INTERACTIVE INFLUENCES OF WILDFIRE AND NONNATIVE SPECIES ON PLANT COMMUNITY SUCCESSION IN HAWAII VOLCANOES NATIONAL PARK

by

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The role of fire as a natural disturbance, its interactions with nonnative species and effects of repeated fires in the Hawaiian Islands have received little investigation. We are unsure of the role fire played in shaping forest structure and composition as well as affecting evolutionary processes of the native biota. Yet, many species do have adaptations that facilitate their capacity to establish, grow, reproduce, and persist on either the individual or the population level when fire occurs. The objectives of this study were to document individual survival and colonization of native Hawaiian species after fire and to examine the potential interactions of nonnative species and fire. Specifically, I hypothesized that (1) many native Hawaiian species would survive and or colonize the postfire environment because they are adapted to a wide array of disturbance events, (2) the interaction of fire and nonnative species would alter native plant community succession because fire would facilitate nonnative species invasions, and the presence of nonnative species would limit native species recovery, and (3) the occurrence of a second fire within one year would result in a more impoverished native flora because sprouts from native surviving trees would be killed by the second fire.

To understand the role of fire in tropical forests of Hawaii and how forest species respond to fire, I established replicate plots (n=5) in burned and unburned areas in five vegetation communities along an elevation/community gradient in Hawaii Volcanoes National Park. At lower elevations the sampled plant communities were two shrub-dominated communities (*Dodonaea viscosa/ Andropogon virginicus* and *Dodonaea/ Nephrolepis multiflora*) and at higher elevations three forest communities (*Metrosideros polymorpha/ Nephrolepis multiflora*, *Metrosideros/ Dicranopteris linearis*, and *Metrosideros/ Cibotium glaucum)*. Fires in all community types were stand-replacing, where >95% of the dominant native woody species were top-killed. Results from this study indicate that many native Hawaiian species had the capacity to survive fire vegetatively and/or established from seed in the postfire environment. Nineteen native tree, shrub and tree fern species survived fire primarily by sprouting from the base. Many of these species also established from seeds or spores postfire. *Metrosideros*, in particular, both exhibited widespread survival (>50%) primarily via basal sprouting and established from seed postfire. In addition, the effects of fire differed across species, populations and vegetation communities along the elevation gradient.

Fire differentially affected the communities with greater differences in composition and structure observed in the three forest communities than the shrub-dominated communities. In the forested communities, fire dramatically altered structure from a closed-canopy *Metrosideros* forest to shrub, fern and herb dominated sites. Understory cover differed between unburned and burned forest sites with reduced cover in the *Nephrolepis* and *Dicranopteris* forests and greater cover in the *Cibotium* forest. In the previously native-dominated *Dicranopteris* and *Cibotium* forest communities,

nonnative species became increasingly abundant following fire suggesting that fire facilitated nonnative species invasion in these communities. The native fern *Dicranopteris linearis* was the most abundant understory species in the unburned sites, but nonnative ferns and vines dominated the understory in the burned sites postfire. Species richness, percent nonnative, and understory diversity were greater in the burned sites two years postfire than the unburned sites for each community. In contrast, in the *Nephrolepis* forest community the nonnative fern *Nephrolepis multiflora* dominated the understory (>50% cover) in both the unburned and burned sites.

Metrosideros survival and recovery, quantified as basal sprout height, elliptical crown area and volume, differed among forest communities. Measures of sprout vigor were greatest two years following fire in the native *Dicranopteris* forest, where understory recovery was slowest presumably due to the thick litter layer that remained following fire acting as a barrier to understory colonization. Postfire vegetation composition and cover of the understory in the *Nephrolepis* and *Cibotium* forests was due largely to vigorous *Nephrolepis multiflora* sprouting and *Paspalum conjugatum* grass invasion, respectively. In addition, *Cibotium glaucum* tree ferns in the subcanopy tier had very high survival rates (>85%) and constitute a large portion of cover in the *Cibotium* forest community. Lower *Metrosideros* sprout growth rates in the *Nephrolepis* and *Cibotium* forest communities suggest that the high survival of tree ferns (*Cibotium* forest) and the rapid establishment of a nonnative-dominated understory (*Nephrolepis* and *Cibotium* forests) may be limiting *Metrosideros* tree recovery during early postfire succession.

The occurrence of two fires in two years in some *Dicranopteris* and *Cibotium* forest communities dramatically increased mortality of *Metrosideros*. In the *Dicranopteris* community, 71% of *Metrosideros* trees survived a single fire, but only 22% survived repeated fires. Similarly in the *Cibotium* community, *Metrosideros* survival was reduced from 48% to 6% following repeated fires. Vegetative survival of the native tree fern *Cibotium glaucum* was also significantly reduced from 93% following a single fire to 56% following a second fire. *Metrosideros* seedling recruitment did not differ between forests that burned once and forests that burned twice. The composition of the understory in both of the sampled communities following repeated fires differed from that of forests that burned once and unburned control forests. Interestingly, the most abundant species in the understories following repeated fires were native sedges (*Cyperus polystachyos*) and shrubs (*Pipturus albidus*). However, these species are typically disturbance oriented short-lived species. Repeated fires resulted in lower *Metrosideros* survival, no significant increase in native tree seedling establishment, and rapid occupation native herbaceous and shrub species, all of which may delay, or even prevent, recovery to native forest dominance.

Fire in the shrub-dominated communities, which were already heavily invaded by nonnative species, had little effect on vegetation composition and structure. These communities were previously modified by past fires (1972 and 1992) and nonnative grass (*Andropogon virginicus*) and fern (*Nephrolepis multiflora*) invasions. Notably absent from these communities were young native tree species suggesting that native forest recovery was not occurring. These communities demonstrate how nonnative species

invasions coupled with repeated fires may alter successional trajectories such that native forest recovery is less likely.

Master of Science thesis of Alison Ainsworth presented on March 13, 2007.

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I understand that my thesis will become part of the permanent collection of Oregon State University Libraries. My signature below authorizes release of my thesis to any reader upon request.

Alison Ainsworth, Author

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INTERACTIVE INFLUENCES OF WILDFIRE AND NONNATIVE SPECIES ON PLANT COMMUNITY SUCCESSION IN HAWAII VOLCANOES NATIONAL PARK

CHAPTER 1. A REVIEW OF FIRE IN HAWAIIAN FORESTS

Alison Ainsworth

INTRODUCTION

Disturbance is defined in the context of a dynamic ecosystem by White and Pickett (1985) as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Examples of disturbance types in ecosystems include: fire, wind, lava flows, hurricanes, floods, and insect and disease outbreaks (White and Pickett 1985). Fire has been well documented to change ecosystem (including resource availability), community, and population structure by creating conditions that selectively favor certain species or creating opportunities for new species to invade (Agee 1993). In many regions of the world scientists have an understanding of fire behavior allowing them to predict the spread of individual fires by linking fuels, weather, and topographic information. However, the effect of fire on the landscape is not well understood or predictable because frequency, intensity, seasonality and extent all vary (Agee 1993).

To fully understand the effects of fire on forest ecosystems, we need to learn how to measure, predict, and interpret the biological and ecological responses to fire (Kauffman 1990). The composition and structure of forests following disturbances are dependent on the adaptations for survival of all species present as well as the capacity of species to invade and establish following disturbance. Species adaptations for survival and colonization are sensitive to both physical plant characteristics and environmental factors (Agee 1993). Species adaptations affect their capacity to establish, grow and reproduce. Traits insuring successful persistence may be characteristics of individuals or of species. Examples of characteristics that promote individual plant survival postfire

include: thick bark, protected buds from dense leaf bases, and basal and epicormic sprouting. Species that persist effectively after fire have these adaptations: seeds that are stimulated to germinate by fire, fire-stimulated flowering, seed storage on plants such as serotinous cones, and windborne seeds (Kauffman 1990). Because vegetation adaptations evolve with the natural processes of the systems in which the species occur, these adaptations are truly adaptations for survival only in certain fire regimes (Kauffman 1990).

Natural disturbances are a major source of heterogeneity in the structure and dynamics of natural communities (Sousa 1984). Ecological disturbances also promote nonnative species invasions (Hobbs and Huenneke 1992, D'Antonio and Dudley 1995). Further, the effects of nonnative species on fire characteristics and the subsequent responses by native species and communities are not well described (especially in the tropics or Hawaii). Species composition can influence both the magnitude (size and severity) of a disturbance and species recovery following disturbance. Concern over changing species composition with increasing biological invasions has grown during the past few decades to include concern on the global scale (Vitousek et al. 1996). Invasive species have demonstrated the capacity to dramatically alter plant community composition, ecosystem function, and succession (D'Antonio and Vitousek 1992). Many studies have demonstrated how species invasions have been promoted by disturbances and the subsequent influences that invasive species have on species present in the invaded ecosystems. However, Mack and D'Antonio (1998) suggested that there is now sufficient evidence to support the hypothesis that the greatest effect an invasive species or functional group can have on ecosystem structure and function is to alter the disturbance

regime thereby changing the successional trajectory. Among the mechanisms by which invaders alter disturbance regimes are to enhance or suppress fire, increase or decrease erosion, increase biotic disturbance, and change the susceptibility of a community to disturbance (Mack and D'Antonio 1998).

Variation in the frequency of disturbance such as a reduced fire-return interval may substantially influence species capacity to survive or persist postfire. Extremely short intervals between fires, particularly those with a single year return interval have reduced woody species densities significantly in temperate and tropical zones. Repeat burning has been shown to increase herbaceous species cover and decrease woody density in both southern pine systems (Cain et al. 1998, Beckage and Stout 2000) and California chaparral (Zedler et al. 1983); yet this phenomenon has not been investigated in tropical ecosystems.

The effect of disturbance such as fire on an individual plant is variable, but often predictable when the physical (age, vigor) and physiological adaptations of the species are known (Agee 1993). To understand how fire affects vegetation at the community and landscape scale the influence of environmental factors on species response to disturbance must be considered. Specifically, the influence of preburn community composition and frequency of fires on the vegetation response postfire has been studied extensively in some regions such as the western United States, but is not well documented in the tropics including Hawaii. Increasing nonnative species invasions, growing human population, increasing wildland-urban interface, and climate change contribute to today's altered fire regimes. It is likely the phenomenon of changing fire-return intervals will become increasingly important in the future.

FIRE EFFECTS IN HAWAII

The natural frequency of disturbances, specifically fires, in Hawaii is poorly understood. Natural fires are believed to have occurred before human settlement (Burney et al. 1995), but determining the historic role of fire is challenging because no annual rings form on the trees eliminating the potential to use fire scar chronologies. The presence of lightning, lava flows, continuous fuels in some ecosystems, and weather conditions that would facilitate fire suggest that fire was part of the disturbance history in Hawaiian island ecosystems. The frequency and severity of those fires would likely have varied by climate, plant composition, and ignition sources.

Anthropogenic fires have occurred since Polynesians arrived in the Hawaiian Islands 2,000 years ago (Kirch 1982) and are an increasing factor as nonnative flammable fuel loads grow, climate changes, and population increases. Historical accounts of Polynesian burning are documented for sections of the coastal lowlands (McEldowney 1979). Anthropogenic burning is believed to be responsible for the widespread deforestation of the coastal lowlands of Hawaii (Kirch 1982). Recent fire history (1924-present) is documented in Hawaii Volcanoes National Park demonstrating a dramatic increase in fire frequency and size in the late 1960s (Smith and Tunison 1992).

The ‘climate’ state factor, specifically temperature and precipitation, is the dominant control on ecosystem structure and function (Jenny 1980, Vitousek and Benning 1995). Temperature and precipitation vary on a fine scale on the island of Hawaii encompassing twenty-six Holdridge life zones (Tosi et al. 2001). Steep climatic gradients are not unique to Hawaii, but are of interest because they often vary

dramatically while other state factors (i.e. substrate) remain relatively constant (Vitousek and Benning 1995). Many woody plants are found across a wide range of habitats in Hawaii (Wagner et al. 1999) thereby controlling for the 'organism' state factor (Vitousek and Benning 1995). Limited colonization due to the island's extreme isolation resulted in low species richness of native flora (Carlquist 1980). This allowed for the 'ecological release' or evolutionary radiation of species across a broad range of ecosystems (Kitayama and Mueller-Dombois 1995, Vitousek and Benning 1995). For example, *Metrosideros polymorpha* a dominant tree in Hawaii, has a wide range of genetic variability (Burton and Mueller-Dombois 1984) and is found across a gradient of substrate age, elevation (0 – 3000 m), and precipitation (<400 mm to >10,000 mm annual rainfall) (Dawson and Stemmerman 1990). A number of shrubs (*Dodonaea viscosa*, *Leptecophylla tameiameiae*, and *Osteomeles anthyllidifolia*) are also found across a wide range of habitats (Wagner et al. 1999). In Hawaii, topography and parent material often lack in variation across the landscape and time or age of substrate are well documented (Vitousek and Benning 1995). Because many state factors can be controlled for, the effects of community caused variation in species response to fire and nonnative species invasion can be studied in relative isolation.

Species adaptations that promote individual survival postfire such as basal and epicormic sprouting (Kauffman 1990) have been documented to exist for some native Hawaiian species including *Metrosideros polymorpha* (Parman and Wampler 1977, Hughes et al. 1991, Tunison et al. 1995, D'Antonio et al. 2000), *Acacia koa* (Tunison et al. 2001) and tree ferns *Cibotium glaucum* and *Sadleria cyathoides* (Vogl 1969, Smith and Tunison 1992). However, little information exists on the percent of those species

that survived fire, the importance of age or size class and if and how survival differ among forest community types.

Wind dispersal and the capacity to establish on bare soil is an adaptation facilitating invasion and establishment postfire (Kauffman 1990) and is also an important characteristic for many native Hawaiian species that can successfully colonize recent lava flows (Mueller-Dombois 1987, Hughes and Vitousek 1993).

Fire severities or the ecological effects of fire on native plant species in Hawaii likely vary across ecosystems, but there has been little quantification of this even though we can control for substrate variables across environmental gradients. The few fire effects studies conducted during the past forty years in Hawaii include many ecosystems: coastal lowlands, seasonally dry woodlands, rainforest, and montane shrubland in Hawaii Volcanoes National Park (Tunison et al. 2001) and tropical montane grassland and shrubland of the Pohakuloa Training Area on the Island of Hawaii (Shaw 1995). D'Antonio et al. (2000) found climate the dominant variable influencing species composition between ecosystems and species response to fire in Hawaii Volcanoes National Park. Variation in native species cover among 14 burned sites in nonnative grasses (*Andropogon virginicus*, *Schizachyrium condensatum*, and *Melinis minutiflora*) and between burned and unburned sites in the seasonally dry woodland and eastern coastal lowlands of Hawaii Volcanoes National Park was best explained by climatic zone when considering fire intensity, time since fire, unburned grass cover, unburned native cover, and identity of the most abundant nonnative grass (D'Antonio et al. 2000).

Two studies in Hawaii examined the species composition along environmental gradients and found nonnative species present where disturbance had facilitated invasion

(Kitayama and Mueller-Dombois 1995, Aplet et al. 1998). Among species currently of greatest concern are nonnative grasses because they are competing with native species for resources, physically excluding species, and altering disturbance regimes. Invasive grass removal experiments in the seasonally dry woodlands of Hawaii Volcanoes National Park show how some nonnative grass species are competing with native species by utilizing resources otherwise used by native woody species. Three years after fire, Hughes and Vitousek (1993) found that nonnative grasses were successfully competing for light with native shrub seedlings. Following grass removal, *Metrosideros* and native shrub species demonstrated a strong growth response and an increase in seedling recruitment (D'Antonio et al. 1998, Mack and D'Antonio 2003a). Even in the absence of fire, nonnative grasses in this community have been shown to reduce growth and recruitment of native species (Hughes and Vitousek 1993, D'Antonio et al. 1998). The lack of germination and establishment of woody species in the presence of invasive nonnative grasses has been attributed to the grasses extensive above ground biomass acting to thwart establishment (D'Antonio and Vitousek 1992, Cabin et al. 2000). Nonnative grass invasions in the seasonally dry woodland of Hawaii serve as an example of invaders that have been shown to alter biomass, fuel composition, structure, moisture, and chemistry thereby facilitating an increase in the frequency, severity, and intensity of fire in seasonally dry woodlands and lowlands (D'Antonio and Vitousek 1992).

RELEVANCE OF RESEARCH IN HAWAII

Hawaii is an ideal place to examine species response to disturbances such as how fire varies with environmental factors because of the steep climatic gradients, the influence of biological invaders, and the recent occurrence of successive fires. This research was initiated to examine the ecological responses of individual species and plant communities to single and repeated wildfires across an elevation/community gradient in Hawaii Volcanoes National Park. Specifically, my objectives were to document individual survival and colonization of native Hawaiian species and to examine the potential for nonnative species and fire interactions to result in a type conversion from native-dominated mesic and wet forests to nonnative-dominated shrublands. I hypothesized that (1) many native Hawaiian species would survive and or colonize the postfire environment because they are adapted to a wide array of disturbance events, (2) the interaction of fire and nonnative species would alter native plant community succession because fire would facilitate species invasions, and the presence of nonnative species would limit native species recovery, and (3) the occurrence of a second fire within one year would result in a more impoverished native flora because sprouts from native surviving trees would be killed by the second fire.

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CHAPTER 2. NATIVE HAWAIIAN WOODY SPECIES RESPONSE TO LAVA-IGNITED WILDFIRES AT HAWAII VOLCANOES NATIONAL PARK

Alison Ainsworth

ABSTRACT

The historic role of fire as a natural disturbance in the Hawaiian Islands has received little investigation and fire effects in the absence of invasive species will never be known. It remains unclear what role fire played in shaping forest structure and composition as well as affecting evolutionary processes of the native biota. It is clear that species have adaptations that facilitate their capacity to establish, grow, reproduce, and persist on either the individual or the species (population) level. To understand the role of fire in tropical forests of Hawaii and how forest species respond to fire, I examined the survival and establishment of native Hawaiian woody species and tree ferns following the 2003 Panauiki and Luhi wildfires which were large naturally-ignited wildland fires that burned across a broad elevation gradient in Hawaii Volcanoes National Park on the Island of Hawaii. I established plots (n=5) in burned and unburned sites for five separate plant community types including two shrub-dominated communities (*Dodonaea viscosa/ Andropogon virginicus* and *Dodonaea/ Nephrolepis multiflora*) and three forest communities (*Metrosideros polymorpha*/ *Nephrolepis*, *Metrosideros/ Dicranopteris linearis*, and *Metrosideros/ Cibotium glaucum)*. Fires in all community types were stand-replacing, where >95% of the dominant native woody species were top-killed.

The native Hawaiian species measured in this study displayed a capacity to survive fire and/or establish from seed following fire. However, the effects of fire differed across species, populations and vegetation communities. Despite the near complete top-kill of the dominant canopy tree *Metrosideros polymorpha*, more than half of the individuals of this species survived fire via basal sprouting. *Metrosideros*

individuals with larger diameters (>20cm diameter at breast height) sprouted in lower percentages than smaller trees. Nineteen native tree, shrub and tree fern species demonstrated the capacity to survive fire vegetatively.

In addition to basal sprouting, many native woody species were successful colonizers in the postfire environment, establishing from seed either contained in the soil seed bank or dispersing onto the site from surrounding unburned areas. This was not surprising considering that most of these species are also the primary colonizers of recent lava flows. Fire appeared to particularly promote seedling establishment of *Dodonaea viscosa*, which was the dominant species in the shrubland communities. The effect of fire on *Metrosideros* seedling recruitment differed among forest communities in that seedling density was greater in the burned sites than unburned sites for the *Nephrolepis* and *Dicranopteris* forests, but the opposite pattern was observed in the *Cibotium* forest community. For all other species in all communities, seedling density either did not change following fire or was significantly higher in the unburned sites.

The widespread persistence and establishment of native Hawaiian species following wildfire demonstrates the adaptations of these plant species to survive fire. It is unclear whether these are evolutionary adaptations to fire or causal adaptations of traits derived in response to other disturbances common in the region (volcanism, landslides, hurricanes, etc.). These adaptations may not be sufficient to insure dominance of native species in the future as the presence of invasive plant and ungulate species will likely dramatically alter postfire succession and dominance in these ecosystems.

INTRODUCTION

Little information exists regarding the historic role of natural fire in the evolution and development of Hawaiian terrestrial ecosystems (LaRosa In press). Determining the historic frequency and extent of fire in the tropics is challenging due to the lack of annual rings, which eliminates the use of traditional dendrochronological methods for determining fire history. A handful of studies that examined pollen data from sediment cores collected in bogs and radiocarbon data from charcoal studies indicate that wildfires occurred in Hawaii prior to European settlement (Mueller-Dombois 1981a, Smith and Tunison 1992, Burney et al. 1995). The occurrence of natural ignition sources including lightning and volcanism (Vogl 1969, Tunison and Leialoha 1988), continuous vegetation cover in many ecosystems (Wagner et al. 1999), and periodic weather conditions that would facilitate fire, further suggest that fire did occur historically and did influence the disturbance history of Hawaiian ecosystems. As is true everywhere the frequency and severity of fires, however, would likely have varied depending on climate, fuel loads and ignition sources.

The response of native woody species to wildland fire provides insights into fire patterns of ecosystems because vegetation adaptations evolve within the context of the natural disturbance regimes of the ecosystems (Kauffman 1990). Species adaptations in ecosystems are linked to their ability to survive, or establish, grow and reproduce in the disturbance regime of their habitat (i.e, type of disturbance, frequency of disturbance and the severity and size of the disturbance)(White and Pickett 1985). Examples of traits that promote survival of individuals during and immediately following fire include: thick

bark, protected buds from dense leaf bases, and basal (subterranean) and epicormic sprouting. Adaptations that facilitate establishment of species or populations, but not the individual following fire include: fire-stimulated germination or flowering, seed storage on plants (e.g., serotinous cones), and wind-borne seeds (Kauffman 1990).

Few studies have examined the effects of fire on native Hawaiian vegetation and the majority of those were in the seasonally dry *Metrosideros* woodlands of Hawaii Volcanoes National Park (Hughes et al. 1991, Hughes and Vitousek 1993, Freifelder et al. 1998, Ley and D'Antonio 1998, D'Antonio et al. 2000, D'Antonio et al. 2001, Mack et al. 2001). Some authors have proposed that the primary disturbance adaptations of native vegetation in Hawaii are in response to weather events and volcanism, and not fire, because fires likely occurred at very long intervals and with limited extent in many Hawaiian ecosystems. They suggest that wildfire has less of an effect on the evolution of much of the Hawaiian flora than other disturbances (Mueller-Dombois 1981a, Smith and Tunison 1992, Mueller-Dombois 2001). Alternatively, Vogl (1969) suggested that the capacity of the dominant wet forest tree ferns to withstand disturbance may be an evolutionary adaptation to fire.

Many Hawaiian species do possess characteristics frequently associated with long fire-return intervals (e.g., thin bark, buried seeds requiring heat or other disturbance to germinate). The few studies that have been conducted examining species response to fire clearly demonstrate that some native plants have the capacity to persist and recover following fire. For example, basal and epicormic sprouting has been documented for *Metrosideros polymorpha,* a dominant tree species of many of the Hawaiian ecosystems, allowing it to survive fire despite very high percentages of top-kill (Parman and Wampler

1977, Hughes et al. 1991, Tunison et al. 1995, D'Antonio et al. 2000). Another dominant native tree, *Acacia koa* has the capacity to sprout following disturbance from dormant buds on roots, with root sprouts reaching the forest canopy within ten years following wildfire (Tunison et al. 2001). In addition this species produces refractory seeds capable of surviving in the soils for decades until fire or other disturbance stimulates germination. The tree ferns *Cibotium glaucum* and *Sadleria cyathoides* lose current fronds following fire, but most survive and rapidly produce new leaves, presumably because the meristematic tissues are protected by frond scales (Smith and Tunison 1992).

Wind dispersal and capacity to establish on bare substrate is a common adaptation that facilitates invasion and establishment following fire (Kauffman 1990). In Hawaii, this is also an important characteristic for many natives that are adapted to successfully colonize recent lava flows (Burton and Mueller-Dombois 1984). *Metrosideros* has long ranging and abundant wind-dispersed seeds (Drake 1992, Hatfield et al. 1996). Prior seedling recruitment has been observed following wildfire in *Metrosideros* dominated wet forests (Tunison et al. 2001). In addition, the seeds of a dominant native shrub species in Hawaiian ecosystems, *Dodonaea viscosa,* were found to break dormancy following exposure to heat (Hodgkinson and Oxley 1990) and have also been found to germinate readily after fire (Hughes et al. 1991, Shaw et al. 1997, D'Antonio et al. 2000).

The capacity to persist following fire is also influenced by environmental conditions before and during the fire which would affect both fire intensity and severity (Kauffman 1990). Weather conditions largely affect fire frequency, size, and behavior (i.e the fire regime of an ecosystem) and species are largely adapted to the fire regime in

which they evolved (Agee 1993). Human alterations of environmental conditions such as fire frequency or intensity or the introduction of nonnative species which affects fuel dynamics may dramatically alter a species response to fire in its environment.

Native Hawaiian woody species response to fire is poorly understood particularly in mesic and wet forest communities. An increased understanding of the ecological response of native species to fire across an elevation/community gradient is needed. I hypothesized that many native Hawaiian species would either survive fire or establish from seed because species in Hawaiian landscapes have been subjected to an array of disturbance events (fires, volcanism, tropical storms, etc). In this study, I measured the response of native Hawaiian woody species and tree ferns for the first two years following lava-ignited wildfires (Kupukupu, Luhi, and Panauiki fires of 2002 and 2003) in five community types across an elevation/environment gradient in Hawaii Volcanoes National Park. The specific objectives of this study were to: (1) examine the survival rates of native Hawaiian trees, tree ferns, and shrubs according to species and size classes following fire; and (2) quantify native woody seedling establishment across this gradient for the first two years following fire. Information from this study should provide insights regarding historic fire regimes in this area and native species response to fire, and will assist managers in evaluating the potential threat of fire to native forest recovery in these unique communities.

METHODS

Study Site

This study was conducted in shrub and forest-dominated communities along an elevation gradient in Hawaii Volcanoes National Park on the Island of Hawaii (Fig. 2.1). Elevation ranged from 350m in the shrub-dominated communities to 825m in wet forest communities; all communities occurred within 5 km of each other. The study area was located on a steep precipitation gradient from dry shrublands to wet forest and encompassed four distinct Holdridge life zones: subtropical basal moist forest, subtropical basal wet forest, subtropical lower mountain moist forest and a subtropical lower mountain wet forest (Tosi et al. 2001).

The study area is located within a 6 km wide band of vegetation between the Mauna Ulu lava flows (1969-1974) and the Puu Oo lava flows (1983-present). Substrate across the gradient consists of relatively young (400 to 750 yr-old) pahoehoe lava flows (smooth ropy texture) with minimal topographic relief (Trusdell et al. 2005). Two basic soil types are present: the Kalapana series and the Makaopuhi series. The Kalapana series are very shallow to shallow (5-50 cm) well drained soils formed in ash deposited over pahoehoe lava with 2-10% slopes, and are classified as Medial, ferrihydritic, isothermic, Lithic Udivitrands. The Makaopuhi series are very shallow to shallow (5-30cm) somewhat poorly drained soils that formed in volcanic ash deposited over pahoehoe lava with 2-10% slopes, and are classified as Medial, ferrihydritic, isothermic, Lithic Hapludands. The shrub-dominated communities are on the Kalapana dry phase

soils, the mesic forest communities are on Kalapana medial course sandy loam and the wet forest community is on Makaopuhi very paragravelly muck (Jasper In press).

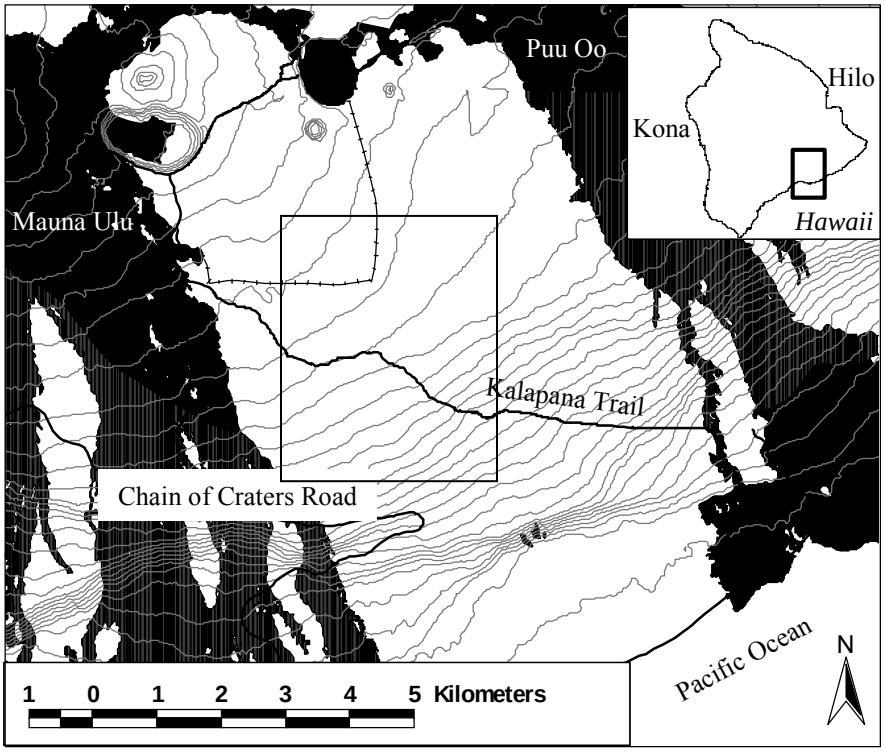


Figure 2.1. Map of the Island of Hawaii depicting the study area between the Mauna Ulu and Puu Oo lava flows above the Chain of Craters Road in Hawaii Volcanoes National Park.

Metrosideros polymorpha is the dominant forest tree across the elevation gradient, but ranges in percent canopy cover from <1 % in the shrublands to >60 % in the mesic forests. The study area contained five major plant communities. The *Dodonaea viscosa/ Andropogon virginicus* community (350-450 m) was dominated by native *Dodonaea* in the shrub layer (~9000 individuals/ha) with the nonnative perennial bunch grass *Andropogon* dominating the understory. A few trees (*Metrosideros*) were scattered across the landscape, but were primarily restricted to lava uplifts where recent past fires did not carry to kill them. This community is located within the mapped boundaries of

past wildfires that occurred in 1972 and 1992 and will be referred to hereafter as the "*Andropogon* shrubland." The *Dodonaea/ Nephrolepis multiflora* shrub-dominated community (450-550 m) is also dominated by *Dodonaea* in the shrub tier (~8500 individuals/ha) with the nonnative fern *Nephrolepis multiflora* dominating the understory. Similar to the *Andropogon* shrubland, remnant *Metrosideros* trees are scattered throughout this community. Burned sites for this community type are located within the 1972 and 1992 wildfire boundaries, and the unburned control sites were within the 1972 wildfire boundary, but not the mapped 1992 boundary (National Park Service 2003). This community will be referred to as the "*Nephrolepis* shrubland." While the tree component of these two communities is now sparse due to the recent fires, historic photos indicate that the area was characterized as relatively open *Metrosideros* woodlands with scattered shrubs and a mixed understory prior to the 1972 wildfire (Hawaii Department of Land and Natural Resources 1966).

The study includes three forest communities that range from mesic to wet. The *Metrosideros*/ *Nephrolepis multiflora* forest community (550-640m) is dominated by *Metrosideros* in the overstory (~700 individuals/ha) and the nonnative fern *Nephrolepis multiflora* in the understory. This community will be referred to as the "*Nephrolepis* forest." The *Metrosideros*/ *Dicranopteris linearis* forest community (640-750m) contains *Metrosideros* in the overstory (~850 individuals/ha) and the native, mat forming fern *Dicranopteris* in the understory. This community will be referred to as the "*Dicranopteris* forest." The *Metrosideros*/ *Cibotium glaucum* forest community (700-850m) has an open canopy overstory of *Metrosideros* (~500individuals/ha) with a native tree fern *Cibotium glaucum* midstory (~2800/ ha) and the native fern *Dicranopteris* and

nonnative grasses in the understory. This community will be referred to as the "*Cibotium* forest."

Lava has been the main ignition source in this area of the Park from 1916 to present (Gassaway et al. 2002). Multiple fires have occurred in the coastal lowlands in the last thirty years and two have burned the areas dominated by the lowland *Andropogon* shrubland and *Nephrolepis* shrubland communities, one in 1972 and once in 1992. Both fires did not spread (>200m) into the *Metrosideros* mesic forest communities (Timothy Tunison, pers. comm.). In May, 2002, the Mother's Day lava flow erupted and on 17 May 2002, the Kupukupu Fire burned 345 ha of wet forest; an additional 1,020 ha of mesic forest and shrub-dominated communities had burned by June, 2002.

The Panauiki Fire (January, 2003) burned 860 ha of *Andropogon and Nephrolepis* shrublands between 60 and 670 m. In May 2003, the Luhi fire burned 2,000 ha across the study area (National Park Service 2003). I established replicate plots (n=5) in each of the five vegetation communities in areas burned in the 2003 Panauiki (shrub-dominated communities) and Luhi (forest communities) wildfires and unburned controls to measure tree and tree fern individual survival and quantify seedling density.

Field Methods

In burned areas for each of the sampled communities, I established five replicate, randomly located 20 x 50m permanent plots and measured the vegetation response one (2004) and two (2005) years following fire. Sample locations were selected based on composition and structure, elevation, fire history and proximity to unburned sites.

Locations were rejected if archeological features such as rock outcrops and walls were observed (in compliance with National Park policy).

Unburned plots were sampled once – two years (2005) following fire except the *Nephrolepis* forest community which was sampled one year (2004) following fire. Unburned plot selection was confounded by two factors: (1) the burns constituted a significant proportion of the total area and; (2) uncertainty as to why the unburned sites did not burn. I selected five replicate reference or unburned plots in each community type based on comparable elevation, and a vegetation composition and structure similar to what I assumed existed in the burned plots before fire. In spite of the difficulties in locating unburned replicates, I am confident they represent conditions similar to those that existed in the burned areas prior to the wildfire based on community structure. Flowering plant nomenclature followed that of Wagner et al. (1999) and tree fern nomenclature followed that of Palmer (2003). Family and complete names for all species encountered can be found in Appendix A.

I sampled trees, tree ferns, shrubs, and woody seedlings using a nested plot design (Fig. 2.2). Shrub species density was measured in six 1 x 5m subplots nested within the 20 x 50m plot. Individuals in the burned plots were recorded as resprouts if the live portion was attached to an older burned stem or base. Surviving individual shrubs were recorded as mature if they demonstrated any sign of reproduction and/or were greater than 50cm in length. Tree seedlings were defined as individuals less than 1.4m tall, and tree fern juveniles (those with fronds <50cm long) were also measured in six 1 x 5m subplots. Trees <10 cm diameter at breast height (dbh; 1.4m in height) and tree ferns <10 cm in diameter at the point below past years frond shed were measured in six nested

subplots (2 x 10m). Trees >10 cm dbh and tree ferns with trunk diameters >10 cm below the past years frond shed were measured in the 20 x 50m plot. Species with individuals that reached reproductive maturity within the first two years following fire were noted.

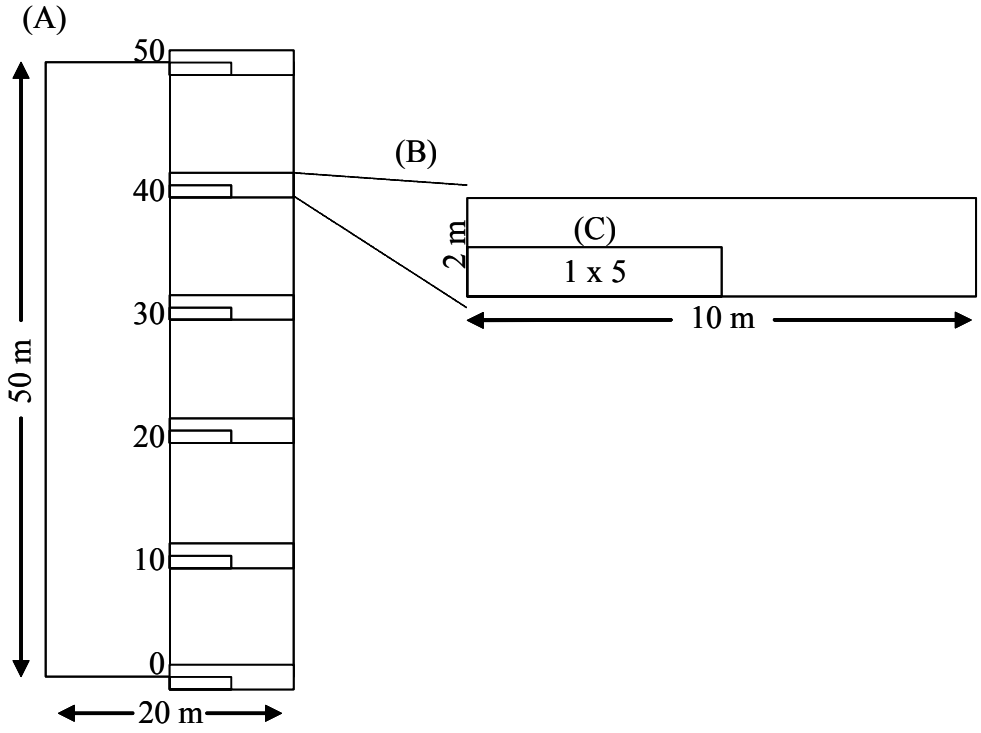


Figure 2.2. Plot layout used to quantify native woody and tree fern species survival and recruitment in burned and unburned sites. (A) All large trees and tree ferns >10cm in diameter were measured in the 20 x 50m plot. (B) Trees and tree ferns <10cm in diameter were measured in six 2 x 10m subplots perpendicular to the center transect at 10m intervals. (C) All trees seedlings (<1.4m in height) and shrubs were measured in six 1 x 5m subplots nested within the 2 x 10m subplots. These data yield composition, density, and tree and shrub survival.

Quantitative measures recorded for all trees in each 20 x 50m plot included: diameter (dbh), crown mortality, plant mortality, and mode of sprouting (basal if it originated from subterranean plant organs at the base of trees <50 cm above ground and epicormic if it originated from dormant meristematic tissue in the bole or mainstems)

(Kauffman 1990). From these data, percent crown mortality and individual plant death were calculated for all trees by species, and by size class for the dominant canopy (*Metrosideros*) and subcanopy (*Cibotium*) species.

Analysis

Native Hawaiian woody species and tree ferns were grouped according to Rowe's classification system. Rowe (1981) developed a broad classification system of plant response to disturbance that incorporates both life history traits of species and characteristics of fire regime. The five categories include: invaders (high dispersal ability), evaders (long lived propagules stored in the soil), avoiders (shade tolerant and slow invaders following fire), resisters (thick bark or an anomalous arrangement of mertistematic tissues that facilitates fire survival), and endurers (ability to sprout) (Rowe 1981). Species often have multiple or changing adaptations and therefore can fit into more than one category. This universal life-form classification is a useful way to examine species response to fire on a per site basis because categories incorporate the influence of environmental factors (Agee 1993).

All statistical analyses were conducted using S+ version 7.0 (Insightful 2005). The sampling unit used in analysis for all parameters was the 20 x 50m plot; therefore for each analysis each treatment had five replicates. Average values were calculated per plot and used in analysis for vegetation parameters that were sampled in subplots (e.g., understory cover, seedlings, small trees and tree ferns). *Metrosideros* percentage survival and population structure were analyzed as two factor ANOVA's with tree diameter size class, community, and size class x community as fixed effects. Differences among

treatments were compared using Tukey's multiple comparison tests. Tree count data used to examine population structure were log base 10 transformed (log +1) to equalize variance. ANOVA and *t*-test analyses were performed at an $\alpha = 0.10$.

Differences in *Cibotium* survival among size classes were compared using nonparametric tests (Kruskal-Wallis Rank Test and Wilcoxon Rank Test for pair-wise comparisons) because the assumptions of ANOVA were not met due to large differences in variance among treatments. Nonparametric tests were also used to detect differences in native species seedling density between treatments and years (unburned vs. one year postfire, and unburned vs. two year postfire) for each community.

RESULTS

Sprouting Response

The wildland fires in this landscape were stand-replacing where over 95% of the overstory *Metrosideros* trees were top-killed. There were very few unburned islands within the fire perimeter. Despite the near complete crown mortality, many native Hawaiian species survived fire across the elevation gradient via vegetative sprouting. Nineteen tree, shrub and tree fern species were observed to have survived fire primarily through basal spouting (Table 2.1). In addition to sprouting from the base or root crown, scattered individuals of three woody species, *Dodonaea*, *Metrosideros,* and *Santalum paniculatum*, also displayed epicormic sprouting. All tree fern and shrub species that survived fire vegetatively had individuals that reached reproductive maturity within the

first two years following fire (Table 2.1). Two tree species *Hedyotis terminalis* and *Santalum* were also observed to be fruiting during the second postfire year.

Table 2.1. Native woody species and tree ferns that survived fire and/or established from seed in the postfire environment. Mode of survival was recorded as vegetative for tree ferns and basal or epicormic sprouting for tree and shrub species. Asterisks denote species with individuals that reached reproductive maturity within two years postfire.

Species	Life Form	Individual Survival			Postfire
		Vegetative	Basal	Epicormic	Seedlings
Broussaisia arguta	Shrub		X		
Cheirodendron trigynum	Tree				X
Cibotium glaucum	Tree fern	X*			X
Cibotium menziesii	Tree fern	X*			
Clermontia hawaiiensis	Shrub				X
Coprosma menziesii	Shrub		X*		X
Dodonaea viscosa	Shrub		X*	X*	X*
Hedyotis terminalis	Tree		X*		X
Ilex anomala	Tree		X		X
Leptecophylla tameiameiae	Shrub		X*		X
Lythrum maritimum	Shrub				X
Melicope clusiifolia	Tree		X		X
Melicope radiata	Tree				X
Metrosideros polymorpha	Tree		X	X	X
Myrsine lessertiana	Tree		X		
Myrsine sandwicensis	Tree		X		
Osteomeles anthyllidifolia	Shrub		X*		
Pipturus albidus	Shrub				X*
Psychotria hawaiiensis	Tree		X		
Sadleria cyatheoides	Tree fern	X*			X
Santalum paniculatum	Tree		X*	X*	
Scaevola chamissoniana	Shrub		X*		
Sida fallax	Shrub				X*
Vaccinium calycinum	Shrub		X*		X
Vaccinium reticulatum	Shrub		X*		X
Total		3	16	3	17

More than half (57%) of the 911 *Metrosideros* trees sampled in the burned communities survived fire through basal sprouting (Fig. 2.3). Survival significantly

differed among diameter classes, where trees with larger diameters (>20cm) were less likely to sprout following fire than those with smaller diameters ($P = 0.05$; Fig. 2.4). The influence of plant size on survival was most pronounced in the *Dicranopteris* forest community, where >70% of the smaller trees (<10cm and 10-20cm) and only 38% of the larger trees (>20cm) survived fire ($P = 0.02$).

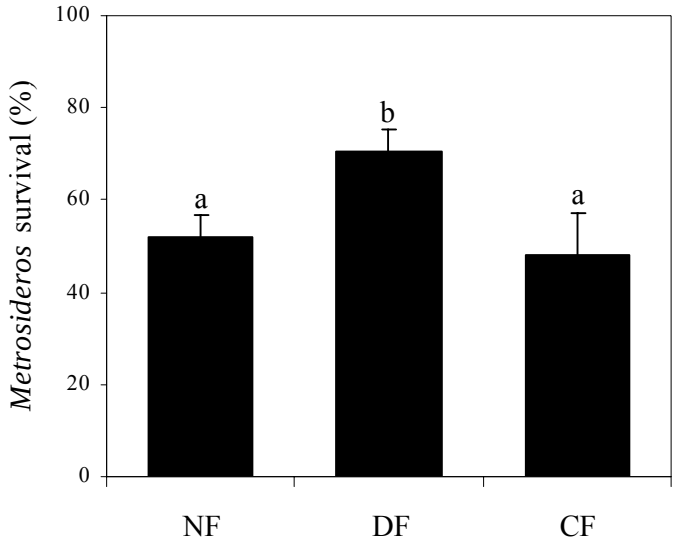


Figure 2.3. *Metrosideros polymorpha* survival differed among three forest communities ($P = 0.07$), with the highest survival in the *Dicranopteris* forest (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest). Data are means +1 SE. Letters indicate significant differences. A total of 911 trees were measured.

Cibotium tree fern survival was >86% following fire (1195 tree ferns sampled). Tree fern size affected rates of survival (Fig. 2.5). Survival was lower (42%) in the smaller size class (<10cm diameter) than the larger classes (10-20cm and >20cm diameter) where over 90% of the individuals possessed live fronds one year postfire ($P < 0.01$). Although there was a difference ($P < 0.10$) in survival between the two larger diameter classes, this difference is probably not ecologically meaningful considering that survival was extremely high (>90%) in both classes (Fig. 2.5). For *Cibotium* individuals

>10cm in diameter, no difference in survival was detected among trunk length classes (<1m, 1-2m, >2m; $P = 0.38$).

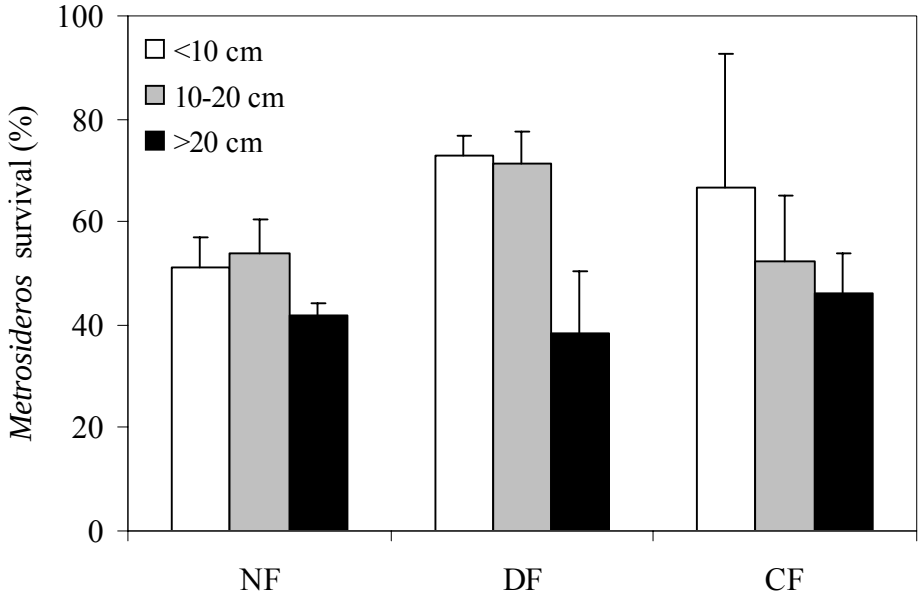


Figure 2.4. *Metrosideros polymorpha* survival differed by diameter size class across the three forest communities ($P = 0.04$), with the greatest mortality in the largest size class (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest). No differences in survival among communities were detected when controlling for size class ($P = 0.36$). Data are means +1 SE.

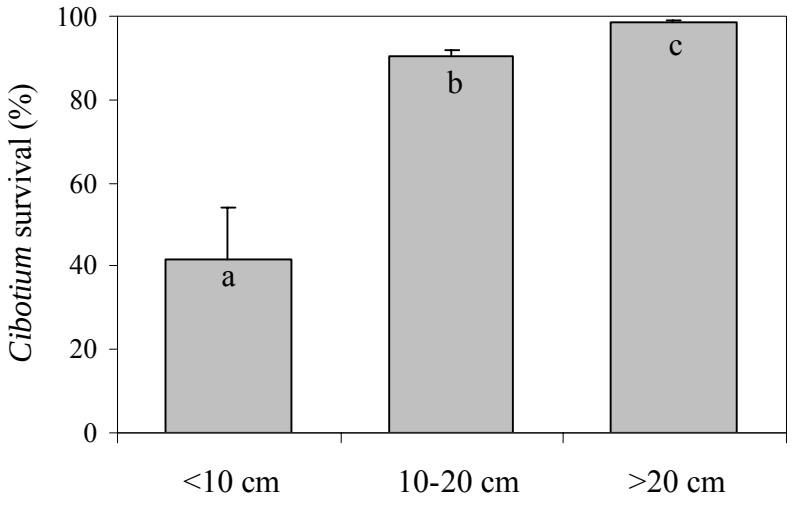


Figure 2.5. *Cibotium glaucum* survival differed by diameter class in the *Cibotium* forest community ($P < 0.01$), with the greatest mortality in the smallest size class. Data are means +1 SE. Letters indicate significant differences. A total of 1195 tree ferns were measured.

Metrosideros total survival (i.e., the percentage of individuals that sprouted) differed among communities with higher survival in the *Dicranopteris* (71%) community than the *Cibotium* (48%) and *Nephrolepis* (52%) forest communities ($P = 0.07$; Fig. 2.3). However, when controlling for differences among size classes (size and community as a 2 factor ANOVA), survival did not differ among communities ($P = 0.04$; Fig. 2.4).

Differences in survival among communities may be partially explained by differences in *Metrosideros* population structure among communities ($P < 0.01$; Fig. 2.6). The population structure of the *Dicranopteris* and *Nephrolepis* forest communities was composed of smaller individuals with greater than 75% of *Metrosideros* trees in the smallest size class. In contrast, the *Cibotium* forest had less than 30% of the trees in the smallest size class and over 50% in the largest size class.

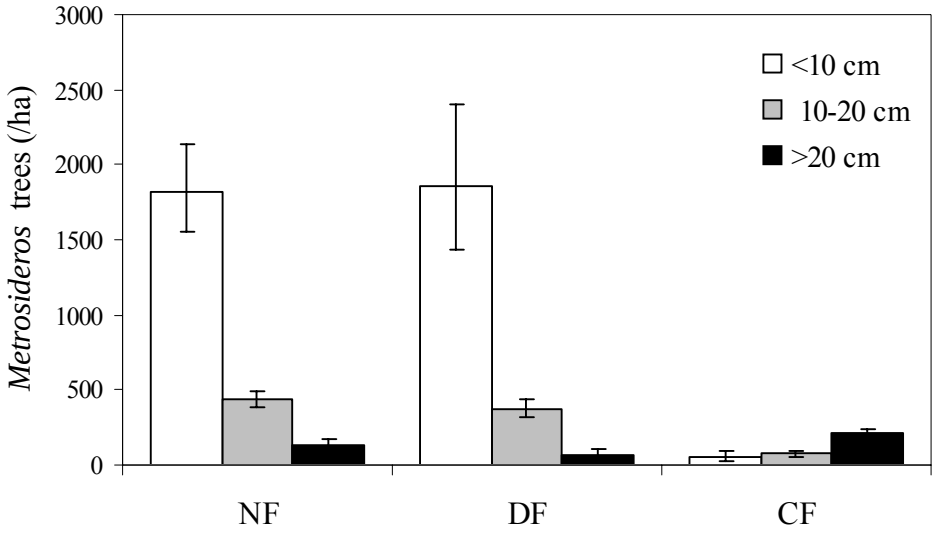


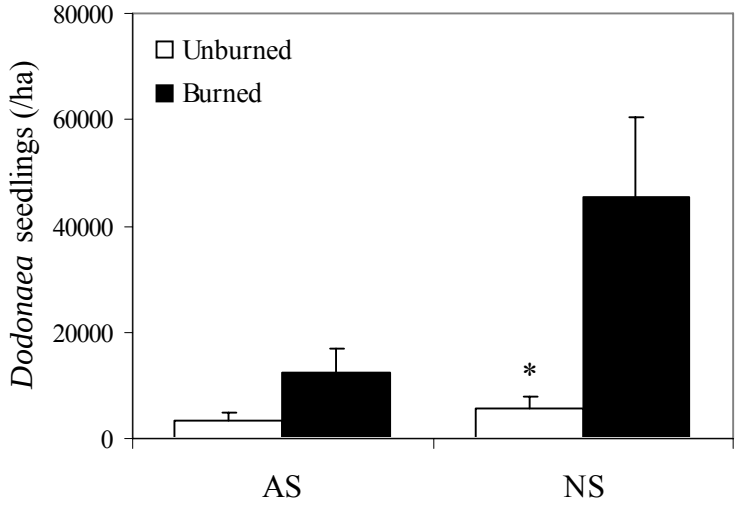
Figure 2.6. The population structure of *Metrosideros polymorpha* differed among the three forest communities ($P < 0.01$; NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest). Data are means ±1 SE. A total of 911 trees were measured.

Seedling Response

Seedlings of 17 native woody species were encountered in the postfire plots (Table 2.1). The majority of these species were present both as seedlings and as sprouts including four tree, six shrub, and two tree fern species. Of the five species present, only as seedlings, two were tree species and three were shrub species. For three shrub species, *Clermontia hawaiiensis*, *Lythrum maritimum*, and *Sida fallax* no dead individuals were found in the burned plots and no live mature individuals were found in the unburned plots suggesting that these species either dispersed into the area from outside or survived a long time in the soil seed bank. Growth and maturation from seed was rapid for three species that flowered within the first two postfire years, *Dodonaea*, *Pipturus albidus*, and *Sida fallax*.

Few shrub species differed in seedling density between unburned and burned sites for any community except *Dodonaea*, the only shrub encountered following fire in all five community types (Table 2.2). *Dodonaea* was the most abundant shrub that was recruited from seed with a density of 3,333/ha in the unburned and 12,333/ha in burned plots of the *Andropogon* shrubland two years postfire ($P = 0.16$; Fig. 2.7A). Similarly in the *Nephrolepis* shrubland, *Dodonaea* dominated the unburned site (5,733/ha) yet had even higher seedling density in the burned site (45,267/ha) two years postfire ($P = 0.01$; Fig. 2.7A). In the forest communities, *Dodonaea* was not encountered in the unburned sites (Table 2.2), but did establish from seed in low densities in the burned sites of the *Nephrolepis* (200/ha; $P = 0.07$), *Dicranopteris* (67/ha; $P = 0.43$), and *Cibotium* (267/ha; $P = 0.18$) forest communities (Fig. 2.7B).

(A) Shrub-dominated communities



(B) Forest communities

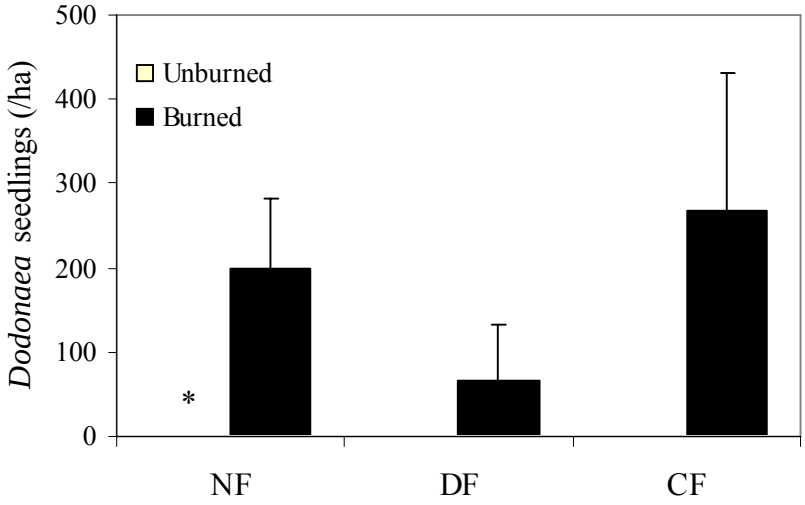


Figure 2.7. *Dodonaea viscosa* seedling density in unburned and burned sites two years postfire for (A) two shrub-dominated communities (AS = *Andropogon* shrubland and NS = *Nephrolepis* shrubland) and (B) three forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest). Means +1 SE are reported and asterisks denote significant differences between treatments for each community.

Table 2.2. Native shrub, tree, and tree fern seedling or juvenile density in unburned (U) and burned (B) sites two years following fire for the three forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, CF = *Cibotium* forest). Mean density per hectare is reported with standard error in parentheses. Asterisks denote significant differences between unburned and burned sites for each community.

Species	NF		DF		CF	
	U	B	U	B	U	B
Shrub species						
Coprosma menziesii	0	0	67(67)	0	133(133)	67(67)
Dodonaea viscosa	0	* 200(82)	0	67(67)	0	267(163)
Labordia hedyosmifolia	0	0	0	0	67(67)	0
Leptecophylla tameiameiae	67(67)	0	0	67(67)	0	0
Pipturus albidus	0	0	0	67(67)	0	67(67)
Vaccinium calycinum	0	0	0	0	133(82)	67(67)
Vaccinium reticulatum	0	0	0	67(67)	0	0
Tree species						
Cheirodendron trigynum	0	0	0	0	133(82)	0
Hedyotis terminalis	0	0	0	67(67)	0	0
Ilex anomala	0	0	0	67(67)	0	133(82)
Melicope clusiifolia	0	0	0	0	400(245)	1,000(350)
Melicope radiata	0	0	0	0	0	67(67)
Metrosideros polymorpha	67(67)	*667(236)	0	*267(125)	8,267(3,165)*	733(386)
Myrsine lessertiana	0	0	0	0	267(125) *	0
Myrsine sandwicensis	0	0	133(82)	0	0	0
Tree fern species						
Cibotium glaucum	0	0	0	333(333)	400(323)	3,200(1,948)
Sadleria cyatheoides	0	0	0	67(67)	0	0

Seedling density for the majority of tree and tree fern species did not differ between unburned and burned sites within each community type (Table 2.2). Fire did appear to affect *Metrosideros* seedling establishment in the forested communities. In the *Nephrolepis* and *Dicranopteris* forests fire promoted seedling establishment. Only one seedling was found in the unburned plots, but two years following fire many more seedlings were found in the burned plots of the *Nephrolepis* (667/ha; $P = 0.06$) and *Dicranopteris* (267/ha; $P = 0.07$) forests (Fig. 2.8). Alternatively, fire in the *Cibotium* forest decreased *Metrosideros* seedling density. In the unburned site seedling density was high (8,267/ha), whereas in the burned site two years postfire seedling density was significantly lower (733/ha; $P = 0.09$; Fig. 2.8). Juveniles of the subcanopy dominant tree fern species, *Cibotium glaucum*, were more abundant in the burned *Cibotium* forest two years following fire (3,200/ha) than the unburned forest (400/ha), but this difference was not significant ($P = 0.16$) due to high variation among plots.

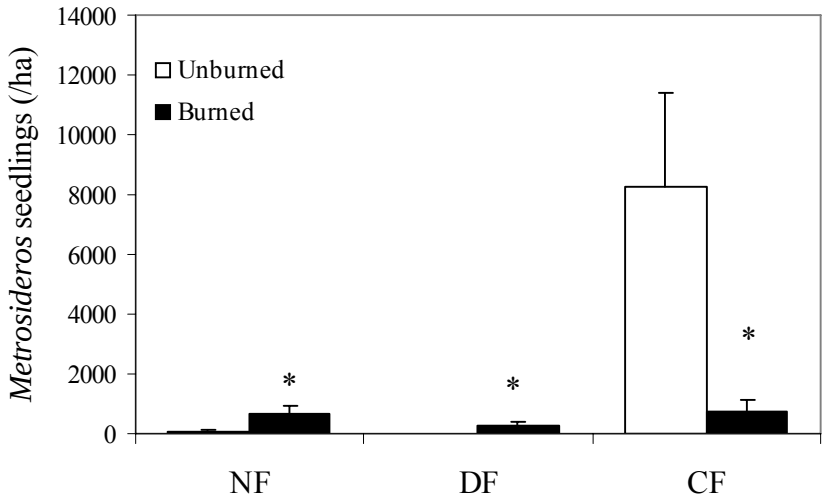


Figure 2.8. *Metrosideros polymorphs* seedling density in unburned and burned sites two years following fire in the forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest and CF = *Cibotium* forest). Means +1 SE are reported and asterisks denote significant differences between treatments for each community.

DISCUSSION

Sprouting Response

Many native Hawaiian woody plants in this study demonstrated some adaptations that facilitated survival by fire. The majority of these species were characteristic of "endurers" (i.e. they were top-killed, but sprouted after fire; Table 2.3). Nearly all tree and shrub sprouts originated from the base or root crown where bark tends to be thickest and where soils provide a great deal of insulation (Agee 1993). Similarly, previous studies following fire in mesic forest, seasonal submontane woodlands, and coastal lowland zones of Hawaii Volcanoes National Park, documented native woody species including *Metrosideros*, *Santalum paniculatum, Dodonaea, Osteomeles anthyllidifolia, Leptecophylla tameiameiae, Coprosma menziesii,* and *Vaccinium reticulatum* sprouting from the base (Warshauer 1974, Parman and Wampler 1977, Tunison et al. 1994, Tunison et al. 1995, D'Antonio et al. 2000, Loh et al. 2004). Yet this study is the first study to present the percent survival of *Metrosideros* and *Cibotium* in the wet forest following fire and how survival differed by species, size class, and plant community across an elevation gradient.

Table 2.3. Native woody species and tree fern plant adaptations that facilitate survival following fire.

Adaptation	Trait	Species
Resistors	protected meristems	Tree ferns (3): *Cibotium* glaucum, *Cibotium menziesii, Sadleria cyathoides*
Endurers	sprouters	Trees (8): *Hedyotis terminalis, Ilex anomala, Melicope clusiifolia, Metrosideros polymorpha, Myrsine lessertiana, Myrsine sandwicense, Psychotria hawaiiensis, Santalum paniculatum*
		Shrubs (8): *Broussaisia arguta, Coprosma menziesii, Dodonaea viscosa, Leptecophylla tameiameiae, Osteomeles anthyllidifolia, Scaevola chamissoniana* , *Vaccinium calycinum, Vaccinium reticulatum*
Invaders	wind-borne seeds	Tree ferns (2): *Cibotium glaucum* and *Sadleria cyathoides Cheirodendron trigynum, Hedyotis terminalis, Ilex anomala, Melicope clusiifolia, Metrosideros polymorpha*
		Shrubs (10): *Clermontia hawaiiensis* , *Coprosma menziesii, Dodonaea viscosa, Leptecophylla tameiameiae, Lythrum maritimum, Melicope radiata, Pipturus albidus, Sida fallax, Vaccinium calycinum, Vaccinium reticulatum*
Evaders	soil seed bank	Trees (1): *Santalum paniculatum* [1]
		Shrubs (3): *Dodonaea viscosa* [1,2] , *Osteomeles anthyllidifolia* [1,2] , *Sida fallax* [1]

[1] R.K.Loh unpublished data. [2] Hughes and Vitousek 1993.

Tree ferns were characteristic of "resistors" in that they survived fire and grew fronds within a few months following fire (Table 2.3). The thick fibrous trunk of tree ferns protected the meristematic tissue from fire. Similarly, *Cibotium* and *Sadleria* species were observed to have recovered from the terminal rhizomes following earlier

lava ignited wildfires (1969-1973) in the region (Warshauer 1974), but percent survival was not quantified in this study. In Australia, tree ferns (*Cyanea* spp) recover rapidly following disturbance such as fire, and logging (Ough and Murphy 2004).

In rare cases some woody species including *Metrosideros*, *Santalum paniculatum*, and *Dodonaea* were also observed to regenerate from epicormic buds along the stem and in the crown. Vegetative reproduction along the trunk for *Metrosideros* individuals has also been observed to occur following wildfire in dry woodlands (Loh et al. 2004) and tree-fall in unburned wet forests (Drake and Mueller-Dombois 1993). Sprouting from the crown provides a competitive advantage over individuals sprouting from the base or establishing from seed (Agee 1993). However, in this study epicormic sprouting was rare, presumably because temperatures extremes and durations during the fire reached lethal levels to kill epicormic buds. All of these species have very thin and in some cases scaly bark (Wagner et al. 1999) offering little protection from heat (Kauffman 1990).

Rapid maturation and reproductive effort following fire is also an adaptation facilitating persistence and establishment in the postfire environment (Kauffman 1990). All eight shrub and three tree fern species that survived fire vegetatively had individuals that reached sexual maturity (i.e., were observed to be flowering and fruiting) within two years following fire (Table 2.1). Additionally two tree species *Hedyotis terminalis* and *Santalum* also had sprouts that reached sexual maturity during the second postfire year. The majority of reproducing *Santalum* across the study area originated from basal or root sprouts, suggesting that flowering for this species was fire-enhanced.

Specific characteristics promoting survival in an individual plant will often change with age (Kauffman 1990). Size class distribution of the dominant tree and tree

fern species influenced rates of survival. I found that postfire survival rates of *Metrosideros* decreased with increasing size. These data support the suggestion made by Tunison et al. (1995) that *Metrosideros* survival following fire is inversely correlated with tree size and is different from results of a previous study in the dry *Metrosideros* woodlands that found mortality to be independent of size class (D'Antonio et al. 2000). Although this trend of increased mortality with age and size has been documented in other tree species such as *Quercus* spp (Griffin 1980), the loss of sprouting capacity usually signifies a shift in the mode of survival to a general thickening of the bark tissue to protect cambial and meristematic tissues (Kauffman and Martin 1990). In this study, the stem and crown of *Metrosideros* trees were extremely sensitive because of the thin-barked nature of all individuals in all size classes. This heat sensitivity is apparent by the near complete crown mortality and paucity of epicormic sprouting following fire.

In contrast to *Metrosideros*, smaller individuals of *Cibotium* (<10cm) were less likely to survive fire than large individuals (>10cm), and survival did not differ among trunk length classes (i.e. tree fern age). High survival of tree ferns was presumably related to their unique morphology in which the meristematic tissue is highly protected by the main trunk and frond bases. Similarly tree ferns in Australia, *Dicksonia* spp and *Cyathea* spp, resprouted following wildfire (Ough and Murphy 2004). However, in this study there appears to be a threshold trunk diameter size (~10cm) for *Cibotium glaucum*, below which the tissues are not protected to a significant extent as evidenced by declining survival in burned plots.

In addition to individual species adaptations to fire, context specific factors such as pre-fire population structure and fuel consumption also greatly influence individual

survival (Agee 1993, D'Antonio et al. 2000). Survival of *Metrosideros* was greatest in the *Dicranopteris* forest community (71%; Fig. 2.3). Differences in population structure between the *Dicranopteris* and *Cibotium* communities explain the lower survival in the *Cibotium* community (48%). The *Cibotium* community appears to be a later successional forest with a greater proportion of trees in the largest size class (Fig. 2.5) which had a lower number of sprouting individuals. No difference in survival among communities was detected when controlling for differences in population structure (Fig. 2.4).

Total survival in the *Nephrolepis* forest community (52%) was significantly lower than in the *Dicranopteris* (71%) community ($P = 0.02$), but population structure between these two young forests was similar (Fig. 2.5). This suggests that the difference in survival may be related to differences in fire characteristics. In the burned *Dicranopteris* forest community, the quantity of unconsumed residual surface fuels was greater than the other two communities. Lower fuel consumption results in lower heat flux around the base of the trees and may explain the higher survival observed in this community. For example in the coastal lowlands and seasonal submontane zones of Hawaii Volcanoes National Park, D'Antonio et al. (2000) found that individual mortality was greater for native Hawaiian woody species in sites where more fuel was consumed. Additional analysis of the fuels data in this region will add to our understanding of fuels, combustion factors and vegetation response.

Seedling Response

In the burned landscape, about the same number of native Hawaiian plant species were encountered as seedlings (17) as sprouts (19). Two tree (*Cheirodondron trigynum*

and *Melicope radiata*) and four shrub species (*Clermontia hawaiiensis*, *Lythrum maritimum*, *Pipturus albidus*, and *Sida fallax*) were observed to be obligate seeders (i.e., no vegetative survival by sprouting). It is not surprising that many native species can be classified as "invaders" (i.e. those that disperse onto the site following fire) according to Rowe's (1981) scheme (Table 2.3) because they have also been observed to be primary colonizers of recent lava flows (Burton and Mueller-Dombois 1984). For example *Metrosideros* is considered an early successional tree species that colonizes new volcanic substrate or gaps created by tree falls and often remains dominant in mature wet forest communities (Mueller-Dombois 1987).

Species with seeds that can survive fire in the soil seed back or on individual plants are classified as "evaders" (Table 2.3). Some of the seedlings detected following fire may also have originated from the soil seed bank, but because I did not sample the soil seed bank in this study the relative importance of the seed bank is unknown. A few previous studies have shown that some native Hawaiian species have the capacity to germinate following high temperature treatments (120° C for 5 minutes) including *Osteomeles*, *Dodonaea* (Hughes and Vitousek 1993), *Santalum* and *Sida* (Loh, unpublished data).

Seedling establishment following fire differed among species and among communities across the elevation gradient of this study. Most species present in the study area did not differ in seedling density between the unburned and burned sites (Table 2.2) except *Metrosideros, Myrsine lessertiana and Dodonaea*. In the *Cibotium* forest community, *Myrsine* seedlings were found (267/ha) in the unburned plots, but no seedlings were found in the burned plots during the first two years postfire suggesting

this species follows the "avoider" strategy of Rowe. Alternatively, the lack of *Myrsine* seedlings detected in the burned site may be attributed to the limited sampling subplot size. Fewer *Metrosideros* seedlings were found in the burned *Cibotium* forest (733/ha) as compared to the unburned *Cibotium* forest (8,267/ha). Lower *Metrosideros* seedling density in the burned plots is not likely due to limited seed source considering the proximity to unburned forests and the dispersal capabilities of these small wind-blown seeds. The competitive advantage of *Metrosideros* is argued to be its superior wind dispersal ability into large gaps (Hatfield et al. 1996). Research on recent lava flows found seed rain or dispersal to be sufficient to saturate available sites and suggested that colonization was limited by the density of "safe sites" or microclimatic conditions necessary for establishment (Drake 1992). Similar to previous studies, the majority of *Metrosideros* seedlings found in the unburned forest were growing on moss substrate on tree fern nurse logs (Burton and Mueller-Dombois 1984). Although tree fern trunks were abundant in the burned sites, mosses were burned off during the fire and conditions on the trunks were presumably drier and less favorable for *Metrosideros* establishment.

These changes in *Metrosideros* seedling density following fire do not necessarily indicate differences in the future forest because this species is not seed limited and is well suited for establishing in canopy gaps. *Metrosideros* seedlings are more likely to establish and have faster growth rates in high light environments (Burton and Mueller-Dombois 1984). Dramatically lower seedling density in the *Cibotium* forest may be inconsequential because there are still large numbers (733/ha) of seedlings in the burned forest presumably with a higher likelihood of reaching the canopy than those seedlings in the unburned forest due to increased light availability following top-kill.

In contrast to the *Cibotium* forest, *Metrosideros* seedling recruitment appeared to be enhanced by fire in the *Nephrolepis* and *Dicranopteris* forests where seedling densities were greater in burned sites (*Nephrolepis*: 667/ha; *Dicranopteris*: 267/ha respectively) than unburned sites (*Nephrolepis*: 67/ha; *Dicranopteris* 0/ha). Similarly, *Metrosideros* seedlings establishment was greater on recent (4-17 year old) landslides than undistrurbed mesic forests on the Island of Hawaii (Restrepo and Vitousek 2001). The *Nephrolepis* and *Dicanopteris* forest communities lacked tree fern nurse logs and the dense fern understory in the unburned sites appeared to limit space for seedling establishment.

The native shrub *Dodonaea* was the only woody species found in all five communities following fire. *Dodonaea* colonized the postfire environment through dispersal (i.e. seeds are enclosed in wind-borne bracts) and from the soil seed bank where high temperatures during fire scarify the seeds (Hodgkinson and Oxley 1990). Therefore *Dodonaea* can be classified as an "evader", "invader", and "endurer" species (Table 2.3).

In the forest communities of this study, no *Dodonaea* shrubs were found in the unburned sites and those in the burned sites established from seed. In the shrubland communities, however, individuals both sprouted and established from seed. This species had higher seedling densities in burned areas than in unburned areas. It is also one of three native woody species to reach sexual maturity from seed within the first two years following fire. Similarly, in previous fire studies at Hawaii Volcanoes National Park, *Dodonaea* seedlings were abundant in burned mesic forest and shrublands (Warshauer 1974), submontane sites (Hughes et al. 1991, Hughes and Vitousek 1993, D'Antonio et al. 2000) and coastal lowlands (Tunison et al. 1994, D'Antonio et al. 2000).

Dodonaea also successfully colonized young (4-17 year old) landslides on the Island of Hawaii (Restrepo and Vitousek 2001).

Many of the native Hawaiian woody species and tree ferns in this study area possessed traits that facilitated or ensured the persistence of individuals and/or species following fire. However, the effects of fire differed among species, populations and preburn vegetation communities. The majority of woody species demonstrated the capacity to sprout, thus conferring these plants with advantages over individuals that establish solely from seed in the postfire environment. It is unclear whether these are evolutionary adaptations to fire or causal adaptations of traits derived in response to other disturbances common in the region (volcanism, landslides, hurricanes, etc.). These adaptations may not be sufficient to insure dominance of native species in the future as the presence of invasive plant and ungulate species will likely dramatically alter postfire succession and dominance in these ecosystems.

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CHAPTER 3. INTERACTIONS OF FIRE AND NONNATIVE SPECIES ACROSS AN ELEVATION/PLANT COMMUNITY GRADIENT IN HAWAII VOLCANOES NATIONAL PARK

Alison Ainsworth

ABSTRACT

Invasive species interacting with fire poses a relatively unknown, but potentially serious, threat to the tropical mesic and wet forests of Hawaii. Fires may create conditions that facilitate the establishment of nonnative species into previously native-dominated plant communities. Once established, the presence of nonnative species in the postfire environment may slow or dramatically alter establishment of native forest species. The objectives of this study were to compare changes in vegetation composition and structure for two years following lava-ignited wildfires in five plant communities arrayed across an environmental gradient of four life zones and comprising a vegetation gradient from shrubland to wet forest. To examine postfire succession, I established replicate plots (n=5) in burned and unburned sites in five separate plant community types along an elevation/environmental gradient in Hawaii Volcanoes National Park, Island of Hawaii. Two shrub-dominated communities (*Dodonaea viscosa/Andropogon virginicus* and *Dodonaea/Nephrolepis multiflora*) and three forest communities (*Metrosideros polymorpha*/ *Nephrolepis*, *Metrosideros/ Dicranopteris linearis*, and *Metrosideros/ Cibotium glaucum)* were investigated.

Fires in all community types were stand-replacing, where >95% of the dominant native woody species were top-killed. Fire differentially affected the communities. The greatest differences between unburned and burned composition and structure were in the three forest communities. Alternatively, relatively few differences were detected in the nonnative-dominated shrubland communities. In the forested communities, structure was dramatically altered by *Metrosideros* canopy mortality. Understory cover differed

between unburned and burned sites for each community with reduced total understory vegetation cover in the *Nephrolepis* and *Dicranopteris* forests and greater cover in the *Cibotium* forest one and two years postfire. Nonnative species became increasingly abundant following fire in the previously native-dominated *Dicranopteris* and *Cibotium* forest communities, suggesting that fire facilitated nonnative species invasion in these communities. The native fern *Dicranopteris linearis* was the most abundant understory species in the unburned sites, but was absent following fire and nonnative ferns and vines had the greatest relative cover and frequency postfire. In contrast, in the *Nephrolepis* forest community the nonnative fern *Nephrolepis multiflora* dominated the understory in both the unburned and burned sites and fewer differences in understory composition were detected following fire.

Metrosideros survival and recovery differed among forest communities. Measures of sprout vigor were greatest two years following fire in the native *Dicranopteris* forest, where understory recovery was slowest presumably due to the thick litter layer that remained following fire acting as a barrier to understory colonization. Postfire vegetation composition and cover of the understory in the *Nephrolepis* forest was due largely to rapid recovery of *Nephrolepis multiflora* cover via sprouting. In the *Cibotium* forest community rapid recolonization of the understory was due to nonnative grass invasion. These results suggest that the rapid establishment of a nonnative-dominated understory is limiting *Metrosideros* tree recovery during early postfire succession.

Lastly, fire in the lowest elevation modified shrubland communities (sites of previous fires in 1972 and 1992) had little effect on vegetation composition and structure.

These modified communities, demonstrate how nonnative species invasions coupled with repeated fires can selectively eliminate fire-sensitive species thereby maintaining the community in an arrested state of succession.

INTRODUCTION

Changes in biodiversity associated with biological invasions of nonnative species are a tremendous concern at local, regional and global scales (Vitousek et al. 1996). Invasive species are a serious threat to native ecosystems because of their capacity to dramatically alter species composition, ecosystem function, and successional trajectories (D'Antonio and Vitousek 1992). Moreover, global climate change is predicted to allow range expansion of many invasive species (Kriticos et al. 2003b, a, Morrison et al. 2005) and is likely to stress native ecosystems thus further increasing the success of some nonnative species (Dukes and Mooney 1999, Asner et al. 2006).

Natural disturbances, a major source of heterogeneity in the structure and dynamics of all natural communities (Sousa 1984), have been documented to facilitate nonnative species invasions in many community types across the globe (Hobbs and Huenneke 1992, D'Antonio and Dudley 1995, Burke and Grime 1996, Bellingham et al. 2005, De Gruchy et al. 2005). In Hawaii, nonnative species invasions into native-dominated communities are also facilitated by natural and human disturbances (Kitayama and Mueller-Dombois 1995, Aplet et al. 1998). According to the fluctuating-resources hypothesis, community invasibility increases with increases in available resources (Davis et al. 2000). Fire can increase available resources at a site by consuming or reducing

predisturbance vegetation (Grime 1979) and increasing nutrient availability (Kauffman 1990) thereby decreasing resource use (Davis et al. 2000) and altering microsite conditions (e.g., light levels, wind speed, and moisture availabilty) in the understory. Nonnative species in Hawaii have been shown to invade sites following an increase in resource availability (Gerrish and Mueller-Dombois 1980, Carino and Daehler 2002, Ostertag and Verville 2002) in some cases creating positive feedbacks for further invasions (Vitousek and Walker 1989, Allison and Vitousek 2004, Hughes and Denslow 2005). Differences in invisibility among differing plant communities or environments following fire are not as well documented in Hawaii. Fire certainly influences species composition and structure (Hughes et al. 1991, Tunison et al. 2001), as well as resource availability.

The interactive effects of nonnative species and fire are not well understood in many ecosystems (Brooks et al. 2004), particularly in the tropics (Cochrane 2003). Species composition can influence both the magnitude of a disturbance and species survival following disturbance. Many studies have demonstrated that species invasions are promoted by disturbance and that invasive species can subsequently have negative impacts on native species assemblages (D'Antonio et al. 1998). However, Mack and D'Antonio (1998) suggested that invasive species can also alter disturbance regimes and, thereby, successional trajectories of the plant communities. Invaders can alter disturbance regimes by enhancing or suppressing fire, increasing or decreasing erosion, and by increasing biotic disturbance (Mack and D'Antonio 1998). For example, nonnative grass invasions in the seasonally dry woodlands of Hawaii alter biomass and

fuel composition, structure, moisture, and chemistry, thereby increasing the probability of an increased frequency and severity of fire (D'Antonio and Vitousek 1992).

The nonnative fern *Nephrolepis multiflora* was not abundant in the East Rift portion of Hawaii Volcanoes National Park until sometime after the 1980's (Jacobi 1989). Following a lava-ignited wildfire in 2002 in this region, *Nephrolepis multiflora* has recovered rapidly from sprouts, consistent with observations in the Caribbean (Rivera et al. 2000). The presence of this recent invasion by *Nephrolepis multiflora* and range expansion by nonnative grasses such as *Paspalum conjugatum* in the mesic and wet forest communities of Hawaii (Pratt et al. 1999) may greatly influence native forest regeneration.

The objectives of this study were to compare changes in vegetation composition and structure for two years following lava-ignited wildfires in five plant communities arrayed across an environmental gradient of four life zones and comprising a vegetation gradient from shrubland to wet forest. I hypothesized that postfire succession of these communities would differ and that nonnative species would alter native plant community succession. Specifically, fire would facilitate species invasions and where nonnative species were abundant following fire they would limit native species recovery. I predicted that: (1) communities dominated by natives prior to fire would have higher nonnative species abundance in burned sites compared to unburned sites (i.e., fire would increase invasibility by nonnative species), and (2) communities dominated by nonnatives prior to fire would not differ in vegetation composition and structure between burned and unburned sites (i.e., fire would not increase invasibility by a different suite of nonnative species). In addition, I predicted that communities where nonnative species

were abundant during early postfire succession would exhibit: (3) faster understory recovery, (4) less native tree species recruitment, and (5) slower recovery rates for surviving trees.

METHODS

Study Site

The study was conducted in shrubland, mesic forest, and wet forest communities along an elevation/precipitation gradient previously described in Chapter 2 (Fig. 2.1). All communities occurred within 5 km of each other along an elevational range of 350m in shrubland communities to 825m in wet forest communities. The study area encompassed four distinct Holdridge life zones: subtropical basal moist forest, subtropical basal wet forest, subtropical lower mountain moist forest and a subtropical lower mountain wet forest (Tosi et al. 2001).

The entire study area was located within a 6 km wide band of vegetation between the Mauna Ulu lava flows (1969-1974) and the Puu Oo lava flows (1983-present). Substrate across the gradient consisted of relatively young (400 to 750 yr-old) pahoehoe lava flows (Trusdell et al. 2005). Two basic soil types were present: the Kalapana series and the Makaopuhi series. The Kalapana series are very shallow to shallow (5-50 cm) well drained soils formed in ash deposited over pahoehoe lava with 2-10% slopes, and are classified as Medial, ferrihydritic, isothermic, Lithic Udivitrands. The Makaopuhi series are very shallow to shallow (5-30cm) somewhat poorly drained soils that formed in volcanic ash deposited over pahoehoe lava with 2-10% slopes, and are classified as

Medial, ferrihydritic, isothermic, Lithic Hapludands. The shrubland communities are on the Kalapana dry phase soils, the mesic forest communities are on Kalapana medial course sandy loam and the wet forest community is on Makaopuhi very paragravelly muck (Jasper In press).

I sampled composition in burned and unburned sites of the five major plant communities within the Luhi and Panauiki fire perimeters. The *Dodonaea viscosa/ Andropogon virginicus* shrubland community (350-450 m) consisted of a native *Dodonaea* shrub layer (~9000 individuals/ha) with the nonnative perennial bunch grass *Andropogon* dominating the understory. A few trees (*Metrosideros*) were scattered across the landscape, but were primarily restricted to lava uplifts and other rocky microsites where fuel loads were insufficient to carry fire during the recent past burn events. This community is located within the mapped boundaries of past wildfires that occurred in 1972 and 1992 and will be referred to hereafter as the "*Andropogon* shrubland." The *Dodonaea/ Nephrolepis multiflora* shrubland community (450-550 m) consisted of a *Dodonaea* native shrub tier (~8500 individuals/ha) with the nonnative fern *Nephrolepis* dominating the understory. Similar to the *Andropogon* shrubland, remnant *Metrosideros* trees were scattered throughout this community. Burned sites for this community type were located within the 1972 and 1992 wildfire boundaries, and the unburned control sites were within the 1972 wildfire boundary but not the 92 boundary according to fire history maps (National Park Service 2003). This community will be referred to as the "*Nephrolepis* shrubland." While the tree component of these first two communities is now sparse due to the recent fires, photos taken prior to the 1972 wildfire indicate that the area was characterized as relatively open *Metrosideros* woodland with

scattered shrubs and a mixed understory (Hawaii Department of Land and Natural Resources 1966).

The study includes three forest communities that range from mesic to wet. The *Metrosideros*/ *Nephrolepis multiflora* forest community (550-640m) was dominated by *Metrosideros* in the overstory (~700 individuals/ha) and the nonnative fern *Nephrolepis multiflora* in the understory. This community will be referred to as the "*Nephrolepis* forest." The *Metrosideros*/*Dicranopteris linearis* forest community (640-750m) contained *Metrosideros* in the overstory (~850 individuals/ha) and the native, mat forming fern *Dicranopteris* in the understory. This community will be referred to as the "*Dicranopteris* forest." The *Metrosideros*/ *Cibotium glaucum* forest community (700-850m) had a more open canopy overstory of *Metrosideros* (~500individuals/ha) with a native tree fern *Cibotium* midstory (~2800/ ha) and variable fern and grass species in the understory. This community will be referred to as the "*Cibotium* forest."

Lava has been the main ignition source in this area of the Park from 1916 to present (Gassaway et al. 2002). Multiple fires have occurred in the coastal lowlands over the last thirty years and two have burned the lowland *Andropogon* shrubland and *Nephrolepis* shrubland communities of this study area. Both fires did not spread (>500m) into the *Metrosideros* mesic forest communities (Timothy Tunison, pers. comm.). In May 2002, the Mother's Day lava flow erupted and on 17 May 2002, the Kupukupu Fire burned 345 ha of wet forest; by June 2002 an additional 1,020 ha of mesic and wet forest had burned. The Panauiki Fire (January, 2003) burned 860 ha of *Andropogon and Nephrolepis* shrublands between 60 and 670 m. In May 2003, the Luhi fire burned 2,000 ha across the study area (National Park Service 2003). I sampled

vegetation composition and structure in permanent plots (n=5) in each of the five vegetation communities in areas burned in the 2003 Panauiki and Luhi wildfires and unburned controls.

Vegetation Sampling

I examined some of the ecological effects of wildfire through comparisons of the vegetation composition and structure in the areas burned by the 2003 wildfires, and surrounding unburned sites. In each of the five communities, I established five replicate, randomly located 20 x 50m permanent plots. Burned areas were sampled the first and second years postfire (2004 and 2005). Burned sample locations were selected based on vegetation composition and structure, elevation, fire history, and proximity to unburned sites. Under the assumption of little year to year variability in understory composition, unburned areas were sampled only once- two years following fire (2005) except for the *Nephrolepis* forest community which was sampled one year following fire (2004). I selected unburned plots in each community type based on comparable elevation, and similar vegetation composition and structure to what appeared to have existed in the burned plots before fire. Flowering plant nomenclature followed that of (Wagner et al. 1999) and fern nomenclature followed that of (Palmer 2003).

All plant species within the plot (20 x 50m) were recorded to compile a species list for each site and constancy for each species was calculated by determining the percent of communities in which each species occurred. Vegetation was measured using a nested plot design (Fig. 3.1). Tree, tree fern and shrub density were sampled as previously described in Chapter 2. Briefly, all large trees (>10cm diameter at breast

height) and tree ferns (>10cm diameter below past years frond shed) were measured in the 20 x 50m plot (Fig. 3.1A). Trees and tree ferns <10cm in diameter were measured in six 2 x 10m subplots (Fig. 3.1B). Tree seedlings (<1.4 height) and shrub density were measured in six 1 x 5m subplots (Fig. 3.1C). The cover of understory plant species (herbs, ferns, and shrubs) was measured for each species to the nearest percent within twelve 1 x 1m nested subplots (Fig. 3.1D). Shrubs were recorded as mature if they demonstrated any sign of reproduction and/or were greater than 50cm in height.

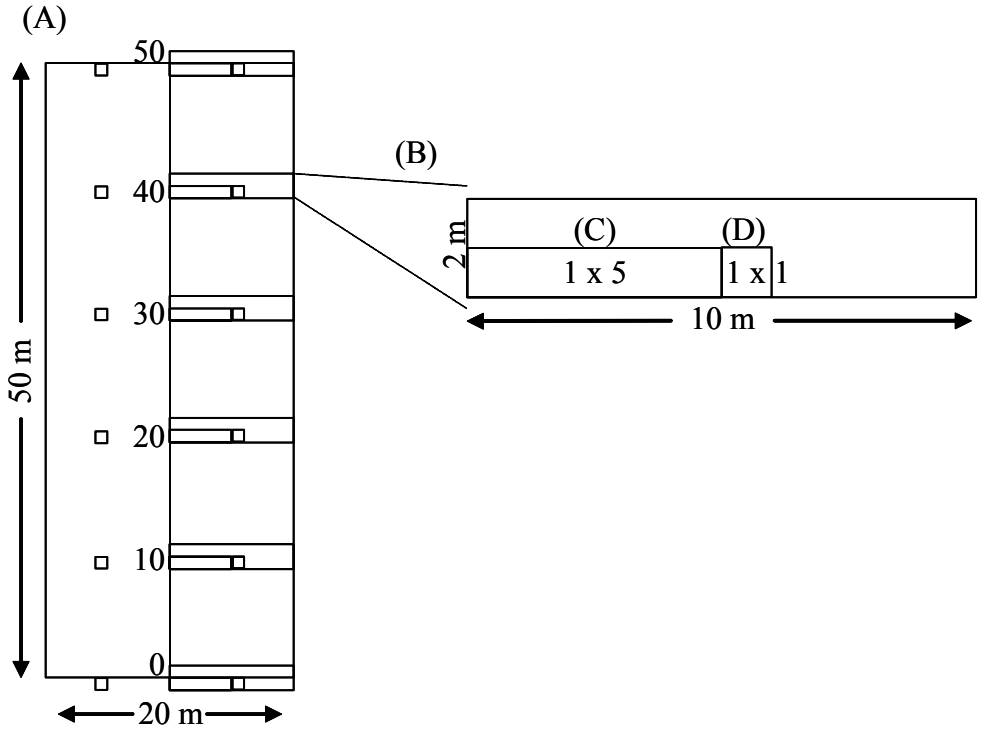


Figure 3.1. Plot layout used to quantify species composition and structure. (A) All large trees and tree ferns >10cm diameter at breast height were measured in the 20 x 50m plot. (B) Trees and tree ferns <10cm diameter were measured in six 2 x 10m subplots perpendicular to the center transect at 10m intervals. (C) All shrubs and trees <1.4m in height were measured in six 1 x 5m subplots nested within the 2 x 10m subplots. (D) Understory (herbaceous and shrub species) cover was measured in twelve 1 x 1m subplots.

Quantitative measures recorded for all trees in each 20 x 50m plot included: the diameter at 1.4 m aboveground (dbh), number of boles at 1.4m, crown mortality, plant mortality, and mode of sprouting (basal if it originated from subterranean plant organs at the base of trees originating <50 cm above ground and epicormic if it originated from dormant meristematic tissue in the bole or mainstems) (Kauffman 1990). From these data, percent crown mortality and individual plant death were calculated for all trees by species, and by size class for the dominant species.

Individual tree sprout growth was quantified by measuring basal sprout height and basal sprout elliptical crown area. Basal sprout height (cm) was calculated as the longest basal sprout per tree, measured from its base to the apical meristem. Elliptical crown area (cm^2) was calculated from crown width measured in two perpendicular directions and the formula:

$$\text{Area} = (W_1 * W_2 * \pi) / 4$$

where W_1 is the maximum diameter (cm) and W_2 is the perpendicular diameter to W_1. Crown volume (cm^3) was then calculated by multiplying the height of the tallest sprout by the elliptical crown area (Mueller-Dombois and Ellenberg 1974, Kauffman and Martin 1990, Sampaio et al. 1993).

Tree and sprout measurements were made one and two years postfire, allowing for quantification of a relative growth rate (RGR). Relative growth rates were compared for the height of the tallest sprout, elliptical crown area, and sprout volume using the formula:

$$RGR = (\ln P_2 - \ln P_1) / t_2 - t_1$$

where P_1 is the parameter measured (height, crown area, or volume) at time one (t_1), and P_2 is the parameter measured at time two (t_2) (Hunt 1982).

Data Analysis

Species presence/absence data are reported as species richness or the number of species per sampled site and per 20 x 50m plot. Additionally, species are categorized as native or nonnative. Understory plant diversity was calculated from the cover data using the Shannon-Wiener Diversity Index (Shannon and Weaver 1949),

$$H' = -\Sigma\, p_i \log p_i$$

where p_i is the relative cover of each species. This index is influenced by both the number of species present and their abundance. Evenness (J') was isolated by dividing the Shannon-Wiener Diversity Index by the logarithm of the average number of species per plot (Pielou 1966, 1969). The maximum value for $J' = 1$ when there was perfect equitability among species.

Relative dominance of understory species within each sampled community treatment was determined by calculating importance values (Mueller-Dombois and Ellenberg 1974). The importance value (IV) of a species was based on relative frequency within 20 x 50m plots and relative cover within 1 x 1m subplots,

$$IV = (F_s/F_t + C_s/C_t)/2 \text{ X } 100$$

where F_s is frequency of a species, F_t is frequency of all species, C_s is cover of a species, and C_t is total combined cover (Mueller-Dombois and Ellenberg 1974). Importance values range from 0 to 100%. Species had high importance values when the average

relative cover within subplots (1 x 1m) was high and species were found in all five plots (20 x 50m) within the community treatment.

The sampling unit used in analysis for all parameters was the 20 x 50m plot; therefore for each analysis each treatment had five replicates. Average values were calculated per plot and used in analysis for vegetation parameters that were sampled in subplots (e.g., understory cover, seedlings, small trees and tree ferns). Species richness and the percent of those species that were nonnative were analyzed across the study gradient as two factor ANOVA's with community, burn, and community x burn as fixed effects. Differences in *Metrosideros* survival, sprout height, sprout elliptical crown area, sprout volume and relative growth rate among forested communities were analyzed using analysis of variance (ANOVA) and Tukey's multiple comparison test. In order to determine the effect of fire in each community separately, differences in many vegetation parameters (species richness, % nonnative, species diversity, understory cover, shrub and tree seedling densities) were compared between sites and years following fire using two sample *t*-tests (unburned vs. burned one year postfire and unburned vs. burned two years postfire). In the *Andropogon* and *Nephrolepis* shrublands, shrub and seedling densities were log base 10 transformed (log + 1) to normalize residuals and nonparametric tests (Wilcoxon Rank Test) were used to compare differences in understory cover. Nonparametric tests were used to examine differences in shrub and seedling density for the three forest communities and species diversity and cover in the Dicranopteris forest because the assumptions of parametric tests were not met due to large differences in variance between burned and unburned sites. ANOVA and *t*-test analyses were performed at an $\alpha = 0.10$. Statistical analyses of species richness, diversity, understory

cover, shrub, seedling and tree density, and measures of tree sprouts were conducted using S+ version 7.0 (Insightful 2005).

Multivariate statistical analysis of community data was based on cover values for all herbaceous and shrub species and was conducted using PC-ORD, Version 4.25 (McCune and Mefford 1999b). To assess differences in understory composition between burned and unburned sites, multi-response permutation procedure (MRPP) was used to test the null hypothesis of no difference between groups. An indicator species analysis (Dufrene and Legendre 1997) was performed to examine relationships of individual species to the burned and unburned sample groups for each community. Species reported as indicators were tested for significance using a Monte Carlo test of 1000 randomizations.

Non-metric multidimensional scaling (NMS) ordination (300 maximum iterations with a stability criterion of 0.0001 standard deviations in stress over the last 15 iterations, with 40 separate runs) with Sørenson distance measures were used to delineate patterns between burned and unburned sites and among communities (Kruskal 1964, Mather 1976). Two or three dimensional solutions were found for ordinations and Monte Carlo was used to test stress and strength of the NMS results. Prior to NMS ordination, species occurring in fewer than two plots were deleted from the data set and all species were relativized by their maximum value to equalize the influence of individual species (McCune and Grace 2002). Plots were rotated to load the burn variable on axis 1, maximizing the proportion of variance represented by that axis. Joint plot overlays (NATIVE, ALIEN, and WOODY), indicate the relative significance of each axis on the

variable by their length and direction. Community data and joint plot overlay matrices and specific NMS test results for each ordination are described in Appendix B.

RESULTS

Vegetation structure was dramatically altered by fire in the forest communities. Fires were stand-replacing in all five communities. There was little postfire live plant cover with very few unburned islands of vegetation remaining. On average, over half (57%) of the *Metrosideros* survived fire through basal sprouting, but survival differed among forested communities (Fig. 2.3). Survival one year following fire was highest in the *Dicranopteris* forest (71%). Although some sprout mortality occurred between postfire years, total survival was >65% (553/ha) two years postfire in this community. In the *Nephrolepis* forest, half of the *Metrosideros* trees had live sprouts one year following fire (52%), but sprout mortality between the first and second years postfire resulted in a second year postfire survival of 34% (238/ha). No sprout mortality occurred in the *Cibotium* forest community between years postfire, but initial survival was lowest in this community (48%; 240/ha).

Measures of sprout vigor including sprout height, elliptical crown area, and volume also differed following fire among forest communities (Fig. 3.2A-B). The RGR of *Metrosideros* basal sprout height between the first and second years postfire was faster in the *Dicranopteris* forest (3.5cm) than the *Nephrolepis* (2.5cm) and the *Cibotium* (1.8cm) forest communities (P <0.01; Table 3.1). By the second year postfire sprout

height (81cm), elliptical crown area (2815cm^2), and volume (270,169cm^3) were also greater in the *Dicranopteris* forest than the other communities (P <0.01; Fig. 3.2B).

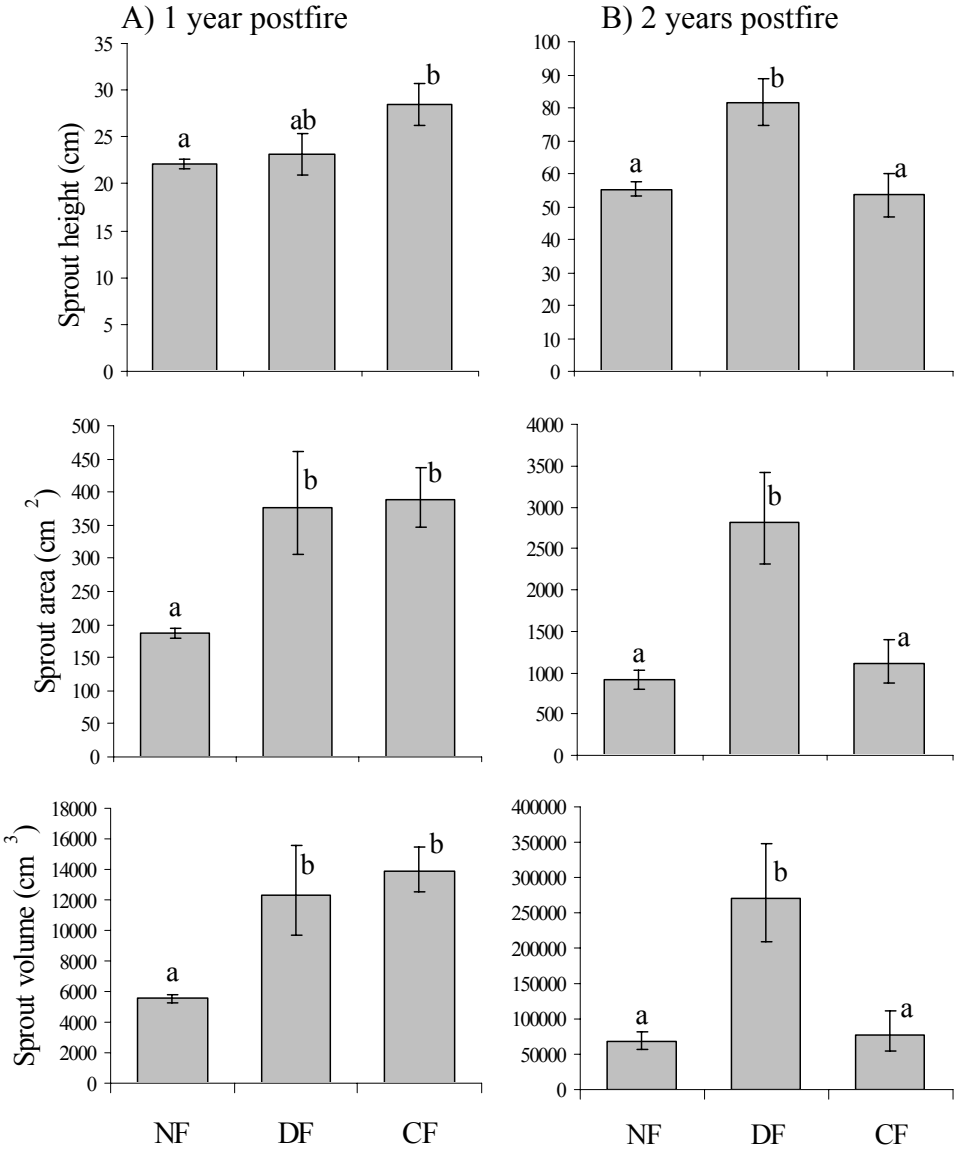


Figure 3.2. *Metrosideros polymorpha* sprout vigor as measured by sprout height (cm), sprout area (cm^2), and volume (cm^3) (A) one and (B) two years postfire in three forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest). Note the difference in scale between postfire years. Means ± 1 SE are shown for sprout height. Backtransformed means ± 1 SE are shown for sprout area and volume.

Table 3.1. Relative growth rate between the first and second years postfire (mean and SE) of *Metrosideros polymorpha* basal sprout height, crown area, and volume for three forest communities (NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest). Significant differences among forest communities for each parameter are denoted by different letters.

	Community	Mean	SE	*P*
Height (cm)	NF	2.494[a]	1.065	<0.01
	DF	3.529[b]	1.071	
	CF	1.846[c]	1.064	
Crown area (cm^2)	NF	4.839[a]	1.175	<0.01
	DF	7.492[a]	1.128	
	CF	2.836[b]	1.230	
Volume (cm^3)	NF	1.289[a]	1.022	<0.01
	DF	1.329[a]	1.018	
	CF	1.178[b]	1.021	

Vegetation response to fire differed widely by species and by plant community type. One hundred and eight species were found across the gradient, 14 trees, 3 tree ferns, 23 shrubs, 6 vines, 15 ferns, and 47 herbs, grasses and sedges (Appendix A). Over half (56%) of these species were native. Species richness per sampled plot (20 x 50m) and the proportion of those species that were nonnative significantly differed between unburned and burned sites (P <0.01), as well as among communities (P <0.01). In the forest communities, in particular, species richness and the proportion of those species that were nonnative was significantly greater in the burned sites than the unburned sites. For both parameters the interaction term was also significant (P <0.01) which indicated that the magnitude of the effect of fire varied from one plant community to the next. For example, species richness in the *Andropogon* shrubland did not differ between the burned plots (11.8) two years postfire and the unburned plots (13; P = 0.25), but in the *Cibotium*

forest species richness was greater in the burned plots (31.4) than the unburned plots (24.4; $P = 0.05$).

Results of the NMS analysis of the understory for all communities combined indicated that community type was more important in explaining differences in community composition than the effects of fire (Fig. 3.3A). The sample units for the five communities separate into forest and shrubland communities along axis 2, which explained a greater percentage of the variation in the data (25%) than the burn axis 1 (20%) even after rotation that maximized the alignment of the burn variable with axis 1. In addition, heterogeneity among plots within each community type differed, as indicated by the difference in polygon size (Fig. 3.3B). The *Dicranopteris* forest, in particular, exhibited much more variation in understory species composition following fire. The understory composition in the burned forest communities more closely resembled the composition in the shrubland communities. This is due to the colonization and range expansion of species found in the shrubland communities including native and nonnative herbs, grasses and sedges into the forest communities postfire. In the unburned communities only one species, nonnative *Nephrolepis multiflora*, was found in all five community types. Two years postfire, *Nephrolepis multiflora*, and five additional species had high constancy values because they were found in the understory of all five community types including, native *Dodonaea viscosa*, *Cyperus polystachyos,* and *Paspalum scrobiculatum*, and nonnative *Andropogon virginicus*, and *Digitaria violascens*.

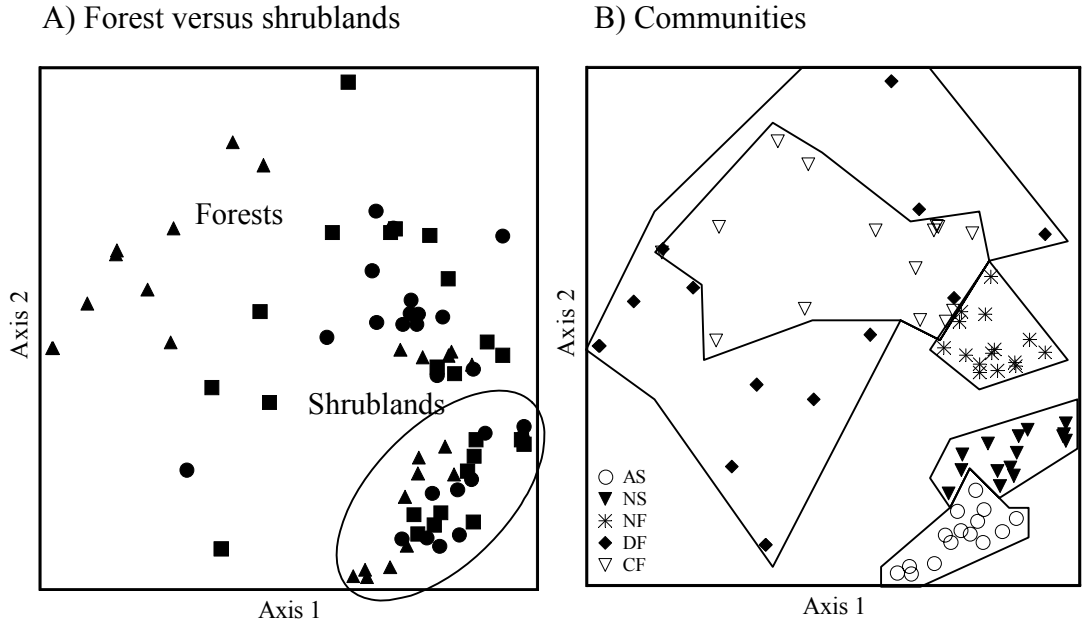


Figure 3.3. (A) Community membership or site differences are more important than burn effect (triangles: unburned; squares: burned 1 year postfire; circles: burned 2 years postfire) in explaining variation in understory community composition. (B) Generated polygons enclose unburned and burned plots one and two years postfire for each community (AS = *Andropogon* shrubland, NS = *Nephrolepis* shrubland, NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest).

The effect of fire on understory community composition differed among the three forest communities, evidenced by differences in the distance in NMS ordination space between plots in burned and unburned sites for each community (Fig. 3.4A-C) and low variance represented by the burn axis 1 (16%). Fire had the least effect in the *Nephrolepis* forest (i.e., shortest distance in ordination space between burned and unburned plots) (Fig. 3.4A). In addition, understory composition in this community became increasingly similar to unburned plots with time since fire. This pattern can be explained by the rapid recovery of the prefire dominant nonnative fern *Nephrolepis multiflora*. In contrast, the understory species composition was dramatically different

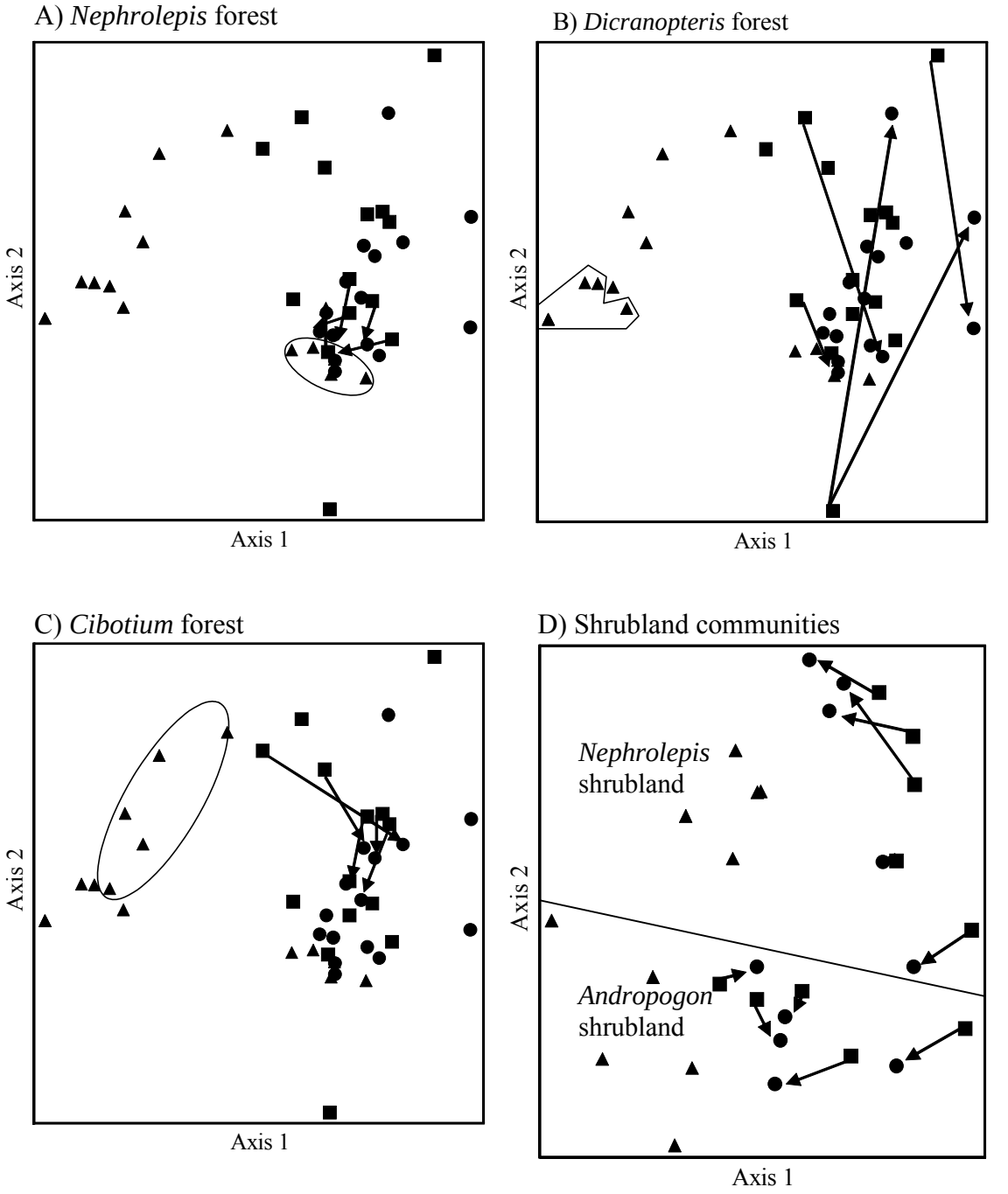


Figure 3.4. Graphical representation of the forested communities (A-C) with unburned plots (triangles) circled and arrows representing the changes in cover within a sample unit between the first (squares) and second (circles) years postfire. Shrubland communities (D) were ordinated separately in order to gain enough resolution to distinguish differences between burned and unburned plots.

following fire in the *Dicranopteris* forest (Fig. 3.4B). The change in composition between the first and second years postfire was also greatest in the *Dicranopteris* forest community, and two years postfire plots were still very dissimilar to the unburned sites. Heterogeneity among unburned plots was greatest in the *Cibotium* forest community shown by greater distances among unburned plots representing greater dissimilarities in community composition as compared to the other forest communities (Fig. 3.4C). However, burned sites in this community one and two years postfire were more similar, demonstrating that community composition became more homogeneous during early postfire succession

Site effect or community was also more important than burn effect in explaining patterns of community composition in the two shrubland communities (Fig. 3.4D). Less than 15% of the variance in composition among plots could be explained by the burn effect. Two years following fire, community composition was more similar to the unburned sites than it was one year following fire, suggesting a resilient vegetation composition for both shrubland communities.

To more clearly separate the effects of fire from the effects of community type, I also analyzed the vegetation data for each of the communities separately.

Andropogon Shrubland

In the unburned site of this community, 19 species were found with an average of 13 species per plot (20 x 50m). Over half (65%) of these species were nonnative. Understory species diversity (H') was 0.340 and Pielou's (*J*') measure of evenness was 0.31. The nonnative grass *Andropogon* (41% cover) and the native shrub *Dodonaea*

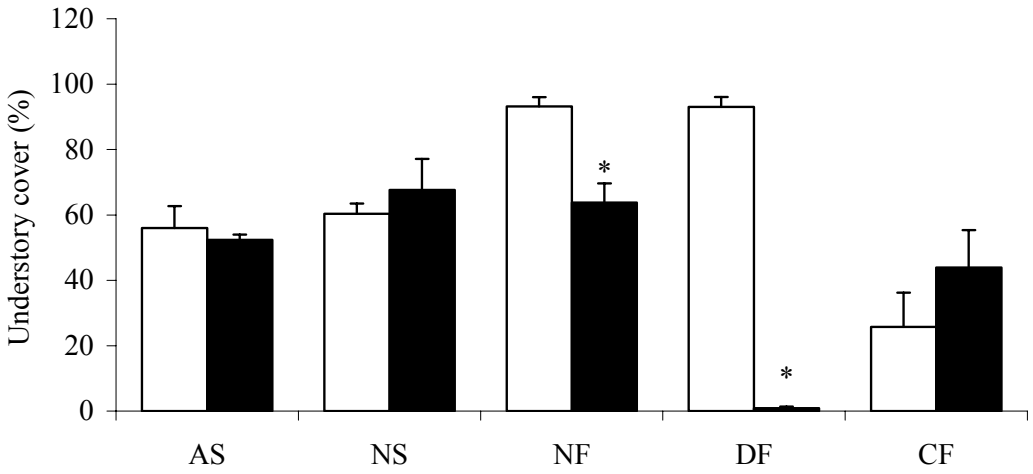
(10% cover) were the most abundant species in the unburned site and together constituted over 90% of the total understory vegetation cover (56%; Table 3.2). The majority of the *Dodonaea* shrubs encountered (11553/ha) were mature individuals. Because *Andropogon* and *Dodonaea* had high relative cover values and were found in all plots within the unburned site, they had high importance values (55% and 21% respectively; Table 3.3). Ten additional species were found in the understory subplots all with an average cover <2% (Table 3.2) and consequently low (<10%) importance values.

In the burned site two years postfire, 22 species were found and average species richness per plot (11.8) did not differ from that of the unburned site (13; $P = 0.25$). The percent of those species that were nonnative (57%) also did not differ from the unburned site (65%; $P = 0.35$). In contrast to species richness, understory diversity was greater in the burned site (H' = 0.514) two years postfire than the unburned site ($P = 0.08$) implying that higher diversity in the burned site is attributed to higher evenness ($J' = 0.48$) among species postfire. Vegetation recolonized quickly following fire primarily through individual survival. Total understory vegetation cover in the burned site one year postfire was 52% and did not differ from unburned site ($P = 0.69$; Fig. 3.5A). Rapid recovery was largely the response of the resilient species - the nonnative *Andropogon* grass and native *Dodonaea* shrub (Table 3.2). Similar to the unburned site, together they comprised the majority of total vegetation cover in the burned site two years postfire (74%) and remained the most important species in the community based on cover and frequency (Table 3.3). *Andropogon* sprouted vigorously from the base such that cover in the burned site (32%) did not differ from cover in the unburned site (41%) one year postfire ($P = 0.25$). The primary mode of recolonization following fire for *Dodonaea* in

Table 3.2. Understory cover (%) by species in the *Andropogon* and *Nephrolepis* shrubland communities in unburned and burned sites two years postfire.

Species		*Andropogon* Shubland				*Nephrolepis* Shrubland			
	Native	Unburned		Burned		Unburned		Burned	
	Status	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Shrub species									
Dodonaea viscosa	Native	10	4.1	6	2.6	16	2.3	29	9.2
Leptecophylla tameiameiae	Native			1	0.5	<1	0.0		
Osteomeles anthyllidifolia	Native					3	0.7		
Sida fallax	Native							<1	0.0
Indigofera suffruticosa	Non			<1	0.1				
Lantana camara	Non	1	0.5			<1	0.3		
Psidium guajava	Non	<1	0.3	1	1.3	<1	0.1		
Herb species									
Cocculus trilobus	Native					<1	0.3	<1	0.1
Cuscuta sandwichiana	Native	<1	0.2					<1	0.0
Waltheria indica	Native	<1	0.3	3	0.9	<1	0.1	3	1.6
Chamaecrista nictitans	Non	<1	0.0	1	0.5			<1	0.1
Desmodium sandwicense	Non			3	0.9	<1	0.1	12	3.2
Nephrolepis multiflora	Non	1	0.5	<1	0.3	33	2.9	21	8.7
Grass/Sedge species									
Chrysopogon aciculatus	Native	<1	0.0	<1	0.2				
Cyperus polystachyos	Native					<1	0.1	1	0.3
Paspalum scrobiculatum	Native	<1	0.0	5	1.5			3	1.4
Andropogon virginicus	Non	41	6.5	38	4.0	6	1.6	2	1.3
Digitaria violascens	Non			<1	0.2			<1	0.1
Melinis minutiflora	Non	<1	0.0			<1	0.1		
Melinis repens	Non	<1	4.9	1	0.9	<1	0.2	1	0.7
Setaria gracilis	Non			<1	0.1			9	5.4
Total Understory Cover		56	6.7	59	4.7	60	3.2	79	15.8

A) 1 year postfire



B) 2 years postfire

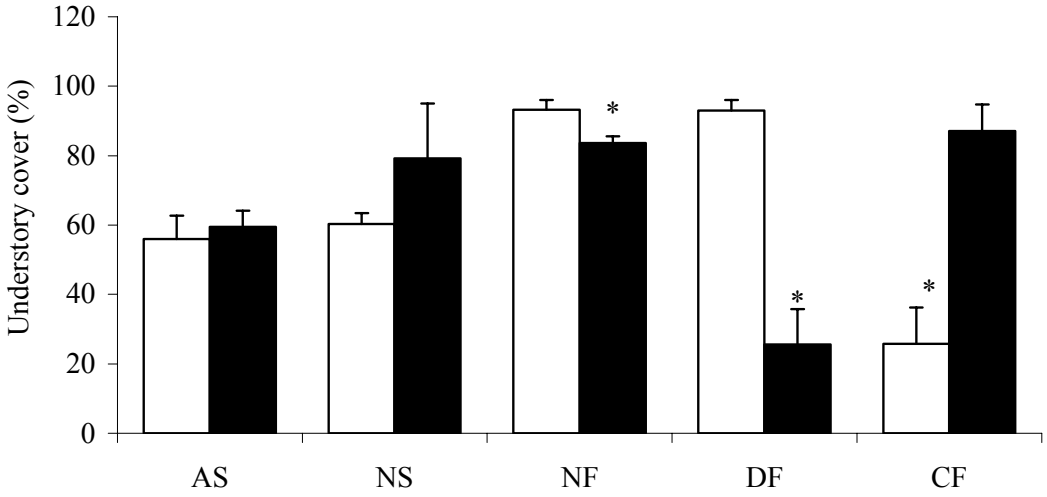


Figure 3.5. Combined understory vegetation cover in the unburned (open bars) and burned (closed bars) sites one (A) and two (B) years postfire for five vegetation communities (AS = *Andropogon* shrubland, NS = *Nephrolepis* shrubland, NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest).

this community was seedling recruitment although individuals did also survive fire by subterranean sprouting. *Dodonaea* cover (4%; $P = 0.20$) and total density (15006/ha; $P = 0.66$) did not differ between unburned and burned sites one year postfire, but the

population distribution did differ with fewer mature shrubs ($P < 0.01$) and more seedlings ($P = 0.07$) in the burned site. Despite similarities between unburned and burned sites differences in community composition existed one (A = 0.16; $P < 0.01$; MRPP) and two (A = 0.13, $P < 0.01$; MRPP) years postfire. These can be attributed to higher cover and frequency of some species in burned plots. For example, the native subshrub *Waltheria indica* was identified as an indicator species despite low cover (3%) because it was found in all burned plots two years postfire (Table 3.3).

Table 3.3. Plant species with high (>10%) importance values (IV) calculated from relative frequency and cover within each group and those identified as indicator species (ISA) based on abundance and faithfulness to a group relative to the other groups for *Andropogon* and *Nephrolepis* shrubland communities two years postfire.

Sites and Species	Life Form	Native Status	Cover (%) Mean	SE	Ave. IV	ISA
Andropogon shrubland						
Unburned						
Andropogon virginicus	Grass	Non	41	6.5	55	-
Dodonaea viscosa	Shrub	Native	10	4.1	21	-
Burned						
Andropogon virginicus	Grass	Non	38	4.0	49	-
Waltheria indica	Subshrub	Native	3	0.9	13	86.6
Dodonaea viscosa	Shrub	Native	6	2.6	12	-
Paspalum scrobiculatum	Grass	Native	5	1.5	-	99.8
Desmodium sandwicense	Grass	Non	3	0.9	-	80.0
Nephrolepis shrubland						
Unburned						
Nephrolepis multiflora	Fern	Non	33	2.9	43	-
Dodonaea viscosa	Shrub	Native	16	2.3	28	-
Andropogon virginicus	Grass	Non	6	1.6	14	-
Osteomeles anthyllidifolia	Shrub	Native	3	0.7	-	100.0
Burned						
Dodonaea viscosa	Shrub	Native	29	9.2	29	-
Nephrolepis multiflora	Fern	Non	21	8.7	23	-
Desmodium sandwicense	Subshrub	Non	12	3.2	16	99.6
Chamaecrista nictatins	Herb	Non	<1	0.1	-	90.0
Paspalum scrobiculatum	Grass	Native	3	1.4	-	80.0

Separation between unburned and burned sites were graphically displayed using NMS ordination (Fig. 3.6) where the burn effect (axis 1) represented the greatest amount of variation in the data (48%). The variable ALIEN represented the combined responses of nonnative species and was correlated with the burned plots (r = 0.59) largely due to the abundance of two nonnative herbs, *Desmodium sandwicense* and *Chamaecrista nictitans*. Indicator species analysis found these species indicators of the burned site despite low cover values (≤3%; Table 3.3) because they were found in the majority of burned plots and rarely found in unburned plots. However, the importance of *Chamaecrista* was temporary because by the second postfire year it was found in fewer of the burned plots than one year postfire (Table 3.3).

Although the variable (NATIVE) which represented the combined responses of native species was not significantly correlated with the burn axis 1 (r = 0.24), two native species *Paspalum scrobiculatum* and *Waltheria indica* were identified as indicators of the burned sites (Table 3.3). The combined response of woody species (WOODY) was not correlated with the burn axis 1 (r = 0.22), but had a strong negative correlation with axis 2 (r = -0.72). No species were identified as indicators of the unburned plots suggesting that there were few species lost via burning in this community (Table 3.3).

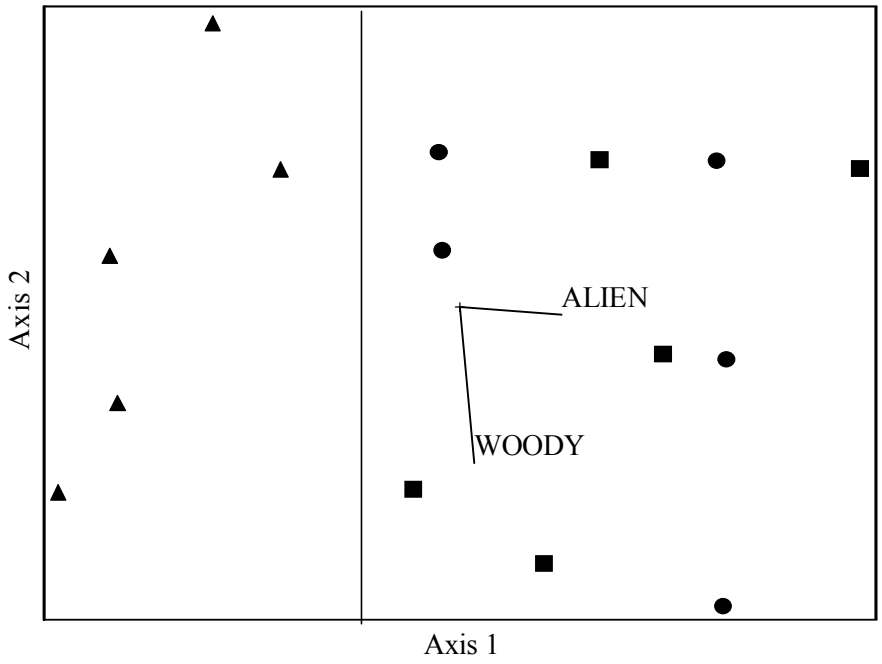


Figure 3.6. Non-metric multidimensional scaling (NMS) ordination depicting the separation of unburned (triangles) and burned plots one (squares) and two (circles) years postfire in the *Andropogon* shrubland. Joint plot overlays of environmental variables exhibit correlations of total nonnative (ALIEN) and woody (WOODY) species abundance with axes.

Nephrolepis Shrubland

In the unburned *Nephrolepis* shrubland, 25 species were found with an average of 15.2 species per plot. Over half (55%) of these species were nonnative. Understory species diversity (H') was 0.510 and evenness (*J*') was 0.43. The nonnative fern *Nephrolepis multiflora* (33%) and the native shrub *Dodonaea* (16%) were the most abundant species in the unburned site and together constituted over 82% of the total understory cover (60%; Table 3.2). *Nephrolepis* and *Dodonaea* were the most important species in the unburned site (43% and 28% respectively) because they had high relative cover values and were found in all plots within the site (Table 3.3). *Andropogon* was also

identified as important in this community because it was found in all plots with an average cover of 6%. Ten additional species were found each with <3% cover (Table 3.2) and consequently low (<10%) importance values.

In the burned site, 31 species were found and species richness per plot was lower one year postfire (11.4) than the unburned site (15.2; $P = 0.06$). However, by the second year postfire species richness (14.2) did not differ from the unburned site (15.2; $P = 0.65$). The percent of those species that were nonnative (63%) also did not differ from the unburned site (55%; $P = 0.19$). Similar to the *Andropogon* shrubland, species diversity (H') was greater in burned plots one (0.657; $P = 0.01$) and two (0.635; $P = 0.05$) years postfire than unburned plots attributed to greater evenness ($J' = 0.55$) among species during early postfire succession. The rate of vegetation recovery was similar to the rapid rate observed in the *Andropogon* shrubland. Understory cover in the burned site was 68% one year postfire and did not differ from the unburned site ($P = 0.60$; Fig. 3.5A). *Nephrolepis* (21% cover) and *Dodonaea* (29% cover) remained the most abundant species postfire. *Dodonaea* cover in the burned site also did not differ from the unburned site one year postfire ($P = 0.82$), but shrub density was 4-fold greater in burned plots (61,445/ha) than in unburned plots (13,649/ha; $P = 0.01$). *Nephrolepis* regenerated primarily by sprouting from rhizomes and one year postfire cover was >25% which did not differ from the unburned site ($P = 0.44$).

Similar to the *Andropogon* shrubland, differences in community composition between unburned and burned sites one (A = 0.23; $P < 0.01$; MRPP) and two (A = 0.20, $P < 0.01$; MRPP) years postfire are due to differences in abundance for some species. Nonnative *Desmodium* had low cover (<1%) in unburned plots and 12% cover in burned

plots two years postfire (Table 3.2). Similarly, the nonnative grass *Setaria gracilis* was not found in the unburned site and had 9% cover in the burned plots two years postfire (Table 3.2). NMS ordination shows the separation of unburned and burned plots along the burn axis 1 which explained 60% of the variation in the data (Fig. 3.7). The variable nonnative species (ALIEN) was correlated with the burned site ($r = 0.61$) and nonnative *Desmodium* and *Chamaecrista nictitans* were identified as indicators of the burned site (Table 3.3). Although the combined response of native species (NATIVE) was not significantly correlated with either axes ($r < 0.02$), the native grass *Paspalum scrobiculatum* was identified as an indicator of the burned site (Table 3.3). In contrast, the native shrub *Osteomeles anthyllidifolia* was absent from the burned site and therefore negatively correlated with axis 1 ($r = -0.81$). *Osteomeles* was identified as an indicator of the unburned site where it covered 3% of the area (Table 3.3). Similar to the *Andropogon* shrubland, the WOODY variable was negatively correlated with axis 2 ($r = -0.47$).

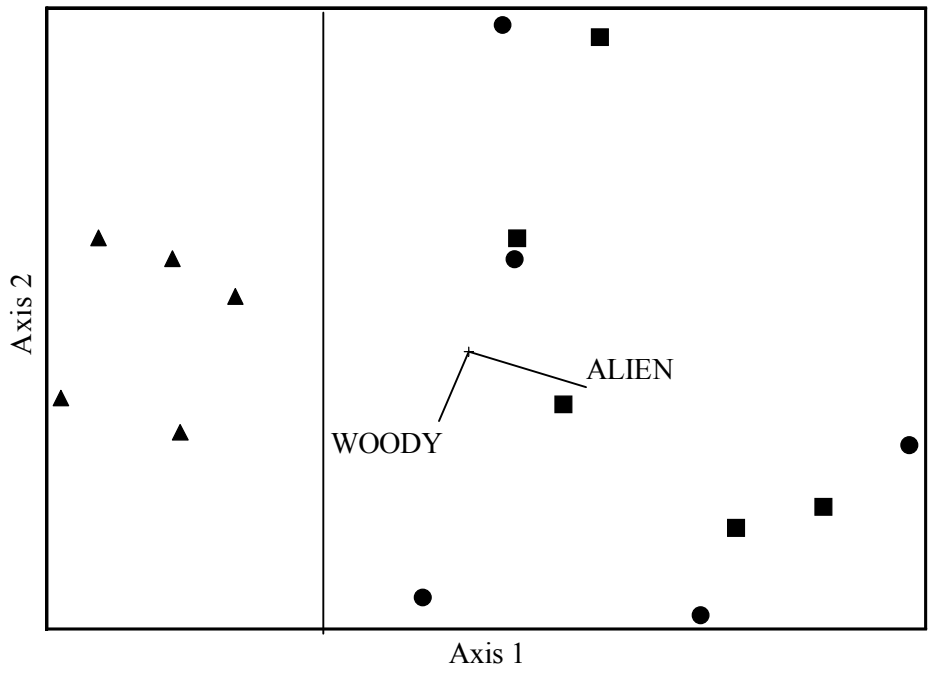


Figure 3.7. NMS ordination depicting the separation of unburned (triangles) and burned plots one (squares) and two (circles) years postfire in the *Andropogon* shrubland. Joint plot overlays of environmental variables exhibit correlations of total nonnative (ALIEN) and woody (WOODY) species abundance with axes.

Nephrolepis Forest

The nonnative fern *Nephrolepis multiflora* dominated the understory of the unburned site in this community with an average cover value of 87% which constituted over 90% of the total understory cover (Table 3.4). Twenty-one species were found with an average of 9.4 species per plot. Understory species diversity (H' = 0.100) and evenness (*J*' = 0.10) were low due to site dominance by nonnative *Nephrolepis* ferns (Table 3.5). The next most abundant species was the native fern *Nephrolepis exaltata* with a cover value of 4% (Table 3.4). Five additional species were present in the understory subplots each with <1% cover. Although nonnative species made up a small percent (22%) of the total

Table 3.4. Understory cover (%) by species in the *Nephrolepis* and *Dicranopteris* forest communities in unburned and burned sites two years postfire.

Species		*Nephrolepis* Forest				*Dicranopteris* Forest			
	Native	Unburned		Burned		Unburned		Burned	
	Status	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Shrub species									
Coprosma menziesii	Native					<1	0.0		
Dodonaea viscosa	Native							2	1.5
Leptecophylla tameiameiae	Native	1	1.0	<1	0.0	<1	0.0	<1	0.0
Pipturus albidus	Native	<1	0.1	<1	0.3			2	2.1
Vaccinium calycinum	Native					<1	0.1		
Rubus rosifolius	Non							<1	0.1
Herb/Fern species									
Cocculus trilobus	Native	<1	0.1	2	1.1	<1	0.0	<1	0.1
Dicranopteris linearis	Native	<1	0.3			91	3.4		
Nephrolepis exaltata	Native	4	2.5			1	0.4		
Pteridium aquilinum	Native							1	1.3
Sphenomeris chinensis	Native					<1	0.0	<1	0.0
Crassocephalum crepidioides	Non							<1	0.0
Desmodium sandwicense	Non			2	1.6				
Nephrolepis multiflora	Non	87	4.7	71	0.8			2	1.0
Passiflora edulis	Non			<1	0.2			11	6.0
Pityrogramma austroamericana	Non							<1	0.1
Grass/Sedge species									
Carex spp	Native							<1	0.1
Cyperus polystachyos	Native			2	0.9			<1	0.4
Isachne distichophylla	Native					<1	0.1	2	1.8
Machaerina mariscoides	Native	<1	0.1	<1	0.1	<1	0.0	2	1.4
Paspalum scrobiculatum	Native			<1	0.1				
Andropogon virginicus	Non			<1	0.0			<1	0.1
Axonopus fissifolius	Non							<1	0.1
Digitaria violascens	Non			1	0.6			<1	0.1
Kyllinga brevifolia	Non			<1	0.0				
Paspalum conjugatum	Non			5	3.3	1	0.5	3	1.8
Setaria gracilis	Non			<1	0.0	<1	0.0		
Total Understory Cover		93	8.8	84	2.0	93	3.1	26	10.2

species richness, nonnative abundance at the site was very high due to the overwhelming dominance of *Nephrolepis multiflora.*

Fire affected the understory community composition such that burned plots significantly differed from unburned plots postfire (1 year: A = 0.13; $P < 0.01$; 2 years: A = 0.08, $P = 0.01$; MRPP). There were nearly twice as many species in the burned site (40) two years after fire than the unburned site. Increased species richness was due to increased nonnative species richness, four nonnative species were found in the unburned site and 27 were found in the burned site two years postfire. Average species richness per plot (17.6; $P < 0.01$), understory diversity (0.233; $P = 0.03$), and evenness ($J' = 0.19$) were also greater than in the unburned site (S = 9.4 species, H' = 0.100, $J' = 0.10$). Combined understory cover was lower in the burned site one (64 %; $P <0.01$) and two (84 %; $P = 0.02$) years postfire than the unburned site but, increased significantly between years ($P = 0.01$; Fig. 3.5A-B). *Nephrolepis multiflora* was the dominant species in the understory of the burned site (>84%) and was present in all plots postfire (Table 3.5). Two years postfire, cover was recorded for 13 additional species in the burned site, but only the nonnative grass *Paspalum conjugatum* had cover exceeding 2% (Table 3.4). NMS analysis of one year postfire data delineated the separation between unburned and burned plots (Fig. 3.8). However, the burn axis 1 (38%) was not more important than axis 2 (44%) in explaining variation in the understory composition. This suggests that the effect of the burn on understory composition was only weakly detected one year postfire due to the rapid recovery of *Nephrolepis multiflora*. The variable nonnative species (ALIEN) was not significantly correlated with the burn axis (r = 0.26). *Nephrolepis multiflora* was negatively correlated (r = -0.81) and identified as an indicator

of the unburned site because abundance and frequency were higher in the unburned site (Table 3.5). The combined responses of native species (NATIVE) was strongly correlated with axis 1 (r = 0.75) due to the colonization of a native sedge, *Cyperus polystachyos*, and native herb, *Solanum americanum* (r >0.60). *Cyperus* was identified as an indicator of the burned site (Table 3.5). Few shrubs were encountered in this community (67 – 266/ha) and densities did not differ between treatments ($P > 0.23$).

Table 3.5. Plant species with high (>10%) importance values (Ave. IV) calculated from relative frequency and cover within each group and those identified as indicator species (ISA) based on abundance and faithfulness to a group relative to the other groups for *Nephrolepis, Dicranopteris* and *Cibotium* forest communities two years postfire.

Sites and Species	Life Form	Native Status	Cover (%) Mean	SE	Ave. IV	ISA
Nephrolepis forest						
Unburned						
Nephrolepis multiflora	Fern	Non	87	4.7	85	55.1
Burned						
Nephrolepis multiflora	Fern	Non	71	0.8	67	-
Paspalum conjugatum	Grass	Non	5	3.3	10	100.0
Cyperus polystachyos	Sedge	Native	2	0.9	-	80.0
Dicranopteris forest						
Unburned						
Dicranopteris linearis	Fern	Native	91	3.4	91	100.0
Burned						
Passiflora edulis	Vine	Non	11	6.0	24	-
Nephrolepis multiflora	Fern	Non	2	1.0	23	100.0
Machaerina mariscoides	Sedge	Native	2	1.4	10	99.5
Cibotium forest						
Unburned						
Dicranopteris linearis	Fern	Native	22	10.7	44	-
Paspalum conjugatum	Grass	Non	2	1.4	24	-
Alyxia oliviformia	Vine	Native	<1	0.2	-	80.0
Burned						
Paspalum conjugatum	Grass	Non	73	7.7	62	97.0
Nephrolepis multiflora	Fern	Non	6	1.4	15	96.8
Dodonaea viscosa	Shrub	Native	2	1.3	-	80.0

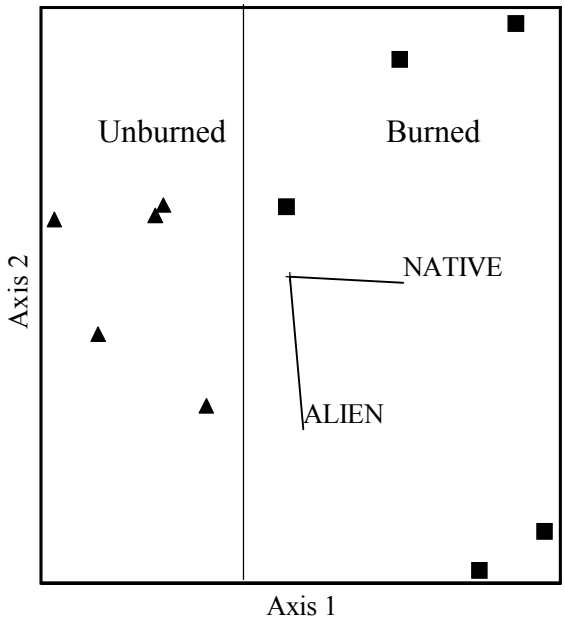


Figure 3.8. NMS ordination depicting the separation of unburned (triangles) and burned plots one year (squares) postfire in the *Nephrolepis* forest. Joint plot overlays of environmental variables show correlations of total native (NATIVE) and nonnative (ALIEN) species abundance with axes.

Dicranopteris Forest

The native fern *Dicranopteris linearis* dominated the understory of the unburned site with an average cover value of 91% (Table 3.4). A total of 29 species were found with an average of 12.8 species per plot. Species diversity (H' = 0.039) and evenness (*J*' = 0.04) were low due to site dominance by *Dicranopteris* ferns. Although ten additional species were recorded in the understory subplots, together they constituted < 2% of the total cover (Table 3.4). Few nonnative species were present and together they constituted < 1% of the total understory cover.

Fire resulted in the most significant and dramatic change in community composition and structure of any of the sampled communities (1 year: A = 0.22; $P <$ 0.01; 2 years: A = 0.24, $P < 0.01$; MRPP). In the burned site, two years postfire 48

species were found and average species richness per plot (23.2; $P = 0.07$), diversity (H' = 0.592; $P = 0.01$), and evenness ($J' = 0.39$) were greater than in the unburned site (S = 12.8; H' = 0.039; $J' = 0.04$). In addition, total understory vegetation cover was dramatically lower in the burned site both one (<1%; $P = 0.01$) and two (26%; $P < 0.01$) years postfire (Fig. 3.5A-B). *Dicranopteris* was absent and nonnative species were the most abundant species following fire. Two years postfire, the nonnative vine *Passiflora edulis* was the most abundant species (11% cover) and had the highest importance value of any species in the community based on relative frequency and abundance (Table 3.5). Several species had 2-3% cover values (Table 3.4), but the nonnative fern *Nephrolepis* and the native sedge *Machaerina mariscoides* were the only species other than *Passiflora* with high (>10%) importance values because they had high frequency values within the community (Table 3.5). The percent of species that were nonnative was greater in the burned site (> 46%) than the unburned site (<1 %) both years postfire ($P < 0.01$).

NMS analysis and ordination graphically illustrate the separation of plots in unburned and burned sites one and two years postfire along axis 1 (Fig. 3.9). Nonnative species (ALIEN) were correlated with axis 1 (r = 0.58), due to the combined effect of many weakly correlated (0.37 < r < 0.45) species including *Passiflora*, *Nephrolepis*, two grass species (*Andropogon* and *Digitaria violescens*), and a shrub species (*Rubus roseafolius*). Two years following fire, *Nephrolepis* was identified as an indicator of the burned site using indicator species analysis. The combined responses of native species (NATIVE) was not significantly correlated with axis 1 (r = -0.27). The extremely high negative correlation of the unburned indicator species *Dicranopteris* with axis 1 (r = -0.96) was offset by weak positive correlations of many native species including

Machaerina mariscoides, which was also identified as an indicator of the burned plots two years postfire (Table 3.5). The WOODY variable was not significantly correlated (r = 0.18) with the burn axis 1 because shrub cover was sparse in unburned and burned plots. In the unburned site two native shrubs, *Leptecophylla* and *Coprosma menziesii*, were encountered in only one plot. In the burned plots four native shrub species (*Dodonaea*, *Leptecophylla*, *Pipturus albidus*, and *Vaccinium reticulatum*) and one nonnative shrub species (*Rubus roseafolius*) established from seed in the postfire environment. However, no single shrub species had cover > 1% or were found in more than 2 of the 5 plots sampled in the burned site.

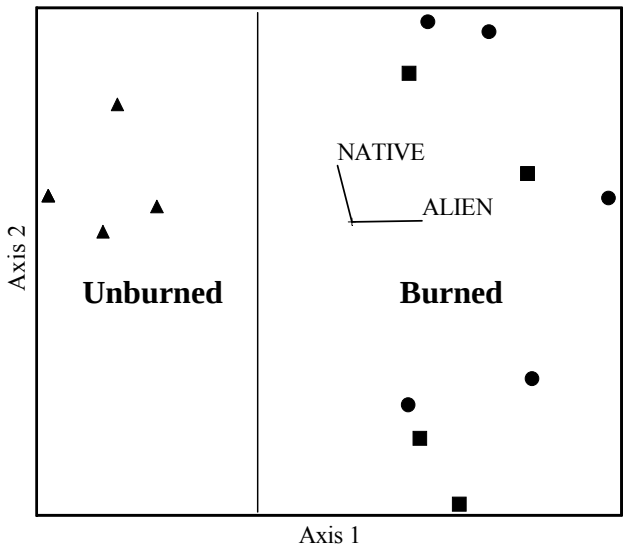


Figure 3.9. NMS ordination depicting the separation of unburned (triangles) and burned plots one (squares) and two (circles) years postfire in the *Dicranopteris* forest. Joint plot overlays of environmental variables show correlations of total native (NATIVE) and nonnative (ALIEN) species abundance with axes.

Cibotium Forest

Species richness was higher in this community than any of the previous unburned communities with a total of 35 species encountered and an average of 24.4 species per

plot. Understory species diversity (H' = 0.218) and evenness (J' = 0.16) were also higher than the previous forest communities. Total understory cover was relatively sparse with a combined cover value of 26%. The native fern *Dicranopteris* was the most abundant species in the understory with a cover value of 11% which constituted 85% of the total understory cover (Table 3.6). The nonnative grass *Paspalum conjugatum* was the next most abundant species with 2% cover, accounting for 8% of the total vegetation understory cover. Despite low cover, *Paspalum* had a high importance value (15%) because it was present in all sampled plots in the unburned forest (Table 3.5). Eleven additional species were present in the understory, but together constituted < 3% cover (Table 3.6). Together nonnative species accounted for 10% of the total understory cover. The effects of fire on understory community composition were substantial such that unburned and burned sites significantly differed postfire (1 year: A = 0.13; $P < 0.01$; 2 years A = 0.15, $P < 0.01$; MRPP). In the burned plots, the number of species found (57) two years postfire was 63% greater than in the unburned plots. Total species richness per plot was greater one (31.6; $P = 0.03$) and two (31.4; $P = 0.05$) years postfire than the unburned site (24.4), but understory diversity (1 year: 0.311; 2 years: 0.292) did not differ from that in the unburned site (H' = 0.218; $P > 0.35$). Evenness was similar between the burned ($J' = 0.20$) and the unburned sites ($J' = 0.16$). Understory recolonization was rapid such that total understory cover was greater in the burned plots one (44%; $P = 0.28$) and two (87%; $P < 0.01$) years postfire than the unburned plots (26%; Fig. 3.5A-B). Higher understory cover in the burned plots can be attributed to colonization and range expansion of the nonnative species *Paspalum conjugatum.* This grass was the most abundant species (73% cover) and made up over 80% of the total understory cover as

Table 3.6. Understory cover (%) by species in the *Cibotium* forest community in unburned and burned sites two years postfire.

Species		*Cibotium* Forest			
	Native	Unburned		Burned	
	Status	Mean	SE	Mean	SE
Shrub species					
Broussaisia arguta	Native	<1	0.1		
Coprosma menziesii	Native	<1	0.3	<1	0.1
Dodonaea viscosa	Native			2	1.3
Labordia hedyosmifolia	Native	<1	0.0		
Pipturus albidus	Native			<1	0.0
Vaccinium calycinum	Native	<1	0.0		
Buddleia asiatica	Non			1	0.8
Pluchea symphytifolia	Non			<1	0.0
Rubus rosifolius	Non			<1	0.3
Herb/Fern species					
Cocculus trilobus	Native	<1	0.0	<1	0.1
Dicranopteris linearis	Native	22	10.7	<1	0.0
Psilotum complanatum	Native	<1	0.0		
Cuphea carthagenensis	Non			<1	0.0
Erechtites valerianifolia	Non			<1	0.0
Nephrolepis multiflora	Non	<1	0.2	6	1.4
Passiflora edulis	Non			1	0.7
Pityrogramma austroamericana	Non			<1	0.0
Sphenomeris chinensis	Non			<1	0.2
Grass/Sedge species					
Carex wahuensis	Native	<1	0.0		
Cyperus polystachyos	Native			<1	0.2
Isachne distichophylla	Native	<1	0.0	1	1.1
Machaerina mariscoides	Native	<1	0.0	<1	0.2
Paspalum scrobiculatum	Native			1	0.7
Andropogon virginicus	Non	<1	0.2	<1	0.4
Melinis minutiflora	Non			<1	0.0
Paspalum conjugatum	Non	2	1.4	73	7.7
Setaria gracilis	Non			<1	0.2
Total Understory Cover		26	10.5	87	7.6

compared to 8% in the unburned plots (Table 3.6). Similarly, *Nephrolepis multiflora* had <1% cover in the unburned plots, but was the second most abundant species (6% cover)

in the burned plots (Table 3.6). *Nephrolepis multiflora* was the only other species with an importance value >10% based on relative abundance within the plot and frequency among plots (Table 3.5). Twenty additional species were present in the understory each with cover values <3% (Table 3.6). Over 40% of the species encountered were nonnative and together constituted over 90% of the total cover during early postfire succession.

Separation between unburned and burned sites were graphically displayed in the NMS ordination (Fig. 3.10) with the burn effect (axis 1) representing the majority of the variation in the data (56%). The combined responses of nonnative species (ALIEN) was highly correlated with the burned plots (r = 0.89) largely due to the abundance of *Paspalum* and *Nephrolepis* (r > 0.67). Although combined native species abundance (NATIVE) was not correlated with the burn (r = -0.13), three native species were negatively correlated with axis 1 including: *Dicranopteris* (r = -0.59), *Alyxia oliviformis* (r = -0.55) and *Carex wahuensis* (r = -0.47). *Alyxia* was the only species identified as a significant indicator of the unburned site (Table 3.5). The combined response of understory woody species (WOODY) was not significantly correlated with either axis (r < 0.45). Total shrub density was higher in burned plots one year postfire (2,734/ha; P = 0.09), but by the second year did not differ (800/ha; P = 0.16) from the unburned plots (333/ha). The most abundant shrubs in the burned site postfire, native *Dodonaea* and nonnative *Rubus*, were not found in the unburned site.

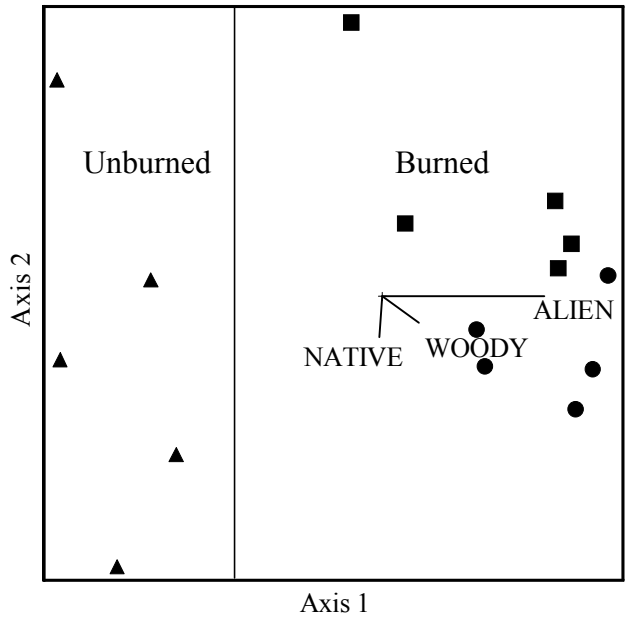


Figure 3.10. NMS ordination depicting the separation of unburned (triangles) and burned plots one (squares) and two (circles) years postfire in the *Cibotium* forest. Joint plot overlays of environmental variables show correlations of total native (NATIVE), nonnative (ALIEN), and woody (WOODY) species abundance with axes.

DISCUSSION

Community Invasibility

The fires of this study were stand-replacing in all five vegetation communities. However, the effects of fire greatly differed among communities. The greatest differences in composition and structure were observed in the forest communities that had a native understory composition prior to fire. In contrast there were fewer changes in the shrubland communities.

Fire dramatically altered community composition and structure in the higher elevation native-dominated forest communities (*Dicranopteris* and *Cibotium* forests) by

creating opportunities for recruitment of a different suite of both native and nonnative species to occur that were adapted to establish in the postfire environment. It was originally hypothesized that increases in nonnative species abundance following fire would be greatest in these two native-dominated forest communities. Prior to fire, the native fern *Dicranopteris* was the most abundant species in both communities, but was virtually absent during early postfire succession (Table 3.4-3.6) and nonnative species richness was increased. In contrast, previous studies in Sri Lanka have suggested that *Dicranopteris linearis* survives fire because the rhizomes are fire-resistant (Maheswaran and Gunatilleke 1988, Ashton et al. 2001). However, others have reported that ferns in the *Dicranopteris* genus including *Dicranopteris linearis* do not regenerate from roots following fire (Holttum 1957, Walker and Boneta 1995), anthropogenic land clearing (Slocum et al. 2004), or insect-caused dieback (Follet et al. 2003). Following a previous wet forest fire (<10 ha) in Hawaii, *Dicranopteris linearis* regained understory dominance, but recovery took over ten years (Tunison et al. 2001). In this study, it may require more time for *Dicranopteris* to regain understory dominance in the *Dicranopteris* and *Cibotium* communities than in the previous studies because the fire was substantially larger leaving few unburned patches and large distances from unburned edges.

Nonnative species dominance in the *Dicranopteris* and *Cibotium* understories following fire could be of particular concern because the order of arrival following disturbance in some instances dictates which species dominate a site (Connell and Slatyer 1977). Prior to fire, *Dicranopteris* dominated the understory in the *Dicranopteris* forest (Table 3.4), likely excluding nonnative species invasion (Russell et al. 1998). In the *Cibotium* forest, *Dicranopteris* was also the most abundant species (Table 3.6), but cover

was substantially lower than in the *Dicranopteris* forest. Following fire the most widespread species in both communities were nonnative and included *Nephrolepis multiflora* and *Paspalum conjugatum* (Table 3.4-6). *Paspalum* cover was extremely high (73%) two years postfire in the *Cibotium* forest. Alternatively, cover for all understory species was low in the *Dicranopteris* forest postfire, but the most important species based on relative cover and frequency among plots were nonnative including *Nephrolepis multiflora*. Both species were found in the unburned plots and were recorded in these forests in the late 1980's (Pratt et al. 1999), but with lower relative cover values. Similarly, *Nephrolepis multiflora* was also one of the most common species colonizing and spreading in *Dicranopteris* dieback areas on Maui, Oahu and Kauai Islands (Follet et al. 2003).

Fire in the *Nephrolepis* forest community also dramatically altered the forest structure by top-killing the overstory *Metrosideros* canopy. However, the effects of fire on the understory composition and structure were less pronounced than in the *Dicranopteris* and *Cibotium* forest communities (Fig. 3.4). The nonnative fern, *Nephrolepis multiflora*, was present prior to fire, and recovered rapidly and maintained site dominance following fire (Table 3.5). Species richness and diversity were greater in burned than unburned sites but, *Nephrolepis multiflora* remained the most abundant species. While this species is clearly quite resilient following fire few studies have documented this. This fern was reported to dominate abandoned pastures that had a recent history of fire in Puerto Rico (Aide et al. 1995, Rivera and Aide 1998) and the Dominican Republic (Rivera et al. 2000). In addition, two different *Nephrolepis* species were found to be abundant in understory communities across the Pacific in sites that had

been selectively logged (Kingston and Waldren 2003), in forest gaps within sites (Whistler 1994), and following hurricanes (Halleck et al. 2004).

In the nonnative-dominated *Andropogon* and *Nephrolepis* shrubland communities few new species were present in the burned sites. The observed increase in species diversity merely reflects an increase in evenness among species due to the reduction in the abundance of the dominants (Table 3.2). The shrubland communities are likely less vulnerable to new species invasions because they have previously been disturbed by fire and the species now dominant are adapted to shorter fire-return intervals (Kauffman 1990).

Do Nonnative Species Inhibit Native Species Recovery?

Invasive species can change the ecosystem response to fire (Mack and D'Antonio 1998). Nonnative species can influence native species recovery and colonization after fire through physical domination of the site and by utilization of limiting resources. In this study, *Metrosideros* recovery and colonization were slower in communities where nonnative species were abundant in the understory during early postfire succession. Nonnative understory herbaceous grass and fern species rapidly occupied the site and physically dominated the postfire environment in the understory of four of the five sampled vegetation communities. Postfire nonnative species site dominance occurred through two pathways: (1) rapid recovery of nonnative grasses and ferns in previously invaded sites (e.g., *Andropogon* shrubland, *Nephrolepis* shrubland, and *Nephrolepis* forest), and (2) colonization and range expansion of nonnative species into previously native-dominated sites (e.g., *Cibotium* forest). In the three lower elevation communities

(shrublands and invaded *Nephrolepis* forest) nonnative grass (*Andropogon*) and fern (*Nephrolepis multiflora*) species present prior to fire recovered rapidly from basal sprouts as predicted. Alternatively, in the highest elevation *Cibotium* community that was native-dominated prior to fire, nonnative grasses invaded and expanded rapidly following fire resulting in dramatic increases in understory cover (Fig. 3.5B). Prior to fire, the dense tree fern subcanopy likely limited understory colonization of herbs by decreasing light on the forest floor (Burton and Mueller-Dombois 1984) and by limiting suitable substrate for germination for some species due to the thick slow decomposing frond litter (Russell and Vitousek 1997). Although tree fern survival was extremely high (>90%), fire temporarily decreased these barriers to colonization by consuming the dense frond litter layer thus altering seedbed conditions and nonnative *Paspalum conjugatum* grass quickly dominated the understory.

Physical site dominance by herbaceous understory species can limit available space for slower growing native species to establish (D'Antonio and Vitousek 1992, Aide et al. 1995, Cabin et al. 2000, Corbin and D'Antonio 2004). In this study, native woody seedling densities (*Dodonaea* and *Metrosideros*) were greater in the burned sites than unburned sites in the *Nephrolepis* and *Dicranopteris* forests (Chapter 2) where understory cover was lower two years postfire (Fig. 3.5B). In the *Cibotium* forest, *Metrosideros* and *Myrsine lessertiana* seedling densities were lower in the burned site (Chapter 2) where understory cover was greater than the unburned site (Fig. 3.5B). These results suggest that high herbaceous cover in the understory (e.g., preburn *Nephrolepis* and *Dicranopteris* and postburn *Cibotium* forests) may inhibit native woody seedling establishment. However, when comparing among the three burned forest communities

no differences were detected in *Dodonaea* and *Metrosideros* seedling densities. These results suggest that barriers to seedling recruitment were similar among communities following fire despite differences in understory recolonization at least during early postfire succession.

The thick litter layer that was not consumed by the fire in the *Dicranopteris* forest community appeared to inhibit species invasion following fire. Greater amounts of unconsumed surface fuel remained in this community as compared to the other communities (C. M. Litton, pers. comm.). In addition, the remaining fuel, primarily a dense litter mat of *Dicranopteris*, was slow to decompose and may effect forest regeneration by limiting light and space on the forest floor (Maheswaran and Gunatilleke 1988, Russell and Vitousek 1997). Seedling germination was inversely proportional to *Dicranopteris* litter depth in a decomposition experiment in Hawaii (Follet et al. 2003). In this study, invading nonnative or native species may gain dominance in the understory of the *Dicranopteris* forest community as the remnant litter layer gradually decomposes. However, it is also possible that *Dicranopteris* ferns may regain dominance over time.

Nonnative species may inhibit the growth and survival of newly established and surviving native species during early postfire succession via superior growth rates and a greater capacity to exploit resources (e.g., light, water, and nutrients). *Metrosideros* recovery, quantified as basal sprout volume, was greatest two years following fire in the native *Dicranopteris* forest (Fig. 3.2B), where understory was much lower than the other two forest communities (Fig. 3.5B). Postfire vegetation composition and cover of the understory in the *Nephrolepis* and *Cibotium* forests was largely that of *Nephrolepis multiflora* and grass invasion, respectively. In these communities *Metrosideros* sprout

growth was greatly reduced (Table 3.1). These results suggest that the rapid establishment of a nonnative-dominated understory decreases the growth of *Metrosideros* regrowth. High tree fern survival and cover may also have contributed to reduced *Metrosideros* regrowth in the *Cibotium* forest community as compared to the other forest communities. In dry woodland sites in Hawaii Volcanoes National Park, nonnative grasses successfully competed for light with native shrub seedlings (Hughes and Vitousek 1993). Further, following grass removal *Metrosideros* and native shrub species demonstrated a strong growth response and increase in seedling recruitment (D'Antonio et al. 1998, Mack and D'Antonio 2003a).

Implications of Fire and Nonnative Species Invasions

The implications of the interactions of fire and nonnative species invasions differed across this elevation/composition gradient. The two lowest elevation shrubland communities (*Andropogon* and *Nephrolepis*) characterize communities in which nonnative grass and fern invasion coupled with ignitions, nonnative ungulates during the past 50 years, and dry conditions have resulted in grass/fern-fire cycles (D'Antonio and Vitousek 1992). Human disturbances, including nonnative species invasions, ungulates, and fire have contributed to the loss of native *Metrosideros* woodlands. Scattered snags and large downed logs on the landscape provide further evidence of the effects of past fires on forest structure in these communities. The conspicuous lack of trees and shrubs except for *Dodonaea* in the unburned sites where fire has not occurred in over 10 years suggests that postfire site dominance by nonnatives persists for many years. The nonnative fern *Nephroplepis multiflora* has dominated abandoned pasture lands for at

least ten years in the Dominican Republic, and likely much longer (Rivera et al. 2000). Similarly, in the dry woodlands of Hawaii Volcanoes National Park, *Dodonaea* and nonnative grasses still dominate former woodland sites that burned over 30 years ago (D'Antonio et al. 2001). Reduced light levels under nonnative grasses (Hughes and Vitousek 1993) and degraded soil conditions including dramatic reductions of N inputs via fixation in grasslands versus unburned woodlands (Ley and D'Antonio 1998, Mack and D'Antonio 2003b) following repeated fires and grass invasion limit the reestablishment of native woody species in this system. These are also likely to be factors limiting reestablishment in our shrub-dominated study sites.

In the *Nephrolepis* forest, nonnative *Nephrolepis multiflora* site dominance appeared to be enhanced by fire. My findings suggest that the rapid recovery of *Nephrolepis multiflora* which physically dominated the understory decreased the re-growth of those *Metrosideros* individuals that did survive fire. Although over half of the *Metrosideros* canopy trees survived fire by sprouting, it is unclear whether they will reestablish a native canopy, especially considering the sprout mortality between the first and second postfire years. In either case, the occurrence of another fire in this community in the near term may convert this remnant woodland into a nonnative *Nephrolepis multiflora* and native *Dodonaea viscosa* shrubland resembling the adjacent *Nephrolepis* shrubland community.

The native *Dicranopteris* forest community was largely intact prior to fire and the majority of trees survived fire by sprouting (>70%). A more rapid regrowth of sprouting *Metrosideros* is expected due to a lesser amount of competition by understory species. However, fire created the opportunity for nonnative ferns to invade the understory thus

expanding the invasion front. If *Nephrolepis multiflora* increases in abundance the burned native *Dicranopteris* forest could resemble the preburn nonnative *Nephrolepis* forest with a native canopy and a mono-dominant nonnative fern in the understory. Alternatively, native *Dicranopteris linearis* may overtop the nonnative grasses and ferns during the next ten years as was observed in a previous smaller fire in the area (Tunison et al. 2001). The future understory composition of this community is uncertain, but the presence of nonnative ferns, coupled with future fires, may alter native forest succession.

The occurrence of fire in the *Cibotium* community created the opportunity for nonnative herbaceous species to expand their range by consuming litter and temporarily decreasing both the *Metrosideros* canopy and *Cibotium* subcanopy. The long term persistence and impact of nonnative *Paspalum conjugatum* grass in the understory is unknown. Unlike the lower elevation mesic forests, *Cibotium* dominated the subcanopy and over 90% survived the fire. Therefore, much of the frond canopy reestablished within a year and now competes for light and nutrients with the understory. Recovery of the tree fern canopy may inhibit establishment and growth of *Metrosideros* trees (Burton and Mueller-Dombois 1984) resulting in a modified community dominated by tree ferns and lacking an emergent *Metrosideros* canopy. Similar to the *Dicranopteris* forest community, the occurrence of additional fires would likely result in increased nonnative species abundance and loss of native forest components. This is a possible scenario with global change. However, under current conditions higher elevation forests are less likely to be readily type converted into nonnative-dominated shrubland communities because higher precipitation and cooler temperatures (Giambelluca et al. 1986) would be less likely to carry fire.

CONCLUSIONS

As predicted, fire facilitated the spread of nonnative species into previously native-dominated understories (*Dicranopteris* and *Cibotium* forests). Some native species also invaded and increased in abundance following fire in these communities, but the most abundant and widespread species were nonnative during early postfire succession. Canopy recovery was significantly slower in forests where nonnative species were abundant during early postfire succession (*Nephrolepis* and *Cibotium* forests) implying that the presence and widespread success of invasive grasses and ferns impacts the structural development of these communities following fire through competition for limiting resources. In the *Cibotium* forest, surviving tree fern individuals also likely compete with *Metrosideros* basal sprouts for resources. Lastly, in the lowest elevation shrubland communities fire had little effect on vegetation composition and structure. These communities were previously modified by past fires. Notably absent from these communities were young native tree species suggesting that native forest recovery was not occurring. These communities demonstrate how nonnative species invasions coupled with repeated fires may alter successional trajectories such that native forest recovery is not likely.

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CHAPTER 4. EFFECTS OF REPEATED FIRES ON NATIVE PLANT COMMUNITY SUCCESSION AT HAWAII VOLCANOES NATIONAL PARK

Alison Ainsworth

ABSTRACT

Fires are a relatively rare event in tropical wet forests and fires in rapid succession represent an uncommon disturbance with significant influences on forest structure and function. Few studies have examined influences of wildland fire in tropical lowland wet forests and even fewer have examined repeated fires in these ecosystems. I had the opportunity to study the effects of this extreme event following the Kupukupu fire in 2002 and the Luhi fire in 2003 at Hawaii Volcanoes National Park. To examine the effects of repeated wildfires (2002-2003) on forest composition and structure, I established replicate plots (n=5) in two native communities which were mesic *Metrosideros polymorpha*/ *Dicranopteris linearis* and wet *Metrosideros*/ *Cibotium glaucum* forests. The first fire was stand replacing where over 95% of the dominant *Metrosideros polymorpha* trees were top-killed. The occurrence of a second fire dramatically increased mortality of *Metrosideros*. In the *Dicranopteris* community, 71% of *Metrosideros* trees survived a single fire, but only 22% survived repeated fires. Similarly in the *Cibotium* community, *Metrosideros* survival was reduced from 48% to 6% following repeated fires. Vegetative survival of the native tree fern *Cibotium glaucum* was also significantly reduced from 93% following a single fire to 56% following a second fire. *Metrosideros* seedling recruitment did not differ between forests that burned once and forests that burned twice. The composition of the understory in both of the sampled communities following repeated fires differed from that of forests that burned once and unburned control forests. Repeated fires resulted in lower *Metrosideros* survival, no significant increase in seedling establishment, and rapid

occupation by aggressive herbaceous species, all of which may delay, or even prevent, recovery to native forest dominance.

INTRODUCTION

Across the Hawaiian Islands, little information exists regarding the historic role of natural fires and to what extent fire influenced the evolution of the native flora. A handful of studies that examined pollen (Burney et al. 1995) and charcoal data (Mueller-Dombois 1981b) show that wildfires occurred in Hawaii prior to Polynesian settlement. In addition, the occurrence of natural ignition sources including lightning and volcanism, continuous vegetation cover in many ecosystems, and periodic weather conditions that would facilitate fire, further suggests that fire did occur historically and did influence the disturbance history of many island ecosystems. The frequency and severity of fires would vary depending on climate, fuel loads and ignition source and little is known on these aspects of fire history in Hawaii. In particular few observations or studies have been conducted on fire and fire effects in the mesic and wet forests. Even less is known about the extreme potential effects on community dynamics of repeated fires in these forests. This is important because fire will probably occur more frequently in Hawaii in the future with increasing human populations, invasive species, and the cascading effects associated with changing climatic conditions. With increases in the frequency of disturbance such as fire, the direct effects of each disturbance event are likely to influence community composition more than traditional successional processes that occur between disturbance events (Zedler et al. 1983).

Variation in the frequency of disturbance such as a reduced fire-return interval may substantially influence species capacity to survive or persist following fire. When fire frequency becomes too high and the fire cycle is shorter than the reproduction cycle for obligate-seeder species, selective extinction is unavoidable (Bradstock and Myerscough 1988). Resprouting responses have also been shown to differ between single and repeated fires (Arthur et al. 1988). Two tree species that were abundant following a single fire in Mexico substantially increased in dominance following repeated fires because not all species present in the tropical forest had the capacity to survive such an extreme event (Miller and Kauffman 1998). Similarly, Slik and Echhorn (2003) observed that rain forest recovery in Indonesia was increasingly difficult with successive fires because species were disproportionately affected. Tropical forest tree densities, live biomass and canopy cover were found to decrease with increasing fire frequency in the Eastern Amazon (Cochrane and Schulze 1999).

Successive fires, particularly those at intervals of only one year have reduced woody species densities significantly in both temperate (Zedler et al. 1983) and tropical zones (Cochrane 2003). Increases in fire frequency typically lead to the dominance of species with short life-cycles such as herbaceous annual species (Keeley 1981). Repeated fires increase herbaceous, often nonnative species cover, and decrease woody density in eastern pine systems (Arthur et al. 1988, Cain et al. 1998, Beckage and Stout 2000), and California chaparral (Zedler et al. 1983). These ecosystems have relatively short fire return intervals to begin with, but successive fires in a few years were considered extreme events that threatened the survival of some species and altered succession (Zedler et al. 1983).

Hughes et al. (1991) compared vegetation between forests burned once and forests burned twice with a seventeen year return interval in the seasonally dry woodland at Hawaii Volcanoes National Park. Fifteen months following fire, the forest that burned twice had greater nonnative grass cover and fewer native woody species than the forest that burned once. Repeated fires in the mesic and wet forest may differ in their effects on native species due to differences in fire frequency, fire characteristics, and climate.

The recent Kupukupu (2002) and Luhi (2003) wildfires at Hawaii Volcanoes National Park provided the opportunity to compare the effects of the extreme disturbance of two repeated fires with those of a single fire relative to unburned control sites in mesic and wet forests. The objective of this study was to examine the effects of two successive lava ignited wildfires on the survival and recovery of species in two native forest communities. I hypothesized that the occurrence of a second fire within one year would result in a more impoverished native flora because sprouts from native surviving trees would be killed by the second fire. I predicted that the effects of repeated fires would be similar between the *Dicranopteris* and *Cibotium* forests. Specifically, in both communities I predicted that twice burned forests would have reduced individual survival of dominant woody species and greater nonnative herbaceous cover than forests that only burned once. I predicted that seedling recruitment would differ between once and twice burned forests due to differences in seed beds.

METHODS

Study Site

This study was conducted in mesic (*Metrosideros polymorpha*/ *Dicranopteris linearis)* and wet (*Metrosideros*/ *Cibotium glaucum*) lowland forests (Wagner et al. 1990) previously described in Chapter 2. These forests range from 550m to 825m in elevation along the southeastern flank of Kilauea Volcano (Fig. 2.1; 19° 20' 11" N and 155° 7' 29" W) in Hawaii Volcanoes National Park, Island of Hawaii. Substrates are 400 to 750 year-old pahoehoe lava flows (Trusdell et al. 2005). Soils are shallow (5-50cm) and were formed in ash deposited over pahoehoe with minimal slope (2-10%). The mesic forest community is lower in elevation and conditions are slightly warmer (19° C), and drier (2160mm mean annual rainfall) than those found in the wet forest community (18° C; 2800mm mean annual rainfall)(Jasper In press).

The two forest communities have *Metrosideros* as the mono-dominant canopy species and differ in elevation and understory composition. The *Metrosideros*/ *Dicranopteris* mesic forest (640-750m), referred to as the "*Dicranopteris* forest", has over 850 trees (>10 cm diameter at breast height) per hectare and contains the native mat forming fern *Dicranopteris* in the understory. The *Metrosideros*/ *Cibotium* wet forest (700-850m), referred to as the "*Cibotium* forest", has a more open overstory canopy (~500/ha). Native tree ferns *Cibotium* form a dense midstory (~2800/ ha) with variable fern and grass species in the understory.

On 17 May 2002 the Kupukupu Fire burned 345 ha of *Cibotium* wet forest. An additional 1020 ha of *Dicranopteris* mesic forest and *Dodonaea viscosa/ Nephrolepis*

multiflora shrubland communities burned between 31 May and 2 June 2002. The fire was contained by August and had burned 1538 hectares. Fire in the forested areas was wind driven and was largely carried by fine fuels consisting of *Nephrolepis* and *Dicranopteris* (Gassaway et al. 2002). Gassaway et al. 2002 reported the postfire burn severity on the understory vegetation, litter/duff layer and canopy following methods described in the draft version of the Fire Monitoring Handbook (USDI National Park Service 2003). In the *Dicranopteris* and *Cibotium* communities, most of the vegetation <2m in height was lightly to moderately consumed. The remaining litter layer (0.2 – 1m) was partially blackened and fire rarely penetrated the duff layer. Scorch heights on trees ranged from 3-15m and >85% of the canopy foliar crowns were scorched (Gassaway et al. 2002). One year later (May 2003), the Luhi fire was ignited by lava and burned over 2000 ha including 400 ha that burned the previous year (National Park Service).

In order to compare the vegetation following repeated fires with a single fire and unburned controls, I established replicate plots in each burn scenario in the mesic *Dicranopteris* and wet *Cibotium* forest communities. Twice burned plots were established in forests that burned in the Kupukupu fire (2002) and reburned one year later in the Luhi fire (2003). Once burned plots (Chapter 3) were established in forests that only burned during the Luhi fire (2003) and unburned controls (Chapter 3) have not burned in recent history.

Vegetation Sampling

Vegetation composition and structure were quantified in the twice burned (2002 and 2003) *Dicranopteris* and *Cibotium* forests using methods identical to those used in

the once burned (2003) and unburned forests (described in Chapter 3). Briefly, five 20 x 50m replicate plots were established in each community and sampled twice- one (2004) and two (2005) years following fire. Twice burned sample locations were randomly selected within the reburn area defined by the 2002 and 2003 GIS fire perimeter maps (National Park Service 2003) and showed signs of repeated fires such as burned basal sprouts. The prefire vegetation composition, structure and elevation were similar to the sampled once burned and unburned forests. In the *Cibotium* forest, the once burned and unburned sites are located in a management unit where feral pigs are controlled (R.K. Loh, pers. comm.). Despite these differences, the unburned controls represent conditions similar to those that existed in the once and twice-burned sites prior to the wildfires based on vegetation composition and structure. Flowering plant nomenclature followed that of Wagner et al. (1999) and fern nomenclature followed that of (Palmer 2003).

Vegetation was measured using a nested plot design (Fig. 3.3). All plant species encountered in the plot were recorded. Herbaceous species canopy cover was estimated to the nearest percent in twelve 1 x 1m subplots. Large trees and tree ferns (>10cm dbh) were measured in the 20 x 50m plot. Trees and tree ferns <10cm dbh were measured in six 2 x 10m subplots and shrubs and trees <1.4m in height were measured in six 1 x 5m subplots. Subplot values were averaged per 20 x 50m plot. Quantitative measures recorded for all trees in each plot included: diameter at breast height, crown mortality, plant mortality, and mode of sprouting. From these data, percent crown mortality and individual plant death were estimated for all trees by species, and by size class for the dominant species.

Data Analysis

Species presence/absence data was summarized in three ways, alpha, beta, and gamma diversity (Whittaker 1972). Alpha diversity is defined as the average species richness or number of species within each plot. Gamma diversity is the total number of species encountered in all sampled plots. Beta diversity represents heterogeneity in species composition among plots within a community and is calculated by dividing gamma diversity by alpha diversity.

Species diversity was also calculated using the Shannon-Wiener Diversity Index H' (base 10)(Shannon and Weaver 1949). Importance values (IV) were calculated for the species in each community treatment (Mueller-Dombois and Ellenberg 1974). The importance value was calculated as the average of the relative frequency within the plot (i.e. the percent of the 12 subplots that contain the species) and the relative cover within each subplot (generated for each understory species in each community treatment using cover data collected in 1 x 1m subplots) for understory species.

The sampling unit used in analysis for all parameters was the 20 x 50m plot; therefore for each analysis each treatment had five replicates. Average values were calculated per plot and used in analysis for vegetation parameters that were sampled in subplots (e.g., understory cover, seedlings, small trees and tree ferns). Statistical analyses on species richness, diversity, tree and tree fern survival, seedling density, and combined understory cover were conducted using S+ version 7.0 (Insightful 2005). Differences in species richness and the percent of those species that were nonnative among unburned, once burned and twice burned treatments were analyzed using one-way ANOVA's and

Tukey's multiple comparisons tests. Nonparametric tests (Kruskal-Wallis and Wilcoxon Rank Test for pairwise comparisons) were used to compare diversity among treatments.

Differences in *Metrosideros* survival and total understory cover (*Cibotium* forest) between once and twice burned forests were analyzed using two sample *t*-tests. Nonparametric tests (Wilcoxon Rank Test) were used to test for differences in *Cibotium* survival, total understory cover (*Dicranopteris* forest) and *Metrosideros* seedling density. ANOVA and *t*-test analyses were performed at an $\alpha = 0.10$.

Statistical analysis of multivariate community data based on percent cover values for all herbaceous and shrub species were conducted using PC-ORD, Version 4.25 (McCune and Mefford 1999a). Multi-response permutation procedure (MRPP) is a non-parametric procedure used to test if there is a difference between groups. MRPP was used to test for differences in composition between twice burned, once burned and unburned sites for each community one and two years following fire. Indicator species analysis (Dufrene and Legendre 1997) was used to describe how well each species separates between groups. Indicator values range from zero to 100% which represents perfect indication meaning that the presence of a species points to that particular group without error. Species reported as indicators were tested for significance using a Monte Carlo test of 1000 randomizations.

Non-metric multidimensional scaling (NMS) ordination (300 maximum iterations with a stability criterion of 0.0001 standard deviations in stress over the last 15 iterations, with 40 separate runs) with Sørenson distance measures were used to delineate patterns between unburned, once and twice burned sites and among communities (Kruskal 1964,

Mather 1976). Three dimensional solutions were found for ordinations and Monte Carlo was used to test stress and strength of the NMS results. Prior to NMS ordination, species occurring in fewer than two plots were deleted from the data set and all species were relativized by their maximum value to equalize the influence of individual species (McCune and Grace 2002). Plots were rotated to load the burn variable on axis 1, maximizing the proportion of variance represented by that axis. Community data matrices and specific NMS test results for each ordination are described in Appendix B.

RESULTS

Dicranopteris Forest

In the unburned *Dicranopteris* forest, a total of 29 species (gamma) were found with an average of 12.8 species (alpha) per 20 x 50m plot (Table 4.1). The majority (85%) of those species were native. Understory species diversity (H'), accounted for evenness among species and richness, was low (0.039) because the native fern *Dicranopteris* dominated the site with an average cover value of 91% (Table 4.2). Although ten additional species were recorded in the understory together they made up less than 2% of the total cover (Table 4.3). Nonnative species constituted less than 1% of the total understory cover.

Following a single fire, the total number of species (48) and the average number of species per plot (23.2) were greater in the once burned forest than the unburned forest (Table 4.1). In contrast to the unburned forest, nearly half (46%) of those species were nonnative (Table 4.1). Understory species diversity (H') was also higher (0.592) in the

once burned forest than in the unburned forest due to both higher species richness and increased evenness among species (Table 4.1). Understory recolonization was quite slow following fire in this forest type. Cover was less than 1% one year following fire and 26% two years following fire (Fig. 4.5A). The nonnative vine *Passiflora edulis* was the most abundant species (11% cover) and considered the most important based on relative

Table 4.1. Plant species diversity in unburned, once and twice burned sites two years postfire for the *Dicranopteris* and *Cibotium* forest communities. Mean and standard error in parentheses are reported. Means with the same letter are not significantly different across site type.

Community	Unburned	Once burned (2003)	Twice burned (2002 and 2003)
Dicranopteris forest			
α diversity	12.8^{a}(3.4)	23.2^{b}(3.5)	22.8^{b}(2.4)
% nonnative (α diversity)	15^{a}(4)	46^{b}(6)	48^{b}(4)
β diversity	2.27	1.9	1.8
γ diversity	29	44	41
Understory diversity (H')	0.039^{a}	0.592^{b}	0.568^{b}
Cibotium forest			
α diversity	24.4^{a}(1.3)	31.4^{b}(2.7)	20.8^{a}(0.5)
% nonnative (α diversity)	14^{a}(2)	42^{b}(2)	41^{b}(2)
β diversity	1.43	1.53	1.59
γ diversity	36	48	33
Understory diversity (H')	0.218	0.292	0.464

frequency and cover within the understory of the once burned forest two years following fire (Table 4.3). Several species had 2-3% cover (Table 4.3), but the nonnative fern *Nephrolepis multiflora* and the native sedge *Machaerina mariscoides* were the only species with high importance values (>10%) because they had high frequency values within the community (Table 4.2). Combined nonnative species cover two years following fire was 17% which accounted for 65% of the total understory cover in the once burned forest.

Table 4.2. Plant species with high (>10) importance values (Ave. IV) calculated from relative frequency and cover within each group and those identified as indicator species (ISA Value) based on abundance and faithfulness to a group relative to the other groups for *Dicranopteris* and *Cibotium* forest communities two years postfire.

Sites and Species	Life Form	Native Status	Cover (%) Mean	SE	Ave. IV	ISA
Dicranopteris forest						
Unburned						
Dicranopteris linearis	Fern	Native	91	3.4	91	99.8
Once burned (2003)						
Passiflora edulis	Vine	Non	11	6.0	24	-
Nephrolepis multiflora	Fern	Non	2	1.0	23	-
Machaerina mariscoides	Sedge	Native	2	1.4	10	-
Twice burned (2002 and 2003)						
Cyperus polystachyos	Sedge	Native	27	6.7	36	88.9
Machaerina mariscoides	Sedge	Native	14	4.7	18	80.7
Nephrolepis multiflora	Fern	Non	9	3.2	17	60.0
Paspalum scrobiculatum	Grass	Native	5	4.6	-	98.5
Stachytarpheta dichotoma	Herb	Non	2	0.9	-	80.0
Cibotium forest						
Unburned						
Dicranopteris linearis	Fern	Native	22	10.7	44	-
Paspalum conjugatum	Grass	Non	2	1.4	24	-
Alyxia oliviformis	Vine	Native	<1	0.2	-	80.0
Once burned (2003)						
Paspalum conjugatum	Grass	Non	73	7.7	62	77.4
Nephrolepis multiflora	Fern	Non	6	1.4	15	61.1
Dodonaea viscosa	Shrub	Native	2	1.3	-	80.0
Twice burned (2002 and 2003)						
Pipturus albidus	Shrub	Native	13	6.7	25	99.9
Passiflora edulis	Vine	Non	12	5.7	22	90.7
Paspalum conjugatum	Grass	Non	19	12.9	20	-
Nephrolepis multiflora	Fern	Non	3	1.2	13	-

Table 4.3. Understory cover (%) by species in the *Dicranopteris* forest community in unburned, once (2003) and twice (2002-2003) burned sites two years postfire.

Species	Native Status	Unburned Mean	Unburned SE	1x Burned Mean	1x Burned SE	2x Burned Mean	2x Burned SE
Shrub species							
Coprosma menziesii	Native	<1	0.0				
Dodonaea viscosa	Native			2	1.5		
Leptecophylla tameiameiae	Native	<1	0.0	<1	0.0	<1	0.1
Pipturus albidus	Native			2	2.1	<1	0.0
Vaccinium calycinum	Native	<1	0.1				
Buddleia asiatica	Non					<1	0.2
Pluchea symphytifolia	Non					<1	0.1
Rubus rosifolius	Non			<1	0.1	<1	0.1
Herb/Fern species							
Cocculus trilobus	Native	<1	0.0	<1	0.1	<1	0.2
Dicranopteris linearis	Native	91	3.4			<1	0.1
Nephrolepis exaltata	Native	1	0.4				
Pteridium aquilinum	Native			1	1.3		
Smilax melastomifolia	Native					1	1.2
Sphenomeris chinensis	Native	<1	0.0	<1	0.0		
Crassocephalum crepidioides	Non			<1	0.0	<1	0.0
Nephrolepis multiflora	Non			2	1.0	9	3.2
Passiflora edulis	Non			11	6.0	6	3.0
Pityrogramma austroamericana	Non			<1	0.1	<1	0.3
Stachytarpheta dichotoma	Non					2	0.9
Tibouchina herbacea	Non					<1	0.0
Grass/Sedge species							
Carex spp	Native			<1	0.1		
Carex wahuensis	Native					<1	0.2
Cyperus polystachyos	Native			<1	0.4	27	6.7
Isachne distichophylla	Native	<1	0.1	2	1.8		
Machaerina mariscoides	Native	<1	0.0	2	1.4	14	4.7
Mariscus hillebrandii	Native					<1	0.1
Paspalum scrobiculatum	Native					5	4.6
Andropogon virginicus	Non			<1	0.1	1	1.1
Axonopus fissifolius	Non			<1	0.1		
Digitaria violascens	Non			<1	0.1		
Fimbristylis dichotoma	Non					<1	0.0
Kyllinga brevifolia	Non					<1	0.1
Paspalum conjugatum	Non	1	0.5	3	1.8	<1	0.1
Sacciolepis indica	Non					<1	0.0
Setaria gracilis	Non	<1	0.0			<1	0.0
Total Understory Cover		93	3.1	26	10.2	66	7.7

Following repeated fires, measures of species diversity were similar to those found following a single fire event. A total of 47 species were found in the twice burned forest with an average of 22.8 species per plot (Table 4.1). Forty-eight percent of those species were nonnative. Understory diversity (H' = 0.568) was also comparable to the once burned forest (Table 4.1). Differences between once and twice burned forests were most pronounced in the understory community composition. Recolonization of herbaceous species in the twice burned forest was rapid. Total combined understory cover was greater in the twice burned forest one (18%) and two (66%) years following fire than the once burned forest (1 year: $P = 0.01$; 2 years: $P = 0.03$; Fig. 4.1A). The native sedge *Cyperus polystachyos*, was the most important and abundant species (absolute cover = 27%) in the twice burned forest and constituted over 40% of the total understory cover (Table 4.2). *Machaerina* and *Nephrolepis* were also important in the twice burned forest and accounted for 21% and 14% of the total understory cover respectively (Table 4.2). Nonnative species cover in the twice burned forest was 19% two years following fire which accounted for 29% of the total understory cover. Many different species were found in the understory of the once and twice burned forests. Thirteen species found in the twice burned forest were not present in the once burned forest (Table 4.3). Similarly, seven species found in the once burned forest were not present in the twice burned forest during early post fire succession (Table 4.3).

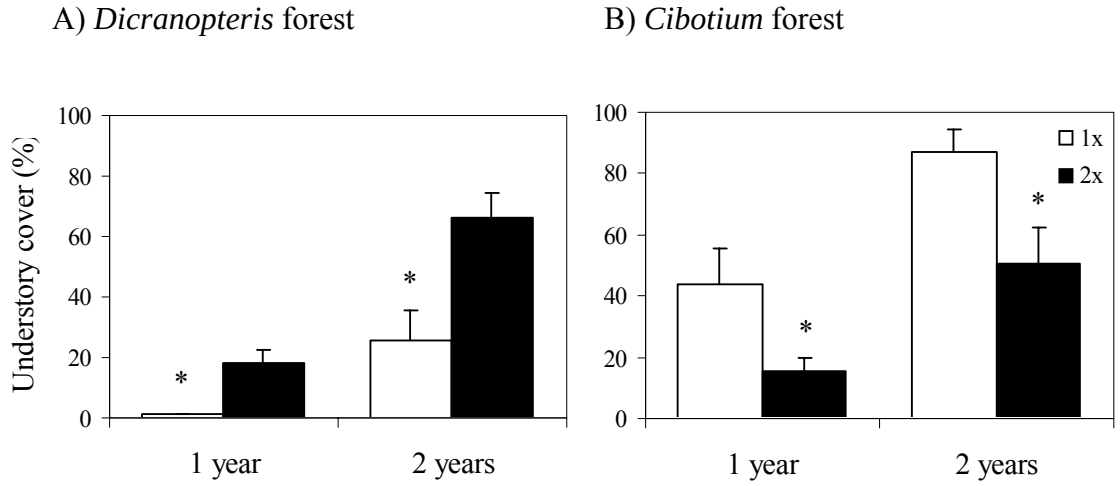

Figure 4.1. In the *Dicranopteris* forest (A), total combined understory cover was greater in the twice burned site (2x) than the once burned site (1x) one ($P = 0.01$) and two ($P = 0.03$) years postfire. In the *Cibotium* forest (B) the opposite pattern was observed, cover was greater in the once burned site (1x) than the twice burned site (2x) one ($P = 0.05$) and two ($P = 0.03$) years postfire.

These differences in understory community composition among unburned, once and twice burned forests were significant one (A = 0.24; $P < 0.01$; MRPP) and two (A = 0.24, $P < 0.01$; MRPP) years following fire. The NMS ordination graphically indicated that the community composition of once and twice burned plots was more similar than the composition in the unburned plots (Fig. 4.2A). Plots separated by treatment along axis 1 (burn) of the ordination which explained 36.4% of the variation in the data. Axis 2 was weakly correlated (r = -0.40) with the combined response of nonnative species and separated the once and twice burned plots and explained 22.4% of the variation in the data. Axis 3 was strongly correlated with the combined response of native species (r = 0.80), but is not displayed in Fig. 4.2 due to lower representation of variation in the data (18.6%).

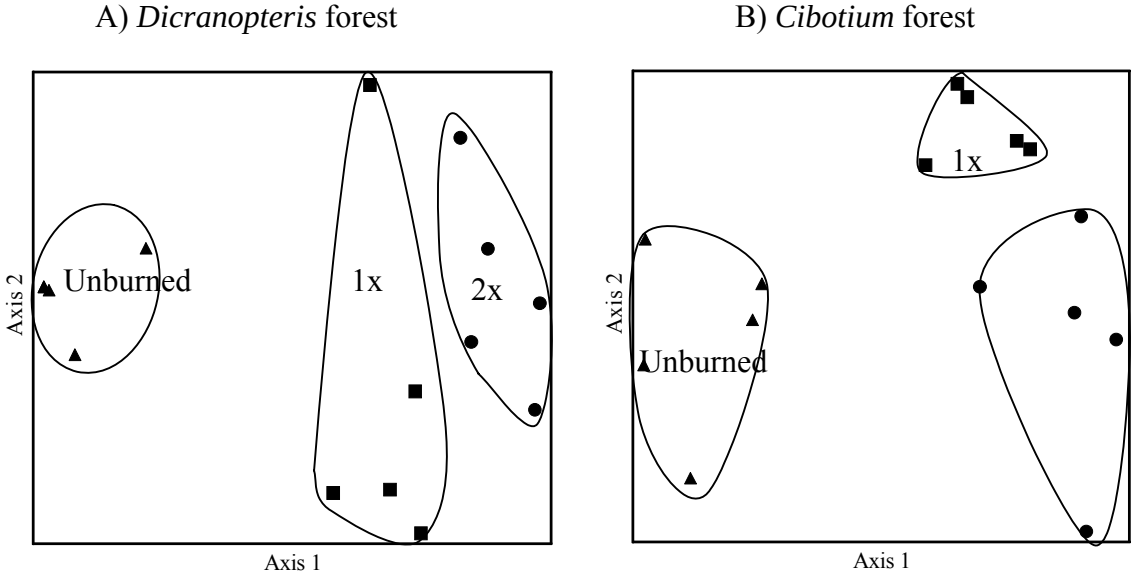

Figure 4.2. Graphical representation of sample units in species space depicting differences in understory community composition among unburned, once (1x) and twice (2x) burned sites two years postfire in the *Dicranopteris* (A) and *Cibotium* (B) forest communities. Axis 1 represents the burn treatment and axis 2 is correlated with nonnative species abundance.

The results of the indicator species analysis showed that the most abundant species in the unburned (*Dicranopteris*) and twice burned (*Cyperus*, *Machaerina*, and *Nephrolepis*) forests were significant indicators of these forest types two years following fire (Table 4.1). *Paspalum scrobiculatum* and *Stachytarpheta dichotoma* were also identified as significant indicators of the twice burned forests despite low cover values (<6%) because they were present in multiple plots and only found in the twice burned forests. Identification of indicator species is useful for indicating different groups or environmental conditions. For instance, the presence of *Paspalum scrobiculatum* (98.5%) in the forest indicated a twice burned site two years following fire for this data set. In the once burned forest, no species yielded an indicator value stronger than expected by chance because frequency and cover were low for all species.

Repeated fires dramatically increased mortality of the sprouting dominant canopy species *Metrosideros* in the *Dicranopteris* forest. Because canopy mortality following the first fire was extremely high (> 99%), differences in fire effects between once and twice burned sites were most pronounced in the sprouting trees. *Metrosideros* survival via basal sprouting was lower in the twice burned forest (22%) than the once burned forest one year following fire (71%; $P < 0.01$; Fig. 4.3). *Metrosideros* seedling density was greater in the twice burned forest (1533/ha) than the once burned forest (267/ha) two years following fire, but this difference was not significant ($P = 0.18$; Fig. 4.4). Similarity between once and twice burned sites suggests that there were few differences in seed bed suitability.

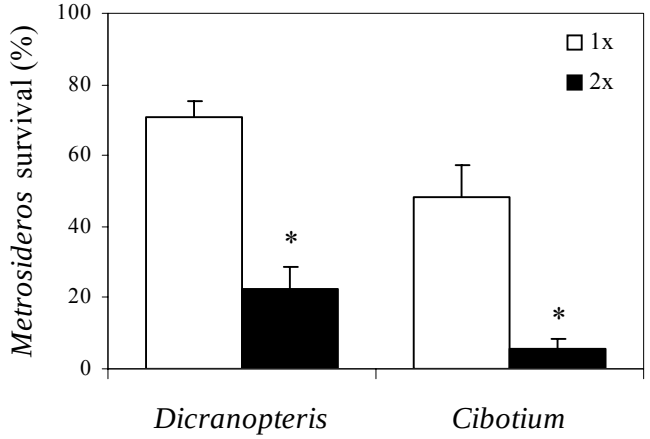

Figure 4.3. *Metrosideros polymorpha* survival via sprouting was lower in the twice burned (2x) sites than the once burned (1x) sites one year following fire in the *Dicranopteris* and *Cibotium* forest communities (P < 0.01).

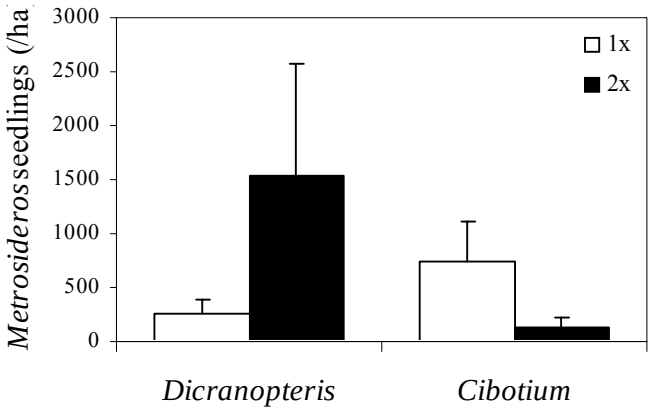

Figure 4.4. *Metrosideros polymorpha* seedling density did not differ between once (1x) and twice (2x) burned sites for either community (*Dicranopteris*: $P = 0.18$; *Cibotium*: $P = 0.36$) however, the direction of change differed.

Cibotium forest

In the unburned *Cibotium* forest, a total of 35 species were found with an average of 24.4 species per 20 x 50m plot (Table 4.1). Similar to the unburned *Dicranopteris* forest the majority (86%) of these species were native. Understory species diversity (H') was higher (0.218) than in the unburned *Dicranopteris* forest due to greater species richness and evenness (Table 4.1). The understory was relatively sparse where the total combined cover was 26%. Similar to the *Dicranopteris* forest, the native fern *Dicranopteris* was the most abundant (cover 22%) and important species in the *Cibotium* forest understory and constituted 85% of the total cover (Table 4.2). The nonnative grass *Paspalum conjugatum* was the next most abundant species (cover 2%) in the unburned forest, but only constituted 8% of the total cover. Despite low cover, *Paspalum conjugatum* had a high (15%) importance because it was present in all sampled plots in the unburned forest. Eleven additional species were present in the understory, but

together constituted <3% cover. Nonnative species accounted for 10% of the total understory cover.

In the once burned *Cibotium* forest, the number of species found (57) was 63% greater than in the unburned forest with an average of 31.4 species per plot (Table 4.1). Nearly half (42%) of those species were nonnative (Table 4.1). Despite higher species richness understory species diversity (H') did not differ between unburned and burned forests ($P = 0.14$; Table 4.1). Understory recolonization was fast following fire in the *Cibotium forest*. Total cover was 87% two years following fire (Fig. 4.1B), largely due to the colonization and range expansion of the nonnative species. *Paspalum conjugatum* was the most abundant species with 73% cover which constituted over 80% of the total understory cover. *Nephrolepis multiflora* was the next most abundant species with 6% cover and was the only other species with an importance value greater than 10% based on relative abundance within the plot and frequency among plots (Table 4.1). Twenty additional species were present in the understory each with cover values <3%. Nonnative species accounted for over 90% of the total understory cover during early postfire succession.

Fewer species were found in the twice burned forest (40) with an average of 20.8 species per 20 x 50m plot than the once burned forest ($P < 0.01$; Table 4.1). Similar to the once burned forest over 40% of those species were nonnative. Understory diversity (H' = 0.464) was also comparable to the once burned forest (Table 4.1). In contrast to the *Dicranopteris* community, the total combined understory cover was lower in the twice burned forest than the once burned forest one ($P = 0.05$) and two ($P = 0.03$) years following fire (Fig. 4.1B). Despite the fact that cover was greater in the once burned

forest, vegetation recolonization in the twice burned forest was still rapid such that within one year the total combined cover was 16% and did not differ from the unburned forest ($P = 0.40$). Total understory cover two years following fire was 51%. *Paspalum conjugatum* was the most abundant species in the understory with 19% cover (Table 4.4). However, the native shrub *Pipturus albidus* was the most important species in the twice burned despite lower cover (13%) because it was encountered more frequently in the plots (Table 4.2). *Passiflora* and *Nephrolepis multiflora* also had high importance values (>10%) calculated from relative abundance and frequency despite lower cover values (12% and 3% respectively). Fourteen additional species were found in the understory of the twice burned forest each with cover values <3% (Table 4.4). Nonnative species accounted for 69% of the total understory cover.

Differences in understory community composition among unburned, once and twice burned *Cibotium* forests were significant one (A = 0.24; $P < 0.01$; MRPP) and two (A = 0.24, $P < 0.01$; MRPP) years following fire. The NMS ordination graphically shows that fire (single or repeated) resulted in changes in community composition depicted by the distance between plots in the unburned and those in either the once or twice burned forests (Fig. 4.2B). Shorter distances between plots that burned as compared to unburned controls indicate that greater changes in community composition occurred following a single fire than changes between once and twice burned sites. That being said, the occurrence of a second fire did result in changes in understory composition as shown by the separation of once and twice burned plots. The ordination was rotated such that axis 1 represented the burned groups and explained 46.5% of the variation in the data. Axis 2 was correlated with the combined cover of

Table 4.4. Understory cover (%) by species in the *Cibotium* forest community in unburned, once (2003) and twice (2002-2003) burned sites two years postfire.

Species	Native Status	Unburned Mean	Unburned SE	1x Burned Mean	1x Burned SE	2x Burned Mean	2x Burned SE
Shrub species							
Broussaisia arguta	Native	<1	0.1				
Coprosma menziesii	Native	<1	0.3	<1	0.1		
Dodonaea viscosa	Native			2	1.3		
Labordia hedyosmifolia	Native	<1	0.0				
Pipturus albidus	Native			<1	0.0	13	6.7
Vaccinium calycinum	Native	<1	0.0				
Buddleia asiatica	Non			1	0.8		
Pluchea symphytifolia	Non			<1	0.0	<1	0.4
Rubus rosifolius	Non			<1	0.3	<1	0.0
Herb/Fern species							
Carex wahuensis	Native	<1	0.0				
Cocculus trilobus	Native	<1	0.0	<1	0.1	<1	0.1
Dicranopteris linearis	Native	22	10.7	<1	0.0	<1	0.1
Psilotum complanatum	Native	<1	0.0				
Smilax melastomifolia	Native					<1	0.4
Cuphea carthagenensis	Non			<1	0.0		
Erechtites valerianifolia	Non			<1	0.0		
Nephrolepis multiflora	Non	<1	0.2	6	1.4	3	1.2
Passiflora edulis	Non			1	0.7	12	5.7
Pityrogramma austroamericana	Non			<1	0.0		
Sphenomeris chinensis	Non			<1	0.2	<1	0.1
Stachytarpheta dichotoma	Non					<1	0.0
Tibouchina herbacea	Non					<1	0.1
Grass/Sedge species							
Cyperus polystachyos	Native			<1	0.2	<1	0.1
Isachne distichophylla	Native	<1	0.0	1	1.1		
Machaerina mariscoides	Native	<1	0.0	<1	0.2	2	1.2
Paspalum scrobiculatum	Native			1	0.7		
Andropogon virginicus	Non	<1	0.2	<1	0.4	<1	0.1
Fimbristylis dichotoma	Non					<1	0.1
Melinis minutiflora	Non			<1	0.0		
Paspalum conjugatum	Non	2	1.4	73	7.7	19	12.9
Sacciolepis indica	Non					<1	0.0
Setaria gracilis	Non			<1	0.2	<1	0.1
Fimbristylis dichotoma	Non					<1	0.1
Total Understory Cover		26	10.5	87	7.6	58	10.6

nonnative species (r = 0.636) and explained 16.9% of the variation in the data. Axis 3 (not shown) represented *Dicranopteris* abundance (r = 0.837) and explained 13.9% of the variation.

The results of the indicator species analysis for the *Cibotium* community differ from those of the *Dicranopteris* community in that the most abundant species in the unburned forest are not significant indicators (Table 4.2). Although *Dicranopteris* and *Paspalum conjugatum* are the most important species within the unburned site based on relative abundance and frequency (Table 4.2), they are not significant indictors of the unburned forest when compared to the burned forests because they are not found in all of the unburned plots (*Dicranopteris*) and they are more abundant in the burn treatments (*Paspalum conjugatum*). Therefore the native vine *Alyxia oliviformis* is the only significant indicator of the unburned forest. In the once burned forest the two most abundant species, *Paspalum conjugatum* and *Nephrolepis*, are significant indicators. The native shrub *Dodonaea viscosa* is also a significant indicator of the once burned forest because it was found in 80% of the plots and was not found in the unburned or twice burned forests. In the twice burned forest, the most abundant species is also *Paspalum conjugatum*. Because cover and frequency were greater in the once burned forest it can not be an indicator of the twice burned forest. Alternatively, *Pipturus* and *Passiflora* were significant indicators of the twice burned forest.

Similar to the *Dicranopteris* forest community, nearly all individuals were top-killed by the first fire and the effects of the second fire were most pronounced in sprouting and recovering trees and tree ferns. *Metrosideros* survival was dramatically reduced following a second fire from 48% survival in the once burned site to 6% survival

in the twice burned site one year following fire ($P < 0.01$; Fig. 4.3). Fewer *Metrosideros* seedlings were found in the twice burned forest (133/ha) than the once burned forest (1000/ha) one year following fire ($P = 0.02$), but by the second postfire year seedling density decreased in the once burned forest (733/ha) and did not differ from the twice burned forest which remained the same ($P = 0.36$; Fig. 4.4). *Cibotium glaucum* survival following a single fire was extremely high (93%), but in the twice burned forest survival was reduced to 56% ($P = 0.01$; Fig. 4.5). *Cibotium* recruitment did not differ between once (3200/ha) and twice burned sites (7533/ha) two years following fire ($P = 0.15$).

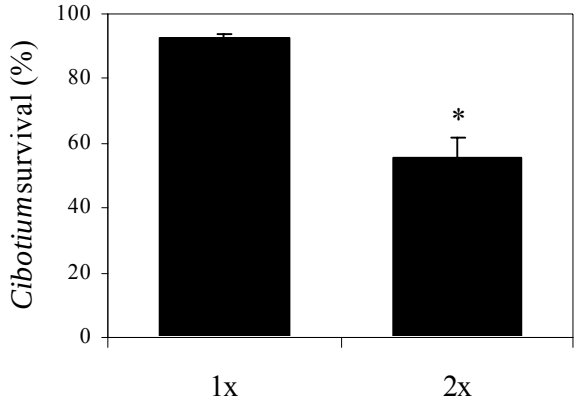

Figure 4.5. *Cibotium glaucum* survival was lower following repeated fires (2x) than a single fire (1x) event in the *Cibotium* forest community ($P = 0.01$).

DISCUSSION

Changes in Vegetation Structure Following Repeated Fires

Repeated fires dramatically increased mortality of the sprouting dominant canopy species *Metrosideros* in the *Dicranopteris* and *Cibotium* forests (Fig. 4.1). Increased canopy tree mortality following repeated fires has also been reported in tropical rain forests in Australia (Fensham et al. 2003) and Indonesia (Slik and Eichhorn 2003). Even in vigorous sprouting shrub species adapted to short fire return intervals (3-5 years) in the California chaparral two successive fires with a one year return interval can result in high mortality (Zedler et al. 1983).

The occurrence of a second fire increases the quantity of biomass consumed by fire which can decrease an individual's capacity to survive fire if the meristematic tissue is damaged (Flinn and Wein 1977). In the *Dicranopteris* and *Cibotium* forests a single fire left unconsumed fuels on site (Gassaway et al. 2002) presumably due to high fuel moisture content at the time of the first burn. Therefore the base of the *Metrosideros* trees probably did not experience extremely high temperatures during the first fire. The second fire likely consumed the remaining litter as well as killing the new sprouts of surviving individuals. Because of the high quantity of dead fine surface fuels in an open environment temperatures may have been higher at the base of the trees during the second fire which may explain the observed reduction in sprouting success. Additionally, the short fire return interval may have prevented surviving trees from building up sufficient carbohydrate reserves to survive another disturbance event (Iwasa and Kubo 1997, Drewa et al. 2002). The basal sprouts of *Metrosideros* are relatively slow growing

(Tunison et al. 1995) and reached less than 30 cm in height during the first twelve months following fire in the mesic and wet forests of this study (Chapter 3). The slow growth rates and apparent heat sensitivity (Chapter 2) in *Metrosideros* explain the low number of individuals that survived such an extreme event as two wildfires in two years.

Repeated fires also greatly increased mortality of the dominant subcanopy tree fern *Cibotium glaucum* in the *Cibotium* wet forest community. *Cibotium* individuals survived fire by resprouting from a terminal bud in the fibrous trunk. Vegetative survival in the once burned forest was extremely high (>90%) and individuals recovered fronds within two months (pers. obs.). It has been suggested that tree ferns evolved in high fire environments (Vogl 1969) and that their anomalous arrangement of meristematic tissue should allow them to survive frequent severe fires (Chapter 2). However, *Cibotium glaucum* survival in the twice burned forest was significantly lower than in the once burned forest in this study (Fig. 4.3).

In contrast to individual survival, *Metrosideros* seedling recruitment was not influenced by the occurrence of a second fire in that density did not significantly differ between once and twice burned forests for either community (Fig. 4.4). Similar findings were reported for rain forests in Indonesia where seedling and small tree densities (<5cm dbh) did not differ between once and twice burned forests (Slik and Eichhorn 2003). Although no differences in seedling density were detected for the *Dicranopteris* and *Cibotium* forests, the effect of repeated fires on *Metrosideros* seedling density differed between communities.

Limitations or barriers to seedling establishment may explain the observed different response of *Metrosideros* seedling recruitment to repeated fires between the

Dicranopteris and *Cibotium* forests. In the *Dicranopteris* forest, it has been hypothesized that the thick remnant *Dicranopteris* litter layer that remained following a single fire created a barrier to seedling establishment by limiting available space and light (Chapter 3). The second fire consumed this litter and the average number of *Metrosideros* seedlings was greater in the twice burned forest (1533/ha) than the once burned forest (267/ha), yet this difference was not significant ($P = 0.18$). The power to detect a difference in this test was very low (< 40%) and with increased sample size variance may have been reduced and the difference may have been significant. In both once and twice burned *Dicranopteris* forests seedling recruitment was significantly greater than in unburned forest where no *Metrosideros* seedlings were observed (Chapter 2). In previous fire studies at Hawaii Volcanoes National Park including coastal lowlands (Tunison et al. 1994), seasonal submontane woodlands (Parman and Wampler 1977, Tunison et al. 1995, Loh et al. 2004), and *Dicranopteris* dominated forests (Tunison et al. 2001) *Metrosideros* seedling recruitment was only documented in the *Dicranopteris* forest.

In the *Cibotium* forest the rapid aggressive recolonization of nonnative *Paspalum conjugatum* following a single fire is suggested to limit available space for *Metrosideros* seedling establishment (Chapter 3). However, the twice burned *Cibotium* wet forest site had significantly less understory cover than the once burned site yet no differences in seedling density. In fact, seedling density was five times greater in the once burned forest (733/ha) than the twice burned forest (133/ha), but the difference was not significant ($P = 0.36$). In both once and twice burned forests, *Metrosideros* seedling density was dramatically less than in the unburned forest where 8267 seedlings per

hectare were recorded (Chapter 2). Although *Metrosideros* germination has been shown to be higher under greater light intensity (Drake 1993) it is still unclear what the limiting factors are for seedling establishment in mesic and wet forests (Burton and Mueller-Dombois 1984, Denslow et al. 2006) especially following fire. In the unburned forest nearly all seedlings were found on moss or bryophyte patches on tree fern nurse logs (Chapter 2). Similarly, previous studies have shown greater tropical forest seedling establishment on tree fern and hardwood coarse woody debris (Ashton 2000, Santiago 2000). It has been suggested that *Metrosideros* seedlings were found in significantly greater numbers establishing on moss covered logs because temperatures tended to be higher and moss is better at retaining moisture (Burton and Mueller-Dombois 1984). Although nurse logs remain in the burned sites of this study, mosses and bryophytes were at least temporarily eliminated by fire. The lack of moss and hotter drier microsite conditions may be limiting recruitment in both burned treatments as compared to the control. Additional research is required to elucidate the conditions necessary for *Metrosideros* recruitment following fire in mesic and wet forest communities.

Nonnative Species

Fire has been shown to promote nonnative herbaceous species invasions in previously native-dominated sites (reviewed in (D'Antonio 2000) including mesic *Dicranopteris* and wet *Cibotium* forests (Chapter 3); therefore the occurrence of a second fire was predicted to further increase nonnative herbaceous species abundance. Herbaceous species were abundant in the understory following repeated fires in both communities, but surprisingly nonnative species were significantly less abundant in the

twice burned forest than the once burned forest. The dominate understory species in the once burned forests included nonnative grass, fern and vine species all of which have the capacity to survive fire by sprouting (Chapter 3). However, the twice burned sites had significantly less cover of these nonnative herbaceous species. Although both forest communities demonstrated similar patterns of increasing native species in the understory following repeated fires, the mechanisms responsible for these shifts appeared to differ between the *Dicranopteris* and *Cibotium* forests.

In the *Dicranopteris* mesic forest, nonnative species made up less than 30% of the understory cover in the twice burned forest as compared to greater than 60% in the once burned forest. Two native sedge species (*Cyperus* and *Machaerina*) accounted for over 60% of the total cover in the twice burned forest. *Cyperus* abundance following repeated fires was somewhat unexpected because this species was not present in the unburned forest and had <1% cover in the once burned forests (Table 4.3). *Machaerina* species have been documented invading after fire in a small (<10 ha) rain forest burn just outside of Hawaii Volcanoes National Park (Tunison et al. 2001). However, the observed abundance in the twice burned forest is also somewhat surprising because this species constituted <1% of the total understory cover in unburned forest and <10% of the total understory cover in once burned forest (Table 4.3).

Differences in composition between once and twice burned *Dicranopteris* mesic forests may be attributed to differences in postfire site conditions. Fires with high heat pulses down into the soil tend to increase individual mortality and eliminate the soil seed bank which favors species that disseminate onto the site (Ryan 2002). In the once burned forest, most of the trees survived via basal sprouting (Chapter 2) and large quantities of

unconsumed *Dicranopteris* fuels remained following fire which suggests that lethal temperatures did not penetrate into the soil. Vegetation recovery was extremely slow because the thick litter layer appeared to create a barrier for vegetation establishment (Chapter 3). The occurrence of a second fire consumed the litter layer and increased tree mortality both of which suggest that the amount of heat released around the base of the trees was high enough to kill a significant number of *Metrosideros* individuals. More *Metrosideros* individuals were killed by the second fire than the first fire in the *Dicranopteris* community. Following repeated fires, understory vegetation recolonization was faster with greater herbaceous cover than in the once burned forest (Fig. 4.1A). The understory consisted of different species including more native species than the once burned forest. The apparent shift from nonnative to native understory dominance following repeated fires may reflect differences in the number of individuals that survived fire, propagule pressure, and/or available nutrients.

In the *Dicranopteris* forest the early postfire colonizing species consisted primarily of native sedges. However, it is unlikely that the limited amount of nonnative grass, fern and vine species in the twice burned forest is due to a lack of propagules because these species are colonizing invading species which tend to have small wind-blown seeds (Wagner et al. 1990). The one exception is the nonnative vine *Passiflora* which is likely transported throughout the region by birds and feral pigs. Alternatively, the second fire may have altered soil conditions such that different species were favored.

Similar to the *Dicranopteris* forest, in the *Cibotium* wet forest the percent of understory cover made up by nonnative species was significantly lower two years following repeated fires (69%) than two years following a single fire event (94%). The

native shrub *Pipturus* constituted over 25% of the total understory cover and was the most important species in the twice burned forest two years following fire. In a previous greenhouse experiment comparing four light treatments, none of the *Pipturus* seedlings grown in shade treatments survived the four month duration of the study (Pattison et al. 1998). *Pipturus* is typically found in high light environments (Wagner et al. 1999) and can be fast growing following disturbance (pers. obs.). It was not found in unburned plots and had <1% cover in once burned plots (Table 4.4). The same nonnative species (*Passiflora, Paspalum conjugatum, and Nephrolepis*) found in the once burned *Dicranopteris* forest were abundant in the once and twice burned *Cibotium* forests (except *Passiflora* which was uncommon in the once burned *Cibotium* forest).

Site differences between the once and twice burned *Cibotium* forests are likely responsible for differences in early postfire composition between forests. In contrast to the *Dicranopteris* forest, a single fire in the wet forest consumed most of the litter and vegetation colonization was rapid following fire. In fact, twelve months following fire the understory cover in the once burned forest was nearly double that in the unburned sites (Chapter 3). Nonnative *Paspalum conjugatum* was responsible for over 90% of the understory cover in the once burned forest and was a primary fuel source for the second fire in the twice burned forest. The occurrence of the second fire killed many surviving and/or colonizing nonnative herbaceous species possibly altering soil conditions and litter thus creating conditions more favorable for *Pipturus* germination. The abundance of native *Pipturus* following repeated fires is probably not due to higher propagule pressure in the twice burned forest as compared to the once burned forest. Although *Pipturus* may be found scattered in mesic and wet forests (Wagner et al. 1990) no dead individuals

were found in the twice burned forest plots. Birds may be dispersing the seeds from outside the immediate region or the shrubs may be germinating from a legacy seed bank released by the consumption of ground fuels. In either case the once burned forest should have a similar likelihood of *Pipturus* propagules suggesting that differences in site conditions between once and twice burned forests are driving differences in composition.

Despite higher native species cover following a second fire, once and twice burned forests in the *Dicranopteris* and *Cibotium* communities had dramatically higher nonnative species diversity and abundance than the unburned forests where native *Dicranopteris* was the most important species in the understory of both communities.

Prospects for Forest Recovery Following Repeated Fires

Repeated fires in the *Dicranopteris* and *Cibotium* forests dramatically altered community composition and reduced surviving canopy and subcanopy individuals. The drastic reduction in live *Metrosideros* individuals is important because this species is a mono-dominant primary and secondary successional species (Mueller-Dombois 1987) that constitutes the majority of the above ground biomass in the forest. *Metrosideros* is slow growing, greater than 137 years were required for closed canopy self-thinned forests to establish on recent lava flows in wet forests sites on the Island of Hawaii (Clarkson 1997). Other studies that used a chronosequence approach predicted up to 300 years may be required for *Metrosideros* self-thinned forests to establish (Drake and Mueller-Dombois 1993). However, forest recovery following fire disturbance should be faster than forest development on a recent lava flow because the soil is already developed. Increased mortality of the subcanopy dominant tree fern *Cibotium* in the *Cibotium* forest

would also alter the community composition and microclimates (Burton and Mueller-Dombois 1984). In Australia, increased tree fern mortality was found to affect microclimate and forest processes (Ough and Murphy 2004). In areas in windward rain forests on Oahu, *Cibotium* species contributed over 25% of the aboveground biomass (Mueller-Dombois et al. 1983, Aplet and Vitousek 1994). Increased tree fern mortality is important because these species were found to have a disproportionately high role in nutrient cycling relative to their biomass in wet forests (Walker and Aplet 1994). For example in wet forest on windward Mauna Loa on the Island of Hawaii, *Cibotium* constituted less than 50% of the aboveground biomass, but fronds accounted for 70% of the N in above ground biomass (Mueller-Dombois et al. 1983). *Cibotium* is slow growing like many native Hawaiian plants and many of the tree ferns killed by fire in this community were likely over 50 years old based on their trunk lengths employing Walker and Aplet's (1994) average growth estimate of 5 cm/year. Dramatic reductions of canopy and subcanopy species following repeated fires accelerate the potential for a type conversion from mesic and wet forest to shrublands or fernlands with significantly lower structural and biological complexity.

The effects of repeated fires on these forests particularly the decrease in *Metrosideros* and tree fern will likely be apparent for a long time. Although many native woody forest species demonstrated the capacity to establish from seed in the postfire environment (Chapter 2), gaps created by canopy and subcanopy mortality are currently being filled by herbaceous species and one native shrub species. Without replacement of dead plants by recruiting tree seedlings *Dicranopteris* and *Cibotium* forests will not resemble prefire forests. Increases in *Metrosideros* recruitment in the future are possible

as snags begin to fall. Clarkson (1997) found the majority of *Metrosideros* seedlings in a young wet forest located on *Metrosideros* logs, but establishing seedlings in these communities will be in competition for space and resources with understory colonizers (Chapter 3). Additionally, in the *Cibotium* forest surviving tree ferns may create a light barrier that inhibits *Metrosideros* establishment even without the presence on an overstory canopy (Burton and Mueller-Dombois 1984).

An expansion of herbaceous species following repeated fires was predicted. However, native sedge and shrub dominance was somewhat surprising. In either case (native versus nonnative), increased herbaceous understory dominance will likely create additional barriers for a rapid native forest recovery (Chapter 3). Previous studies have suggested that herbaceous species in the understory have the potential to limit regrowth of surviving individuals through competition for resources (Hughes and Vitousek 1993, Denslow et al. 2006). Additionally increases in fine fuels in the understory would increases the probability of future fires. In the *Cibotium* forest, the aggressive colonization of a nonnative grass following fire provided fuel for the second fire one year later. In contrast, understory recolonization was slow in the *Dicranopteris* forest following fire due to unconsumed litter which then provided fuel for the second fire. Aggressive herbaceous colonizers may provide fuels for future fires with different chemicals, arrangement and moisture of extinction levels in the burned *Dicranopteris* forest sites particularly when the litter decomposes and recolonization occurs in the once burned forest.

Clearly additional time and research are required to determine how meaningful these early postfire differences are and whether they will result in diverging successional

pathways. Although it is very interesting that native sedges and shrubs colonized the twice burned forests, these are not tree species and this positive response is overshadowed by the dramatic increase in canopy mortality following a second fire. Only direct monitoring in the future will tell how long it will take for *Dicranopteris* and *Cibotium* forests to recover following a single fire at this site with the influence of nonnative species (Chapter 3). However, this study clearly demonstrates that the occurrence of a second fire reduces the rate of recovery by killing regenerating canopy and subcanopy individuals. If another fire were to occur in the near future, additional reductions in individual survival and changes in composition are predicted. Reduced fire return intervals appear to pose a serious threat to *Metrosideros* dominated forests in this region.

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CHAPTER 5. CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE WORK

Alison Ainsworth

This study quantified vegetation composition and structure one and two years postfire in five vegetation communities at Hawaii Volcanoes National Park. Fires in all community types were stand-replacing, where >95% of the dominant native woody species were top-killed. However, many native and nonnative species demonstrated the capacity to survive fire vegetatively and to colonize the postfire environment. The effects of fire differed by species, populations, and preburn vegetation communities along the elevation/community gradient.

Results from this study indicate that many native Hawaiian species have the capacity to survive fire vegetatively and/or establish from seed in the postfire environment. *Metrosideros polymorpha*, in particular, exhibited widespread survival (>50%) following fire, primarily via basal sprouting. Individual survival differed among diameter classes, where trees with larger diameters (>20cm diameter) were less likely to sprout than those with smaller diameters. This pattern was particularly evident in the *Dicranopteris* forest community where over 70% of the smaller trees sprouted and only 38% of the larger trees sprouted. Survival also differed among size class for the subcanopy dominant tree fern *Cibotium glaucum* in the *Cibotium* forest community, but the opposite pattern was observed where smaller tree ferns were less likely to survive fire than larger (>10cm diameter) individuals. These results indicate that the rate of recovery for a community following fire will be influenced by the population structure of the preburn vegetation community.

Seventeen native Hawaiian trees, tree ferns and shrubs established from seed in the postfire environment. Many of these are the same species that also survived fire by sprouting most notably *Metrosideros* and *Dodonaea*. It is not surprising that many native

species established from seed in the postfire environment because they are the primary colonizers of recent lava flows. Similar to sprouting response, seedling establishment following fire differed among species and communities. The native shrub *Dodonaea viscosa* was the only woody species found in all five community types postfire. In addition, it was one of only three native species to flower from seed within the first two postfire years. In contrast to *Dodonaea*, *Metrosideros* seedlings were only found in the forested communities and density differed between unburned and burned sites. In the *Nephrolepis* and *Dicranopteris* forests, recruitment appeared to be enhanced by fire in that seedling densities were greater in the burned plots than the unburned plots. However, in the *Cibotium* forest the opposite pattern was observed where 733/ha seedlings were found in the burned plots as compared to 8267/ha in the unburned plots. This dramatic difference in density may not necessarily lead to differences in the future forest because *Metrosideros* is a gap-phase species and seedlings have been shown to have faster growth rates in high light environments. Additional time and research are required to determine if and when *Metrosideros* seedlings and sprouts will regain the forest canopy in these sites.

Although many native Hawaiian species demonstrated the capacity to survive fire vegetatively and colonize the postfire environment, it remains unclear whether these are fire-influenced adaptations from the evolutionary history of this flora, or merely fortuitous adaptations derived in response to other disturbances common in the area such as volcanism, hurricanes and landslides. Nonnative species including flora and fauna have been present to some extent in these forest communities for over 100 years; therefore it is difficult and not necessarily that relevant to interpret the effects of these

fires on native species response in a historical context. Further research on fire history and plant response to fire throughout the Hawaiian archipelago is needed to determine the importance of fire in the evolution of the native flora.

Many nonnative species also demonstrated the capacity to survive fire by sprouting and established from seed in the postfire environment. Fire appeared to facilitate nonnative species invasion into previously native-dominated understories. In the three forest communities, species richness was greater in the burned sites than the unburned sites two years following fire. Greater species richness following fire in the forests can largely be attributed to nonnative species colonization. The percent of nonnative species found in each forest community was dramatically greater in the burned plots than the unburned plots. Similarly, understory composition differed between unburned and burned sites in the two previously native-dominated forests (*Dicranopteris* and *Cibotium*). The native fern *Dicranopteris linearis* was the most abundant species prior to fire, but was absent during early postfire succession and nonnative grasses, ferns and vines were the most abundant species in the understory. These results provide evidence that fire facilitated the spread of nonnative species into previously native-dominated understories. In contrast, fire in the lowest elevation shrubland communities, which were already heavily invaded by nonnative species, had little effect on vegetation composition and structure. These fire-modified communities demonstrate how nonnative species invasions coupled with repeated fires can selectively eliminate fire-sensitive native species and maintain the community in an arrested state of succession largely dominated by nonnatives.

Native *Metrosideros* sprout growth was significantly slower in forests with heavily invaded understories, implying that the presence and widespread success of invasive grasses and ferns is impacting the structural development of these communities. Total understory cover was dramatically lower in native-dominated *Dicranopteris* forest (26%) than invaded *Nephrolepis* (83%) or *Cibotium* forests (86%). This difference was due to vigorous fern sprouting and grass invasion, respectively and the effects of a large residual litter layer in the *Dicranopteris* forest. *Metrosideros* sprout growth also differed across communities, where the opposite pattern was observed with the greatest sprout growth in the community with the slowest understory recovery. These results suggest that the rapid establishment of nonnative understory fern and grass species and the high tree fern survival rate (>85%) may be limiting native *Metrosideros* tree recovery through competition for resources.

In summary we found evidence that fire facilitated nonnative species invasion in the mesic *Dicranopteris* and *Cibotium* wet forests of Hawaii Volcanoes National Park. In both communities nonnative species replaced native *Dicranopteris* ferns in the understory postfire. Sites that were dominated by nonnative species immediately following fire demonstrated slower *Metrosideros* recovery postfire. In the *Nephrolepis* community ferns rapidly recovered by sprouting whereas in the wet *Cibotium* forest grass (*Paspalum conjugatum*) colonized quickly greatly increasing the understory cover postfire. The fact that canopy recovery was significantly slower in the invaded forests than the *Dicranopteris* forest site suggests these nonnative species may be inhibiting native species recovery postfire. At least in the short term the rapid reaccumulation of nonnative fine fuels coupled with an altered microclimate postfire may create a positive

feedback facilitating more frequent fires, but additional time and research are required to determine if the interaction of nonnative species and fire in these communities will lead to the establishment of a fern-fire cycle that precludes native species establishment and persistence. Each successive fire is predicted to result in reduced individual survival and potentially more widespread invasion by nonnative species and subsequently greater barriers to native forest recovery.

This study provides quantitative data on vegetation recovery following single and repeated fires across an elevation/community gradient at Hawaii Volcanoes National Park. These data are important for resource management prioritization within the park and should also be valuable on a wider scale to fire and plant ecologists. Very few studies have quantitatively examined the effects of wildfire on vegetation composition and structure in Hawaii.

Results from this study indicate that nonnative species pose a serious threat to native Hawaiian mesic and wet forest recovery following fire. Control following fire of ubiquitous herbaceous nonnative species such as *Nephrolepis multiflora* and *Paspalum conjugatum*, is probably not feasible on a large scale. However, data from this study suggests that localized control around individual *Metrosideros* trees may increase sprout growth rates and individual survival during early postfire succession. It remains unclear whether these observed differences in growth would be noticeable even in as short a time frame as ten years. Therefore, additional research is needed to identify the mechanisms responsible for this apparently competitive interaction between understory herbaceous species and recovering *Metrosideros* individuals.

Additional research is needed in order to manage for the long term integrity of these unique forests found in this volcanically active region of Hawaii Volcanoes National Park. Suggested research goals include: determination of weather conditions necessary for fire spread, native and nonnative fuel properties, influence of current and future climate change on fire characteristics and postfire recovery, identification of mechanisms by which nonnative species limit native species recovery postfire, invasion potential of *Nephrolepis multiflora* in the absence of fire, and long term effects of the early postfire patterns reported in this study (i.e. will the presence of nonnative species and future fires ultimately result in a type conversion from native forests to nonnative shrubland communities across this gradient?).

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APPENDICES

APPENDIX A. PLANT SPECIES LIST

Plant species list for the elevation/community gradient at Hawaii Volcanoes National Park. 109 plant species were identified in 0.10 ha plots located in unburned (U), once burned (1xB) and twice burned (2xB) sites for five community types (AS- *Andropogon* shrubland, NS – *Nephrolepis* shrubland, NF – *Nephrolepis* forest, DF – *Dicranopteris* forest, CF – *Cibotium* forest). Plant species are categorized by life form and native or nonnative status.

Species	Family	Life Form	Native Status	AS		NS		NF		DF			CF		
				U	B	U	B	U	B	U	1xB	2xB	U	1xB	2xB
Ageratina riparia (Regel) R. King & H. Robinson	Asteraceae	Herb	Non											X	
Alyxia oliviformis Gaud.	Apocynaceae	Vine	Native					X		X			X	X	
Andropogon virginicus L.	Poaceae	Grass	Non	X	X	X	X		X		X	X		X	X
Antidesma platyphyllum H. Mann	Euphorbiaceae	Tree	Native										X		
Arundina graminifolia (D. Don) Hochr.	Orchidaceae	Herb	Non				X								
Asclepias physocarpa (E. Mey.) Schlechter	Asclepiadaceae	Herb	Non				X								
Axonopus fissifolius (Raddi) Kuhlm.	Poaceae	Grass	Non								X	X			
Bothriochloa barbinodis (Lag.) Herter	Poaceae	Grass	Non											X	
Broussaisia arguta Gaud.	Hydrangeaceae	Shrub	Native										X	X	
Buddleia asiatica Lour.	Buddleiaceae	Shrub	Non				X		X		X	X		X	X
Bulbostylis capillaris (L.) C. B. Clarke	Cyperaceae	Sedge	Non	X	X	X	X								
Canthium odoratum (G. Forester) Seem.	Rubiaceae	Tree	Native			X									
Carex spp	Cyperaceae	Sedge	Native								X	X			
Carex wahuensis C. A. Mey.	Cyperaceae	Sedge	Native						X	X	X	X	X	X	X
Chamaecrista nictitans (L.) Moench	Fabaceae	Herb	Non	X	X	X	X		X			X			
Cheirodendron trigynum (Gaud.) A. Heller	Araliaceae	Tree	Native							X			X	X	
Chrysopogon aciculatus (Retz.) Trin.	Poaceae	Grass	Native	X	X	X									

Species	Family	Life Form	Native Status	AS		NS		NF		DF			CF		
				U	B	U	B	U	B	U	1xB	2xB	U	1xB	2xB
Cibotium glaucum (Sm.) Hook and Arn.	Dicksoniaceae	Tree fern	Native					X		X	X	X	X	X	X
Cibotium menziesii Hook.	Dicksoniaceae	Tree fern	Native										X	X	X
Clermontia hawaiiensis (Hillebr.) Rock	Campanulaceae	Shrub	Native												X
Clermontia parviflora Gaud. Ex A. Gray	Campanulaceae	Shrub	Native											X	X
Cocculus trilobus (Thunb.) DC	Menispermaceae	Vine	Native			X	X	X	X	X	X	X	X	X	X
Cordyline fruticosa (L.) A. Chev.	Agavaceae	Shrub	Native					X			X				
Conyza canadensis (L.) Cronq.	Asteraceae	Herb	Non						X		X			X	
Coprosma menziesii A. Gray	Rubiaceae	Shrub	Native					X		X	X		X	X	
Crassocephalum crepidioides (Benth.) S. Moore	Asteraceae	Herb	Non			X			X		X	X		X	X
Crotalaria pallida Aiton	Fabaceae	Subshrub	Non		X										
Cuphea carthagenensis (Jacq.) Macbr.	Lythraceae	Herb	Non											X	X
Cuscuta sandwichiana Choisy	Cuscutaceae	Vine	Native	X	X		X								
Cyperus polystachyos Rottb.	Cyperaceae	Sedge	Native		X	X	X		X		X	X		X	X
Desmodium sandwicense E. Mey.	Fabaceae	Subshrub	Non		X	X	X		X		X	X			
Dianella sandwicensis Hook. & Arnott	Liliaceae	Herb	Native					X	X			X			
Dicranopteris linearis (Burm. F.) Underw.	Gleicheniaceae	Fern	Native					X		X	X	X	X	X	X
Digitaria violascens Link	Poaceae	Grass	Non		X	X	X		X		X	X		X	
Dodonaea viscosa Jacq.	Sapindaceae	Shrub	Native	X	X	X	X		X	X	X	X	X	X	X

Species	Family	Life Form	Native Status	AS		NS		NF		DF			CF		
				U	B	U	B	U	B	U	1xB	2xB	U	1xB	2xB
Elaphoglossum crassifolium (Gaudich.) W. R. Anderson & Crosby	Lomariopsidaceae	Fern	Native										X		
Emilia fosbergii Nicolson	Asteraceae	Herb	Non			X									
Erechtites valerianifolia (Wolf) DC	Asteraceae	Herb	Non					X		X	X		X	X	
Fimbristylis dichotoma (L.) Vahl	Cyperaceae	Sedge	Non			X		X		X	X		X	X	
Gnaphalium purpureum L.	Asteraceae	Herb	Non										X		
Grammitis tenella Kaulf.	Grammitidaceae	Fern	Native										X		
Hedychium flavescens N. Carey ex Roscoe	Zingiberaceae	Herb	Non								X				
Hedyotis hillebrandii (Fosb.) W. L. Wagner & Herbst	Rubiaceae	Shrub	Native								X				
Hedyotis terminalis (Hook. & Arnott) W. L. Wagner & Herbst	Rubiaceae	Tree	Native					X		X	X		X	X	
Heteropogon contortus (L.) P. Beauv. Ex Roem. & Schult.	Poaceae	Grass	Native	X											
Ilex anomala Hook. & Arnott	Aquifoliaceae	Tree	Native							X	X		X	X	X
Indigofera suffruticosa Mill.	Fabaceae	Shrub	Non		X		X		X						
Isachne distichophylla Munro ex Hillebr.	Poaceae	Grass	Native							X	X		X	X	X
Kyllinga brevifolia Rottb.	Cyperaceae	Sedge	Non						X		X	X			
Labordia hedyosmifolia Baill.	Loganiaceae	Shrub	Native										X		
Lantana camara L.	Verbenaceae	Shrub	Non	X	X	X	X		X						

Species	Family	Life Form	Native Status	AS U	AS B	NS U	NS B	NF U	NF B	DF U	DF 1xB	DF 2xB	CF U	CF 1xB	CF 2xB
Leptecophylla tameiameiae (Cham. & Schlechtend.) F. v. Muell.	Epacridaceae	Shrub	Native	X	X	X	X	X	X	X	X	X			X
Lycopodium spp	Lycopodiaceae	Fern	Native							X					
Lythrum maritimum Kunth	Lythraceae	Shrub	Native											X	
Machaerina angustifolia (Gaud.) T. Koyama	Cyperaceae	Sedge	Native							X		X			
Machaerina mariscoides (Gaud.) J. Kern	Cyperaceae	Sedge	Native					X	X	X	X	X	X	X	X
Mariscus hillebrandii (Boeck.) T. Koyama	Cyperaceae	Sedge	Native	X		X			X		X	X			
Mecodium recurvum (Gaudich.) Copel.	Hymenophllaceae	Fern	Native										X		
Melicope clusiifolia (A. Gray) T. Hartley & B. Stone	Rutaceae	Tree	Native								X		X	X	X
Melicope radiata (St. John) T. Hartley & B. Stone	Rutaceae	Tree	Native										X	X	
Melinis minutiflora P. Beauv.	Poaceae	Grass	Non	X	X	X	X		X					X	
Melinis repens (Willd.) Zizka	Poaceae	Grass	Non	X	X	X	X		X		X	X			
Metrosideros polymorpha Gaud.	Myrtaceae	Tree	Native		X	X	X	X	X	X	X	X	X	X	X
Morella faya (Ait.) Wilbur	Myricaceae	Tree	Non							X			X	X	
Myrsine lessertiana A. DC	Myrsinaceae	Tree	Native					X	X	X			X	X	
Myrsine sandwicensis A. DC	Myrsinaceae	Tree	Native					X		X	X		X	X	
Nephrolepis cordifolia (L.) C. Presl	Nephrolepidaceae	Fern	Native					X							

Species	Family	Life Form	Native Status	AS U	AS B	NS U	NS B	NF U	NF B	DF U	DF 1xB	DF 2xB	CF U	CF 1xB	CF 2xB
Nephrolepis exaltata (L.) Schott subsp. *hawaiiensis* W. H. Wagner	Nephrolepidaceae	Fern	Native							X					
Nephrolepis exalta x *multiflora*	Nephrolepidaceae	Fern	Non					X							
Nephrolepis multiflora (Roxb.) F. M. Jarrett ex. C. V. Morton	Nephrolepidaceae	Fern	Non	X	X	X	X	X	X	X	X	X	X	X	X
Oplismenus hirtellus (L.) P. Beauv.	Poaceae	Grass	Non											X	
Osteomeles anthyllidifolia (Sm.) Lindl.	Rosaceae	Shrub	Native	X	X	X	X								
Paspalum conjugatum Bergius	Poaceae	Grass	Non					X	X	X	X	X	X	X	X
Paspalum scrobiculatum L.	Poaceae	Grass	Native	X	X		X		X	X	X	X		X	X
Passiflora edulis Sims	Passifloraceae	Vine	Non						X		X	X	X	X	X
Passiflora foetida L.	Passifloraceae	Vine	Non				X		X						
Peperomia hypoleuca Miq.	Piperaceae	Herb	Native										X		
Phaius tankarvilleae (Banks ex L'Her.) Blume	Orchidaceae	Herb	Non										X	X	
Phymatosorus grossus (Langsd. & Fisch.) Brownlie	Polypodiaceae	Fern	Non	X		X									
Physalis peruviana L.	Solanaceae	Subshrub	Non						X		X	X			X
Pipturus albidus (Hook. & Arnott) A. Gray	Urticaceae	Shrub	Native					X	X		X	X		X	X
Pityrogramma austroamericana Domin	Pteridaceae	Fern	Non						X	X	X	X		X	X
Pluchea symphytifolia (Mill.) Gillis	Asteraceae	Shrub	Non	X		X	X		X		X	X		X	X

Species	Family	Life Form	Native Status	AS		NS		NF		DF			CF		
				U	B	U	B	U	B	U	1xB	2xB	U	1xB	2xB
Psidium cattleianum Sabine	Myrtaceae	Tree	Non						X	X	X		X	X	X
Psidium guajava L.	Myrtaceae	Shrub	Non	X	X	X	X								
Psilotum complanatum Sw.	Psilotaceae	Fern	Native										X	X	
Psilotum nudum (L.) P. Beauv.	Psilotaceae	Fern	Native											X	X
Psychotria hawaiiensis (A. Gray) Fosb.	Rubiaceae	Tree	Native					X					X	X	
Pteridium aquilinum (L.) Kuhn var. *decompositum* (Gaudich.) R. M. Tyron	Dennstaedtiaceae	Fern	Native								X				
Rubus rosifolius Sm.	Rosaceae	Shrub	Non								X	X		X	X
Sacciolepis indica (L.) Chase	Poaceae	Grass	Non								X	X		X	X
Sadleria cyatheoides Kaulf.	Blechnaceae	Tree fern	Native					X		X	X	X			X
Santalum paniculatum Hook. & Arnott	Santalaceae	Tree	Native							X		X	X	X	
Scaevola chamissoniana Gaud.	Goodeniaceae	Shrub	Native											X*	
Schizachyrium condensatum (Kunth) Nees	Poaceae	Grass	Non						X		X	X		X	
Setaria gracilis Kunth	Poaceae	Grass	Non		X	X	X	X	X	X		X		X	X
Sida fallax Walp.	Malvaceae	Shrub	Native				X								
Sida rhombifolia L.	Malvaceae	Shrub	Non						X						
Smilax melastomifolia Sm.	Smilacaceae	Vine	Native									X			X
Solanum americanum Mill.	Solanaceae	Subshrub	Native				X		X		X	X			X

* *Scaevola* was observed in the once burned *Cibotium* forest, but did not occur in any of the sample plots.

Species	Family	Life Form	Native Status	AS		NS		NF		DF			CF		
				U	B	U	B	U	B	U	1xB	2xB	U	1xB	2xB
Sphenomeris chinensis (L.) Maxon	Lindsaeaceae	Fern	Native					X			X	X		X	X
Sporobolus africanus (Poir.) Robyns & Tournay	Poaceae	Grass	Non									X			
Stachytarpheta dichotoma (Ruiz & Pav.) Vahl	Stachytarpheta	Subshrub	Non				X		X			X		X	X
Tibouchina herbacea (DC) Cogn.	Melastomataceae	Subshrub	Non						X			X			X
Vaccinium calycinum Sm.	Ericaceae	Shrub	Native							X		X	X	X	
Vaccinium reticulatum Sm.	Ericaceae	Shrub	Native								X	X			
Waltheria indica L.	Sterculiaceae	Subshrub	Native	X	X	X	X					X			
Wikstroemia spp	Thymelaeaceae	Shrub	Native			X									
Youngia japonica (L.) DC	Asteraceae	Herb	Non											X	

APPENDIX B. NON-METRIC MULTIDIMENSIONAL SCALING ANALYSES

Database Preparation

Community data matrices were generated from species percent cover estimates for each non-metric multidimensional scaling analysis and consisted of the number of plots analyzed and the number of species present within those plots. Uncommon species defined as those that only occurred in one plot of the study were removed from the data matrix in order to reduce noise and strengthen the pattern of community composition. The data matrices for each analysis are summarized in Table App.B1. To equalize the influence of individual species all species were relatavized by their maximum value. Outliers were recognized when the Sørenson distance between any two plots in species space was greater than 2.0 standard deviations of the grand mean Sørenson distance calculated for all plots.

Group membership matrices consisted of plots and 1 or 2 groupings. Plots were grouped by frequency of burn (unburned, once burned or twice burned) and where applicable by *a priori* community designations (*Cibotium* forest, *Dicranopteris* forest, *Nephrolepis* forest, *Nephrolepis* shrubland or *Andropogon* shrubland). Species trait matrices were generated for individual community analysis (Chapter 3) consisting of 3 traits and the number of species. Traits identified each species in the analysis as native (NATIVE) or nonnative (ALIEN), and those that were woody (WOODY). Community data matrices were multiplied by the trait matrices generating joint plot overlay matrices that consisted of plots and traits. In order to assign group membership and overlay

species trait matrices simultaneously on plots in species space the group membership matrices were added to each plot x trait matrix. The resultant overlay or joint plot matrices consisted of rows identifying plots and columns representing group membership (burn frequency and community type) and the magnitude or number of species with each trait (native, nonnative and woody).

Data Analysis

Patterns of community composition for all matrices were extracted and graphically displayed using nonmetric multidimensional scaling using Sørenson distances. Forty runs were conducted of the real data using a random starting configuration and 50 runs were conducted of the randomized data for a Monte Carlo test of significance. Two and three dimensional solutions were selected for all analyses and dimensionality was assessed using a graph of stress as a function of dimensionality (scree plot) and the Monte Carlo test results. Stability of the final solution was examined with a graph of stress versus iteration number and the stability criterion set to 10^{-4}. Plots were ordinated in species space with overlays from the grouping and trait matrix and the community matrices. Ordinations were rotated using an orthogonal technique to align burn frequency along axis 1 to ease the interpretation of the relationship between grouping and trait variables with community composition. Final dimensionality, stress, number of iterations and rotation angle are summarized for each analysis in Table App.B1. The total variation in the data accounted for by each axis (Table App.B2) and the correlation of each trait with the axis 1 representing burn frequency (Table App.B3) are reported.

Table App.B1. Community matrices, dimensions, outliers, NMS axes chosen in the solution, stress, number of iterations and degrees rotated to align the burn variable with axis 1 for each NMS analysis reported in the text (U = unburned, 1x = once burned, 2x = twice burned, 1y = 1 year postfire, 2y = 2 years postfire; AS = *Andropogon* shrubland, NS = *Nephrolepis* shrubland, NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest).

Figure	Matrix	Dimension (plotxspp)	Outlier	NMS	Stess	Iteration	Rotation (deg)
3.2, 3.3	All (U-1x1y-1x2y)	75 x 46	none	3D	15.9	182	88
3.4A-C	Forest (U-1x1y-1x2y)	45 x 35	1*	3D	16.9	248	222
3.4D	Shrubland (U-1x1y-1x2y)	30 x 21	none	3D	10.6	82	139
3.7A	AS (U-1x1y-1x2y)	15 x 17	none	2D	13.3	151	300
3.7B	NS (U-1x1y-1x2y)	15 x 16	none	2D	0.82	57	132
3.8A	NF (U vs. 1x1y)	10 x 10	none	2D	6.37	98	97
3.8B	DF (U-1x1y-1x2y)	15 x 17	none	3D	10.4	181	280
3.8C	CF (U-1x1y-1x2y)	15 x 25	none	2D	15.7	69	129
4.2A	DF (U-1x2y-2x2y)	15 x 21	none	3D	9.07	64	178
4.2B	CF (U-1x2y-2x2y)	15 x 24	none	3D	8.36	89	119

* Outlier plot was retained in the analysis (= 2.19 standard deviations away from mean).

Table App.B2. The percent of variation in understory community composition represented by each NMS axis following rigid rotation maximizing the alignment of the burn variable with axis 1 (AS = *Andropogon* shrubland, NS = *Nephrolepis* shrubland, NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest).

	Combined Communities single fire			Individual Communities single fire					repeated fires	
NMS	All	Forests	Shrublands	AS	NS	NF	DF	CF	DF	CF
Axis	3.2&3.3*	3.4A-C	3.4D	3.7A	3.7B	3.8A	3.8B	3.8C	4.2A	4.2B
1	20.3	16.3	11.7	48.3	60.2	37.6	20.6	55.6	36.4	46.5
2	24.6	19.6	48.8	24.9	26.9	43.9	23.7	18.2	22.4	16.9
3	15.5	21.8	27.3	-	-	-	24	-	18.6	13.9
Total	60.4	57.8	87.8	73.1	87.1	81.5	68.3	73.8	77.4	77.3

* Figure in text.

Table App.B3. Correlation (*r*) values for joint plot overlays of environmental variables with the burn axis 1 (AS = *Andropogon* shrubland, NS = *Nephrolepis* shrubland, NF = *Nephrolepis* forest, DF = *Dicranopteris* forest, and CF = *Cibotium* forest).

	AS 3.7A	NS 3.7B	NF 3.8A	DF 3.8B	CF 3.8C
NATIVE	0.24	0.02	0.75*	-0.27	-0.13
ALIEN	0.59*	0.61*	0.26	0.58*	0.89*
WOODY	0.22	-0.31	na	0.18	0.43

* significant (r >0.45)