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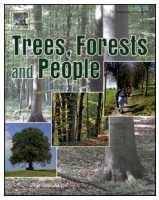

Ecosystem response to management of an invasive N_2-fixing tree in Hawai'i

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ABSTRACT

Many non-native tree species are recognized as problematic to ecosystems they have invaded, and subsequent control efforts have met with varying levels of success. *Falcataria falcata* is a fast-growing, N-fixing tree that has aggressively invaded landscapes across the Hawaiian Archipelago. Due to their ability to alter Hawai'i's native forest ecosystems, large stature at maturity, and potential for catastrophic tree fall, *F. falcata* stands pose threats to Hawai'i's native forests, residential communities, and agricultural lands. We investigated responses to chemical control of *F. falcata* stands immediately after control and during ensuing initial stages of succession. Herbicide treatment of *F. falcata* stands increased litter inputs of N and P that translated to increased soil nutrient availability. Such increases were exploited by extant understory vegetation consisting of non-native grasses and forbs that formed a continuous layer to severely limit the documented maximum potential germination of nearly 8 million *F. falcata* seedlings per hectare. Although trajectories of post-control vegetation development were dominated by non-native species in this case, control strategies could be employed to incorporate purposeful plantings of native Hawaiian species, non-native but bio-culturally important species, or desired agricultural species. In the absence of such interventions, however, non-native vegetation dominance following *F. falcata* control presents a daunting barrier to any hope for native species establishment. Overall, findings indicated that *F. falcata* control is possible and feasible where understory vegetation is allowed to respond to increased light and nutrient resources and limit potential seedbank recruitment that would otherwise lead to *F. falcata* stand reestablishment.

Introduction

Non-native species invasions continue to threaten and degrade the integrity, functioning, and persistence of ecosystems world-wide (Mooney et al., 2005; Lodge et al., 2006). Although only recently recognized as prominent within invasive species taxa, many introduced non-native trees are now widely acknowledged as capable of causing significant damage to both natural and human-built environments (Richardson and Rejmánek 2011; van Wilgen et al. 2012). A body of scientific literature exists that investigates patterns, dynamics, and impacts of invasive trees (e.g., Ehrenfeld 2003, Webster et al. 2006, Shackleton et al. 2014), and some information is available concerning control and management of invasive tree species and their response to such management actions, including the response of invaded ecosystems to such actions (Kettering and Adams 2011; Hulme 2006; Loh and Daehler 2008; Hughes et al. 2012, Marchante et al. 2008).

Invasive trees capable of symbiotic N_2-fixation are widely acknowledged as increasing soil N availability via increased N content in litterfall, and elevated soil N availability may persist long after the mature individuals responsible for such litterfall have ceased to exist (D'Antonio and Meyerson 2002; Loh and Daehler 2007; Grove et al. 2015). In such cases, species poised to exploit increases in nutrients and light, such as non-native grasses and forbs, may be more likely to dominate initial stages of post-control succession than more desirable native species (Hughes and Vitousek 1993; Maron and Connors 1996; Nsikani et al. 2017). Non-native invasive trees may also deposit abundant and persistent seedbanks that promote their return to dominance after mature individuals have been successfully treated and controlled

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(Newsome and Noble 1986; Lonsdale et al. 1988; Baskin and Baskin 1998; D'Antonio and Meyerson 2002). Increased understanding of the ecological characteristics of non-native tree species, and the ecosystems in which they invade, may provide insights that lead to the development of appropriate and effective methods of control (D'Antonio and Meyerson 2002). Such understanding may reveal characteristics that hinder reestablishment of seedlings and saplings of controlled tree species (Hughes et al. 2012).

Falcataria falcata, until recently known as *Falcataria moluccana* and commonly known as albizia in Hawai'i, is a large, fast-growing tree native to the Malaysian peninsula, Indonesia, Papua New Guinea, and Solomon Islands; it has become naturalized in continental Africa, Asia, and many Caribbean and Pacific Islands, including Hawai'i (Hughes et al. 2024). Currently, an estimated 4 million *F. falcata* trees occur across the Hawaiian Islands, and large trees (i.e., > 25 cm diameter at breast height or DBH) account for 720,000 of that total (Owen et al. 2021). *F. falcata* is an early successional, shade intolerant, pioneer species that outcompetes and displaces other tree species as a function of its symbiotic nitrogen-fixing capacity, rapid growth rate, and copious long-lived seedbank. Stands of the tree have invaded and transformed the composition, structure, and function of Hawai'i's remnant lowland wet forests (Hughes and Denslow 2005; Hughes and Uowolo 2006; Hughes et al. 2024). Due to their large stature at maturity (i.e., > 30 m in height) and brittle large branches and limbs, *F. falcata* stands also pose a serious threat to residential communities and agricultural lands in Hawai'i and elsewhere in the Pacific (Butler 2014; Niemiec et al. 2020; Hughes et al. 2024). Conventional efforts to remove *F. falcata* stands, typically involving the costly use of large machinery (e.g., bulldozers), clears vegetation and disturbs soils in ways that often lead to explosive germination of *F. falcata* seedbanks representing the next generation of monospecific canopy tree dominants. Recently, new techniques employing herbicide applications have proven successful in controlling large stands of *F. falcata* (Hughes et al. 2024).

Our objectives here were to better understand and document community and ecosystem responses to broad-scale chemical control of *F. falcata* stands immediately after control as well throughout subsequent months and years. We aimed to answer two main questions. First, how is soil and vegetation nutrient status altered - both initially and over time - in response to herbicide control of *F. falcata* stands? Second, how does understory vegetation - including *F. falcata* seed germination - respond to changes in post-control resource availability? To answer these questions, we documented dynamics of specific parameters of litter, soil, and plant tissue nutrients across study sites along the windward coast of Hawai'i Island. We also characterized post-control *F. falcata* seedling recruitment under differing shade conditions likely to affect such recruitment, and we measured the composition and structure of understory vegetation cover. We compared these parameters and their dynamics through time in forest stands where all *F. falcata* individuals were killed via herbicide application and in adjacent stands in which *F. falcata* trees were not similarly treated. In so doing, we documented how the legacy of *F. falcata* stands shaped ecosystem response following their control, which in turn influenced potential *F. falcata* recruitment and re-establishment.

Methods

Study site descriptions

Research was conducted at five distinct and widely separated locations along the windward coast of Hawai'i Island (Fig. 1, Table 1); locations were arrayed across 3 different volcanoes spanning ca. 75,000 years of soil development (Wolfe and Morris 1996). Situated at relatively low elevations, the climate of each study site was relatively warm and wet (Table 1). Mean annual precipitation (MAP) ranged from 3308 mm y^{-1} at the Keonepoko site to 5750 mm y^{-1} at the Honomū site (Giambelluca et al. 2013). Mean annual temperature (MAP) scaled with elevation and ranged from 19.8° C at the Honomū site to 22.6° C at the Pana'ewa site (Table 1; Giambelluca et al. 2014).

Plant communities at all sites were best characterized as thoroughly invaded by non-native species in the understory and dominated in all cases by the presence of tall, contiguous overstory canopies of the invasive non-native tree, *F. falcata*. Diameter at breast height (DBH) of

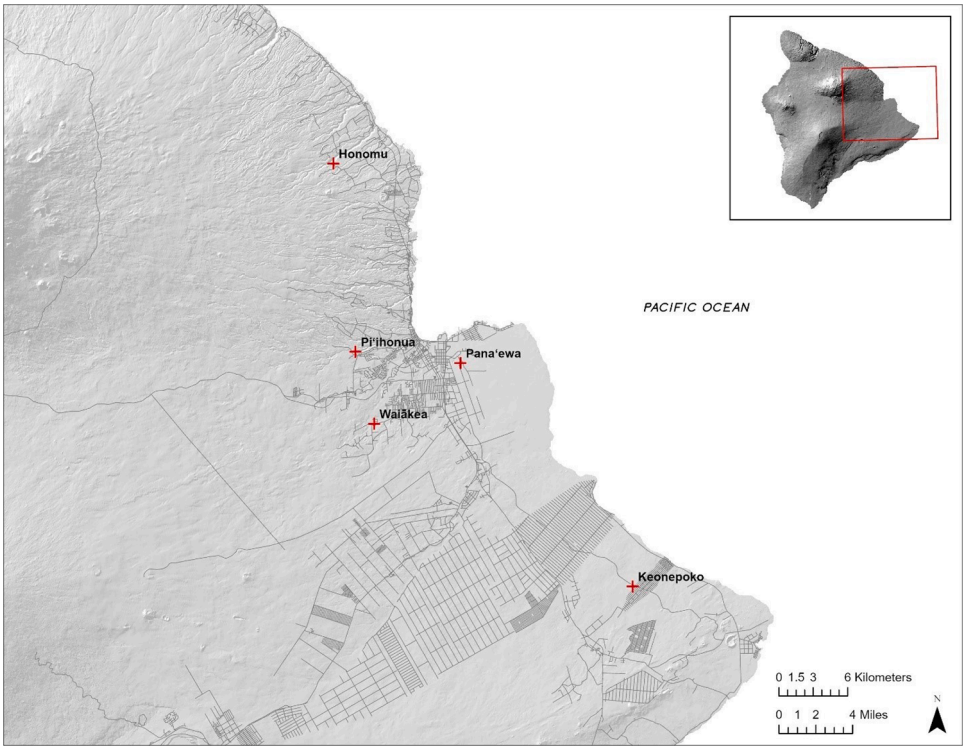

Fig. 1. Windward coast of Hawai'i Island indicating locations of the five study sites.

Table 1
Names, locations, and environmental characteristics of study sites.

Site Name	Land Manager	Location (UTM: 5Q)	Elev. (m)	Volcano, Substrate Age (YBP)	Lava/ Substrate Type	MAT (°C)	MAP (mm)	Average *F. falcata* DBH (cm)	Herbicide Treatment Date
Keonepoko	DOFAW	0297,311 m E, 2163,750 m N	84	Kilauea, 200–750	pahoehoe	22.4	3308	76	10/12/2015
Pana'ewa	DHHL	0285,439 m E, 2179,341 m N	28	Mauna Loa, 750–1500	a'a	22.6	3376	70	6/9/2016
Waiākea	Private	0277,996 m E, 2175,744 m N	225	Mauna Loa, 750–1500	pahoehoe	20.9	4677	84	12/1/2015
Pi'ihonua	DHHL	0276,635 m E, 2181,622 m N	274	Mauna Kea, 5–10 x 10^3	mineral soil	20.5	4729	81	4/7/2015
Honomū	Private	0274,641 m E, 2196,537 m N	378	Mauna Kea, 65–75 x 10^3	mineral soil	19.8	5750	53	7/2/2015

Note: DOFAW denotes Division of Forestry and Wildlife within the Hawaii State Department of Land and Natural Resources.
DHHL denotes Department of Hawaiian Homelands. "MAT" denotes mean annual temperature. "MAP" denotes mean annual precipitation. Average *F. falcata* diameter at breast height (DBH) determined for each site from twenty selected trees. "Herbicide treatment date" denotes date that all *F. falcata* individuals of given stands received lethal doses of aminopyralid herbicide.

mature *F. falcata* trees within study sites averaged 76 cm and ranged from 53 cm at the Honomū site to 84 cm at the Waiākea site (Table 1), heights of *F. falcata* stands ranged from 30 to 40 m. Common subcanopy trees and shrubs included non-native species *Psidium cattleyanum, Melastoma candidum*, and *Miconia crenata* (formerly *Clidemia hirta*). Common understory species included the non-native grasses *Melinis minutiflora, Panicum maximum, Paspalum conjugatum*, and *Setaria palmifolia*. The non-native vine, *Paederia foetida* was also common at multiple sites.

Sample design and methods

Each of the five study sites consisted of several hectares divided into two roughly equal sections (i.e., ca. 2 to 3 ha, respectively) defined as "Treated" and "Untreated" (Fig. 2). Within Treated sections, all *F. falcata* trees, saplings, and seedlings that were present received a lethal dose of the herbicide aminopyralid via an incision point application method whereby 9 cm long incisions were cut into the sap wood at 10 cm intervals at breast height around the circumference of each *F. falcata* tree. Each incision was filled (i.e., ca. 0.5 ml/incision) with undiluted herbicide using narrow-necked laboratory squeeze bottles (Hughes et al. 2024, www.biisc.org/incision-point-application). *F. falcata* is extremely sensitive to aminopyralid herbicide, and its application typically resulted in total canopy leaf abscission and mortality approximately two weeks after application. Where initial applications failed to completely kill given trees in Treated areas, herbicide was re-applied to ensure 100 % mortality of *F. falcata* trees within Treated plots of each study site (Fig. 2). Herbicide treatments were staggered in time among the five study areas, and all stands were treated within 14 months of one another (i.e., April 2015 to June 2016) (Table 1). Once dead, *F. falcata* snags within Treated plots decomposed at a relatively rapid rate; snags were reduced to foreshortened trunks lacking large limbs or branches that were ca. 33 % of their original height following 3.5 years since treatment (Hughes, unpublished data).

Prior to herbicide control of designated *F. falcata* trees within each study site (Fig. 2), we established a nested sampling design encompassed within a single 50 m x 100 m sample plot (i.e., 0.5 ha) centered in both Treated and Untreated sections (Fig. 1, Table 1). All litter, soil, and vegetation measurements and samples were collected within each 0.5 ha plot arranged variously and systematically around three sampling foci located at 25 m, 50 m, and 75 m points along the central axis of each 0.5 ha plot (Fig. 3).

Litterfall

We collected litterfall from Treated and Non-Treated sections of each study site from sets of 43 x 43 cm litter traps arranged as three pairs located and secured on the forest floor at 25, 50, and 75 m points along the 100 m central axis of each plot (Fig. 3). Litter traps of each pair were

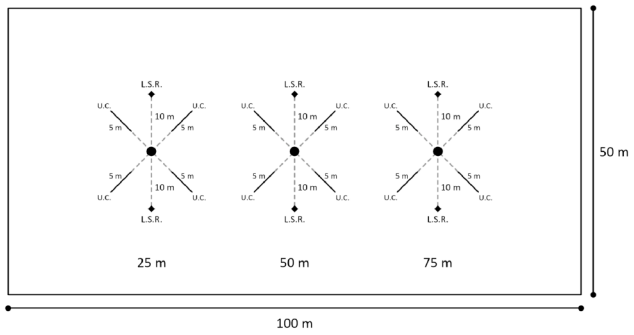

Fig. 3. Diagram of sampling design for Treated and Untreated sections at each study site. Sampling foci were located at 25, 50, and 75 m of the 0.5 ha sample plot. "U.C." denotes each of four 5 m transects along which understory cover was measured at each sampling foci. "L.S.R." denotes locations of litter traps, seedling quadrats, and soil sampling areas.

Fig. 2. Arial images of Untreated and Treated areas within the Honomū study site which represent management treatments for each of the other five study sites. Image on left ("1″) indicates intact *Falcataria falcata* canopy ca. 30 m in height across the study site; "A" indicates approximate location of the Untreated plot, and "B" indicates location of the Treated plot. Image on right ("2") indicates the Untreated (A) and Treated (B) plots approximately 30 months following herbicide application of *F. falcata* trees and subsequent whole canopy leaf loss of stands in Treated plots.

placed in opposing perpendicular directions 10 m from each of the three central sample foci points, resulting in 6 subsamples per 0.5 ha plot of the five study sites (Fig. 3). Litterfall was collected from traps each month over the course of the first year immediately following herbicide application; this was done to capture litterfall resulting from the initial wholesale canopy leaf abscission following herbicide application. Monthly litter collections included all leaves and stems < 10 cm diameter that fell within the confines of traps. Collected litter was sorted into the following three tissue type categories: 1) *F. falcata* leaves, seeds, and seedpods; 2) *F. falcata* wood < 10 cm in diameter; 3) all other litter mass, including all non-*F. falcata* wood material < 10 cm in diameter. Sorted samples were dried to a constant mass at 70 °C and weighed. For each tissue type, values from each plot were averaged by month for Treated and Untreated sections of each of the five study sites.

Litter tissue concentrations of nitrogen and phosphorus (i.e., N and P) were determined from composited samples of the three sorted litter types from Treated and Untreated plots of the five study sites. Within each Treated and Untreated plot, all 12 monthly collections from all six litter traps within a given plot (i.e., 72 samples) were combined by designated tissue type. Once composited, dried samples were ground to pass through a 32-mesh screen (0.5 mm) using a Wiley Mill and analyzed for N % by induction furnace methods using a LECO CN-200 Analyzer (LECO, St. Joseph, Michigan, USA; Bremner 1996, Nelson and Sommers 1996). Composite samples were dry-ashed and analyzed in solution using a Jarrell Ash ICP (Thermo Jarrell Ash, Franklin, Massachusetts, USA) to determine P % (Kuo 1996). Mass of N and P in litter inputs were estimated by multiplying litter mass values of each monthly litter collection of each litter type in Treated and Untreated sections of study sites by the respective N and P concentration values of each litter type from each treatment type within each study site.

Available soil nutrient indices

Indices of available soil nitrogen (NO_3^--N and NH_4^+-N) and phosphorus (PO_4^{3-}-P) were measured in each site using resin bags (Binkley and Matson 1983) placed within each site for one-month in-situ periods at 4-month intervals during the first year after herbicide application and at 6-month intervals during the subsequent 19 months after herbicide treatment. This schedule resulted in six in-situ sampling intervals over the course of 31 months following herbicide treatment. A pair of resin bags, one for NO_3^--N and NH_4^+-N and one for PO_4^{3-}-P, were placed at a 5 cm soil depth at designated distances and orientations from each of the six litter traps located in Treated and Untreated 0.5 ha plot, resulting in 12 resin bags (i.e., 6 in Treated plots and 6 in Untreated plots) in each plot during each in-situ sampling interval (Fig. 3). Resin bags were 6 x 7.5 cm and made of monofilament polyester silkscreen fabric (86 mesh) and filled with 6 g of mixed-bed exchange resin beads (IONAC NM-60 H1/OH2 form, type I, beads,16– 50 Mesh; J. T. Baker; Phillipsburg, New Jersey, USA). Bags were recovered after approximately 28 days, rinsed with deionized water to remove attached soil, and vigorously shaken to remove excess water. Bags destined for NO_3^--N and NH_4^+-N analysis were immersed in 100 mL of 2 mol/L KCl solution in sealed sample cups and placed on an oscillating shaker table for six hours. Bags destined for PO_4^{3-}-P analysis were immersed in 100 mL of 0.5 mol/L HCl solution and treated in the same manner. Resulting KCl extracts were analyzed colorimetrically for NO3 2-N and NH4 1-N (Technicon AAI Sampler [Technicon, Emeryville, California, USA] and Scientific AC 200 Colorimeter [Westco Scientific Instruments; Danbury, Connecticut, USA]), and HCl extracts were analyzed colorimetrically for PO_4^{3-}-P (Scientific AS 140 [Westco Scientific Instruments; Danbury, Connecticut, USA] and Scientific AC 200 Colorimeter) at the Analytical Laboratory of the University of Hawai'i at Hilo (Kuo 1996; Mulvaney 1996). Resin bags that had been exposed to the air or damaged by animals in the field were discarded. Results were expressed as μgram ion per gram resin per day and represent relative indices of soil inorganic N and P availability rather than actual inorganic N and P pool sizes or transformation rates (Binkley and Matson 1983). In all cases, in-situ resin bag sampling intervals were conducted simultaneously in Treated and Untreated plots at each study site to ensure that resin bag sets in the two treatment types had experienced identical temperature and precipitation conditions throughout respective in-situ sampling periods.

Leaf tissue nutrient dynamics

We used N- and P-mass/area ratios of *Miconia crenata* leaves as a bioassay of available vegetation N and P status and dynamics through post-control vegetation response. *M. crenata*, an invasive non-native understory shrub, was appropriate for this use as it was common across Treated and Untreated plots in all study sites. We collected five foliar samples consisting of approximately 40 fully-expanded sun leaves from multiple mature *M. crenata* individuals haphazardly selected and collected from within Treated and Untreated 0.5 ha plots at each study site. Collections occurred at 6-month intervals, beginning immediately following herbicide control of *F. falcata* individuals in Treated plots and continuing for 30 months to provide six sample points in time at each study site. Total leaf area of fresh *M. crenata* foliar samples was determined by passing them through an LI 3100 Area Meter (LI-COR Inc., Lincoln Nebraska, USA); foliar samples were subsequently dried to a constant mass at 70° C. These values – dried mass divided by fresh leaf area - provided a leaf mass per area value for each foliar sample. Dried samples were ground to pass through a 32-mesh screen (0.5 mm) using a Wiley Mill and analyzed for N % and P % in the same manner as was conducted and previously detailed for litterfall tissue.

F. falcata seedling dynamics

Maximum potential *F. falcata* seedling germination in the presence and absence of vegetative cover was determined for Treated and Untreated plots of each study site using three pairs of one m^2 quadrats located 8 m away in opposing pre-determined directions from each of the three central sample foci points (Fig. 3). Within each pair of quadrats, one was designated as "cleared", and the other was designated as "vegetated". In cleared quadrats, all understory vegetation < 2 m in height was removed down to bare ground and maintained as such for the duration of the study; in vegetated quadrats understory vegetation was not removed, resulting in three cleared and three vegetated quadrats within each Treated and Untreated plot. *F. falcata* germinant surveys were conducted at monthly intervals within Treated and Untreated plots at each study site over the course of the first year immediately following herbicide treatment of *F. falcata* stands. All *F. falcata* seedlings encountered within each quadrat were tallied and subsequently removed during monthly surveys. Where necessary, encroaching non-*F. falcata* vegetation was removed from cleared plots during monthly survey visits to maintain the status of cleared quadrats. Summed monthly survey tallies provided annual seed germination values for each quadrat.

Understory plant cover

Percent cover of understory vegetation < 2 m in height within Treated and Untreated plots was sampled immediately after herbicide application of *F. falcata* trees in Treated plots (T_0) and again after 30 months of post-control vegetation response (T_{30}). Percent cover was sampled using a modified point intercept method (Mueller-Dombois and Ellenberg 1974) along four, 5 m long transect lines emanating in opposing directions (i.e., generally N, S, E, and W) from the three sampling foci locations of each plot (Fig. 3). At each 0.5 m mark along each 5 m long transect, we lowered a straight sampling rod down through understory vegetation and recorded identity of any species that touched the rod. This resulted in 10 sample points per transect line, 40 sample points per subplot, and 120 sample points per plot for each

6-month sampling interval (Fig. 3). In many instances the sampling rod hit *Multiple species* at a given sample point, resulting in total cover values > 100 %. We corrected for this by dividing the number of "hits" for a given species by the total number of "hits" along the combined 120 sample points of the twelve transects in each plot. We also recorded height of the tallest understory species at each sample point, and where the sample pole failed to hit vegetation as it descended, "no cover" was recorded.

Stem density of and basal area of saplings of F. falcata

We determined the degree to which *F. falcata* saplings reestablished and grew following herbicide control of mature *F. falcata* stands in each study site at the end of the 30-month post-control interval. Within each of the five 0.5 ha Treated plots, we measured and recorded diameter (DBH) of all *F. falcata* saplings that were encountered.

Statistical design and analysis

Statistical Design and Analysis

In all cases, given parameters (e.g., litterfall, understory cover, and *F. falcata* seedlings) were subsampled within Treated and Untreated plots, and subsamples were averaged to provide a single value for each plot in each study site (i.e., $n = 5$); parameter values from the five study sites were averaged to provide a mean value ($\pm$ one standard error) for Treated and Untreated areas, respectively. We used paired *t*-tests, pairing Treated and Untreated values of a given site, to identify statistical differences between Treated and Untreated plots ($P \leq 0.05$). In many cases we measured given parameters at various times throughout initial stages of post-control succession to identify temporal dynamics between Treated and Untreated areas based on paired *t*-tests (Systat version 13.0). Differences in C:N values and concentrations of N and P in litterfall constituents between Untreated and Treated plots were evaluated using non-parametric Kruskal-Wallis Tests (P-values $\leq$ 0.05). Differences in maximum potential *F. falcata* seedling germination among vegetated and cleared quadrats in Untreated and Treated plots were determined by analysis of variance and post-hoc Tukey tests (P-values $\leq$ 0.05).

Regarding post-control understory vegetation dynamics, we employed Hierarchical Cluster Analysis (Systat version 13.0) to discern similarities and differences in collective understory cover values among sites measured immediately after herbicide control (T_0) as well as 30 months post-control (T_{30}). Analyses employed Centroid linkage and Euclidian distance parameters. Relative cover values provided a numerical basis by which to make comparisons of understory vegetation based on all species present at given sites, time periods, and treatment types. Statistical analyses were conducted using Systat version 13. We also evaluated differences among common species contributors to understory cover using Kruskal-Wallis non-parametric tests of individual species cover values in Treatment plots of each of the five study sites immediately after control of *F. falcata* stands (i.e., T0) and following 30 months of post control vegetation response (i.e., T30).

Results

Temporal dynamics of litterfall

F. falcata litter dynamics in herbicide-treated plots differed markedly from those of Untreated plots. Monthly total litter mass values in Untreated plots were relatively stable throughout the 12-month measurement period; average monthly values ranged between 0.9 and 1.7 Mg ha^{-1}, owing primarily to the steady deposition of canopy leaf litter under intact mature *F. falcata* canopies (Fig. 4a). In contrast, litterfall values of Treated plots were double those of Untreated plots one month after herbicide control of *F. falcata* trees in Treated plots. This increase was due to wholesale abscission of nearly canopy leaves as *F. falcata* trees

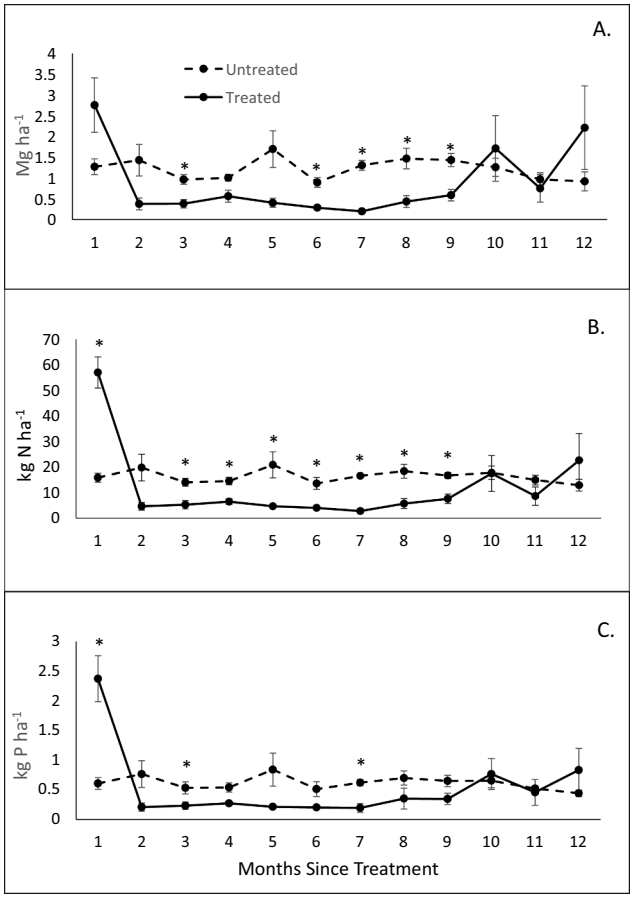

Fig. 4. Monthly mean values ($\pm$ one S.E.) of litter mass (A.), nitrogen mass in litter (B.), and phosphorus mass in litter (C.) within Untreated and Treated plots of the five study sites during the twelve-month period following control of *F. falcata* stands in Treated plots. Asterisks (*) denote significant differences between Untreated and Treated plots at each monthly time step determined by paired *t*-tests (P-value $\leq$ 0.05).

died (Fig. 4a). Following initial canopy leaf litter deposition, monthly litter mass values in Treated plots declined below those of Untreated plots as *F. falcata* leaf litter fall ceased entirely in Treated plots (Fig. 4a). Treated and Untreated values of total litter mass converged in months 10, 11, and 12 as sloughing of small wood debris (i.e., small stems and branches) by decomposing standing dead trees increased litterfall values in Treatment plots (Fig. 4a).

F. falcata leaf tissue exhibited significantly higher %N and %P values,

Table 2
Mean ($\pm$ one standard error) concentrations of N and P, and C to N ratios, of the three tissue types in Untreated and Treated plots of the five study sites.

Tissue type	Untreated				Treated		
				%N			
F. falcata leaves	1.37	$\pm$	0.06	*	2.13	$\pm$	0.10
F. falcata wood	0.65	$\pm$	0.04		0.78	$\pm$	0.07
Other	0.88	$\pm$	0.07		1.09	$\pm$	0.10
				%P			
F. falcata leaves	0.05	$\pm$	0.01	*	0.09	$\pm$	0.01
F. falcata wood	0.03	$\pm$	0.003		0.03	$\pm$	0.003
Other	0.05	$\pm$	0.01		0.08	$\pm$	0.02
				C:N			
F. falcata leaves	22.51	$\pm$	1.62	*	15.39	$\pm$	0.53
F. falcata wood	49.53	$\pm$	2.87		43.03	$\pm$	4.19
Other	34.64	$\pm$	2.99		29.02	$\pm$	3.40

Note: Asterisks (*) denote significant differences in tissue-type values between Untreated and Treated sites (Nonparametric Kruskal-Wallis Tests; $P \leq 0.05$).

and lower C:N values, in litterfall from Treated plots compared to *F. falcata* leaf tissue of Untreated plots (Table 2). In contrast, %N, %P, and C:N values of *F. falcata* wood and "other" tissue types did not differ between Untreated and Treated plots (Table 2).

Dynamics of N and P mass in litterfall were similar those of litter mass (Fig. 4a), but differences between Untreated and Treated plots were amplified in important ways. N and P mass in monthly total litter values were relatively consistent between months in Untreated plots, ranging from 13 to 21 kg ha^{-1} and from 0.5 to 0.8 kg ha^{-1}, respectively (Fig. 4b and 4c). Canopy leaf abscission within the first month following herbicide treatment resulted in litterfall N and P mass inputs in Treated plots that were 3.6 times and 3.9 times higher than Untreated plots, respectively (Fig. 4b and 4c). Thereafter, litter N mass values in Treated plots declined below those of Untreated plots three to nine months after herbicide treatment, before rising again to levels seen in Untreated plots as inputs from falling dead *F. falcata* stems, twigs, and small branches increased (Fig. 4b). Monthly litter P mass values in Treated plots also declined significantly below those of Untreated plot values during a subset of months following initial whole canopy leaf abscission (i.e., months 3 and 7), but did not differ significantly from Untreated plot values between 4 and 6 month and 8 to 12 month periods following herbicide treatment.

Indices of available soil N and P

Temporal dynamics of available soil N and P indices in Untreated and Treated plots generally followed documented annual litterfall dynamics, but in a manner that was attenuated over the course of 30 months. Available soil inorganic N (i.e., NO_3^--*N* + NH_4^+-N) values in Untreated plots were relatively stable across the 30-month sampling period, with average values ranging from 45 to 81 μg N g resin^{-1} day^{-1} (Fig. 5a). In contrast, inorganic N values in Treated plots were substantially elevated relative to Untreated plot values during the initial 6-month sample period (Fig. 5a). Throughout the following two years average soil inorganic N values of Treated plots declined and converged with values of Untreated plots. After 31 months of post-control vegetation response, soil inorganic N values in Treated plots had declined to the point that values in Untreated plots were 5 times greater than those of Treated plots (Fig. 5a). Average values of soil inorganic P (PO_4^{3-}-P) ranged from 0.32 to 0.89 μg P g resin^{-1} day^{-1} in Untreated plots (Fig. 5b), and values did not differ between Treated and Untreated plots at any of the six temporal sampling points (Fig. 5b).

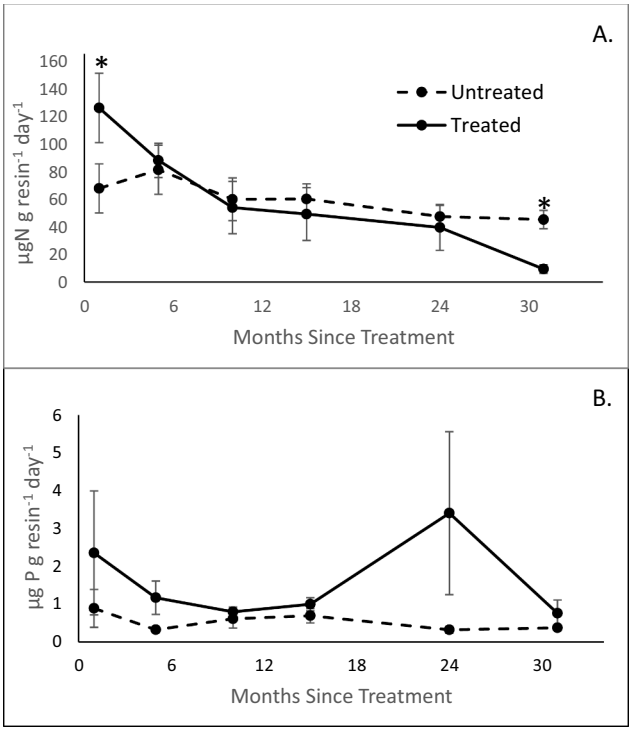

Fig. 5. Mean values (± one S.E.) of resin-captured (A.) soil inorganic nitrogen (NO_3^--N and NH_4^+-N) and (B.) soil inorganic phosphorus (PO_4^{3-}-P) within Untreated and Treated plots of the five study sites during the 31-month period following control of *F. falcata* stands in Treated plots. Asterisks (*) denote significant differences between Untreated and Treated plots at each sampling interval determined by paired *t*-tests (P-value ≤ 0.05).

M. crenata foliar structural and nutrient dynamics

M. crenata leaf mass per area (LMA) and nutrient status differed between Untreated and Treated plots across the six temporal sample periods. Average LMA values did not differ between Untreated and Treated plots immediately following herbicide treatment of *F. falcata* stands in Treated plots, but they diverged and were consistently higher in Treated plots compared to Untreated plots at every temporal sample point thereafter. Average LMA values were 26 % to 55 % higher in Treated plots compared to Untreated plot temporal counterparts (Fig. 6a). Following dynamics of LMA, foliar N mass values initially did not differ between Untreated and Treated plots, but they were 31 to 48 % higher in Treated relative to Untreated plots at 6-, 12-, 18-, and 24-month sample intervals before converging again at the 30-month sample interval (Fig. 6b). Foliar P mass values exhibited dynamics similar to foliar N mass values; Treated plot values were 44 to 60 % higher than Untreated plot counterparts at 6-, 12-, 18-, and 24-month intervals, and did not differ from one another at both 0- and 30-month time intervals.

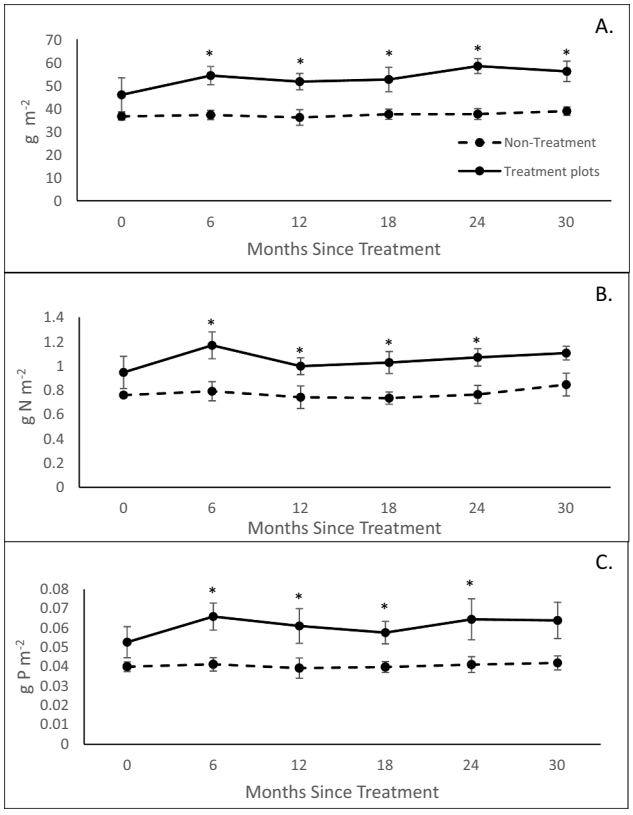

Fig. 6. Mean values (± one S.E.) of *Miconia crenata* leaf mass per area (A.), nitrogen mass per area (B.), and phosphorus mass per area (C.) within Untreated and Treated plots of the five study sites during the 30-month period following control of *F. falcata* stands in Treated plots. Asterisks (*) denote significant differences between Untreated and Treated plots at each sampling interval determined by paired *t*-tests (P-value ≤ 0.05).

Understory species composition, percent bare ground, and height

Multi-variate cluster analyses of species' contributions to understory cover immediately after herbicide treatment (i.e., T_0) and 30 months later (i.e., T_{30}) revealed decipherable patterns among Treated and Untreated plots of the five study sites. Relative species contributions to cover of Untreated plots exhibited little to no apparent change between T_0 and T_{30}, as species cover values of both intervals for each study site were grouped most closely with each other (Fig. 7a); this not surprisingly indicated little to no change in composition and dominance of understory species over time. In Treated plots, three of the five sites (i.e., Waiākea, Keonepoko, and Pana'ewa) also exhibited congruency between T_0 and T_{30} interval measures, as seen in Untreated plots (Fig. 7a and 7b). However, understory species composition differed distinctly between T_0 and T_{30} measures of Treated plots in Honomū and Pi'ihonua study sites; T_{30} values of those sites were most closely grouped with each other, and they were most distinct from all other sites and time intervals, including T_0 values of Honomū and Pi'ihonua sites that were most closely grouped with each other (Fig. 7b).

That measures of Honomū and Pi'ihonua Treated plots grouped together, and diverged from all other sites and time intervals, indicated temporal changes in species composition within those Treated plots. Their similarity (Fig. 7b) was explained by sharp increases in *Melinis minutiflora* relative cover in Treated plots of both sites after 30 months post-treatment response; cover of this grass species increased from 4 % to 73 % and from 0 % to 40 %, respectively (Table 3). The Treatment

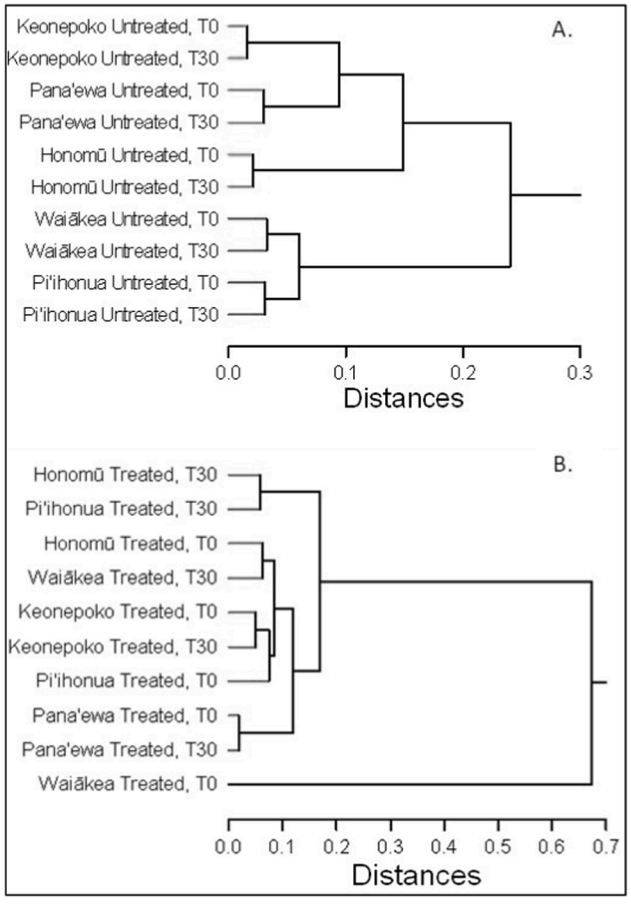

Fig. 7. Hierarchical Cluster Analysis of relative cover of all species encountered in Untreated (A.) and Treated (B.) determined both at the time of control of *F. falcata* stands in Treated sites (i.e., "T0") and 30 months after control F. falcata stands in Treated sites (i.e., "T30") to discern similarities and differences in collective understory cover values among sites. Analyses employed Centroid linkage and Euclidian distance parameters.

plot in the Honomū site also exhibited significant declines over time (i.e., from T_0 to T_{30}) regarding relative cover of *M. crenata, Paspalum conjugatum* and *Torenia asiatica*. Relative cover of *Rubus rosifolius* declined with time in the Pi'ihonua Treatment plot (Table 3). Relative cover of the woody shrub, *Lantana camara*, and vine, *Paederia foetida*, increased over time in the Keonepoko Treatment plot, and incidence of bare ground declined significantly over time in Treatment plots of both Keonepoko and Waiākea study sites (Table 3). Considering all Treatment plots of all sites, native Hawaiian species were rarely encountered; only *Scleria Testcea* – a native grass – and *Hibiscus tiliaceus* - a putatively native tree - were among the 24 species that individually accounted for $\geq$ 5 % of total relative cover at any given Treatment plot. All other species – 22 in total – were non-native introductions (Table 3) (Wagner et al., 1999). Similarly, understory cover of Untreated plots - whether measured immediately after herbicide control (T_0) or 30 months later (T_{30}) - was overwhelmingly comprised of non-native species. Dominant contributors to percent cover values of Untreated plots included *Psidium cattleianum, Setaria palmifolia, Miconia crenata, Arthrostema ciliatum, Oplismenus hirtellus, Melastoma candidum,* and *Rubus rosifolius* (data not shown).

Percent cover of bare ground decreased with time in Treated plots (Fig. 8A). At the time of herbicide treatment and immediately prior to wholesale *F. falcata* canopy leaf abscission, percent bare ground in Treatment plots averaged 15 % across study sites. Thereafter, bare ground ranged from 1 % to 5 % of total cover in Treated plots during the subsequent 30 months of post-treatment vegetation response and differed significantly from Untreated plot values only at 24 months following treatment (Fig. 8A).

Average height of understory cover did not differ between Treated and Untreated plots immediately following herbicide treatment of *F. falcata* stands in Treated plots (Fig. 8B). However, average understory canopy height in Treated plots was significantly greater than that of Untreated plots at all subsequent sampling points in time; Treated plots exhibited understory canopy heights at 6-, 12-, 18-, 24-, and 30-month sampling points that were 31 % to 46 % greater than those of their Untreated plot counterparts (Fig. 8B).

Maximum potential F. falcata seedling germination

Maximum potential *F. falcata* seedling germination over the course of the year following herbicide treatment was constrained by both understory and overstory cover. Regarding Untreated plots over which a contiguous *F. falcata* overstory remained, the quadrats where understory vegetation remained intact, and quadrats where understory vegetation was cleared averaged 12 and 33 *F. falcata* seedlings m^{-2} $year^{-1}$, respectively (Fig. 9). Similarly, quadrats in Treated plots above which the *F. falcata* overstory no longer existed but where understory vegetation remained intact averaged maximum potential germination of 70 *F. falcata* seedlings m^{-2} $year^{-1}$. Levels of maximum potential germination of the three shaded conditions did not differ from one another (Fig. 9). In contrast, maximum potential *F. falcata* seedling germination in quadrats lacking both understory vegetation and a *F. falcata* overstory canopy exhibited levels of germination (i.e., 764 seedlings m^{-2} $year^{-1}$) that were an order of magnitude greater than the three shaded treatments (Fig. 9); this value for cleared quadrats in Treated plots translated to maximum potential annual germination rates of 7.6 million *F. falcata* seedlings per hectare.

F. falcata sapling abundance and size

Establishment of *F. falcata* saplings and small trees within Treated plots was limited and sparse over the 30-month monitoring period following herbicide treatment. Density of post-control saplings, i.e., those that established and grew above forest understories following wholesale chemical treatment of all detected *F. falcata* trees and saplings in Treated plots, ranged from 4 to 63 individuals ha^{-1} in Pana'ewa and

Table 3
Relative percent cover values (mean ± one standard error) of understory species in Treatment plots of each of the five research study sites immediately after herbicide treatment of *F. falcata* stands (i.e. T0) and 30 months since herbicide treatment (i.e., T30).

	Honomū							Pi'ihonua							Keonepoko							Pana'ewa						Waiākea						
Genus species	T0				T30			T0				T30			T0				T30			T0				T30		T0				T30		
Arthrostema ciliatum (forb)																												2	+	2		18	+	9
Cecropia obtusifolia (woody)															5	+	2		6	+	2													
Commelina diffusa (forb)	3	+	2		5	+	2	6	+	3		7	+	3																				
Hibiscus tiliaceus (woody) (native)																						6	+	3		0	+	0						
Justica betonica (forb)																						21	+	10		13	+	7						
Lantana camara (woody)															2	+	2	*	15	+	5													
Macaranga mappa (woody)																						8	+	4		17	+	6						
Melastoma candidum (woody)	7	+	3		13	+	8	10	+	4		8	+	4	16	+	5		4	+	2								9	+	3		6	+	4
Melinus minutiflora (grass)	4	+	3	*	73	+	11	0	+	0	*	40	+	13																				
Miconia crenata (woody)	40	+	6	*	0	+	0	12	+	6		6	+	4															26	+	5		26	+	8
Oplismenus hirtellus (grass)															18	+	6	*	0	+	0													
Paederia foetida (vine)								9	+	4		11	+	4	0	+	0	*	9	+	4	5	+	3		9	+	5						
Panicum maximum (grass)								32	+	9		23	+	8																				
Paspalum conjugatum (grass)	33	+	7	*	0	+	0																											
Passiflora edulis (vine)															6	+	3		8	+	5													
Phymatosorus grossus (fern)																						8	+	4		10	+	5						
Psidium cattleianum (woody)															7	+	5		19	+	9	19	+	7		9	+	5	13	+	5		13	+	5
Rubus rosifolius (woody)								18	+	7	*	1	+	1																				
Scleria testacea (grass) (native)															6	+	3		9	+	3													
Setaria palmifolia (grass)								6	+	4		3	+	2															13	+	6		15	+	4
Sphagneticola trilobata (forb)																													2	+	2		12	+	6
Stachytarpheta dichotoma (woody)															9	+	3		17	+	6													
Thunbergia laurifolia (vine)																						0	+	0		13	+	9						
Torenia asiatica (forb)	6	+	2	*	0	+	0																											
< 5 % cover species	8	+	3		8	+	5	8	+	4		1	+	1	9	+	3		11	+	5	10	+	5		8	+	4	13	+	5		8	+	3
Bare ground	2	+	1		0	+	0	1	+	1		0	+	0	23	+	6	*	3	+	2	23	+	4		21	+	6	23	+	5	*	2	+	1

Note: Significant differences in species-specific T0 and T30 percent cover values within a given site are denoted by an asterisk and based on.
Kruskal-Wallis non-parametric tests ($P < 0.05$). Significant differences between T0 and T30 "< 5 % cover species" values were not determined due to the multi-species nature of those values.

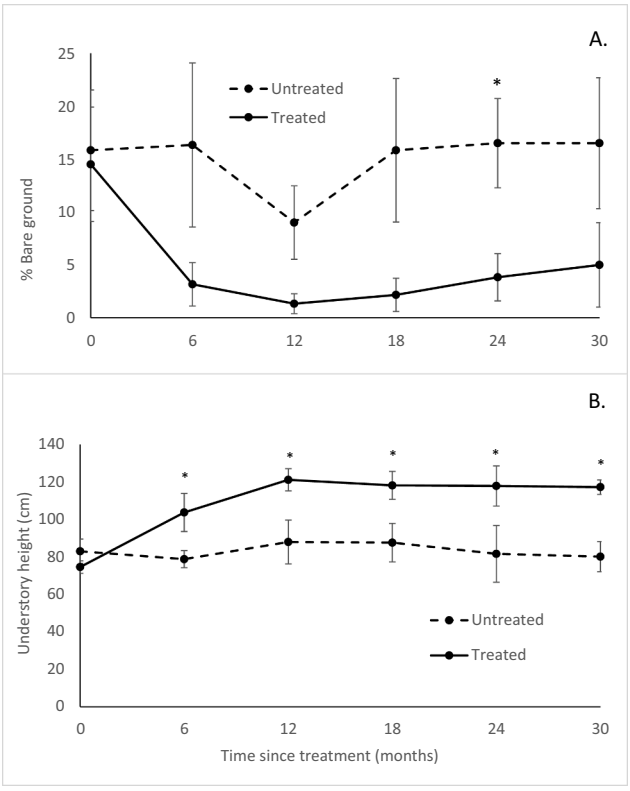

Fig. 8. Mean values (± one S.E.) of percent bare ground (A.) and understory canopy height within Untreated and Treated plots of the five study sites throughout the 30-month period following control of *F. falcata* stands in Treated plots. Asterisks (*) denote significant differences between Untreated and Treated plots at each sampling interval determined by paired *t*-tests (P-value ≤ 0.05).

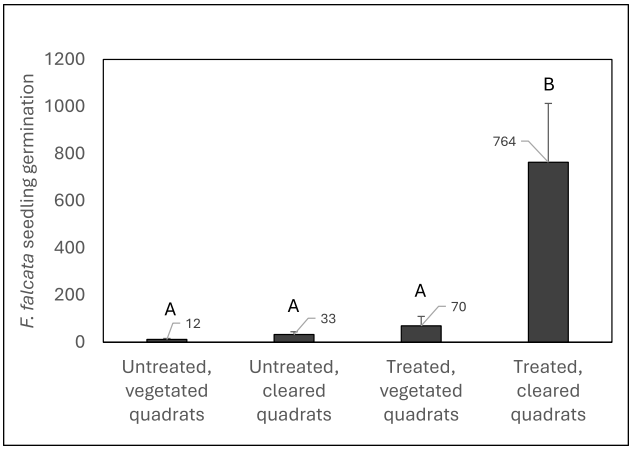

Fig. 9. Mean values (± one S.E.) of maximum potential annual *F. falcata* seedling germination in cleared and vegetated quadrats in Untreated and Treated plots (individuals m^2 $year^{-1}$). Quadrats were censused monthly over the course of one year following control of *F. falcata* stands in Treated plots. Categories that share the same letter did not differ significantly from one another based on Analysis of Variance accompanied by post-hoc Tukey tests (P value ≤ 0.05).

Keonepoko study sites respectively; values averaged 18 individuals ha^{-1} overall (Table 4). Average stem diameters ranged from just 3 to 11 cm in Pana'ewa and Pi'ihonua sites, respectively, and exhibited an overall average diameter of 6 cm (Table 4). Basal diameter of reestablishing *F. falcata* trees averaged a mere 0.034 m^2 ha^{-1}.

Discussion

Afzal et al. (2023) asserted that effective management of invasive plant species benefits from a comprehensive understanding of the specific traits of the invasive species as well as those of the invaded ecosystem. Our results documented and evaluated ecosystem response to control of a non-native, invasive tree (Kettering and Adams 2011). Viewed together, results portrayed an effective management scenario whereby large stands of non-native invasive *F. falcata* trees were killed via target-specific, low dose herbicide treatment, and post-mortality plant community response proceeded to constrain the maximum potential germination of an estimated 7.6 million *F. falcata* seedlings ha^{-1} to actual establishment of only 18 saplings ha^{-1} during the first 3 years after treatment. Prior results of Hughes and Denslow (2005) indicated that contiguous overstory *F. falcata* leaf canopies reduced light availability to 20 % of ambient, and combined understory vegetation and *F. falcata* canopies reduced light to ca. 5 % of ambient. Further, results of Hughes and Vitousek (1993) found that post-disturbance M. *minutiflora* establishment, a phenomenon documented here, led to available light levels 1.5 % of ambient. Elsewhere and previously, Luken and Mattimiro (1991) showed that removal of *Lonicera maakii* (Amur honeyscuckle) infestations stimulated rigorous post-control resprouting of L. *maakii* basal stems and seed germination. An early successional pioneer species, *F. falcata* requires high light conditions to persist and grow at all stages of its life cycle, including the germination of copious seedbanks produced by trees as soon they reach reproductive maturity at four years of age (Soerianegara and Lemmens 1993; Hughes et al. 2024). As such, the rapid growth and thorough occupation of the understory by species present prior to herbicide treatment of the *F. falcata* overstory proved the critical mechanism by which post-disturbance *F. falcata* seed germination and subsequent tree reestablishment was constrained across the study sites.

Results also showed that herbicide-induced death of *F. falcata* stands manifested as wholesale canopy leaf abscission within two to three weeks following treatment, leading to large inputs of plant available N and P to an extant understory plant community coincidently experiencing increased light availability due to the removal of said overstory *F. falcata* canopy. *F. falcata*'s symbiotic N-fixing capacity enables trees to acquire and store large pools of N within its broad canopies (Hughes and Denslow 2005), and the 57 kg N ha^{-1} deposited during the first month after herbicide treatment of stands represented 30 % of the total annual N deposition from intact *F. falcata* stands in Untreated plots.

Sharp increases in nutrient inputs via litterfall following herbicide control of *F. falcata* stands translated to concomitant increases in plant available soil nutrients that were exploited by extant understory vegetation – primarily non-native grasses and forbs. This allowed vegetation to rapidly form a thick and continuous understory layer evidenced by documented increases in understory canopy height and low incidence of exposed bare ground as post-disturbance vegetation response progressed in Treated plots. N enrichment resulting from disturbance has often accelerated colonization by fast growing grass and forb species (Milberg et al. 1999; Davis et al. 2000; Grove et al. 2015). Nsikani et al. (2017) found that control of the non-native, N-fixing tree, *Acacia saligna*, increased soil nitrogen significantly up to ten years following control, and Yelenik et al. (2004) showed that soils beneath *A. saligna* stands promoted secondary invasions of non-native weedy species over reestablishment of desirable native species. Similarly, in studies of the effects of a widespread moth outbreak across extensive areas of native *Acacia koa* forest on Hawai'i Island, Banko et al. (2022) showed that N rich caterpillar frass inputs under defoliated forests significantly increased soil N availability which in turn led to increased foliar N content of understory non-native grasses in outbreak areas.

Post-herbicide plant community dynamics described here agreed with Hughes et al. (2012) who showed that girdling and killing of mature non-native *F. falcata* trees within otherwise native-dominated forests of American Samoa created gaps that were rapidly colonized

Table 4
Mean values (± one standard error) of *F. falcata* sapling stem density, average stem diameter, and basal area encountered within Treated plots of each study site documented throughout the 30-month period following herbicide treatment of *F. falcata* stands.

Site	Stem density (stems ha^{-1})			Average stem diameter DBH (cm)			Basal area (m^2 ha^{-1})		
Honomū	15.8	±	7.3	4.5	±	0.9	0.024	±	0.013
Pi'ihonua	5.0	±	0.0	11.3	±	7.1	0.071	±	0.064
Keonepoko	63.3	±	18.0	3.4	±	0.4	0.063	±	0.011
Pana'ewa	3.8	±	1.3	3.3	±	1.0	0.003	±	0.001
Waiākea	4.2	±	1.7	5.3	±	1.4	0.009	±	0.004
All sites	18.4	±	11.5	5.5	±	1.5	0.034	±	0.014

by native tree species capable of exploiting increased available soil N resulting from the prior occupation of *F. falcata* stands (Hughes et al. 2012). *F. falcata* seedlings were abundant in *F. falcata*-invaded forest stands of American Samoa, but they were effectively absent following only 3 years of forest recovery; a result likely due to overstory canopy shade cast by reestablishing native trees (Hughes et al. 2012).

Considering management of *Morella faya*, an invasive non-native N-fixing tree capable of altering composition, structure and function of native Hawaiian ecosystems (Vitousek and Walker 1989), Loh and Daehler (2008) examined how different removal approaches (i.e., logging, girdling, and incremental girdling) resulted in distinct responses; logging *M. faya* stands resulted in sharp increases in nutrient and light availability – as seen in our study as well – that led to rapid establishment of non-native species (Pons 1992; Probert 1992). In contrast, girdling and incremental girdling dampened resource availability and encouraged establishment of slower to establish native species, including preferred dominant canopy species from nearby native-dominated rain forest (Loh and Daehler 2008).

Whereas objectives of Loh and Daehler (2007 and 2008) were to explore potential best management practices to remove *M. faya* in a manner that encouraged native plant reestablishment, our objectives focused instead on understanding whether response processes following herbicide control of mature *F. falcata* stands could break the cycle of *F. falcata* seed germination, tree reestablishment, and return to stand dominance. As results clearly indicated, native Hawaiian plant species were virtually non-existent from all five sites in our study; of the 24 understory plant species that contributed >5 % to the total relative cover of any plot at any site; only two native species – *H. tiliaceus* and *S. Testacea,* a small tree and sedge, respectively – were present at only one of the five study sites. Instead, aggressive non-native grasses and shrubs such as *M. minutiflora, P. maximum, Setaria p*almifolia, *Lantana camara*, and *M. crenata* dominated post-control vegetation response. These species constrained *F. falcata* seedling germination, sapling re-establishment, and return to canopy dominance throughout post-control development. However, and unlike native-dominated vegetation recovery following *F. falcata* control in American Samoa (Hughes et al. 2012), non-native vegetation dominance following *F. falcata* control documented here presents a daunting barrier to native species establishment, as shown previously and elsewhere (Holl et al. 2000; Kanowski et al. 2009; Yelenik and D'Antonio 2013).

As N-fixing tree species, *F. falcata* stands have been shown capable of increasing nutrient – and particularly N – inputs, storage, and cycling. Hughes and Denslow (2005); Hughes and Uowolo (2006), and Hughes et al. (2012) documented elevated N inputs via litterfall, elevated decomposition rates, and concomitant increases in soil N availability in *F. falcata* invaded forests compared to adjacent native-dominated forests in both Hawai'i and American Samoa, and *F. falcata* stands increased soil N availability and cycling in *Eucalyptus* tree plantations on Hawai'i Island (Binkley et al. 1992 and Binkley 1997). Vitousek et al. (1987) and Vitousek and Walker (1989) demonstrated patterns and mechanisms by which invasive, N-fixing tree species alter ecosystem functions by increasing N stocks and cycling where they establish. Untreated plots in our study conformed to patterns of elevated N inputs and availability that we expected established mature stands of *F. falcata* to exhibit, and they provided the status quo against which post-herbicide ecosystem response could be compared.

Herbicide treatment of mature *F. falcata* stands in our study resulted in two profound changes with respect to available soil nutrients and their fate. Firstly, as noted, herbicide treatment killed the entire stand, abruptly ending the elevated N inputs and cycling sustained by intact stands as documented by Untreated plots of our study. Secondly, wholesale canopy leaf abscission immediately following herbicide treatment led to a spike in both N and P availability that could be tracked in soils and vegetation during subsequent vegetation response. In a similar fashion, Grove et al. (2015) documented an initial pulse of inorganic N in soils one month after herbicide-induced mortality and leaf abscission of the invasive N-fixing shrub, *Cytisus scoparus* (aka scotch broom) in Douglas fir forests; after 10 months of post-control community response, however, soil inorganic N levels were 70 % less than levels beneath untreated, intact *C. scoparus* stands. In contrast, elevated levels of soil N continued for 14 years following hurricane-induced mortality the invasive N-fixing species, *Robinia pseudoacacia*, in coastal forests of Northeastern United States (Von Holle et al. 2013).

Even though post-control whole-canopy leaf abscission resulted in a significant spike in litter inputs of P as well as N, that spike did not manifest in an increase of inorganic P in soils as seen with regard to available soil N. Grove et al. (2015) also did not see an increase in soil available P following stand mortality of *C. scoparius*; they surmised that any post-mortem spike in P released from litter decomposition might have been immediately taken up by fast growing plants colonizing their study plots. Indeed, our findings showed clear and substantial uptake of both N and P resulting in sustained elevated levels of those nutrients (i.e., at least 2.5 years post herbicide treatment) in foliar tissue of *M. crenata* individuals present in herbicide treated *F. falcata* stands compared to those present in Untreated *F. falcata* stands. Although dynamics of nutrient uptake and retention were not characterized for other common colonizing understory species (e.g., *M. minutiflora*, L. *camara, P. maximum*), the rapid growth and increased canopy volume exhibited by understory vegetation provided an expectation that foliar nutrient dynamics documented for *M. crenata* would be exhibited by other understory species as well. Taken together, results conformed to those of Vitousek (1977) and Quinn et al. (2018), evincing a mechanism whereby nutrient legacies of *F. falcata* stands were absorbed and retained by co-occurring plant species whose resultant biomass effectively excluded *F. falcata* seedlings and saplings during the initial stages of secondary invasion.

In most cases, desired goals of invasive species control efforts include reestablishment of native species and communities displaced by said non-native species; colonization and subsequent dominance by rapidly growing non-native species – often invasive grasses and forbs - during initial stages of post-control succession is typically considered an unfortunate outcome, if not an abject failure (D'Antonio and Meyerson 2002). Control of *F. falcata* within invaded portions of Ameran Samoa's otherwise native-dominated forests resulted in the ideal scenario of rapid establishment by native pioneer tree species and suppression of

F. falcata seedling and sapling reestablishment (Hughes et al. 2012). In contrast, Nsikani et al. (2018) documented that even after invasive N-fixing trees were cut down and physically removed from ecosystems, the soil legacy effects of transformed microbial communities, depleted native seedbanks, increased available soil N, and dominance by undesirable weed species represented daunting barriers to purposeful restoration efforts. In the case of *F. falcata* post-control vegetation dynamics studied here, re-establishment by native species was not expected due to their scarcity in and around the study areas; these were areas that had experienced significant disturbance (i.e., fire, and/or conversion to agriculture) prior to *F. falcata* stand establishment, and they were dominated by non-native species. Instead, objectives of this study primarily were to understand whether, how, and to what extent *F. falcata* stands could be eliminated from areas in a manner that constrained *F. falcata* seedling recruitment and subsequent reestablishment leading to overstory dominance once again.

In the long term, however, it remains to be seen whether *F. falcata* re-establishment will continue to be constrained in these study sites as post-control succession proceeds. *F. falcata* seeds retain 70 % to 90 % viability following 18 months in storage (Soerianegara and Lemmons 1993), and it is possible for some fraction of extant seedbanks to remain viable much longer, creating conditions for eventual germination and establishment (Milton and Hall 1981). Indeed, although our results documented how expanding understory vegetation limited secondary invasion by F. falcata, low numbers of saplings did still establish over the course of the study. In addition, Yelenik and D'Antonio (2013) showed that non-native grass invasion and dominance may lead to declines in soil N availability that provide opportunities for secondary invasion by non-native, N_2-fixing trees. Similarly, our results documenting eventual declines in available soil N with non-native grass and shrub establishment may portend future opportunities for secondary invasion by *F. falcata* individuals within understory light gaps, and additional management in the form of targeted herbicide treatment would likely be necessary to remove them from areas of interest before they become mature, full-sized trees.

Conclusions

In parts of the Pacific and elsewhere, *F. falcata* establishment and growth is encouraged to increase soil nutrient availability, increase stand productivity, and provide shade to important commercial crops (e.g., coffee) (Hughes et al. 2024). However, *F. falcata* forests also present a major obstacle to persistence of native forests (Hughes and Denslow 2005), a threat to residential communities (Hughes et al. 2024), and barriers to establishment of sustainable agroforestry systems (Hastings et al. 2023), all of which constitute important concerns for land managers of Hawai'i and elsewhere in the Pacific. Our results regarding ecosystem dynamics following herbicide-control of mature *F. falcata* stands documented an increase in nutrient availability relative to untreated sites. This led to conditions favorable to rapid establishment of non-*F. falcata* understory vegetation that constrained germination of the extant *F. falcata* seedbank and broke the cycle of *F. falcata* dominance. As such, effective control and management of this large, fast-growing, and disruptive non-native invasive tree was possible by exploiting its "Achilles heel" – i.e., shade intolerance. Although trajectories of post-control vegetation studied here were dominated by non-native species, control strategies could be employed in future efforts that incorporate purposeful plantings of native Hawaiian plants, non-native but bio-culturally important plants, or agriculturally important plants. Desired species could be planted either before or immediately following herbicide treatment of mature F. falcata stands to take maximum advantage of the increased resources (i.e., light and nutrients) our study documented. In prior studies, Lincoln et al. (2023) identified extensive areas of agroforestry and novel forests (i.e., forests managed for resource production) across the Hawaiian Archipelago prior to European contact, including areas currently occupied by mature stands of *F. falcata*. Further, DiManno et al. (2023) showed that purposeful planting of desirable tree species in previously invaded lowland wet forests of Hawai'i can successfully grow, persist, and exclude undesirable weeds – including shade intolerant trees such as *F. falcata* - via control of available resources (e.g., light and nutrients). As such, the potential to convert undesirable *F. falcata* stands to productive agroforest systems is high, and the societal imperative to do so exists (Hastings et al. 2023). Our results indicate that management activities to control *F. falcata* stands and replace them with more desirable forests and agricultural systems can succeed at local, watershed, and landscape scales in Hawai'i and elsewhere in the Pacific when and where relevant ecological factors, characteristics, and contexts are heeded.

CRediT authorship contribution statement

R.Flint Hughes: Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Caitlin Morrison:** Project administration, Methodology, Investigation, Data curation. **Edward Bufil:** Investigation, Formal analysis, Data curation. **James Leary:** Writing – review & editing, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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