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Impacts of *Falcataria moluccana* Invasion on Decomposition in Hawaiian Lowland Wet Forests: The Importance of Stand-level Controls

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Abstract

Invasive species have the capacity to substantially alter soil processes, including rates of litter decomposition. Currently, the few remaining native-dominated lowland wet forests in Hawai'i are being invaded by *Falcataria moluccana*, a large, fast-growing, N_2-fixing tree. In this study, we sought to determine the extent to which *Falcataria* invasion alters decomposition in these lowland wet forests, and whether changes resulted from differences in litter substrate type, lava flow age and type, forest stand type and associated soil biota, or some combination of these factors. We measured decomposition rates and nitrogen (N) and phosphorus (P) dynamics of *Metrosideros polymorpha* and *Falcataria* leaf litter in native-dominated and *Falcataria*-invaded stands on 48- and 300-year-old a'a lava flows and a 213-year-old pāhoehoe flow in the Puna district of eastern Hawai'i. Despite significant differences in the initial quality of *Metrosideros* and *Falcataria* litter, in nearly all cases mass remaining of the two litter types did not differ within a given forest stand, whether native-dominated or invaded. Instead, stand type accounted for large differences in the decomposition of both litter types, and litter decomposed two to 10 times faster in *Falcataria*-invaded stands than it did in their native-dominated counterparts on each lava flow. Dynamics of N (that is, immobilization or release) during decomposition were affected by stand, litter, and lava flow type; P dynamics were affected by stand and flow type, but not litter type. Although not definitive proof of causality, the decay rates of both species were positively correlated to previously measured inputs of N mass and P mass via litterfall as well as availability of soil N and P, characteristics that all increased substantially with *Falcataria* invasion. Given the degree of change to a host of ecosystem processes, including decomposition, after invasion by *Falcataria*, these transformed forest ecosystems may best be viewed as fundamentally new and different, in both structure and function, from the native ecosystems they have replaced.

Key words: *Metrosideros polymorpha*; nitrogen; phosphorus; albizia; primary succession; mass loss; invasive species; ecosystem processes; nutrient availability; lava flows.

Introduction

Exotic species are capable of impacting ecosystems through a variety of mechanisms that can be classified into three broad groups: (a) altered trophic structure (Savidge 1987), (b) altered disturbance frequencies or intensities (Mack and D'Antonio 1998), and (c) altered resource supply or utilization (Vitousek 1990). Increasing attention has focused on this last mechanism, which includes the role invasive species play in changing soil properties

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and processes (Ehrenfeld 2003). This may include the alteration of organic inputs to soils through changes in net primary production (NPP), the quantity and quality of litter inputs, soil nitrogen (N) and phosphorus (P) mineralization and nitrification rates, and soil carbon (C) and nutrient pools. In concert with, or as a consequence of, the aforementioned changes, exotic species invasions may also alter rates of litter decomposition, in turn leading to changes in ecosystem-scale nutrient cycling and rates of productivity (Vitousek and Farrington 1997; Allison and Vitousek 2004).

The decomposition of litterfall is determined by (a) climate (that is, temperature and moisture); (b) the physical and chemical characteristics of the decomposing material, such as surface-to-volume ratios and concentrations and ratios of C, N, and P; and (c) nutrient availability and the composition and activity of soil biota within the site of decomposition (Swift and others 1979; Lavelle 1997). Previous studies have shown that litter and site characteristics affect rates of decomposition within native-dominated forests sampled across a gradient of soil development in Hawai'i that varied systematically with respect to N and P availability (Vitousek and others 1997; Hobbie and Vitousek 2000). Plant species themselves are capable of influencing rates of decomposition by changing the chemistry of litter inputs (Hobbie 1992); and when exotic species invade an ecosystem, such invasions also may alter the determinants of decomposition—including changes to the soil biotic community—although relatively few examples are available from the literature. Using selected native and nonnative species common to wet forests of Hawai'i, Allison and Vitousek (2004) found that high-quality litter of selected invasive species decomposed more rapidly than comparatively low-quality litter of selected native species. In montane Hawaiian rainforests containing native-dominated stands and stands of the nonnative tree, *Fraxinus uhdei*, differences in litter quality affected decomposition rates, whereas differences in stand characteristics did not (Rothstein and others 2004). Vitousek and Walker (1989) demonstrated that the N-fixing tree, *Myrica faya* (now known as *Morella faya*), altered decomposition rates in areas of Hawai'i Volcanoes National Park that it had invaded; *Myrica* litter decomposed faster than litter of the dominant native tree, *Metrosideros polymorpha*, under both *Myrica* or *Metrosideros* canopies, and *Myrica* litter decomposed faster under *Myrica* canopies than under *Metrosideros* canopies. Windham (2001) found that litter type, but not where that litter was located, affected decomposition rates in native *Spartina*-dominated marshes invaded by an exotic grass species (*Phragmites*); *Spartina* litter decomposed faster than *Phragmites* litter under both canopy types. In seasonally dry woodlands of Hawai'i, rates of decomposition were higher in grass-invaded areas than in woodlands where grass had been removed; differences were attributed to the higher decomposability of exotic grass litter and increased decomposition of native litter from woodland+grass sites—a case in which altered site or stand characteristics indirectly influenced litter quality (Mack and D'Antonio 2003).

Falcataria molucanna (albizia), a large, fast-growing, N_2-fixing tree, is currently invading the few remaining expanses of native-dominated lowland wet forests undergoing primary succession on young lava flows in the Puna district of Hawai'i. Prior research has shown that *Falcataria* is capable of substantially increasing both the quantity and quality of litterfall; inputs of N via litterfall were four to 55 times greater, and P inputs were two to 28 times greater, in *Falcataria*-invaded stands than in their native-dominated counterparts on 48-, 213-, and 300-year-old lava flows. These increased inputs also corresponded to sharp increases in both available soil N (17- to 121-fold) and P (two- to 24-fold) (Hughes and Denslow 2005). Given increased inputs and availabilities of N and P, we hypothesized commensurate increases in rates of litter decomposition after *Falcataria* invasion, but we were uncertain whether the hypothesized increases would result from differences in the chemistry of the dominant litter types, differences in the respective C and nutrient inputs between the native-dominated and *Falcataria*-invaded stands, corresponding differences in the composition and activity of soil biota (Zou 1993), or some combination of those factors.

Our objectives were to determine the degree to which *Falcataria* invasion alters rates of decomposition in previously native-dominated lowland wet forests of Hawai'i, and whether the changes differ with respect to lava flow age and type. We also sought to evaluate the relative importance of litter chemistry and stand-level characteristics in controlling decomposition rates in native-dominated and *Falcataria*-invaded forest stands. To do so, we measured decomposition rates of *Metrosideros* and *Falcataria* leaf litter, the dominant contributors to litterfall in native-dominated and *Falcataria*-invaded stands, respectively, in paired native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-year-old lava flows of eastern Hawai'i. Further, we investigated the associations between decomposition rates and previously measured

inputs of N and P mass via litterfall and soil N and P availability among forest stands as an additional assessment of the importance of stand-level controls on decomposition.

Methods

Study Sites

The experiment was conducted in study sites established in lowland wet forest stands located within the Malama Ki (19°26′53″N, 154°51′40″W) and Keauohana (19°25′11″N, 154°57′14″W) state forest reserves in the easternmost portion of the windward side of the Island of Hawai'i. Study sites were the same as those used previously to investigate the impacts of *Falcataria* invasion on rates of litterfall, soil nutrient availability, and forest structure of lowland wet forests (Hughes and Denslow 2005). Both forest reserves are located in the Puna district of Hawai'i, USA, and are in close proximity to one another (that is, less than 10 km). The climate is warm and wet, with a mean annual temperature of approximately 23°C and a mean annual precipitation of approximately 2,500 mm (Giambelluca and others 1986; Sanderson 1993). Study sites in Malama Ki Forest Reserve were located on 213-year-old lava flows of the pāhoehoe lava type (that is, smooth and ropy), whereas study sites at Keauohana Forest Reserve were located on two lava flows of the a'a type (that is, 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 before present. Each lava flow is part of the lower East Rift Zone of the active shield volcano, Kilauea. Parent material is tholeiitic basalt, with little variation in chemical composition among flows (Moore and Trusdell 1991).

Vegetation on these relatively young lava flows has been classified as lowland wet forest, and native-dominated vegetation typically consists of single cohort stands of *Metrosideros polymorpha* and associated native understory tree and shrub species (Wagner and others 1999; Mueller-Dombois and Fosberg 1998). Prior to invasion by *Falcataria*, native-dominated primary succession on these young lava flows is characterized by gradual accumulations of biomass strongly constrained by N availability. The lava parent material contains little N (Vitousek and others 1993), and native plants capable of N fixation are conspicuously absent (Vitousek 1994), although the N-fixing lichen *Stereocaulon vulcani* is abundant on lava flows of the region prior to forest canopy closure (Crews and others 2001).

The N_2-fixing tree *Falcataria* was introduced to Hawai'i from Indonesia in 1917 (Rock 1920) and planted extensively throughout the Hawaiian Islands as part of efforts to reforest degraded watersheds (Nelson 1965). *Falcataria* forms symbiotic associations with *Rhizobium* bacteria, a characteristic of many leguminous plants, and has been shown to be capable of high levels of N fixation under a variety of conditions (Binkley and Giardina 1997). This tree is remarkable for its rapid growth; tree heights may reach 10 m in 2-year-old stands (Walters 1971). Mature *Falcataria* trees can reach heights greater than 30 m and produce broad-spreading crowns with diameters commensurate to their height. Where *Falcataria* stands become established, they often form monospecific canopies that overtop lower-stature native trees, including *Metrosideros*. Prior research indicates that *Metrosideros* trees suffer nearly 100% mortality when overtopped by invading *Falcataria* trees (Hughes and Denslow 2005).

Study sites were established in relatively intact native-dominated forest stands as well as in stands invaded by *Falcataria* on each of three lava flows (Table 1). Native-dominated *Metrosideros* stands likely approximate the age of the respective lava flows on which they occur. *Metrosideros* is an early pioneer on young lava flows (that is, less than 100 years old), and probably established as juvenile cohort stands on each of the three lava flows studied here within the first 30 years of primary succession (Mueller-Dombois and Fosberg 1998). In contrast, based on archived aerial photos (Hawai'i Department of Land and Natural Resources 1993), *Falcataria* populations were not present within any of the study sites in 1965 and likely established less than 30 years ago. To ensure that the native and invaded study areas differed only with regard to the presence of *Falcataria*, we examined the aforementioned aerial photos and located plots beyond (native stands) and behind (invaded stands) the active invasion front of *Falcataria*. Size-class distributions of *Metrosideros* snags and stumps at invaded sites indicated that, prior to invasion by *Falcataria*, these stands were similar in structure to adjacent native stands (Hughes and Denslow 2005).

Experimental Design

Decomposition experiments were carried out using recently senesced *Metrosideros* and *Falcataria* leaf litter collected once every 2 weeks from sets of 2×2 m permeable plastic tarps; *Metrosideros* and *Falcataria* leaf litter was gathered from tarps located in native-dominated stands on the 300-year-old (y.o.) lava flow and *Falcataria*-invaded stands on the 231-

Table 1. Description of the Six Study Sites

Site	Forest Reserve Location	Lava Flow Type	Lava Flow Age[a] (y)	Under or Away from *Falcataria* Canopies
48-year-old native stand	Keauohana	'A'ā	48	Away
48-year-old invaded stand	Keauohana	'A'ā	48	Under
213-year-old native stand	Malama Ki	Pāhoehoe	213	Away
213-year-old invaded stand	Malama Ki	Pāhoehoe	213	Under
300-year-old native stand	Keauohana	'A'ā	200–400	Away
300-year-old invaded stand	Keauohana	'A'ā	200–400	Under

[a]*Lava flow age is expressed as the number of years prior to initiation of the study.*

y.o. lava flow, respectively. Litter collections were conducted within these two stands because they provided the most abundant source of each respective litter type, and these two litter types were subsequently deployed in each of the six stand/lava flow combinations. After collection, leaf litter was dried to a constant mass at 50°C. A 5-g sample of a given species was placed in a 12.5 × 12.5 cm litterbag made from fiberglass window screen material (1-mm mesh size) and the bag was sewn shut with cotton/nylon thread. We made 300 litterbags for each species. Within each of the six study sites, sampling stations were randomly located at roughly 20-m intervals along two 100-m transects (that is, 10 stations per site). Five bags of each species were tethered along 2-m lengths of high-test fishing line placed on the substrate surface and anchored by a flagging stake at each sampling station; *Metrosideros* litterbag lines were oriented 180° from *Falcataria* litterbag lines at each station. One randomly selected litterbag of each species was retrieved from stations within each site after 0.5, 1, 3, 6, and 12 months of incubation (that is, 10 samples of each litter type/site/incubation period). On retrieval, mineral soil and debris was carefully removed from remaining leaf material, and samples were dried to a constant mass at 70°C. Initial mass of each sample, determined at 50°C, was adjusted for by using a 50°–70°C dry mass correction factor specific to each litter type. After mass determination, the 10 replicate bags of a given leaf species at each harvest were grouped into five pairs, and each pair was composited and analyzed for total C, N, and P (n = 5). In addition, initial C, N, and P concentrations of both litter types were determined from five grab samples taken from the respective pooled litter collections prior to placement in litterbags. Specific leaf area (SLA) of initial litter was determined by calculating the area of grab samples of known mass using an LI-3100 area meter (LI-COR, Lincoln, NE, USA). All tissue samples were ground to pass through a 32-mesh screen (0.5-mm) using a Wiley mill and analyzed for %C and %N by induction furnace methods using a LECO CN-200 Analyzer (LECO, St. Joseph, MI, USA) (Nelson and Sommers 1996; Bremner 1996). Samples were dry-ashed and analyzed in solution using a Jarrell Ash ICP (Thermo Jarrel Ash, Franklin MA, USA) to determine %P (Kuo 1996). Lignin concentration of initial litter samples was also estimated from five grab samples of each litter type. Samples were sequentially extracted using dichloromethane (non–polar extractable), 100°C H_2O (polar extractable), and separated into acid-soluble and acid-insoluble fractions using sulfuric acid, with the former fraction approximating cellulose and the latter approximating lignin or lignin-based material (McClaugherty and others 1985). Fractions were calculated on an ash-free basis and expressed as a percentage of the initial litter material.

Calculations and Statistical Analysis

We estimated annual decomposition constants (k values) for the two litter types at each of the six study sites by fitting mass loss over time to the single negative exponential model (Jenny and others 1949; Olson 1963):

$$M_t/M_o = e^{-kt}$$

where M_t/M_o is the proportion of the original mass remaining at time t; t is the elapsed time in years; and k is the decay rate constant. Because litterbag collections at each time-step were not separated by plot for each litter type and stand type combination, plot-specific k values could not be generated. Instead, k values for treatment combinations were estimated from pooled values of the 10 plots/litter type/forest stand across the five collection periods (that is, 0.5, 1, 3, 6, and 12 month periods) and presented with associated SE values, adjusted

Table 2. Initial Physical and Chemical Characteristics (mean ± 1 SE) of *Metrosideros* and *Falcataria* Leaf Litter Decomposed in Native-dominated and *Falcataria*-invaded Stands of Lowland Wet Forests in Hawai'i

Parameter	*Metrosideros*	*Falcataria*	*P* Value
Specific leaf area ($cm^2\ g^{-1}$)	52 ± 0.42	140 ± 3.4	[b]
%C	51 ± 0.06	47 ± 0.07	[b]
%N	0.32 ± 0.007	1.4 ± 0.003	[b]
%P	0.03 ± 0.001	0.03 ± 0.002	[a]
C:N	157 ± 3.4	33 ± 0.11	[b]
C:P	1821 ± 57	1383 ± 66	[b]
N:P	12 ± 0.20	42 ± 1.9	[b]
Cellulose (%)	43 ± 0.45	38 ± 0.14	[b]
Water-soluble polyphenols (%)	8.0 ± 0.13	2.4 ± 0.02	[b]
Lignin (%)	31 ± 0.81	41 ± 0.17	[b]
Lignin:N	95 ± 2.3	28 ± 0.08	[b]

C, carbon; N, nitrogen; P, phosphorus.
[a] $P < 0.05$.
[b] $P < 0.01$.

R^2 values, and 95% confidence intervals (CI). We evaluated differences among the mean values for % of initial N and P, and initial mass remaining at the end of 1 year using analysis of variance (ANOVA) that enabled different variances for each litter type, stand type, and lava flow age combination, followed by Tukey's (HSD) test on all possible combinations (SAS/STAT software, version 8.02, SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513, USA).

Differences between the initial chemical characteristics of *Metrosideros* and *Falcataria* litter were determined using two-tailed *t*-tests that assumed unequal variance (Systat, version 8.0 for Windows, Systat Software, Incorporated, 501 Canal Blvd, Suite E Point Richmond, CA 94804-2028 USA). In all cases, a significance level of 5% was used. In addition, linear regression analysis was used to investigate relationships between decay rate constants (k) of *Metrosideros* and *Falcataria* leaf litter and (a) annual inputs of N and P mass via litter and (b) indices of surface soil N and P availability (that is, resin-captured soil N and P). Litter inputs of N and P were measured throughout the duration of the decomposition experiment from monthly collections of litter traps located within each stand type on each lava flow; indices of soil N and P availability were measured during the same time period from sets of resin bags incubated within each stand type on each lava flow (Hughes and Denslow 2005).

Results

Initial Litter Characteristics

The initial physical and chemical characteristics of *Metrosideros* and *Falcataria* litter differed substantially with regard to both physical and chemical parameters. Specific leaf area (SLA), N concentration, and N:P ratio were three to four times greater in *Falcataria* than in *Metrosideros* litter. Phosphorus and lignin concentrations were 23% and 32% higher, respectively, in *Falcataria* litter. In addition, C:N and lignin:N ratios were three and four times greater in *Metrosideros* litter relative to *Falcataria* litter; moreover, % polyphenol, % cellulose, % C, and C:P ratios of *Metrosideros* litter were significantly higher as well (Table 2).

Mass Remaining, k Values, and Mean Residence Times

Effect of Forest Stand Type. Both *Metrosideros* and *Falcataria* litter decayed more rapidly in *Falcataria*-invaded stands than in native-dominated stands. Remaining mass of *Metrosideros* and *Falcataria* litter was 13 and nine times greater, respectively, in the native-dominated stand than in the invaded stand on the youngest (48 y.o.) lava flow. Remaining mass of both litter types was two times greater in the native stand than in invaded stands on the 213-y.o. flow and seven times greater in native stands than in invaded stands on the 300-y.o flow (Table 3, and Figure 1).

Effect of Litter Type. Despite substantial differences between *Metrosideros* and *Falcataria* litter types with regard to initial physical and chemical characteristics, in most cases the percentage of litter remaining after 1 year did not differ significantly between litter types within a given forest stand, whether native-dominated or invaded, on the three lava flows (Table 3, and Figure 1). The only exception was in the native stand on the 48-y.o. a'a

Table 3. Percentage of Initial Litter, N, and P Mass (mean ± SE) Remaining of *Metrosideros* and *Falcataria* Leaf Litter after a 1-year Period of Decompostion in Native-dominated and *Falcataria*-invaded Stands on 48-, 213-, and 300-Year-Old Lava Flows

Stand/Leaf Tissue Type	Mass Remaining	95% CI		% N Remaining	95% CI		% P Remaining	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
48-year-old a'a lava									
Native/*Metrosideros*	72.5 ± 1.6 c	9.0	76.0	106.3 ± 2.3 e, f	101.1	111.4	48.6 ± 1.0 b	46.2	50.9
Native/*Falcataria*	57.9 ± 1.8 b	53.9	61.8	86.4 ± 2.6 c, d	80.5	92.4	52.9 ± 1.6 b	49.3	56.5
Invaded/*Metrosideros*	5.5 ± 0.9 a	3.6	7.5	21.9 ± 3.4 a, b	12.0	28.1	13.0 ± 2.1 a	7.1	16.7
Invaded/*Falcataria*	6.3 ± 1.3 a	3.4	9.2	10.3 ± 2.1 a	5.5	15.1	11.6 ± 2.4 a	6.2	17.1
213-year-old pāhoehoe lava									
Native/*Metrosideros*	57.2 ± 3.1 b, d	50.1	64.3	117.8 ± 6.4 f	105.9	135.6	72.4 ± 4.0 c	65.1	83.4
Native/*Falcataria*	59.7 ± 2.7 b, c	53.6	65.9	92.7 ± 4.2 d, e	83.2	102.3	66.9 ± 3.0 c, d	60.0	73.8
Invaded/*Metrosideros*	27.6 ± 2.9 e	21.0	34.2	131.7 ± 14.0 d, e, f	100.0	163.3	68.2 ± 7.2 b, c, d	51.8	84.6
Invaded/*Falcataria*	28.9 ± 6.4 a, d, e	14.5	43.2	50.7 ± 11.2 b, c, g	25.5	75.9	58.2 ± 12.8 b, c, d	29.2	87.1
300-year-old a'a lava									
Native/*Metrosideros*	31.3 ± 3.0 e	24.6	38.0	100.8 ± 9.6 d, e, f	80.5	119.3	49.2 ± 4.7 b, d	40.3	59.3
Native/*Falcataria*	36.7 ± 3.9 d, e	27.9	45.5	56.4 ± 6.0 g	42.8	70.0	50.9 ± 5.4 b, d	38.6	63.1
Invaded/*Metrosideros*	4.2 ± 1.7 a	0.3	8.1	16.2 ± 7.2 a, b	1.4	34.3	7.7 ± 3.4 a	0.6	16.4
Invaded/*Falcataria*	5.3 ± 2.0 a	0.9	9.7	8.7 ± 3.2 a	1.4	16.0	7.5 ± 2.8 a	1.2	13.8

N, nitrogen; P, phosphorus; CI, confidence interval.
For a given parameter, mean values that share the same letter did not differ significantly from one another ($P < 0.05$).

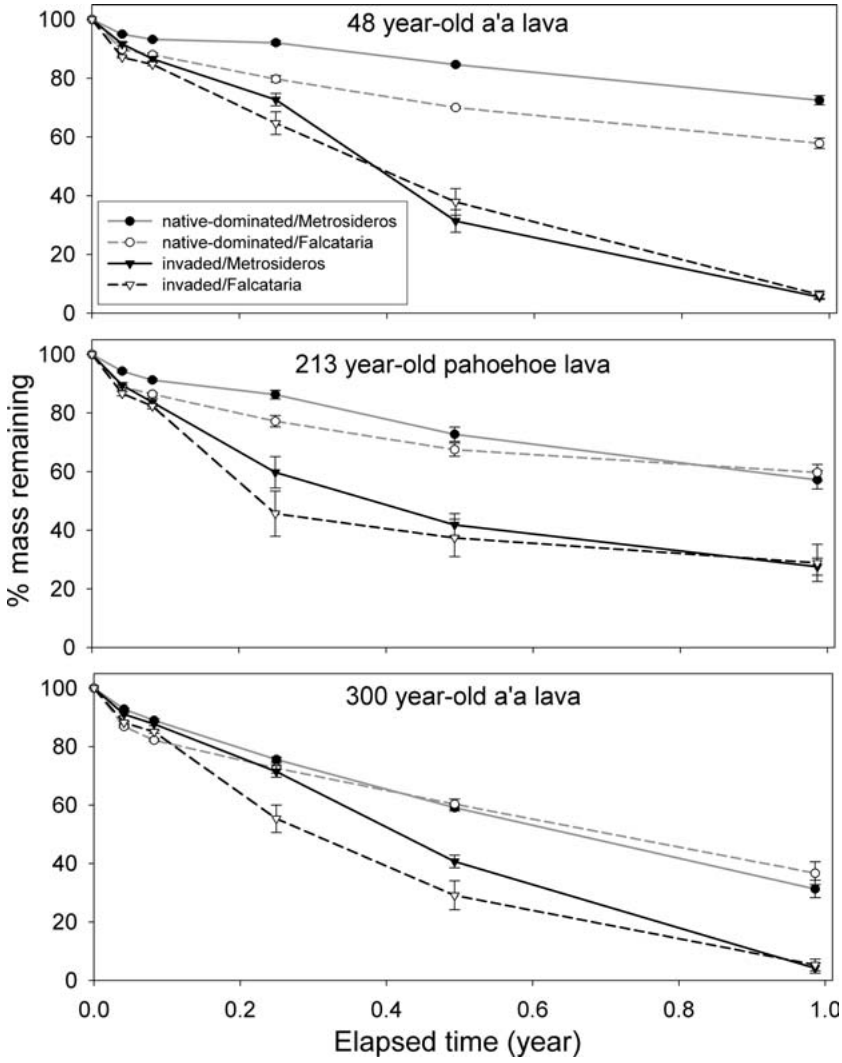

Figure 1. Percent of initial mass of *Metrosideros* and *Falcataria* leaf litter remaining (mean ± 1 SE) during 1-year incubations in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-year-old lava flows in lowland wet forests of Hawai'i.

flow, where significantly less *Falcataria* litter mass remained (58% of initial mass) compared to that of *Metrosideros* litter (73% of initial mass) after 1 year.

Effect of Flow Type and Age. Flow type and age affected decomposition rates, but the effects were species- and forest stand–specific. For *Metrosideros* litter decomposed in native stands, mass remaining was highest on the 48-y.o. a'a flow, intermediate on the 213-y.o. pāhoehoe flow, and lowest on the 300-y.o. a'a flow. For *Falcataria* litter decomposed in the native stands, significantly more mass remained on the pāhoehoe and younger a'a flows than on the older a'a flow. In invaded stands, mass remaining of *Metrosideros* litter on the two a'a flows was significantly less than that left on the intermediate-aged pāhoehoe flow. The mass of *Falcataria* litter remaining after 1 year did not differ among invaded stands on the three lava flows (Table 3, and Figure 1).

Decay rate constants (k) and mean residence times (MRT = 1/k) of both species followed patterns very similar to % mass remaining values; both parameters spanned an order of magnitude among combinations of species/forest stand/lava flow type. Decay rate constants were as low as 0.30 (3.32-y MRT) for *Metrosideros* litter in the native stand on the 48-y.o. a'a flow and as high as 3.49 (0.29-y MRT) for *Metrosideros* litter in the invaded stand on the 300-y.o. a'a flow (Table 4). Moreover, k-values of both species tended to be higher, and MRT values lower, in invaded stands than in native stands of all three lava flows. Both species decomposed at similar rates within a given stand and flow, except for the native stand on the youngest (48-y.o.) a'a flow, where *Falcataria* litter decayed 70% faster than *Metrosideros* litter (Table 4). Lastly, decay constants for both species were generally greater, and MRT values smaller, in invaded stands

Table 4. Decomposition Rate Constants (k) for Mass Loss (mean ± 1 SE) and Mean Residence Time (1/k) for *Metrosideros* and *Falcataria* Leaf Litter Decomposed in Native-dominated and *Falcataria* -invaded Stands on Three Lava Flows in Eastern Hawai'i.

			95% CI		
Lava Flow/Stand/Species	k (y^{-1})	adj. R^2	Lower	Upper	MRT (y)
48-year-old a'a lava					
Native stand/*Metrosideros*	0.30 ± 0.01	0.91	0.28	0.33	3.32
Native stand/*Falcataria*	0.51 ± 0.02	0.91	0.47	0.56	1.94
Invaded stand/*Metrosideros*	3.04 ± 0.11	0.93	2.83	3.26	0.33
Invaded stand/*Falcataria*	2.97 ± 0.15	0.86	2.66	3.28	0.34
213-year-old pāhoehoe lava					
Native stand/*Metrosideros*	0.56 ± 0.03	0.84	0.50	0.63	1.78
Native stand/*Falcataria*	0.49 ± 0.04	0.74	0.41	0.56	2.04
Invaded stand/*Metrosideros*	1.37 ± 0.10	0.76	1.17	1.56	0.73
Invaded stand/*Falcataria*	1.50 ± 0.20	0.47	1.09	1.91	0.67
300 year-old a'a lava					
Native stand/*Metrosideros*	1.19 ± 0.05	0.92	1.09	1.28	0.84
Native stand/*Falcataria*	1.00 ± 0.06	0.82	0.88	1.12	1.00
Invaded stand/*Metrosideros*	3.49 ± 0.17	0.87	3.14	3.84	0.29
Invaded stand/*Falcataria*	3.41 ± 0.19	0.84	3.03	3.79	0.29

MRT, mean residence time; CI, confidence interval.

on a'a flows than in invaded stands on pāhoehoe flows.

Nitrogen and Phosphorus Immobilization and Release from Litter

Effect of Forest Stand Type. The fraction of initial N remaining after 1 year for litter of both species generally was smaller for invaded than native stands (Table 3, and Figure 2). The only exception was that forest stand type did not affect the fraction of N remaining in *Metrosideros* litter on the pāhoehoe flow. The fraction of initial P remaining after 1 year was also less for invaded than native stands, but only on a'a flows. Stand type had no effect on the fraction of P remaining for either species on the pāhoehoe flow.

Effect of Litter Type. In native-dominated stands, *Falcataria* litter released more of its initial N than *Metrosideros* litter (Figure 2). However, invaded stands growing on a'a tended to mute species differences in N retention to the point where they were no longer statistically significant (Table 3). Species had no effect on the fraction of initial P remaining after 1 year, whether in native-dominated or invaded stands.

Effect of Lava Flow Type and Age. Flow effects on N dynamics were variable (Table 3). For *Metrosideros* litter in native-dominated stands, there was no flow effect, in terms of either flow age or type, on the fraction of initial N remaining after 1 year. For *Falcataria* litter, flow age had an effect in native-dominated stands: the fraction of initial N remaining was significantly smaller on the 300-y.o. flow than on the younger flows. Invasion, however, resulted in greater release of N from *Metrosideros* and *Falcataria* litter on a'a than pāhoehoe lava, but the age of a'a lava had no effect on N retention by either species. In general, litter of both species retained more P on pāhoehoe than on a'a lava, but the age of the a'a flow had no significant effect on P retention after 1 year (Figure 3).

Relationships between Litter Inputs and Decomposition Rates

Decomposition rates (k constants) of both species were positively correlated to inputs of N and P mass in litterfall (Figures 4a, and b); as litter inputs increased with *Falcataria* invasion, decomposition rate constants increased as well. Decomposition rates were also positively correlated with indices of soil N and P availability (Figure 4c, and d).

Discussion

Ecosystem processes such as decomposition are controlled as much by individual plant species as by inherent edaphic or climatic factors (Hobbie 1992). If invasive species are able to alter characteristics such as stand-level nutrient supply, they should also alter rates of decomposition. Our results indi-

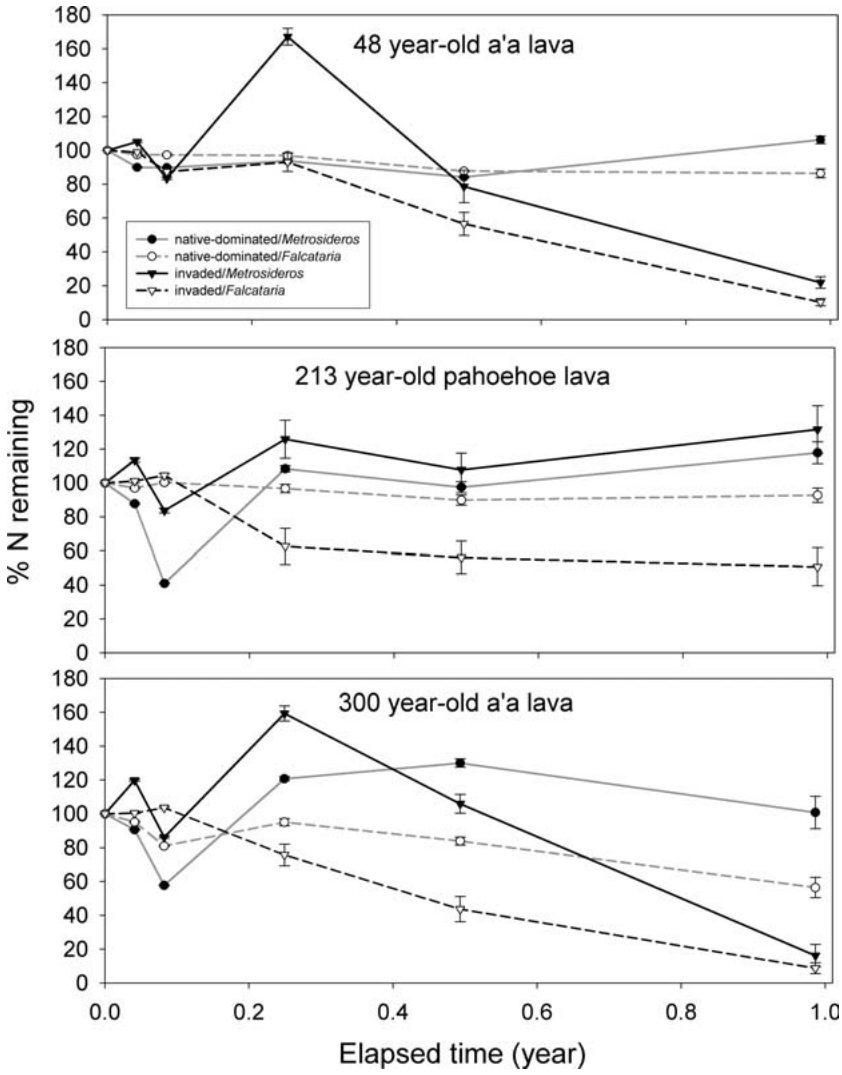

Figure 2. Percent of initial nitrogen (N) remaining (mean ± 1 SE) in decomposing *Metrosideros* and *Falcataria* leaf litter during 1-year incubations in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-year-old lava flows in lowland wet forests of Hawai'i.

cate that invasion of *Falcataria* into the N-limited lowland wet forests studied here does exactly that: Invasion not only resulted in increased inputs of N and P via litterfall and increased soil N and P availability (Hughes and Denslow 2005), it also increased rates of decomposition. *Falcataria* and *Metrosideros* litter decayed six and 10 times faster, respectively, in the invaded stand on the 48-y.o. flow compared to its native counterpart, and both species decomposed two to three times faster in invaded than native stands on the 213- and 300-y.o. lava flows.

These results agree with other studies that document invasion-mediated changes in decomposition rates (Vitousek and Walker 1989; Mack and D'Antonio 2003). Moreover, these patterns are similar to the results of previous research demonstrating systematic increases in decomposition rates with increasing quantities of N and P in litterfall and decreasing stand-level N- and P-use efficiencies in native-dominated montane forests (Vitousek and others 1997; Herbert and Fownes 1999; Ostertag and Hobbie 1999). Thus, invasion by *Falcataria* produces, in a relatively short time, changes in ecosystem processes, including decomposition, that are similar to changes that take place over long successional and soil-development intervals.

The finding that decomposition rates increased in concert with stand-level increases in nutrient availability and cycling initiated and sustained by *Falcataria* invasion contrasts with the results of Rothstein and others (2004), who found that stand type had little or no effect on decomposition in native- and non-native-dominated montane rainforests of Hawai'i. This contrast is likely a result of differences in inherent characteristics of both the nonnative tree species and the soil substrate of the

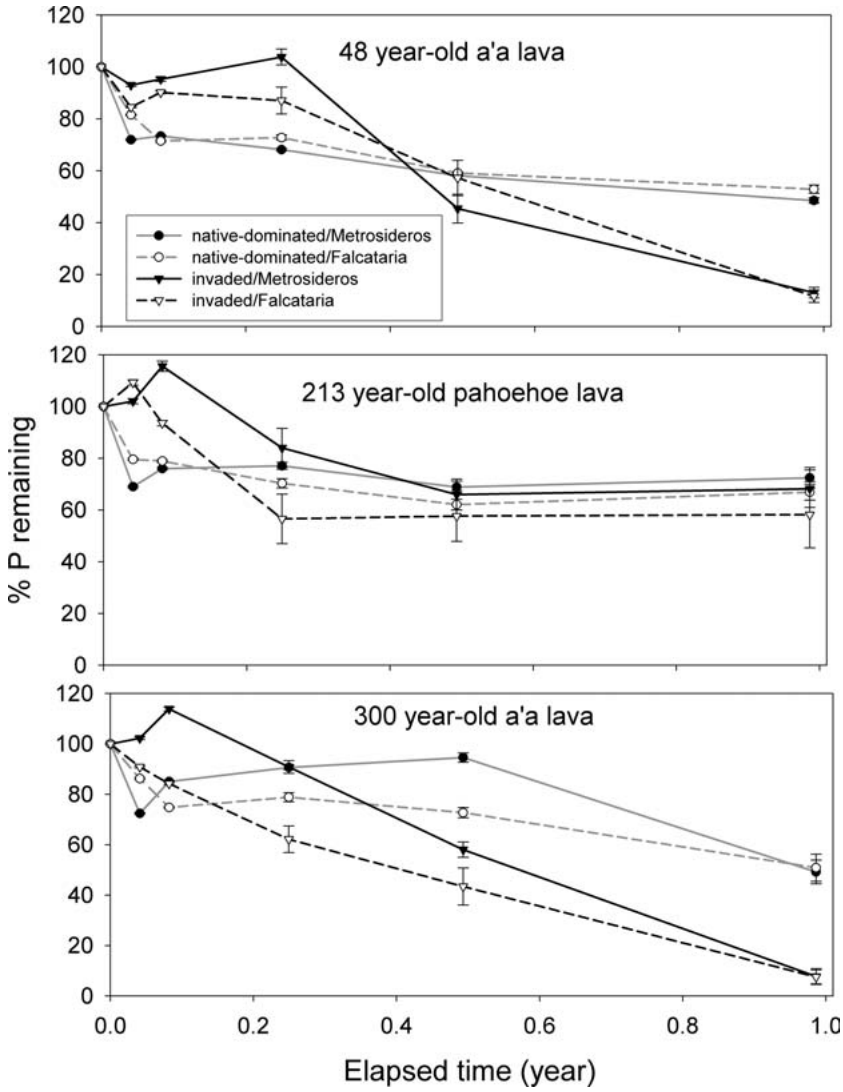

Figure 3. Percent of initial phosphorus (P) remaining (mean ± 1 SE) in decomposing *Metrosideros* and *Falcataria* leaf litter during 1-year incubations in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-year-old lava flows in lowland wet forests of Hawai'i.

respective studies. Productivity on the young lava flows (that is, less than 400 years old) studied here are N-limited (Vitousek and others 1993), and *Falcataria* invasion dramatically increases N supply and cycling (Hughes and Denslow 2005). The forests studied by Rothstein and others (2004) occurred on soils derived from tephra-covered, 5,000-year-old lava flows in which both N and P are relatively more abundant than in the young soils of Puna (Vitousek 2004). In addition, although litter chemistry differed between *Metrosideros* and *Fraxinus*, the latter is not an N_2-fixing species capable of increasing N inputs far above those of the native-dominated forest it has replaced.

As an N_2-fixing species, *Falcataria* is expected to produce higher-quality litter that decomposes more readily than litter from nonfixing species such as *Metrosideros*. Initial characteristics of the two litter types bore this out; specific leaf area and %N and %P were higher, and polyphenol concentrations, C:N, C:P, and lignin:N were lower, in *Falcataria* litter than in *Metrosideros* litter. A suite of invasive species common to Hawaiian forests have been shown to produce higher-quality litter (for example, higher concentrations of soluble C and lower concentrations of condensed tannins) than that of selected native species, and such differences correspond to faster decomposition rates for those invasive species relative to the natives (Allison and Vitousek 2004). Decomposition rates have also been shown to be inversely related to initial litter lignin:N ratios (Mellilo and others 1982), ratios that in this study were significantly higher for *Metrosideros* litter than for *Falcataria* litter. Consequently, we expected *Falcataria* litter to decompose faster than *Metrosideros* litter at a given site. Instead we found that decay rates were generally similar for both species. Similarly, Smith and others (1998)

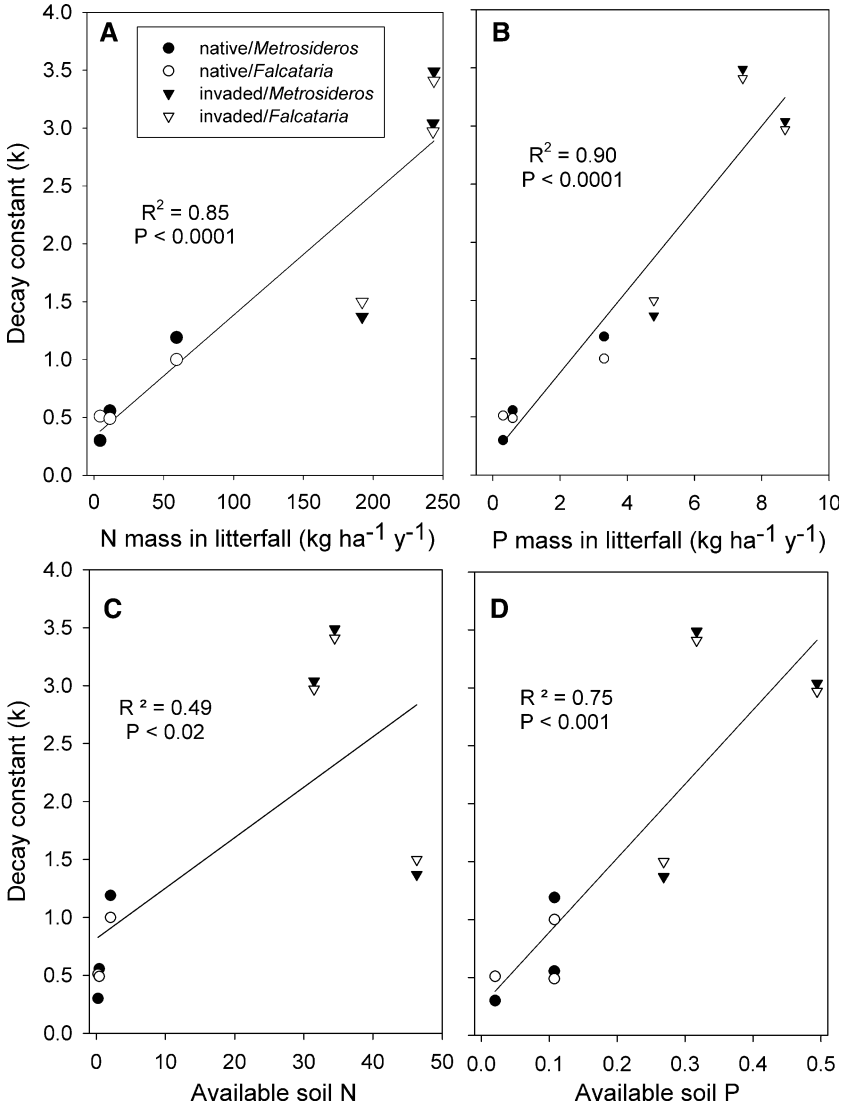

Figure 4. Relationship of decomposition rate constants (k) of *Metrosideros* and *Falcataria* leaf litter to stand-level **A** annual litter nitrogen (N) input, **B**, annual litter phosphorus (P) input, **C**, resin-captured soil N, and **D** resin-captured soil P in native-dominated and *Falcataria*-invaded stands on 48-, 213-, and 300-year-old lava flows in lowland wet forests of Hawai'i. Annual litter input and resin-captured N and P values for each stand are from Hughes and Denslow (2005).

found no relation between initial litter chemistry and decay rates in field experiments within lowland primary forest and plantation stands of Amazonia despite broad variation in the initial chemistry of the litter types deployed (that is, C fractions, and N and polyphenol concentrations).

Possible explanations for why the two species decomposed at roughly the same rate in the majority of forest stands may be found in differences in their C quality and N concentration. High litter lignin concentrations generally correspond to slower decomposition rates by affecting the availability of C and nutrients to decomposer communities (Aber and Mellilo 1982; Berendse and others 1987; Berg and McClaugherty 1989). In experiments conducted in montane forests of Hawai'i, Hobbie (2000) found that decomposition rates were inversely related to initial concentrations of lignin, which ranged from 12% to 18%, whereas litter N concentrations were poorly correlated with decomposition rates even in sites where N availability limited aboveground net primary productivity (Ostertag and Hobbie 1999; Hobbie and Vitousek 2000). The approximate 50% change in lignin noted by Hobbie (2000) is comparable to the 30% difference in lignin concentrations between *Falcataria* and *Metrosideros* litter types in this study. This difference, combined with significantly greater cellulose concentrations in *Metrosideros* litter, might counteract the effects of three-fold greater concentrations of N in *Falcataria* than *Metrosideros* litter and account for similarities in decay rates of the two species. Alternatively, Berg (2000) presented evidence, and possible mechanisms, whereby litter with high lignin and N concentrations may decompose quite slowly, at least during the latter stages of decomposition in temperate ecosystems. In our study, initial concentrations of both lignin

and N were significantly higher in *Falcataria* than *Metrosideros* litter; such differences, in combination, may account for the similar decomposition rates of the two litter types at five of the six study sites. Palm and Sanchez (1991) suggested that high polyphenol concentrations, rather than high lignin concentrations, may constrain decomposition rates of tropical legume litter. Our results did not support that suggestion; polyphenol concentrations were over two times higher in *Metrosideros* litter than in *Falcataria* litter, yet patterns of mass loss were similar for the two litter types in most cases.

In contrast to mass loss, which was primarily controlled by differences between native and invaded forest stands, both litter and stand type influenced accumulation and release of N from litter. Although the large release of N from litter of both species in invaded stands relative to native stands was in part a simple manifestation of more rapid mass loss in the former sites, substantial differences in soil N availability and demand between sites also likely played a role (Hughes and Denslow 2005). Net accumulation of N in decomposing litter resulting from microbial immobilization is indicative of N limitation within an ecosystem (Aber and Mellilo 1991; Prescott 1995), whereas net N release corresponds to N availability in excess of microbial needs. The sole exception to this general pattern (that is, accumulation in native stands, release in invaded stands) occurred on the pāhoehoe flow, where decomposing *Metrosideros* litter accumulated more N in the invaded forest than in the native forest.

Differences in net N release between the two species within given stands underscores the importance of litter chemistry in controlling soil N dynamics, particularly in the N-limited, native-dominated sites. In each of the native stands, as well as the invaded stand on the pāhoehoe flow, net N release from *Falcataria* litter was significantly greater than N release from *Metrosideros* litter. In fact, after 1 year of decomposition, *Metrosideros* litter had as much or more N as was found at the start of the study. In contrast, both species released substantial amounts of N (78% to 91% of initial) in invaded stands on the a'a flows, where N was relatively abundant and unlikely to constrain the decomposer activity. It should be noted, however, that in these latter cases where net release of N—expressed as a percentage of the initial values—was roughly similar for the two litter types, the initial N content of *Falcataria* litter was over four times greater than that of *Metrosideros* litter. Such a difference resulted in substantially greater absolute amounts of N released from *Falcataria* litter for a given percent change from the initial litter N values, and provides a mechanism for increased N availability within invaded stands.

The results of the present study and those of Hughes and Denslow (2005) show that *Falcataria* invasion changes several distinct, but linked, ecosystem parameters, that collectively create a self-reinforcing mechanism to increase the cycling and availability of N in lowland forests. First, the replacement of *Metrosideros* by *Falcataria* resulted in four- to 55-fold increases in N inputs in litterfall. Second, both decomposition and net N release during decomposition were significantly greater in invaded than native-dominated stands. Lastly, *Falcataria*-invaded stands had 17- to 121-fold greater availability of soil N than native stands. A similar self-reinforcing mechanism has been postulated should the native tree fern *Cibotium glaucum* be replaced by the introduced tree fern *Sphaeropteris cooperi* in montane forests of Hawai'i (Allison and Vitousek 2004). *S. cooperi* not only produces much more litter than *C. glaucum*, its litter is more nutrient-rich and nutrient release is consequently much more rapid.

Although statistically significant, initial P concentrations were only 20% greater in *Falcataria* than *Metrosideros* litter and whereas P dynamics differed somewhat between species within given stands during early stages of decomposition, by the end of 1 year differences in the net release of P between the two species were small. Stand type, rather than litter type, controlled P dynamics on a given lava flow. Generally, net release of P from litter of both species was significantly greater on invaded than native-dominated sites. We suspect that P availability accounted for this difference. Increased P release during decomposition has been associated with stand-level increases in P availability (Vitousek and Farrington 1997); and at our study sites, inputs of P in litterfall and concentrations of resin extractable soil P were indeed greater in invaded stands relative to native stands (Hughes and Denslow 2005). *Falcataria* invasion might also enhance the release of P from decomposing litter by stimulating microbial production of phosphatase, an enzyme involved in P mineralization (Duff and others 1994). Soil phosphatase concentrations typically increase in response to either low P availability or high P demand (Olander and Vitousek 2000). Soil phosphatase levels were two to four times greater in the invaded than the native stands that we studied (Allison and others 2006), although it is not clear whether such changes were the direct effect of *Falcataria* invasion (that is, root exudates) or an indirect effect of invasion on microbial production of that enzyme.

In addition to exhibiting strong differences between native and invaded sites, patterns of mass loss and N and P accumulation or release also differed notably between the pāhoehoe substrate and both a'a substrates, particularly in invaded stands. Decay rates and release of both N and P from decomposing litter were generally lower on the pāhoehoe substrate than the two a'a substrates. This was likely due to differences in substrate texture; although both lava types are chemically quite similar (Moore and Trusdell 1991), the a'a lava flows consist of rough-textured, blocky rocks and the pāhoehoe lava flows consist of relatively smooth planar surfaces. As a consequence, the surface area available for mineral weathering is lower for pāhoehoe than a'a, and the availability of rock-derived nutrients such as P should be lower as well. Results of fertilization experiments conducted in early successional montane forests on young a'a and pāhoehoe lava flows (Raich and others 1996) suggest that productivity was more nutrient-limited on pāhoehoe flows compared to a'a flows and that forest productivity on both flow types was more nutrient-limited than similarly aged tephra, which consists of a mix of easily weathered cinder and fine-ash deposits. Our results suggest similar lava substrate controls on decomposition dynamics such that nutrient release—particularly of P—would be greater on more readily weathered a'a substrates than on the pāhoehoe substrate.

Clearly, our results provide evidence for stand-level control of decomposition rates and the role that *Falcataria* invasion plays in altering stand-level characteristics. Litter inputs and soil availability of both N and P increased dramatically with *Falcataria* invasion (Hughes and Denslow 2005), and those increases were positively correlated with increased decomposition rates in invaded sites (Figure 4). In conjunction with these increases, *Falcataria* invasion has also altered the composition (that is, fungal–bacterial ratios) and activity (that is, enzyme production) of the decomposer community (Allison and others forthcoming)—an alteration that would be expected to affect nutrient availability and cycling (González and Zou 1999; Liu and Zou 2002). In tree plantations on Hawai'i Island, Zou (1998) documented significantly more earthworms within stands of *Falcataria* than stands of *Eucalyptus saligna*, increases that coincided with increased litter production and higher N concentrations of fine litter in *Falcataria* stands. In addition, invasion by *Myrica*, another N_2-fixing species, increased macro-invertebrate (that is, earthworm) populations in montane forests of Hawai'i (Aplet 1990), and those increases coincided with higher rates of decomposition (Vitousek and Walker 1989). Invasion by nonnative shrub species in temperate forest ecosystems also led to substantial changes in both microbial community structure and function (Kourtev and others 2002). We suspect that *Falcataria* invasion leads to similar increases in macro-invertebrate populations, including amphipods (Taltridae), which preliminary evidence indicates were more abundant in *Falcataria*-invaded stands than in their native-dominated counterparts (P. Klawinski unpublished). Our results suggest that the proximal causes for increased decomposition rates in *Falcataria*-invaded stands are likely the dual and linked increases in nutrient inputs from albizia litterfall (Hughes and Denslow 2005) and changes in soil biota communities (Zou and Bashkin 1998; Allison and others 2006).

Overall, these findings demonstrate the degree to which an invasive species such as *Falcataria* increases rates of decomposition well above those of native-dominated forest stands. They also show that increased decomposition rates may not necessarily be influenced as much by species differences in litter chemistry as by large and sustained increases in nutrient inputs via litterfall and coincidental changes in soil biota that result from stand-level replacement of *Metrosideros* by *Falcataria*. In this case, the biotic and abiotic characteristics of the stand in which the litter was located proved to be stronger determinants of decomposition than the inherent physical and chemical characteristics of that litter. As shown here and in previous studies (Ehrenfeld and others 2001; Vitousek and Walker 1989), invasive species such as *Falcataria* have the capacity to establish positive feedbacks that affect numerous ecosystem processes, thereby utterly transforming the way these forests function and develop. Rather than thinking of them as native ecosystems compromised to a lesser or greater degree by one or more nonnative species, these invaded and transformed systems may best be considered as ''new forests'', in the sense described by Lugo and Helmer (2004), in that they are fundamentally different—both in structure and function—from the native ecosystems they have replaced.

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