ECOSYSTEMS

Ecosystem and Restoration Consequences of Invasive Woody Species Removal in Hawaiian Lowland Wet Forest

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ABSTRACT

A removal experiment was used to examine the restoration potential of a lowland wet forest in Hawaii, a remnant forest type that has been heavily invaded by non-native species and in which there is very little native species regeneration. All non-native woody and herbaceous biomass (approximately 45% of basal area) was removed in four 100-m^2 removal plots; plots were followed for a three-year period. Removal plots had a lower leaf area index, higher air temperatures, higher afternoon soil temperatures, and lower relative humidity than control plots. Removal plots had 40% less litterfall mass and similarly reduced nutrient inputs. Leaf litter decomposition rates were much slower in the removal plots, due more to site quality than litter quality. However, soil N and P were not different between treatments. Native species had a distinct suite of leaf traits (greater integrated water use efficiency, lower mass-based leaf nutrient concentrations, and lower specific leaf area). Despite major environmental changes in the removal plots, native species' diameter growth and litterfall productivity were not significantly greater after removal, testifying to the slow response capabilities of native Hawaiian trees. Our results are consistent with the expectation that native species are conservative in regards to resource use and may not strongly respond to canopy removal, at least at the adult stage. Management strategies will have to incorporate the slow growth rate of Hawaiian species and the fact that weeding may be required to suppress expansion and nutrient inputs of introduced species.

Key words: aboveground biomass; *Metrosideros polymorpha*; non-native species; nutrient cycling; productivity; resource availability.

INTRODUCTION

Few ecosystems remain pristine, and those that maintain major native biodiversity components are increasingly being threatened by non-native species. One approach to studying these invaded ecosystems is the use of removal experiments, which can serve as proxies in ecosystems in which there are no longer uninvaded areas. Removal

experiments can be used to examine the competitive effect of a dominant species, the response of remaining vegetation, the response to disturbance created during the act of removal, or the biotic and abiotic consequences of biomass loss (Diaz and others 2003). Critical questions that need to be addressed include understanding how removal of key species affects ecosystem functioning (Zavaleta and others 2001; Diaz and others 2003) and whether the impacts and legacy of invasive species are reversible.

An excellent place to examine these questions is Hawaii, where it is estimated that half of the flora is non-native (Wagner and others 1999). Hawaiian ecosystems have shown a high degree of invasibility, due in part to disharmonic biota, high endemism, and low species diversity (Simberloff 1995; Denslow 2003). This investigation examines removal of woody invasive species in a tropical lowland wet forest in Hawaii. Hawaiian lowland wet forests (LWF) are rare and exist today only in remnant patches, mainly on the islands of Hawaii and Kauai on sites not well suited for agriculture (Price and others 2007). A recent survey of remnant communities found although these forests are invaded, they are still important reservoirs of native biodiversity (Zimmerman and others 2008). On older sites (>300-year-old substrates) native species can still dominate basal area through the presence of large, old canopy trees, but introduced species dominate in terms of abundance and density, and very little regeneration of native species is occurring.

Unfortunately, deforestation and lack of written documents mean that there is very limited information on the species composition or functioning of intact native LWF, unlike the better studied montane forests that have more intact canopies (Vitousek 2004). We therefore lack an important baseline in understanding the impacts of local extinction and introduced species. Despite the decline of these forests, little to nothing is known about the response of native species to competition, the potential for lowland forest restoration, or the resilience of the forests once the obvious threats of invasive animal and plant species are removed. Although it is likely that removal will have ecosystem-level impacts, the benefits to native species are unclear because many native Hawaiian species are conservative in their resource use (Baruch and Goldstein 1999; Daehler 2003) and may not be able to take advantage of additional resources. We address two major themes in this article: (1) how removal of biomass influences resource availability and productivity and (2) whether native species

benefit from removal, making it an effective part of a restoration effort.

MATERIALS AND METHODS

Study Site

The study site is a 107-acre lowland wet forest in the southern portion of the Keaukaha Military Reservation (KMR) immediately south of the Hilo Airport on the eastern coast of Hawaii Island (Figure 1). It is about 30 m in elevation and is situated on a 750- to 1500-year-old 'a'ā lava flow. Rainfall, as determined by the Hilo Airport, averages 3280 mm y^{-1}. The forest is an example of primary succession and is not believed to have undergone major human disturbances although some human presence was likely because the ancient Hawaiian foot path, the Puna Trail, runs through the property. Canopy height ranged from 23 to 35 m. The forest was fenced in 2002 to exclude pigs (center of exclosure is at 19°42.15 N, 155°2.40 W). The site is classified as LWF, based on the definitions of greater than 2500 mm precipitation at 1000 m and greater than 3000 mm at sea level (Price and others 2007), and on vegetation descriptions of Gagné and Cuddihy (1999).

Soils at the site are classified as isohyperthermic Typic Udifolists of the Papai Series—extremely cobbly, well-drained soils overlying 'a'ā lava. This soil series is found in gently sloping areas (2–10%) on windward slopes of Mauna Loa, and is high in
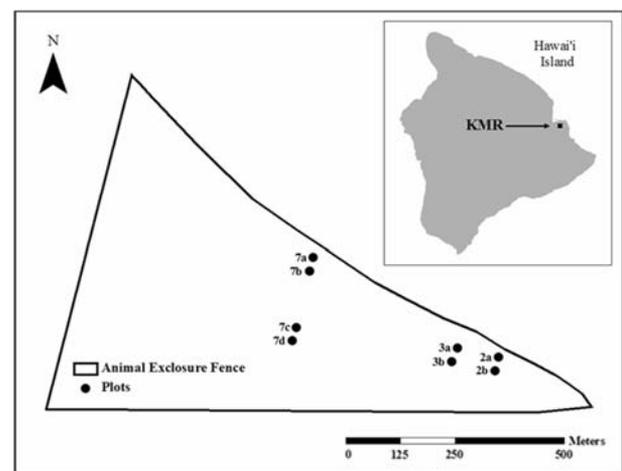
Figure 1. Map of Keaukaha Military Reservation study area, showing location within the Hawai'i Island (*inset*), and within the site, the location of our eight study paired control and removal plots.

organic matter (30–50% in the top 10 cm). In the top 26 cm, soils have an ECEC of 35–117 meq/100 g and are acidic (pH range 5.1–5.5) (Patrick Niemeyer, personal communication). Soils are likely to be N-limited based on their age and other work in Hawaii (Vitousek 2004).

The KMR site is dominated by ʻōhiʻa (*Metrosideros polymorpha*) and lama (*Diospyros sandwicensis*) in the overstory, and various shrubs, small trees, and ferns in the midstory and understory; this ʻōhiʻa/lama forest community is currently found only on the eastern side of the island of Hawaiʻi (Gagné and Cuddihy 1999). Numerous non-native species have invaded this forest type, most notably the trees strawberry guava (*Psidium cattleianum*), bingabing (*Macaranga mappa*), melastoma (*Melastoma septemnervium*), albizia (*Falcataria moluccana*), and the shrub *Clidemia hirta* (Zimmerman and others 2008). The latter three species are listed on the Hawaii state Noxious Weed List. Introduced animals common in these forests includes pigs (*Sus scrofa*), mongoose (*Herpestes auropunctatus*), rats, and a variety of birds. The main native and non-native species at the KMR site are listed in Table 1; none of these are N-fixers. An inventory at this site showed that for woody species the basal area of stems 2.0 cm or larger DBH was 19.8 m^2 ha^{-1} for native species and 16.4 m^2 ha^{-1} for woody introduced species, with a density of 1591 native stems/ha and 17,199 introduced stems/ha (Zimmerman and others 2008). Although the overstory remains largely native, younger individuals in the forest are mainly non-native, and non-native species may soon dominate this forest.

Experimental Design

Four pairs of control and removal plots were setup along three permanent transects at the KMR site. Control plots were located approximately 20 m away from the removal plots. All plots were 10 × 10 m^2. In April–June 2004 all introduced species were removed, leaving only seedlings and adult forms of the native species. With the exception of *Pandanus tectorius*, few to no native midstory species are present in this forest. To minimize potential edge effects, invasive species were also cleared from a 2.5-m perimeter buffer around the removal plots. Trees were removed by hand or saws and cut stumps were immediately dosed with a triclopyr-based herbicide (Garlon 4, Dow Agro-Sciences LLC). This basal bark treatment was very effective as less than five stems resprouted. Herbaceous vegetation and small shrubs were hand pulled. All material removed was separated by species, and then further separated into leaf and wood components. The wet weight of all material was measured in the field and the biomass was removed from the plots. To determine dry weight, three sub-samples per plot each of leaf and wood material were dried at 70°C to determine a wet/dry weight conversion factor for each species.

Leaf Area Index and Microclimate

Two LAI-2000 Plant Canopy Analyzers (LI-COR, Lincoln, Nebraska) were used to estimate leaf area index (LAI). Measurements were taken before the removal treatment was applied and on five occasions thereafter; light was surveyed in all four corners of the plot, facing toward the center. We

Table 1. Major Native and Non-Native Species at the KMR Site

Species	Family	RA (%)	RF (%)	RD (%)	RC (%)
Native					
Cibotium spp	Dickinsoniaceae	1.14	7.14	4.5	
Diospyros sandwicensis	Ebenaceae	1.31	9.52	6.53	
Metrosideros polymorpha	Myrtaceae	6.4	11.9	38.72	
Psychotria hawaiiensis	Rubiaceae	5.09	9.52	2.11	
Non-native					
Cecropia obtusifolia	Cecropiaceae	3.55	10.71	8.85	
Clidemia hirta	Melastomataceae		8.08		7.21
Macaranga mappa	Euphorbiaceae	5.16	8.33	4.93	
Melastoma septenervium	Melastomataceae	56.31	11.9	20.81	
Psidium cattleianum	Myrtaceae	15.5	11.9	8.71	

Values are for individuals >2 cm dbh, with the exception of the herbaceous Clidemia. Data are from Zimmerman and others (2008). Cibotium is a tree fern. RA = relative abundance, RF = relative frequency, RD = relative dominance, RC = relative cover. The native Pandanus tectorius is present at KMR but was not present in Zimmerman's plots.

sampled at very low sun angles using a 45-degree view cap to best capture sky conditions. Each simultaneous measurement in the open field faced the same compass direction as the measurement in the plot, and also used the 45-degree cap. LAI was calculated from simultaneous measurements in the plot and in an open pasture adjacent to the forest, using post correctional software (FV2000, LI-COR Inc.). The average LAI of each plot was compared using Mann–Whitney tests. A repeated measures ANOVA with time as a random effect was run to determine if LAI changed through time. All statistical analyses used JMP version 3.1 (SAS Institute 1995) unless stated otherwise.

Air temperature, soil temperature, and relative humidity were measured in some of the paired plots for at least six months between June 2004 and March 2005. HOBO H8 Pro series temperature and humidity sensors (Onset Computer Corp., Pocasset, Massachusetts) were placed 1 m from the northeast corner of the plots at a height of about 20 cm (or a depth of about 10 cm for soil temperature); data were recorded every 15 min prior to averaging hourly by month. Paired *t*-tests were applied across a 24-h period to examine differences in control versus removal plots.

Growth of Trees and Emerging Understory Weeds

Spring-loaded dendrometer bands were placed at 1.35 m height on native trees to assess growth rate. In March 2004, bands were placed on trees with greater than 2 cm diameter. Because native trees often have very slow diameter growth, bands were left to settle for 7 months before scoring. Increment growth measurements were taken in 2005, 2006, and 2007. Circumference growth on the dendrometer was converted to diameter, and growth rate was analyzed both as annual diameter increment (cm y^{-1}) and as relative growth rate ((Δ diameter $\times$ 100)/initial diameter). Changes were measured with DBH tapes if trees were greater than 2.0 cm DBH but too small for dendrometer bands. Because each plot contained only around a dozen native trees, plots were pooled and analysis was done on an individual tree basis using Mann–Whitney tests.

In the 40 months following removal, we conducted five weedings, with the first initiated 6 months after removal. All non-native species were pulled up by their roots and weighed after drying for a minimum of 48 h at 70°C. Biomass was separated by species for the first three weedings, but not for the last two weedings. The data are expressed as g/day to account for the fact that intervals between weedings were not identical.

Canopy Leaf Characteristics

Sun leaves were collected from the canopy using a shotgun in June 2005 to better understand leaf characteristics of the most common species (four native, four non-native). Up to five sunlit individuals per species were collected from the forest across all eight plots. Samples were analyzed for N, P, C, leaf water content, leaf area, specific leaf area, δ^{13}C (an index of integrated water-use efficiency), and δ^{15}N. Nutrient analyses were done at the University of Hawaii at Hilo Analytical Laboratory. Isotopes were measured on a Thermo-Finnigan Delta V IRMS (Waltham, Massachusetts) attached to a Costech ECS 4010 CN Elemental Analyzer (Valencia, California). P was measured on a Pulse Autoanalyzer III with Autosampler IV (Saskatoon, SK, Canada). Either Mann–Whitney or *t*-tests were used to compare native and introduced species, depending on the homogeneity of variance. All leaf traits were analyzed separately by *t*-tests or Mann–Whitney tests, depending on equality of variance, and then grouped together for a principal components analysis using Primer 5 (version 5.2.9) (Clarke and Gorley 2001).

Litterfall Mass and Nutrients

Litterfall collection began in November 2004 using littertraps (40×40 cm^2) made from plant trays lined with fiberglass window screening. At four randomly chosen locations (one in each quarter of the plot), a group of four littertraps (covering 80×80 cm^2 area) were set out. For 2 years, litter was collected biweekly and separated and categorized by different leaf species, native and non-native reproductive material, wood, and miscellaneous. Each collection was dried at 70°C and weighed.

Litterfall nutrients were assayed on a subset of litter collected over a 4-month period in Year 1. Litter was ground using a Wiley mill (20 mesh) and samples were bulked across dates. C and N were determined on a Costech ECS 4010 CN Elemental Analyzer (Valencia, California), and other nutrients on a Varian Vista MPX ICP-OES Spectrometer (Palo Alto, California).

Examination of litterfall mass and nutrients was conducted with a two-way ANOVA with treatment and origin (native or introduced) as main effects. Mann–Whitney rank tests were used to compare between removal and control plots for individual species' leaves and other sorted categories.

Leaf Litter Decomposition

Leaf litterfall from the first year of collection was used for a decomposition experiment. Although leaf litter had been previously oven-dried, and this may affect litter decomposition to a small degree, the purpose of the experiment was to determine the relative differences in decay rate between species and treatments. Approximately 5 g of six species (with the exception of 4.0 g of *Diospyros*) were placed in 10×10 cm^2 bags made of 1-mm mesh fiberglass window screen. Each bag received litter from a single well-mixed source bag for that species (a common litter experiment). Six litter bags (one for each species) were attached 20 cm apart on a string. There were three designated locations for litter bags in each plot and each of these locations received four strings (each was collected on a different date). The bags were placed in the field in March 2007 and litter collections occurred at 35, 67, 95 and 182 days.

Decomposition rate constants (k values) were calculated by species for each plot. Both linear and exponential models were tested, and the latter were found to be superior based on R^2 values. The three sub-replicate k values per time point per plot were averaged, and a k value for a given species in a given plot was considered the replicate. Two-way ANOVA was run on the 48 k values (4 plots $\times$ 6 species $\times$ 2 treatments), with treatment and species as main effects. Tukey tests were used to compare species within a treatment.

Soil Nutrient Availability

Available soil N (as NO_3^- and NH_4^+) and P (as PO_4^{3-}) were measured at each plot using ion exchange resin bags. The 6.5×7.5-cm^2 resin bags were composed of monofilament polyester silkscreen fabric (86 mesh) and filled with 6.0 g of mixed-bed exchange resin (IONAC NM-60 H+/OH$^-$ form, type

I). A 10% HCl acid bath solution was used to rinse all materials in contact with the mixed resin beads prior to filling the bags. Following the acid wash, all materials were rinsed with deionized water. In October of 2006, 64 resin bags were buried at a depth of 4–6 cm in the plots (four N and four P bags per plot). Bags were recovered after 27 days and rinsed with deionized water to remove the excess soil and debris. Bags designated for NO_3^- and NH_4^+ analysis were extracted using a 1 M KCl solution, and samples for PO_4^{3-} analysis were extracted with a 0.5 M HCl solution. Resin bags were placed into extraction solutions and shaken at 3500 rpm for 14 h. Approximately 15 ml of each extraction solution was transferred into scintillation vials and analyzed on a Pulse Autoanalyzer III with Autosampler IV (Saskatoon, SK, Canada). A Mann–Whitney test was used to analyze differences between treatments.

RESULTS

Biomass Removed

Biomass removed ranged from 288 to 928 kg/100 m^2 plot, with *Macaranga* and *Melastoma* as the two species with the most biomass. Based on the figures reported in Zimmerman and others (2008), about 45% the forest basal area was removed. There was considerable variation among plots in species composition on small spatial scales (Table 2). However, the removal species corresponded well with the previous vegetation survey of the forest (Table 1).

Leaf Area Index and Microclimate

Prior to treatment there was no significant difference between removal and control plots, with LAI of the forest approximately 5.5 m^2 leaf/m^2 ground

Table 2. Biomass of Non-Native Species Harvested from the Four Removal Plots

Species	Biomass (kg)					Composition (all plots)	
	Plot 2A	Plot 3A	Plot 7B	Plot 7D	Total	% Leaves	% Wood
Alstonia scholaris	0.0	0.0	102.6	0.0	102.6	3.4	96.6
Cecropia obtusifolia	74.9	65.2	75.5	0.0	215.6	0.7	99.3
Clidemia hirta	5.7	8.5	0.2	7.1	21.5	32.3	67.7
Macaranga mappa	32.1	119.4	583.1	299.0	1033.6	3.0	97.0
Melastoma septemnervium	172.8	106.0	125.4	75.8	479.9	5.2	94.8
Other herbaceous	0.00	0.01	0.01	0.00	0.01	100.0	0.0
Psidium cattleianum	2.6	26.4	16.1	62.6	107.8	9.4	90.6
Psidium guajava	0.0	0.0	25.0	0.0	25.0	0.8	99.2
Total	288.1	325.5	928.0	444.4	1986.0		
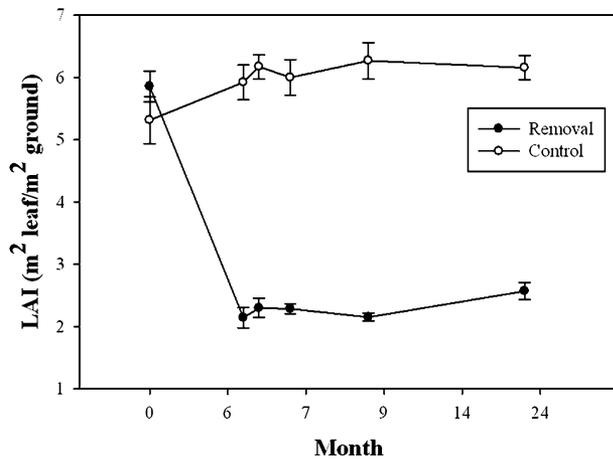
Figure 2. Leaf area index (and SE) during pre-removal (Feb 2004) and five post-removal time points.

(Figure 2). After treatment, removal plots had significantly lower LAI on every date ($P = 0.02$ for each test), with LAI being reduced to approximately 2 m^2 leaf/m^2 ground. Using repeated measures, the only significant difference was before and after treatment; after the removal plots were created there was no increase in LAI with time in either the control or removal plots.

The diurnal signature of microclimatic conditions was significantly different between treatments (Figure 3). Paired *t*-tests showed that relative humidity was significantly lower in removal plots ($t = 3.23$, df = 23, $P < 0.004$) and that air temperature was significantly greater in removal plots ($t = -4.45$, df = 23, $P < 0.001$). Taken over the entire 24-h period, the soil temperature was not significantly different between treatments, but there were differences in the diurnal pattern. Compared to the control plots, the removal plots had cooler soil temperatures from 10:00 p.m. to noon and warmer temperatures in the afternoon.

Growth of Trees and Emerging Understory Weeds

There was no significant difference in tree diameter growth between removal and control plots for any of the three native species. Both relative growth rate and diameter increment were extremely variable among individuals (Figure 4). Growth rates were extremely slow for tropical forest trees—with averages ranging from 0.01 to 0.19 cm per year.

Removal led to a large influx of new weeds, which appear to have come primarily from the seed bank (unpublished experiments). In the first weeding, which occurred approximately 7 months post-removal, there was an average of 12.38 g day^{-1} m^{-2}
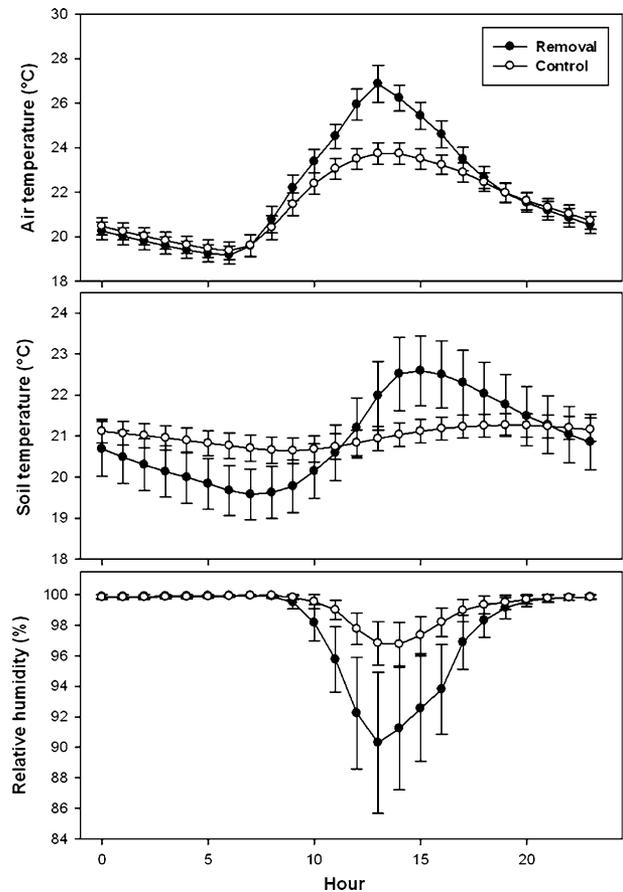
Figure 3. Microclimate of the control and removal plots. Data points represent averages over 6–9 months; bars represent SE. Note different scales on the *y*-axes.

of biomass in the four removal plots, but by the second weeding this value was down to 0.41 g day^{-1} m^{-2}. Although the total went up slightly in the third and the fourth weeding (0.77 and 0.88 g day^{-1} m^{-2}, respectively), it was 0.46 g day^{-1} m^{-2} at the fifth weeding.

Canopy Leaf Characteristics

As a group, the native species had δ^{13}C values that were significantly less negative than the non-native species ($P < 0.01$) (Figure 5). This indicates that natives tend to have greater integrated water-use efficiency. *Melastoma* and *Psidium* had the lowest δ^{13}C values and are thus the least efficient water users, but these species as well as *Psychotria* were generally shorter than the others and their δ^{13}C values may potentially be influenced by carbon dioxide recycling (Sternberg and others 1989). Native species also had significantly more positive δ^{15}N values ($P < 0.02$). Additionally, native species as a group were lower in leaf area ($P = 0.09$,
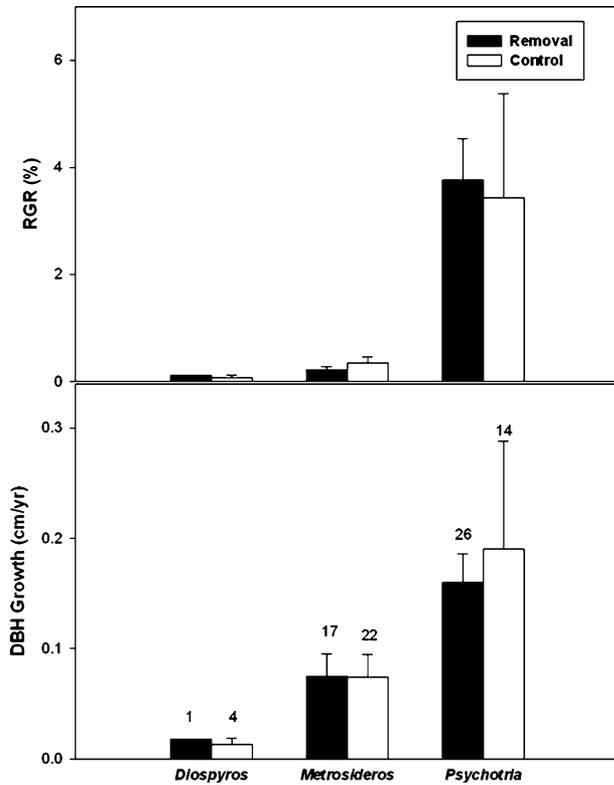
Figure 4. Diameter growth (+SE) of the three native tree species, *Diospyros sandwicensis*, *Metrosideros polymorpha*, and *Psychotria hawaiiensis*. Growth is presented either as relative growth rate, which takes into account initial size, or absolute diameter increment. Values above *bars* in the lower panel represent the sample sizes for both data sets.
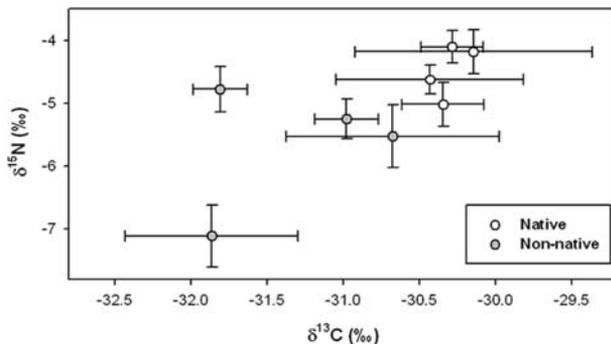
Figure 5. Isotope values for $\delta^{13}C$ and $\delta^{15}N$ for four common native and non-native species. *Dots* represent means and *bars* represent SE in both directions.

Mann–Whitney test), SLA ($P < 0.001$, Mann–Whitney test), N_{mass} ($P = 0.007$, Mann–Whitney test), P_{mass} ($P = 0.07$, Kruskal Wallis test), but higher in N_{area} ($P = 0.02$, t-test), P_{area} ($P = 0.001$, t-test), and C ($P = 0.0001$, t-test).

Litterfall Mass and Nutrients

The total litterfall averaged over the 2-year period was 515.4 g m^{-2} y^{-1} in removal plots and 851.6 g m^{-2} y^{-1} in control plots. In both years, total litterfall in the control plots was significantly greater than the removal plots ($P = 0.02$ for each test) (Table 3). In Year 1, removal plots had significantly less non-native leaves ($P = 0.02$) and miscellaneous material than control plots ($P = 0.02$). In Year 2, both of those two terms were still significant ($P = 0.02$ and 0.04, respectively), but removal plots also had less non-native reproductive material ($P = 0.02$) and wood ($P = 0.04$). Some litter from outside the removal plots was clearly blowing into the plots because the removal plots did contain some leaves of non-native species (Table 3). *Metrosideros* was the species with the greatest amount of litter, followed by *Melastoma* and *Cecropia* (Table 3). Although removal of introduced species had a large effect on total litterfall, productivity of the native species leaf litter was not enhanced (Figure 6).

Litterfall nutrient concentrations of K, Mg, P, Ca, and N were significantly greater in introduced species than in native species (Figure 7). Carbon was lower in non-native species (averaging 38.0% vs. 46.5% in native species). However, for a given species, nutrient concentrations in litterfall were generally not different between the control and removal plots, except that *Cecropia* had higher K concentrations and *Psychotria* had greater C in removal plots, whereas *Metrosideros* had greater Al concentrations in control plots (Appendix 1, see supplementary material). Miscellaneous, native reproductive and non-native reproductive material differed in C, P, and Ca concentrations, and wood differed in Al levels (Appendix 1, see supplementary material).

Litterfall mass averaged over the 2-year period was multiplied by nutrient concentrations, resulting in an estimate of annual nutrient inputs via aboveground litter in this forest (Appendix 2, see supplementary material). The invaded control areas are receiving more nutrients to the forest floor than the removal plots: control plots are enriched by a factor of 1.5 for K, 1.9 for Mg, 4.7 for Al, 1.3 for Na, 1.6 for P, 1.9 for Ca, 1.8 for N, and 1.6 for C.

Leaf Litter Decomposition and Soil Nutrient Availability

There was a significant effect of treatment on decomposition ($F_{1,36} = 5.97$, $P < 0.0001$), with control plots averaging k values of 1.59 ± 0.45 y^{-1} and removal plots averaging 0.88 ± 0.15 y^{-1}.

Table 3. Litterfall Mass in g m^{-2} y^{-1} in Control and Removal Plots

| | Year 1 | | | | Year 2 | | | |
| | Removal | | Control | | Removal | | Control | |
	Avg	SE	Avg	SE	Avg	SE	Avg	SE
Native leaves								
Metrosideros polymorpha	231.5	45.0	225.0	40.7	224.7	38.0	198.0	35.2
Pandanus tectorius	1.4	0.8	37.8	33.7	1.1	0.7	40.2	39.4
Diospyros sandwicensis	16.7	3.5	34.7	21.0	15.9	5.7	30.8	18.9
Psychotria hawaiiensis	34.9	17.7	19.2	11.0	36.8	17.2	17.7	12.2
Alyxia oliviformis	1.8	1.6	1.4	1.3	0.1	0.1	1.2	1.1
Non-native Leaves								
Melastoma septemnervium	24.6	10.7	135.0	33.3	16.1	9.0	128.7	38.9
Cecropia obtusifolia	46.7	8.8	93.1	20.5	61.7	28.1	100.0	14.7
Macaranga mappa	10.5	6.3	42.4	12.4	23.8	14.9	47.2	33.5
Clidemia hirta	5.4	2.4	15.6	4.9	2.6	0.9	30.9	4.8
Trema orientalis	0.4	0.4	5.8	5.8	0.2	0.1	5.4	5.2
Vines	4.4	3.1	5.6	3.8	2.4	1.9	4.4	2.6
Psidium cattleianum	0.4	0.3	5.5	3.0	0.9	0.6	14.0	8.1
Mangifera indica	0.2	0.2	3.6	3.6	0.0	0.0	1.5	1.5
Cordyline fruticosa	0.0	0.0	3.1	3.1	0.0	0.0	1.2	1.1
Falcataria moluccana	0.0	0.0	1.8	1.5	0.1	0.1	2.7	2.7
Ferns	0.4	0.1	1.0	0.5	0.4	0.3	1.0	0.4
Alstonia scholaris	2.7	2.6	0.6	0.4	3.3	3.3	0.1	0.1
Oplismenus hirtellus	0.008	0.008	0.006	0.006	0.004	0.004	0.009	0.009
Other								
Wood	73.4	8.6	117.9	21.2	74.2	17.6	150.4	17.6
Misc.	30.2	3.0	46.4	4.2	38.3	8.4	63.7	7.2
Native reproductive	37.0	15.4	31.3	3.9	26.0	8.6	28.8	7.9
Non-native reproductive	6.7	2.4	22.5	7.3	6.2	0.4	33.2	6.3
Total	496	47.05	802	64.1	534.7	42.7	901.1	31.4

Averages represent four plots, although every species may not have been found in all plots.
Values are listed from most to least abundant in control plots.
Vines represent both Dioscorea pentaphylla and Paedaria foetida.
Ferns represent Blechnum occidentale and Christella parasitica.

Slower decomposition rates in the removal plots were strikingly consistent across species (Figure 8). For example, decomposition rates in control plots were almost doubled for all three native species, suggesting a strong treatment effect. In addition, both the species effect ($F_{5,36} = 12.18$, $P < 0.0001$) and the species*treatment term ($F_{5,36} = 0.011$) were significant. *Melastoma* had a decomposition rate that was much faster than any other species; differences between the remaining native and non-native species were much smaller (Figure 8).

Resin-available nutrients 2.5 years after the treatments were applied were not significantly different between removal and control plots for NH_4^+, total N, and PO_4^{3-}, but NO_3^- was close to significant ($P = 0.07$). There was greater variability in the removal plots (Table 4).

DISCUSSION

Consequences of Biomass Loss and Native Species' Responses

Removal experiments can be powerful tools for examining the mechanisms of impacts of specific species or the functional consequences of biomass removal. Most removal experiments carried out to date have removed herbaceous vegetation either in grasslands (Wardle and others 1999; Symstad and Tilman 2001) or in tree/grass systems (D'Antonio and others 1998; Simmons and others 2007). Although herbaceous-dominated systems may be easier to work with logistically, woody vegetation may affect resource availability quite differently, due to potentially greater shading, longer-lived tissues, deeper rooting patterns, and different litter
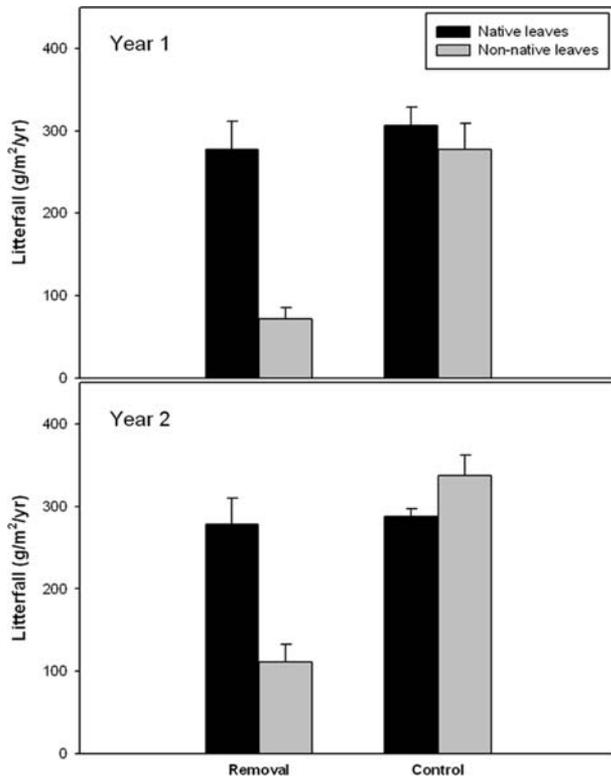
Figure 6. Average litter mass of leaves (+SE) from native and non-native species. Leaffall was calculated on an annual basis from littertraps left out for a 2-year period. There were significantly fewer non-native leaves in the removal plots in both years, but native leaffall did not differ between removal and control plots.

Figure 7. Average (+SE) nutrient concentrations for native and non-native species. Data represent the main effect of species origin from a two-way ANOVA and are thus pooled across treatments and plots. Significance symbolized by $*P \le 0.05$, $**P \le 0.01$, and $***P \le 0.001$.

quality. Of the prior experiments involving removal of tree biomass (Holmes and Cowling 1997; Yelenik and others 2004; Loh and Daehler 2007), to our knowledge this is the only multispecies removal study conducted in a tropical forest. The multispecies approach essentially lumps all non-native species together, precluding the possibility of identifying consequences specific to particular species or functional group removed (Wardle and others 1999; Symstad and Tilman 2001). To partially overcome this limitation, we have quantified most variables by species. However, in this study, it is impossible to know if removal plot differences were due to species identity or simply the loss of biomass. Our main objective therefore was not to ascribe effects to invasive species but to quantify plot conditions after removal to determine if removal could be part of a successful management strategy for these invaded forests.

Removal of biomass had a variety of abiotic and biotic effects, and responses may occur at different time scales. Some abiotic effects such as higher light

levels (Figure 2), reduced leaf area within 1–10 m from the ground (Wong 2007), and altered microclimate (Figure 3) are short-term responses to the removal. Other predicted effects such as increased productivity of native species, in terms of tree growth and litterfall, were not seen over this 3-year period. Perhaps this is not surprising, given that the average leaf lifespan of *Metrosideros* was 2.5 years in N-limited montane forest (Cordell and others 2001). The native trees may either be responding to the treatments very slowly and still undetectably, or they may be unable to respond at all. The only evidence for an allocation shift comes from small changes in some nutrient concentrations in native reproductive material in the removal plots (Appendix 1, see supplementary material). Tree growth was highly variable after removal, and the observed growth rates were quite slow, often an order of magnitude slower than what is typically reported for tropical forests (Baker and others 2003). However, values for *Metrosideros* were similar to its growth rate in montane wet forest
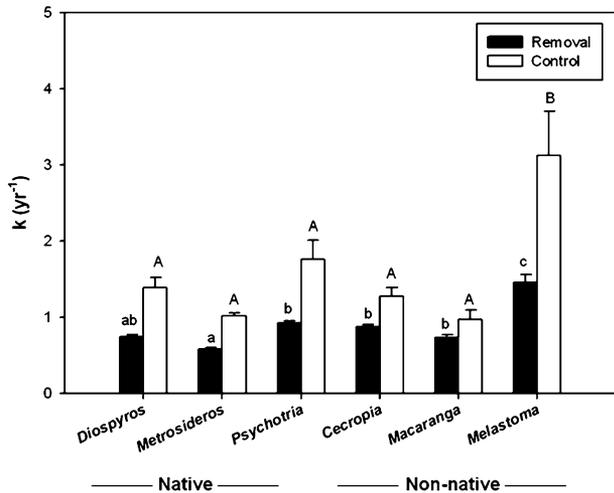
Figure 8. Decomposition rate constants (k values + SE) for control and removal plots by species. Removal plots had significantly lower decomposition rates for all species. Letters within a treatment show significant differences among species.

(1–2 mm y^{-1}) (Gerrish and others 1988; Gerrish and Mueller-Dombois 1999). Although growth rates of the native species are slow, we want to stress that the invaded forest is quite productive under the present environmental conditions. Globally, the litterfall productivity in the invaded areas puts this forest in the top 20% of tropical forests reviewed by Clark and others (2001). The decomposition k values of 0.58 y^{-1} (removal) and 1.01 y^{-1} (control) are higher than most Hawaiian montane wet forests, where values range from 0.16 to 1.06 y^{-1}, but are generally less than 0.5 y^{-1} (Vitousek and others 1994; Vitousek 1998; Ostertag and Hobbie 1999; Austin and Vitousek 2000). The site, if originally stocked with higher densities of native trees, may have been a highly productive lowland tropical forest.

There was a lack of connection between litterfall and soil nutrients in our study that was unexpected. Removal plots had lower total litterfall mass and nutrient inputs, and slower decomposition rates. Because of lower inputs it is likely that removal plots will have slower rates of nutrient cycling. However, removal of non-natives did not affect soil nutrients when measured 2.5 years after removal (Table 4). It is possible that our one-time sampling did not adequately capture soil nutrient trends, although our results were similar to our preliminary sampling 6 months earlier (results not shown). Because we observed that most species have similar litter nutrient concentrations and mass in both treatments (Appendix 1, see supplementary material), we conclude that uptake by native species may not increase with reduced competition. Therefore, it is possible that the lower input per area is balanced by lower uptake per area in the removal plots due to the loss of approximately half the basal area. Alternatively, invasion may not have altered soil nutrients—a similar result was observed in secondary forests in the Seychelles, where they found faster decomposition rates of invasive species litter but small soil nutrient differences (Kueffer and others 2008). Both hypotheses suggest that litter plays a dominant role over soils in short-term nutrient cycling, common in many tropical forests where annual nutrient fluxes are mainly through litterfall inputs (Vitousek and Denslow 1986). Soils at this site consist of organic matter and cobbles, so it seems reasonable that plants may be getting most of their nutrition from recent organic matter. We do not have data on rooting patterns, and it is possible that native and non-native trees may have different belowground allocation and root turnover patterns. The soil characteristics at this site preclude adequate sampling to address this question. However, from a restoration perspective, the lack of a soil effect is encouraging, because enriched soils tend to foster greater invasion (Ehrenfeld 2003).

Our results suggest that native species generally have limited plasticity in resource use, at least in the short term. Based on the C isotopes, native species may use water more efficiently (Figure 5), although CO_2 recycling from the forest understory

Table 4. Soil N and P Levels from Ion Exchange Resin Bags

	$NO_3^- + NO_2^-$		NH_4^+		Total N		PO_4^{3-}	
	Average	SE	Average	SE	Average	SE	Average	SE
Control	2.24	0.68	12.72	0.98	14.95	1.51	0.90	0.75
Removal	6.12	3.29	12.69	1.66	18.80	3.79	0.13	0.15
	$P = 0.07$		n.s.		n.s.		n.s.	

$n = 4$, values expressed as µg/g resin/day.

cannot be ruled out (Sternberg and others 1989). The $\delta^{15}N$ data are more difficult to interpret (Adams and Grierson 2001), but examining both isotopes together indicates that native species are isotopically distinct (Figure 5). Native and non-native leaves appear to be distinguishable based on their leaf traits with natives tending to have leaves that maximize photosynthesis per area (represented by N_{area}) and introduced species tending to have larger, thinner leaves that allocate more to the enzyme RUBISCO (represented by higher N_{mass}). The slow growth rate and conservative nutrient use of many Hawaiian plant species (Baruch and Goldstein 1999; Harrington and others 2001) provides further support for the hypothesis that patterns of productivity and nutrient cycling after invasion will not favor native species.

Conservation and Restoration Potential of Tropical Lowland Wet Forest

LWF represent a unique and rare ecosystem in Hawaii, and a reservoir of native biodiversity. *Metrosideros* provides an important nectar and insect source for many of Hawaii's native honeycreeper species (Perkins 1903; Scott and others 1986), a group of native birds that are one of the most cited examples of remarkable adaptive radiation (Ziegler 2002). Additionally, native bird populations below 1300 m elevation have been decimated by the introduction of the southern house mosquito (*Culex quinquefasciatus*) and the avian malaria parasite (*Plasmodium relictum*) (Woodworth and others 2005). Recent evidence suggests that at least one species, the Hawaii 'Amakihi (*Hemignathus virens*) has increased in prevalence at below 326 m (Spiegel and others 2006), which may be due to either the increased resistance by the bird host or decreased virulence by the parasite (Woodworth and others 2005). Without LWF habitat the possibility of evolution of resistance to malaria and the recovery of native birds will not exist (Kilpatrick 2006).

Comparison of replicated control and removal plots offers an opportunity to examine the efficacy of invasive species management as part of a restoration strategy (D'Antonio and Chambers 2006). This study demonstrates that the biomass removed is having strong ecosystem consequences on LWF in Hawaii. In contrast to many other studies of ecosystem-level effects of invasion, the main invaders are not N-fixers (for example, Vitousek and Walker 1989; Stock and others 1995; Maron and Connors 1996; Hughes and Denslow 2005). Rather, invasive species in this site have a variety of competitive advantages including shade tolerance, high specific leaf area, and lower construction costs (Wong 2007), high leaf area (*Macaranga*), high nutrient litter with fast decomposition rates (*Melastoma*), and vegetative reproduction (*Melastoma* and *Psidium*). The combination of these traits has led to a dense understory and midstory and some canopy emergence (*Cecropia*, *Macaranga*), a forest structure that may have been different from pristine LWF. Unfortunately, due to the absence of information on pre-human species distributions or light environments, we do not know if the introduced species invaded "empty niches" or displaced other species. However, this invaded site averages 2% light in the understory, with many areas at less than 1% (Wong 2007). Other wet forests dominated by *Metrosideros* range from 5% to 10% light (Burton and Mueller-Dombois 1984; Pattison and others 1998). Given the fact that the canopy dominants *Metrosideros* and *Diospyros* are not regenerating in the shade, but that 3 years after removal *Metrosideros* seedlings were observed as well as a tenfold increase in *Psychotria* seedlings (Cordell and others in press), we conclude that canopy opening is critical to avoid complete conversion of these forests to exotic-dominated systems. Although the native species were not responsive as adults to the changes in resource availability with removal, seedlings may be the strongest beneficiaries of removal as a management strategy.

Our experience in creating and sustaining the removal plots suggests that controlling invasive species will be labor intensive and may not be feasible at a regional scale. We removed about 500 kg/100 m^2 and this required, approximately 40 person-hours per 100 m^2. The removal also led to a flush of new weeds and the first weeding removed about 50 kg/100 m^2. To maintain the removal plots, we anticipate weeding at 6–12 month intervals for the foreseeable future. It is likely that most of the emergent weeds were from the seed bank, although the small plots meant that edge effects were highly likely and some seeds may have come in from adjacent areas. Other research at this site has shown that the seed bank is entirely non-native whereas the seed rain contains native species (Cordell and others in press). An alternative strategy is partial canopy opening through girdling, shown to be effective when combined with seed addition in *Morella faya*-dominated montane forest in Hawai'i (Loh and Daehler 2007, 2008). One encouraging result from this study is that KMR soils do not appear enriched in nutrients and with early weeding it may be possible to deplete most of the seed bank. Restoration strategies will have to

incorporate the slow growth and resource use properties of native species, and that some degree of weeding may be required. Without intervention, LWF in Hawaii is an ecosystem that is destined to become dominated by highly invasive species, and the future of the endemic lowland flora and fauna is uncertain.

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