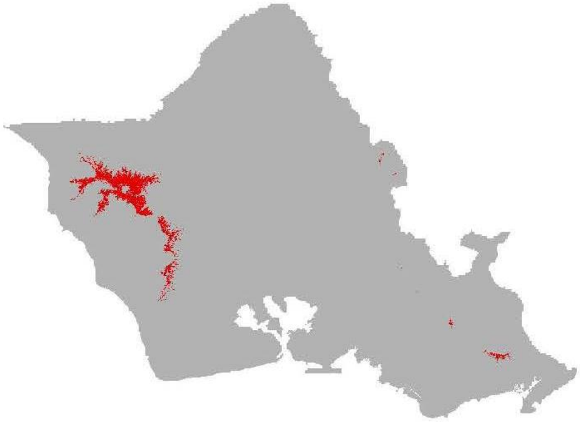
Species Name	AUC Value	LTP Threshold	Standard Deviation	Minimum Predicted Presence Area
Abutilon sandwicense	0.9886	0.2495	0.003	0.0524
Alectryon macrococcus macrococcus	0.9866	0.1759	0.001	0.0529
Erythrina sandwicensis	0.9836	0.3606	0.007	0.0535
Eugenia koolauensis	0.9731	0.1862	0.010	0.1553
Euphorbia celastroides kaenana	0.9706	0.2662	0.010	0.1289
Euphorbia herbstii	0.9831	0.286	0.008	0.0477
Flueggea neowawraea	0.9872	0.1776	0.002	0.0556
Hibiscus brackenridgei mokuleianas	0.9898	0.3659	0.002	0.0385
Pleomele forbesii	0.9854	0.22	0.003	0.0635
Pritachardia kaalae	0.993	0.1931	0.002	0.0358
Pteralyxia macrocarpa	0.9834	0.1501	0.003	0.0778

Appendix S2: Habitat Suitability Models

Figure S1: 10m models of *A. sandwicense, A. macrococcus, E. sandwicensis, E. kooauensis, E. celastroides, E. herbstii, F. neowawraea, H. brackenridgei, P. forbessi, P. kaalae, P. macrocarpa* (from left to right, top to bottom)







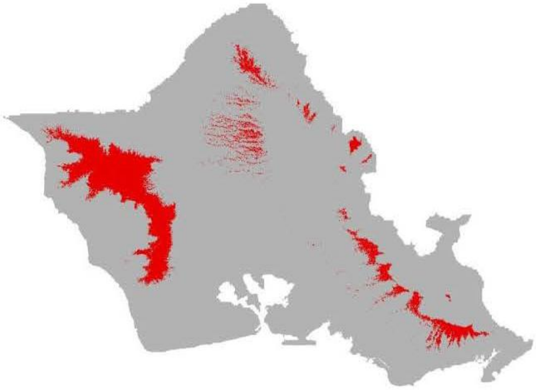
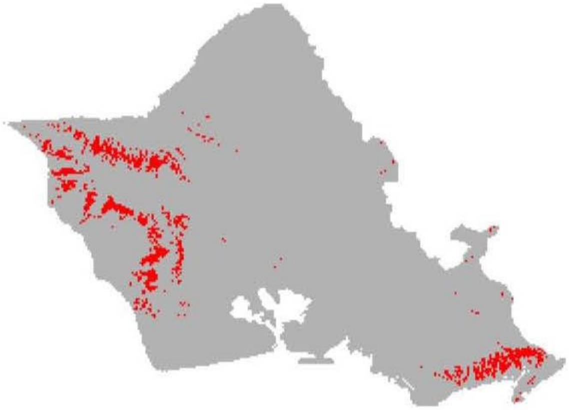
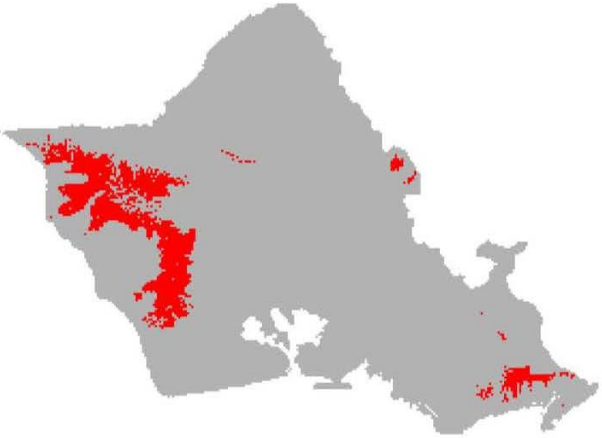


Figure S2: 250m models of *A. sandwicense, A. macrococcus, E. sandwicensis, E. kooauensis, E. celastroides, E. herbstii, F. neowawraea, H. brackenridgei, P. forbessi, P. kaalae, P. macrocarpa* (from left to right, top to bottom)





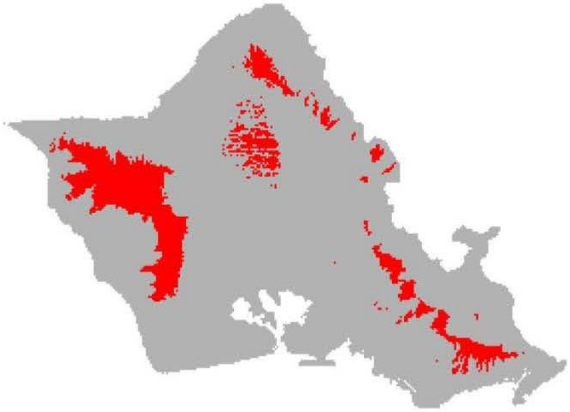
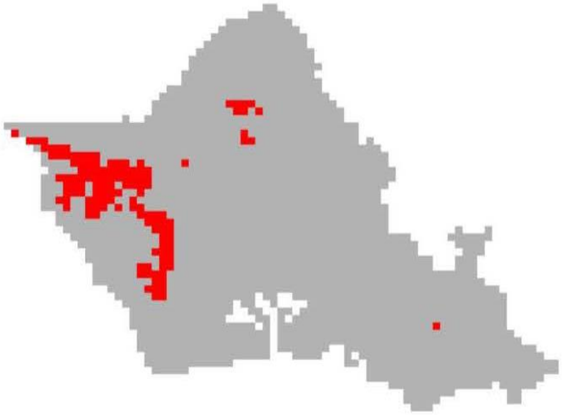
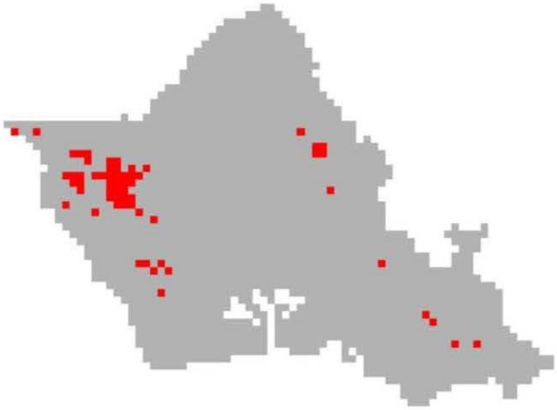
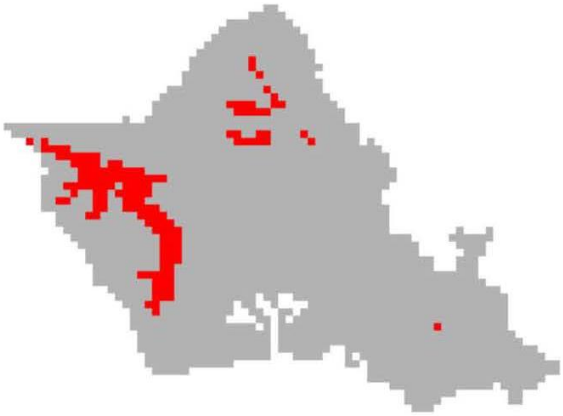


Figure S3: 1 km models of *A. sandwicense, A. macrococcus, E. sandwicensis, E. kooauensis, E. celastroides, E. herbstii, F. neowawraea, H. brackenridgei, P. forbessi, P. kaalae, P. macrocarpa* (from left to right, top to bottom)







CHAPTER 4

4. Management implications for the reintroduction of an endangered Hawaiian dry forest plant in a highly degraded habitat

4.1 Abstract

Tropical dry forests are one of the most endangered forest types worldwide. In Hawaii, over 90% of the dry forest has been destroyed and 45% of all plant species have been listed as federally threatened or endangered. Although restoration may help preserve the dry forest fragments which remain, reintroduction is necessary to maintain viable population sizes and expand a species range. The goals of this research were to reintroduce *Hibiscus brackenridgei mokuleinus,* the state flower of Hawaii and a federally endangered species, into its historical range on Oahu. We determine the environmental variables contributing to plant survival and growth, assess the effectiveness of a reintroduction program with minimal management, and evaluate the potential for habitat suitability models to assist in reintroduction site selection. In December 2013, fifty individuals were grown from cuttings and transplanted in eight different sites. Invasive species removal occurred at the initial time of planting, after three months, six months, and nine months. Height measurements were taken four times over the course of two years. After two years, there was 52% survival and significant average plant growth of 107.835 cm (± 11.6 cm). Overall, plants survived and grew the most in sites with greater soil water content, steeper slopes, higher annual precipitation, lower soil bulk density, slightly acidic soil pH, and a lower soil C:N ratio. The 10 m habitat suitability models were significantly positively correlated with total plant growth and survivorship and suggest that 10 m models should be used

for planting H. brackenridgei mokuleinus in the future. These findings provide insight into environmental variables and models which should be considered prior to planting as well as the intensity of site management which should occur post reintroduction.

4.2 Introduction

Over the next century, it is estimated that the global plant extinction rate will increase by a factor of ten (Ricketts et al., 2005b; Thuiller, 2007). One widely used method to help preserve populations of endangered species is native species reintroductions which involves releasing wild or captive-bred individuals into novel or historical habitats (Armstrong and Seddon, 2008, 2008; Lipsey et al., 2007; Seddon et al., 2007). Habitat restoration without the use of introduced individuals is the ideal method used to help a species recover from a low population number due to its minimal manipulation of the native landscape (Menges, 2008). However, spontaneous recovery of a native population may be hindered by a species' transient seed banks (Thompson, 1997a) as well as dispersal limitations (Clark et al., 2007a). The resulting deficiency in naturally occurring propagules necessitates species reintroduction as a means to increase the likelihood of species survival (Luijten et al., 2002; Pavlik, 1996; Van Groenendael et al., 1998).

Despite the frequent use of reintroduction as a method for species conservation, there has been minimal documentation of protocols and results following reintroduction projects (Bottin et al., 2007; Godefroid et al., 2011). The case studies which do exist tend to appear outside of the scientific literature resulting in ambiguous interpretations of results as well as difficulties reproducing methods (Fischer and Lindenmayer, 2000; Godefroid et al., 2011; Hodder and Bullock, 1997). Furthermore, only 33% of reported plant reintroduction projects tend to be successful (Godefroid et al., 2011). Previous studies have found that factors favoring the survival of reintroduced plants include transplanting seedlings, cuttings, or individuals from tissue culture (Wang et al., 2006) rather than directly seeding at the restoration site (Guerrant Jr and Kaye, 2007; Maschinski and Wright, 2006), reintroducing large numbers of individuals across a wide spatial distribution (Pavlik, 1996), obtaining individuals with high genetic variation, and finally, pre and post-planting management of the reintroduced individuals (Godefroid et al., 2011). Common assessments of reintroduction success include individual survival, plant growth, and reproduction (Menges, 2008). In many cases, especially for rare species, the ideal habitat for the target species, as well as the species biology, is not known (Kaye, 2008). One way to determine optimal environmental conditions is to vary the habitat types in which individuals are reintroduced. Measurements of individual plant growth are then used to indicate whether a particular site is suitable or not for a given species (Menges, 2008).

Another growing and cost-effective tool for reintroduction site selection is habitat suitability modeling (HSM) which uses statistical modeling to predict the potential geographic distribution of a species by measuring the relationship between a species' spatial distribution and select environmental variables (Franklin, 2009a; Guisan et al., 2006; Loiselle et al., 2003; Pearson et al., 2007). Despite the use of HSMs to identify sites for endangered plant species reintroduction and habitat conservation (Butler, 2009; Gallardo and Aldridge, 2013; Gogol-Prokurat, 2011; Guisan et al., 2006; Loiselle et al., 2003; Pearson et al., 2007; Thompson, 1997a; Wilson et al., 2013), few studies have tested their effectiveness by reintroducing individuals across varying degrees of habitat suitability and evaluating plant establishment.

Tropical dry forests in Hawaii are among the most endangered forest types in the world with 45% of endemic trees and shrubs on the federal threatened and endangered species list (Pau et al., 2009). Although there have been efforts to preserve endangered dry forest species, most reintroduction attempts have proven unsuccessful. A handful of restoration studies have evaluated the effect of outplanting strategies (Burney and Burney, 2007; Cordell et al., 2008), removing grass (Jarrod M. Thaxton et al., 2012) or using fences (Cabin et al., 2002b, 2000) on the success of species reintroductions in Hawaii's dry forest, however, none have evaluated the influence of environmental variables such as temperature, rainfall, topography, and soil factors. Furthermore, few studies globally, and none in Hawaii, have compared HSM results with restoration success.

Hibiscus brackenridgei, the state flower of Hawaii, is a federally listed endangered species found in the Hawaiian dry forest (Wagner et al., 1999). The species is native to lowland dry/mesic forests and shrublands and occurs on slopes, cliffs, and arid ledges between elevations of 24-490 meters (Mansker 2002). On Oahu, the subspecies *Hibiscus brackenridgei mokuleianus* is scattered throughout the Wai'anae Mountains from Puu Pane to Kealia-Kawaihapai and the Dillingham Military Reservation (U.S. Fish and Wildlife 1999; Oahu Army Natural Resources Program 2010). According to the US Fish and Wildlife Service, only five populations are known to remain on Oahu (Mansker 2002; Oahu Army Natural Resources Program 2010). A major threat to this species, as well all Hawaiian dry forest species, has been the increasing rate and extent of wildfires caused by the expansion of invasive grasses in dry forest habitat. In particular, a major fire in the Waialua region of the Waianae mountains in August 2007 devastated much of Oahu's dry forest habitat leading to the decline in approximately 97% of *H. brackenridgei mokuleinus* individuals (Oahu Army Natural Resources Program, 2010). Although *H. brackenridgei mokuleinus* has been a top conservation priority for the Oahu Army Natural Resources Department, only a handful of reintroduced plants have successfully established. Thus, there is a need for understanding which environmental conditions are most ideal for restoring *H.brackenridgei mokuleinus* as well potential methods for improving reintroduction success.

This study has three primary questions. First, can reintroduced *H. brackenridgei mokuleinus* individuals successfully establish with minimal management? Second, which environmental factors are associated with the restoration success of endangered *H. brackenridgei mokuleinus* on Oahu? Finally, how effective are habitat suitability models in predicting growth and survival of reintroduced individuals? In addition to these questions, a management objective of this study is to increase the population of *H. brackenridgei mokuleinus* and expand its current range into new sites with similar environmental conditions to areas in which the species is currently found.

4.3 Methods

4.3.1 Study Area

This experiment was conducted in a highly degraded dry forest habitat located within the Mokuleia region of the Wai'anae Mountains on Oahu (Fig. 1). The Mokuleia region is found on the north-facing side of the Wai'anae mountains, and includes the East Makaleha Valley to Kealia (Hatheway, 1952). Steep ridges and deep gulches in the region result in diverse microhabitats and ultimately, high endemism (Hatheway, 1952). The area receives between 26 and 118 cm of annual precipitation and is characterized by a dry season of approximately 7 months (Giambelluca et al., 2013). The soils consist primarily of entisols, inceptisols, and oxisols (Hawaii Statewide Planning and GIS Program, 2016). Historically, the region contained over 50 native species and the most widespread were *Erythrina sandwicensis, Canthium odoratum, Sapindus oahuensis*, *Dracaena aurea*, *Osmathus sandwicensis,* and *Reynoldsia sandwicensis* (Hatheway, 1952). However, the region has experienced a severe decline in native populations due to competition by exotic species including *Prosopis chilensis, Leucaena glauca, Panicum maximus* (Oahu Army Natural Resources Program, 2010).

4.3.2 Experimental Design

Field work was conducted from November 2013 through February 2016 in order to reintroduce and monitor individuals of *H. brackenridgei mokuleinus* and evaluate the environmental factors influencing reintroduction success. Sites were chosen based on state permits (P-185) and accessibility, and only areas without native species cover were considered. During the wet season (December 12th and 13th, 2013), 50 individuals of *H. brackenridgei mokuleinus* were planted at eight sites with varying elevations, slope, aspect, and soil conditions in the Mokuleia region of the Waianae mountain range on Oahu, Hawaii (Table 1). Two sites were located at Ka'ena point (19 m, 21 m) and six sites were located along an elevational gradient along Kealia trail (82 m, 108 m, 127 m, 133 m, 270 m, and 310 m). Each site was prepared using an application of an herbicide treatment (2% glyphosate) followed by manual removal of all non-native vegetation. Clippings from wild *H. brackenridgei mokuleinus* individuals were obtained by the OANRP and grown at Hui Ku Maoli Ola native plant nursery for three months. A week after vegetation removal, the individuals were planted at each site within 1-2 m of each other over the course of two days. Ten individuals were planted at each of the two sites at Ka'ena point and five individuals were planted at each of the six sites along the Kealia trail. All plants were planted in the open with the exceptions of site 3 which was planted under the canopy of *Sapindus oahuensis*. Volcanic rocks were placed around the planted individuals to provide stabilization and limit surface moisture loss. Each individual received 1 liter of water at the time of initial planting and another liter two days following. Subsequent vegetation removal occurred 3 months (March 2014), 6 months (June 2014), and 9 months (September 2014) after the initial planting ((https://www.youtube.com/watch?v=cGzq4Za80aI). No other management of the sites occurred after September 2014.

4.3.3 Plant Height and Environmental Factors

Measurements of plant survival and growth were taken every three months until February 2015. Soil moisture was obtained from bulk density measurements and soil nitrogen content was analyzed by comparing percent carbon, percent nitrogen, and carbon to nitrogen ratios for each site and all individuals.

The variables used in the statistical analyses included soil moisture and nutrient measurements obtained from soil samples as well as elevation, slope, aspect, precipitation, and temperature data obtained from spatial data available in a Geographic Information Systems (GIS) format. Mean monthly temperature and precipitation grids were provided by T. Giambelluca at a 250 m resolution (Giambelluca et al., 2013) and stastically downscaled to 10 m using bilinear interpolation. In this process, the four nearest grid cells to the target cell are weighted based on its distance to the target cell and then averaged (Newbold et al., 2009). Annual temperature and annual precipitation were derived from the mean monthly climate dataset using ArcGIS 10.1. Elevation data was downloaded from the U.S. Geological Survey National Elevation Dataset (NED) at a 10 m resolution (U.S. Geological Survey, 2015). Slope and aspect were calculated using ArcGIS 10.1. Aspect was calculated in degrees and reclassified to represent categorical classes (N, NE, NW, S, SE, SW, E, W). Soil order was obtained at a 10 m resolution (Hawaii Statewide Planning and GIS Program, 2016).

The HSM from Rovzar et al. (2016) was tested for this research (Rovzar et al., 2016). Models at a 1 km and 10 m resolution model were created for *H. brackenridgei mokuleinus* based on elevation, topography, soil, and climate variables using the MaxEnt (maximum-entropy) version 3.3.3k algorithm (Phillips et al., 2006b). Maxent has been found to produce robust results for studies involving rare or endangered species which often have limited and spatially biased presence data (Elith et al., 2006; Loiselle et al., 2008; Pearson et al., 2007). An additional benefit of Maxent is that it measures variable contribution to the predicted distribution and thus, allows for an assessment of variable importance to a species' occupied habitat (Kumar and Stohlgren, 2009; Ortega-Huerta and Peterson, 2008).

4.3.4 Soil Analysis

Soil samples were taken in November 2013 prior to outplanting. Two soil cores from 0 to 10 cm were taken at each site using a 2.5 cm diameter soil probe. Cores from each site were pooled to provide one representative sample. Bulk density was measured from 0 to 10 cm back from an undisturbed face of a 20 cm pit at each site using three cores from a 2.5 cm diameter soil probe. The corer was inserted and excavated to minimize soil loss. The cores from each site were pooled to give one representative sample and a subsample for each site was oven dried at 105°C in order to calculate grams of dry soil cm^{-3}. Separate subsamples for each site were air-dried, sieved, and then ground for C and N analyses. A Costech Elemental Analyzer was used to conduct total C and N analyses using atropine as standards and between 56 and 58 mg of each sample (Costech Analytical, Valencia, CA, USA).

4.3.5 Statistical Analyses

All statistical analyses were run using SPSS Statistics version 23 (IBM, USA). Descriptive statistics were used to compare plant survival between sites. A two-tailed, paired t-test was performed to test if plant growth for all individuals was statistically significant. One-way analysis of variance (ANOVA) was used to evaluate if plant growth rate varied across five dates (12/11/13, 03/15/14, 02/14/15, 09/09/15, 02/18/16) at the reintroduction sites as well as to evaluate if plant growth rate varied between each site. A Pearson Correlation (2-tailed) was performed to assess correlations between each variable and overall growth as well as to determine correlated variables. This metric was also used to examine the relationship between plant growth and survivorship and the predicted probability of its success based on an HSM at 1 km and 10 m . A general linear model (GLM) was run to determine the relationship between total plant height and a suite of environmental variables including elevation, slope, aspect, annual precipitation, annual temperature, soil water concentration (%), soil C:N ratio, soil pH, and soil bulk density. Group effect was also tested by adding the site number as a fixed effect in the model.

4.4 Results

4.4.1 Survivorship and Growth

After three months, there was an 88% survival rate for all individuals. In particular, there was 100% mortality under the *Sapindus* canopy (Kealia Trail site 1). Survivorship decreased to 72% after 14 months, 70% after 21 months, and 52% after 25 months. At Kaena Point, there was 35% survival for both sites while all remaining sites at Kealia Trail had 63.3% survival. An ANOVA of survival between each group was statistically significant ($F = 4.258$, $df = 7$, $p < 0.01$). Growth for all surviving individuals was statistically significant (t = 9.3, df = 25, $p < 0.01$) and the mean growth was 107.84 cm (± 11.6 cm) (Fig. 2). Average plant growth after 3, 14, 21, and 25 months was 23.49 cm/month, 8.36 cm/month, 6.02 cm/month, and 5.19 cm/month, respectively. An ANOVA between each time period suggests that the difference in height between each time period is significantly different (F = 13.585, df = 3, $p < 0.05$). An ANOVA of average total growth between each group was statistically significant (F = 21.836, df = 7, $p < 0.01$) suggesting that site location was important in determining overall growth (Table 2).

4.4.2 General Linear Model

Results from the GLM suggest the model is highly statistically significant (F = 13.339, df = 12, $p < 0.001$) and show an r square value of 0.812. Site number was a highly statistically significant (F = 4.797, df = 3, p = 0.006) factor, suggesting clustering in the dataset and the importance of the site location in affecting overall plant growth.

No other variables in the model were found to be significant. Furthermore, no variables were found to be significant when univariate GLM was performed and total growth regressed against each predictor variable individually.

4.4.3 Relationships with growth

Total growth was significantly positively correlated with water percent by mass, slope, and annual precipitation (Pearson's correlation, $p < 0.05$; Table 3). Total growth was significantly negatively correlated with aspect and bulk density ($p < 0.05$). Water percent by mass was significantly positively correlated with slope and negatively correlated with bulk density ($p < 0.05$). Slope was significantly negatively correlated with aspect, annual temperature, pH, and bulk density, and significantly positively correlated with annual precipitation ($p < 0.05$). Annual precipitation was significantly positively correlated with the C:N ratio and negatively with annual temperature, aspect, and soil pH ($p < 0.05$). The C:N ratio was significantly negatively correlated with pH ($p < 0.05$).

4.4.4 Comparisons with Habitat Suitability Models

Based on a 10 m HSM for *H. brackenridgei*, the site predicted to be most suitable for reintroduction was Kealia Trail site 5 (65.8%) and the least suitable site was Kaena Point site 2 (0.6%) (Fig. 3). The most suitable reintroduction sites predicted by a 1 km HSM were Kealia Trail sites 5 and 6 (54.9%), while the least suitable sites were predicted to be Kaena point sites 1 and 2 (18.6%). There was a significant positive correlation between total growth and the 10 m HSM ($r = 0.299$, $p < 0.05$) and the 1 km HSM ($r = 0.302$, $p < 0.05$). There was no significant correlation between survivorship and the 1 km HSM ($r = 0.246$, $p = 0.083$) but there was a significant positive correlation between survivorship and the 10 m HSM ($r = 0.318$, $p < 0.05$).

4.5 Discussion

4.5.1 Reintroduction Outcomes

Overall, there was 52% survival with 26 out of 50 planted individuals surviving across all sites. A meta-analysis of 249 plant species reintroductions worldwide found the average survival to be 52% (Godefroid et al., 2011) and tropical dry forest species outplantings on the island of Hawaii had an overall survival rate of 30%, and 45% survival rate for *Hibiscus brackenridgei* (Cordell et al., 2008). Although this percentage may seem high, the authors consider this reintroduction project to be a success due to comparisons with previous reintroduction projects for this species during this particular year. In January 2013, the OANRP planted in a similar dry forest area on Oahu with double the number of individuals ($n = 102$) and had 51% survival as of 1/27/16. Our reintroduction approach involved minimal management in order to best understand the ideal reintroduction habitat for the species. Despite limited management, many of the individuals were able to persist.

The outplanting of *H. brackenridgei mokuleinus* increased the wild population in the Mokuleia region of the Waianae mountains. Based on the one-way ANOVA results, the growth rate was significantly different at each time period, and showed a slowing pattern over time. Peak growth was greatest in the first few months and dramatically decreased after 21 months. This finding suggests that management efforts for the species would be most effective during the first year and half after reintroduction. An important measure of reintroduction success is the ability for reintroduced plants to produce viable offspring (Godefroid et al., 2011; Maschinski and Wright, 2006; Menges, 2008). Although both flowering and seeding have been observed by the reintroduced individuals, to date, there are no observations of regeneration. This appears to be common in the restoration of tropical dry forest species (Cordell et al., 2008). Possible reasons include competition for light with non-native grasses and lack of barren substrates needed for germination. Dispersal agents for *H. brackenridgei* are unknown, however, seeds from cultivated individuals can remain viable up to 15 years (Oahu Army Natural Resources Program, 2010). It is interesting to note that flowering for this subspecies typically does not occur until the plants are two to four years old (Oahu Army Natural Resources Program, 2010). For the reintroduced plants in this study, flowering was observed after 3 months.

4.5.2 Importance of Environmental Variables

Both total growth and survival were significantly different between each site suggesting that the location and attributes of each site were important predictors in reintroduction success. This is further supported by regression results which suggest that site is a significant variable influencing total growth observed for all individuals. In particular, both sites at Ka’ena Point as well as the lowest site and two highest sites at Kealia trail had the lowest overall growth. Compared to all the sites, the Kaena Point sites are characterized by lower annual precipitation (805.9 mm), warmer annual temperature (23.6 °C), a lower elevation (20 m), and a less steep slope (21°). The two highest sites at Kealia Trail (sites 5 and 6) have lower soil pH (4.3) relative to the other sites. In contrast, sites 2, 3, and 4 at Kealia Trail experienced the highest survival and growth. These sites are characterized by steeper slopes (36.9°), a higher water percent by mass (45.7%), slightly acidic soils (pH = 5.3), and lower soil bulk density (0.69 g/cm^3).

Considering individuals at all sites, plants with the highest growth tended to occur in places that had steeper slopes, higher annual precipitation, soils higher in moisture, lower bulk density, and a lower C:N ratio. Wild individuals of *H.brackenridgei mokuleinus* tend to be found on steep slopes so it is unsurprising that individuals planted on steeper slopes had higher total growth. The occurrence of the species on steeper slopes might not necessarily be a preference for the species, but rather, have lower competition with other species which may require flatter surfaces for growth. Although *H. brackenridgei mokuleinus* is a drought tolerant species, the result that individuals in sites with higher soil water content and higher annual precipitation had higher total growth suggests that water may be a limiting factor for the reintroduction of this species in its dry forest habitat. It is projected climate change will cause a decline of the trade winds which will ultimately influence rainfall patterns by causing long periods of both drought and flooding (Loope and Giambelluca, 1998; Rovzar et al. 2013). The dramatic fluctuations in rainfall could pose a threat to the reintroduction success of not just this species, but all other Hawaiian plants, especially those in dry forest habitats which are already water stressed.

In addition to areas with higher water availability, reintroduced plants with the highest growth were found in sites with lower bulk density. Bulk density refers to the ratio of the soil mass to the volume of soil particles and pore spaces for a given sample and provides insights into soil compaction (Blake, 1965). In general, plants will grow best under intermediate soil densities (Avidsson and Hakansson, 1991; Boone, 1986). Soils which are too hard hinder water and nutrient uptake by the plant's roots which have difficulty penetrating the soil while soils which are too soft do not provide enough contact with the root to enable optimal uptake of nutrients and water (Herkelrath et al., 1977; Kooistra et al., 1992). A lower C:N ratio suggests that more nitrogen is found in the soils at sites where plants grew most. Nitrogen is essential for plant growth and is considered to be the most limiting nutrient to primary productivity in a variety of ecosystems, including Hawaii's dry forest (Binkley, 1986; Haas et al., 1957; Lee et al., 1983; Vitousek and Howarth, 1991).

4.5.3 Reliability of Habitat Suitability Models

Results from Pearson's correlation suggest that both the 10 m and 1 km HSM were significantly positively correlated with total plant growth. Furthermore, survivorship was also significant positively correlated with the 10 m HSM. These significant correlations suggest that the planted individuals had greater growth and survivorship in areas predicted to be more suitable for *H. brackenridgei mokuleinus*, especially for the 10 m HSM. One of the most cited reasons for the failure of a reintroduction project is unsuitable habitat (Godefroid et al., 2011). Through the use of HSM, managers may better determine sites and permit locations which would provide a more suitable environment for the target species (Rovzar et al., 2016). Indeed, there were a number of 10 m HSM locations with predicted probabilities of > 70% where reintroductions should be tested in the future.

4.5.4 Management Implications

Invasive species have been identified as one of the key drivers of native species decline both worldwide and in Hawaii (Cabin et al., 2002b; Thaxton et al., 2010). In particular, *M. maximus* dominates most lowland areas of Oahu and poses a major threat to native species in the Waianae region by affecting resource availability, such as access to nutrients and sunlight (Ammondt et al., 2013; D'Antonio and Vitousek, 1992). The maximum height for *M. maximus* (Guinea Grass) has been found to be around 105 cm in open grasslands and 72 cm in forests (Ellsworth et al., 2014). Previous research suggests that *M. maximus* grows 39-94% faster than native Hawaiian plants (Ammondt and Litton, 2012) and thus, must be managed so it does not outcompete natives for sunlight. Our results suggest that invasive species removal at reintroduced *H. brackenridgei mokuleinus* sites should be conducted periodically for at least 14 months, the time in which some of the individuals were above the maximum height threshold for *P. maximus*. After 14 months, little to no invasive species management may be necessary to reduce the impact of *P. maximus* on the livelihood of *H. brackenridgei mokuleinus*.

Resources for conservation management are often limited resulting in the need to select optimal sites for endangered species reintroduction. Site selection for the reintroduction of this species, and potentially others found in similar habitats, should consider the variables identified in this study as important drivers in plant survival and growth. Choosing sites with adequate soil water content, exposure to higher rainfall, slightly acidic pH, lower bulk density, and steeper slopes should result in greater survival and growth of reintroduced individuals. Future outplanting should follow an adaptive management strategy (Burney and Burney, 2007). For instance, sites 2, 3, and 4 along the Kealia trail clearly had the highest survival and growth rates, and future outplantings should be conducted within and between these sites with a greater number of individuals planted. This along with results from habitat suitability models should result in higher survival and growth rates for *H. brackenridgei mokuleinus* in the future.

4.6 Conclusion

Our study illustrates that reintroduction of an endangered species is possible with minimal management in a highly degraded habitat. In order to be most effective, management of sites for *H. brackenridgei mokuleinus* should be most frequent in the months after reintroducing individuals, but may not be necessary after the first year post-transplant when the individuals are large enough to compete with fast-growing invasive species. Important limitations of this study is the number of individuals in our sample size and the number of groups. Unfortunately, both of these factors were restricted due to permit regulations and the number of cuttings which could be obtained. In future reintroduction studies, increasing both of these factors will allow for a greater understanding into which environmental variables affect plant growth and survival most.

4.7 Acknowledgements

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4.8 Figures

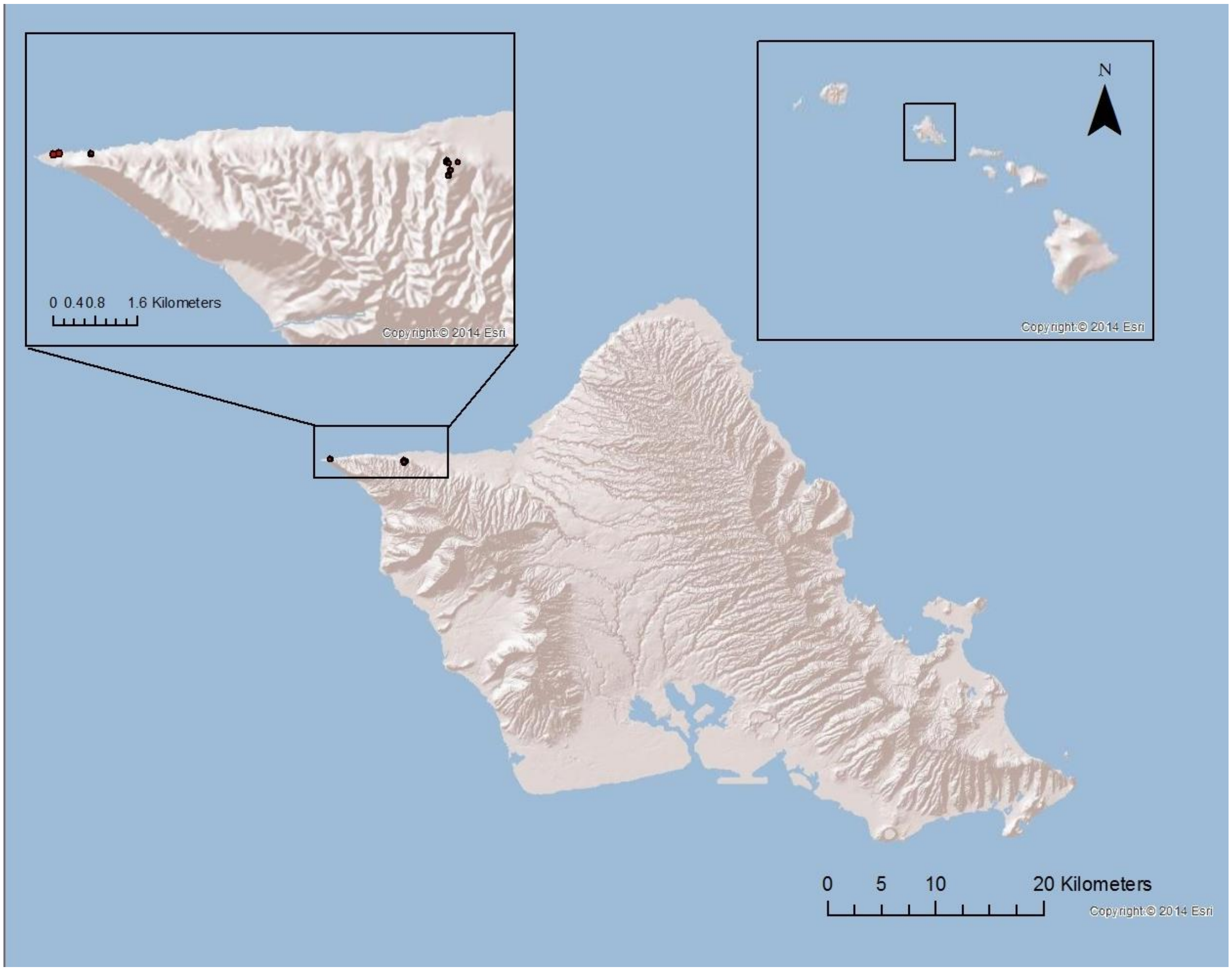


Figure 1: Map of study location. This study contains 8 sites at two locations: Kaena Point and Kealia Trail (from west to east).

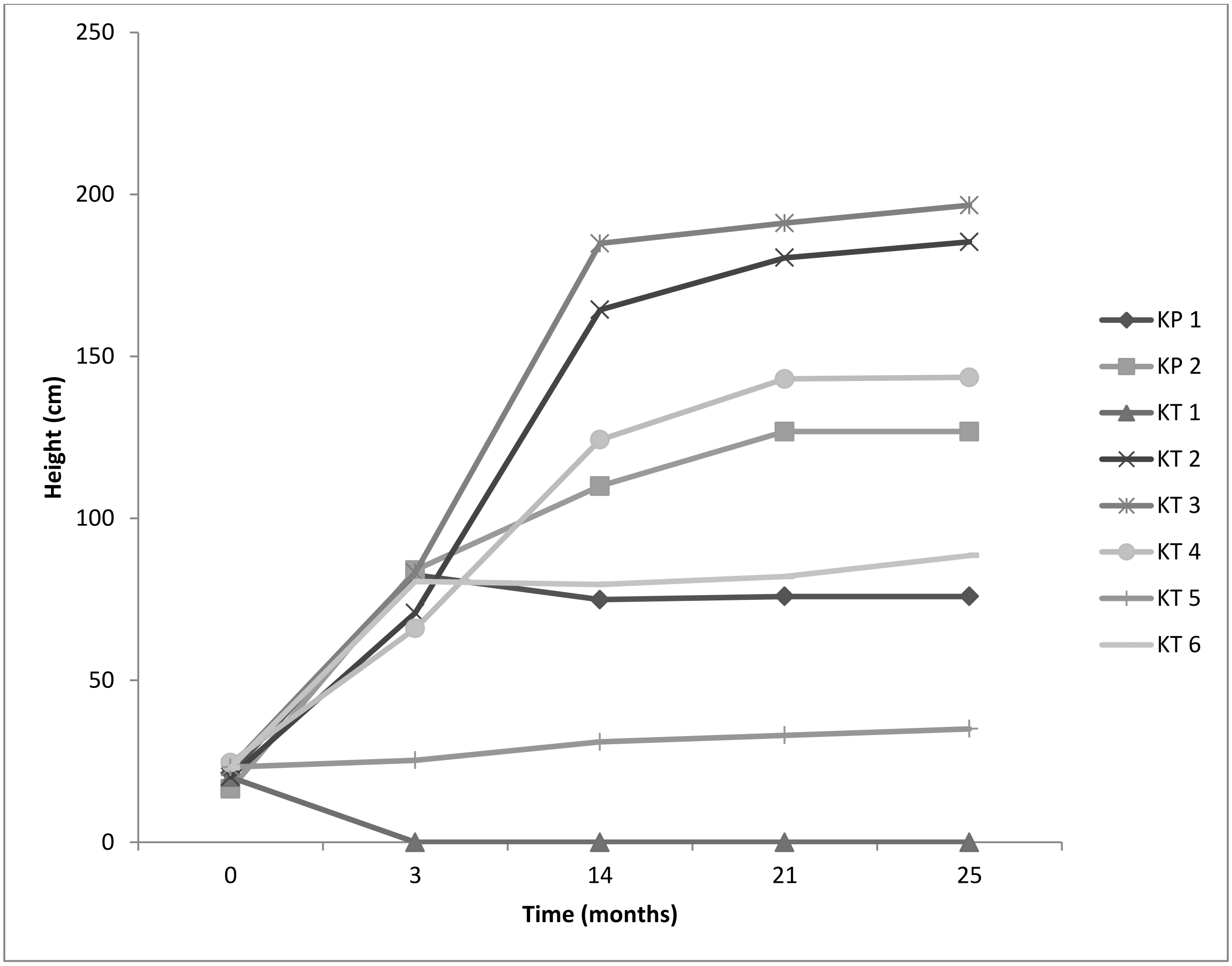
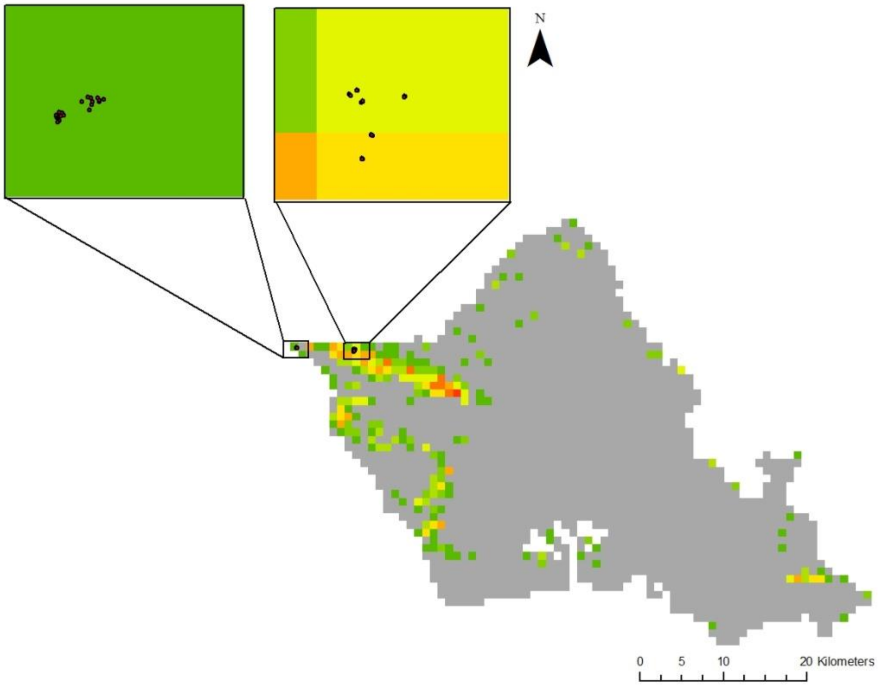


Figure 2: The above figure shows average growth over 25 months for surviving individuals at each site (KP = Kaena Point, KT = Kealia Trail)


N
0
5
10
20 Kilometers

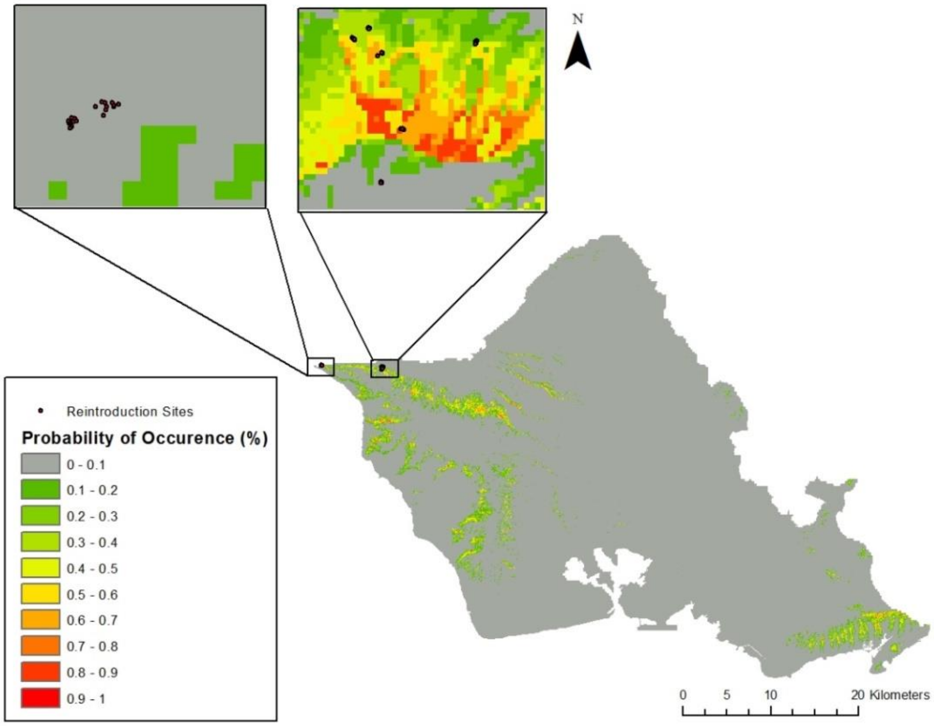

N
Reintroduction Sites
Probability of Occurence (%)
0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1
0
5
10
20 Kilometers

Figure 3: Illustrated above are the reintroduced individuals overlain on habitat suitability models at a 10 m and 1 km resolution for *H. brackenridgei mokuleinus*

4.9 Tables

Sites	Elevation (m)	Slope (°)	Aspect	Average Annual Temperature (°C)	Average Annual Precipitation (mm)	Water % (by mass)	C:N ratio	Soil pH	Bulk density
Kaena Point 1	19	21.9	N	23.6	805.9	24.7	20.0	6.06	0.804
Kaena Point 2	21	20.8	N	23.6	805.9	36.8	24.7	5.75	0.734
Kealia Trail 1	82	33	N	23	909.1	35.7	25.2	5.06	0.74
Kealia Trail 2	108	37.7	N	22.9	911	40.3	20.3	5.36	0.717
Kealia Trail 3	127	36.3	NE	23	908.9	52.4	24.5	5.24	0.658
Kealia Trail 4	133	36.8	N	22.8	911.7	44.3	23.7	5.3	0.693
Kealia Trail 5	270	32.6	N	22.3	921.2	33.7	27.0	4.2	0.753
Kealia Trail 6	310	21.2	NE	22	928.3	32.8	29.0	4.7	0.758

Table 1: The above table shows the environmental variable values at each reintroduction site including elevation, slope, aspect, average annual temperature, average annual precipitation, water percent by mass, the C:N ratio, soil pH, and soil bulk density

	KP 1	KP 2	KT 1	KT 2	KT 3	KT 4	KT 5	KT 6	Total
N	10	10	5	5	5	5	5	5	50
Avg. Growth (cm)	54.56	110.25	0	165.12	173.45	118.9	11.8	65.5	87.4
No. Surviving	5	2	0	5	5	4	3	2	26
Percent Survival	50	20	0	100	100	80	60	40	52

Table 2: The table above displays the average total growth and survival for each site (KP = Kaena Point, KT = Kealia Trail)

	Water % (by mass)	Slope	Aspect (degrees)	Annual Temp	Annual Precipitation	C:N ratio	pH	Bulk density
Total Growth	.514**	.592**	-.378**	-.081	.330**	-.197	.052	-.326*
Water % (by mass)	1.00	.463**	-.252	.074	.197	-.221	-.119	-.549**
Slope	0.463**	1.00	-.788**	-.376**	.717**	.137	-.382**	-.401**
Aspect	-.252	-.788**	1.00	.833**	-.993**	-.372**	.718**	.329*
Annual Temp	.074	-.376**	.833**	1.00	-.892**	-.462**	.815**	.138
Annual Precip	.197	.717**	-.993**	-.892**	1.00	.402**	-.757**	-.303
C:N ratio	-.221	.137	-.372**	-.462**	.402**	1.00	-.309*	.149
pH	-.119	-.382**	.718**	.815**	-.757**	-.309*	1.00	.273
Bulk density	-.549**	-.401**	.329*	.138	-.303*	.149	.273	1.00

Table 3: The above table shows Pearson's correlation coefficient between total growth and all variables as well as between variables. Correlations significant at the 0.01 level (2-tailed) are indicated by **. Correlations significant at the 0.05 level (2-tailed) are indicated by *

4.10 References

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4.11 Supporting Information

Link to time-lapse of plant growth over first three months:
https://www.youtube.com/watch?v=cGzq4Za80aI

CHAPTER 5

5. An evaluation of the composition, extent, and changes in Hawaii's dry forest using two remotely sensed products

5.1 Abstract

Globally, land cover changes resulting from anthropogenic activities represent the greatest threat to biodiversity. Remote sensing is a powerful tool which can be used to monitor landscape dynamics, quantify habitat loss and fragmentation, and assess the effectiveness of conservation management for a particular ecosystem. Despite the rapid increase in remote sensing products over the past decade, research is needed to explore and test the utility of spaceborne sensors for conservation and management of protected areas and to develop standard and repeatable GIS and remote sensing methods, protocols, and products that can be used across all protected areas. Tropical dry forests in Hawaii are one of the most endangered forest types in the world and have been identified as an understudied ecosystem in need of increased research attention. This research uses GIS to examine two remotely sensed datasets, the GAP Analysis Project and Global Forest Change products, and determine the extent and conservation status of tropical dry forests in Hawaii in order to understand the current state of the ecosystem and inform future management. We found that native dry forest species cover 1,771.9 km^2 of the Hawaiian Islands and account for 18.4% of dry habitat and 10.8% of the total area of the islands. The reserves on all of the islands experienced a decline in forest cover between 2000 and 2014. Oahu contains the smallest area of native dry forest cover as well as the lowest percentage of native dry forest

cover relative to its size (23.7 km^2 and 1.5%, respectively), and thus, was identified as having the most endangered forest. Non-native species dominate all of the islands and comprise three of the top four vegetation types found in the dry regions of Hawaii. These findings demonstrate the possibility of using freely available data for a first order assessment of ecosystem health and provide an updated measurement of remaining dry forest habitat in Hawaii.

5.2 Introduction

It is well-established that biodiversity is greatly threatened by human activity (Gaston, 2005; Myers et al., 2000). In particular, land cover changes such as those linked to human-induced habitat loss, fragmentation, and degradation represent the largest current threat to species worldwide (Chapin III et al., 2000; Gaston, 2005; Gillespie et al., 2008; Menon et al., 2001). Remote sensing can be used to derive metrics on fragmentation, often in the form of landscape pattern and connectivity indices, that are calculated from a thematic map produced by image classification analysis (Foody, 2002; Gillespie, 2005; Kupfer, 2012; Sun and Southworth, 2013). Remote sensing may also be applied to monitoring a habitat of interest with a one-class classification approach adopted to focus management efforts and resources on one particular ecosystem (Boyd et al., 2006; Sanchez-Hernandez et al., 2007). This method can also reduce problems associated with not satisfying the assumptions of an exhaustively defined set of classes that is commonly made in a standard classification analysis. Indeed, Hansen et al. (2013) recently used this one-class classification approach to map the worldwide spatial extent of all forests at a 30 m pixel resolution using Landsat imagery (Hansen et al., 2013). In addition to estimating forest extent and fragmentation, spaceborne sensors can also be used to quantify anthropogenic impacts in the form of forest loss, fire, and human disturbance at a global spatial scale (Giglio et al., 2006; Laurance et al., 2012; Small et al., 2005). Thus, there are a number of remote sensing metrics associated with climate, vegetation extent and condition, and anthropogenic disturbance that might improve conservation management.

Protected areas are widely regarded as one of the most successful measures implemented for the conservation of biodiversity, drawing upon traditional and community-based approaches, governance regimes, scientific and traditional knowledge, and contemporary practices of governments and conservation agencies (IUCN, 2013). Given the limited resources available for conservation efforts, it is critical that reserves are strategically planned to ensure the most effective protection of biodiversity and the most efficient use of land (Kupfer, 2012; Nagendra et al., 2013). A systematic approach to conservation planning generally prioritizes representativeness, persistence, and complementarity principles in reserve design (Margules and Pressey, 2000). In the past decade, remote sensing of protected areas has grown rapidly as exemplified by the number of scientific articles and reviews that use satellite imagery to assess land cover change, as well as techniques to model and monitor biodiversity and natural resource issues in individual protected areas (Fraser et al., 2009; Gillespie et al., 2014; Secades et al., 2014). However, the science has not been able to keep pace with the rapid accumulation of useful remote sensing data, the environmental changes that are occurring around the world, and real world information needs of natural resource managers, the conservation community, and the public in the over 100,000 decreed protected areas (UNEP and IUCN, 2009). Furthermore, the applications of spatial analysis tools and spaceborne remote sensing for protected areas has not been fully realized to date (Secades et al., 2014). Thus, there is a need to explore and test the utility of spaceborne sensors for conservation and management of protected areas and to develop standard and repeatable GIS and remote sensing methods, protocols, and products that can be used across all protected areas (Gaveau et al., 2009; Laurance et al., 2012; Nagendra et al., 2013).

Globally, tropical dry forests are one of the most endangered and least-studied forest types (Aide et al., 2013; Gillespie et al., 2012; Janzen, 1988; Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). This is especially true for Hawaiian dry forest which has 45% of its endemic trees and shrubs listed as federally threatened or endangered (Pau et al., 2009). Hawaii’s dry forest and dry scrub ecosystems contain over 25% of all endangered plant species in Hawaii, which accounts for 38% of all endangered and threatened plant species in the United States (Cabin et al., 2000; Sakai et al., 2002). Historically, Hawaiian dry forest ecosystems occurred between 0-1,500 m elevation on the rain shadow side of the islands (Cuddihy et al., 1989; Cuddihy and Stone, 1990; Stone et al., 1992) and contained high species richness and endemism compared with other habitats in Hawaii (Rock, 1913). Since European arrival, over 90% of the dry forest area has been destroyed resulting in widespread species loss (Bruegmann, 1996; Cabin et al., 2000; Sakai et al., 2002). Today, native dry forest habitat occurs in fragmented patches containing only a few rare and endangered individuals (Cabin et al., 2000). Although much of Hawaii’s dry forest has been lost, preservation of remaining fragments is both biologically and culturally significant, due to the high degree of endemic and rare species as well as the importance of many of these endangered species to native Hawaiian culture (Anderson-Fung and Maly, 2002).

Today, the distribution, diversity, and composition of dry forests in Hawaii are the result of significant human impact (fire, agriculture, development) and ecological changes (invasive species) (Cabin et al., 2004, 2002; Gillespie et al., 2008; Weller et al., 2011). Researchers have stated that over 90% of the original dry forest coverage has been eliminated in Hawaii, however, the actual extent of native dry forest cover may be as low as 1% (Bruegmann, 1996). The ambiguity regarding dry forest extent is further compounded by a general lack of knowledge on the biology, ecology, and distribution of endangered species found in Hawaii (Caujapé-Castells et al., 2010).

The aim of this study is to determine the extent and conservation status of tropical dry forests in Hawaii through the use of remote sensing and GIS technologies in order to understand the current state of the ecosystem and inform future management. We undertake this work with two major goals. First, we quantify the extent and composition of remaining native dry forest fragments on six of the main Hawaiian Islands using high-resolution geographic information system (GIS) data on climate and land cover. Second, we evaluate the effectiveness of reserves in protecting dry forest habitat by determining the percent of dry forest habitat found in reserves on each island.

5.3 Methods

5.3.1 Study Site

This research was conducted for the six main Hawaiian Islands located at the southeastern end of the archipelago including Kauai, Oahu, Molokai, Lanai, Maui, and the island of Hawaii (Big Island). The Hawaiian Islands cover 16, 634 km^2 and are the result of an active hot spot in the middle of the Pacific Ocean. The islands range in age from 5.1 my old (Kauai) to less than 0.5

my old (the Big Island) (Clague, 1996). Elevations range from sea level to 4,205 m on Mauna Kea, resulting in a diverse vegetation zones. The climate is predominantly controlled by orographic precipitation in which the north-easterly tradewinds bring heavy rainfall to the windward side of volcanic mountains resulting in drier conditions on the leeward side (Giambelluca et al., 2013). Mean annual precipitation is highly variable (50 cm to 715 cm) with the rainy season occurring from November to March and the dry season persisting from April through October (Walker, 1990). Mean temperature ranges from 15.7°C to 23.8°C (Giambelluca et al., 2013). Historically, native tropical dry forests, scrublands, and grasslands occurred at low elevations and on the rainshadow or dry sides of volcanic mountains (Cuddihy et al., 1989) .

5.3.2 Estimation of Dry Forest Cover and Composition

The extent and composition of remaining native dry forests throughout the Hawaiian Islands was estimated using climate data, the Hawaii Gap Analysis Project dataset, and the Global Forest Change dataset. The extent of the dry region on the Hawaiian Islands was provided by Price et al. (2012) and contains four moisture zones (arid, very dry, moderate dry, and seasonal mesic) that historically contained native tropical dry forest taxa (Price et al., 2012). The moisture zones were defined based on a moisture availability index derived from mean annual precipitation and potential evapotranspiration data provided by Giambelluca et al. 2013 (Giambelluca et al., 2013; Price et al., 2012). This climate dataset was created based on rainfall observations at more than 1200 sites in Hawaii, estimates derived from PRISM rainfall analysis (Daly, 2006), NEXRAD radar rainfall observations, MM5 mesoscale meteorological model simulations, and vegetation patterns (Giambelluca et al., 2013). Incorporating multiple datasets improves the overall accuracy of the climate predictions and enables estimates to be made in remote regions where rain gauge data is unavailable.

Land cover classifications were obtained from the 2008 Hawaii Gap Analysis Project which contains 37 state-wide land cover classes generated using Landsat TM imagery at a 30-meter pixel resolution from 1999 to 2005 with an overall accuracy of 44.13% (Kappa = 0.42) (Matsuwaki and Gibson, 2008). Twelve native forest land cover classes occur within the dry forest moisture zones including: (1) closed *Acacia-Metrosideros* forest, (2) closed *Metrosideros* forest, (3) closed *Pouteria* forest, (4) *Acacia* forest, (5) *Sophora* / *Myoporum* / native trees, (6) native mesic to dry forest and shrubland, (7) *Metrosideros-Cheirodendron* forest, (8) *Nestegis-Diospyros* forest, (9) open *Acacia-Sophora* forest, (10) open *Acacia-Metrosideros* forest, (11) open *Metrosideros* forest, and (12) *Metrosideros* forest. There are also nine vegetation types that also contain native species: (1) mixed native-alien forest, (2) mixed native-alien shrubs and grasses, (3) native coastal vegetation, (4) *Dodonaea* shrubland, (5) native dry cliff vegetation, (6) native shrubland/ sparse *Metrosideros,* (7) native wet cliff vegetation, (8) open *Gossypium* shrubland, and (9) *Dicranopteris* shrubland.

Forest cover extent and changes were estimated using the Global Forest Change dataset provided by the Hansen et al. (2013). This comprehensive dataset uses a time-series of Landsat TM imagery at a 30 m pixel resolution to provide an estimation of tree canopy cover in the year 2000, total forest loss between 2000 and 2014, and total forest cover gain between 2000 and 2012 (Hansen et al., 2013). The current extent of total forest in the dry region of Hawaii was calculated using ArcGIS 10.2.2 by adding forest cover gain to and subtracting forest cover loss from tree cover in the year 2000.

Land cover classification from the Gap Analysis Program, current forest cover data from the Global Forest Change dataset, and tropical dry forest moisture zones from Price et al. (2012) were overlaid in ArcGIS 10.2.2 to identify the extent and composition of remaining native dry forests on Kauai, Oahu, Molokai, Lanai, Maui, and the Big Island. Vegetation type was reclassified as native or non-native conservatively such that all native species could be accounted for (e.g. the ‘mixed native and alien forest’ class was classified as native). Natural reserve boundaries used in this analysis were acquired from the State of Hawaii GIS data system and are current to 2016 (Hawaii Statewide Planning and GIS Program, 2016). The reserve boundaries were overlaid with both the Global Forest Change and GAP Analysis datasets to identify the extent of native dry forest currently protected. The island containing the least amount of native dry forest as well as the lowest percentage of native dry forest protected was identified as having the most endangered dry forests in the Hawaiian Islands and a top priority for conservation management.

5.4 Results

5.4.1 Native Species Cover

Results from the Gap Analysis Project analysis show that native dry forest species cover 1,771.9 km^2 of the Hawaiian Islands and account for 18.4% of dry habitat and 10.8% of the total area of the islands (Table 1; Figure 2). The Big Island has the greatest area of dry habitat with 5571.4 km^2 while Lanai has the highest percent of dry habitat relative to its size (96.4%). The largest area of native dry forest cover as well as the highest percentage of native dry forest cover relative to the island size is found on the Big Island (1529.2 km^2 and 14.7%, respectively). Oahu contains the smallest area of native dry forest cover as well as the lowest percentage of native dry forest cover relative to its size (23.7 km^2 and 1.5%, respectively). The overall reserve area across all the islands is 3, 347.3 km^2 which accounts for 34.8% of Hawaii's dry region. Molokai and Oahu have the smallest dry forest area found in reserves relative to the island size with 34.3 km^2 (6.6%) and 88.7 km^2 (7.75%) protected, respectively. For all the islands, 292.1 km^2 of native dry forest cover is in protected areas which accounts for 35% of total native dry forest cover. The Big Island contains both the largest area of native dry forest cover as well as the largest percent of total native dry forest cover found in reserves (979.9 km^2 and 64.1%, respectively). The most dominant vegetation type in the dry region of the Hawaiian Islands is 'alien grassland' which covers 2301.0 km^2 or 14.0% of their total area. The next most abundant vegetation type is 'native shrubland/ sparse ohia' (1196.8 km^2 or 7.3%) followed by 'alien shrubland' (859.7 km^2 or 5.2%) and 'alien forest' (713.7 km^2 or 4.3%).

5.4.2 Global Forest Change

Based on Hansen et al. data combined with Price et al. climate zones, the dry forest habitat covers 2, 577.1 km^2 or 15.7% of the Hawaiian Islands (Table 2; Figure 3). This estimate does not account for differences between native and non-native species and is solely an estimation of total tree cover in the year 2014. The net loss of dry forest habitat between 2000 and 2014 across all of the Hawaiian Islands was 239.2 km^2 or 2.5% of the dry region. Oahu and Kauai had the greatest net loss in forest cover, with 128.2 km2 or 11.2% of the dry region and 86.1 km^2 or 11.1% of the dry region lost. Interestingly, there was a slight net forest cover gain on the Big Island of 22.1 km^2 or 0.4% of the dry region. On all of the Hawaiian islands, the natural reserves experienced a small net loss in forest cover when accounting for both forest loss and gain over the 14 year period (54.92 km^2, 1.8% of the total reserve area). Reserves on the Big Island had the largest net loss in forest cover (52.1 km^2, 1.97% of total reserve area) followed by reserves on Oahu (0.68 km^2, 0.63% of the total island reserve area).

5.5 Discussion

5.5.1 Dry Forest Extent, Changes, and Composition

It is difficult to estimate the amount of dry forest lost on the Hawaiian Islands due to a lack of paleoecological and historical data of dry forest extent available from before the arrival of the Polynesians or Europeans (Athens, 1997; Vitousek et al., 2004). However, we show that with advances in GIS and remote sensing technologies, it is possible to measure current forest cover as well as changes over the past two decades. Results from our GIS analysis using the GAP Analysis Project data suggest that native Hawaiian dry forest species occupy only 10.8% of the total area of the Hawaiian Islands. Previous estimates of native Hawaiian dry forest habitat state that 10% of the original forest cover remains (Bruegmann, 1996) and our findings corroborate this value. However, two factors suggest to the authors that the percentage of native dry forest is less than this reported value. First, the GAP Analysis Project for Hawaii includes only images through the year 2005. In the past decade, it is likely that some of the native forest cover has been replaced with non-native species. Furthermore, analysis of the Global Forest Change dataset shows that there has been a net loss of total forest cover on the islands between the year 2000 and 2015. Second, our classification of native species was conservative and included some non-native species under the class ‘mixed native-alien forest’ and ‘mixed native-alien shrubs and grasses’. Of the 10.8% remaining, only about 35% of native dry forest species cover is found in reserves. Thus, the total protected native dry forest habitat in Hawaii is about 3.8%. Changes in forest cover of reserves between the years 2000 and 2014 in the dry forest region of Hawaii were overall found to be a net loss of 3.2%. Although it is possible to estimate forest gain or loss from the Global Forest Change dataset, it is unclear whether the change is attributed to changes in native or non-native species distributions. Surprisingly, our results show a slight net gain in forest cover on the Big Island while all of the other islands had net losses in forest cover. Overlaying the GAP analysis data suggests that this land is mixed native and non-native forest cover. Overlaying landownership data shows that this land is privately owned by a ranch. Based on these factors, the authors conclude that the primary region of tree growth is likely non-native species.

Our results indicate that three out of the four most dominant vegetation types across all of the Hawaiian Islands contain non-native species. Worldwide, it is expected that climate change will lead to an increase in exotic species invasions and fire (Diez et al., 2012; DM Richardson et al., 2000; Hellmann et al., 2008; Hobbs, 2000). This is especially concerning for ecosystems such as Hawaii's dry forests which are prone to periods of drought. Prolonged dry events will likely increase the number of fires and subsequently, enable the expansion of invasive grasses in Hawaii's dry forest habitat (Hughes et al., 1991; Smith and Tunison, 1992). This grass-fire cycle in which fire facilitates the expansion of exotic grasses which then increases the likelihood of fire has been cited as a major threat to Hawaii's dry forest ecosystems (D'Antonio and Vitousek, 1992; Hughes et al., 1991). By understanding the geographic location and overall extent of exotic vegetation, conservation managers can better estimate fuel loads and take preventative action to prevent massive wildfires.

5.5.2 Management Implications

Although all of the islands collectively have low native dry forest cover (10.8%), Oahu contains only 1.5% native cover, of which only 0.75% is found in protected areas (Table 1). Furthermore, between the year 2000 and 2014 Oahu experienced an 11.2% decline in total forest cover found in the dry region (Table 2). Although there are no federal national parks or national forests on Oahu, federal agencies are undertaking the most extensive dry forest restoration projects. State agencies are involved with limited restoration projects on land within the extensive State Natural Area Reserve System and Forest Reserve System. The City and County of Honolulu have undertaken a number of excellent education projects concerning native species in botanical gardens in the lowlands of Oahu. These micro-restoration or gardening projects are important for educating the general public about native species that used to occur in the heavy developed urban lowlands (Hobbs 2007). There are a number of non-profit organizations involved in restoring native dry forest species on private land. These organizations work primarily in densely populated areas in the lowlands of Oahu. Despite the multiple agencies involved in conservation management on Oahu, many projects are highly underfunded. In order for restoration projects to receive greater funding, it is imperative that the state of the dry forest be quantified so that it can be considered a high conservation priority. Our study provides an assessment of the current state of Hawaii’s dry forest which can provide insight into the management of remaining dry forest fragments as well as target areas of exotic species removal.

5.6 Conclusion

The last estimate of Hawaii’s dry forest occurred over two decades ago and was based solely on field observations (Bruegmann, 1996). This study utilizes two distinct datasets derived from remotely sensed imagery in order to estimate the Hawaiian dry forest extent and composition, as well as determine the overall conservation status of dry forest on each of the Hawaiian Islands. While our focus was to measure the dry forest extent across all the main islands, there is potential for more local high-resolution quantification of canopy cover to improve estimates of remaining dry forest extent on Hawaii. For example, Morales et al. (2008) successfully quantified canopy cover in a dry forest site on Big Island using high spatial resolution (1-m^2) Ikonos-2 satellite data (Morales et al., 2008). Although measuring forest extent and composition at high resolution may be ideal, often times this data is either unavailable or expensive for remote areas such as Hawaii. In our study, we show that it is possible to use freely available data for a first order assessment of ecosystem health. Ultimately, the most robust estimation of an ecosystem's conservation status will combine both field methods and remote sensing/GIS technologies in order to provide a complete assessment of its current state and monitor changes over time.

5.7 Acknowledgements

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5.8 Figures

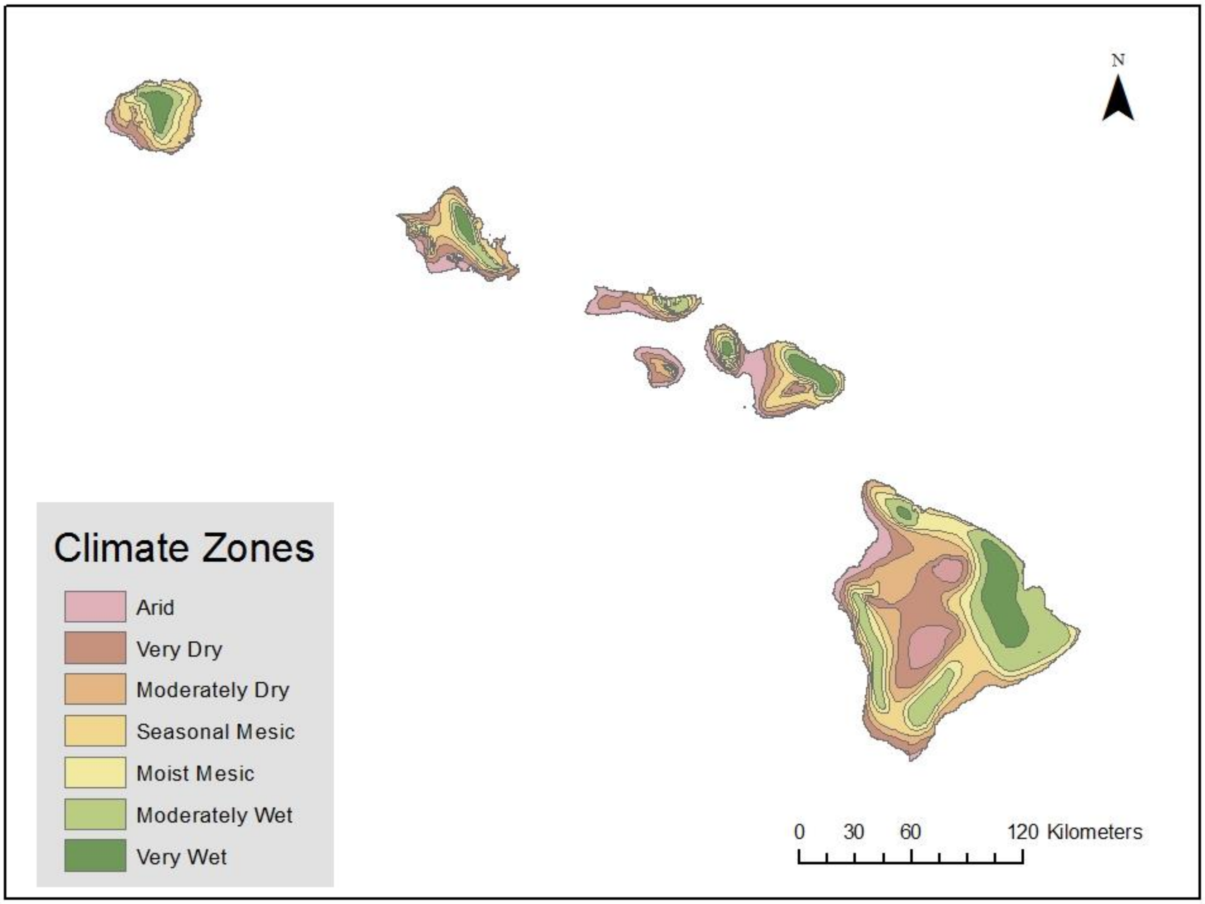

Figure 1: The above figure displays the climate zones from Price et al. 2012 of the six main Hawaiian Islands from oldest to youngest (left to right): Kauai, Oahu, Molokai, Lanai, Maui, and the Big Island

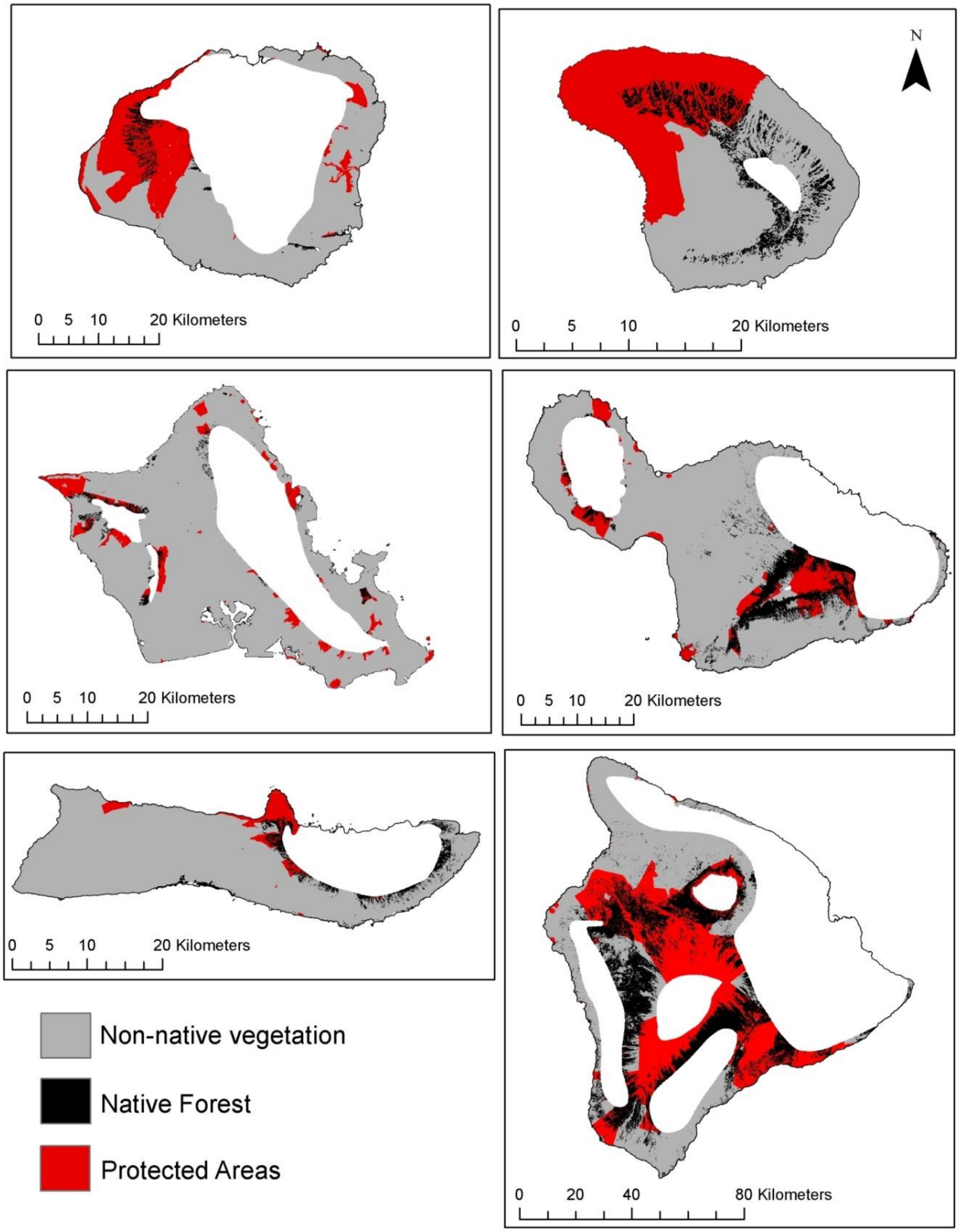

Figure 2: The above image shows native forest found in protected areas based on the GAP Analysis landcover dataset

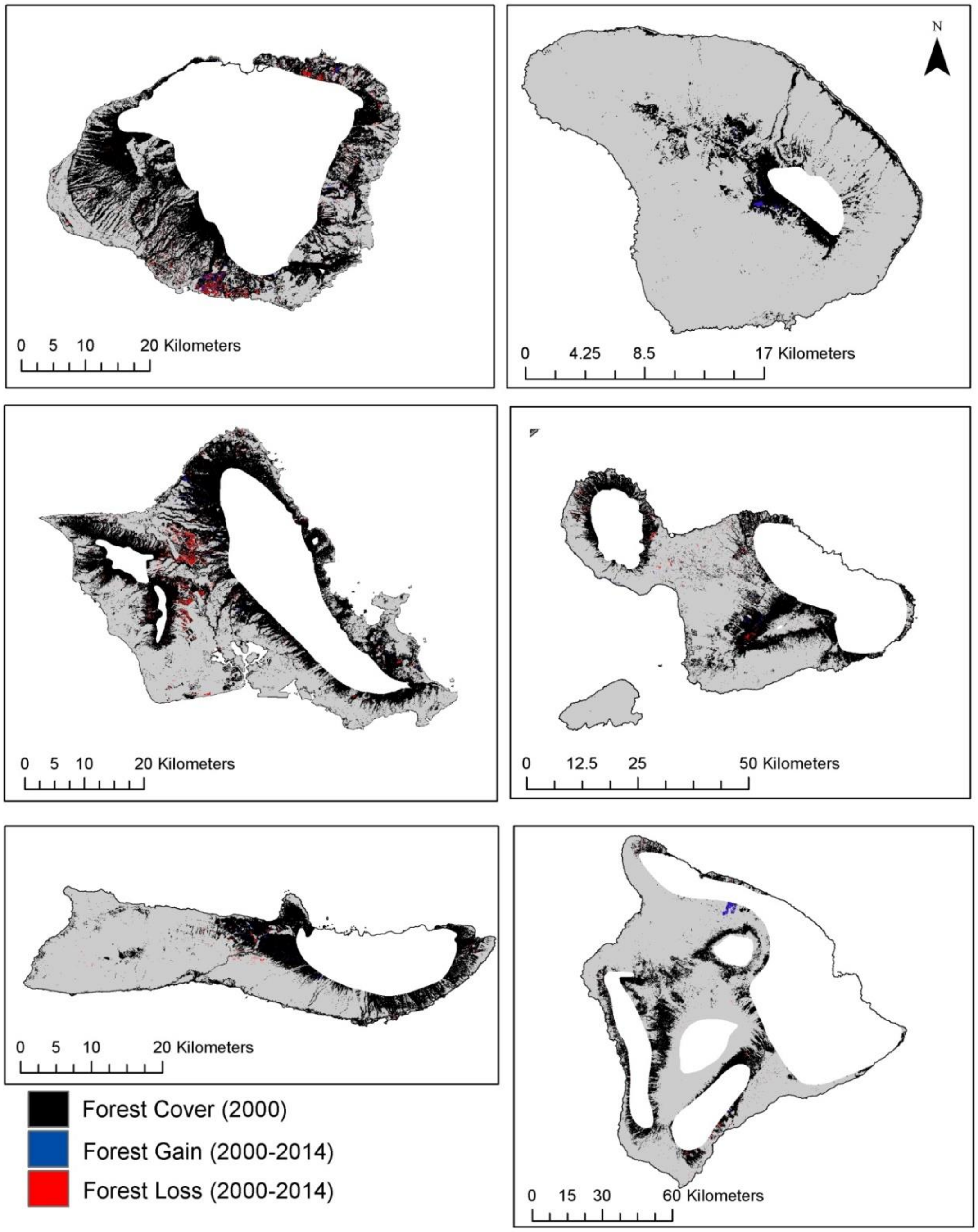

Figure 3: The above figure shows dry forest cover from the year 2000, forest gain (2000 – 2014), and forest loss (2000-2014) for the six major Hawaiian Islands based on the Global Forest Change dataset

5.9 Tables

Island	Island size km^2	Dry region km^2	Native Dry Forest km^2 (% of total island)	Dry Reserve Area (% of dry area)	Native Dry Forest in Reserves km^2 (% of native cover)
All	16451.5	9623.5	1771.9 (10.8)	3347.3 (34.8)	292.1 (35.0)
Kauai	1430.6	775.7	24.3 (1.7)	233.0 (30.0)	20.1 (82.7)
Oahu	1547.9	1144.1	23.7 (1.5)	88.7 (7.75)	11.8 (49.8)
Molokai	674.6	521.5	26.1 (3.9)	34.3 (6.6)	6.9 (26.4)
Lanai	365.4	352.3	38.4 (10.5)	139.9 (39.7)	16.7 (43.5)
Maui	1999.5	1258.5	129.5 (6.5)	171.7 (13.6)	62.8 (48.5)
Big Island	10433.5 (20.3)	5571.4	1529.2 (14.7)	2679.7 (48.1)	979.9 (64.1)

Table 1: The above table details the area and percent of native dry forest on the Hawaiian Islands and in reserves on each island based on the GAP Analysis Project data and climate data from Price et al. 2012

Island	Forest Cover km^2 (% of island)	Gain km^2 (% of dry area)	Loss km^2 (% of dry area)	Cover in Reserves km^2 (% of total forest cover)	Reserve Gain km^2 (% of reserve)	Reserve Loss km^2 (% of reserve)
All	2577.1 (15.7)	182.6 (1.9)	421.8 (4.4)	740 (28.7)	3.68 (0.12)	58.6 (1.8)
Kauai	419.5 (29.3)	18.6 (2.4)	104.7 (13.5)	157.1 (37.4)	0.08 (0.01)	1.74 (0.26)
Oahu	499.8 (32.3)	16.0 (1.4)	144.2(12.6)	70.5 (13.8)	0.02 (0.01)	0.70 (0.63)
Molokai	128.1 (19.0)	0.68 (0.13)	1.6 (0.31)	25.9 (19.8)	0.06 (0.04)	0.34 (0.22)
Lanai	28.8 (8.2)	0.32 (0.092)	0.030 (0.0086)	5.1 (16.8)	0.002 (0.003)	0.008 (0.005)
Maui	368.7 (29.3)	18.9 (1.5)	65.4 (5.2)	99.6 (27.0)	0.06 (0.04)	0.34 (0.22)
Big Island	1132.2 (20.3)	128.1 (2.3)	105.9 (1.9)	381.8 (33.7)	3.44 (0.13)	55.5 (2.1)

Table 2: The table above lists current forest cover, forest loss, and forest gain between 2000 and 2014 for the total dry region and for reserves based on the Global Forest Change datastet

Gap Analysis Class	Area (km^2)
M: Mixed Native-Alien Forest	21.16
NG: Deschampsia Grassland	3.72
NS: Aalii Shrubland	34.75
NS: Native Coastal Vegetation	0.15
NS: Native Dry Cliff Vegetation	3.35
NS: Native Shrubland / Sparse Ohia (native shrubs)	1196.83
NS: Native Wet Cliff Vegetation	0.88
NS: Open Mao Shrubland	0.47
NS: Uluhe Shrubland	2.34
NT: Closed Hala Forest	1.31
NT: Closed Koa-Ohia Forest	62.19
NT: Closed Pouteria Forest (native trees)	0.05
NT: Koa Forest	2.33
NT: Mamane / Naio / Native Trees	120.75
NT: Native Mesic to Dry Forest and Shrubland	7.71
NT: Native Wet Forest and Shrubland	0.5
NT: Ohia Forest	0.9
NT: Olopua-Lama Forest	0.52
NT: Open Koa-Mamane Forest	88.31
NT: Open Koa-Ohia Forest	182.9
NT: Open Ohia Forest	134.26
Undefined	4.18
W: Water	30.23

W: Wetland Vegetation	7.65
X: Agriculture	600.05
X: High Intensity Developed	117.91
X: Low Intensity Developed	316.7
XG: Alien Grassland	2301.01
XS: Alien Shrubland	859.73
XT: Alien Forest	713.69
XT: Kiawe Forest and Shrubland	564.54
Y: Uncharacterized Forest	37.83
Y: Uncharacterized Open-Sparse Vegetation	181.16
Y: Uncharacterized Shrubland	4.36
Z: Very Sparse Vegetation to Unvegetated	2156.62

Table 3: GAP classifications and their associated areas for all of the Hawaiian Islands

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CHAPTER 6

6. Conclusion

6.1 Summary

This dissertation uses field-based methods, habitat suitability modeling, GIS, and analyses of remotely sensed data to quantify the conservation status of Hawaii's dry forest and inform management decisions regarding the reintroduction of endangered species. Each chapter is formatted as a peer-reviewed academic journal article and is published, in review, or in preparation for submission. For conservation management to be effective it is essential to understand the current state of an ecosystem and test scientifically derived techniques with the goal of creating a standard and repeatable protocol for monitoring and restoring threatened habitat. Each chapter in this dissertation serves to accomplish this goal for Hawaii's dry forest by using different methods that either provide insight into potential methods to inform endangered species reintroductions or into the conservation status of this ecosystem. The following paragraphs summarize the key findings of each chapter.

Chapter 2 provides an overview of the past and present degradation of Hawaii's dry forest and highlights areas that could benefit from additional research. Major threats to Hawaii's dry forest include deforestation, land development, pigs, non-native ungulate grazing, invasive species, and fire. A thorough review of the literature suggests that most research has been focused on understanding the impact of invasive grasses and fire on Hawaii's dry forest while fewer studies have examined the impacts of pigs and livestock grazing. This is likely because invasive grasses and fires associated with their expansion have the ability to destroy remaining dry forest fragments over a very short time-scale. Furthermore, it was found that there needs to be greater efforts towards quantifying the impacts posed by different threats in order to understand which factor is most important to manage. It is recommended that threats be assessed annually to evaluate the rate at which a threat can cause changes in dry forest ecosystems. While previous research has shown the aboveground forest degradation caused by different threats, greater research should evaluate the impacts on belowground process such as nutrient cycling, which influences aboveground dynamics. Overall, there remains a great need for research in all areas concerning Hawaii's dry forest as little is known regarding the historical state of the ecosystem, its current extent and distribution, and potential methods for preserving and restoring remaining fragments.

Chapter 3 utilizes habitat suitability modeling to determine the best methods for modeling rare or endangered species in regions with rugged topography, such as Hawaii. Habitat suitability models were created for 11 rare and endangered species in Hawaii's dry forest in order to determine the most appropriate spatial scale and environmental variables that should be used for modeling species in regions with diverse topography. Results from this study suggest that high resolution topography data may be a better option than relying solely on coarse climate grids, especially when HSMs are used to inform endangered plant reintroductions on small islands. The relative importance of the environmental metrics did not vary across spatial scales with soil great group contributing most to the models, followed by elevation, and mean precipitation of the driest quarter. Only 1.2% of the total area of niche overlap for eight species is currently found in protected areas. Overall, this study shows that species distribution models are useful for predicting habitat suitability at all scales (1 km, 250 m, 10 m), environmental metrics do not change across scales but high resolution data on soils, topography, and precipitation are needed, and 10 m resolution data are the best for informing restoration decisions for the endangered species on Hawaii and other oceanic islands.

Chapter 4 involves the reintroduction of *Hibiscus brackenridgei mokuleinus*, the state flower of Hawaii and a federally endangered species, into its historical and highly degraded habitat on Oahu. In December 2013, fifty individuals were grown from cuttings and transplanted in eight different sites. After the initial planting, there was minimal management of the reintroduction sites. After two years, 52% of the plants survived and had an average growth of 107.8 cm (± 11.6 cm). Sites with the greatest plant survival and growth had greater soil water content, steeper slopes, higher annual precipitation, lower soil bulk density, slightly acidic soil pH, and a lower soil C:N ratio. In addition, habitat suitability models were significantly, positively correlated with total plant growth suggesting they may be useful for reintroduction site selection. Results from this study suggest that management of sites is most important in the months immediately following reintroduction, but may not be necessary after the first year post-transplant when individuals are large enough to compete with fast-growing invasive species. Overall, choosing sites with adequate soil water content, exposure to higher rainfall, slightly acidic pH, lower bulk density, and steeper slopes should result in greater survival and growth of reintroduced individuals.

Chapter 5 evaluates the current extent of Hawaii’s dry forest, changes over the past decade, and composition using two remotely sensed datasets: the GAP Analysis Project and Global Forest Change datasets. Measurements of dry forest extent based on the GAP Analysis dataset corroborate the previously estimated value (10%). However, the estimates from this study are likely higher than actual because only images through the year 2005 are considered in the GAP Analysis Project dataset and it is likely that some of the native forest covered has been replaced by non-native species. Furthermore, estimations from the Global Forest Change dataset are even greater (15.7%). However, this measurement does not discriminate between native and non-native species and only provides insight into the percent of tree cover in the dry regions of Hawaii. Further analysis of the Global Forest Change dataset suggests that there has been a net loss of total forest cover on the islands and in reserves between 2000 and 2014. Finally, analysis of the GAP Analysis Project dataset suggests that three of the four most dominant vegetation types across all of the Hawaiian Islands contain non-native species. This is especially concerning considering the predictions that global climate change will favor the expansion of invasive grasslands in Hawaii and subsequently, increase the frequency of fires.

6.2 Research Contributions

In addition to the scientific findings discussed throughout this dissertation, several products that may be of use to both the scientific community and conservation managers are as follows:

1. A review of the history of Hawaii's dry forest and contemporary issues faced by this highly endangered ecosystems
2. Habitat suitability models for 11 native Hawaiian dry forest species (10 endangered, and one rare) which may assist with multi-species reintroduction site selection on Oahu

3. Guidelines for reintroduction site selection on Oahu and an assessment of important environmental variables to consider based on a reintroduction study of endangered *Hibiscus brackenridgei mokuleinas*
4. An evaluation of the current extent and composition of Hawaii’s dry forest and changes which have occurred over the past decade