

INVASION BY A N₂-FIXING TREE ALTERS FUNCTION AND STRUCTURE IN WET LOWLAND FORESTS OF HAWAII

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Abstract. Invasive species pose major threats to the integrity and functioning of ecosystems. When such species alter ecosystem processes, they have the potential to change the environmental context in which other species survive and reproduce and may also facilitate the invasion of additional species. We describe impacts of an invasive N₂-fixing tree, *Falcataria moluccana*, on some of the last intact remnants of native wet lowland forest undergoing primary succession on 48-, 213-, and 300-yr-old lava flows of Kilauea Volcano on the island of Hawai'i. We measured litterfall, soil nitrogen (N) and phosphorus (P) availability, light availability, species composition, and forest structure in native-dominated stands and in stands invaded by *Falcataria*. Litter inputs increased 1.3–8.6 times, N mass of litterfall increased 4–55 times, and P mass of litterfall increased 2–28 times in invaded stands relative to native stands. C:N and C:P ratios of litterfall were lower, and N:P ratios higher, in invaded stands relative to native stands. Resin-captured soil N and P values were 17–121 and 2–24 times greater, respectively, in invaded stands relative to native stands on each of the three lava flows. Native species accounted for nearly 100% of total basal area and stem density in native stands, while alien species accounted for 68–99% of total basal area, and 82–91% of total stem density, in invaded stands. Compositional changes following *Falcataria* invasion were due both to increases in alien species, particularly *Psidium cattleianum*, and decreases in native species, particularly *Metrosideros polymorpha*. Results provide a clear example of how invasive tree species, by modifying the function and structure of the ecosystems that they invade, can facilitate invasion by additional nonnative species and eliminate dominant native species. Given the rarity and limited extent of remaining native-dominated wet lowland forests in Hawaii, and the degree to which *Falcataria* invasion alters them, we expect that the continued existence of these unique ecosystems will be determined, in large part, by the spread of this invasive species.

Key words: carbon; facilitation; *Falcataria moluccana*; invasion; light availability; litterfall; *Metrosideros*; nitrogen; phosphorus; primary succession; *Psidium*.

INTRODUCTION

Invasive species that alter biological processes or disturbance regimes pose a substantial threat to native communities because they not only compete for limited resources, but also change the environmental context in which other species survive and reproduce (Vitousek et al. 1987, D'Antonio 2000). Vitousek and Walker (1989) demonstrated that a single invasive species, by increasing nitrogen (N) inputs and availability, was capable of altering ecosystem processes, and perhaps the trajectory of ecosystem development as well. They speculated that such species might ultimately facilitate the invasion of other alien species. Where invasive species cause such changes within rare plant assemblages, their impact on biodiversity is potentially devastating.

Facilitation, the process by which one or more species promotes the establishment, persistence, or spread of other species, has been documented in native-dominated communities and those invaded by alien species

(Callaway 1995, Maron and Connors 1996, Yelenik et al. 2004). Invasibility may increase with increased nutrient supply (Huenneke et al. 1990, Davis et al. 2000, Ostertag and Verville 2002) or altered disturbance regimes (Mack and D'Antonio 1998, Mack et al. 2001). When invasive species alter such characteristics, they may facilitate the invasion of other species, even promoting a cascade of multiple species invasions that substantially alters ecosystem structure and composition—an invasional meltdown (Simberloff and Von Holle 1999).

Diversity and abundance of nonnative species appear correlated with site fertility (Gerrish and Mueller-Dombois 1980, Bridgewater and Backshall 1981, Stohlgren et al. 1999). In Hawaii, N availability likely constrains the establishment of many exotic species on recent lava flows where rates of net primary productivity and decomposition are low and limited by N availability (Vitousek et al. 1993, Vitousek and Farrington 1997). However, such N limitation may also make these young lava flows more susceptible to invasion by nonnative, N₂-fixing species, and such invasions have led to increased nitrogen cycling within ecosystems of Hawaii,

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California, and South Africa (Vitousek and Walker 1989, Stock et al. 1995, Maron and Connors 1996).

Within the Hawaiian Islands, native-dominated wet lowland forests are rare, limited in extent, and primarily found in the eastern portion of the island of Hawai'i (Mueller-Dombois and Fosberg 1998, Wagner et al. 1999). In their un-invaded state, these ecosystems typically consist of monotypic stands of the native tree *Metrosideros polymorpha*, which dominates the initial stages of primary succession on 30-yr-old to 200-yr-old lava flows. On less common, older substrates (i.e., those ≥ 300 years in age) a variety of other native tree species co-occur with *Metrosideros* individuals (Atkinson 1970). Though these native forests once covered much of the windward low-elevation (<500 m) portions of the main Hawaiian islands, most were converted to agriculture or human habitation both during Polynesian occupation prior to 1600 AD and with the advent of plantation agriculture following European contact in the late 1700s (Kirch 1982, Cuddihy and Stone 1990). Examples of this forested ecosystem still remain in eastern Hawai'i because over 90% of the region comprises lava substrates <750 years in age (Moore and Trusdell 1991) that were generally considered unsuitable for most agricultural activities.

Unfortunately, these few remaining stands of native-dominated wet lowland forest are currently being invaded by the alien N_2 -fixing tree, *Falcataria moluccana* (Miquel) Barneby and Grimes (formerly known as *Albizia falcataria* (L.) Fosberg and *Paraserianthes falcataria* (L.) Nielsen). Native to the Moluccas, New Guinea, New Britain, and the Solomon Islands (Wagner et al. 1999), *Falcataria* first was introduced to Hawai'i in 1917 (Rock 1920) and planted extensively throughout the main Hawaiian Islands during the 1920s to 1950s as part of efforts to reforest degraded watersheds (Nelson 1965). It grows well on a variety of soil types, including degraded sites (Otsamo 2000) and acidic or nutrient-poor soils (DeBell et al. 1989, Panjaitan et al. 1993), and is among the fastest growing trees in Hawaii (Walters 1971). In the last 20 years, scattered plantations of albizia have been established with the intention of capitalizing on its fast growth and nitrogen fixation capacity for short-rotation forestry applications (Binkley and Giardina 1997, DeBell et al. 1997). We hypothesized that when *Falcataria* invades early successional lowland forests growing on young nitrogen-limited lava flows of eastern Hawai'i, it increases nutrient availability and cycling that in turn leads to compositional and structural changes to those ecosystems.

The objectives of this research were two-fold. First, we sought to determine how invasion by *Falcataria* into native-dominated wet lowland forests alters resource availability, including understory light levels. Second, we asked whether *Falcataria* invasion alters forest structure and facilitates the invasion of other alien species. To address these objectives, we compared inputs of C, N, and P via litterfall, soil N and P avail-

ability, light availability, species composition, and forest structure in native-dominated and *Falcataria*-invaded stands growing on three lava flows that differ in age and represent points along primary succession within these systems. We also measured the foliar nutrient status of *Psidium cattleianum* within each forest stand to evaluate the response of this nonnative species to the changes imposed by *Falcataria*.

METHODS

Study sites

Study sites were established within Malama Ki (19°26'53" N, 154°51'40" W) and Keauohana (19°25'11" N, 154°57'14" W) State Forest Reserves. Both reserves are located in the Puna District of Hawaii, USA, and are in close proximity to one another (i.e., within 10 km). The climate is warm and wet, with a mean annual temperature of $\sim 23^\circ\text{C}$ and mean annual precipitation of ~ 2500 mm (Giambelluca et al. 1986, Sanderson 1993). All study sites were located on lava flows of the lower East Rift Zone of the active shield volcano, Kilauea. Parent material is tholeiitic basalt with little variation in chemical composition among lava flows (Moore and Trusdell 1991). Study sites in Malama Ki Forest Reserve were located on a 213-yr-old lava flow of the pahoehoe lava type (i.e., smooth and ropy), and study sites in Keauohana Forest Reserve were located on two lava flows of the a'a type (i.e., rough and blocky) that were 48 and 200–400 years in age, respectively. For the sake of simplicity we refer to flow ages as 48, 213, and 300 years old.

Vegetation on these young lava flows has been classified as wet lowland forest, and native-dominated stands typically consist of single cohort stands of *Metrosideros* (Mueller-Dombois and Fosberg 1998). Associated native tree species include *Diospyros sandwicensis* and *Psychotria hawaiiensis* within stands of Keauohana Forest Reserve and *Psydrax odorata*, *Diospyros*, and *Pandanus tectoris* within stands of Malama Ki Forest Reserve (Wagner et al. 1999).

Stands invaded by *Falcataria* in both Keauohana and Malama Ki Forest Reserves are notable for the overstory canopy dominance of *Falcataria*. This species is known for its rapid growth and large size at maturity; canopy heights can reach 10 m in 2-yr-old stands, and 20-yr-old individuals may be 30 m tall with trunk diameters up to 80 cm (Walters 1971). In mature stands, the broad umbrella-shaped canopies of large individuals often coalesce into one extensive monotypic canopy capable of covering hectares to square kilometers. *Falcataria* naturalizes near recorded plantings (Nelson and Schubert 1976), and preliminary analysis of remotely sensed imagery indicates that *Falcataria* has spread from planted populations into native-dominated forests of both Malama Ki and Keauohana Forest Reserves (T. Benning, *personal communication*).

TABLE 1. Description of the six study sites sampled in Hawaii.

Stand type/lava flow age [†]	Forest reserve location	Lava flow type	Under or away from <i>Falcataria</i> canopies
Native/48-yr-old	Keauohana	a'a	away
Invaded/48-yr-old	Keauohana	a'a	under
Native/213-yr-old	Malama Ki	pahoehoe	away
Invaded/213-yr-old	Malama Ki	pahoehoe	under
Native/300-yr-old	Keauohana	a'a	away
Invaded/300-yr-old	Keauohana	a'a	under

[†] Lava flow age is expressed as the number of years before the present time. The age 300-yr-old represents a range from 200 to 400 years old.

Six study sites were established on the three lava flows (Table 1). Pairs of study sites were established on each flow in relatively intact native-dominated forest (native stands) as well as in forests invaded by *Falcataria* (invaded stands). To ensure that native and invaded study areas differed only in the presence of *Falcataria*, we examined archived aerial photos of each study area (Hawaii Department of Land and Natural Resources 1993) and located plots beyond (native stands) and behind (invaded stands) the active invasion front of *Falcataria*. Size-class distributions of *Metrosideros* snags and stumps within invaded sites provided additional evidence that prior to invasion these stands were similar in structure to adjacent native stands.

Vegetation composition and structure

Two 100-m transects were established within each of the six study sites. Five 0.01-ha circular plots (11.28 m in diameter) were located randomly within each 20-m segment of each transect ($n = 10$ plots/site). We quantified woody species composition and stand structure within each plot using a nested plot design. Diameter at breast height (dbh) was measured and species recorded for all live and dead woody stems >2.0 cm dbh rooted within each 0.01-ha plot. All woody stems >1.3 m in height but <2.0 cm dbh were counted and identified to species in a 0.002-ha circular subplot nested within the larger plot.

Litterfall mass and composition

Litterfall was collected at each site in $0.18 \text{ m}^2 \times 6$ cm deep trays lined with 2-mm mesh fiberglass to ensure complete capture of litterfall and provide adequate drainage. One litter trap was placed within each of the 10 sampling plots at each site. Litter was collected monthly between February 2002 and January 2003, and samples were collected from all traps at all study sites on the same sampling day. Collected litter was sorted into the following categories: *Falcataria* leaves, *Falcataria* wood, *Metrosideros* leaves, *Psidium* leaves, leaves from all other species, wood from all other species, and other types of tissue from all species (e.g., flowers or fruit). *Falcataria*, *Metrosideros*, and *Psidium* litter components were distinguished from other components because these species contributed the majority of litter to each of the study sites. 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 at each study site. Monthly values were summed to estimate annual litterfall biomass inputs by tissue type.

Nutrient concentrations were determined from five composited monthly samples of each litter type. Samples were ground to pass through a 32-mesh screen (0.5 mm) using a Wiley Mill and analyzed for percentage of C and percentage of N by induction furnace methods using a LECO CN-200 Analyzer (LECO, St. Joseph, Michigan, USA; Bremner 1996, Nelson and Sommers 1996). Samples were dry ashed and analyzed in solution using a Jarrell Ash ICP (Thermo Jarrell Ash, Franklin, Massachusetts, USA) to determine percentage of P (Kuo 1996). C, N, and P concentrations were determined for dominant litter types at each site. For example, *Falcataria* leaves were a dominant component at the 48-, 213-, and 300-yr-old invaded sites, and site-specific concentrations of C, N, and P were consequently determined for this litter type. Where litter types contributed relatively little to total litterfall (i.e., $<15\%$), general, non-site-specific concentrations were used to estimate inputs. For example, C, N, and P concentrations of "other leaf" and "other wood" tissue types were determined only at the 300-yr-old native forest site, and these values were used to estimate inputs from the same litter types encountered at other sites. Mass of C, N, and P in litter inputs at sites were estimated by multiplying biomass values for each litter category by the respective C, N, and P concentrations of that litter type.

Soil N and P availability

Available soil N (NO_3^- -N and NH_4^+ -N) and P (PO_4^{3-} -P) were measured at each site using resin bags (Binkley and Matson 1983). Each 6×7.5 cm resin bag was made of monofilament polyester silkscreen fabric (86 mesh), filled with 6 g of mixed-bed exchange resin (IONAC NM-60 H^+/OH^- form, type I, beads, 16–50 Mesh; J. T. Baker; Phillipsburg, New Jersey, USA). At the beginning of a given sampling period, two resin bags were placed 5 cm deep within each plot ($n = 10$ pairs/study site). Bags were recovered after 28 days, rinsed with deionized water to remove attached soil, and shaken vigorously to remove excess water. Bags

designated 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 a shaker table for six hours. Bags designated for PO_4^{3-} -P analysis were immersed in 100 mL of 0.5 mol/L HCl solution and treated in the same manner. After shaking, KCl extracts were analyzed colorimetrically for NO_3^- -N and NH_4^+ -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) by the Agricultural Diagnostic Service Center, University of Hawaii, Manoa (Kuo 1996, Mulvaney 1996). Resin-captured N was measured quarterly (April, July, and October of 2002, and January of 2003); resin-captured P was measured over the last three of the four sample periods ($n = 10$ per stand for each sample period). In a few instances resin bags were damaged by animals in the field, and these samples were discarded from subsequent analyses. Results are expressed as μg ion per g resin per day and represent indices of soil inorganic N and P availability rather than actual inorganic N and P pool sizes or transformation rates.

Foliar N and P concentrations of *Psidium cattleianum*

Concentrations of N and P in foliage of *Psidium cattleianum* were determined from five grab samples of fully expanded leaves collected from the upper canopy of individuals of this species at each site. Each grab sample included leaves collected from two individuals during April of 2004. Samples were oven dried at 70°C to a constant mass, ground, and analyzed for total tissue N and P, as described for litter.

Light availability

Photosynthetically active radiation (PAR) was measured between March and May of 2003 at both sub-canopy and soil surface levels using LI-COR quantum sensors coupled to LI-COR LI-250 light meters (LI-COR Environmental; Lincoln, Nebraska, USA). Below-canopy PAR was measured well below the overstory but above the understory tree canopy (at a height of ~ 7.25 m) using sensors placed on extension poles. Two PAR readings were collected at points 3 m in opposing cardinal directions from the center point of each plot along each transect. Below-canopy readings coincided with readings from a PAR sensor located in an adjacent open area with an unobstructed view of the sky (i.e., no obstructions within 38° of the zenith in any cardinal direction) to estimate above-canopy incident radiation. Above- and below-canopy measures were located as close to one another as possible, and readings from the sensors were logged simultaneously. PAR at the soil surface was estimated from sensors

placed on the forest floor. Light availability was calculated as percentage of light transmitted (subcanopy or soil surface PAR divided by above-canopy PAR).

Statistical analysis

In all cases, results from each of the six stands (native and invaded stand pairs on each of the three lava flows) are presented and discussed as site means \pm SE of the untransformed data. Differences among native and invaded stands on the three lava flows with regard to litter inputs ($n = 10$ per stand), foliar nutrient concentrations of *Psidium* ($n = 5$ per stand), and light availability ($n = 10$ per stand) were analyzed using Analysis of Variance (ANOVA) and Tukey-Kramer multiple comparisons (SAS/STAT software, Version 8.02, SAS Institute, Cary, North Carolina, USA). Stem basal area and density values ($n = 10$ per stand) as well as resin-captured N and P values were analyzed using ANOVA with post-hoc Tukey's tests to determine (1) differences between native and invaded stands on a given flow, and (2) differences among flows for a given stand type ($P = 0.05$). Prior to analysis, data sets were transformed [$\log(1 + x)$] to increase the normality of distributions while allowing for different variances for each lava flow age/stand type combination (SAS/STAT software, Version 8.02). Because resin-captured N and P values of each site did not differ systematically among seasonal sampling periods based on repeated-measures analysis, values from all sampling periods were pooled prior to analysis (i.e., $n = 40$ per stand for N, and $n = 30$ per stand for P). Histograms of stem densities of dominant species were used to evaluate structural and compositional differences among sites.

RESULTS

Litter inputs

Litter inputs in invaded stands were 8.6, 4.9, and 1.3 times greater than native stands on the 48-, 213-, and 300-yr-old lava flows, respectively. In native stands, annual litter inputs were lowest on the 48- and 213-yr-old flows (1.2 and 2.4 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and increased significantly to 8.5 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ on the 300-yr-old flow (Fig. 1A). Inputs of *Metrosideros* leaves accounted for 84%, 69%, and 50% of total litter inputs in native stands on the 48-, 213-, and 300-yr-old flows, respectively. Total litter mass did not differ significantly among invaded stands, ranging from 10.3 to 11.3 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Inputs of *Falcataria* leaf and wood litter accounted for 81–95% of litter inputs in invaded stands.

Concentrations of N and P in *Falcataria* leaf litter in invaded stands ranged between 2% and 2.9% and between 0.05% and 0.10%, respectively (Table 2). *Falcataria* wood litter ranged from 1.1% to 1.4% N and from 0.03% to 0.05% P. Concentrations of N and P in *Metrosideros* leaf litter ranged from 0.3% to 0.6% N and from 0.02% to 0.04% P among native stands.

Nitrogen mass in litterfall was 55, 17, and 4 times greater in invaded stands relative to native stands on

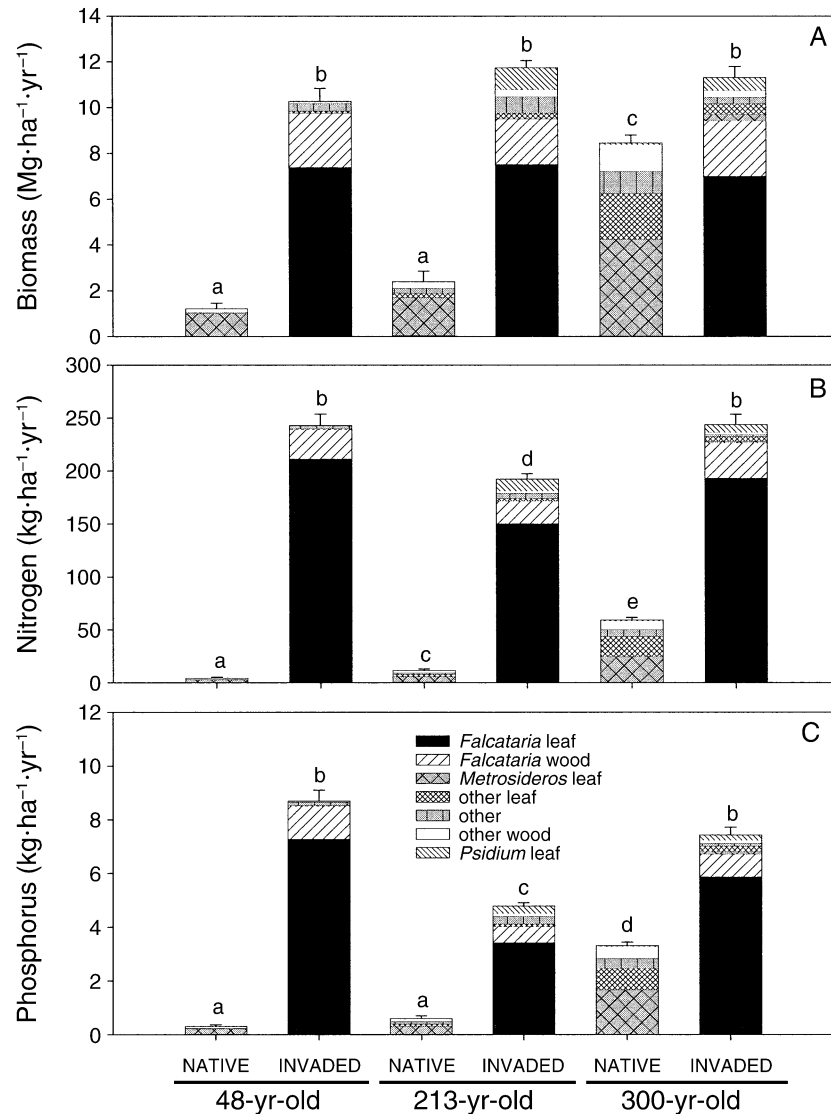


FIG. 1. Annual inputs (means + SE) of (A) biomass, (B) N mass, and (C) P mass via litterfall, and the relative contributions of various species to those inputs, in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-yr-old lava flows in eastern Hawai'i. Mean values that share the same lowercase letter did not differ significantly from one another (Tukey's test, $P \leq 0.05$).

48-, 213-, and 300-yr-old flows, respectively. In native stands, litterfall N mass increased with increasing flow age (Fig. 1B). *Metrosideros* leaf litter exhibited relatively low percentage of N values in all sites and accounted for 70, 44, and 42% of total N mass in litterfall of native stands on the 48-, 213-, 300-yr-old flows. In invaded stands, N mass ranged from 192 kg·ha⁻¹·yr⁻¹ on the 48-yr-old flow to 243 kg·ha⁻¹·yr⁻¹ on the 213- and 300-yr-old flows. *Falcataria* leaf and wood litter accounted for 89–98% of N mass in litter of those stands.

Phosphorus mass in litterfall was 28, 8, and 2 times greater in invaded stands relative to native stands on the 48-, 213-, and 300-yr-old flows, respectively (Fig. 1C). In native stands, P inputs were relatively low on

the 48- and 213-yr-old flows and significantly higher on the 300-yr-old flow, with *Metrosideros* leaves dominating total P inputs on each flow. In invaded stands, inputs of P ranged from 4.8 kg·ha⁻¹·yr⁻¹ on the 213-yr-old flows to 7.4 and 8.9 kg·ha⁻¹·yr⁻¹ on the 48- and 300-yr-old flows, respectively. As with N inputs, *Falcataria* leaf and wood litter dominated annual P inputs at invaded sites, representing 84–98% of total inputs.

In addition to absolute increases in inputs of biomass and N and P mass, litter quality increased with *Falcataria* invasion as well (Fig. 2). C:N of litterfall was 3–7 times greater, and C:P was 2–4 times greater, in native stands relative to their invaded counterparts. In contrast, litterfall N:P was 2 times greater in each of

TABLE 2. Concentrations (means \pm SE) of C, N, and P in dominant litter types collected from litter traps over the course of one year.

Tissue type, by stand type/lava flow age	Concentration (%)		
	C	N	P
<i>Falcataria</i> leaf			
Invaded/48-yr-old	48 \pm 0.21	2.86 \pm 0.05	0.098 \pm 0.0051
Invaded/213-yr-old	48 \pm 0.10	2.00 \pm 0.09	0.046 \pm 0.0034
Invaded/300-yr-old	48 \pm 0.20	2.76 \pm 0.06	0.084 \pm 0.0038
<i>Falcataria</i> wood			
Invaded/48-yr-old	47 \pm 0.23	1.17 \pm 0.07	0.051 \pm 0.0064
Invaded/300-yr-old	47 \pm 0.12	1.37 \pm 0.05	0.035 \pm 0.0034
Invaded/213-yr-old	48 \pm 0.24	1.07 \pm 0.11	0.030 \pm 0.0079
<i>Metrosideros</i> leaf			
Native/48-yr-old	50 \pm 1.28	0.30 \pm 0.01	0.023 \pm 0.0012
Native/213-yr-old	52 \pm 0.10	0.31 \pm 0.01	0.018 \pm 0.0006
Native/300-yr-old	51 \pm 0.14	0.59 \pm 0.03	0.039 \pm 0.0016
<i>Psidium</i> leaf			
Invaded/213-yr-old	45 \pm 0.05	1.16 \pm 0.02	0.029 \pm 0.0009
Invaded/300-yr-old	45 \pm 0.14	1.26 \pm 0.05	0.035 \pm 0.0016
Other leaf			
Native/300-yr-old	48 \pm 0.18	0.94 \pm 0.04	0.040 \pm 0.0022
Other wood			
Native/300-yr-old	51 \pm 0.19	0.68 \pm 0.08	0.038 \pm 0.0035

the invaded stands relative to their native-dominated counterparts.

Soil N and P availability

Resin-captured soil N (i.e., combined NO_3^- -N and NH_4^+ -N) values were 121, 106, and 17 times higher in invaded stands relative to their native counterparts on the 48-, 213-, and 300-yr-old lava flows, respectively (Fig. 3A). Resin-captured soil P (PO_4^{3-} -P) values were 24, 2, and 3 times higher in invaded stands relative to their native counterparts on the 48-, 213-, and 300-yr-old flows, respectively (Fig. 3B). Among native stands, resin-captured N values were significantly higher on the 300-yr-old flow compared to the two younger flows, and resin-captured P values were significantly lower on the 48-yr-old flow relative to the two older flows. In contrast, N and P values did not differ significantly among invaded stands.

Foliar N and P concentrations of *Psidium*

Foliar N concentrations of *Psidium* increased substantially with increasing age in native stands, but were consistently high in the invaded stands (Fig. 4A). In the native stand on the 300-yr-old lava flow, foliar N values were as high as those of invaded stands on each of the three flows. Similarly, foliar P values of *Psidium* were significantly higher in the native-dominated stand on the 300-yr-old flow relative to native stands on the two younger flows (Fig. 4B). Values were significantly higher in the invaded stands relative to native stands on both the 48- and 213-yr-old flows, and did not differ significantly among invaded stands and the native stand on the 300-yr-old flow.

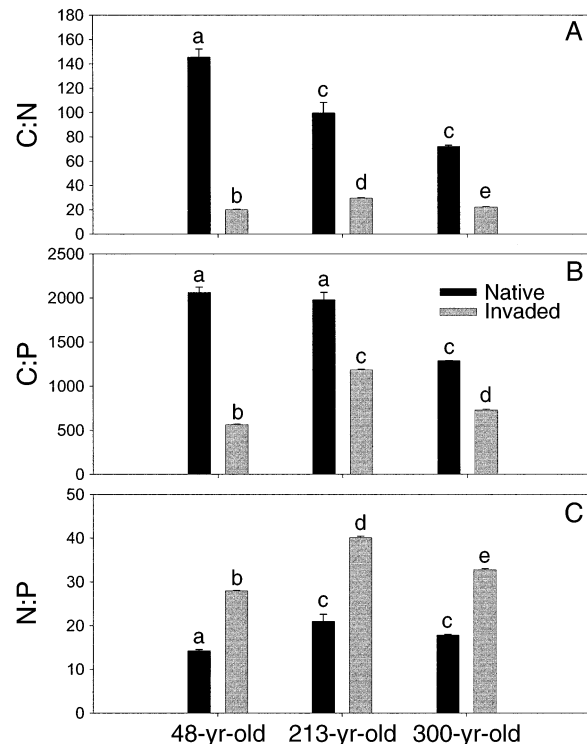


FIG. 2. Ratios (means \pm SE) of nutrients C, N, and P in annual litter inputs of native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-yr-old lava flows in eastern Hawai'i. Mean values that share the same lowercase letter did not differ significantly from one another (Tukey's test, $P \leq 0.05$).

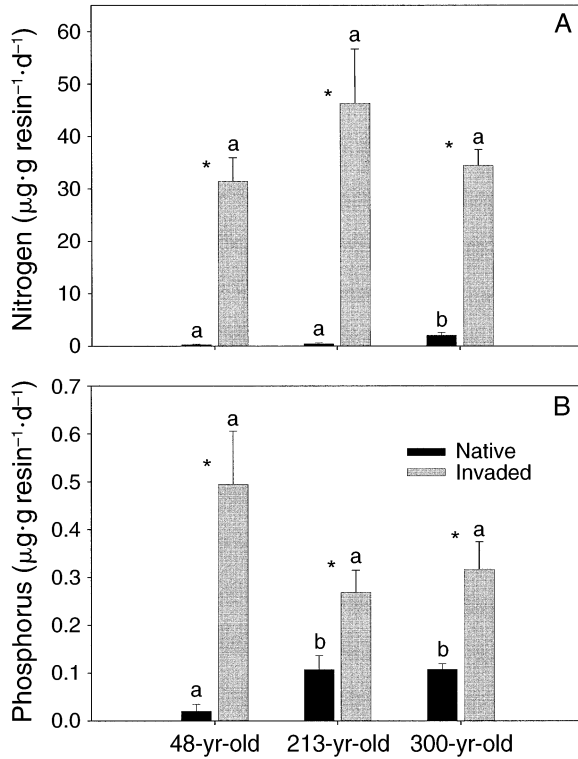


FIG. 3. Values (means + SE) for resin-captured (A) N and (B) P in surface soils of native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-yr-old lava flows in eastern Hawai'i. An asterisk denotes that native-dominated and *Falcataria*-invaded treatments of a given lava flow differed significantly from one another (Tukey's test, $P \leq 0.05$). Mean values of stands of a common type (i.e., native or invaded) that share the same letter did not differ significantly from one another (Tukey's test, $P \leq 0.05$).

Light availability

Light availability at both forest floor and subcanopy levels differed with respect to lava flow age in the native-dominated stands and between native and invaded stands on the two younger lava flows. Subcanopy light levels were greatest in the relatively open-canopied native stands of the 48- and 213-yr-old flows (Fig. 5A) and declined in the native stand on the 300-yr-old flow. Regardless of flow age, all three invaded stands exhibited low light levels similar to those of the native stand on the 300-yr-old flow. Light availability at the forest floor was lower than at the subcanopy level within each stand, but followed a pattern similar to subcanopy levels with respect to forest type and flow age (Fig. 5B). In native stands, light availability at the forest floor decreased with increasing flow age, from 85% of ambient on the 48-yr-old flow to 2% of ambient on the 300-yr-old flow. Forest floor light availability was relatively low among all invaded stands and those values did not differ from that of the native stand on the 300-yr-old flow.

Stand level basal area and stem density

The composition of stand basal area (BA; stems >2 cm dbh) differed markedly between native and invaded stands on each of the three lava flows. In native stands, native species accounted for nearly 100% of total BA on all three flows (Table 3), while alien species accounted for 68–99% of total BA in the invaded stands. Total BA increased with increasing flow age among native stands, and such increases were driven primarily by increases in *Metrosideros*. While *Metrosideros* dominated total BA of native stands on the two younger flows (100% and 98%, respectively), two native understory tree species, *Psychotria hawaiiensis* and *Diospyros sandwicensis*, as "other native species," accounted for 28% of total stand BA on the 300-yr-old flow. In contrast to native stands, invaded stands showed no pattern of increase in total BA with flow age (Table 3). Total BA was 13 times greater in the invaded stand than in the native stand on the 48-yr-old flow, but did not differ between native and invaded stands on the 213- and 300-yr-old flows. *Falcataria* accounted for 98%, 72%, and 57% of total BA in invaded stands of the 48-, 213-, and 300-yr-old flows, respectively. While a primary contributor to total BA

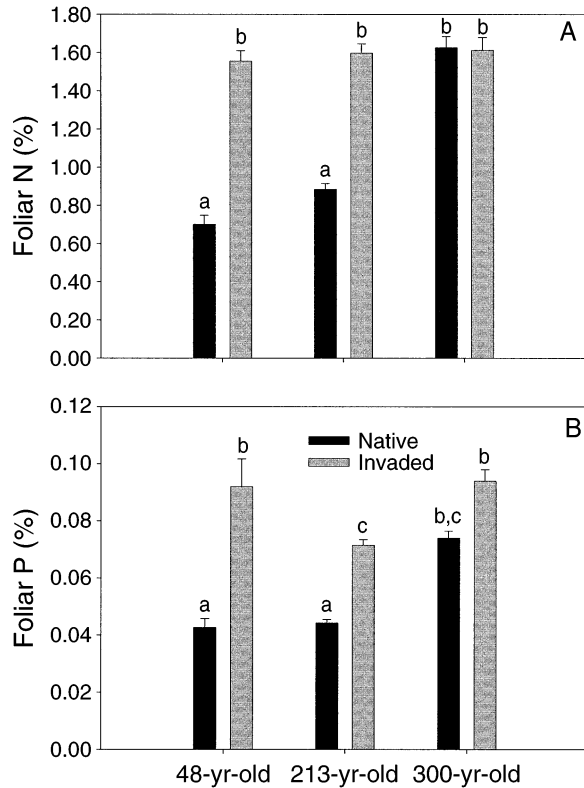


FIG. 4. Concentrations (means + SE) of (A) N and (B) P in the foliage of the nonnative tree, *Psidium cattleianum*, in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-yr-old lava flows in eastern Hawai'i. Mean values that share the same lowercase letter did not differ significantly from one another (Tukey's test, $P \leq 0.05$).

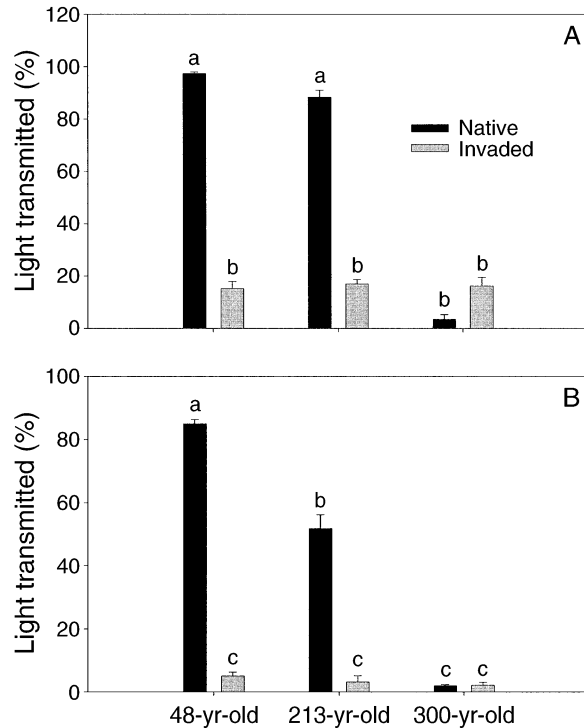


FIG. 5. Values (means + SE) of light availability measured at (A) subcanopy and (B) forest floor levels in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-yr-old lava flows in eastern Hawai'i. Mean values that share the same lowercase letter did not differ significantly from one another (Tukey's test, $P \leq 0.05$).

in each of the native stands, *Metrosideros* was relatively scarce in invaded stands, accounting for at most 20% of total BA (Table 3). Further, live individuals accounted for 94–100% of *Metrosideros* BA in native stands, but dead individuals accounted for 68–100% of *Metrosideros* BA in invaded stands.

Densities of woody stems followed patterns similar to those of stand-level BA; native species accounted for 96–100% of stem density in native stands of the three flows. In invaded stands, nonnative species accounted for 82–91% of total stem density (Table 3). *Falcataria* individuals accounted for 30% of total stems of the invaded stand on the 48-yr-old flow, and *Psidium* accounted for 49–89% of total stems in the three invaded stands. Total stem densities were three and five times greater in invaded stands compared to their native counterparts on the 213-, and 300-yr-old flows, respectively. Though the mean value of total stem density was two times higher in the invaded stand compared to the native stand on the 48-yr-old flow, this difference was not significant. *Psidium* densities were significantly higher in invaded stands relative to native stands on all three flows and accounted for differences in total stem density between native and invaded stands.

Forest structure

Size class distributions of live stems differed substantially among lava flows and between native and invaded stands on each flow (Fig. 6). On the 48-yr-old flow, the native stand was characterized by many small *Metrosideros* individuals (Fig. 6A), while the invaded stand was notable for the absence of live *Metrosideros* individuals and high densities of small (0–5 cm) *Psidium* stems and larger (>30 cm) *Falcataria* individuals (Fig. 6B).

The native stand of the 213-yr-old flow was characterized by a shift in *Metrosideros* stems to larger diameter classes relative to its 48-yr-old flow counterpart. In contrast, live *Metrosideros* stems were absent from the invaded stand of 213-yr-old flow, which instead consisted of high frequencies of small diameter *Psidium* stems and numerous large *Falcataria* individuals (Fig. 6D).

The native stand of the 300-yr-old flow was characterized by few large *Metrosideros* individuals and large numbers of other native tree species (e.g., *Psychotria* and *Diospyros*) in small to intermediate diameter classes. *Psidium* individuals were also present, but at relatively low frequencies (Fig. 6E). The invaded stand was characterized by few large *Metrosideros* and *Falcataria* individuals, high numbers of small diameter *Psidium* stems, and moderate numbers of *Psychotria* and *Diospyros* in the small to intermediate diameter classes (Fig. 6F).

DISCUSSION

Our results demonstrate that invasion by *Falcataria* substantially alters the functioning of native-dominated lowland forest ecosystems of Hawai'i by significantly increasing the input, availability, and cycling of nutrients. Not only did biomass and N and P mass inputs via litterfall increase in invaded stands relative to their native counterparts on each lava flow, but litter quality, reflected in lower C:N and C:P ratios and higher N:P ratios, increased as well. Increased litter quantity and quality also coincided with, and likely led to, large increases in both soil N and P availability in *Falcataria*-invaded stands relative to their native-dominated counterparts.

Such process-level changes with *Falcataria* invasion are consistent with those reported for young volcanic sites in Hawai'i Volcanoes National Park where the nonnative N₂-fixing tree *Myrica faya* increased N inputs above background levels (i.e., from 4.2 kg·ha⁻¹·yr⁻¹ to 22.5 kg·ha⁻¹·yr⁻¹), leading to significant increases in soil N availability (Vitousek and Walker 1989). Similarly, invasion by the N₂-fixing *Acacia* species into strandveld ecosystems of South Africa also increased soil nitrogen mineralization rates (Stock et al. 1995).

As expected for forests in the early stages of primary succession, litterfall in native stands on the 48- and 213-yr-old flows were at the low end of litterfall values

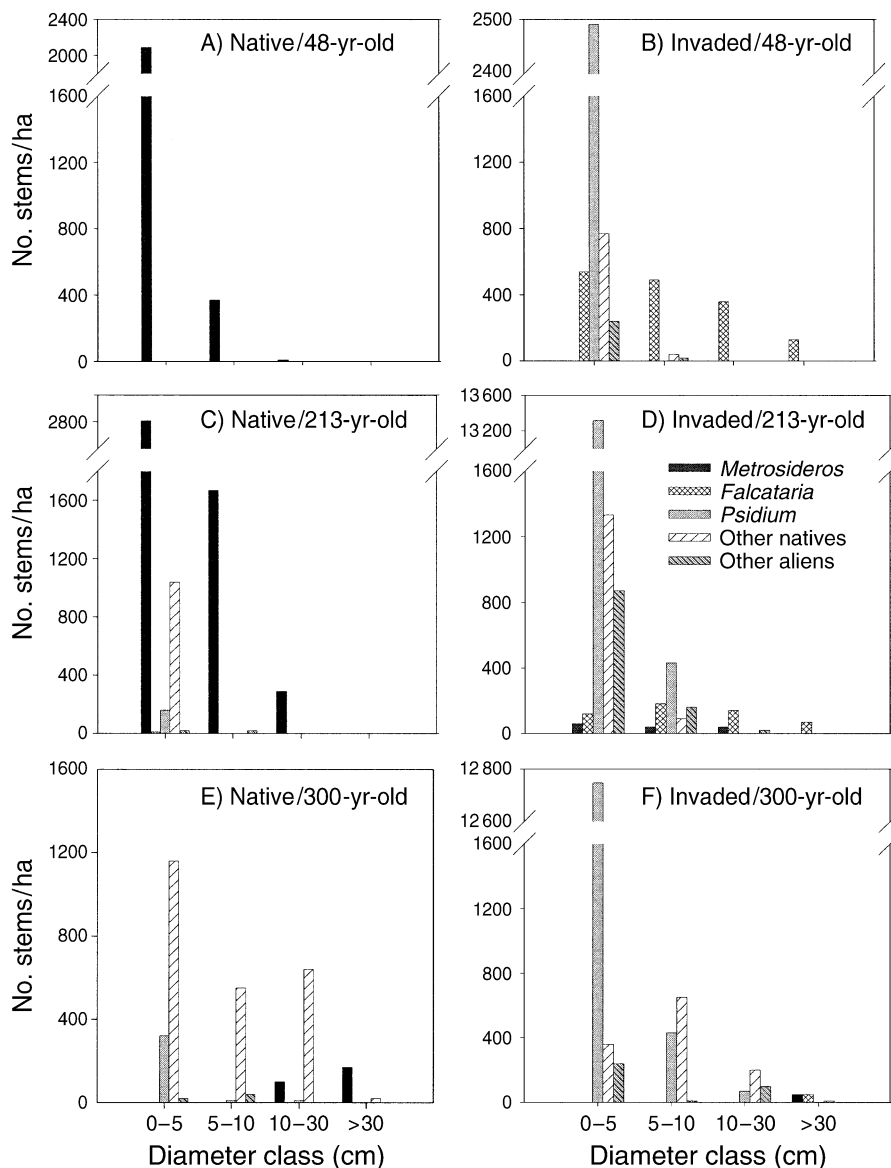


FIG. 6. Histograms of woody stem frequencies at (A, C, and E) native and (B, D, and F) invaded stands on 48-, 213-, and 300-yr-old lava flows in eastern Hawai'i. The "other natives" category refers to native species other than *Metrosideros*; the "other aliens" category refers to alien species other than *Falcataria* and *Psidium*. Stems are grouped by diameter class (cm) measured at 1.3 m height.

for tropical forests reported by Clark et al. (2001), and mass of N and P in litterfall of all three native-dominated stands were lower than the range for each of these elements reported by Vitousek and Sanford (1986) for a broad set of tropical forests. In contrast, litterfall rates for each of the three invaded stands were high regardless of flow age. Litterfall N mass values among the set of invaded stands were high as well, while litterfall P mass values were in the mid to high range of those reported for lowland and montane moist tropical forests (Vitousek and Sanford 1986).

It is not surprising that *Falcataria* increased inputs and availability of N in these early successional forests.

In native-dominated forests studied here and elsewhere in Hawaii, primary succession is characterized by a gradual biomass accumulation constrained by N limitation on young lava substrates (Vitousek et al. 1993). Constraints on primary production imposed by N limitation (Harrington et al. 2001) are further exacerbated by the lack of native N_2 -fixing plants in early successional forests even though such species are represented in Hawaii's flora (Wagner et al. 1999). Where plants capable of symbiotic nitrogen fixation are absent during primary succession, N stocks are derived from cyanobacteria, heterotrophic bacteria, and atmospheric inputs (i.e., precipitation and dryfall). Previous studies

TABLE 3. (A) Stand-level stem density and (B) basal area values (means with SE in parentheses) of woody species encountered within each study site.

Species	48-yr-old lava flow		213-yr-old lava flow		300-yr-old lava flow	
	Native	Invaded	Native	Invaded	Native	Invaded
A) Stem density (no. stems/ha)						
<i>Metrosideros polymorpha</i> (live)	2471 ^{a,α} (283)	0 ^{b,α} (0)	4770 ^{a,β} (566)	140 ^{b,α} (129)	270 ^{a,ω} (50)	50 ^{b,α} (27)
<i>Metrosideros polymorpha</i> (dead)	0 ^{a,β} (0)	470 ^{b,β} (144)	510 ^{a,α} (85)	1460 ^{b,α} (169)	50 ^{a,β} (22)	270 ^{b,β} (50)
<i>Falcataria moluccana</i> †	0 ^{a,α} (0)	1520 ^{b,α} (233)	10 ^{a,α} (10)	510 ^{b,β} (113)	0 ^{a,α} (0)	50 ^{b,ω} (17)
<i>Psidium cattleianum</i> †	0 ^{a,α} (0)	2491 ^{b,α} (788)	160 ^{a,α} (122)	13 747 ^{b,β} (2237)	340 ^{a,α} (318)	13 247 ^{b,β} (2351)
Other native species	0 ^{a,α} (0)	930 ^{b,α} (292)	1040 ^{a,β} (323)	1421 ^{a,α} (451)	2430 ^{a,β} (241)	1220 ^{b,α} (259)
Other alien species	0 ^{a,α} (0)	140 ^{b,α,β} (58)	40 ^{a,α} (22)	1050 ^{b,α} (344)	0 ^{a,α} (0)	350 ^{a,β} (236)
Total (live)	2471 ^{a,β} (283)	5082 ^{a,α} (103)	6021 ^{a,α} (744)	16 868 ^{b,β} (2521)	3040 ^{a,β} (480)	14 918 ^{b,β} (2306)
B) Basal area (m ² /ha)						
<i>Metrosideros polymorpha</i> (live)	2.4 ^{a,α} (0.3)	0.0 ^{b,α} (0.0)	13.0 ^{a,β} (1.6)	0.7 ^{b,α} (0.6)	36.8 ^{a,β} (5.8)	11.4 ^{b,α} (6.0)
<i>Metrosideros polymorpha</i> (dead)	0.0 ^{b,α} (0.0)	0.1 ^{b,α} (0.0)	0.8 ^{a,β} (0.2)	4.6 ^{b,β} (0.6)	1.4 ^{a,α,β} (0.8)	24.0 ^{b,ω} (5.0)
<i>Falcataria moluccana</i> †	0.0 ^{a,α} (0.0)	32.4 ^{b,α} (8.4)	0.0 ^{a,α} (0.0)	14.9 ^{b,α} (3.9)	0.0 ^{a,α} (0.0)	32.6 ^{b,α} (16.1)
<i>Psidium cattleianum</i> †	0.0 ^{a,α} (0.0)	0.2 ^{b,α} (0.1)	0.0 ^{a,α} (0.0)	3.3 ^{b,β} (0.7)	0.2 ^{a,α} (0.1)	3.7 ^{b,β} (0.9)
Other native species	0.0 ^{a,α} (0.0)	0.3 ^{b,α} (0.2)	0.2 ^{a,β} (0.1)	0.5 ^{b,α} (0.1)	17.5 ^{a,ω} (1.1)	6.7 ^{b,β} (0.8)
Other alien species	0.0 ^{a,α} (0.0)	0.2 ^{a,α} (0.1)	0.1 ^{a,α} (0.1)	1.4 ^{b,β} (0.4)	0.0 ^{a,α} (0.0)	2.8 ^{a,α,β} (2.6)
Total (live)	2.4 ^{a,α} (0.3)	33.1 ^{b,α} (8.4)	13.4 ^{a,β} (1.7)	20.8 ^{a,α} (3.6)	54.6 ^{a,ω} (5.6)	57.3 ^{a,α} (22.7)

Notes: Stem density measures include all stems >1.3 m in height. Basal area measures include all stems >2 cm dbh. Total species values do not include dead *Metrosideros* values. Within a given row, values from native and invaded stands on the same lava flow that share the same Roman letter did not differ significantly (Tukey's test $P \leq 0.05$). Values of common stand types across the three lava flows that share the same Greek letter did not differ significantly (Tukey's test $P \leq 0.05$).

† Alien species.

of N₂-fixing lichens on recent lava flows in Hawaii documented inputs between 0.02 and 0.45 kg N·ha⁻¹·yr⁻¹ (Kurina and Vitousek 2001). In relatively young (300-yr-old) montane wet forest stands in Hawaii, estimated inputs from asymbiotic, heterotrophic bacteria on *Metrosideros* leaf litter were 1.25 kg N·ha⁻¹·yr⁻¹ (Crews et al. 2001), and combined inputs from bryophytes, lichens, and decaying wood were estimated to be 0.2 kg N·ha⁻¹·yr⁻¹ (Matzek and Vitousek 2003). Atmospheric N inputs from precipitation, dry deposition, and background cloudwater measured in native-dominated *Metrosideros* forests of Hawai'i Volcanoes National Park averaged 1.01, 0.4, and 5.8 kg N·ha⁻¹·yr⁻¹, respectively (Carrillo et al. 2002, Vitousek 2004). In the wet lowland forests studied here, where cloudwater likely does not play an important role, atmospheric inputs, largely to due precipitation, are estimated to be ~2 kg N·ha⁻¹·yr⁻¹ (P. M. Vitousek, *personal communication*). Even when taken together, the

above inputs are low compared to estimates of 18.5 kg N·ha⁻¹·yr⁻¹ accompanying invasion by the N₂-fixing tree *Myrica faya* on young volcanic substrates (Vitousek and Walker 1989), and inputs inferred from four-fold to 55-fold increases in the annual cycling of N through litterfall accompanying recent *Falcataria* invasion.

In a temperate system of North America, Bormann and Sidle (1990) found that establishment of N₂-fixing alders increased both plant biomass and net primary productivity during primary succession on substrates exposed following glacial retreat. In warm-temperate forests of Japan, accumulations of biomass and nutrients during early stages of primary succession on lava flows were greater than those of similar forests in Hawaii (Kamijo et al. 2002). Such differences were attributed to the dominance of *Alnus sieboldiana*, an N₂-fixing alder species, during the early stages of primary succession in Japan, and an absence of such N₂-fixing

plants during primary succession in Hawaii. Clearly, the lack of N₂-fixing vascular plants during early stages of primary succession in wet lowland forests of Hawaii constrains stand and ecosystem development and is a fundamental characteristic of these ecosystems (Crews et al. 2001). Our results from native stands studied here bear this out in that both inputs of N via litterfall and soil N availability increased gradually with increasing flow and forest stand age. However, any constraints to N availability imposed by flow age are diminished by *Falcataria* invasion.

Interestingly, *Falcataria* increased inputs and availability of P as well as N. In contrast, Pearson and Vitousek (2002) found that resin-captured P values were significantly lower in stands dominated by *Acacia koa*, an N₂-fixing tree, relative to stands dominated by *Metrosideros*, a non-N₂-fixing tree, along a gradient of increasing soil age in Hawaii. Further, *Falcataria* significantly increased soil N supply but decreased soil P availability in plantation settings in Hawaii; resin-captured P values under 15–17-yr-old *Eucalyptus saligna* stands were double those in adjacent *Falcataria* stands of the same age even though the latter stands cycled as much P as the former (Binkley and Ryan 1998, Binkley et al. 2000, Kaye et al. 2000). Our results indicated not only that *Falcataria* increased P supply from litterfall, but that soil P availabilities increased as well. Such discrepancies regarding the effect of *Falcataria* on soil P availability may be due to differences in soil age. During the early stages of soil development, most soil P is bound in primary mineral phosphates and is relatively available for plant uptake, but with increased soil weathering the fraction of total soil P in forms available to plants declines (Crews et al. 1995, Schlesinger et al. 1998). Sites studied by Binkley et al. (2000) were located on ~65 000-yr-old ash-derived soils that had been intensively cultivated for sugar cane production for 65 years (Bashkin and Binkley 1998), and thus may be relatively depleted in plant available P. In contrast, sites studied here consisted of thin and patchy accumulations of soil organic matter overlaying relatively unweathered 48–300-yr-old lava flows. If *Falcataria* is readily able to access primary mineral phosphates, it may be able to moderate potential P limitation on these young substrates. Increased allocation to root biomass is one way to increase access to mineral P, and *Falcataria* stands have been shown to allocate 30% more C to belowground biomass than adjacent *Eucalyptus saligna* stands in plantations on the Big Island of Hawai'i (Binkley et al. 2000). Though not measured here, enhanced association between *Falcataria* and its mycorrhizal symbionts also may have increased the supply and cycling of P in invaded stands. Both *Metrosideros* and *Falcataria* have been classified as arbuscular mycorrhizal (Binkley and Giardina 1997, Treseder and Allen 2002), but *Falcataria* may allocate relatively more carbon to mycorrhizal symbionts in or-

der to gain greater access to mineral and organic phosphorus.

In addition to altering ecosystem processes, *Falcataria* changed both the composition and structure of wet lowland forests from strongly native dominated to strongly alien dominated. Such changes were due to increased numbers of alien species as well as decreased numbers of native species in invaded stands relative to native stands. Results suggest that increases in *Psidium* basal area and density in stands invaded by *Falcataria* may be due in part to increased N and P supply. *Psidium*, an understory tree species native to Brazil (Wagner et al. 1999), is capable of forming dense stands in both disturbed areas and intact forests of Hawai'i, and is considered a serious management problem in many natural areas (Huenneke and Vitousek 1990). Differences in *Psidium* abundance between native and adjacent invaded stands were striking; very few *Psidium* stems were encountered in native stands on the 213-yr-old flow and none were present in native stands on the 48-yr-old flow, while large numbers were encountered in adjacent *Falcataria*-invaded stands on these two flows. Comparison of foliar N and P concentrations of *Psidium* found in native and invaded stands supports the facilitative effect of *Falcataria*; foliar N and P concentrations of *Psidium* were significantly higher in invaded stands relative to native stands on both 48- and 213-yr-old flows. Though not definitive evidence, increased foliar nutrient concentrations likely reflect increased soil nutrient availability and are positively correlated with photosynthetic capacity (Vitousek and Sanford 1986), which may translate to increased relative growth rates. Given that light levels were low in invaded stands, it is unlikely that stand structure or canopy openness contributed significantly to *Psidium* spread, though other factors not measured here also may be responsible (e.g., changes in water availability, relative humidity, or temperature). Nonetheless, increased soil N availability has been implicated in the spread of other nonnative species elsewhere (Huenneke et al. 1990, Maron and Connors 1996, Yelenik et al. 2004), and we suspect this to be the case in these early successional scenarios.

Although *Psidium* density and basal area values were higher in the invaded stand relative to the native stand on the 300-yr-old flow, *Psidium* densities were found to be equally high (i.e., 15 400 stems/ha) in nearby forest stands on 300-yr-old flows that had not yet been invaded by *Falcataria* (R. F. Hughes, unpublished data), suggesting that *Psidium* invasion does not require the presence of *Falcataria* stands at that more advanced point of primary succession. Concentrations of N and P in *Psidium* foliage from native stands on the 300-yr-old flow support this reasoning; while *Falcataria* invasion was associated with significantly higher values for foliar percentages of N and P for *Psidium* on the younger flows, it did not appear to increase the

foliar N and P status of *Psidium* beyond those of the native forest on the 300-yr-old flow.

In addition to facilitating *Psidium* on the two youngest flows, *Falcataria* invasion also was associated with declines in populations of *Metrosideros* on all three flows. The set of native stands studied here represent an approximate chronosequence of primary succession in these wet lowland forest ecosystems, a process dominated by *Metrosideros* stand development. Comparing forest structure along a gradient of increasing lava flow age on windward slopes of Mauna Loa, Hawai'i, Drake and Mueller-Dombois (1993) described primary succession in wet forests as one of direct succession in which the initial pioneer, *Metrosideros*, maintains overstory dominance throughout primary succession, with populations typically undergoing self-thinning processes leading to decreased stem density and increased basal area. *Metrosideros* populations establish on young lava flows at all elevations on the wet windward sides of Kilauea and Mauna Loa Volcanoes and persist as a dominant species with increasing flow age (Atkinson 1970, Aplet and Vitousek 1994, Kitayama et al. 1995). The reduction in *Metrosideros* populations associated with invasion of *Falcataria* likely is due to reduced light availability, although other factors such as increased competition for water may contribute. Seedlings of *Metrosideros* are relatively shade intolerant (Burton and Mueller-Dombois 1984), and this intolerance may extend to mature individuals as well. Regardless of proximate causes, the loss of *Metrosideros* represents a profound compositional and structural change to these forests.

In contrast, other native woody species did persist under *Falcataria* canopies. Both density and basal area of native woody species other than *Metrosideros* (e.g., *Pipturus albidus*, *Diospyros*, *Psychotria*, and *Psydrax*) increased in invaded stands compared to native stands on both 48- and 213-yr-old flows, and other native species persisted in the invaded stand on the 300-yr-old flow, though at lower densities relative to the native stand. That these native understory tree species are tolerant of, and could benefit from, the presence of *Falcataria* may be due to their shade tolerance. None are prevalent during early stages of primary succession in wet forests of Hawai'i (Atkinson 1970, Aplet and Vitousek 1994, Kitayama et al. 1995); instead, they appear during later stages, although *Pipturus* is also a common pioneer species in disturbed areas. Given their tolerance to low light conditions, it is not surprising that these species persist to some degree in *Falcataria*-invaded stands where soil N and P availabilities have increased substantially. However, their densities were quite low relative to those of *Psidium*. We expect that as *Psidium* populations increase in these stands, the persistence of remaining native tree species will be compromised due to increased interspecific competition.

Invasive species, particularly those that fix N, have the capacity to alter soil processes and may consequently alter the susceptibility of a given ecosystem to invasion by additional nonnative species (Vitousek and Walker 1989, Ehrenfeld 2003). Our findings provide a clear example of the degree to which alien species modify the function, composition, and structure of systems they invade; invasion by *Falcataria* into Hawai'i's wet lowland forests significantly increased inputs, cycling, and availability of both N and P, thereby facilitating other nonnative species and eliminating previously dominant native species.

Given the necessity to protect the integrity of these last few examples of native wet lowland forest ecosystems of Hawai'i, our results are alarming. Intact remnants of these forests, particularly the more developed and compositionally diverse stands found on lava flows ~300 years in age, are rare and largely restricted to eastern Hawai'i. They are unique to Hawai'i, and distinct from other tropical and subtropical wet lowland forests in both form and function, because they are dominated by species endemic to Hawai'i. They are unique within Hawai'i, and distinct from more widespread montane forests, because of the specific environmental conditions (i.e., temperature and precipitation) that determine their community composition and development. Because *Falcataria* invasion fundamentally alters both the structure and function of these ecosystems, it poses an immediate threat to their existence. Consequently, the degree to which *Falcataria* continues to spread across the lowland regions of eastern Hawai'i will, to a large extent, determine the fate of these unique forests—whether they persist into the future or disappear from the ecosystems of Hawaii and, by extension, those of the world as well.

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