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Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i

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Abstract Physiological traits that contribute to the establishment and spread of invasive plant species could also have impacts on ecosystem processes. The traits prevalent in many invasive plants, such as high specific leaf areas, rapid growth rates, and elevated leaf nutrient concentrations, improve litter quality and should increase rates of decomposition and nutrient cycling. To test for these ecosystem impacts, we measured initial leaf litter properties, decomposition rates, and nutrient dynamics in 11 understory plants from the Hawaiian islands in control and nitrogen + phosphorus fertilized plots. These included five common native species, four of which were ferns, and six aggressive invasive species, including five angiosperms and one fern. We found a 50-fold variation in leaf litter decay rates, with natives decaying at rates of 0.2–2.3 year^{-1} and invaders at 1.4–9.3 year^{-1}. This difference was driven by very low decomposition rates in native fern litter. Fertilization significantly increased the decay rates of leaf litter from two native and two invasive species. Most invasive litter types lost nitrogen and phosphorus more rapidly and in larger quantities than comparable native litter types. All litter types except three native ferns lost nitrogen after 100 days of decomposition, and all litter types except the most recalcitrant native ferns lost >50% of initial phosphorus by the end of the experiment (204–735 days). If invasive understory plants displace native species, nutrient cycling rates could increase dramatically due to rapid decomposition and nutrient release from invasive litter. Such changes are likely to cause a positive feedback to invasion in Hawai'i because many invasive plants thrive on nutrient-rich soils.

Keywords Litter decomposition · Nitrogen · Phosphorus · Invasive species · Fertilization

Introduction

Although human activities have increased invasion rates worldwide, island ecosystems are particularly susceptible to plant invasions due to low competitive ability of island species, lack of invader-specific pathogens and herbivores, and/or greater propagule pressure (Denslow 2003; Dewalt et al. 2004; Lonsdale 1999; Mack et al. 2000; Vitousek et al. 1995b). Humans and pre-existing invasive species can also alter disturbance regimes, thereby facilitating new invasions (Lonsdale 1999; Mack and D'Antonio 1998; Simberloff and Von Holle 1999). In the Hawaiian Islands, these impacts are readily apparent as hundreds of exotic plants have significantly transformed native ecosystems (Vitousek et al. 1987; Wester 1992). For some invaders, such as pyrophytic grasses and the nitrogen-fixer *Myrica faya*, the ecosystem impacts are dramatic and well understood (Hughes et al. 1991; Mack and D'Antonio 2003; Vitousek and Walker 1989), but for most species the ecosystem consequences of invasion are unknown.

One likely connection between invasion and ecosystem impact is through the physiological characteristics of invasive species. In Hawai'i and elsewhere, invaders sometimes exhibit a common suite of traits that allows them to become established and dominate native plant communities (Baruch and Goldstein 1999; Rejmanek and Richardson 1996). In a study of 34 native and 30 invasive species in Hawai'i, Baruch and Goldstein (1999) found that invaders had significantly higher specific leaf area (SLA) and photosynthetic rates and lower leaf construction costs than natives. These traits may contribute to faster growth rates for invaders (Lambers and Poorter 1992; Reich et al. 1997), thereby conferring a competitive advantage over native species.

Because leaf physiological traits also directly affect litter quality and decomposition, invasive species have the potential to affect ecosystem processes through their litter

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inputs. In eastern deciduous forests, certain invasive understory shrubs can increase soil pH, nitrification rates, and litter inputs to soil, thereby altering the soil environment to their advantage (Ehrenfeld et al. 2001). Such positive feedbacks to invasion are common in many ecosystems, although negative feedbacks are also well documented (Ehrenfeld 2003).

The direction of an invasion feedback may depend on soil nutrient availability—in nutrient-poor Hawaiian ecosystems, invasion may stimulate nutrient cycling and lead to a positive feedback. For many Hawaiian invaders, high SLA and low leaf construction costs result in thin, soft leaves that should be more accessible to decomposers in the soil. High rates of growth and photosynthesis require greater concentrations of nitrogen (N) and phosphorus (P) in invader leaves to support photosynthetic machinery and metabolism, which should lead to higher litter nutrient content (Baruch and Goldstein 1999). Litter quality may also improve relative to native species if invaders are less nutrient-conservative and retranslocate a lower fraction of leaf nutrients during senescence. Finally, rapid growth rates and leaf turnover in Hawaiian invasive species could amplify any differences in litter quality through increases in litter production.

We hypothesized that the physiological characteristics of invasive plants would affect their litter chemistry and lead to differences in litter decomposition and nutrient cycling. To test this prediction, we compared the decomposition rates and N and P dynamics of leaf litter from five native and six invasive plant species of Hawaiian wet forests. We also examined the effect of N+P fertilization on litter decomposition and nutrient dynamics, because invasive plants often establish in nutrient rich soils (Huenneke et al. 1990; Ostertag and Verville 2002) and could increase nutrient availability through their litter inputs. If fertilization preferentially accelerates the decomposition and nutrient cycling of invasive litter, then we would expect a positive feedback where invasion facilitates colonization by other plants with high nutrient demands and growth rates (Carino and Daehler 2002).

Materials and methods

Choice of study species

Although our species are not necessarily a representative sample of native and exotic Hawaiian flora, we deliberately selected some of the most abundant native plants and aggressive invaders of forest understories. We chose four native fern species because Hawaiian wet forest understories are generally fern-dominated, with the exact species composition varying according to geologic age (Mueller-Dombois 1992). Native *Cibotium* tree ferns are dominant or sub-dominant species across a wide range of mesic-wet Hawaiian forests, especially on younger substrates (Kitayama and Mueller-Dombois 1995; Kitayama et al. 1995), and may contribute up to 35% of litter production (Vitousek et al. 1995a). We chose the native fern *Dicranopteris linearis* because it forms dense monospecific stands, especially on young substrates, and may contribute up to 74% of net primary productivity in some locations (Russell et al. 1998). The remaining native ferns were *Diplazium sandwichianum*, common on intermediate-aged, rich soils, and *Elaphoglossum alatum*, which is locally abundant on highly weathered soils of Kauai (Kitayama and Mueller-Dombois 1995). Few native angiosperms dominate Hawaiian understories to the extent of ferns, so we selected the shrub *Vaccinium calycinum* as the sole representative of native understory angiosperms. Members of the genus *Vaccinium* are typical examples of the low-nutrient, slow-growth habit of many native Hawaiian angiosperms.

In contrast to the native flora, the vast majority of invasive plant species are angiosperms (Vitousek et al. 1987), and invasions in mesic-wet Hawaiian ecosystems usually cause a shift from fern to angiosperm dominance in the understory. Therefore we collected litter from the invasive ginger *Hedychium gardnerianum*, the invasive grass *Setaria palmifolia*, and three members of the family Melastomataceae, all of which aggressively invade native ecosystems in Hawai’i (Dewalt et al. 2004; Medeiros et al. 1992; Ostertag and Verville 2002; Smith 1992; Wagner et al. 1999; Wester and Wood 1977; S. Allison, personal observation). Relative to angiosperms, few invasive fern species threaten Hawaiian ecosystems. However, we chose to study litter from the Australian tree fern *Sphaeropteris cooperi* because it aggressively replaces *Cibotium* tree ferns on the island of O’ahu (Durand and Goldstein 2001b; Medeiros et al. 1992).

Litter collection

We collected leaf litter in July 2000, from sites on the islands of Hawai’i, O’ahu, and Kauai. Samples of unsenesced tissue were also collected at each site to determine SLA and nutrient retranslocation efficiencies. Although the foliar chemistry of some of our study species varies with substrate age (Vitousek et al. 1995c), none of our litter collections were done in nutrient-rich sites. We measured the surface area of fresh leaves with a Delta-T leaf area meter and used the oven dry mass (70°C) of the leaf sample to calculate SLA. Litter was collected by harvesting senesced leaves from the plant or retrieving recently fallen leaves from the ground. Each litter sample was air dried to constant mass and thoroughly homogenized. Subsamples were withdrawn to determine air dry/oven dry (70°C) mass conversion ratios and initial litter properties. The remaining litter was divided into 2 g subsamples and placed in 1 mm mesh fiberglass window screen bags, which allowed access by most soil invertebrates (Hobbie and Vitousek 2000).

Site description and design

In September 2000, we deployed litter bags in a wet tropical forest site at 150 m elevation on the Island of Hawai'i, USA (19°40′N, 155°4′W). Rainfall is abundant (3,500–4,500 mm year^{-1}) and aseasonal (Giambelluca et al. 1986), mean annual temperature is 23°C, and the substrate is 1,400 year old basalt with shallow, poorly developed soils and a patchy litter layer and root mat. The vegetation is a closed-canopy forest with a mixture of native and exotic trees and understory plants, and the dominant canopy species are *Psidium cattleianum* (exotic) and *Metrosideros polymorpha* (native).

Five litterbags of each litter type were placed in four fertilized and four control plots (5×5 m) in a flat, 1 ha area. Fertilizer was applied at a rate of 100 kg ha^{-1} N and 100 kg ha^{-1} P at the initiation of the experiment and 50 kg ha^{-1} N and 50 kg ha^{-1} P at 4, 8, and 16 months after initiation (Vitousek and Farrington 1997). Litter collections occurred at 14, 47, 86, 152, and 204 days (rapidly decaying species), 14, 47, 86, 204, and 402 days (intermediate species), or 14, 86, 204, 402, and 735 days (slowly decaying species). After removing roots and soil particles, litter was oven dried (70°C), weighed, and ground in a Wiley mill for nutrient analyses.

Litter chemistry

We analyzed total N and P content in litter and plant tissue samples using Kjeldahl digestion followed by colorimetric assay on an Alpkem autoanalyzer (OI Analytical, Wilsonville, Ore., USA). Samples were run with NIST 1515 apple leaves as standards, and recoveries (mean ± SD) were 95±8% for N and 96±9% for P. We calculated percent N and P retranslocation during leaf senescence as [1−(litter nutrient concentration)/(foliar nutrient concentration)]×100.

Statistical analyses

To facilitate comparison among litter decay rates, we used SAS PROC NLIN (SAS 2001) to determine annual litter decomposition constants (*k*-values) for each litter type in each plot by fitting mass loss over time to the negative exponential model

$$M_t = M_0\,\mathrm{e}^{-kt}$$

where M_0 is the initial litter mass and M_t is the mass at time t in years (Olson 1963). These *k*-values were then log-transformed to improve normality and subjected to analysis of variance (ANOVA, SAS PROC GLM) with fertilization and litter type as fixed factors. Because we were interested in comparisons of natives versus invaders and ferns versus angiosperms, we grouped the 11 litter types into these categories and ran separate ANOVAs. We used repeated-measures ANOVA (SAS PROC MIXED, spatial power covariance structure) to test for the effects of fertilization, litter type, and sampling date on litter N and P concentrations. We also present litter nutrient content as a percentage of the initial value to show net litter nutrient retention or loss over time. These nutrient contents were also subjected to repeated-measures ANOVA. P concentrations and litter P contents were log- and square root-transformed, respectively, prior to analyses to improve normality.

Results

Litter decay rates

Litter decomposition rates varied nearly two orders of magnitude by litter type ($F_{10,66}$=172.3, P<0.001), with exponential decay constants from <0.2 to >8 year^{-1} (Table 1). Decomposition rates were significantly greater for invasive than native species ($F_{1,84}$ =110.6, P<0.001), and significantly greater in angiosperms than in ferns

Table 1 Mean (± SE) decomposition rate constants of fern and angiosperm litter in control and fertilized plots *n*=3–4. Significant fertilizer effect denoted by * P<0.10, ** P<0.01. Data from Allison and Vitousek (2004)

Litter type	*k*-value (year^{-1})			
	Control mean(± SE)		Fertilized mean(± SE)	
Ferns				
C. glaucum (Cyatheaceae) (Native)	0.50	(0.07, 0.06)	0.56	(0.08, 0.07)
D. linearis (Gleichenaceae)(Native)	0.18	(0.04, 0.03)	0.31	(0.08, 0.07)**
D. sandwichianum (Athyriaceae) (Native)	1.12	(0.17, 0.15)	1.10	(0.08, 0.08)
E. alatum (Lomariopsidaceae) (Native)	0.48	(0.08, 0.07)	0.58	(0.04, 0.04)
S. cooperi (Cyatheaceae) (Invader)	2.42	(0.33, 0.29)	4.41	(0.70, 0.61)**
Angiosperms				
V. calycinum (Ericaceae) (Native)	1.65	(0.07, 0.06)	2.31	(0.14, 0.13)*
H. gardnerianum (Zingiberaceae) (Invader)	1.42	(0.26, 0.22)	2.02	(0.17, 0.16)*
S. palmifolia (Poaceae) (Invader)	1.39	(0.04, 0.04)	1.56	(0.17, 0.16)
Clidemia hirta (Melastomataceae) (Invader)	8.19	(1.08, 0.96)	9.20	(0.86, 0.78)
Miconia calvescens (Melastomataceae) (Invader)	4.92	(0.76, 0.66)	6.26	(0.82, 0.72)
Tibouchina herbacaea (Melastomataceae) (Invader)	7.80	(0.75, 0.69)	9.28	(0.88, 0.80)

($F_{1,84}$=69.1, P<0.001), with the highest values observed in the Melastome litter types (*Clidemia*, *Miconia*, *Tibouchina*). Fertilization with N and P significantly increased decomposition rates ($F_{1,66}$=21.9, P<0.001), especially in *Dicranopteris* and *Sphaeropteris* litter (Table 1). The invasive tree fern *Sphaeropteris cooperi* decomposed at a rate of 2.42 year^{-1} in control plots, five times the rate of the native tree fern *Cibotium glaucum* (Table 1).

Foliar and litter properties

Plant tissue and litter properties differed strongly between native and invasive litter types, consistent with the higher decomposition rates of the invaders (Table 2). All of the invasive leaves had SLA>167 cm^2 g^{-1}, while native leaf SLA was <144 cm^2 g^{-1} except in *Diplazium* (Table 2). Angiosperm SLA exceeded fern SLA, except for the ferns *Diplazium* and *Sphaeropteris* with SLAs of 227 and 183 cm^2 g^{-1}, respectively (Table 2). Invasive angiosperms generally had high SLA (>200 cm^2 g^{-1}, except *Hedychium*). Litter nutrient concentrations were similar when comparing natives to invaders or ferns to angiosperms. However, within angiosperms and ferns, nutrient concentrations of invaders usually exceeded those of natives. Among the ferns, the invader *Sphaeropteris* had the highest litter P concentration (1.18 mg g^{-1}) and second highest litter N concentration (12.9 mg g^{-1}, Table 2). Within angiosperm litter, most of the invaders had higher nutrient concentrations than the native *Vaccinium* (Table 2). *Sphaeropteris* also retranslocated a much smaller fraction of P during leaf senescence than the native ferns (Table 2).

Litter nutrient dynamics

Nutrient dynamics in litter from natives versus invaders and ferns versus angiosperms reflected nutrient concentrations in the initial litter. In control plots, litter N concentrations increased over time in both native and invasive litter (Figs. 1a–b, 2a–b; ANOVA, P<0.001 for time effect). Phosphorus concentrations (Figs. 1c–d, 2c–d) declined or remained constant in litter types with high initial P concentrations, such as *Diplazium* (Fig. 1d) and *Sphaeropteris* (Fig. 2c; P<0.001 for litter type × time interaction). Fertilization increased litter N concentrations across all litter types (Figs. 1a–b, 2a–b; P<0.001 for fertilization effect), although the increase was small in the fast-decaying Melastomes (Fig. 2b). Litter P concentrations increased more dramatically in response to fertilization (Figs. 1c–d, 2c–d), especially in invaders, where they reached values >0.25% in *Setaria* and the Melastomes (Fig. 2c-d; P<0.001 for fertilization × litter type interaction).

We expressed litter nutrient contents as a percentage of the initial value to show net gains (immobilization) and losses of nutrients from each litter type during decomposition. In comparison to native litter (Fig. 3, solid symbols), invasive litter (open symbols) showed a much stronger tendency to release nutrients (ANOVA, P<0.001 for native/invasive effect on N and P contents). High decomposition rates caused rapid losses of initial N and P content from invasive litter (Fig. 3 open symbols; P<0.001 for native/invasive × time effect on N and P contents); all three Melastome litter types began to lose nutrients so rapidly that >50% of initial N and P was lost by 86 days (Fig. 3c–d). *Hedychium* was the only invasive litter type that ever immobilized N (Fig. 3c). By contrast, all of the natives immobilized N at some point during decomposition, and *Elaphoglossum* and *Cibotium* litter did not

Table 2 Specific leaf area (SLA) and foliar and litter nutrient properties of ferns and angiosperms. n=5–7 for SLA and foliar nutrient concentrations and n=3–4 for litter nutrient concentrations. *M* Melastome. SLA and litter nutrients from Allison and Vitousek (2004)

Litter Type	Mean (SE)					Retranslocation[a] (%)	
	SLA (cm^2 g^{-1})	Foliar N (mg g^{-1})	Foliar P (mg g^{-1})	Litter N (mg g^{-1})	Litter P (mg g^{-1})	N	P
Ferns							
C. glaucum (Native)	114 (8)	14.0 (0.5)	1.04 (0.11)	7.5 (0.2)	0.35 (0.01)	46	66
D. linearis (Native)	112 (7)	8.7 (0.4)	0.59 (0.06)	5.3 (0.4)	0.25 (0.02)	39	57
D. sandwichianum (Native)	227 (19)	21.5 (0.6)	2.40 (0.40)	14.2 (0.8)	0.80 (0.04)	34	67
E. alatum (Native)	95 (5)	8.1 (0.8)	0.57 (0.05)	4.9 (0.2)	0.19 (0.01)	40	67
S. cooperi (Invader)	183 (5)	20.5 (0.5)	1.38 (0.08)	12.9 (0.3)	1.18 (0.03)	37	14
Angiosperms							
V. calycinum (Native)	144 (2)	10.5 (0.2)	0.60 (0.01)	5.6 (0.5)	0.28 (0.04)	47	54
H. gardnerianum (Invader)	167 (12)	14.8 (1.2)	1.10 (0.19)	3.8 (0.0)	0.26 (0.02)	75	76
S. palmifolia (Invader)	237 (11)	19.2 (0.8)	1.45 (0.06)	6.8 (0.5)	0.37 (0.02)	64	74
C. hirta (M) (Invader)	204 (19)	15.6 (0.7)	0.73 (0.05)	7.5 (0.2)	0.27 (0.01)	52	64
M. calvescens (M) (Invader)	202 (13)	19.2 (0.7)	1.21 (0.16)	10.2 (0.9)	0.54 (0.04)	47	55
T. herbacaea (M) (Invader)	267 (12)	19.7 (0.8)	0.98 (0.04)	7.8 (0.1)	0.45 (0.01)	60	54

[a] Minimum value uncorrected for whole-leaf mass loss during senescence

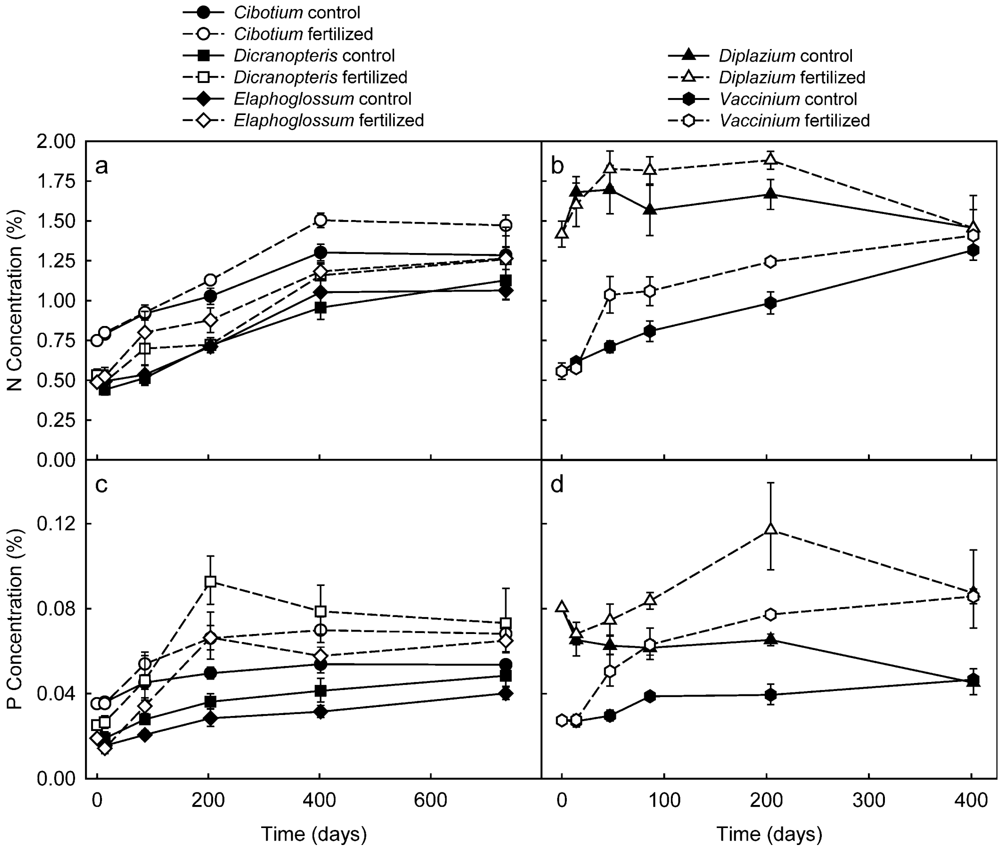

Fig. 1a–d Mean (± SE) nutrient concentrations in native litter over time for nitrogen (**a**,**b**) and phosphorus (**c**,**d**). *n*=4

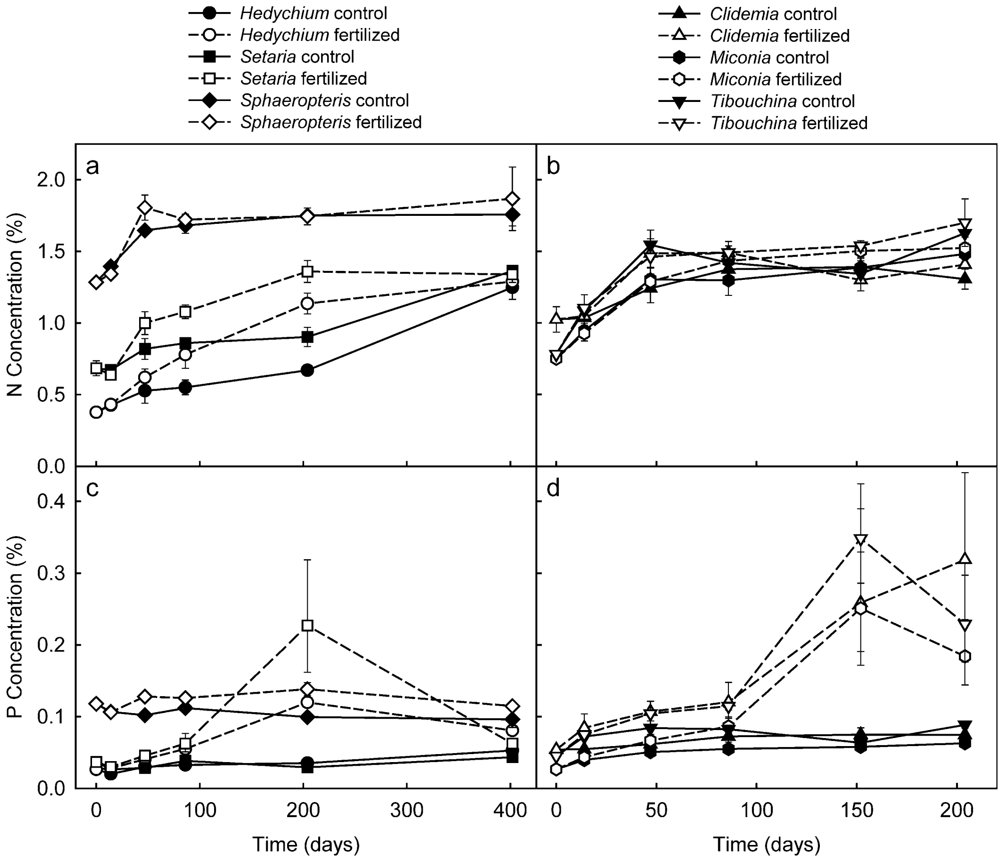

Fig. 2a–d Mean (± SE) nutrient concentrations in invasive litter over time for nitrogen (**a**, **b**) and phosphorus (**c**, **d**). *n*=4

release N at all until after 1 year of decomposition (Fig. 3a). Compared to angiosperms, ferns retained more nutrients in their litter, with the exception of the invasive *Sphaeropteris* and the native *Diplazium*, which resembled angiosperms in their N and P losses (Fig. 3a–b). Only native ferns were able to retain >50% of initial P by the last sampling date (Fig. 3b), and the native *Dicranopteris* was the only litter type that retained N (147%) and P (130%) by the end of the experiment (Fig. 3a–b).

Discussion

Several of our results strongly suggest that invasive litter inputs could contribute to a positive feedback between invasion and nutrient cycling in Hawaiian rainforest ecosystems. We found that some of the most widespread invasive plants in Hawai'i produce litter that decomposes many times faster than the dominant native species (Table 1). During decomposition, this litter releases larger quantities of N and P at faster rates than native litter (Fig. 3), such that nutrients contained in litterfall rapidly become available in the soil below invasive plants. In addition, fertilization with N and P accelerated the decomposition of *Sphaeropteris* and *Hedychium* (Table 1), suggesting that fertile sites will become even more so following invasion by these species. Native litter from *Dicranopteris* and *Vaccinium* also decomposed faster under fertilization, although this effect would only be important under *Vaccinium* because *Dicranopteris* decomposes so slowly, even when fertilized. To complete a positive feedback, invaders would have to be more successful under the high nutrient conditions generated by invasive litter inputs, a trend which has been observed in Hawai'i and elsewhere (Ehrenfeld et al. 2001; Gerrish and Mueller-Dombois 1980; Hobbs and Huenneke 1992; Huenneke et al. 1990; Ostertag and Verville 2002).

Feedbacks to nutrient cycling and invasion originate from the physiological traits of the plants competing in an ecosystem. Our results show that invaders produce litter of higher quality than most natives (except for the native *Diplazium*), with high nutrient and soluble carbon content, high SLA, and low concentrations of condensed tannins (Table 2, Allison and Vitousek 2004). In Hawai'i, most invasive plants are angiosperms (Vitousek et al. 1987), and they could dramatically increase nutrient turnover by displacing native ferns that dominate the understory. Rapid nutrient losses from most angiosperm litter types contrast strongly with high N and P retention in litter from three of four native ferns (>50%, Fig. 3a–b). Nutrient retention in fern litter should drive slower nutrient cycling in fern-dominated understories, and may result from microbial responses to fern litter chemistry (Allison and Vitousek 2004) and/or low fern decay rates (four times lower on average compared to angiosperm litter). The only native fern to lose N and P rapidly was *Diplazium*, probably because of its relatively high decomposition rate (Table 1) and high initial N and P concentrations (Table 2).

While the invasion of angiosperms into fern-dominated understories may be the main driver of higher decompo-

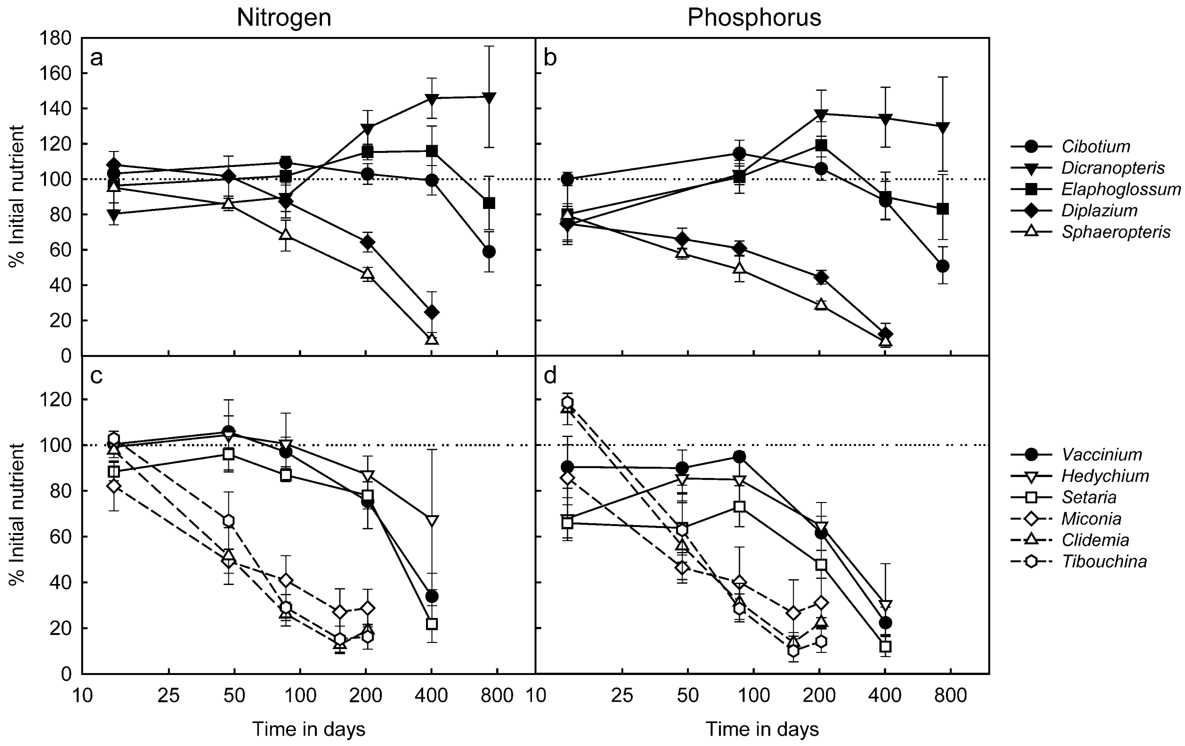

Fig. 3a–d Mean (± SE) litter nitrogen (**a**,**c**) and phosphorus (**b**,**d**) in terms of percent initial nutrient content for ferns (**a**,**b**) and angiosperms (**c**,**d**) in control plots (*n*=4). *Closed symbol* native; *open symbol* invader; *dashed lines* Melastome. Values *above dotted horizontal line* represent nutrient immobilization; values *below* represent nutrient loss. Note log scale on *x*-axis

sition and nutrient cycling rates, our results suggest that some invasive ferns, such as *Sphaeropteris*, could also stimulate increased nutrient turnover. *Sphaeropteris* produces litter that contains nearly twice as much N, three times as much P, and decomposes five times faster than litter from the native tree fern (*Cibotium*) that it displaces. These characteristics lead to rapid losses of N and P from decomposing *Sphaeropteris* litter (Fig. 3a–b), which could increase soil nutrient availability.

The contrast we observed between native and invasive nutrient dynamics strongly suggests that plant physiological traits do affect soil processes through litter quality differences. This effect is expected for N-fixing canopy trees such as *M. faya* (Vitousek and Walker 1989), but we found that even non-N-fixing plants have the potential to alter nutrient cycles by producing litter that decays rapidly without immobilizing nutrients. Ehrenfeld (2001) found a similar pattern in a New Jersey, USA, eastern deciduous forest where the shrub *Berberis thunbergii* accelerated nutrient cycling by producing litter that contained 20–80% more N and decayed three to six times faster than native species litter. In Hawaiian invaders, we suspect that physiological traits associated with superior growth and resource acquisition (Baruch and Goldstein 1999) also drive high rates of litter decomposition and nutrient cycling. Cornelissen et al. (1999) found such a relationship in the flora of Argentina and Great Britain, where litter decomposition rates correlated with leaf physiological traits involved in herbivore defense.

Invaders are likely to profoundly affect ecosystem processes in Hawai'i because of their dominance and ability to displace native species. The Melastomataceae are a particularly aggressive taxon; despite eradication efforts, *M. calvescens* has invaded several hundred hectares of wet forest on Maui and poses a serious threat on the island of Hawai'i where at least one monospecific stand is established (Medeiros and Loope 1997). Since it was first reported in 1941, *Clidemia hirta* has spread to >100,000 ha on O'ahu, and large populations have become established on all of the major Hawaiian islands (Smith 1992). *Clidemia* also spreads rapidly following disturbance by pigs, hurricanes, and fires (Peters 2001; Smith 1992; Wester and Wood 1977). Although locally abundant in disturbed areas on windward Hawai'i (Wagner et al. 1999), *T. herbacaea* has recently invaded remote and relatively undisturbed wet forests on the islands of Maui and Hawai'i (K. Kitayama, P.M. Vitousek, personal observation).

Our other invasive study species also represent widely distributed threats to native wet forest ecosystems. *S. cooperi* may displace native *Cibotium* tree ferns and is found on four of the Hawaiian islands, including Maui, where several populations have invaded over 200 ha (Baruch and Goldstein 1999; Medeiros et al. 1992; Wilson 1996). The grass *S. palmifolia* is also common in wet forests across four of the Hawaiian islands (Wagner et al. 1999). In montane forests, *H. gardnerianum* has become a prominent understory shrub (Ostertag and Verville 2002), with its cover approaching 100% in some areas on the islands of Kauai and Hawai'i.

In order for these invasions to change nutrient fluxes at the ecosystem scale, the invaders must not only displace natives, but also produce significant amounts of litter. We know that native species such as *Cibotium* and *Dicranopteris* may produce large amounts of litter in some sites (Russell et al. 1998; Vitousek et al. 1995a), but few data exist on the productivity of our invasive understory species. However, many invasive species in Hawai'i, including the Melastomes and *Sphaeropteris*, have high photosynthetic and growth rates compared to native species (Baruch and Goldstein 1999; Baruch et al. 2000; Durand and Goldstein 2001a). We speculate that these traits in combination with the clear dominance of our invaders would cause their litter inputs to meet or exceed those of displaced natives. For example, *Sphaeropteris* ferns growing on O'ahu were found to produce ten times as many fronds (of similar size) as adjacent *Cibotium* tree ferns (Durand and Goldstein 2001b). Therefore, a transition from *Cibotium* to *Sphaeropteris* dominance would increase ecosystem nutrient cycling rates many-fold because invader litter inputs would be much higher, contain more nutrients, and decay five times faster. Under these conditions, *Sphaeropteris* and other invaders are likely to persist or increase because decaying, nutrient rich litter could meet the high nutrient demands of invasive plants.

The litter decomposition rates and nutrient dynamics of invasive species also have implications for soil development and ecosystem nutrient losses. One important characteristic of Hawaiian ferns is that they contribute to soil formation on young basaltic substrates by producing large quantities of recalcitrant litter (Russell and Vitousek 1997). In contrast to the native litter types, which generally decompose slowly and immobilize nutrients, litter from invasive species (especially Melastomes) decays rapidly and immediately releases nutrients (Fig. 3). Substrates under these invasive plants are therefore unlikely to accumulate organic matter, and nutrients in the litter would be subject to leaching. On recent lava flows, the establishment of non-N-fixing invaders instead of native species could eventually slow the process of primary succession after an initial period of elevated nutrient cycling rates.

In addition to physiological and growth rate advantages, nutrient feedbacks may be one of the mechanisms controlling the rate of spread of invasive plant species (Ehrenfeld 2003). Even without prominent physiological differences such as the ability to fix atmospheric N, some invasive species may cause positive feedbacks to nutrient availability that could facilitate subsequent invasion. The same traits that allow these invasive plants to grow rapidly and compete for resources may also stimulate nutrient cycling through increases in litter quality and production. In Hawaiian and other nutrient-poor ecosystems, the ability to increase nutrient cycling rates during the course of invasion may be an important trait that contributes to invader success.

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