Vegetation Patterns in Lowland Wet Forests of Hawai'i

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by

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Stands in Brilliant Composition

Here the forest pockets proclaim themselves in plain view
Uttering an ancient essence and origin beyond human
Stands in brilliant composition
The green growth entwined, by branch and by root

A fragile glimpse that in itself supersedes strife
A niche not nebulous to those embraced
Shading the order of diminishing grandeur
Far into the moss covered bottoms

And this I treasure
For so lovely is apportioned the diversity of lives
Beyond the appetite of impenetrable invasion
These lasting remains in lingering potency
Hover, between the likely and the possible

C. J. Dupuis

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Abstract

The easternmost part of the Big Island contains some of Hawai'i's last remaining native lowland wet forests. My goals in this study were to examine how substrate age and elevation influence the degree of invasion present in this lower elevation (< 300 m) region by assessing native and non-native canopy cover of trees, to evaluate native-dominated communities for the influence of substrate age and elevation on diversity and species composition, to examine canopy conditions surrounding rare plant occurrences, and to identify priority areas for restoration. I focused on East Hawai'i's five forest reserves using Braun-Blanquet cover estimate methods to assess vegetation patterns. Plots were stratified to represent combinations of variables including three categories of substrate age (< 200 yrs, 200-750 yrs, >750 yrs), and three elevation zones (< 100 m, 101-200 m, 201-300 m). I analyzed 291 plots, of which 125 had a native-dominated canopy. On intermediate flows, absolute cover of native tree species was higher when compared to young flows; relative cover of native tree species was higher, and absolute cover of non-native species was lower, when compared to older substrates. On young flows, absolute cover of native trees equaled that of non-native trees. The oldest substrate proved to be most degraded, with the relative cover of native trees being lower than on other substrates. At native-dominated sites, there was higher native species richness on intermediate substrates relative to the young, and higher non-native species richness on the older substrate when compared to the young. Young and old substrates had higher numbers of non-native species than they did native species. There was a greater relative canopy cover of native trees where rare plants occur compared to plots where they do not occur. All 34 individuals from rare species were entirely on the 200-750 year old substrate. Together, these trends point to intermediate age substrates as holding the most intact native assemblages and highest potential for restoration.

Chapter I

Native and Non-native Plant Community Comparison

Introduction

As an isolated, tropical archipelago, Hawai'i is home to a rich native flora; current taxonomy suggests that there are 1009 native angiosperms of which 90% are endemic (Wagner *et al.,* 1999), 54% being single-island, and 43% being single-volcano endemics (Price, 2004). High endemism rates are the result of its isolated position in the central Pacific Ocean, which has restricted natural colonization events during its 30 million year history (Price and Clague, 2002). By the mid-1600s, Hawai'i's lowland vegetation was dramatically altered as a result of deforestation and agriculture, with the Hawaiian population reaching a peak of up to one million people (Kelly, 1983; Kirch, 1985). Though the first Hawaiians introduced 40 -50 animal and plant species (Kirch, 1982; Nagata, 1985), the number of introduced species has increased dramatically since the arrival of Europeans in the late 18th century (Cuddihy and Stone, 1990). An estimated 8,000 plant species have been introduced in Hawai'i over the past two centuries (Sax and Gaines, 2008), and with more than 1,000 of them being naturalized (Wagner *et al.,* 1999), the number of non-native species established in the wild has exceeded native species' numbers (Sax and Gaines, 2008). Over time, additional introductions have become naturalized (Wagner and Herbst, 2002), some of which may present a threat to native forests in the future. According to Sax and Gaines (2008), the doubling of plant richness across oceanic islands is based on a current 1:1 ratio of naturalized to native species, and at the current rate of change, the average ratio is projected to be 3:2 by 2060. Despite an increase in biodiversity on local and regional levels, the global exchange between species diminishes endemism rates by contributing to species extinctions, and a decline in biodiversity on a global level (Wilson, 1992; Davis, 2003).

Invasive species are today a principal threat to many of the world's island systems (MacDonald *et al.,* 1991; Walker and Steffen, 1997; Wilcove *et al.,* 1998; Chazdon, 2008); they are one of the greatest threats to native biodiversity throughout the Hawaiian Island chain (Smith 1985; Vitousek, 1990). The vulnerability of Hawai'i's forest ecosystems to invasion by exotic species is the result of its isolated location, in combination with numerous historical events (Smith 1985; Cuddihy and Stone, 1990; Vitousek, 1990; Denslow and DeWalt, 2008; Sax and Gaines, 2008). Among the most significant human disturbance events to affect Hawai'i's ecosystems statewide was a large scale out-planting of 948 exotic species into forest reserves between 1910 and 1960. Although the purpose for this enterprise was to restore Hawai'i's degrading watersheds, this greatly accelerated the spread of invasive species (Woodcock, 2007).

Though present-day plant distribution patterns reflect a number of factors, increased loss in habitat is a prominent threat to the survival of native species, as an increase in the population size of introduced species directly corresponds with the reduction in the native species' population size (Davis, 2003). Some of the effects of invasive species on native plant communities include competition for water or nutrients (Smith, 1985; Kagawa *et al.,* 2009; Cavaleri and Sack, 2010), and displacement through shading or recruitment suppression (Smith, 1985; Vitousek, 1987; Stone *et al.,* 1992). Invasive species have the potential of altering whole ecosystems by changing fire, soil, and water regimes, affecting nutrient cycling, developing monotypic stands or facilitating other non-native species (Smith 1985; Vitousek, 1987; Vitousek, 1990; Chornesky, 2003; Ehrenfeld, 2003). According to Vitousek *et al.* (1987), this has been the case in ecosystems at higher elevations in Hawai'i Volcanoes National Park, where nitrogen fixing *Myrica faya* was found to quadruple nitrogen inputs. Fixed nitrogen expands the resource base for the whole ecosystem by becoming available in soil nutrient pools. Other invasive species may change ecosystem function by altering the trophic structure of an invaded area or the frequency and/or intensity of disturbance events (Smith, 1985; Vitousek, 1990; Stone *et al.,* 1992).

In lowland wet forests (LWF) of Hawai'i, land conversion by agriculture and residential development has increasingly fragmented the landscape, greatly facilitating its vulnerability to alien invasion, and has had degrading effects on native plant communities (Cuddihy and Stone, 1990). For these forests, albizia *(Falcataria moluccana)* assumes a nitrogen-fixing role, altering ecosystem processes and development (Hughes and Denslow, 2005; Hughes and Uowolo, 2006; Zimmerman *et al.,* 2008). Other key species in LWF such as strawberry guava (*Psidium cattleianum*) and *Melastoma septemnervium*, though not nitrogen fixing, pose a similar breadth of impact on the native environment (Atkinson, 1970; Uowolo and Denslow, 2008; Zimmerman *et al.,* 2008).

In spite of current invasion levels, the largest remnants of native LWF are found on the easternmost part of the Big Island. With remnant forest patches spanning a range of successional stages, wet lowlands of East Hawai'i provide a model system for the study of impacts on native rainforests by invasive species (Atkinson, 1970; Uowolo and Denslow, 2008; Zimmerman *et al.,* 2008). This study examines factors influencing the invasion patterns of native LWF in seeking to understand the degree of their invasion on a landscape scale. Though a number of factors may have some degree of effect on plant distribution patterns, substrate age and elevation represent a significant influence based on a number of studies (Aplet *et al.,* 1994; Hughes and Denslow, 2006; Zimmerman *et al.,* 2008). According to Zimmerman *et al.,* (2008), younger substrates (<200yrs) are primarily composed of the native ʻōhiʻa *(Metrosideros polymorpha)*, substrates greater than 300 years old are becoming increasingly compromised by invasive species, and substrates greater than 500 years old are heavily invaded.

In order to more thoroughly understand invasion patterns in LWF, I compare canopy cover of native and non-native-dominated communities with respect to substrate age and elevation on a broad landscape level. My questions include: Do both native and non-native species have a greater absolute canopy cover on older sites than on younger sites? Is the relative canopy cover of native trees greater on younger sites than on older sites when compared to non-native tree species? How does the effect of elevation influence native and non-native plant distribution patterns? Understanding general trends in the canopy cover of LWF vegetation can help identify priority areas, and inform restoration efforts for the few relatively intact segments of remaining wet native forests in the lower elevation regions of Hawai'i.

Methods

Site description

The overall climate on low windward slopes of Kilauea Volcano is warm and wet with a mean annual temperature of approximately 23° Celsius (Juvik and Juvik, 1998). Because elevation ranges from sea level to 300 meters, temperature alone is unlikely to influence variation in plant composition and structure. However, rainfall at higher elevations within this region is 4,000 mm/yr and decreases to 2,000 mm/yr along the coast (Juvik and Juvik, 1998), contributing a certain degree to variation. In the lowland tropical environment, many plants partition themselves according to salt tolerance levels along the elevation gradient (Atkinson, 1970; Gagne and Cuddihy, 1999). Hence, elevation co-varies with salt spray exposure as well as moisture with distance from the coast. Although Atkinson (1970) did not observe trends related to substrate type, Zimmerman *et al.* (2008) suggest that it may have an important role in the distribution of species. Due to heavy groundcover, it is however often difficult to determine whether the substrate in a plot area is made up of the more rugged ‘a‘a or smoother pahoehoe substrate. Despite the possible influence of substrate type and other factors on vegetation composition and structure, as naturally occurring variables expressed in the landscape, substrate age and elevation provide adequate variation.

Field Methods

The focus of my study was on lowland wet forest in the five forest reserves of East Hawai'i: Nānāwale, Kaniahiku, Halepua‘a, Malama-Kī, and Keauohana (Fig. 1). I conducted an extensive survey to assess the current vegetation composition of the eastern portion of the Island of Hawai'i on a landscape scale. Initial reconnaissance and a Geographical Information System (GIS) aided me in establishing potential plot locations. Previous surveys such as a Halepua’a forest reserve survey (Clarke *et al.,* 1979) and a botanical reconnaissance of Malama-Kī forest reserve (Clarke *et al.,* 1981) were also utilized to aid site selection.

I developed individual maps for each reserve using GIS with relevant data: elevation, reserve boundaries, residential areas, roads, land-ownership and land-use patterns, and substrate age. These data aided in the establishment of predetermined transect lines and potential plot locations. Coordinates were entered into a GPS unit prior to entering the field in order to help guide field navigation. Transect lines paralleled reserve boundary lines and were kept a minimum of 50 meters from them in order to avoid confounding factors resulting from edge effects. The sampling design also maintained a minimum distance of 50 meters between transects and plots. The interval between plots and transects on the maps varied depending on the size of the reserve, however the systematic layout offered a basic guideline from which 50m intervals could be determined in the field between established points. In some cases where sample zones were limited in size, such as with substrates greater than 750 years, systematic points were specifically placed to maximize the number of potential plots for the area, while maintaining the minimum required distance between points, thereby appearing more clustered on the map (Fig. A1). In order to evenly distribute my samples and represent the general vegetation patterns of LWF, systematic plots were stratified to represent different substrate ages: younger lava flows, also known as historic flows, date from 1790 up to the present day (now slightly more than 200 years, but considered as < 200 years in this study); intermediate substrate between 200-750 years; and older lava flows greater than 750 years in age (Fig. A2). Substrate age classes were based on those of the Geologic Map of the Island of Hawai'i (Wolfe and Morris, 1996). To ensure even distribution across the elevation gradient I stratified my samples across three elevation zones (<100 m, 101-200 m, 201-300 m), however elevation data used for analyses were based on continuous values representing a range of elevation up to 300 meters (Fig. A3).

From the large set of pre-defined potential plots, selection of plots to be sampled focused on the easiest points of entry, such as roads. My goal was to achieve a minimum of 10 samples each for all 18 sampling zones. In some cases where reserves do not include all combinations of variables, I established plots elsewhere in the region in order to achieve a sufficient sample size. For most of the sampling zones, much more than the minimum was achieved, with the exception of native-dominated sites on older substrate, at the middle elevation range, where there simply was not enough representation.

When arriving at each point, I established a station along the transect using the point as its center. A measuring tape was used in order to clearly visualize which plant species were within a 5.6 meter radius of the 100 m^2 circular plot. Each square meter represented 1% of the total area aiding quantification in the estimation process. The modest size of the plots offers the advantage of being able to produce a large sample size of widely dispersed plots, contributing to more objectivity and accuracy in the overall estimation of cover. On the other hand, smaller plots may represent highly localized conditions in a heterogeneous natural landscape.

For each plot beginning with the uppermost layer, I conducted a basic assessment in which I estimated and recorded the height class and cover class of all native and non-native tree species greater than 3 meters in height employing the Braun-Blanquet cover class estimation method (Mueller-Dombois *et al.,* 1974). The Braun-Blanquet method is designed to quantify a large number of plots over a broad area as efficiently as possible, affording it high levels of accuracy through large sample size but with limited precision for individual plots. Limited precision is the result of some broad categories for which the mid-value was utilized in the analyses. On the other hand, these categories were beneficial for the accuracy of estimations in the field. It was straightforward for team members to agree on the percent cover of a given species due to the small size of a plot, and the layout of Braun-Blanquet categories. Height layers utilized in this component of the study were the upper canopy (>20 m), mid canopy (10-20 m), lower canopy (5-10 m), and tree ferns/short trees (3-5m); cover classes were defined as : <1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-95% and 95-100%. Assessments began with species at the highest canopy level, and included all of its estimated cover from various heights into the layer in which it was most dominant. A total of 291 plots of 100 m^2 were assessed throughout the five reserves (Figures A4- A7); all of these received a basic assessment, and a subset of 125 plots (which had ≥ 66.6% relative cover of native canopy) received a detailed assessment (Table A1, A1b; see chapter 2).

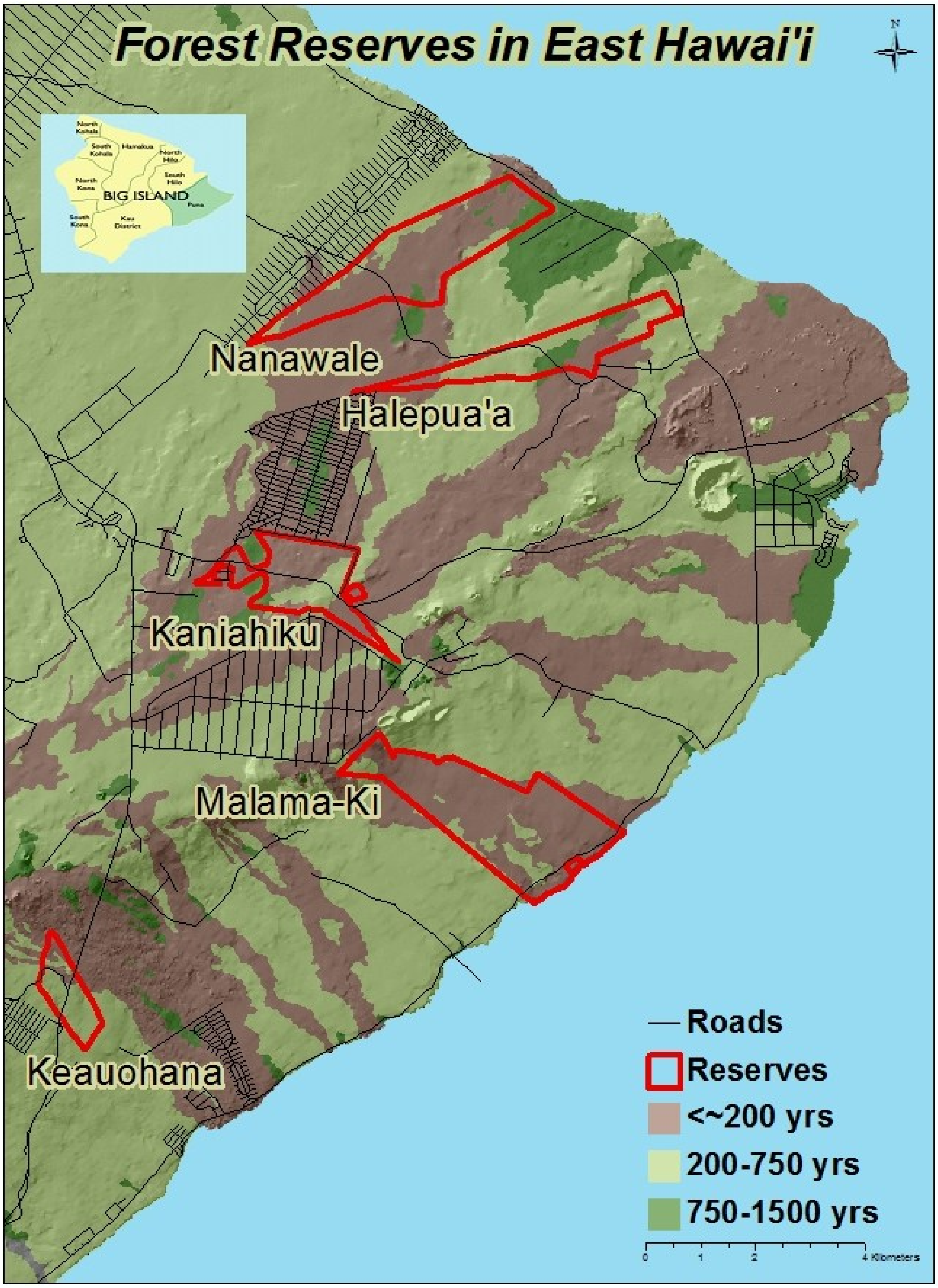

Fig.1: Study location with forest reserves in East Hawai'i.

Statistical analysis

The data for total cover of non-native trees have a slight bi-modal tendency due to heavily invaded areas contrasting with strongly intact ones, and data for total cover of native trees were slightly skewed; nonetheless equal variance patterns and normality in the distribution of the residuals were acceptable for parametric analyses. Hence, a basic one-way ANOVA analysis using Minitab 16 was used for all analyses in this chapter. Tests were run to determine whether both native and non-native species have greater absolute cover on older sites than on younger sites, and whether native tree species have a greater relative canopy cover on younger sites than on older sites when compared to non-native tree species. Dependent variables were absolute canopy cover of native trees, absolute canopy cover of non-native trees, and relative canopy cover of native trees; the independent variable examined was substrate age class. In addition, elevation was treated as a continuous variable for a correlation analysis to test the significance of the relationship between elevation and cover for all data, and for each substrate age class. A Bonferroni correction was conducted to adjust the p-value in order to counteract any problems possibly resulting from multiple comparisons. Hence, if the p-value for the response variable exceeded $p = 0.009$, the correlation was determined insignificant.

Results:

Substrate Age

A total of 291 plots were analyzed in terms of their canopy cover. According to substrate age categories, sample sizes were 103 for the young, 89 for the intermediate, and 97 for the old substrate. Intermediate substrate (90%) was greater in absolute percent canopy cover of native trees ($F_{2,286} = 5.87$; $p = 0.003$), when compared to young substrate (62%). For non-native tree species the average in total absolute percent cover was 68%, 50% and 84% from youngest to oldest substrate. In this case absolute cover on the young was similar to both medium and old aged sites, though there was a significant difference between the medium and old sites ($F_{2, 286} = 7.74$; $p = 0.001$) (Fig. 2).

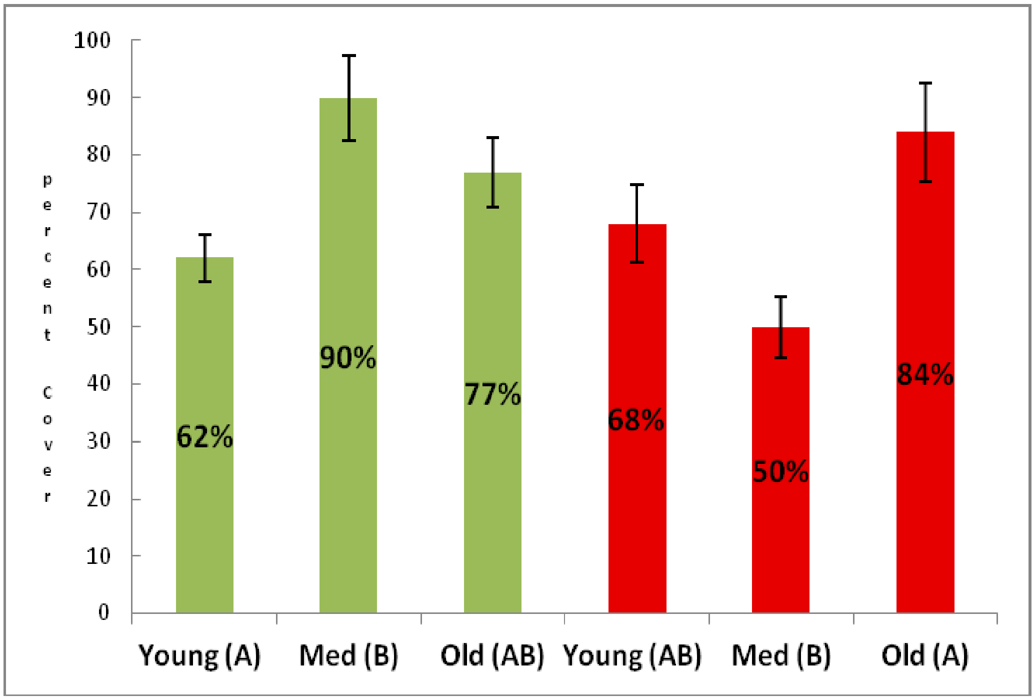

Fig. 2: Average absolute percent cover of native (green) and non-native trees (red) with standard error bars, in three substrate ages categories (< 200 yrs, 200-750 yrs, > 750 yrs) Different letters (A, B) show significance ($p \leq 0.05$) across substrate ages, with the native and non-native species tested separately.

Relative cover of native trees on young (60%) and intermediate (62%) substrates was equivalent, and their values were both greater than on older substrate (48%) ($F_{2, 286} = 4.56$; $p = 0.011$) (Fig. 3).

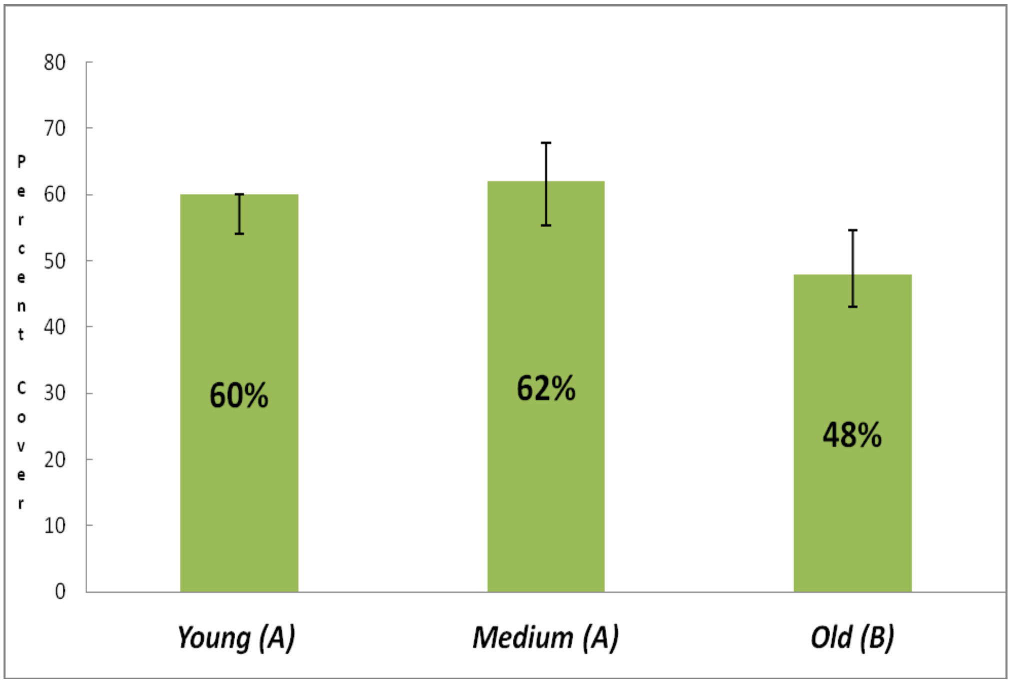

Fig. 3: Average relative percent canopy cover and standard error of native trees in three substrate ages categories (< 200 yrs, 200- 750 yrs, > 750 yrs). Different letters (A, B) show significance ($p \leq 0.05$) across substrate ages, with the native and non-native species tested separately.

Elevation

Canopy cover had no relationship to elevation when looking at all of the data for the region, but when isolating different age substrates, total cover of native trees was negatively correlated with elevation on young substrates ($r = - 0.387$, $p= 0.001$), meaning that canopy cover was highest at the lowest elevation on this particular substrate age (Table A2). These results are based on a Bonferroni correction ($p= 0.009$) due to multiple comparisons.

Dominant species in LWF

Species making up the greatest proportion of absolute canopy cover in LWF of East Hawai'i in general were (in descending order): ‘ōhi‘a *(Metrosideros polymorpha)* (44%), strawberry guava (*Psidium cattleianum)* (30%), hala *(Pandanus tectorius)* (30% strictly in the lowest 100 m), lama (*Diospyros sandwicensis)* (8%), kōpiko *(Psychotria hawaiiensis)* (8%), albizia (*Falcataria moluccana)* (8%), *Cecropia obtusifolia* (7%) *Melastoma septemnervium* (5%), and ironwood (*Casuarina equisetifolia)* (3%) (Fig. 4 and Table A3). The distribution of dominant species according to substrate age and elevation are represented in Figures 5 and 6, and in Table A3.

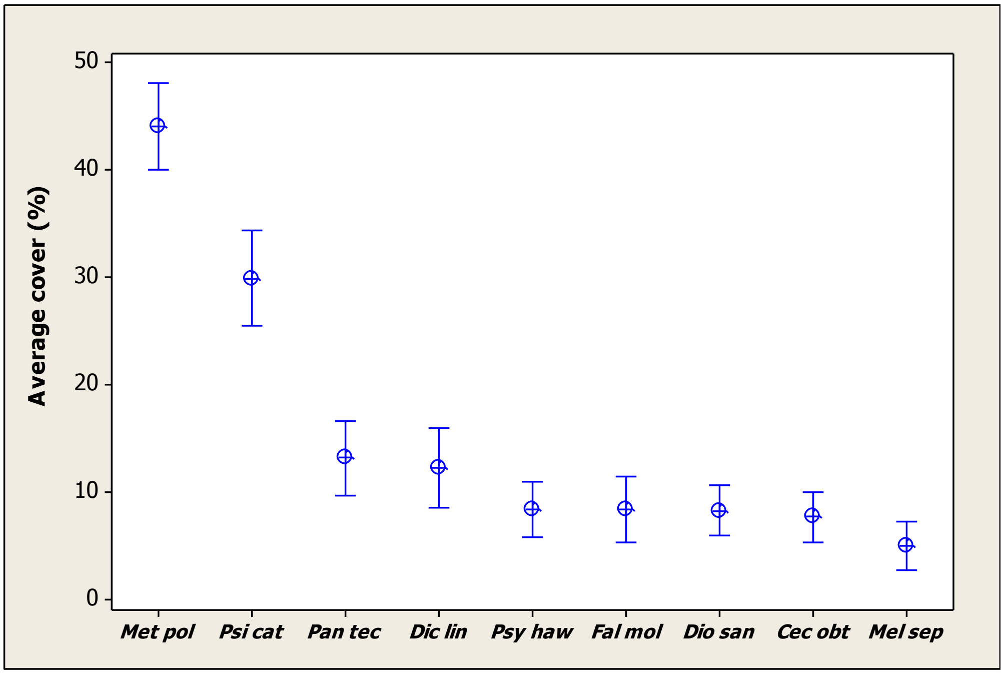

Fig. 4: Average cover in descending order for dominant native and non-native tree species with 95% CI bars in LWF of East Hawai'i (Refer to Table A3 for full species names).

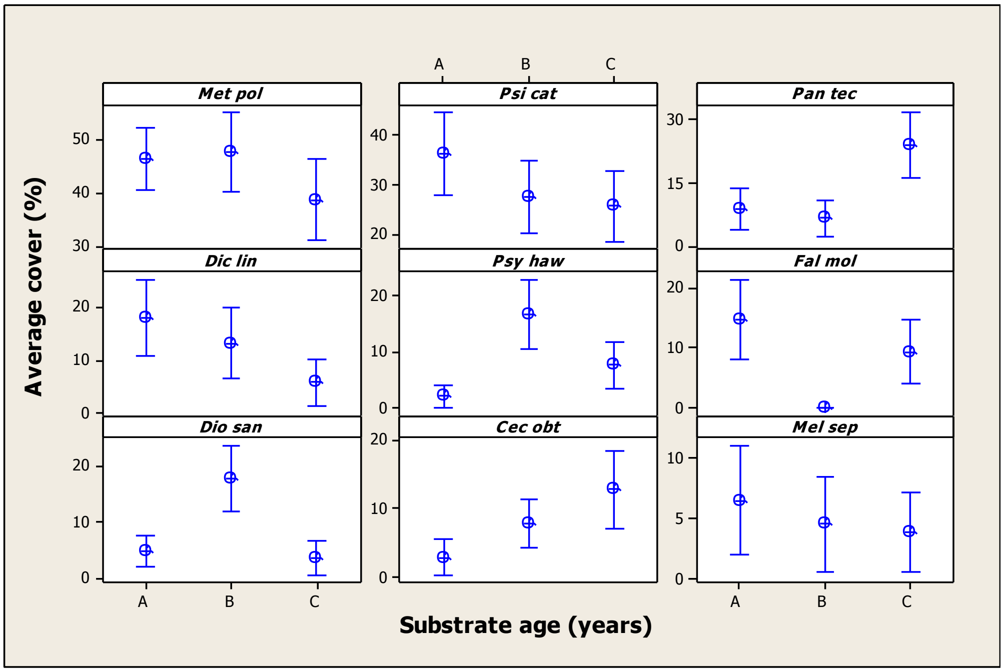

Fig. 5: Average cover with 95% CI bars for dominant tree species in lowland wet forests of East Hawai'i according to substrate age (A= < 200 yrs, B= 200-750 yrs, C= > 750 yrs) (Refer to Table A3 for full species' names).

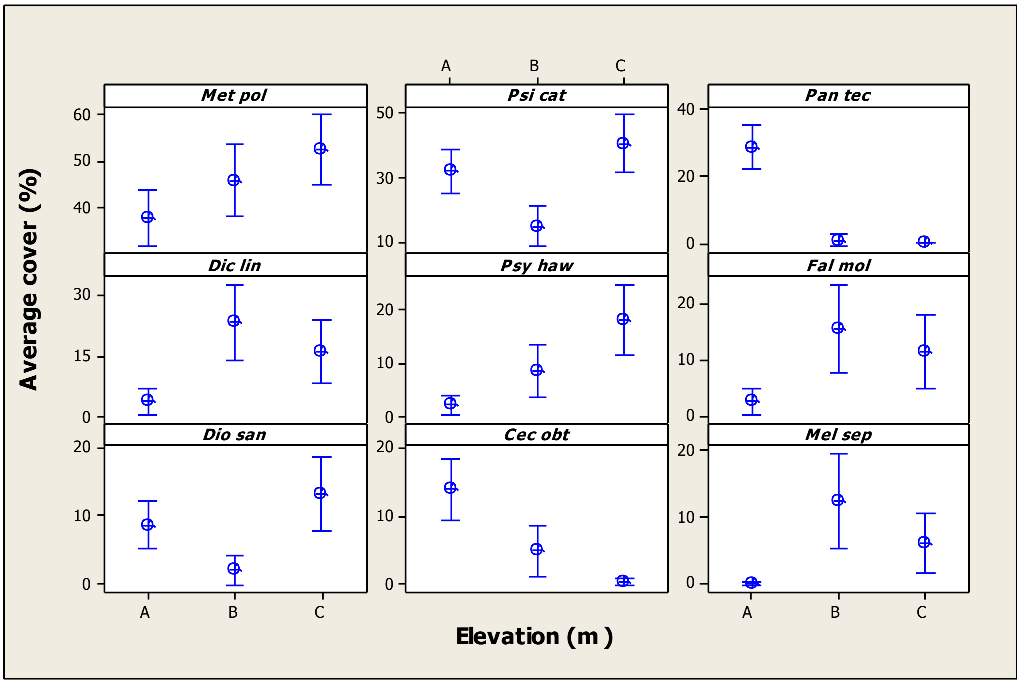

Fig. 6: Average cover with 95% CI bars for dominant tree species in LWF of East Hawai'i according to elevation zones (A= < 100 m, B= 101-200 m, C= 201-300 m) (Refer to Table A3 for full species' names).

Canopy Structure

In order to understand structural patterns of the forest I examined the percent cover of canopy species according to height for plant communities at each substrate age. On young substrate, the 5-10 m height class contains the greatest percentage of both native and non-native cover (25% and 33% respectively), as canopy trees are in early succession stages, not having reached full maturity and height and /or may be stunted due to low nutrient availability. On both the intermediate and the old substrates, non-native species dominate the two lower height classes, while native species dominate the two upper layers. This pattern is strongly accentuated on the intermediate substrate with native species exceeding non-native species (27% and 5% respectively at 10-20 m; 31% and 2% respectively at > 20 m) (Fig. 7).

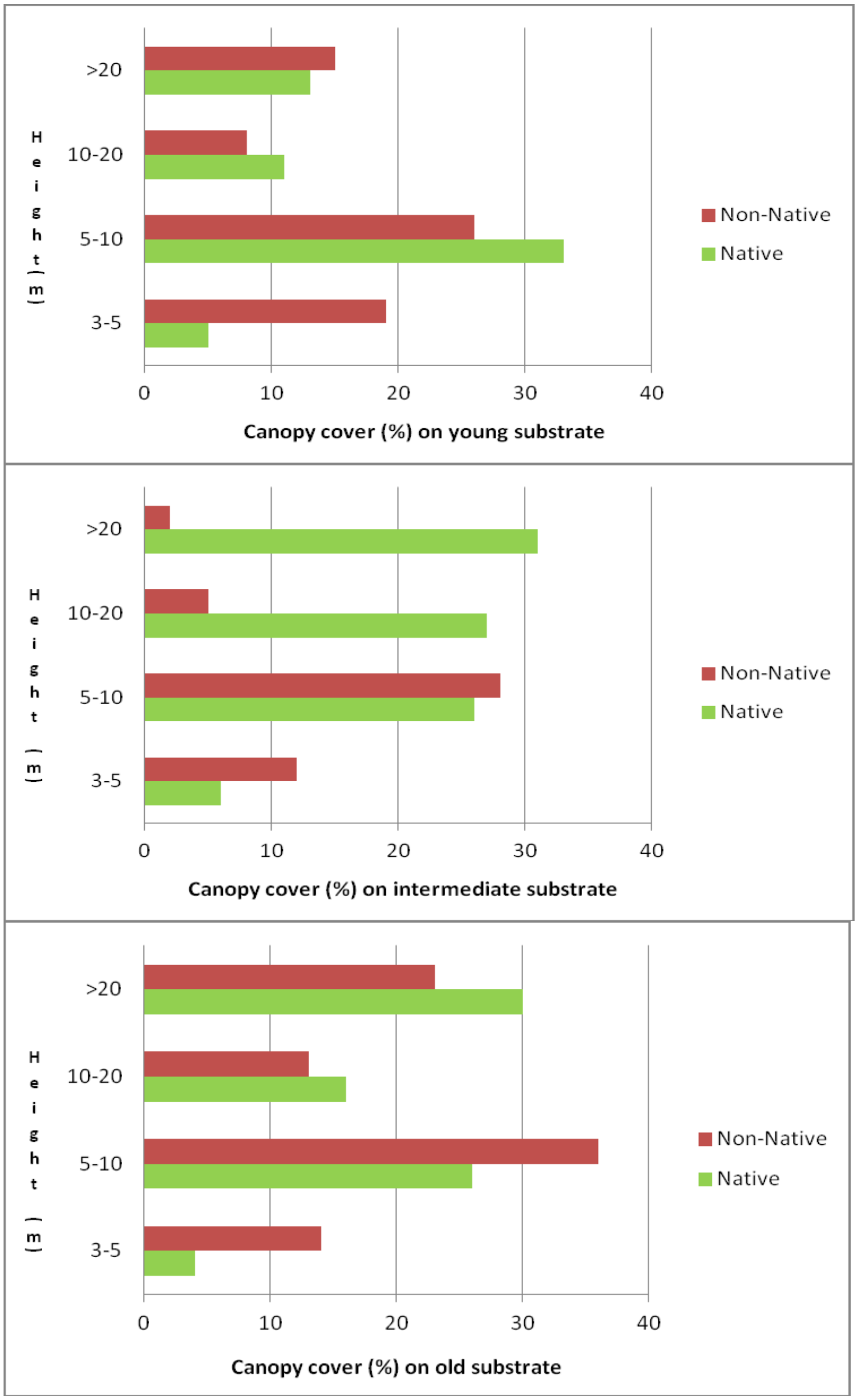

Fig. 7: Percent cover of native (green) and non-native (red) canopy species according to height categories by substrate age (< 200 yrs, 200-750 yrs, > 750 yrs).

Discussion

Canopy cover on younger substrate (< 200 years)

Lowland wet forests as represented in this study exhibit several trends that can help us understand the nature of canopy invasion. Although the overall substrate of Kilauea volcano is very young due to volcanic activity, difference in age contributes significantly to community composition patterns (Zimmerman *et al.,* 2008). Based on my study, the absolute cover of native and non-native trees was equivalent on young flows, and although the relative cover of native trees was equivalent between young and intermediate flows, it was lower than expected on the young flows based on prior studies in lowland wet forests of Hawai'i (Zimmerman *et al.,* 2008). According to Zimmerman *et al.* (2008), younger sites of < 200 years were composed largely of ‘ōhi‘a *(Metrosideros polymorpha)*, this being attributed to native species having better adaptability to very early succession stages. Although there are similar trends that have been observed, a number of my study results were different from other LWF studies such as Zimmerman *et al.* (2008), Hughes and Denslow (2005), and Carlson *et al.* (2007), but they are not directly comparable quantitatively because these studies measured density and basal area whereas I measured canopy cover. Density, basal area and vegetation cover measures are all standard forest inventory measures, however they can produce different results. Appropriate measures depend a great deal on the species involved, as different species will have greater proportions of stems, basal area and foliage. At large scales, basal area is a reasonable indicator of trunk surface area (Franzreb, 1985), vegetation cover a reasonable indicator of foliage surface area (O’Donnell and Dilks, 1987), and stem density is useful in making distinction between species (Smith, 1977). For the purpose of my study, I found that an estimation of canopy cover was most appropriate because it was important to achieve a large sample size over a broad area.

Based on cover values obtained in my study, though *M. polymorpha* still maintains a dominant presence on young substrates, substantial invasion by a number of non-native species occurs. Though it is possible that open niches were occupied by exotic species without native populations being affected; occupation of space by alien species on these substrates may be affecting current native species abundance patterns, and most certainly will into the future.

Fine (2002), suggested that forests in early succession phases are most vulnerable to invasion, particularly on islands, because exotic species will tend to form monospecific stands that can persist throughout the successional trajectory. Many tropical island regions that have been cleared for subsistence agriculture and other human developments, such as the Caribbean islands and Madagascar, are today invaded by exotic species that have long-lasting effects on forest succession patterns as exotic species inhibit native species regeneration (Brown and Gurevitch, 2004; Chazdon, 2008). Because of the extent of environmental degradation found on islands, the effects of exotic species extend beyond disturbed areas. In Hawai'i, undisturbed native forests are altered through invasion (Smith, 1985). Forest invaders occur on numerous other islands, such as Jamaica (Bellingham *et al.,* 2005), the Galapagos (MacDonald *et al.,* 1988), the Seychelles (Fleischmann, 1997), and Papua New Guinea (Roger and Hartemink, 2000). Many continental tropical forests on the other hand, do not have the same degree of invasive species issues as do island forest systems despite appropriate physical conditions, as ecological interactions (competition, pests, functional group diversity, ect.) make it more difficult. (Denslow and DeWalt, 2008).

Remaining LWF of Hawai'i are themselves fragments surrounded by a highly disturbed landscape with continued development and land-use pressures. They are also heavily fragmented due to volcanic activity periodically sending fingers of lava down-slope into existing forests

(Aplet and Vitousek, 1994). Though it is unknown what the particular effects of fragmentation are, their impact depend on a number of factors, such as local species composition, meta-population dynamics, ecosystem type and matrix utilization (Brudvig *et al.,* 2009; Flaspohler *et al.,* 2010). The size, shape and connectivity of a lava flow, differing ages and invasion levels of bordering flows, and micro-topography, are important determinants of species distribution, while larger, more undisturbed areas are more likely to be intact (Brudvig *et al.,* 2009; Flaspohler *et al.,* 2010). If a forested area is on a narrow strip, or borders invaded adjacent flows, proximity of seeds or propagules of certain invasive species can accelerate their invasion and affect succession patterns on a long-term basis (Flaspohler *et al.,* 2010). Factors such as these could have caused greater invasion levels on some of the young substrates I sampled when compared to those sampled by Zimmerman *et al.* (2008).

There are a number of other influences which may confound this study. These include accessibility, distance to roads, size of plots and substrate type. Invasive species control has been done on a community volunteer basis in Halepua'a and Keauohana over the past decade as well. These efforts however probably affected my data minimally because I avoided working directly in the most intensive areas.

Few studies have evaluated the factors involved in the distribution of plant species relative to roadsides on oceanic islands (Arteaga *et al.,* 2009). Roads are a major source for alien species establishment into remote environments (Parendes and Jones, 2000; Pauchard and Alaback, 2004; Dietz and Edwards, 2006). A recent study on the Canary archipelago by Arteaga *et al.* (2009), found that roadside conditions such as aspect, slope, width of corridor, and soil cover, all have influence on species richness. A number of additional factors, such as elevation, area, topography, and distance to propagule sources, also influence plant distribution patterns along roads in the Canary Islands (Rejmanek *et al.,* 2005).

Although I made use of the easiest points of access into forest reserves, for the most part, my plots were perpendicular to and away from roadsides, and those paralleling the roadside in the higher elevation zone of Keauohana, consisted of both native-dominated (4 plots on the 1955 flow), and invaded terrain (6 plots on the 1790 flow/ both considered in this study as younger flows). These particular plots were located on flows narrow in width, between a road and intermediate substrates (Fig. A7). Therefore they may have been more invaded than young flows deeper into larger tracts of the more common *M. polymorpha / D. linearis* forest type. Ample representation of this forest type was collected on large tracts of young substrates in Kaniahiku, Malama-Kī, and Nānāwale. Nevertheless, this forest type is likely under-represented in my study because equivalent sample sizes were achieved for both native and non-native forest types regardless of the greater proportions of native *M. polymorpha / D. linearis* forest likely occurring on young substrates. Had sampling been stratified by the proportional area occupied by a given lava flow age, results may have been different.

Substrate type is another of the factors that may be confounding my study results, as it has been found to have some determining influence on species distribution patterns as well (Zimmerman *et al.,* 2008). For instance, Atkinson (1970) observed that the *M. polymorpha / D. linearis* forest type was predominantly on young pahoehoe substrates. According to Zimmerman *et al.* (2008), species assemblages growing on pahoehoe versus ʻaʻa lava flows had clear distinctions for both native and non-native species, with species such as *P. tectorius* and *P. cattleianum* being more common on pahoehoe substrates, while *D. sandwicensis* and *M. septemnervium* were more common on the ʻaʻa substrate type of older flows.

In spite of possible effects resulting from confounding factors, invasion levels were noteworthy in areas surveyed on substrates less than 200 years. Despite the inhospitable nature of young lava soils, the over-story of young substrates, though often dominated by *M. polymorpha*, also had a large amount of non-native species' canopy cover by *P. cattleianum* (37%), *F. moluccana* (15%), and *M. septemnervium* (7%). Based on the averages of my data, the highest amount of cover for each of these species was actually found on the youngest substrate when compared to other aged flows, however, species were not tested individually according to study variables.

Although *M. polymorpha* requires considerable light, many non-native species may have a competitive advantage over native ones when considering the high levels of light prevalent in early succession stages (Zimmerman *et al.,* 2008; Cordell *et al.,* 2009). Alien species also have an advantage over *M. polymorpha* due to its comparatively slow growing nature (Muller-Dombois, 1987). And although native species have developed a long-term adaptation to limited soil conditions, any advantage is likely reduced with increased rates of fertility by nitrogen fixing species such as *F. moluccana*, nurturing earlier invasion (Hughes and Denslow, 2005).

In lowland wet forests, biological changes due to nitrogen deposition are pivotal in the replacement of *M. polymorpha* forests by *F. moluccana* (Hughes and Denslow, 2005; Zimmerman *et al.,* 2008). Introduced from Indonesia in 1917 (Rock, 1920), *F. moluccana* has been extensively researched, and shown to have devastating effects on native plant assemblages, and on the functioning and structure of LWF of Hawai'i (Hughes and Denslow, 2005). A study of LWF by Hughes and Denslow (2005) determined that *M. polymorpha* made up 20% of composition in the *F. moluccana* invaded stands, but 68-100% of dead individuals. Size-class distributions of *M. polymorpha* snags and stumps indicated that invaded stands were once similar to those found in adjacent native ones (Hughes and Uowolo, 2006). These measures are an indication of the rapid spread of exotic species into the native LWF, where *F. moluccana* became established less than 35 years ago (Hughes and Denslow 2005; Hughes and Uowolo, 2006). Mono-dominant stands of this species have become established on other isolated Pacific Islands such as Mo'orea in French Polynesia, where it was also brought in to restore degraded lands (in the 1960s) (Minnich, 2009). Its spread has been positively correlated to percent bare soil in disturbed open areas (Long, 1999) where there are fewer large trees and less native biodiversity (Minnich, 2009). In my study, *F. moluccana* represented a large portion of invaded lands on young lava flows of Keauohana, Kaniahiku and lower Malama-Kī, yet a decline was evident with distance from the roadways.

Though *F. moluccana* clearly facilitates the success of *P. catteianum* in LWF, *P. cattleianum* appear to be occurring in healthy stands without the facilitative effects of *F. moluccana*. Whereas Hughes and Denslow (2005) found relatively few *P. cattleianum* stems on the 1790 flow, and almost none on the 1955 flow within native stands, they found large numbers of them in the *F. moluccana* invaded stands on the same flows. The present study located *P. catteianum,* on young substrates in the absence of *F. moluccana* and away from roadsides along an entire transect in lower Malama-Kī, in upper Malama-Kī, and in large areas of east Halepua'a.

Due to numerous advantageous traits, *P. cattleianum,* native to Brazil, has been recognized since the 1950s as one of the State's most disruptive weeds, threatening at least 77 plant species in Hawaii (State of Hawai'i Dept. of Agriculture, 2011). Early stages of primary succession on young volcanic sites have been dominated by aggressive alien populations of *P. cattleianum* on other islands as well, such as Tahiti and La Reunion in the Mascarene Islands, where it is among the most threatening invasive species (MacDonald, 1991). *P. cattleianum* has a different effect than *F. moluccana* on LWF as it forms dense thickets that exclude rather than facilitate other plant species through direct competition for resources (Uowolo and Denslow, 2008; Zimmerman *et al.,* 2008). Despite the fact that its seeds do not remain viable beyond a three month period, their abundant germination rate and dispersal by bird and feral pigs (Uowolo and Denslow, 2008), and the plants ability to grow vegetatively (Huenekke and Vitousek, 1990), are largely responsible for this species' prolific spread. As the most successful invasive species throughout LWF, its growing prevalence is having a large impact on native forest composition and biodiversity on all substrate ages found in LWF.

Canopy cover on intermediate substrate (200-750 years)

Intermediate substrates, ranging between 200 and 750 years, may have more optimal conditions for the success of native species when compared to other aged substrates that are more heavily invaded. On these flows, absolute cover of native tree species was higher when compared to the young. When compared to older substrates, non-native absolute cover was lower and native relative cover was higher. When looking at total basal area of native species, Zimmerman *et al.* (2008) also found higher values for native species than for non-native species, with the largest values occurring between 200-750 years. It may be that this substrate age provides a certain balance between conditions found on younger and older flows. Young substrates consist of forests in early succession phases with many open niche areas and poor soil conditions; hence it is not surprising to find less absolute cover of native trees on these sites when compared to intermediate ones. On the other hand, forests in later succession stages, as found on older substrates, experience higher levels of disturbance (Muller-Dombois, 1987; Zimmerman *et al.,* 2008). It is possible that forests on intermediate substrate have not yet reached the successional stage wherein replacement of aged trees is occurring on a large scale.

This stage has been described by others as a second stage of primary succession, when forest composition is more diverse and complex (Aplet and Vitousek, 1994; Kitayama *et al.,* 1995; Aplet *et al.,* 1998; Vitousek 2004). Though it is difficult to know the reasons why some areas support more intact native composition than others, it is possible that a closed canopy layer may have offered the forest more resistance to invasive species by providing levels of shade and nutrients less conducive to the success of alien species (Zimmerman *et al.,* 2008; Ostertag *et al.,* 2009). Zimmerman *et al.* (2008) determined however that on substrates greater than 400 years, densities of non-native saplings were greater than those of native saplings. Forests on intermediate substrates in my study may generally have a more intact canopy layer based on cover values, but Zimmerman *et al.* (2008) may have detected earlier invasion patterns represented in the understory, as cover estimates in my study only focused on layers greater than 3 meters, which largely would have excluded saplings. Native tree recruitment levels on flows between 200 and 750 years may in fact be compromised by the superior fitness of non-native species in the understory layers of the forest (Zimmerman *et al.,* 2008). On the other hand, it is possible that the relatively intact native canopy of these forests may hinder the growth of the non-native saplings.

Canopy cover on older substrate (> 750 years)

Non-native absolute cover of trees was higher on old substrates than on the intermediate substrates, and the relative cover of native trees was lower than on all other substrates. Hence, the oldest substrate (>750yrs) proved to be most degraded, as suggested by Zimmerman *et al.* (2008). On older substrates with greater resource availability (Kitayama and Mueller-Dombois, 1995; Aplet and Vitousek, 1994), invasive alien species are capable of constraining native plant recruitment, and of altering wet lowland forest succession patterns (Hughes and Denslow, 2005).

Because nutrient accumulates with increased lava flow age (Vitousek *et al.,* 1992; Hughes and Denslow, 2005), older substrates may also have more history of human disturbance such as with early agriculture (Cuddihy and Stone, 1990).

Atkinson (1970) observed how the process of invasion by non-native species was expedited by open gaps in the forest canopy. ‘Ōhi‘a die-back, a natural phenomenon that happens in ‘ōhi‘a forests over time, as well as death of old trees, occur in later succession stages such as found on > 750 year old substrate (Muller-Dombois, 1987). In more disturbed areas with abundant sources of seeds, due to numerous competitive advantages and dispersal by wind, pigs and birds, openings in the native forest canopy are more likely to be filled with alien rather than native species (Baruch and Goldstein, 1999; Loh and Daehler, 2007; Cordell *et al.,* 2009). According to a comparison study of leaf traits between 34 native and 30 invasive species with similar growth forms, and found in similar habitats along the Mauna Loa volcano slope, invasive species were found to have a number of advantages over non-native species in many traits (Baruch and Goldstein, 1999). In that study, non-native species on older flows with richer soils captured limiting resources 15% more efficiently than did native species. On older substrates of LWF, increased resource availability and slower resource use by native species may fuel alien advantage (Daehler 2003; Denslow 2003).

Although there is a substantially smaller proportion of the area with substrate greater than 750 years in LWF, and a larger proportion of non-native species, there are nonetheless forest pockets that are relatively native in composition, for instance adjacent to the native-dominated forest on intermediate substrate in central Halepua‘a, and in a number of areas of Kaniahiku.

Canopy cover according to elevation

Elevation has been recognized by earlier studies to be a significant factor when looking at species composition patterns (Aplet *et al.,* 1994), particularly for volcanic high islands because they contain numerous biomes which provide high levels of heterogeneity (Mueller-Dumbois, 2002). In LWF of Hawai'i absolute cover of native trees was negatively correlated with elevation on young substrates. This pattern is predominantly due to the combination of hala *(Pandanus tectorius),* found in abundance strictly at the lowest elevation, and uluhe *(Dicranopteris linearis*), a fern that increases in cover with increased elevation, tending to dominate large areas and restrict other plant life (Atkinson, 1970).

There was an abundance of invasive species throughout the elevation gradient particularly on the young and old substrate as reflected by absolute cover values. *P. cattleianum* was abundant at all elevations, while at higher elevations, there was an abundance of *F. moluccana,* and *M. septemnervium*. At lower elevations the most abundant non-native species was *C. obtusifolia* (and likely *C. equisetifolia,* though not clearly indicated in this study) (Fig. 6).

Dominant species in LWF

A mixture of native and non-native species dominated the canopy layers in LWF with the native *M. polymorpha* being the most dominant tree on all substrate ages, closely followed by the invasive *P. cattleianum*. The native *P. tectorius*, *P. hawaiiensis,* and *D. sandwicensis,* as well as the non-native *F. moluccana*, *M. septemnervium* and *C. obtusifolia* are important contributors to the lowland wet forest in terms of canopy cover (see Table A3 for average cover values; or Figures A4- A7 for native and non-native dominated plots). According to a study in which woody species richness and stem density data were collected for the Puna region, dominant species were *M. polymorpha* (53%) and *Casuarina equisetifolia* (10%) in terms of basal area;

and dominant species were *P. cattleianum* (30%) and *M. septemnervium* (12%) in terms of the largest percentage of stems (Carlson *et al.,* 2007). In a study comparing these measures done in New Zealand forests, the proportion of dominant local tree species estimated by basal area was two times greater than that of cover, and ten times greater than that of stem density (Spurr and Warburton, 1991).

Although results based on vegetation cover measures in the current study differ somewhat from Carlson (2007) in terms of the order of species' dominance, there are some fundamental similarities. In the present study however, though *M. septemnervium* averaged 5% canopy cover, there was an abundance of it below the 3 meter canopy layer in the understory, which was not considered in this canopy assessment, but that would account for some of the difference in dominance compared to the findings of Carlson *et al.* (2007). Also, while *C. equisetifolia* forms abundant mono-specific stands along the coastline, this species was not adequately represented in my study because data were not collected in those areas. Other introduced tree species such as *Schefflera actinophylla*, *Trema orientalis* and *Melochia umbellata,* are also quite abundant in LWF of Hawai'i. Though these forests are occupied by a number of exotic species, there was yet a strong presence of native species making up their canopy cover.

Canopy structure

On both the intermediate and the old substrates, native species dominated the two upper height layers, while non-native species dominated the two lower layers of the canopy. *M. polymorpha* accounted for a majority of the upper canopy cover at all substrate ages. Although seed germination and regeneration is constrained due to the abundance of introduced species dominating the understory of LWF (Ostertag *et al.,* 2009), *M. polymorpha* being the tallest and most dominant native tree, is beneficial when considering restoration prospects in terms of seed production and distribution. All of the middle and upper-canopy native tree species such as *P. hawaiiensis, D. sandwicensis*, and *M. lessertiana,* provide sources of seed and the necessary shade to nurture native seedlings (Ostertag *et al.,* 2009). Though lower canopy layers are largely dominated by non-native species at this point, control of exotic species in the sub-canopy layers of more intact areas is likely to be more successful under healthy upper canopy conditions.

Management Implications

Remaining lowland wet forests of Hawai'i are today reservoirs of rare native biodiversity. Protection of this unique environment would support native communities, providing habitat for native bird species such the ‘amakihi *(Hemignathus virens),* the ‘apapane *(Himatione sanguine),* and the Hawaiian hawk (‘io, or *Buteo solitarius)* (Woodworth *et al.,* 2005; Hughes, Kobsa and Hart, pers. comm); and rare plant species, such as ha‘iwale (*Cyrtandra nanawalensis),* which is entirely restricted to this region (Wagner *et al.,* 1999), and proposed for federal listing as endangered. Its co-occurrence with rare species such as ‘ohe *(Tetraplasandra hawaiensis),* opuhe (*Urera glabra),* and hame *(Antidesma platyphyllum),* (the latter species is not considered rare but is uncommon at this elevation), makes for a unique forest type.

As we lose many island environments to urbanization, agriculture and invasive species, adequate conservation policies are in urgent need of implementation (Strasberg *et al.,* 2005). Between non-native species being able to colonize the young lava substrates that once were the exclusive domain of early-succession native species, and a rising trend of non-native species effectively excluding native ones on older substrates, the loss of native forests will continue if efforts are not made to protect and restore them where they still remain (Hughes and Denslow, 2005; Hughes and Uowolo, 2006; Zimmerman *et al.,* 2008).

The similarity of absolute cover between non-native and native species on young substrates, higher native absolute cover and lower non-native absolute cover on intermediate substrates, and lower relative cover of native species on older flows, are vegetation patterns that may offer guidance to restoration planning. On the basis of these general cover trends, we might conclude that restoration holds the greatest potential on 200-750 year-old lava flows over other more degraded flows, as they would require much less restoration effort and yield greater results. High invasion levels on substrates older than 750 years suggest that, for the most part, older flows are too heavily impacted by invasive species to receive highest priority for restoration. Though native-dominated forests are most likely to be found on intermediate substrate, this does not imply that we should prioritize them at the exclusion of other substrates as priority may need to be based on the overall condition, location, and size of a forest area. There are for instance extensive areas of the *M. polymorpha* / *D. linearis* forest type on young substrates that are generally resistant to invasion due to the suppressive effect of *D. linearis.* It would be effective to target invasive individuals found among them, particularly where available open niches remain. The current impact of invasive species on young substrates calls for early detection and rapid response because young forests represent the future of LWF.

Maintaining representative areas of all of Hawai'i's ecosystem types is a major long-term goal of conservation (Anderson *et al.,* 1999). While it would be ideal to preserve large tracts of every native forest type, priority has been given to higher elevations and less developed regions of Hawai'i that show more promise for conservation efforts. It is important, however, to encompass the full range of biodiversity across the entire elevation gradient into coastal communities (Anderson *et al.,* 1999). The findings of this study indicate an important turning point in the composition of lowland wet forests. Despite the current level of invasion, the potential to reverse trends and to nurture native community resistance and resilience in certain areas remains a realistic prospect.

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Chapter II

Species Composition of Native-dominated Communities

Introduction:

Much of the world's threatened biodiversity, and 80% of recorded extinctions, are found on islands (Groombridge, 1992). Approximately half of plant species are concentrated in biodiversity hotspots covering only 2.3% of the earth's surface, and among them are the islands of Hawai'i (Myers *et al.,* 2000; Mittermeier, 2004). The Hawaiian Island chain is home to more than 1,009 native angiosperms, of which 90% are endemic (Wagner *et al.,* 1999), 54% are single-island, and 43% are single-volcano endemics (Price, 2004). High endemism rates are the result of its isolated position in the central Pacific Ocean, which has restricted natural colonization events during its 30 million year history (Price and Clague, 2002). Its tall mountains provide steep environmental gradients, and therefore a high diversity of habitats and species' specialization over a small geographical area (Mueller-Dombois, 2002). Because many native species in Hawai'i have evolved and adapted as specialists they often inhabit a narrow niche breadth (Price and Wagner, 2004). Furthermore, with little previous competition over many thousands of years, native populations evolved to be small, slow growing, and less effective at competing against the more recently introduced, fast growing and well-dispersed alien generalists (Loope and Mueller-Dombois, 1989; Cuddihy and Stone, 1990; Baruch and Goldstein, 1999; Chornesky, 2003). These many factors contribute to species loss and extinctions in most of Hawai'i's ecosystems (Sakai *et al.,* 2002). Despite 9% of native plant species having gone extinct historically, the Hawaiian island chain, with its high degree of endemism, affords an important contribution to global species richness (Sakai *et al.,* 2002).

Loss of native species and extinctions are the result of habitat loss, species invasions, human exploitation, pollution, disease, and climate change, all of which have had an impact on the niche space and distribution of species affecting community compositions in Hawai'i (Sax and Gaines, 2008). With a general increase in global surface temperatures over the past 30 years (Giambelluca *et al.,* 2008), rainforest ecosystems in Hawai'i may be vulnerable to the effects of climate change. A projected 5-10% reduction in wet season precipitation could cause severe stress to endemic species in the future (Timm and Henry, 2009). Land use changes combined with climate changes can make it challenging for species to shift their ranges, and issues of biological invasion may become exacerbated (Benning *et al.,* 2002). Some of Hawai'i's ecosystems, such as cloud forests and alpine grasslands, are most vulnerable to temperature change, however all vegetation communities are susceptible to changing environmental conditions (Crausbay and Hotchkiss, 2010). Rare and endangered species may not be able to withstand projected changes in climate. With rising temperatures affecting levels of potential rainfall, it is most likely that climate-change-induced-drought, combined with the numerous vulnerabilities particular to plant communities of Hawai'i, will present a formidable challenge to their integrity (Parry *et al.,* 2001; Arnell, 2004).

Although we cannot adequately keep track of species loss, let alone the particular role of invasion on these losses (Sax and Gaines, 2008), invasive species are recognized as one of the greatest threats to native biodiversity throughout the Hawaiian island chain (Smith 1985; Vitousek, 1990). With the introduction of approximately 8,000 plant species on the Hawaiian Islands over the past two centuries, there has been a local and regional increase in biodiversity (Sax and Gaines, 2008). Increased dispersal rates of introduced species among communities however, ultimately diminishes endemism within them, contributing further to species extinctions and a decline in biodiversity on a global level (Davis, 2003).

Land conversion to agriculture and residential development has increasingly fragmented the landscape in lowland wet forests (LWF), greatly facilitating its vulnerability to alien invasion, and having degrading effects on its native plant communities (Cuddihy and Stone, 1990). The largest remnants of lower elevation wet native forests, one of the most threatened habitat types in Hawaii, are found on the easternmost part of the Big Island. These forests provide habitat for rare and endangered species such as ha'iwale (*Cyrtandra nanawalensis),* which is entirely restricted to this region (St. John, 1987) and proposed for federal listing as endangered , 'ohe *(Tetraplasandra hawaiensis),* opuhe (*Urera glabra),* and hame *(Antidesma platyphyllum),* (the latter which is not considered rare but is uncommon at low elevations) (Wagner *et al.,* 1999). Despite the 'amakihi *(Hemignathus virens)* having previously abandoned LWF due to avian malaria susceptibility, Woodworth *et al.* (2005) demonstrated that they comprise from 24.5% to 51.9% of the avian community at three low-elevation forests (55-270 m) over the past decade, having perhaps developed resistance to the disease. The 'apapane *(Himatione sanguine)* has also been sighted in LWF by a number of people in recent years, and the region is inhabited by Hawai'i's native hawk, the endangered 'io *(Buteo solitarius)* (Hughes, Kobsa and Hart, pers. comm.). Protection of this unique environment would support native communities, providing habitat for rare and endangered species while adding to global biodiversity (Davis 2003). Unless properly managed LWF are subject to complete replacement by non-native communities (Zimmerman *et al.,* 2008).

This chapter focuses on vegetation composition of native-dominated communities (> 66.6% relative cover of native trees) and rare species in order to more specifically distinguish plant distribution patterns of a native LWF. Here I seek to understand the trends behind diversity of species, forest composition, and rare plant occurrences. What are the abundance patterns of native and non-native species in the understory of forests with a relatively intact native canopy? How is biodiversity influenced by substrate age in these forests? Do substrate age and elevation have a major effect on species composition patterns? What are the canopy conditions under which rare species occur? Understanding the intricacies of the native-dominated LWF environment is important if we are to succeed in restoring, expanding, and protecting them.

Methods:

This segment of my study incorporates methods found in Chapter I, and more detailed methods for native-dominated sites and rare plant locations. Despite a majority of plots being dominated by non-native tree species, I collected sufficient data to include a representative range of plots dominated by native tree species evenly distributed across the study variables. Native canopy plots were established when they met a criterion of ≥ 66.6% relative canopy cover of native tree species. For these plots, I conducted a detailed assessment in which cover class and height class were recorded for all species present within the plot boundaries, employing the Braun-Blanquet method (Mueller-Dombois *et al.,* 1974). Unlike for basic plots, all height layers were surveyed in this portion of the study, including the upper canopy (> 20 m), mid canopy (10-20 m), lower canopy (5-10 m), and tree ferns/short trees (3-5 m), shrubs (1-3 m), herbs (0.5-1 m), ground (0-0.5 m), vines and epiphytes (variable heights). For detailed plots, I also measured the diameter at breast height (DBH) of the largest tree species present within the plot. A total of 291 plots of 100 m^2 were completed throughout the five reserves, all of which received a basic assessment of native and non-native tree canopy species ≥ 3 m in height, and from which a subset of 125 plots ($\geq$ 66.6% relative cover of native canopy) received a detailed assessment (Tables A1 and A1b; Figures A4- A7).

Whenever rare species were encountered in the field, additional plots were established to characterize the canopy structure surrounding them, with rare species located at the center of the 100 m^2 plot. A group of designated rare species were determined a priori that include: ha‘iwale (*Cyrtandra nanawalensis),* opuhe (*Urera glabra)*, ‘ohe *(Tetraplasandra hawaiensis),* and hame *(Antidesma platyphyllum)*. The latter species is not considered rare but is uncommonly found at this elevation. Though some individuals of all of these species were encountered, the majority of rare plant plot locations consisted of *C. nanawalensis.* In some cases rare plant points that had been mapped prior to this project were also assessed (Clarke *et al.,* 1979; Clarke, *et al.,* 1981, Kobsa, unpub. data). Although only canopy layers were surveyed for statistical analysis of rare plants, detailed data were gathered in order to facilitate a more elaborate study of understory composition patterns in the future. For this study, a total of 34 rare species plots were compared with all 291 other plots in terms of canopy cover using the four highest Braun-Blanquet canopy layers ($\geq$ 3 meters).

Statistical Analyses:

Species richness

Species richness was measured as the number of native and non-native species for each plot. To assess native species richness in relation to substrate age in native tree dominated areas, a one-way ANOVA evaluated the mean number of species present in the three categories of substrate age (< 200 yrs, 200-750 yrs, > 750 yrs). Due to a slightly uneven pattern in the distribution of the residuals, I conducted a $\log_{10}$ transformation in order to test the significance of these data. I also conducted a t-test to compare native versus non-native diversity according to substrate age in order to confirm what appeared to be a significant difference.

Forest composition and structure

In order to assess how species composition of more intact areas varies with respect to substrate age and elevation, I conducted a multivariate analysis using non-metric multi-dimensional scaling (NMS), using the PRIMER- E v. 6 ordination program in order to visualize clustering of similar sites. A resemblance matrix was created for plots according to the three substrate age categories and the three elevation categories (< 100 m, 101-200 m, 201-300 m). I then tested for significance of these factors using ANOSIM within the Primer program. Results were determined based on 999 data permutations.

Rare species

In order to compare the relative proportion of native tree cover for rare species plots to all 291 basic plots, I conducted a t-test for basic comparison of the means using Minitab 16. Data for all 34 rare plant points did not contribute to basic canopy cover analyses, and rare plant individuals were not included in the estimations of cover for rare plant points.

Diameter of largest tree

A basic ANOVA was conducted to test the diameter in centimeters of the largest tree for each native dominated plot according to three substrate age categories (< 200 yrs, 200-750 yrs, > 750 yrs).

Results

Species richness

When looking at the native-dominated plots, a one-way ANOVA of the log10 transformed species count indicated that the average number of native species on intermediate lava flows (4.2 spp. ; minimum 1, maximum 10) was greater than on young lava flows (2.4 spp.) ($F_{2, 122} = 10.86$; p = 0.001). The average number of non-native species was greater on the old substrate (5.2 spp.; minimum 0, maximum 12) than the young (3.7 spp.), ($F_{2, 122} = 2.98$; p = 0.054; Fig. 8). A two sample t-test comparing the number of native and non-native species according to substrate age indicated a higher number of non-native species on younger substrate (t= -2.53; p= 0.013; DF= 88), as well as older substrate (t= -4.07; p= 0.001; DF= 76). A maximum of 15 species was found when considering both native and non-native species within a plot. The Shannon Wiener index value was $H^{'} = 4.35$ across all substrates and elevations, indicating a moderately even spread in species.

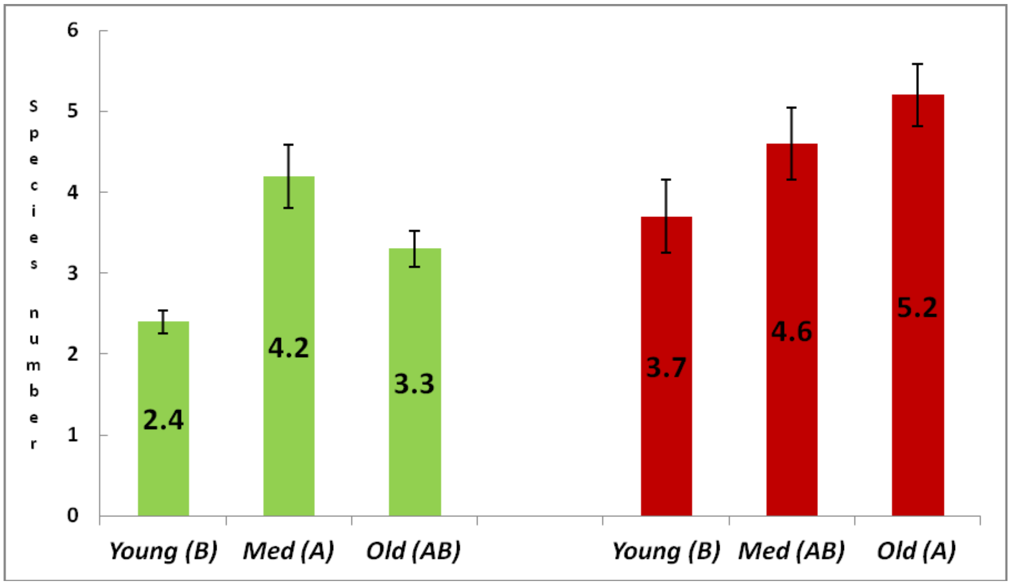

Fig. 8: Average number of native (green) and non-native (red) species with standard error bars, in three substrate ages categories (< 200 yrs, 200-750 yrs, > 750 yrs). Separate tests were done for native and non-native species, with different letters (A versus B) being significant (p-value $\leq$ 0.05).

Forest composition and structure / Ordination

Multivariate ecological data analysis scores (NMS) indicated variance in compositional patterns of more native intact forest areas with respect to substrate age (R= 0.112; p= 0.001) (Fig. 9), and elevation (R= 0.222; p= 0.001) (Fig.10) with a stress value of 21.5 in the two dimensions. Though in both cases there was a significant separation in species community patterns, considerable overlap was evident.

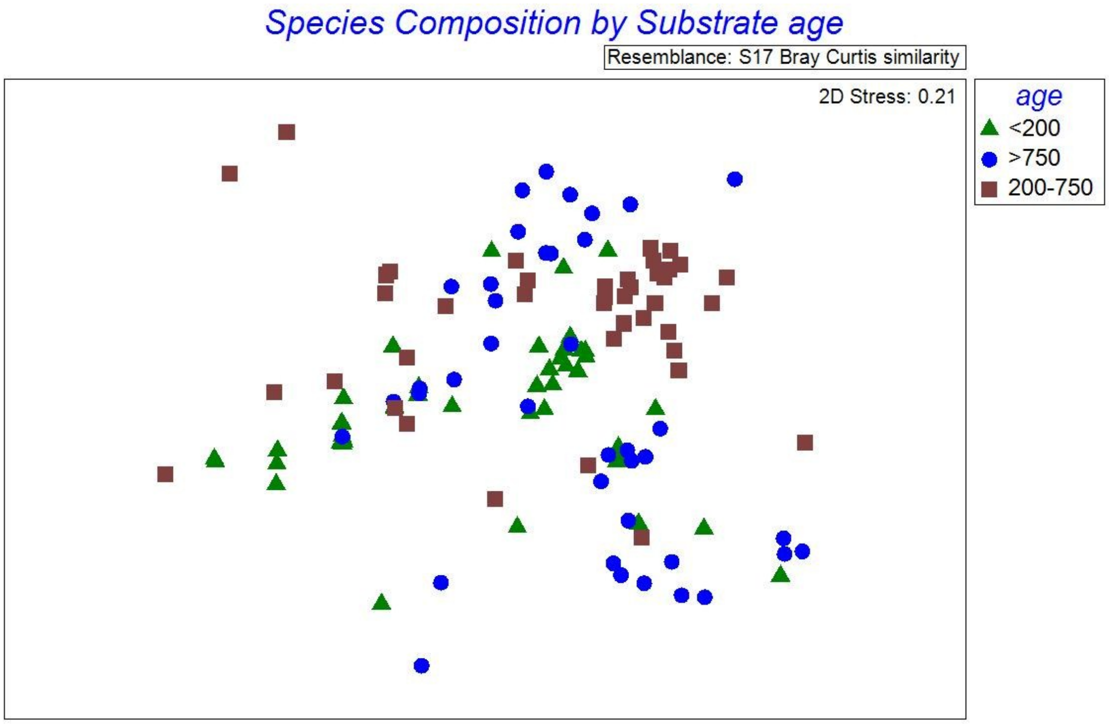

Fig. 9: Plots according to non-metric multi-dimensional scaling (NMS) indicating compositional patterns with different colors/shapes representing the three substrate ages.

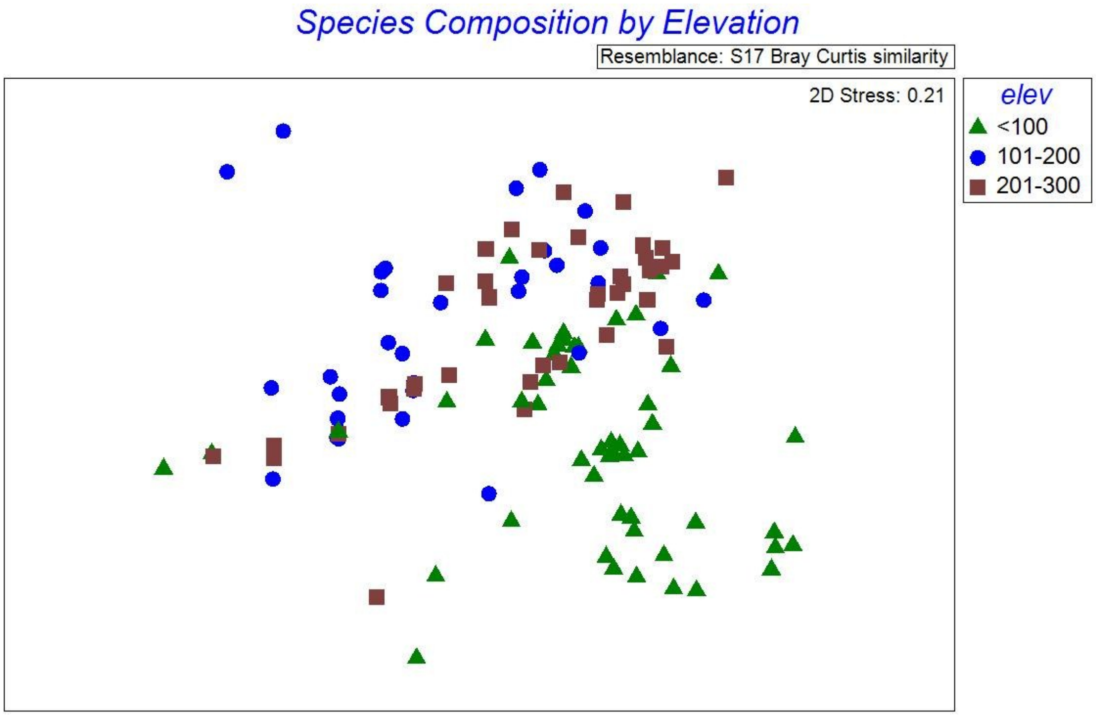

Fig. 10: Plots according to non-metric multi-dimensional scaling (NMS) indicating compositional patterns with different colors/shapes representing the three elevation zones.

Rare species

A t-test indicated greater relative canopy cover of native trees where rare plants occur (72%) compared to all 291 plots where they do not occur (57%, $t = 2.95$; $p = 0.005$; $df = 45$; Fig.11). All 34 rare individuals (total of four rare species) were on the 200-750 year substrate.

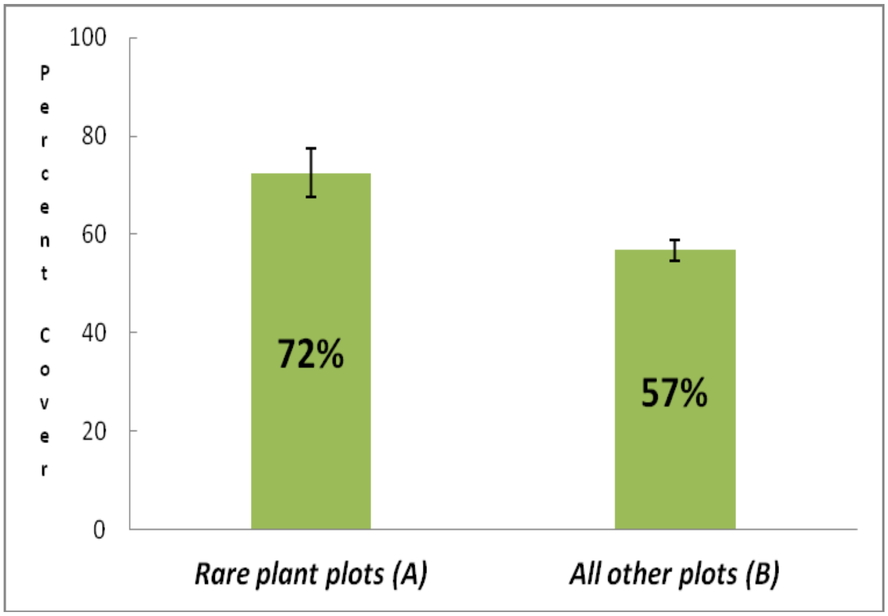

Fig. 11: Average relative percent canopy cover and standard error of native trees for rare plant plots compared to all other plots. Different letters (A, B) show significance ($p \leq 0.05$).

Largest trees

The average diameter in centimeters of the largest tree in native-dominated plots was lower on the young (24 cm, $n = 43$, range = 61 cm), than on intermediate (49 cm, $n = 30$, range = 66 cm), and older flows (46 cm, $F_{2, 102} = 29.35$; $p = 0.001$; $n = 32$, range = 85 cm; Fig.12).

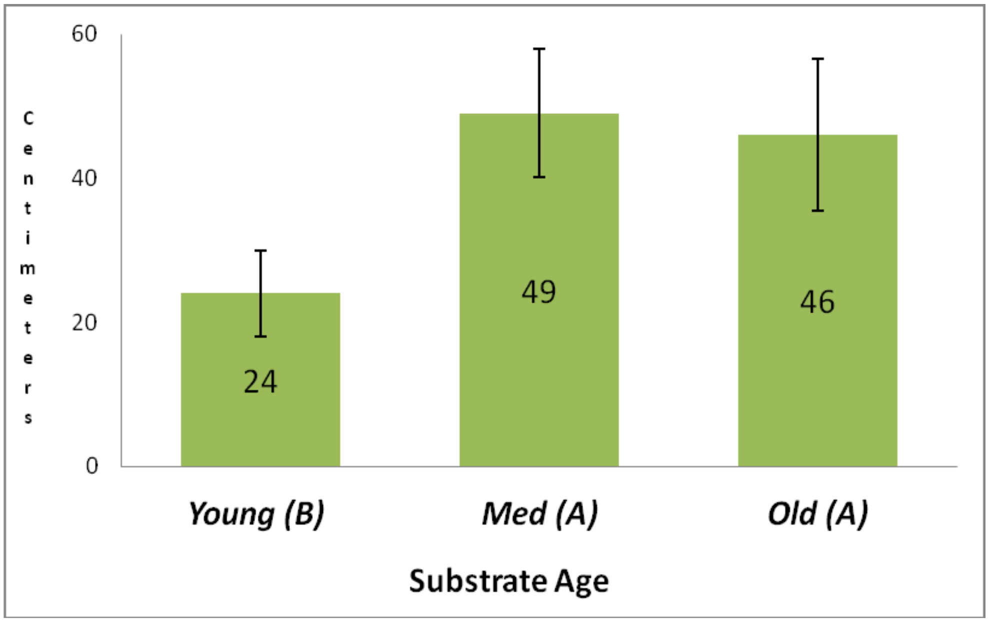

Fig. 12: Average diameter in centimeters and standard error of largest tree according to three substrate age categories (< 200 yrs, 200-750 yrs, > 750 yrs), in native dominated plots.

General cover data summary

Species making up the greatest proportion of canopy cover in native-dominated LWF of East Hawai'i were (in descending order): ‘ōhi‘a *(Metrosideros polymorpha)* (61%), uluhe (*Dicranopteris linearis)* (23%), hala (*Pandanus tectorius)* (20% average / 50% at lowest elevation), kōpiko (*Psychotria hawaiiensis)* (15%), strawberry guava (*Psidium cattleianum)* (15%), lama (*Diospyros sandwicensis)* (9%), *Melastoma septemnervium* (9% understory), *Clidemia hirta* (8%), ‘ie‘ie *(Freycinetia arborea)* (6%), hāpu‘u (*Cibotium* spp.) (3%), ‘ekaha (*Asplenium normale)* (3%), ‘ala‘ala wai nui (*Peperomia* spp.) (2%), and *Cecropia obtusifolia* (2%) (Fig. 13).

Sorenson’s index of similarity suggested 59% similarity in species between the young and medium substrate; 65% between the medium and old; and 69% between the young and the old substrate. All substrate ages shared a number of the more dominant native species such as *M.*

polymorpha, D. sandwicensis, P. hawaiiensis, Cibotium spp.., *D. linearis, A. nidus* and *F. arborea.* Non-native species that shared all three substrate ages were *P. cattleianum, M. septemnervium* and *M. umbellata*. (For averages in cover of dominant species according to substrate age and elevation categories, refer to Figures14and 15; and Table A3.) The ranking of all species from most to least abundant according to the three substrate age categories showed a relatively small number of species having much greater cover than most. The trend was similar between all ages, with the youngest appearing to support slightly less species evenness than the other two substrates ages (Fig.16).

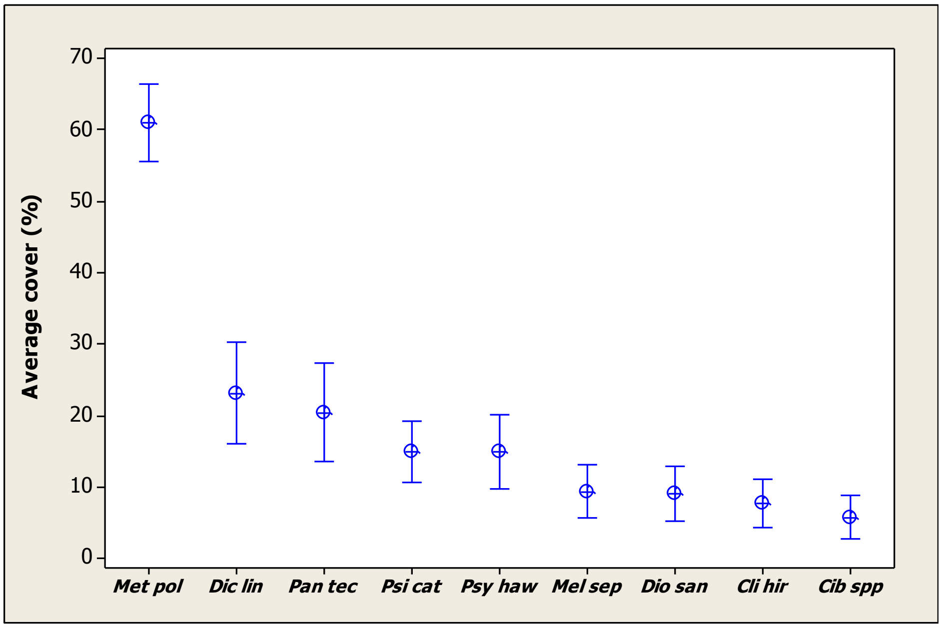

Fig. 13: Average percent cover with 95% CI bars for dominant species in descending order, in native-dominated lowland wet forests of Hawai'i.

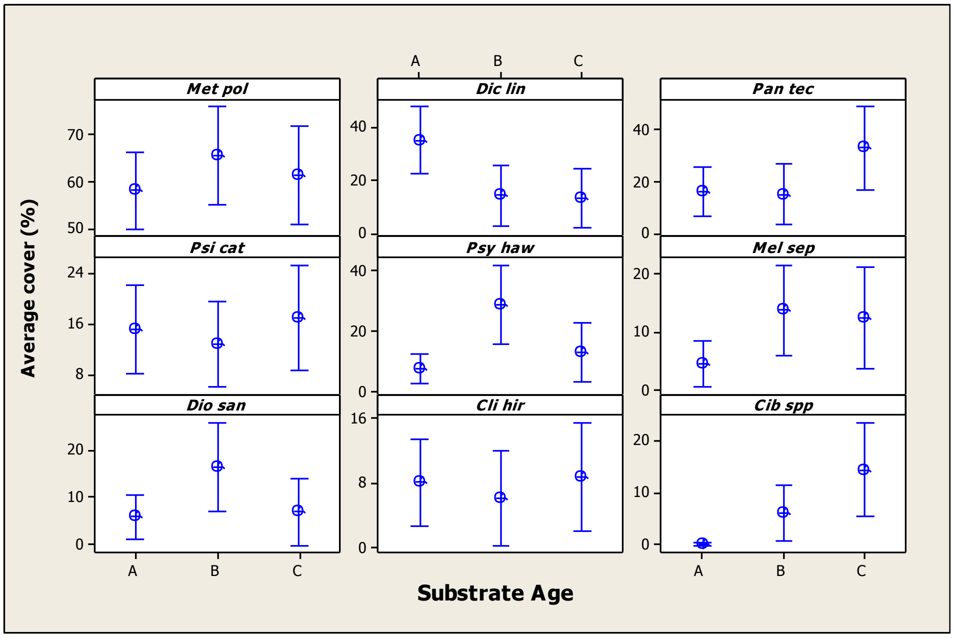

Fig. 14: Average percent cover with 95% CI bars for dominant species according to three substrates age categories (A= < 200 yrs, B= 200-750 yrs, C= > 750 yrs), in native dominated lowland wet forests of Hawai'i.

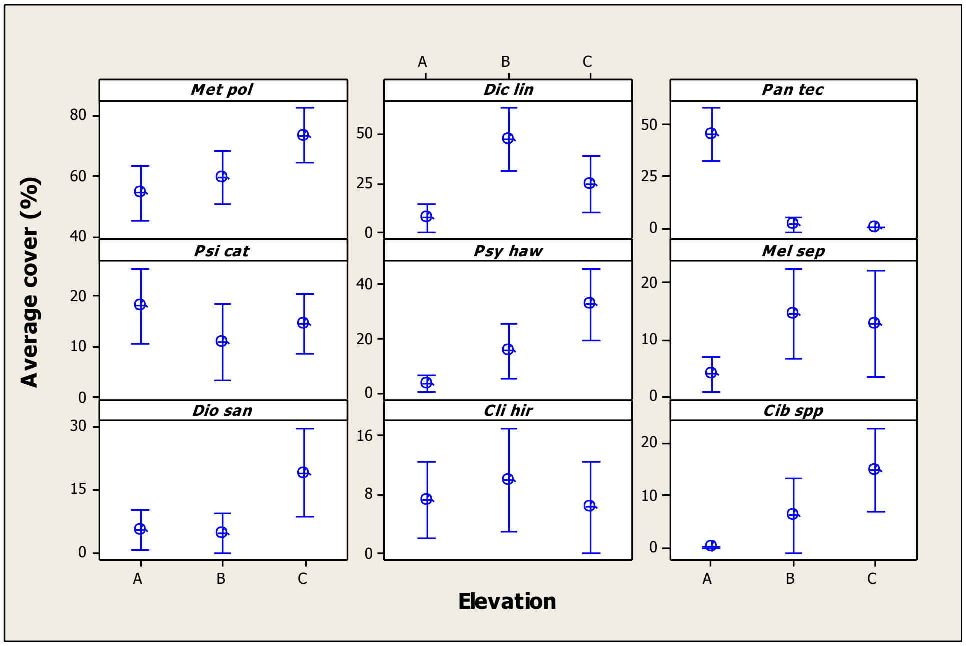

Fig. 15: Average percent cover with 95% CI bars for dominant species according to three elevation zones (A= < 100 m, B= 101-200 m, C= 201-300 m) in lowland wet forests of Hawai'i.

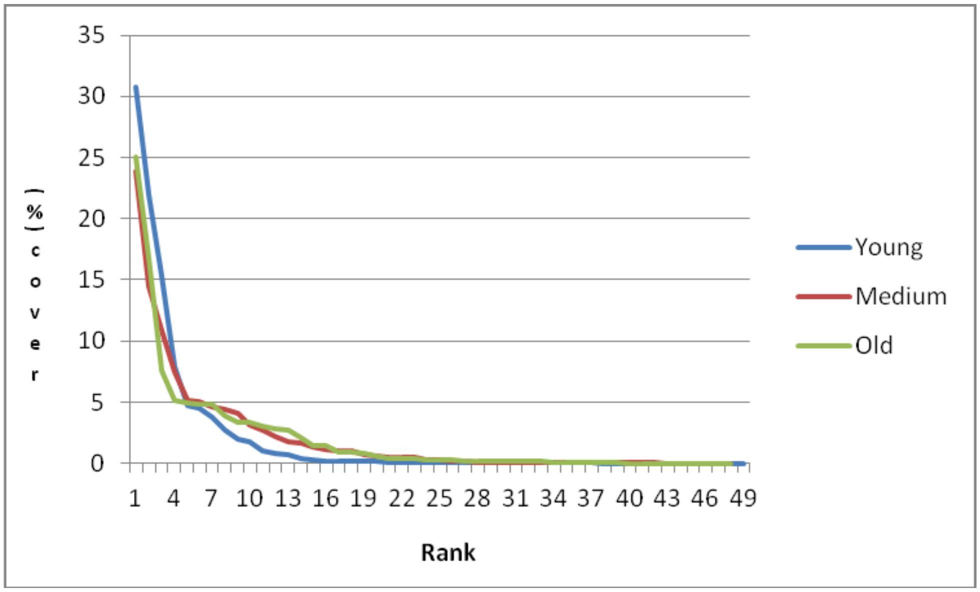

Fig. 16: Average percent relative cover of all species from most to least abundant in lowland wet forests of East Hawai'i. Colors indicate the order in relation to three substrate categories (<200 yrs, 200-750 yrs, > 750 yrs).

Discussion:

Species richness

In a number of ways, the patterns of species richness paralleled those of absolute and relative native cover when considering the effects of substrate age. Intermediate substrate had greater species richness than young substrate, and on both younger and older substrates there was a greater number of non-native species than there were native species. High levels of biodiversity however, were not expected on young substrates, because early succession forest is characterized by poor soils and an abundance of open niches. Later succession forests on older substrates on the other hand, have more natural disturbances occurring such as the death of old trees and perhaps ‘ōhi‘a die-back (Muller-Dombois, 1987). With soils here being more developed and having greater resource availability (Aplet and Vitousek, 1994; Ostertag and Verville, 2002; Hughes and Denslow, 2005), there may also be a history of anthropogenic disturbance such as agriculture (Cuddihy and Stone, 1990). The invasion process by certain non-native species is facilitated on older substrates due to increased gaps in the canopy layer (Atkinson, 1970). Such open areas are likely to be filled by alien invasive species due to their competitive advantages with regards to higher levels of light and soil nutrient, as well as reproductive abilities (Baruch, 1999; Denslow, 2003; Loh and Daehler, 2007; Cordell *et al.,* 2009).

Case (1990) suggests that invasion susceptibility is limited by community size and strength of competition, and that community-level properties determine invasion success. A hypothesis worth testing is whether intermediate substrate areas may have more richness in native species and community resistance due to native canopy integrity. Forests on intermediate substrate are undergoing what a number of studies have qualified as a second stage of primary succession, which consists of a more diverse and complex composition, and provides a closed canopy in which a number of native woody species increase in dominance (Atkinson, 1970; Aplet and Vitousek, 1994; Kitayama *et al.,* 1995; Aplet *et al.,* 1998; Vitousek, 2004). In this case, a more intact canopy layer may be enhancing forest resistance to invasion (Case, 1990). According to Atkinson (1969), a closed canopy should occur at some point between 137 and 300 years, hence these forests may have been in a closed canopy succession stage with the introduction of many invasive species since the early 1800s. With the lack of disturbance and open gaps, invasive species on these substrates may have had less opportunity to invade. Furthermore, community ecology theory presents a concept of “limiting similarity,” predicting that invasive species are not likely to establish themselves if native species with similar traits occupy available niches (Emery 2007). Within relatively intact native forests such as more commonly found between 200 and 750 years, well established plant communities may be less susceptible, and or more resistant to invasion, but this speculation requires experimental testing.

There was a total of 75 species identified in the study altogether, 30 of which were native, and 45 of which were non-native species (between 48 and 51 species on each substrate age). In the understory there were 47 species identified, 21 of which were native and 26 of which were non-native species. Although these forests are dominated by native species in canopy cover, there is a greater number of non-native species on all but the middle aged substrate, which support roughly equivalent numbers of native and non-native understory species. Though results are not quantitatively comparable due to varying measures, the Zimmerman *et al.* study of 2008 determined that densities of non-native saplings were greater than that of native saplings on substrates greater than 400 years. Based on their study, they noted the possibility that 200-300 year old forest development in LWF may represent a threshold in which nutrient limitation no longer constrains native or non-native species. In my study there was no difference in the number of non-native species between young (< 200 yrs), and intermediate substrates (200 - 750 yrs). And although sites greater than 750 years, were higher in the number of non-native species than sites less than 200 years as expected based on Zimmerman *et al.* (2008), the number of non-native species now occurring on young substrates was remarkable given that Zimmerman *et al.* (2008) had determined it to be composed primarily of ʻōhiʻa (*Metrosideros polymorpha*). Note however that density and vegetation cover, though standard forest inventory measures, can produce different results as different species will have greater proportions of stems and foliage, therefore appropriate measures depend a great deal on the species involved. At large scales vegetation cover is a reasonable indicator of foliage surface area (O'Donnell and Dilks, 1987), and was appropriate for the purpose of my study. The invasion level found on young substrates may partly be due to keystone nitrogen fixing species such as albizia *(Falcataria moluccana)* facilitating the success of numerous non-native species by providing a surplus of nutrients (Hughes and Denslow, 2005; Hughes and Uowolo, 2006; Zimmerman *et al.,* 2008).

Despite native dominance of the canopy layer on intermediate substrate, *Psidium cattleianum*, *Melastoma septemnervium,* and *Clidemia hirta* are relatively successful in the lower canopy and shrub layers. These particular species were also recognized by Atkinson *et al.* (1970), Zimmerman *et al.* (2008), and Ostertag *et al.* (2009) as notable invaders in this forest type. Through direct competition for natural resources such as increased water use *(*Kagawa *et al.,* 2009; Cavaleri and Sack, 2010), invasive species such as these change the environment in Hawai'i so dramatically, that they can preempt native species entirely (Hughes and Denslow, 2005; Hughes and Uowolo, 2006; Zimmerman *et al.,* 2008). In this case, *Psidium cattleianum*, *Melastoma septemnervium,* and *Clidemia hirta* all have their maximum cover on middle aged substrates, where most richness and cover of native species are found. These data point to a problematic future for areas now more intact, where native and rare species have the potential of being displaced by encroaching invaders. Their proximity and aggressive regeneration patterns, aided by bird and feral pig activity (Denslow, 2003; Cordell *et al.,* 2009) underscore the urgency of control efforts.

Vegetation cover however, outweighs the importance of richness when looking at dynamics of invasion. The number of species may be insignificant if they have low levels of cover, however it may be a question of time before some of these species become problematic. Not all non-native species pose the same degree of threat to native communities; many in fact may be facilitative of native species establishment and continued existence (Simberloff and Von Holle, 1999). In certain novel system areas, a higher number of species, be they native or non-native, adds to biodiversity and can be beneficial to ecosystem function (Hobbs *et al.,* 2009).

Though the presence of an alien species takes up space that would otherwise be available to a native species, the greater percentage of introductions is not aggressive in nature (Vitousek *et al.,* 1987; Stone *et al.,* 1992; Ewel and Putz, 2004). There are in fact a small number of "super invaders" that can outperform co-existing native species for any given habitat (Daehler, 2003). Of the 8,000 naturalized species found in Hawai'i, most of which were introduced in the 20th century (Cuddihy and Stone, 1990), less than 100 of them pose a serious threat to native forests (Smith, 1985). Identification of alien species that are most harmful to native assemblages is essential in order to inform adequate eradication and/or control measures.

Forest composition and structure

Non-metric multi-dimensional scaling (NMS) demonstrated a clustering of sites according to substrate age and elevation, however other factors contribute to a visible degree of overlap between them (Figures 10 and 11). These may be founded in substrate type, disturbances such as agricultural development, and open gaps in the forest canopy due to fallen trees. A study of ecosystem development on lava flows of Mauna Loa also found elevation (in terms of precipitation and temperature) and substrate age, to be strongly correlated with species composition (Aplet *et al.,* 1998). Some of the clustering patterns in my study, as represented by NMS scores on younger substrates, may be partly representing ‘ōhi‘a (*Metrosideros polymorpha)*/ uluhe *(Dicronopteris linearis)* forest communities that dominate a large portion of LWF landscape on young substrates due to their open niche environment (Atkinson, 1970). These forests have a wide variability of abundance patterns, and are most commonly found on mid-elevation windward slopes of the Hawaiian Islands (Atkinson, 1970; Russell *et al.,* 1998). They later become dominated by *M. polymorpha* as its canopy matures, eventually shading out the sun-demanding fern on older flows (Russell *et al.,* 1998). The coexistence of *M. polymorpha* and *D. linearis* in early succession native forests inhibits seedling establishment by other native and non-native species alike (Russell *et al.,* 1998). The suppression of alien species' invasion by *D. linearis* (Atkinson, 1970) and its eventual replacement by *M. polymorpha* on young substrates, may preserve the potential for future development of native forest.

On medium-aged substrate at higher elevations, a more complex vegetation community includes species such as *M. polymorpha*, *D. linearis,* kōpiko *(Psychotria hawaiiensis),* kōlea *(Myrsine lessertiana),* hāpu‘u (*Cibotium* spp.*.),*'ie‘ie *(Freycinetia arborea)* and ‘ekaha *(Asplenium nidus)*. Older substrates likely represented in this cluster, may also be contributing to some dissipation in the pattern due to the extent of its invasion by non-native species.

A distinct *M. polymorpha* / hala *(Pandanus tectorius*) forest type occurs at the lowest elevation on older lava flows. According to a botanical reconnaissance of Malama-Kī forest reserve (Clarke *et al.,* 1981), closed *M. polymorpha / D. sandwicensis* / *P. tectorius* forests were once present near the coast and also contained *P. hawaiiensis*. Much of the lower region is now heavily invaded by numerous invasive species. Although small pockets of these forests still exist in Malama-Kī, ongoing invasion can largely be attributed to the historic patterns of disturbance that increase with proximity to the coast due to development (Cuddihy and Stone, 1990). The lower abundance of *D. sandwicensis* and *P. hawaiiensis* at these coastal areas may partly be linked to hala itself, as Atkinson (1970) stated that even *M. polymorpha* decreases, and may disappear in advanced stages of succession, giving way to monospecific stands of *P. tectorius.* Higher resistance to invasion by *P. tectorius* may be due partly to a heavy and persistent leaf litter and/or a greater adaptability to salt spray exposure than the dwindling *D. sandwicensis* and *P. hawaiiensis* (Atkinson, 1970; Wagner *et al.,* 1999). The increase in their cover with increased elevation is likely due to increased moisture as suggested by Atkinson (1970).

Unlike for many other tropical forest systems, a single tree species, in this case, *M. polymorpha,* is the major tree during primary succession as well as the dominant climax tree (Drake and Mueller-Dombois, 1993). Hawai'i has a simple forest structure with a depauperate flora (Carlquist, 1974), lacking late successional species that in species-rich continental systems would replace pioneer species (Mueller-Dombois, 1987). There is no identification of a wholesale species replacement as substrate ages according to the Sorenson's index of similarity. Dominant native species are mostly the same on all substrates, but with a few less species on the oldest substrate, perhaps as they are being replaced by non-native species. Interestingly, the greatest similarity exists between the young and the old substrates, likely due to higher levels of non-native presence. High endemism, low species diversity, nutrient limitation in early stages of forest development, and the disharmonic nature of native flora in later succession stages, creates specific disadvantages to native species in later succession (Simberloff, 1995; Denslow, 2003; Zimmerman *et al.,* 2008). The rank abundance diagram of LWF confirms these general trends. There is a small number of species having much greater cover than most for all substrate ages, and slightly less evenness of species on the youngest substrate perhaps due to the dominant presence of ‘ōhi‘a and uluhe on young substrates. Simpler systems have less evenness because a few species will dominate the open niche space, whereas in diverse assemblages such as found in the Amazon, evenness is low because a large number for each species is comparably rare (Mueller-Dombois, 1987).

Rare species

It is remarkable that all 34 rare species' locations (among a total of four rare species) were entirely on the 200-750 year old substrate, and occurred in areas where the relative canopy cover of native trees was greater than for the average plot in LWF. As was observed in chapter I, the intermediate substrate appears to provide more favorable conditions for native plant communities, and native plant communities may provide more favorable conditions for rare species. Younger substrates may not offer rare species adequate nutrient or shade levels for their survival (Aplet *et al.,* 1998), and older substrates may be too heavily invaded with species that render the environment inhospitable (Ehrenfeld, 2003; Zimmerman *et al.,* 2008). On intermediate substrates, invasion by exotic plant species may not yet have altered nutrient dynamics and compositional patterns (Ehrenfeld, 2003).

Little is known about rare species presence and distribution patterns in LWF, as it is difficult to obtain this type of information, specifically in the tropics where it is most needed (Groombridge, 1992). This can be attributed to the fact that distribution patterns are complex and reflect numerous interacting relationships between plant and habitat (Scmida and Ellner, 1984), specifically in heterogeneous environments such as found in Hawai'i (Mueller-Dombois, 2002) . Rare species may not always have been rare. They may be more susceptible to environmental changes occurring with the degradation of native forest habitat for a number of different reasons (Gaston, 1994). Native and rare species are prone to extinction due to loss of genetic variation, and susceptible to the consequences of habitat fragmentation because of their population size. Many fragmented habitats are becoming unable to support small populations due to insufficient gene flow caused through isolation (Honnay and Jacquemyn, 2007). For this reason, rare species may have an importance and possible utility as indicator species for the selection of conservation sites in preserving biodiversity. According to a study in the eastern United States, conservation plans based on indicators encompassed 84% of other species of interest (Lawler *et al.,* 2003). The higher native canopy conditions surrounding rare plant species suggests that areas in which they are found are important priority areas for conservation.

When examining past studies that focused on rare and endangered species of two LWF reserves, Halepuaʻa (Clarke *et al.,* 1979), and Malama-Kī (Clarke *et al.,* 1981), a decline in the presence of rare native species was observed. For instance, approximately 25 mature ʻohe (*Tetraplasandra hawaiiensis)* individuals were mapped in Halepuaʻa by Clarke *et al.* (1979). Though we cannot be certain that all individuals have been found, of seventeen trees since located by Ann Kobsa (pers. comm.), thirteen have died since 2007 due to bark damage at the base of trees by feral pigs, and the four remaining individuals have probably survived due to being fenced. Of five haʻiwale *(Cyrtandra nanawalensis)* clusters located in Halepuaʻa by Ann Kobsa in past years, only two remain. Although a few rare species were located in more native-dominated forest land of upper Malama-Kī, in attempting to relocate over 150 colonies of *C. nanawalensis,* observed by Clarke *et al.* (1981) in an older ʻkipukaʼ of lower Malama-Kī, none were located in the present survey, likely due to invasion and/or drying and warming trends. These trends suggest that populations are declining despite having persisted in more intact forest areas. Identifying limiting factors and key threats of rare species in LWF would be invaluable in order to facilitate management.

Future Restoration

In designing native plant communities that can resist invasion by more harmful exotic species, it may be necessary to attain some form of equilibrium between native and introduced species within buffer zones that help protect core areas (Ewel and Putz, 2004; Hobbs *et al.,* 2009). In many areas of LWF today, fully native composition is no longer a realistic restoration aim, as they are for the most part composed of a mixture of native and non-native species. In these cases it may be essential to accept a novel forest system approach that can procure alternative forms of diversity and secure ecosystem function (Ewel and Putz, 2004; Hobbs *et al.,* 2009). Key invasive species must be targeted in these areas, in order to maintain some form of ecological balance. For native plant communities that are already mostly intact, novel system ideals are unnecessary because it is still realistic for these areas to be restored to a native state.

Though certain control measures are essential to restoring Hawai'i's fragile ecosystems (Ostertag *et al.,* 2009), equally important is native plant propagation to help fill open gaps and niches before they are taken by more aggressive alien species, in the many cases where recruitment levels need supplemental support (Loh and Daehler, 2007). In some areas, invasive species control measures will naturally facilitate native plant recruitment (Cordell *et al.,* 2009). According to Loh and Daehler (2007) however, a diverse native forest is not as probable in opened gap areas caused by removing or killing invasive species, due to seed limitation for many native species. Seed supplementation and out-planting can prove to be more successful in establishing a variety of species, such as was found in upland restoration efforts involving the girdling of *Myrica faya* (Loh and Daehler, 2007). In seeking to reassemble native plant communities that are resistant to exotic species invasion, further studies of native plants, including rare species that may best compete in particular micro-environments based on traits that confer invasion resistance, are an important constituent to restoration efforts (Funk *et al.,* 2008). Studies in propagation techniques best suited for individual species, which could improve the efficacy of both propagation and out-planting protocol, would be of great benefit as well.

Managing lowland wet forests most effectively will require cooperation between our conservation agencies, policy makers, scientific community, and community volunteers. According to Daehler (2003), most environments could likely be managed in such a way that native species have a greater advantage by altering disturbance regimes and resource levels. Beyond restoration however, the State of Hawai'i's Natural Areas Reserve System (NARS) or other resource management entity could ensure more institutionalized protection of remaining native lowland wet forest reservoirs.

Conclusion

A number of patterns observed in this study together highlight the intermediate substrate age as an important conservation target. This substrate age was the only one that came out with significant differences in every one of the conducted analyses. The most striking pattern, which did not require a test, was that 100% of all rare species individuals or clusters were located on this substrate. Rare plant locations had a greater relative cover of native species than the average plot, which did not have rare plant occurrences. In addition to the vegetation cover patterns determined in chapter I, there was higher diversity of species here than on young substrates, and it was the only substrate upon which the richness of non-native species was equivalent, and not greater than native species. In areas where the forest may be inherently less vulnerable to invasion, and where more native abundance and diversity occurs, restoration efforts have a stronger likelihood of succeeding. Invasive species, such as *Psidium cattleianum*, *Melastoma septemnervium,* and *Clidemia hirta*, which have taken root in open pockets of these relatively intact forests, are important target species for control. In spite of non-native richness in the understory of these forests, intermediate aged substrates are more likely to be intact, and perhaps represent the better conservation target in general, as they would require considerably less effort to restore than more heavily degraded forest on other lava flows. Prioritizing more sizable and intact forest areas wherever they remain however may be key in effectively managing LWF.

Despite the strong presence of non-native species, there are substantial areas that are native-dominated in the canopy as well as understory layers, and that make up important priority areas for LWF. Based on this study, the three most important areas to consider for restoration and conservation are: the lower part of Keauohana, the center of Halepua'a, and the top of Malama-Kī, due to their extent of relatively intact native forest assemblages (Fig. A8). These, as well as other native forest areas, could be restored by joining several native-dominated pockets with minimally invaded area between them.

The invasion now occurring on younger substrates by a number of invasive species presents a challenging prospect. The future of native forests depends on the prioritization of these substrates as well, particularly where beginning signs of invasion occur. Young flows, where rare species are not currently found represent areas where they would more likely be found in the future if they are protected and managed appropriately. And though higher elevations in these LWF are more rich and abundant in native species, conserving native representations of coastal communities, such as *M. polymorpha/ P. tectorius* forests, is also important.

Remaining lowland wet forests of Hawai'i are unique and invaluable. Their surviving biota is of great biological significance (Howarth *et al.,* 1988), and presents an important opportunity for restoration and conservation. Each location must be regarded on an individual basis as far as restoration is concerned, especially because of the great deal of variability and biogeographic complexity inherent in the landscape. Quantifying the effects of substrate age and elevation on forest composition and structure in LWF has provided a potential basis for more effective restoration of native plant community assemblages in lower elevation forests of East Hawai'i.

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Appendix

Table A1. Number of basic (B = all canopy trees > 3 m), and detailed (D = all species present) plots completed across three categories of substrate age (< 200 yrs, 200-750 yrs, > 750 yrs.), and three elevation zones (< 100 m, 101- 200 m, 201- 300 m).

	<200 Years	**200-750 Years**	**>750 Years**
≤ 100 Meters	29B / 19D *Total:* **48**	20B / 10D *Total:* **30**	27 B / 22D *Total:* **49**
101-200 Meters	13B / 16D *Total:* **29**	11B / 16D *Total:* **27**	16 B / 4D *Total:* **20**
201-300 Meters	15B / 9D *Total:* **24**	20B / 16D *Total:* **36**	13B / 13D *Total:* **26**

Table A1b. Number of plots completed on each reserve with a breakdown according to the type of assessment conducted based on the proportion of native to non-native canopy tree cover.

Reserves	**Detailed plots**	**Basic Plots**	**Total Plots**
Halepua'a	29	24	53
Kaniahiku	26	49	75
Keauohana	23	25	48
Malama-Kī	16	46	62
Nānāwale	24	20	44

Table A2. Pearson Correlation Analysis for absolute cover non-native trees (ACNNT), absolute cover of native trees (ACNT), absolute cover of all trees (ACAT), and relative cover of native trees (RCNT) according to elevation. Given are r values and the significance of the correlation (* indicates significance).

	ACNNT	**ACNT**	**ACAT**	**RCNT**
All data				
Elevation (m)	-0.037	0.082	0.038	0.081
p-value	0.535	0.166	0.521	0.168
Young substrate				
Elevation (m)	0.114	-0.387	-0.129	-0.080
p-value	0.253	< **0.001***	0.198	0.424
Medium substrate				
Elevation (m)	-0.172	0.256	0.143	0.258
p-value	0.102	0.014	0.173	0.013
Old substrate				
Elevation (m)	-0.083	0.199	0.109	0.108
p-value	0.424	0.054	0.291	0.298

Table A3. Average percent cover of dominant species for all basic and detailed sites according to substrate age and elevation.

Average % cover of most dominant species for all basic data

	Substrate (yrs)			Elevation (m)			
Native Species	**<200**	**200-750**	**>750**	**<100**	**101-200**	**201-300**	**Avg. % cover**
Metrosideros polymorpha	46	48	39	38	46	52	**44**
Pandanus tectorius	9	7	24	29	1	0	**13**
Dicranopteris linearis	18	13	6	4	23	16	**12**
Psychotria hawaiiensis	2	17	8	2	9	18	**8**
Diospyros sandwicensis	5	18	4	9	2	13	**8**
Cibotium glaucum	0	2	1	0	0	3	**1**
Cibotium menziesii	0	0	2	0	1	2	**1**
Non-native Species							
Psidium cattleianum	36	28	26	32	15	40	**32**
Falcataria moluccana	15	0	9	3	16	11	**8**
Cecropia obtusifolia	3	8	13	14	5	0	**8**
Melastoma septemnervium	7	5	4	0	13	6	**5**
Melochia umbellata	0	3	5	3	2	3	**3**
Schefflera actinophylla	2	3	1	4	0	0	**2**
Trema orientalis	2	0	3	1	2	3	**2**

Average % cover of most dominant species in native-dominated forest

	Substrate (yrs)			Elevation (m)			Avg.% cover
Native Species	**<200**	**200-750**	**>750**	**<100**	**101-200**	**201-300**	
Metrosideros polymorpha	57	68	59	54	60	71	**61**
Dicranopteris linearis	40	15	12	7	47	22	**23**
Pandanus tectorius	15	9	39	45	2	0	**20**
Psychotria hawaiiensis	4	31	12	3	13	32	**15**
Diospyros sandwicensis	1	21	6	6	5	18	**9**
Freycinetia arborea	0	14	2	2	8	11	**6**
Cibotium glaucum	0	4	2	0	0	10	**3**
Cibotium menziesii	0	0	4	0	5	5	**3**
Asplenium nidus	8	5	2	1	3	7	**3**
Peperomia spp..	0	5	0	0	1	5	**2**
Non-native Species							
Psidium cattleianum	9	16	12	11	11	14	**15**
Melastoma septemnervium	5	13	10	4	15	13	**9**
Clidemia hirta	3	13	8	7	10	6	**8**
Cecropia obtusifolia	0	3	3	4	1	1	**2**

Table A4. Sorenson's index of similarity for all species by age for all basic data. Full names for abbrevations given in plant list (Table A5).

Native species				**N-Native Species**		
Young	**Med**	**Old**		**Young**	**Med**	**Old**
Met pol	*Met pol*	*Met pol*		*Psi cat*	*Psi cat*	*Psi cat*
Dio san	*Dio san*	*Dio san*		*Psi gua*	*Psi gua*	*Psi gua*
Psy haw	*Psy haw*	*Psy haw*			*Psi pin*	*Psi pin*
Myr les	*Myr les*			*Fal mol*		*Fal mol*
Pan tec	*Pan tec*	*Pan tec*		*Cec obt*	*Cec obt*	*Cec obt*
Cib gla	*Cib gla*	*Cib gla*		*Man ind*	*Man ind*	*Man ind*
Cib men	*Cib men*	*Cib men*			*Per ame*	*Per ame*
Dic lin	*Dic lin*	*Dic lin*		*Mel umb*	*Mel umb*	*Mel umb*
Asp nid	*Asp nid*	*Asp nid*		*Tre ori*	*Tre ori*	*Tre ori*
Fre arb	*Fre arb*	*Fre arb*		*Cas equ*		*Cas equ*
Pip alb	*Pip alb*			*Sch act*	*Sch act*	*Sch act*
	Chr cya			*Mac map*		
	Sad cya					*Fic mic*
	Aly oli			*Syz jam*		
Coc tri	*Coc tri*	*Coc tri*		*Clu ros*	*Clu ros*	*Clu ros*
	Muc gig	*Muc gig*		*Mel sep*	*Mel sep*	*Mel sep*
Psi nud		*Psi nud*		*Tet bic*	*Tet bic*	
Hap elo	*Hap elo*				*Mic cal*	*Mic cal*
Ela spp.	*Ela* spp.	*Ela* spp.				*Cof ara*
	Ade tam	*Ade tam*		*Sch ter*		
Ade lav	*Ade lav*	*Ade lav*		*Cli hir*	*Cli hir*	*Cli hir*
	Pep spp.	*Pep* spp.		*Nep mul*	*Nep mul*	*Nep mul*
	Van cyr			*Chr par*	*Chr par*	*Chr par*
Lep tam		*Lep tam*		*Phy gro*	*Phy gro*	*Phy gro*
Mac ang	*Mac ang*	*Mac ang*			*Phl aur*	
Lyc cer					*Rub ros*	
Sca cor		*Sca cor*		*Opo men*	*Opo men*	*Opo men*
Sch tes				*Thu fra*	*Thu fra*	*Thu fra*
Wis san					*Sta urt*	
	Ipo spp.			*Orc spp.*	*Orc spp.*	*Orc spp.*
	Ale mol	*Ale mol*		*Aru bam*	*Aru bam*	*Aru bam*
		Coc nuc		*NN grass*	*NN grass*	*NN grass*
Ter cat				*Pae foe*	*Pae foe*	*Pae foe*
		Hib til			*Palm* spp.	
Mor cit	*Mor cit*			*Beg hir*	*Beg hir*	
		Bam spp.			*Sen mik*	
Cor fru		*Cor fru*			*Des* spp.	*Des* spp.
Dis pen	*Dis pen*	*Dis pen*		*Plu sym*		*Plu sym*
		Zin Zer		*Dio wil*		
Pas edu		*Pas edu*				

Table 4b. Sorenson's index of similarity for all species by age for native-dominated sites.

Native Species				**Non-native**		
Young	**Med**	**Old**		**Young**	**Med**	**Old**
Met pol	*Met pol*	*Met pol*		*Mac map*		
Dio san	*Dio san*	*Dio san*		*Syz jam*		
Psy haw	*Psy haw*	*Psy haw*		*Clu ros*		*Clu ros*
Myr les	*Myr les*			*Sch act*		*Sch act*
Pan tec	*Pan tec*	*Pan tec*		*Mel sep*	*Mel sep*	*Mel sep*
Cib gla	*Cib gla*	*Cib gla*				*Mic cal*
Cib men	*Cib men*	*Cib men*			*Mic cal*	
Dic lin	*Dic lin*	*Dic lin*		*Cli hir*	*Cli hir*	*Cli hir*
Asp nid	*Asp nid*	*Asp nid*			*Cof ara*	*Cof ara*
Fre arb	*Fre arb*	*Fre arb*			*Sch ter*	
	Pip alb				*Tet bic*	
Coc tri		*Coc tri*		*Nep mul*	*Nep mul*	*Nep mul*
	Chr cya			*Chr par*	*Chr par*	*Chr par*
Psi nud		*Psi nud*		*Phy gro*	*Phy gro*	*Phy gro*
Hap elo				*Phl aur*	*Phl aur*	
	Sad cya				*Rub ros*	
	Aly oli			*Opo men*	*Opo men*	*Opo men*
	Muc gig			*Thu fra*	*Thu fra*	*Thu fra*
	Hap elo				*Sta urt*	
	Ela spp.	*Ela* spp.		*Orc* spp.	*Orc* spp.	*Orc* spp.
	Ade tam	*Ade tam*		*Aru bam*	*Aru bam*	*Aru bam*
Ade lav	*Ade lav*	*Ade lav*		*Beg hir*	*Beg hir*	
	Pep spp.	*Pep* spp.		*Pae foe*	*Pae foe*	*Pae foe*
		Lep tam			*Palm* spp.	
Mac ang	*Mac ang*	*Mac ang*			*Des* spp.	*Des* spp.
		Lyc cer		*NN Grass*	*NN Grass*	*NN Grass*
Sca cor		*Sca cor*			*Ale mol*	
Sch tes				*Pas edu*		
Wis fur				*Plu Sym*		*Plu Sym*
Non-native species						*Coc nuc*
Psi cat	*Psi cat*	*Psi cat*				*Bam spp.*
Psi gua	*Psi gua*	*Psi gua*		*Dio Wil*		
	Psi pin			*Dio wil*		
Fal mol		*Fal mol*		*Plu sym*		
Cer obt	*Cer obt*	*Cer obt*		*Mor cit*		
		Man ind		*Cor fru*	*Cor fru*	*Cor fru*
Mel umb	*Mel umb*	*Mel umb*		*Dis pen*	*Dis pen*	*Dis pen*
Cas equ		*Cas equ*				*Zin Zer*
	Tre ori					

Table A5. Native, non-native, and Polynesian introduced plant list of lowland wet forest plots.

Lowland Wet Forest Native Plot Plant List				
Family	***Genus***	***Species***	**Common Name**	**Class**
Grammitidaceae	*Adenophorus*	*tamariscinus*	Wahine noho mauna	pteri
Acanthospereae	*Adenostemma*	*lavenia*	Kāmanamana	dicot
Apocynaceae	*Alyxia*	*oliviformis*	Maile	dicot
Phyllanthaceae	*Antidesma*	*platyphyllum*	Hamehame	dicot
Aspleniaceae	*Asplenium*	*nidus*	‘Ekaha	pteri
Asteliaceae	*Astelia*	*menziesiana*	Pā'iniu	mono
Thelypteridaceae	*Christella*	*cyatheoides*	kīkawaio	pteri
Dicksoniaceae	*Cibotium*	*glaucum*	Hāpu‘u pulu	pteri
Dicksoniaceae	*Cibotium*	*menziesii*	Hāpu‘u ‘i‘i	pteri
Menispermaceae	*Cocculus*	*trilobus*	Huehue	dicot
Fabaceae	*Desmodium*	spp.	Desmodium	dicot
Gleicheniaceae	*Dicranopteris*	*linearis*	Uluhe	pteri
Ebenaceae	*Diospyros*	*sandwicensis*	Lama	dicot
Dryopteridaceae	*Dryopteris*	*wallichiana*	Laukahi	pteri
Lomariopsidaceae	*Elaphoglossum*	spp.	Stag's tongue	pteri
Pandanaceae	*Freycinetia*	*arborea*	‘Ie‘ie	mono
Vittariaceae	*Haplopteris*	*elongata*	Ohe'ohe shoe string	pteri
Malvaceae	*Hibiscus*	*tiliaceus*	Hau	dicot
Convolvulaceae	*Ipomoea*	spp.	Morning glory	dicot
Ericaceae	*Leptocophylla*	*tamaeiameiae*	Pūkiawe	dicot
Lycopodiaceae	*Lycopodiella*	*cernua*	wawai'iole	pteri
Cyperaceae	*Machaerina*	*angustifolia*	Uki	sedge
Myrtaceae	*Metrosideros*	*polymorpha*	‘Ōhi‘a	dicot
Dennstaedtiaceae	*Microlepia*	*strigosa*	Palapalai	pteri
Fabaceae	*Mucuna*	*gigantea*	Sea bean	dicot
Myrsinaceae	*Myrsine*	*lessertiana*	Kōlea lau nui	dicot
Nephrolepidaceae	*Nephrolepis*	*exaltata*	Ni'ani'au/ kupukupu	pteri
Pandaneceae	*Pandanus*	*tectorius*	Hala	mono
Piperaceae	*Peperomia*	spp.	‘Ala ala wai nui	dicot
Urticaceae	*Pipturus*	*albidus*	Māmaki	dicot
Thelypteridaceae	*Pneumatopteris*	*hundsoniana*	Laukahi	pteri
Psilotaceae	*Psilotum*	*nudum*	Moa / wisk fern	pteri
Rubiaceae	*Psychotria*	*hawaiiensis*	Kōpiko ‘ula	dicot
Rubiaceae	*Psydrax*	*odorata*	Alahe'e	dicot
Blechnaceae	*Sadleria*	*cyatheoides*	‘Ama‘u	pteri
Goodeniaceae	*Scaevola*	*coriacea*	Naupaka	dicot
Cyperaceae	*Scheria*	*testaceae*	Sedge	mono
Araliaceae	*Tetraplasandra*	*hawaiensis*	Ohe	dicot
Urticaceae	*Urera*	*glabra*	Ōpuhe	dicot
Hymennophyllaceae	*Vandenboschia*	*cyrtotheca*	Kīlau	pteri
Thymelaeaceae	*Wikstroemia*	*sandwicensis*	‘Ākia	dicot

Lowland Wet Forest Non- Native Plot Plant List				
Family	***Genus***	***Species***	**Hawaiian/Common**	**Class**
Bignoniaceae	*Begonia*	*asiatica*	African Tulip	dicot
Begoniaceae	*Begonia*	*hirtella*	Begonia	dicot
Casuarinaceae	*Casuarina*	*equisetifolia*	Ironwood	dicot
Cecropiaceae	*Cecropia*	*obtusifolia*	Cecropia	dicot
Thelypteridaceae	*Christella*	*parasitica*	Kikawaiō	pteri
Melastomataceae	*Clidemia*	*hirta*	Koster's curse	dicot
Clusiaceae	*Clusia*	*rosea*	Autograph tree	dicot
Rubiaceae	*Coffea*	*arabica*	Coffee	dicot
Fabaceae	*Dioclea*	*wilsonii*	Sea bean	dicot
Fabaceae	*Falcataria*	*moluccana*	Albizia	dicot
Moraceae	*Ficus*	*microcarpa*	Banyan	dicot
Verbenaceae	*Lantana*	*camara*	Lantana	dicot
Euphorbiaceae	*Macaranga*	*mappa*	Bingabing	dicot
Anacardiaceae	*Mangifera*	*indica*	Mango	dicot
Melastomataceae	*Melastoma*	*septemnervium*	Purple flower	dicot
Solanaceae	*Melochia*	*umbellata*	Melochia	dicot
Melastomataceae	*Miconia*	*calvescens*	Miconia	dicot
Nephrolepidaceae	*Nephrolepis*	*multiflora*	Sword fern	pteri
Poaceae	*Oplismenus*	*hirtellus*	Basket grass	mono
Orchidaceae	*Orchid*	spp.	Orchid	dicot
Rubiaceae	*Paederia*	*foetida*	Pilau Maile	dicot
Passifloraceae	*Passiflora*	*edulis*	Lilikoi	dicot
Lauracea	*Persea*	*americana*	Avocado	dicot
Polipodiaceae	*Phlebodium*	*aureum*	Laua'e like	pteri
Polipodiaceae	*Phymatosorus*	*grossus*	Laua'e	pteri
Asteraceae	*Pluchea*	*symphytifolia*	Sour bush	dicot
Myrtaceae	*Psidium*	*cattleianum*	Strawberry guava	dicot
Myrtaceae	*Psidium*	*guajava*	Common guava	dicot
Rosaceae	*Rubus*	*rosifolius*	Thimble berry	dicot
Arailiaceae	*Schefflera*	*actinophylla*	Octopus Tree	dicot
Anacardiaceae	*Schinus*	*terebinthifolius*	Christmas Berry	dicot
Asteraceae	*Senecio*	*mikanioides*	German ivy	dicot
Verbenaceae	*Stachytarpheta*	*urticifolia*	Vervain	dicot
Myrtaceae	*Syzygium*	*cumini*	Java plum	dicot
Myrtaceae	*Syzygium*	*jambos*	Rose Apple	dicot
Melastomataceae	*Tetrazygia*	*bicolor*	White flower	dicot
Acanthaceae	*Thunbergia*	*fragrans*	Sweet clockvine	dicot
Ulmaceae (Elm)	*Trema*	*orientalis*	Gun powder	dicot

Polynesian Introduction Plot Plant List				
Family	**Genus**	**Species**	**Common Name**	**Division**
Euphorbiaceae	*Aleurites*	*moluccana*	Kukui	dicot
Bambuseae	*Bamboo*	spp.	Bamboo	dicot
Arecaceae	*Cocos*	*nucifera*	Coconut / Niu	dicot
Agavaceae	*Cordyline*	*fruticosa*	Ti	dicot
Dioscoriaceae	*Dioscorea*	*pentaphylla*	Polynesian yam	mono
Malvaceae	*Hibiscus*	*tiliaceus*	Hau	dicot
Rubiaceae	*Morinda*	*citrifolia*	Noni	dicot
Clusiaceae	*Terminalia*	*catappa*	Kamani	dicot
Zingiberaceae	*Zingiber*	*zerumbet*	Awapuhi	dicot

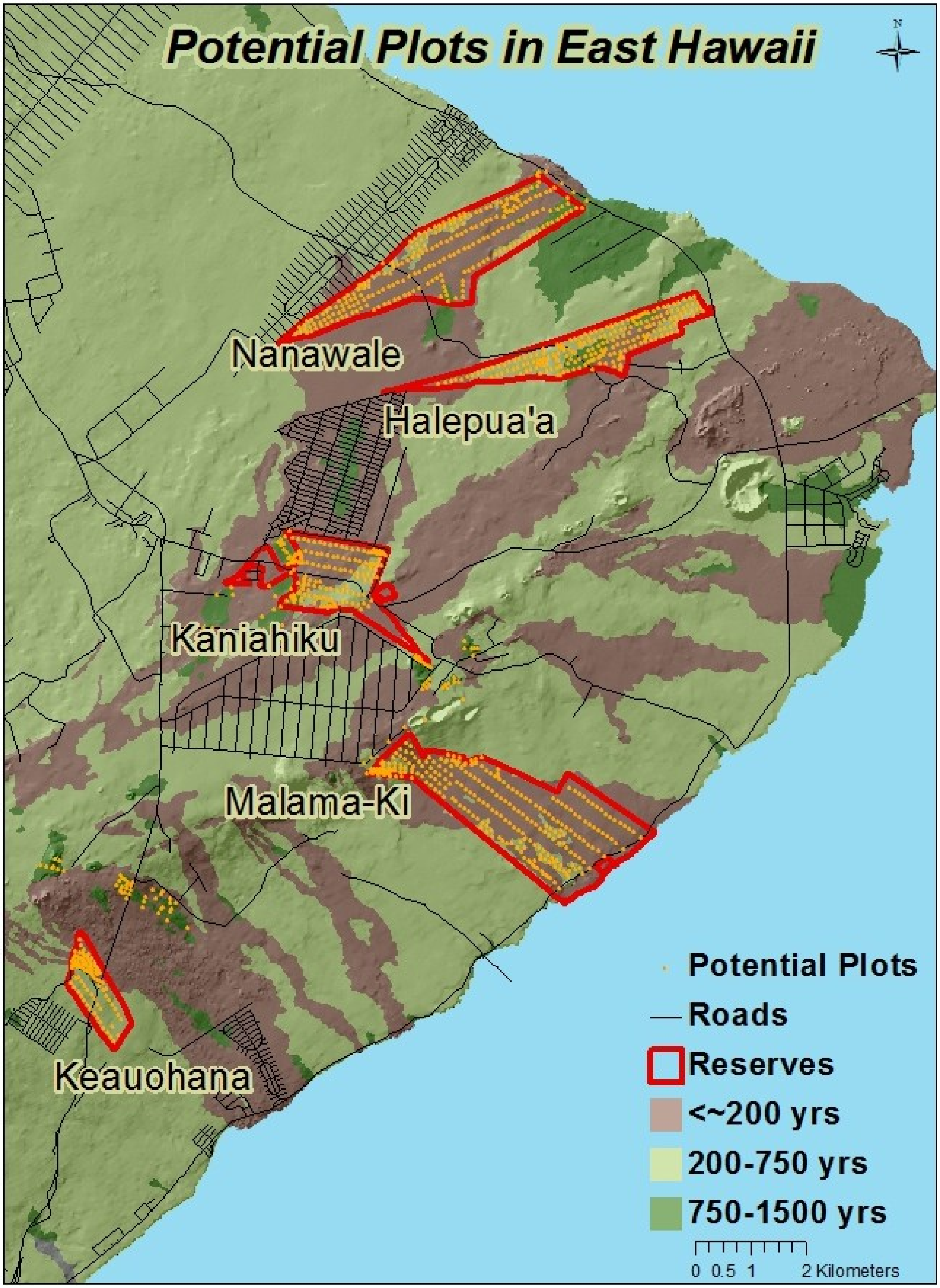

Fig. A1. Systematic layout of potential plots across reserves in East Hawai'i.

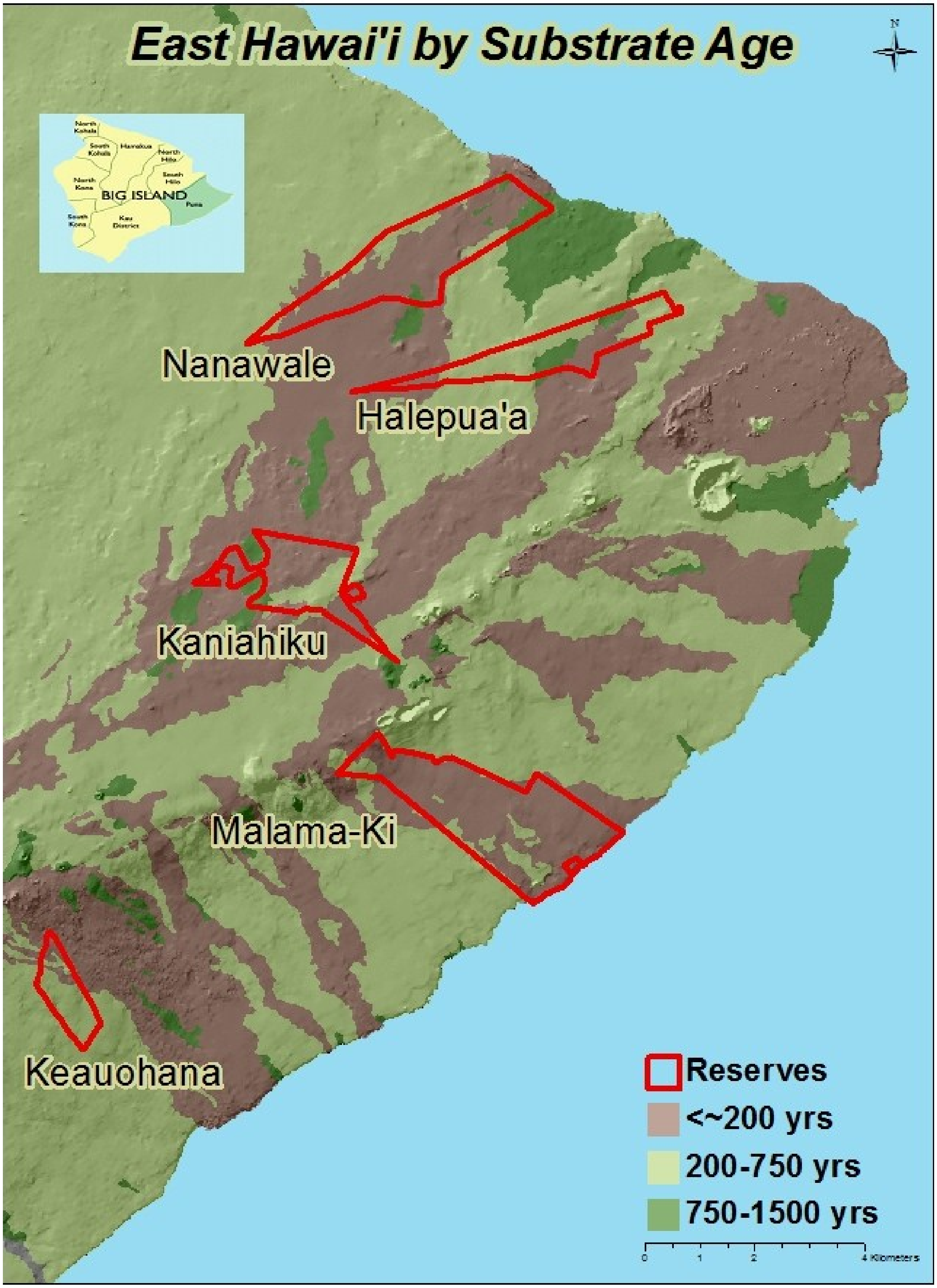

Fig. A2. East Hawai'i according to substrate age categories (< 200 yrs, 200-750 yrs, > 750 yrs.)

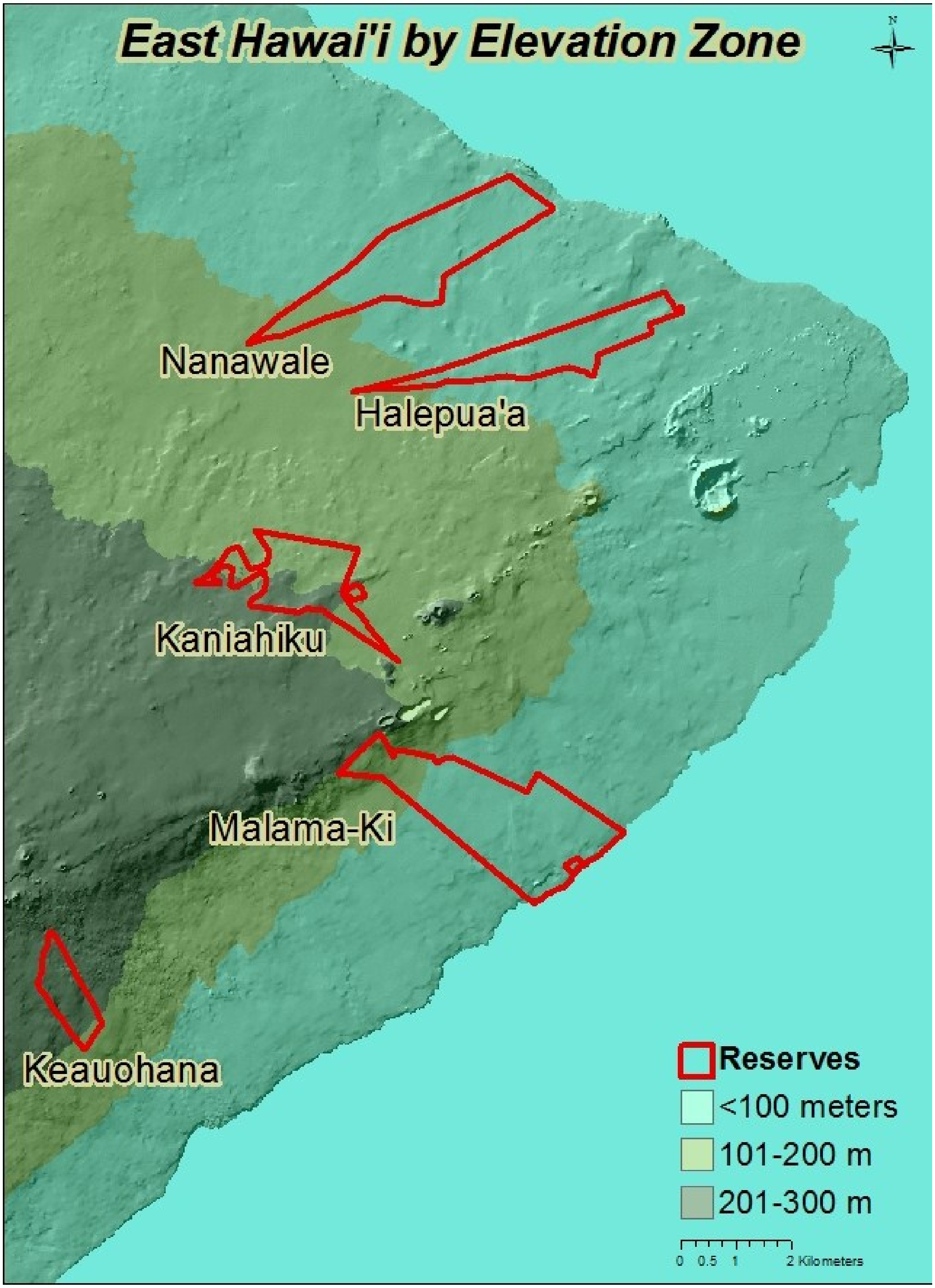

Fig. A3. East Hawai'i according to three elevation zones (≤ 100 m, 101-200 m, 201-300 m).

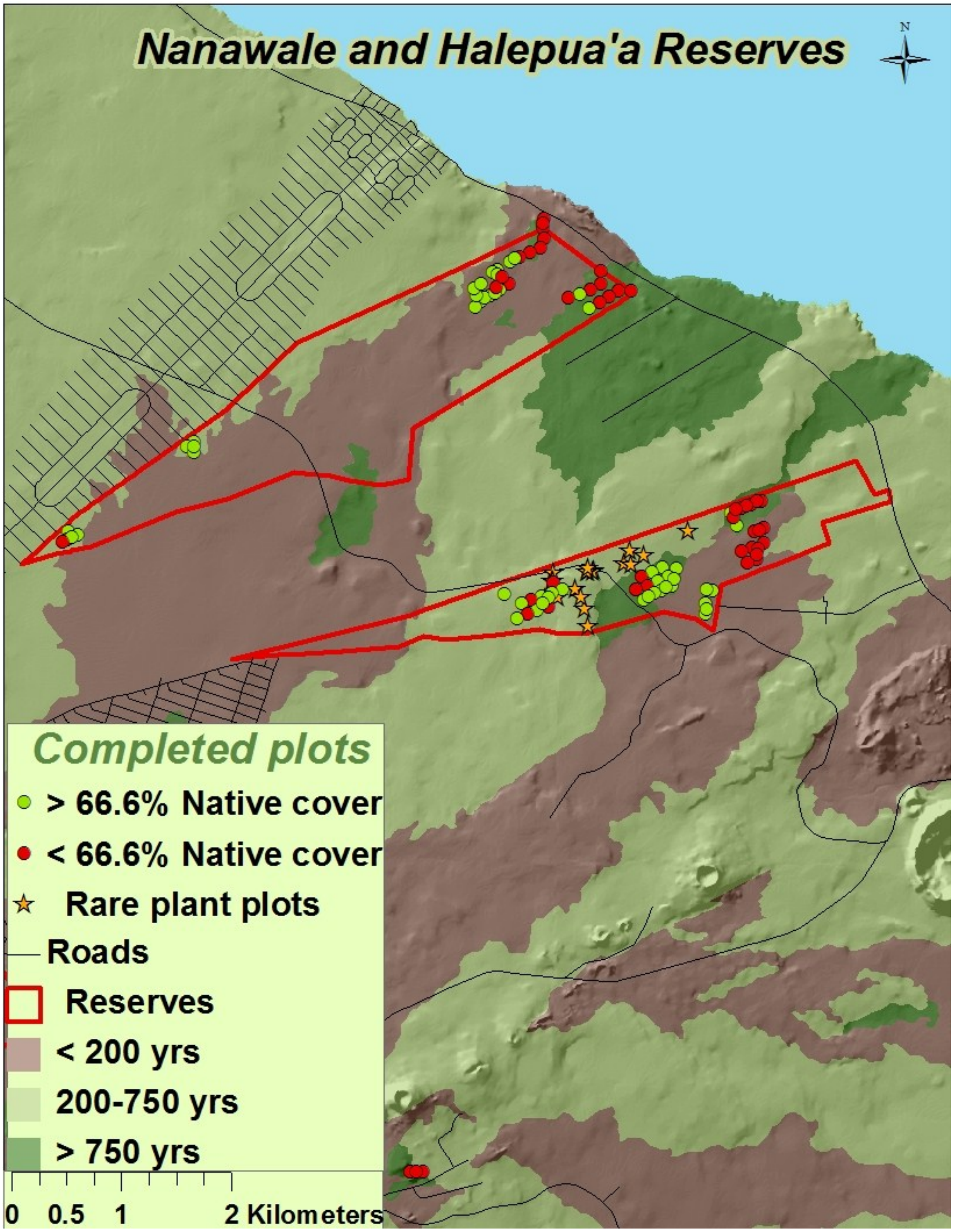

Fig. A4. Completed native-dominated plots, non-native-dominated plots and rare plant plots for Nānāwale and Halepua'a forest reserves**.**

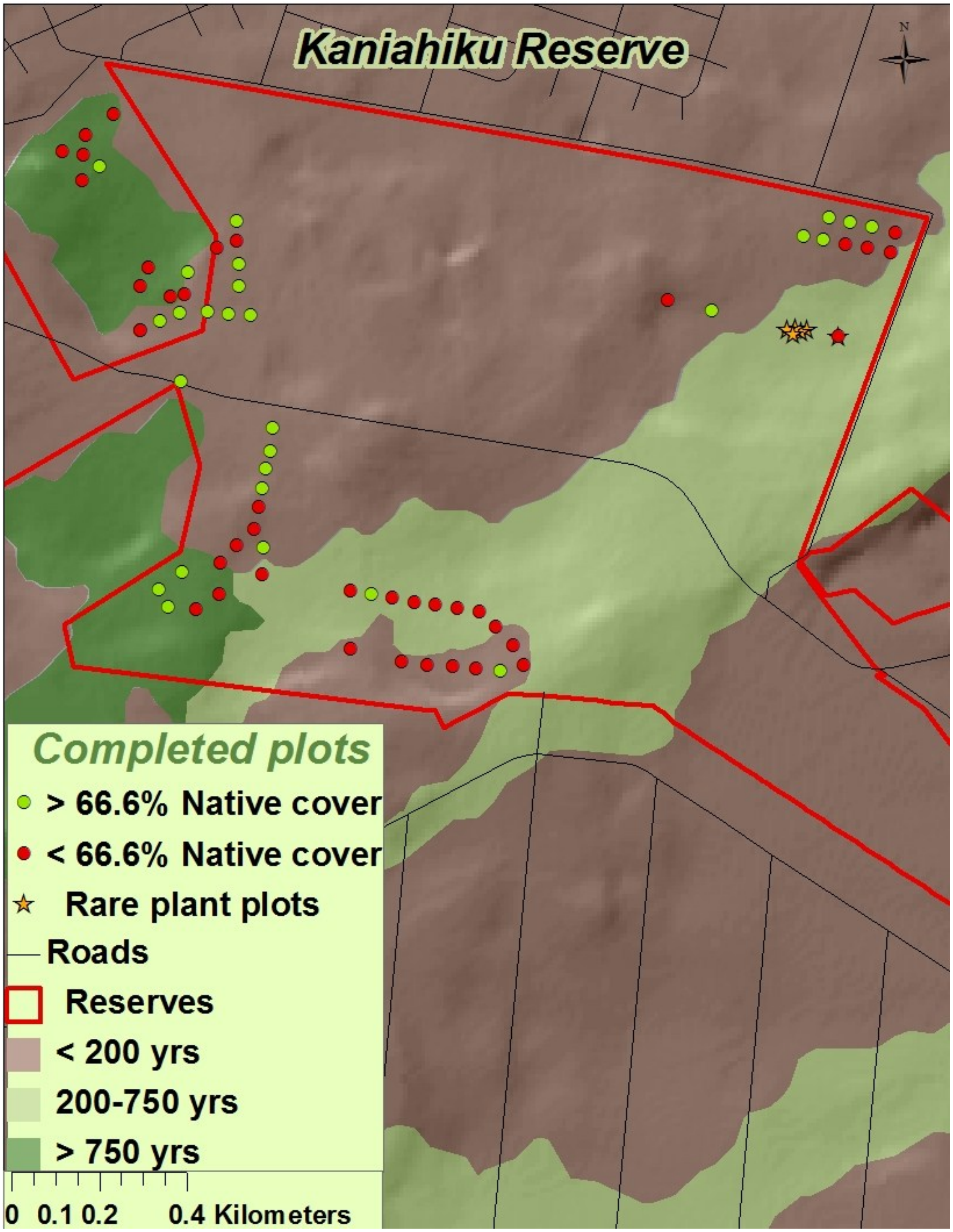

Fig. A5. Completed native-dominated plots, non-native-dominated plots and rare plant plots for Kaniahiku Reserve.

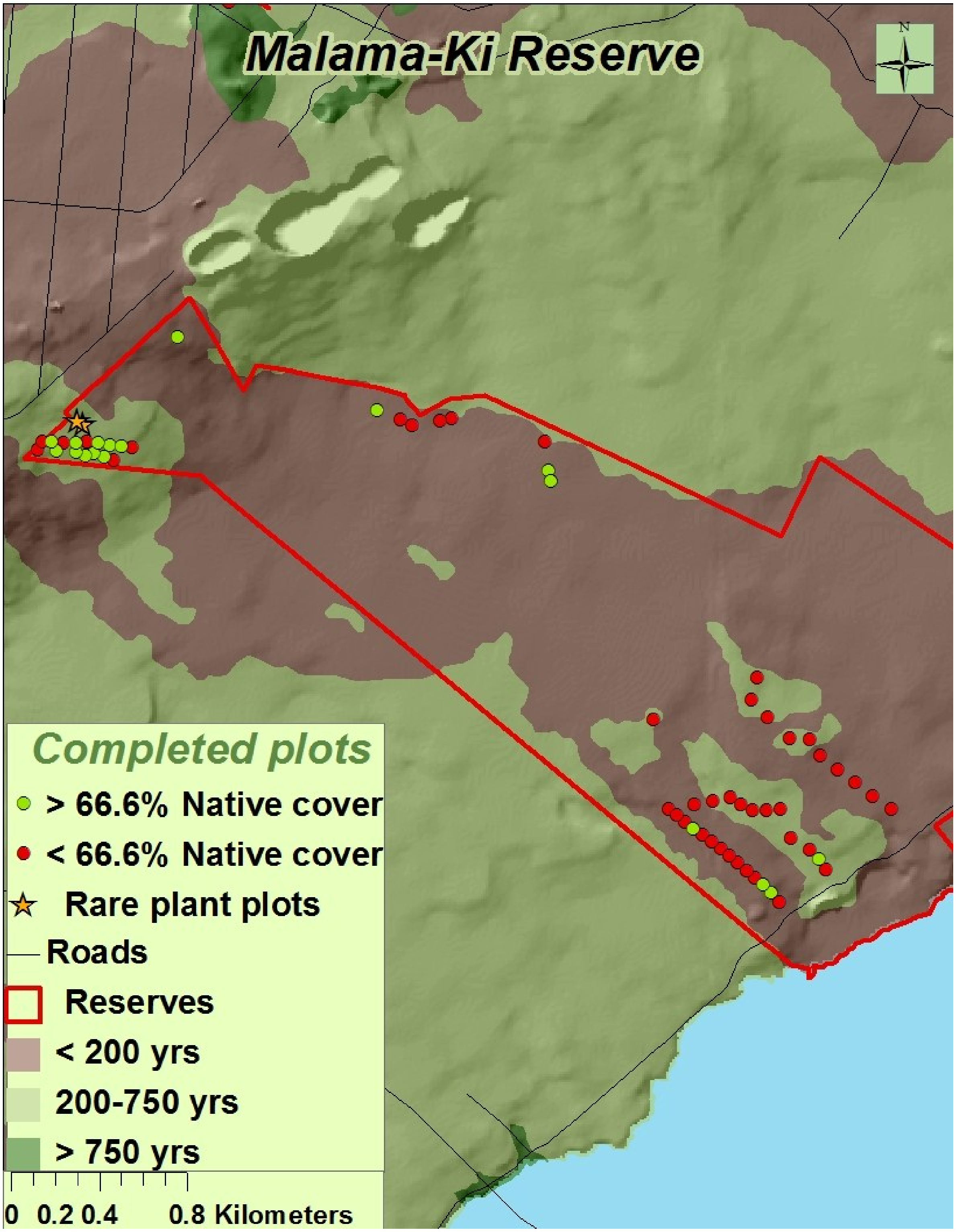

Fig. A6. Completed native-dominated plots, non-native-dominated plots and rare plant plots for Malama-Kī Reserve.

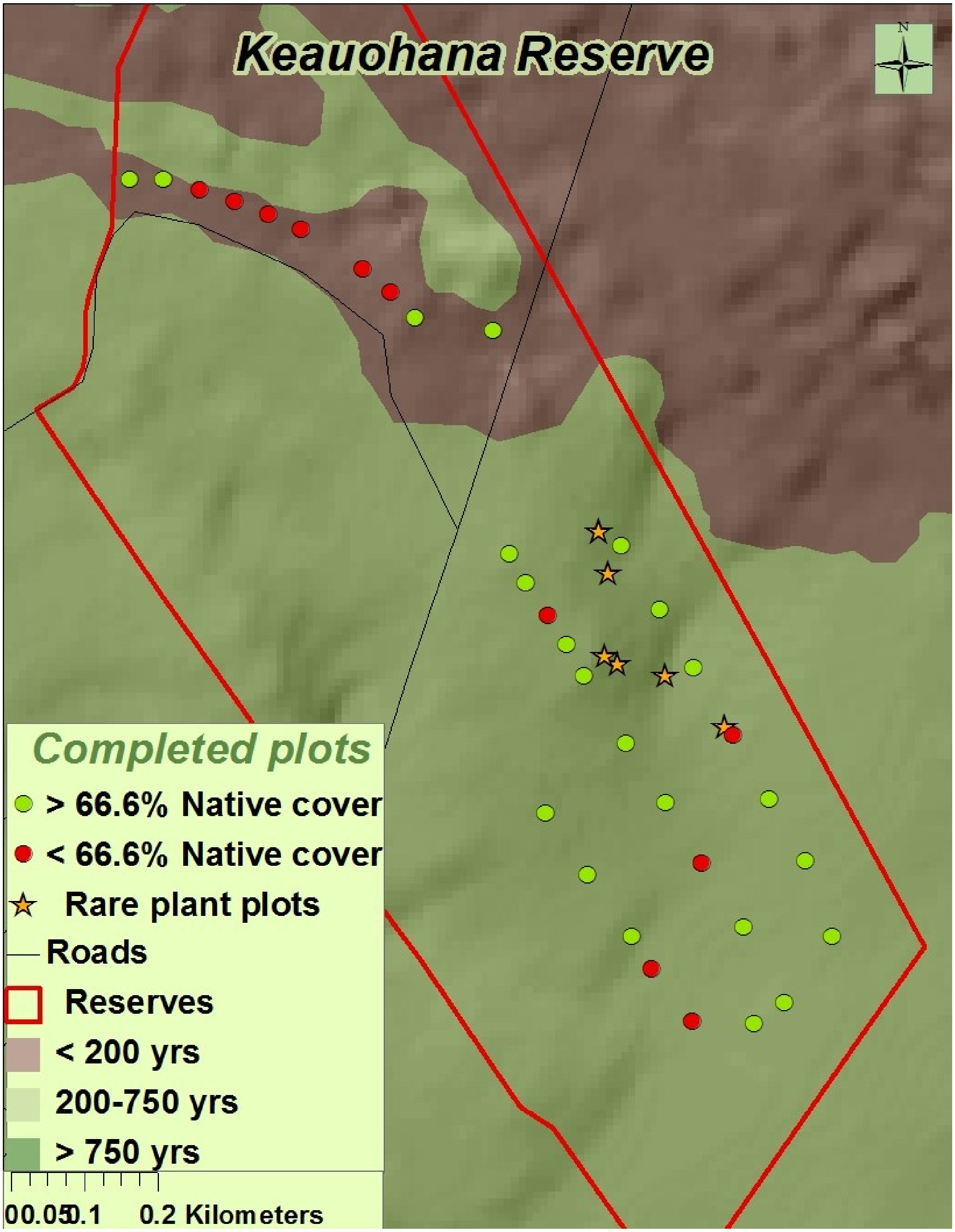

Fig. A7. Completed native-dominated plots, non-native-dominated plots and rare plant plots for Keauohana Reserve.

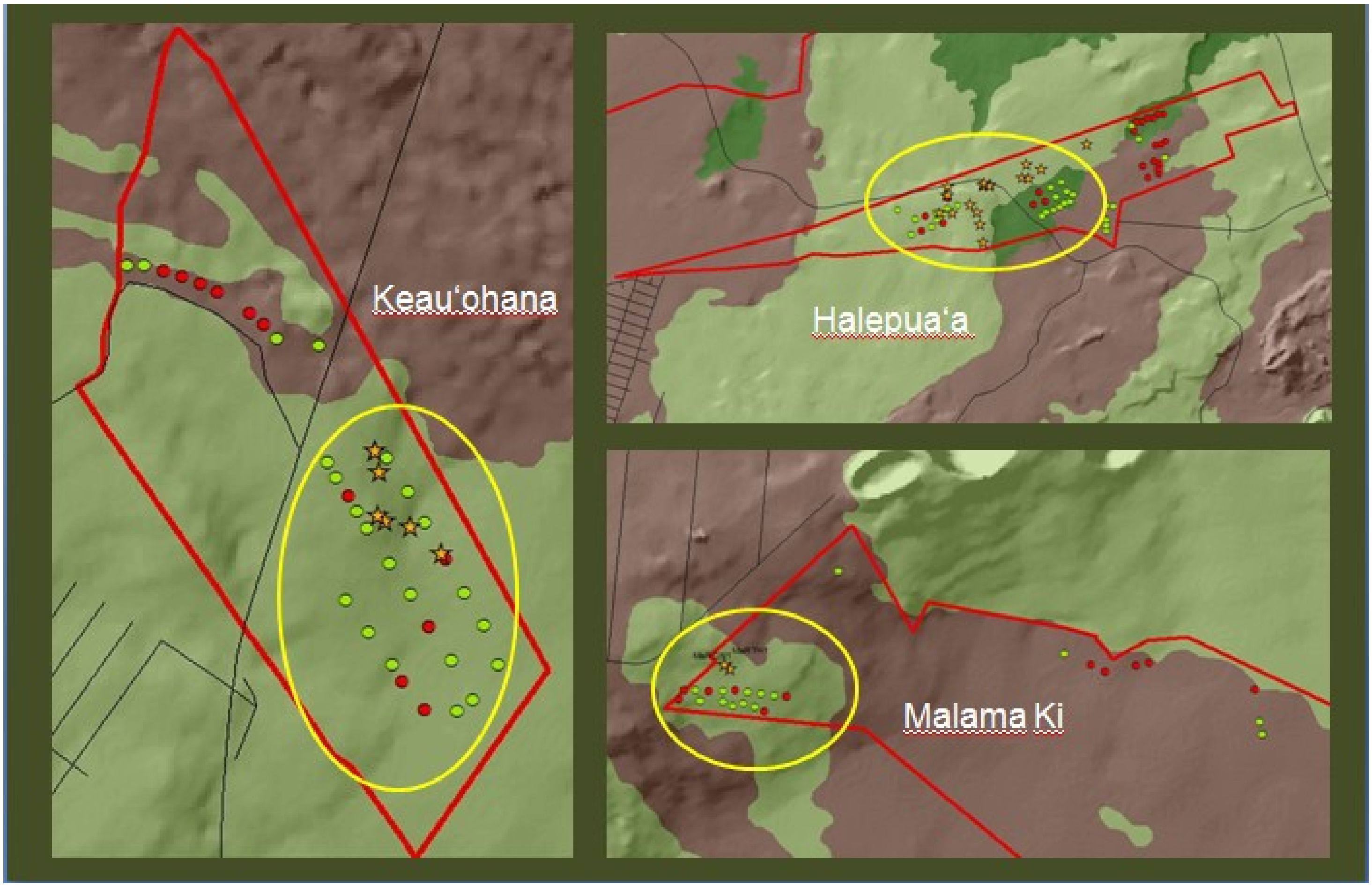

Fig. A8. Priority areas for restoration in LWF of East Hawai'i.

Brief Biography

Born in North Ontario, Canada, Cindy Jocelyne Dupuis, also known as Jaya, has been developing a self-sustainable farm on the big Island of Hawaii since 1989. She is dedicated to preserving native biodiversity in Hawai'i as a unique location with delicate endemic plant life. Jaya has been doing restoration work in lowland wet forests of the Puna District since 2006, both in the control of invasive species as well as native plant propagation. In her continued work she will be seeking for funding to help restore and manage priority areas identified in this study. She would like to support local as well as global community awareness and enthusiasm for native forest ecosystems and environmental balance.