

Interactions of Fire and Nonnative Species Across an Elevation/Plant Community Gradient in Hawaii Volcanoes National Park

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ABSTRACT

Invasive species interacting with fires pose a relatively unknown, but potentially serious, threat to the tropical forests of Hawaii. Fires may create conditions that facilitate species invasions, but the degree to which this occurs in different tropical plant communities has not been quantified. We documented the survival and establishment of plant species for 2 yr following 2003 wildfires in tropical moist and wet forest life zones in Hawaii Volcanoes National Park, Hawaii. Fires were ignited by lava flows and burned across a steep environmental gradient encompassing two previously burned shrub-dominated communities and three *Metrosideros polymorpha* forest communities. Fires in all community types were stand replacing, where > 95 percent of overstory trees were top killed. Over half (> 57%) of the trees survived via basal sprouting, but sprout growth differed among forest communities. Sprout growth (> 250,000 cm³) was greatest in the forest community where postfire understory cover was lowest presumably due to thick native *Dicranopteris linearis* fern litter that remained postfire. In contrast, *M. polymorpha* sprout growth was much slower (< 100,000 cm³) in the two forest communities where there was rapid understory recovery of nonnative ferns *Nephrolepis multiflora* and invasive grasses *Paspalum conjugatum*. These results suggest that the rapid establishment of an invasive-dominated understory limited recovery of the overstory dominant *M. polymorpha*. In contrast to the three forest communities, there were few changes in vegetation composition in the shrubland communities. Nonnative species invasions coupled with repeated fires selectively eliminated fire-sensitive species thereby maintaining these communities in dominance of primarily nonnative, fire-resilient, species.

Key words: disturbance; invasive species; *Metrosideros polymorpha*; sprouting; tropical forest.

CHANGES IN BIODIVERSITY ASSOCIATED WITH BIOLOGICAL INVASIONS OF nonnative species are a tremendous concern at local, regional, and global scales (Vitousek *et al.* 1996). Nonnative or 'alien species' are species capable of propagating that are not native to that ecosystem (Presidential Documents 1999). In ecosystems where alien species persist 'naturalized species' may be applied to those that are widespread and capable of reproducing frequently (Richardson *et al.* 2000). If nonnative or naturalized species are likely to cause economic or environmental harm they are considered 'invasive species' (Presidential Documents 1999). 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 & Vitousek 1992). Moreover, global climate change and altered disturbance regimes are predicted to allow range expansion of many invasive species (Kriticos *et al.* 2003a, b; Morrison *et al.* 2005). These stresses to native ecosystems will likely increase the capacity of some naturalized species to dominate plant communities such that they will become invasive (Dukes &

Mooney 1999, Asner *et al.* 2006). To improve our understanding of invasion ecology and make future predictions it is essential to examine both the susceptibility of native communities to invasion and determine the potentials of invasiveness and naturalization of alien species (Richardson & Pysek 2006). Studies of potential responses of alien species are particularly needed in geographical regions previously underrepresented such as oceanic islands (Crall *et al.* 2006, Pysek *et al.* 2008).

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 & Huenneke 1992, D'Antonio & Dudley 1995, Kitayama & Mueller-Dombois 1995, Burke & Grime 1996, Aplet *et al.* 1998, Bellingham *et al.* 2005, De Gruchy *et al.* 2005). 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 availability). In the Hawaiian Islands, nonnative species have been shown to invade sites following disturbances and the concomitant increases in resource availability (Gerrish & Mueller-Dombois 1980, Carino & Daehler 2002, Ostertag &

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Verville 2002) in some cases creating feedbacks for further invasions (Vitousek & Walker 1989, Allison & Vitousek 2004, Hughes & Denslow 2005). No studies have addressed the fundamental ecological issue of community invasibility by examining differences in invasibility among multiple plant communities subjected to the same disturbance or series of disturbance events.

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. In addition, Mack and D'Antonio (1998) suggested that invasive species can alter disturbance regimes (*e.g.*, enhancing or suppressing fire, increasing or decreasing erosion) and, thereby, successional trajectories of the plant communities. For example, nonnative grass invasions in the seasonally dry woodlands of Hawaii alter biomass and fuel composition, structure, moisture, and chemistry, increasing the probability of an increased frequency and severity of fire (D'Antonio & Vitousek 1992).

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

The objectives of this study were to compare changes in vegetation composition and structure for 2 yr following lava-ignited wildfires in five plant communities arrayed across an environmental gradient of four life zones (Tosi *et al.* 2001), and comprising a vegetation gradient from shrubland to wet forest. We 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. We predicted that: (1) communities dominated by natives before fire would have higher nonnative species abundance in burned sites compared with unburned sites (*i.e.*, fire would increase invasibility by nonnative species), and (2) communities dominated by nonnatives before 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, we predicted that communities where nonnative species were abundant during early postfire succession would exhibit: (3) faster understory recovery (*i.e.*, fewer differences in postfire composition and cover), (4) lower native tree species recruitment, and (5) slower recovery rates for surviving trees.

METHODS

STUDY SITE.—The study site is located within Hawaii Volcanoes National Park (19°20'11" N, 155°729' W) on the east slope of Kilauea volcano at 350–825 m elevation on the Island of Hawaii (Fig. 1). Precipitation varies across this steep gradient from dry

shrublands to wet forest. Substrate consists of young (400–750 yr-old) pahoehoe lava flows (Trusdell *et al.* 2005) overlain by shallow (5–50 cm) soils derived from volcanic ash (Kalapana and Makaopuhi series; Jasper 2007). Detailed site descriptions are provided in Ainsworth and Kauffman (2009).

Community response to fire was examined in five communities across the elevation gradient (Table 1). Communities share a single dominant forest tree species, *Metrosideros polymorpha*, but vary widely in tree density and percent canopy cover (< 1% shrublands to > 60% mesic forests). The two lowest elevation communities (*Andropogon* and *Nephrolepis* shrublands) have been disturbed by past human-ignited fires and at the time of the study only contained remnant *M. polymorpha* trees restricted to rock outcrops. Historic photos of this region suggest that these communities were *M. polymorpha* woodlands with scattered shrubs and a mixed understory before 1972 (Hawaii Department of Land and Natural Resources 1966). Today, native *Dodonaea viscosa* shrubs (8500–9000 individuals/ha) dominate these communities. Understory differs with nonnative perennial bunch grasses (*Andropogon virginicus*) at 350–450 m in the '*Andropogon* shrubland' and nonnative *N. multiflora* ferns at 450–550 m in '*Nephrolepis* shrubland.'

The three forest communities (*Nephrolepis*, *Dicranopteris*, and *Cibotium* forests) have canopies dominated by *M. polymorpha* (500–800/ha) and no known history of fire disturbance. The lowest elevation forest occurring at 550–640 m is ecotonal to the *Nephrolepis* shrubland and is dominated by nonnative *N. multiflora* ferns in the understory. The *Dicranopteris* forest (640–750 m) is dominated by native mat-forming ferns (*Dicranopteris linearis*) in the understory. The highest elevation and wettest community sampled has an open canopy of *M. polymorpha*, abundant native tree ferns *Cibotium glaucum* in the midstory, and native ferns and nonnative grasses in the understory.

Volcanic lava flows have been the primary ignition source for wildland fires in this area of Hawaii Volcanoes National Park since at least 1916 (Gassaway *et al.* 2002). Multiple fires have occurred in the coastal lowlands over the last 30 yr and two have burned the shrubland communities of this study area. In 2002, a new lava outbreak ignited the Kupukupu Fire that burned 1400 ha of forest. Nine months later the Panau Iki Fire (January 2003) burned 860 ha of *Andropogon* and *Nephrolepis* shrublands. In May 2003, the Luhi Fire burned 2000 ha across the study area (National Park Service 2003). We sampled vegetation composition and structure in permanent plots ($N=5$) in each of the five vegetation communities in areas burned in the 2003 Panau Iki and Luhi wildfires and unburned controls.

VEGETATION SAMPLING.—We examined ecological effects of wildfire through comparisons of the vegetation composition and structure in the areas burned by the 2003 wildfires, and adjacent unburned sites. In each of the five communities, we established five replicates, randomly located 20 × 50 m 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 annual variability in

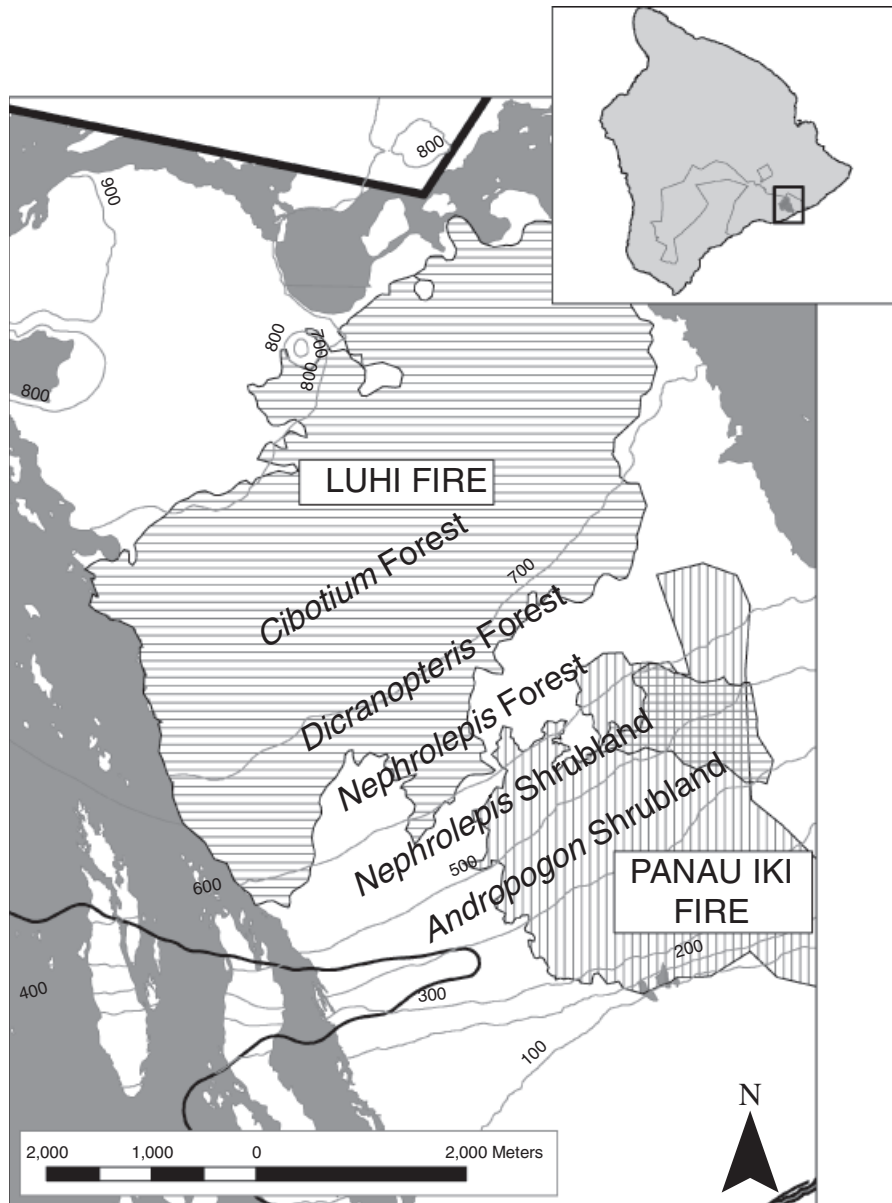


FIGURE 1. Shrubland and forest communities burned during the Luhi and Panau Iki wildfires (2003) in Hawaii Volcanoes National Park on Hawaii Island.

understory composition, unburned areas were sampled only once, 2 yr following fire (2005), except for the *Nephrolepis* forest community which was sampled 1 yr following fire (2004). We 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). Invasive and likely to become invasive species designations for nonnative species are from the Hawaii Weed Risk Assessment (Daehler *et al.* 2004, Daehler & Denslow 2009).

All plant species within the plot (20×50 m) were recorded. Cover of understory plant species (herbs, ferns, and shrubs) was measured for each species to the nearest percent within twelve

1×1 m subplots. Woody tree, shrub, and tree fern species survival and density by size were reported in Ainsworth and Kauffman (2009). Individual *M. polymorpha* tree sprout growth was quantified for all trees within each plot by measuring basal sprout height and basal sprout elliptical crown area. Basal sprout height (cm) was calculated as the longest basal sprout per tree, elliptical crown area (cm^2) was calculated from crown width measured in two perpendicular directions, and crown volume (cm^3) was then calculated by multiplying the height of the tallest sprout by the elliptical crown area (Mueller-Dombois & Ellenberg 1974, Kauffman & Martin 1990, Sampaio *et al.* 1993).

DATA ANALYSIS.—Measures of understory plant diversity were calculated from the cover data using the Shannon–Wiener Diversity

TABLE 1. Elevation, dominant canopy species and density, and dominant understory or midstory species for communities sampled.

Community	Elevation (m)	Dominant canopy (density/ha), understory dominant species
<i>Andropogon</i> shrubland	350–450	<i>Dodonaea viscosa</i> (8500/ha), <i>Andropogon virginicus</i>
<i>Nephrolepis</i> shrubland	450–550	<i>D. viscosa</i> (8500/ha), <i>Nephrolepis multiflora</i>
<i>Nephrolepis</i> forest	550–640	<i>Metrosideros polymorpha</i> (700/ha), <i>N. multiflora</i>
<i>Dicranopteris</i> forest	640–750	<i>M. polymorpha</i> (850/ha), <i>Dicranopteris linearis</i>
<i>Cibotium</i> forest	750–825	<i>M. polymorpha</i> (500/ha), <i>Cibotium glaucum</i>

Index (Shannon & Weaver 1949) and by calculating evenness (J') (Pielou 1966, 1969). Species richness and the percent of those species that were nonnative were analyzed across the study gradient as two-factor analysis of variance's (ANOVA's) with community, burn, and community \times burn as fixed effects. Differences in *M. polymorpha* sprout volume among forested communities were analyzed using ANOVA and Tukey's multiple comparison tests. To determine the effect of fire in each community separately, differences in many vegetation parameters (species richness, nonnative composition, species diversity, and understory cover) were compared between sites and years following fire using two sample *t*-tests (unburned vs. burned 1-yr postfire and unburned vs. burned 2-yr postfire). Nonparametric tests (Wilcoxon rank test) were used to compare differences in understory cover (shrublands and *Dicranopteris* forest) and species diversity (*Dicranopteris* forest). ANOVA and *t*-test analyses were performed at an $\alpha = 0.1$ to increase the power ($1 - \beta$). Multivariate statistical analysis of community data was based on cover values for all herbaceous and shrub species (McCune & Mefford 1999). Nonmetric multidimensional scaling (NMS) ordination was used to delineate patterns between burned and unburned sites and among communities (Kruskal 1964, Mather 1976). Additional test details are available in Ainsworth (2007).

RESULTS

While the wildland fires were stand replacing in all five communities, over half (57%) of the *M. polymorpha* survived fire through basal sprouting (Ainsworth & Kauffman 2009). The rates of sprout growth of *M. polymorpha*, however, differed among communities and by the second year postfire sprout volume was greater in the *Dicranopteris* forest than the other communities (Fig. 2).

There were dramatic differences in vegetation response to fire among the sampled plant communities. 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. Over half (56%) of these species were native. Species richness and the proportion of those species that were nonnative differed between unburned and burned sites ($P < 0.01$), as well as among commu-

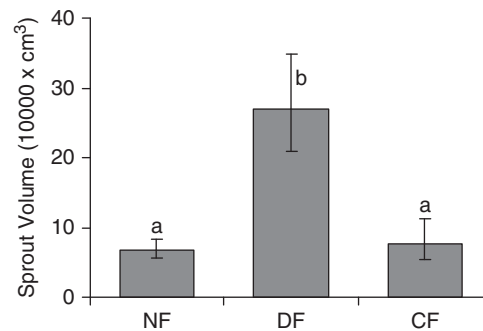


FIGURE 2. Differences in *Metrosideros polymorpha* growth as measured by sprout volume (cm^3) 2-yr postfire in three forest communities (NF, *Nephrolepis* forest; DF, *Dicranopteris* forest; and CF, *Cibotium* forest). Backtransformed means ± 1 SE are shown.

nities ($P < 0.01$). In the forest communities, species richness and the proportion of those species that were nonnative were significantly greater in the burned sites than the unburned sites. For both parameters the interaction term was also significant ($P < 0.01$), clearly reflecting the different postfire responses of the plant communities (Figs. 3 and 4).

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. 3A). The sample units for the five communities separated 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. 3B). The *Dicranopteris* and *Cibotium* forests, in particular, exhibited much more variation in understory species composition than the *Nephrolepis* forest or the nonnative-dominated shrublands demonstrating that the dominance by nonnatives lower community heterogeneity and hence landscape biodiversity (Fig. 3B). The understory composition in the burned forest communities more closely resembled the composition in the shrubland communities. To separate the effects of fire from the effects of community type, we analyzed the vegetation data for each community separately.

ANDROPOGON SHRUBLAND.—Over half (65%) of the 19 species found in the unburned site were nonnative including invasive *Lantana camara* and *Psidium guajava*. Nonnative *A. virginicus* and native *D. viscosa* were most abundant and together constituted > 90 percent of the total understory vegetation cover (Table S1) contributing to low species diversity ($H' = 0.340$) and evenness ($J' = 0.31$). In the burned site 2-yr postfire, 22 species were found (57% nonnative). Vegetation recolonized quickly following fire such that combined cover 1-yr postfire did not differ from the unburned site ($P = 0.69$; Fig. 4). Rapid recovery was largely the response of the resilient species—*A. virginicus* and *D. viscosa* (Table S1). *Andropogon virginicus* sprouted vigorously from the base whereas *D. viscosa*

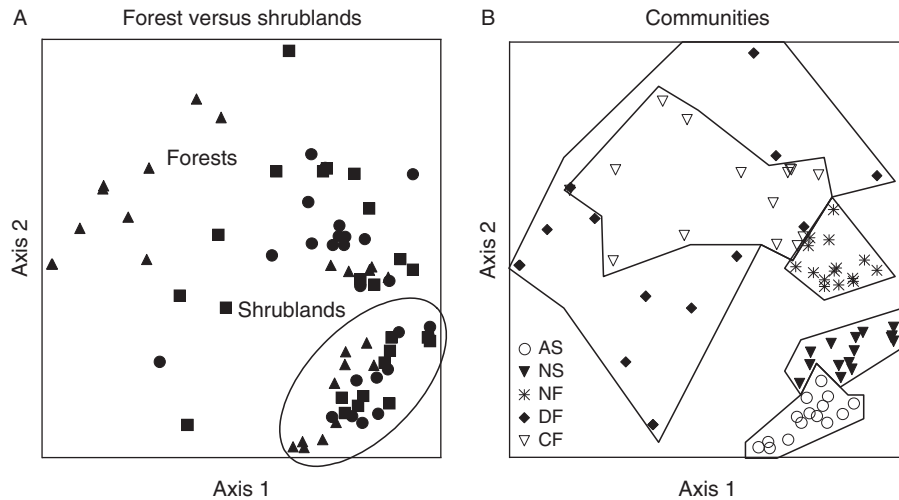


FIGURE 3. (A) Community membership or site differences are more important than burn effect (triangles: unburned; squares: burned 1-yr postfire; circles: burned 2-yr postfire) in explaining variation in understory community composition. (B) Generated polygons enclose unburned and burned plots 1- and 2-yr postfire for each community (AS, *Andropogon* shrubland; NS, *Nephrolepis* shrubland; NF, *Nephrolepis* forest; DF, *Dicranopteris* forest; and CF, *Cibotium* forest).

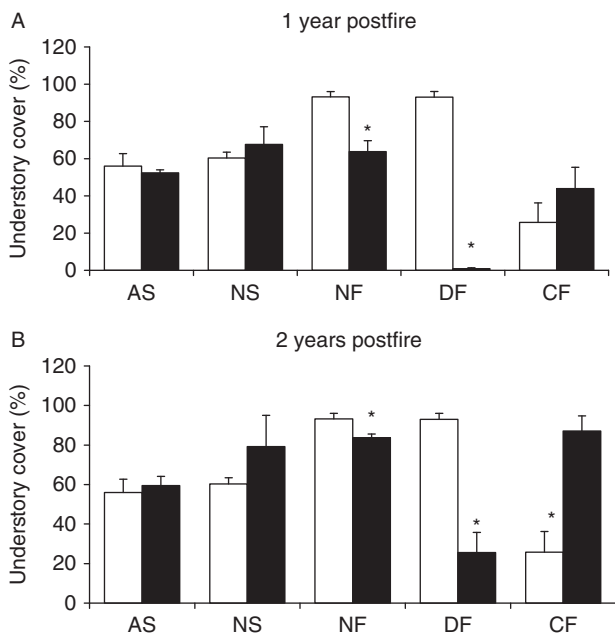


FIGURE 4. Combined understory vegetation cover in the unburned (open bars) and burned (closed bars) sites (A) 1-yr and (B) 2-yr postfire for five vegetation communities (AS, *Andropogon* shrubland; NS, *Nephrolepis* shrubland; NF, *Nephrolepis* forest; DF, *Dicranopteris* forest; and CF, *Cibotium* forest).

primarily recolonized from seed. Invasive *P. guajava* and 'likely to become invasive' *Indigofera suffruticosa* were also present postfire (1% cover). Understory diversity (0.514; $P=0.08$) and evenness (0.48) were higher in the burned site 2-yr postfire.

NEPHROLEPIS SHRUBLAND.—Twenty-five species were found and over half (55%) were nonnative including invasive *L. camara* and *P. guajava*. The most abundant species, *N. multiflora* (33%) and

D. viscosa (16%), constituted > 82 percent of the total understory cover (Table S1). Understory species diversity (0.510) and evenness (0.43) were somewhat higher than the slightly more xeric *Andropogon* shrubland. In the burned site, 31 species were found (63% nonnative). The rate of vegetation recovery was similar to the rapid rate observed in the *Andropogon* shrubland and understory cover in the burned site 1-yr postfire did not differ from the unburned site ($P=0.60$; Fig. 4A). *Nephrolepis multiflora* regenerated primarily by sprouting from rhizomes and along with *D. viscosa* remained the most abundant species postfire (Table S1). Species diversity was greater in burned plots 1-yr (0.657; $P=0.01$) and 2-yr (0.635; $P=0.05$) postfire attributable to greater evenness (0.55) among species during early postfire succession.

NEPHROLEPIS FOREST.—Although 21 species were found (22% nonnative), understory species diversity (0.100) and evenness (0.10) were low due to the overwhelming dominance of nonnative *N. multiflora* with 87 percent cover (Table S1). In the burned site, there were nearly twice as many species (40) 2-yr postfire primarily due to nonnative species colonization. Understory diversity (0.233; $P=0.03$) and evenness (0.19) were greater in the burned compared with the unburned site, but remained lower than the shrublands. *Nephrolepis multiflora* remained the dominant species and was present in all plots postfire. Combined understory cover was lower in the burned site 1-yr (64%; $P<0.01$) and 2-yr (84%; $P=0.02$) postfire but increased significantly between years ($P=0.01$; Figs. 4A and B).

DICRANOPTERIS FOREST.—Twenty-nine species were found with extremely low understory species diversity (0.039) and evenness (0.04) due to site dominance by the native fern *D. linearis* with 91 percent cover (Table S1). Few nonnative species were present and together they constituted < 1 percent 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. In the burned site 2-yr postfire, 48 species (> 46% nonnative) were found with increased diversity (0.592; $P = 0.01$) and evenness (0.39). Total understory vegetation cover was far lower in the burned site both 1-yr (< 1%; $P = 0.01$) and 2-yr (26%; $P < 0.01$) postfire (Figs. 4A and B). The native fern *D. linearis* was absent and nonnative species were the most abundant species following fire. Invasive *P. conjugatum* had higher relative cover (12%) following fire than in the unburned site (< 2%) and two potentially invasive species colonized the postfire environment (*Rubus rosifolius* and *Axonopus fissifolius*). The nonnative vine *Passiflora edulis* was the most abundant species (11% cover).

CIBOTIUM FOREST.—Species richness was the highest of all unburned sampled communities with a total of 35 species encountered (10% nonnative). Species diversity (0.218) and evenness (0.16) were also higher than the other forest communities. Total understory cover was relatively sparse with a combined cover value of 26 percent; *D. linearis* is the most abundant species (Table S1). In the burned plots, the number of species found (57) 2-yr postfire was 63 percent greater than in the unburned plots and 40 percent were nonnative. Despite increased richness, understory diversity (0.292) was similar to the unburned site. Total understory cover was greater in the burned plots 1-yr (44%; $P = 0.28$) and 2-yr (87%; $P < 0.01$) postfire than the unburned plots (Figs. 4A and B) largely due to the dramatic expansion of the invasive grass *P. conjugatum* (Table S1). This grass was the most abundant species following fire with 73 percent cover as compared with 2 percent in the unburned plots. Similarly, *N. multiflora* had < 1 percent cover in the unburned plots, but was the second most abundant species (6% cover) in the burned plots. Two potentially invasive shrubs (*Buddleia asiatica* and *R. rosifolius*) colonized the postfire environment.

DISCUSSION

COMMUNITY INVASIBILITY.—The stand-replacement fire converted three tropical wet forest communities into early seral herbaceous-dominated communities. The fires likely increased resource availability (sunlight, water availability, and nutrients) thereby creating opportunities for recruitment of a different suite of both native and nonnative species. As predicted, the communities dominated by natives before fire had higher nonnative species abundance in burned sites compared with unburned sites. These results support the fluctuating-resources hypothesis, in that community invasibility increased for the forest communities with increases in available resources. Before fire, native *D. linearis* was the most abundant understory species in the two native forest communities, but was virtually absent during early postfire succession. The effect of fire on *D. linearis* has been shown to differ ranging from rapid regrowth from living tissue in Sri Lanka (Maheswaran & Gunatilleke 1988, Ashton *et al.* 2001), to slow (> 10 yr) recovery from expanding unburned patches in Hawaii (Tunison *et al.* 2001), and even no regeneration following fire and other disturbances (Holttum 1957, Walker & Boneta 1995). *Dicranopteris linearis* recovery in this study is likely to be slow because fires completely killed fern indi-

viduals and few patches were left unburned from which to recolonize. Slow recovery is of particular concern because the order of arrival following disturbance can dictate which species dominate a site (Connell & Slatyer 1977).

In contrast to the forest communities, fire had little effect on the structure and composition of the shrubland. Fire did not increase invasibility in these communities. Differences in invasibility among communities in this study were inversely related to the 'level of invasion' or abundance of nonnative species in each community before fire. These results emphasize the importance of community composition before disturbance when predicting vulnerability to invasion by new species. Previous theories that focused on native species richness as a proxy for community invasibility (*e.g.*, Elton's biotic resistance hypothesis, 1958) as opposed to community composition are likely to be less applicable as nonnative species become increasingly abundant on a global scale. Species identity, particularly disturbance adaptations in this study, as well as abundance are likely to be important indicators of invasibility. For example, the shrubland communities are likely less vulnerable to new species invasions because they have previously burned and the species now dominant are adapted to shorter fire-return intervals (Kauffman 1990). Even in previously invaded communities or completely novel habitats, invasibility is important because not all invasive species are equal in their economic or environmental impacts.

DO NONNATIVE SPECIES INHIBIT NATIVE SPECIES RECOVERY?—Invasive species may alter ecosystem responses to fire (Mack & D'Antonio 1998). Four of the five communities sampled were dominated by nonnative species during early postfire succession. Site dominance occurred through two pathways: (1) rapid recovery of nonnative grasses and ferns where they dominated before fire (*e.g.*, *Andropogon* shrubland, *Nephrolepis* shrubland, and *Nephrolepis* forest), and (2) colonization and range expansion of the invasive grass *P. conjugatum* into previously native-dominated sites (*e.g.*, *Cibotium* forest). The rapid recovery of nonnative grasses and ferns where they dominated before fire were expected, but the extent of *P. conjugatum* expansion in the *Cibotium* forest was not. *Paspalum conjugatum* was present in the unburned plots and was recorded in these forests in the late 1980s (Pratt *et al.* 1999), but with lower relative cover. Fire appeared to temporarily decrease barriers to understory colonization through increased light availability (Burton & Mueller-Dombois 1984) due to canopy and subcanopy mortality (Ainsworth & Kauffman 2009) and by consuming the slow to decompose dense frond litter layer (Russell & Vitousek 1997) thus altering seedbed conditions for a rapid establishment of invasive *P. conjugatum* grass in the understory.

Physical site dominance by nonnative herbaceous understory species can limit available space for slower-growing native species to establish (D'Antonio & Vitousek 1992, Aide *et al.* 1995, Cabin *et al.* 2000, Corbin & D'Antonio 2004). Despite large differences in understory cover following fire among communities, native woody seedling densities did not differ among the three forest communities (Ainsworth & Kauffman 2009). Presumably the rapid recovery of nonnative *N. multiflora* and colonization of grasses following fire inhibited seedling establishment. Alternatively,

regrowth of *D. linearis* was virtually absent and the thick litter layer that was not consumed by the fire in this community appeared to diminish seedling establishment of all species following fire. The remaining fuel, primarily a dense litter mat of *D. linearis*, was slow to decompose and may affect forest regeneration by limiting light and space on the forest floor (Maheswaran & Gunatilleke 1988, Russell & Vitousek 1997). Seedling germination was inversely proportional to *D. linearis* 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. It is also possible, however, that *D. linearis* ferns may regain dominance over time.

Metrosideros polymorpha sprout growth was greatest in the native *Dicranopteris* forest, where understory competition was much lower than the other two forest communities where postfire understories were dominated by nonnative species. These results suggest that the rapid establishment of a nonnative-dominated understory decreases the growth of *M. polymorpha* sprouts. Similar results were found in dry woodland sites in Hawaii, where nonnative grasses competed for light with native shrub seedlings (Hughes *et al.* 1991, Hughes & Vitousek 1993). At this site, grass removal resulted in a strong growth response by *M. polymorpha* and native shrubs with increases in seedling recruitment (D'Antonio *et al.* 1998, Mack & D'Antonio 2003). In this study, the dominance of *N. multiflora* to the exclusion of other species (Fig. 4B) suggests that this nonnative fern may be altering the successional trajectory of these mesic and wet forests and should be considered an invasive species in Hawaii.

IMPLICATIONS OF FIRE AND NONNATIVE SPECIES INVASIONS.—In the two lowest elevation shrubland communities, the combination of nonnative species (plants and ungulates), coupled with ignitions have created an alien species–fire cycle (D'Antonio & Vitousek 1992) resulting in the loss of native *M. polymorpha* woodlands. The conspicuous lack of trees and shrubs except for *D. viscosa* in the unburned shrubland sites where fire has not occurred in over 10 yr suggests that postfire site dominance by these grasses and ferns will persist for many years.

In the mesic forest communities (*Nephrolepis* and *Dicranopteris* forests) over half of the *M. polymorpha* canopy trees initially survived fire by sprouting, but mortality increased between the first and second postfire years (Ainsworth 2007). Because of the open nature of these sites coupled with a continuous herbaceous cover or litter layer additional fires are possible. The occurrence of another fire could convert these forests to communities dominated by nonnative herbs and shrubs more closely resembling the adjacent shrubland communities.

Fire is a rare occurrence in tropical wet forests that comprise the *Cibotium* community. Following fire nonnative species expanded their range. The long-term persistence and impact of invasive *P. conjugatum* grass in the understory are unknown. Unlike the lower elevation mesic forests, *C. glaucum* dominated the subcanopy and over 90 percent survived the fire (Ainsworth & Kauffman 2009). Therefore, much of the frond canopy reestablished within a year decreasing light and nutrient availability to the understory.

Tree ferns were observed to create suitable sites of seedling establishment of *M. polymorpha*, but the rapid recovery of the fern canopy may slow their growth into canopy dominance (Burton & Mueller-Dombois 1984). 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. Although currently these cooler, wetter, and higher elevation forests (Giambelluca *et al.* 1986) are less likely to be readily type converted into nonnative-dominated shrubland communities, this is a possible scenario with global change creating conditions for increased fire frequencies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Understory species mean percent cover and standard error in unburned and burned sites 2-yr postfire in the sampled communities.*

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