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Novel forests maintain ecosystem processes after the decline of native tree species

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Abstract. The positive relationship between species diversity (richness and evenness) and critical ecosystem functions, such as productivity, carbon storage, and nutrient cycling, is often used to predict the consequences of extinction. At regional scales, however, plant species richness is mostly increasing rather than decreasing because successful plant species introductions far outnumber extinctions. If these regional increases in richness lead to local increases in diversity, a reasonable prediction is that productivity, carbon storage, and nutrient cycling will increase following invasion, yet this prediction has rarely been tested empirically. We tested this prediction in novel forest communities dominated by introduced species (~90% basal area) in lowland Hawaiian rain forests by comparing their functionality to that of native forests. We conducted our comparison along a natural gradient of increasing nitrogen availability, allowing for a more detailed examination of the role of plant functional trait differences (specifically, N₂ fixation) in driving possible changes to ecosystem function. Hawaii is emblematic of regional patterns of species change; it has much higher regional plant richness than it did historically, due to >1000 plant species introductions and only ~71 known plant extinctions, resulting in an ~100% increase in richness. At local scales, we found that novel forests had significantly higher tree species richness and higher diversity of dominant tree species. We further found that aboveground biomass, productivity, nutrient turnover (as measured by soil-available and litter-cycled nitrogen and phosphorus), and belowground carbon storage either did not differ significantly or were significantly greater in novel relative to native forests. We found that the addition of introduced N₂-fixing tree species on N-limited substrates had the strongest effect on ecosystem function, a pattern found by previous empirical tests. Our results support empirical predictions of the functional effects of diversity, but they also suggest basic ecosystem processes will continue even after dramatic losses of native species diversity if simple functional roles are provided by introduced species. Because large portions of the Earth's surface are undergoing similar transitions from native to novel ecosystems, our results are likely to be broadly applicable.

Key words: biodiversity–ecosystem function paradigm; diversity–productivity relationship; new forests; no-analog communities; novel ecosystems.

INTRODUCTION

Declining local diversity (richness and evenness) can impair the basic biogeochemical functioning of ecosystems, such as productivity, carbon storage, and nutrient cycling (Naeem et al. 1994, Tilman et al. 1997a, Hector et al. 1999, Hooper et al. 2005, Spehn et al. 2005, Fargione et al. 2007). However, while the relationship between diversity and function (known as the biodiversity–ecosystem function paradigm; Naeem 2002) has often been used to predict the possible effects of extinction (e.g., Naeem et al. 1999), the effects of increasing local diversity due to invasion have rarely

been considered (but see Wilsey et al. 2009). Stachowicz and Tilman (2005) argued that “there are virtually no data to address” the functional implications of increased diversity due to invasion, and the Millennium Ecosystem Assessment report stated that invasion was “not a relevant increase in biodiversity” (MEA 2005:21). The notion that invasion may stabilize or increase ecosystem function by increasing local diversity has also been cited anecdotally as a criticism of the biodiversity–ecosystem function paradigm (Srivastava and Vellend 2005), but empirical tests of this hypothesis have been few. When biodiversity–ecosystem function theory has considered invasion, questions have focused almost exclusively on whether higher diversity communities are more resistant to invasion (i.e., whether diversity reduces invasibility; Fridley et al. 2007). The results of these studies indeed suggest that diversity limits invasion at the local scale (Knops et al. 1999, Naeem et al. 2000, Symstad 2000, Kennedy et al. 2002, Fargione et al. 2003, Pfisterer et al.

Manuscript received 6 June 2011; revised 23 November 2011; accepted 28 November 2011. Corresponding Editor: H. A. L. Henry.

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2004, Fargione and Tilman 2005), but in many cases, they also suggest that diversity increases following invasion, and the functional implications of these diversity increases are rarely addressed.

The functional implications of the spread of introduced species via invasion are growing in importance globally. Introduced species now dominate a large fraction of Earth's land surface, forming novel ecosystems (i.e., variously called "new," "no-analog," or "emerging" ecosystems; Lugo and Helmer 2004, Hobbs et al. 2006, Mascaro et al. 2008, Seastedt et al. 2008, Hobbs et al. 2009, Lugo 2009, Martinez 2010, Martinez et al. 2010, Bridgewater et al. 2011, Chai and Tanner 2011). Although invasion can lead to monotypic dominance, species diversity in novel ecosystems is a complex product of changes in species richness and evenness acting at multiple spatial scales (Wardle et al. 2011). Globally, introduced species unequivocally cause extinctions (Vitousek et al. 1997, Castro et al. 2010), but at regional scales, plant species richness appears to be increasing because plant invasions far outnumber extinctions (Sax and Gaines 2003). For example, many oceanic island systems, including large archipelagos such as New Zealand and Hawaii, are now estimated to contain 100% more plant species than they did prior to human colonization (Sax and Gaines 2008). Continental regions such as California and South Africa have also experienced large increases in regional plant species richness (Macdonald and Richardson 1986, Sax 2002, Seabloom et al. 2006). Such increases are not necessarily expressed at the local scale, however. While regional richness has increased in Wisconsin, for example, local richness has declined in most sites because native species ranges are declining faster than introduced species ranges are expanding (Rooney and Waller 2008). Furthermore, if local richness does increase following invasion, declining evenness may cause diversity to decline if most introduced species tend to be rare (Cleland et al. 2004). Thus, the local diversity of novel ecosystems is the product of simultaneous losses of native species and additions of introduced species and their respective abundances, and can be lower, higher, or unchanged relative to historical native ecosystems.

Hawaii is emblematic of global changes in species diversity, with high rates of native plant extinction and even higher rates of plant introduction. Seventy-one vascular plant species are known to have become extinct in Hawaii over the past ~1700 years, while at least 1090 introduced plant species have become naturalized during this period: an approximate doubling of its pre-human contact flora (Sax et al. 2002). More than 8000 species are also cultivated in Hawaii, and more of these become naturalized each year (Wagner et al. 1999). Combined, these changes have major implications for the local diversity of Hawaiian ecosystems and lead to two basic questions in the context of the biodiversity–ecosystem function paradigm: (1) Is local diversity (i.e., of both native and introduced species) decreasing or increasing

in Hawaiian ecosystems? (2) Does the direction of diversity change correspond in sign with the direction of functional change? For example, do increases in diversity translate to greater productivity, carbon storage, and or a greater rate of nutrient turnover? We addressed these questions in lowland Hawai'i Island by comparing tree species diversity and ecosystem functioning between residual native forests, and novel forests dominated by introduced tree species (i.e., by >90% of basal area). Based on regional trends in species richness, we hypothesized that (1) local net tree species richness and diversity would be higher in novel forests than in native forests, and (2) basic functional metrics in novel forests (in terms of productivity, aboveground and belowground carbon storage, and nitrogen and phosphorus turnover) would meet or exceed levels found in native forests. Taken together, these hypotheses follow the mechanistic prediction of the biodiversity–ecosystem function paradigm, although in the direction of increasing rather than decreasing diversity.

In experimental work, the functional outcomes of diversity shifts are influenced not only by the richness and evenness of species, but also by the relative changes in plant functional traits (Hooper and Vitousek 1997, Lavorel and Garnier 2002, Spehn et al. 2002). Introduced species can alter the biogeochemistry of ecosystems in a similar way (Ehrenfeld 2003), particularly when they possess plant functional traits not represented in the native flora (Versfeld and van Wilgen 1986, Vitousek et al. 1987). Alternatively, introduced species that differ little in functional traits compared to native species may have little effect, if any, on biogeochemistry (Wedin and Pastor 1993). Thus, a third question was: (3) How does the transition in plant functional traits between native ecosystems and novel ecosystems influence the functional outcomes of diversity change? To address this question, we compared native and novel forest functioning along a natural gradient in nitrogen availability with increasing lava flow age. In native Hawaiian forests, primary succession on recent lava flows begins with nearly zero available nitrogen, which takes several centuries to accumulate (Vitousek and Farrington 1997). Along this same gradient, novel forests tend to be dominated by introduced trees with N₂-fixing symbioses on young, N-limited substrates (Vitousek et al. 1987, Hughes and Denslow 2005) and by non-fixing pioneer trees on older substrates (Mascaro et al. 2008, Zimmerman et al. 2008). Because each of these functional types is essentially absent from the native lowland flora (Wagner et al. 1999), comparing native and novel forests along this gradient affords a contrast of two different functional trait transitions (i.e., native trees vs. N₂-fixing introduced trees, and native trees vs. non-fixing introduced trees). In results of experimental biodiversity studies, N₂-fixing species are typically associated with a greater impact on ecosystem functioning than non-fixing species (e.g., Spehn et al. 2005). Thus, we hypothesized that (3) the disparity

TABLE 1. Characteristics of 17 tropical wet forest sites on Hawai'i Island, USA.

Site	Substrate type	Substrate age (yr)	Basal area (m ² /ha)	Treatment dominance (%)	Dominant species	Plot area (ha)
Native						
N1	'a'a	53	2	100	<i>Metrosideros polymorpha</i>	0.25
N2	'a'a	168	13 ± 1	100	<i>M. polymorpha</i>	1.0
N3	pah	218	13	99	<i>M. polymorpha</i>	0.25
N4	pah	218	7 ± 1	96	<i>M. polymorpha</i>	1.0
N5	'a'a	300	52	100	<i>M. polymorpha</i>	0.25
N7	pah	575	40 ± 2	77	<i>M. polymorpha</i>	1.0
N8	'a'a	575	39 ± 6	84	<i>M. polymorpha</i>	1.0
N9	p/a	1125	37 ± 3	82	<i>M. polymorpha</i>	1.0
Novel						
E1	'a'a	53	31	99	<i>Falcataria moluccana</i>	0.25
E2	'a'a	168	38 ± 3	83	<i>Casuarina equisetifolia</i>	1.0
E3	p/a	168	43 ± 3	100	<i>C. equisetifolia</i>	1.0
E4	pah	218	26	95	<i>F. moluccana</i>	0.25
E5	pah	218	22 ± 3	97	<i>C. equisetifolia</i>	1.0
E6	'a'a	300	50	80	<i>F. moluccana</i>	0.25
E7	pah	575	33 ± 5	94	<i>Cecropia obtusifolia</i>	1.0
E8	p/a	575	36 ± 3	87	<i>C. obtusifolia</i>	1.0
E9	pah	1125	41 ± 3	92	<i>Psidium cattleianum</i>	1.0

Notes: Ages are exact historical ages (to date of productivity estimates) up to and including 218-year-old sites, after which they represent median values following the stratigraphy of Wolfe and Morris (1996). Substrates are either 'a'a (rough, crinkle type), pahoehoe (pah; dense and ropy), or pahoehoe with thin surface ash deposits (p/a). Treatment dominance reflects the relative basal area (%; mean ± SE [variation was not available for six sites where large trees were sampled in single plot]) in native species for the native sites, and introduced species for the novel sites. At the novel sites, an introduced species was the most dominant species in all cases.

between native and novel forest functioning would be greatest on younger lava flows where novel forests are dominated by N₂-fixing species.

METHODS

Study area

We conducted this study in the districts of Hilo and Puna on the windward side of Hawai'i Island (for natural and ecological histories of the Hawaiian Islands, see Mueller-Dombois and Fosberg 1998, Wagner et al. 1999, Vitousek 2004). We selected 17 lowland forest sites that were dominated either by native (eight sites) or introduced (nine sites) tree species (Table 1). Species brought by Polynesian peoples were considered introduced (Wagner et al. 1999). We considered a forest to be dominated if at least 75% of its mean basal area was in native or introduced trees (Table 1). The native sites averaged 91% ± 3% (mean ± SE) native basal area, and our novel sites averaged 92% ± 2% introduced basal area. With this dominance criterion, sites were therefore selected nonrandomly. All sites are at or below ~1000 m above sea level (a.s.l.), with 2500 to 4000 mm of rainfall per year and no apparent seasonality (Appendix A; Giambelluca et al. 1986), and are considered subtropical wet forest (Holdridge et al. 1971, Tosi et al. 2001, Price et al. 2007). Parent material age (hereafter substrate age) ranged from 53 years to 1125 years. Three young lava flows were dated by historical observation, while the remaining flows were dated stratigraphically by Wolfe and Morris (1996) (Table 1). Our native and novel gradients contain balanced sampling of two substrate

types (pahoehoe and 'a'a) across a range of age groups (Table 1). In this ecosystem, substrate age is a proxy for nitrogen (N) availability, which strongly limits forest productivity (Vitousek and Farrington 1997).

We excluded sites with evidence of agricultural activity or mechanized alteration of the substrate such as tilling. Novel forest sites on substrates ≤300 years old were likely never disturbed prior to invasion by introduced species; they were previously either native-dominated forests or barren lava flows as confirmed by inspection of aerial photography and standing dead snags of the native *Metrosideros polymorpha* (ohia) found at the sites. The native sites on young substrates have simply not yet been invaded; in all cases they are found at the leading edge of an advancing invasion front. Novel forest sites on substrates >300 years old showed evidence of previous canopy disturbance by humans (cutting is a probable cause, as some large areas are totally devoid of old *M. polymorpha* trees, while others contain residual patches); however, these sites were all in closed-canopy forest in their earliest aerial photographs (1960s) and remained free of canopy disturbance after that time. All of the sites (native and novel) on substrates >300 years old also show other small disturbances such as rock piles and hunting activity. While we excluded plantations, all the novel forests on Hawai'i appear to be the product of human activity in the form of propagules from widespread tree planting particularly during the Great Depression and later aerial seeding (Little and Skolmen 1989, Woodcock 2003).

Stand structure and species composition

We measured forest composition and structure in 10 circular randomly selected plots at each site (Table 1). We established six sites (three native, three novel) in 2001 in which we sampled 10 plots with a 5.64 m radius and measured the diameter at breast height (dbh; 1.3 m from ground) of all stems ≥ 2 cm dbh (0.1 ha total area; Hughes and Denslow 2005, Hughes and Uowolo 2006). We extended our sampling of large trees (≥ 20 cm dbh) to a single 0.25-ha plot at these six sites to capture their spatial heterogeneity. Between 2003 and 2007, we added 11 additional sites (five native, six novel) to expand the substrate age gradient. In 10 plots at these later sites, we measured the dbh of all stems ≥ 2 cm within a 9 m radius circle, and all trees ≥ 30 cm dbh an 18-m radius circle (1.0 ha total area). For all sites, the plots were placed along 1–4 transects (depending on the size of the lava flow underlying each site), with plot edges at least 10 m apart. We identified to species 99% of all stems and created morphospecies in four cases where identification could not be determined. We collected voucher specimens for all morphospecies for submission to Bishop Museum (Honolulu, Hawaii, USA).

Our native forests were dominated almost exclusively by *M. polymorpha*, with the abundance of short-stature native tree species increasing with increasing substrate age: primarily *Diospyros sandwicensis* (lama) and *Pandanus tectorius* (hala). Novel forests on young substrates were dominated by either *Falcataria moluccana* (albizia) or *Casuarina equisetifolia* (ironwood), both of which have symbiotic relationships with N_2 -fixing microorganisms (hereafter " N_2 -fixers"), with understories primarily composed of introduced *Psidium cattleianum* (strawberry guava). On older substrates, novel forests were dominated by introduced pioneer tree species, such as *Cecropia obtusifolia* (trumpet tree) and *Melochia umbellata* (melochia); the oldest site was dominated by *P. cattleianum*. Structurally, all novel forests (including the youngest *Falcataria*-dominated site) were closed-canopy forests, whereas the native forests do not achieve canopy closure until sometime between the 218-year-old site and the 300-year-old site. Due to the dominance criterion used in site selection (see *Study area*), most native sites contained some introduced species and most novel sites contained some native species. For comprehensive stem density and basal area, see Appendices B–E.

We compared tree species richness (the total number of native and introduced tree species ≥ 2 cm in diameter) and large-tree diversity using a modified version of the Shannon index (indexed to relative basal area rather than relative density) between the native and novel forest sites. We used a modified Shannon index because larger trees were of greater interest in terms of their influence on ecosystem function (i.e., due to large canopies, high litter inputs, and so on) than were small, but abundant trees. In the youngest native site, only *M. polymorpha* was present, prohibiting an estimate of

Shannon's diversity; we considered the diversity of this monotypic site to be zero.

To give our plot-level comparisons context, we summarized regional changes to tree species richness on the Hawaiian Islands. We organized all angiosperm tree species listed as native extant, native extinct, or naturalized (i.e., introduced and reproducing without human assistance) according to their maximum heights listed by Wagner et al. (1999). Species were considered to be "trees" based on their growth form rather than a taxonomic distinction.

Aboveground biomass and aboveground biomass increment

We measured aboveground biomass (AGB) using a combination of local and global allometric models. We applied locally derived species-specific diameter-to-biomass equations for the two most common species in our data set up to a maximum size class for the available models (*M. polymorpha* to 30 cm dbh and *P. cattleianum* to 20 cm dbh), as well as growth-form specific models for tree ferns and lianas (59% of stems, 9/52 species; Schnitzer et al. 2006, Asner et al. 2011). For the remaining species and larger *M. polymorpha* and *P. cattleianum* individuals, we used a global model for wet tropical forests from Chave et al. (i.e., "Model 1," 2005). In addition to diameter, the Chave model requires inputs of height and wood density. We estimated height using species-specific diameter-to-height allometric equations (26% of stems, 12/52 species), or a regional diameter-to-height model (15% of stems, 33/52 species). Wood density estimates for these 45 species came from a combination of field samples (23% of stems, 8/45 species), a global wood density database (73% of stems, 33/45 species; Zanne et al. 2009) and a default regional wood density value for Oceania of 0.55 g/cm³ (4% of stems, 10/45 species; Chave et al. 2009). For an accounting of all allometric equations and wood density values used see Appendices F and G.

We modeled AGB increment (i.e., the change in AGB over time) using dendrometer bands to measure the relative growth rate (RGR, cm·cm⁻¹·yr⁻¹) of 6.7% of the trees in our study ($n = 924$). We used a minimum of 20 bands for the most dominant species at each site and randomly allocated additional bands among less common species at each site. After initial placement, we allowed all the bands to attain tension for a minimum of eight months and scored them in January 2008. We then revisited the bands in January 2009 to quantify annual growth. Using these data, we created a matrix of mean RGRs by species and site (Appendices H and I) and assigned RGR estimates to each species \times site pair to the remaining individuals to model AGB increment. If a species had no bands at a particular site, we assigned the mean RGR value for that species across all sites within its treatment group (i.e., native or novel). A few remaining species were so rare as to have no bands at any sites in their treatment group, and for these species

we applied the mean RGR value of that site; these species were so rare that including or excluding them had no effect on the significance levels of our results.

Litterfall and aboveground net primary productivity

We collected all leaf litter and woody stems ≤ 1 cm diameter (follows Clark et al. 2001) in five traps at 20-m intervals along a 100-m transect at each site (85 total traps) over a 36-h period each month from April of 2008 until March of 2009. Traps were $0.18 \text{ m}^2 \times 6$ cm deep and were lined with 2-mm fiberglass screen. We dried all samples to constant mass at 70°C in a forced-air oven and weighed them. For each trap, we combined samples for all months to determine annual litterfall mass and nutrient chemistry. We ground the entire sample from each trap in a Model 4 Wiley Mill to pass a 0.5-mm mesh sieve. We determined C and N content using combustion methods in a Analytical Elemental Combustion System 4010 (Costech Analytical, Valencia, California, USA). We determined P content using colorimetry in a Bran-Luebbe Auto Analyzer 3 (SPX Corporation, Charlotte, North Carolina, USA). Nutrient analyses were conducted at the Ecosystems Analysis Lab, University of Nebraska, Lincoln (UNL), Nebraska, USA. We calculated aboveground net primary productivity (ANPP) as the sum of litterfall and AGB increment.

Soil nitrogen and phosphorus availability

We measured available soil N (NO_3^- -N and NH_4^+ -N) and P (PO_4^{3-} -P) using resin bags (Binkley and Matson 1983) in February 2009. For each bag, we sewed 6 g of mixed-bed ion-exchange resin (IONAC NM-60 H^+/OH^- form, type I, beads, 16–50 mesh; J. T. Baker, Phillipsburg, New Jersey, USA) into a 6×7.5 cm section of monofilament polyester silkscreen (86 mesh). We placed 20 bags at each site (5 cm below the soil surface), 10 designated for N and 10 for P extraction. We spaced the bags along each 100-m litterfall transect by placing two pairs of bags on either end of a 10-m side transect perpendicular to each main transect and collected them after 28 d.

We immersed the N-designated bags in 100 mL of 1 mol/L KCl solution and the P-designated bags in 100 mL of 0.5 mol/L HCl. We placed the samples on a shaker table for 6 h. From the KCl extracts, we determined NO_3^- -N and NH_4^+ -N content using colorimetry in a Bran-Luebbe Auto Analyzer 3 at the Ecosystems Analysis Lab, UNL. From the HCl extracts, we determined PO_4^{3-} -P content using colorimetry in a Pulse Instruments Auto Analyzer 2 at the Marine Science Lab, University of Hawai'i, Hilo, Hawaii, USA.

Aboveground nutrient-use efficiency

We estimated aboveground N- and P-use efficiency by estimating the fraction of ANPP for each unit of N and P lost to litter or stored in wood (Vitousek 1982). We measured the amount of N and P lost to litter as the N

and P mass in one year's sample of litter. We estimated the wood fraction of aboveground biomass increment using a global model:

$$\text{AGW} = \text{AGB} - 0.113 \times \text{AGB}^{0.7565}$$

where AGW is aboveground wood mass and AGB is total aboveground biomass ($r^2 = 0.91$; modified from Enquist and Niklas 2002). To estimate the amount of N and P stored to wood, we sampled wood N and P content for 14 common species, at a subset of sites (12/17) using a combination of saw-cut sections and cores. For dominant species (see Table 1), 10 separate trees were composited to create one sample at a site; for other species, three trees were used. We considered the possible influence of site on wood nutrient content, and found that only *Psidium* differed significantly in wood N content (but not P content) by site. On sites that were dominated by the N_2 -fixing species *Falcataria* and *Casuarina*, *Psidium* wood N content was significantly higher than on other sites dominated by either native species or non- N_2 -fixing introduced species. Thus, when estimating NUE and PUE, we used species-specific values for wood chemistry for all sites with the exception of *Psidium*, where we applied separate values on N_2 -fixing-dominated or non- N_2 -fixing-dominated sites. For species without field-based wood chemistry estimates, we used mean values for native and introduced (i.e., non- N_2 -fixing) trees. Including or excluding these species had no effect on the significance levels of our results.

Belowground carbon and nitrogen stocks

Shallow, rocky soils dominate young substrates on Hawai'i and preclude the possibility of coring. We sampled soil carbon stocks using small soil pits designed to capture the entire soil column (method follows Litton et al. 2008). At each site, we located 10 pits in a stratified random design (one pit randomly located in each forest structure plot). We collected standing litter (excluding stems > 1 cm diameter) within a 25×25 cm frame. Within this 25×25 cm space, we used a 22.7-km (50-pound) rock bar to create a pit by removing all material excluding coarse roots (> 1 cm diameter) to a straight depth of 50 cm or to unweathered basalt (i.e., blue rock containing no organic material). Because young Hawaiian soils tend to be shallow, this method typically recovered the entire soil column. However, the pits varied in size and shape due to substrate heterogeneity. Thus, we measured the depth of each pit (as a mean of nine equally distributed points on the pit floor) and measured the volume by backfilling each pit with fine cinder. From the depth (D) and volume (V), we determined the effective surface area (SA) of the pit according to $\text{SA} = \text{V}/\text{D}$.

We separated litter in the field and sorted all other material from each pit into four categories (roots ≤ 1 cm, fine soil ≤ 2 mm, coarse material between 2 and 5 mm exclusive, and rock material ≥ 5 mm) using a

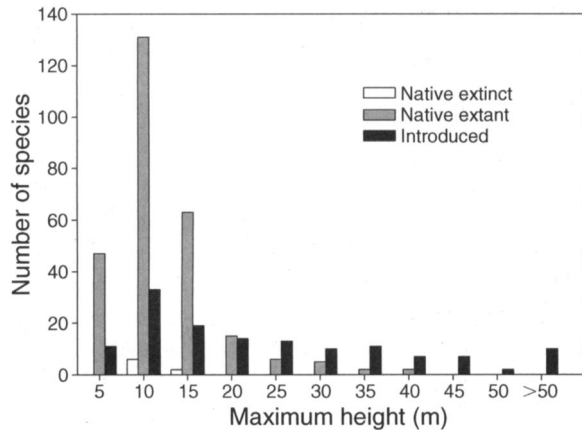


FIG. 1. An example of the regional-scale tree diversity changes underway in the Hawaiian archipelago, USA. The heights of 408 tree species reported by Wagner et al. (1999) as native extinct, native extant, or introduced and naturalized show that not only has tree richness increased regionally, but that tree size is more broadly varied as a consequence.

combination of sieving, hand-picking of roots, and brushing of rocks to remove loose soil. We dried all material to constant mass at 70°C in a forced-air oven. We ground the entire litter and root samples from each pit in either a Model 4 Wiley Mill or a Mini Wiley Mill (depending on the sample size; Thomas Scientific, Swedesboro, New Jersey, USA) to pass a 0.5-mm sieve. We homogenized the fine-soil pool and ground a subsample with a mortar and pestle to pass a 0.5-mm sieve. We determined the organic matter content of a ~30-cm³ subsample of each non-rock pool (including the unground coarse fraction) by incubation in an Isotemp Muffle Furnace (Fisher Scientific, Pittsburgh, Pennsylvania, USA) at 500°C for 8 h (i.e., loss on ignition; Robertson et al. 1999). For the rock fraction, we used a ~1-kg subsample and incubated for 12 h.

We determined C and N content of the litter, root, and fine soil samples using combustion methods in a Costech Analytical Elemental Combustion System 4010 at the Ecosystems Analysis Lab, UNL. We used the C-to-OM (organic matter) and N-to-OM ratios in the fine fraction to estimate the C and N content in the coarse and rock fractions for each pit.

Statistical analyses

We compared each community (richness, diversity), and ecosystem variable (AGB, litterfall, AGB increment, ANPP, soil-available N and P, N and P mass in litterfall, NUE and PUE, belowground C and N storage, belowground C:N ratios) between novel and native forests using analysis of covariance (ANCOVA), with substrate age as the covariate, forest type ("native" or "novel") as fixed factors and forest type × substrate age as the interaction term.

For each variable with a significant interaction between forest type and substrate age, we used

confidence interval analyses to determine the point along the age gradient at which novel and native forests diverged into significance or converged onto lack of significance.

For each variable we fit two linear models as follows:

$$y_{\text{Native}} = a_1 + b_1 \log_{10}(\text{Age}) + \varepsilon_{\text{Native}}$$

$$y_{\text{Novel}} = a_2 + b_2 \log_{10}(\text{Age}) + \varepsilon_{\text{Novel}}$$

where $\varepsilon_{\text{Native}} \sim N(0, \sigma_{\text{Native}}^2)$ and $\varepsilon_{\text{Novel}} \sim N(0, \sigma_{\text{Novel}}^2)$. The intersection of the two lines occurs (when $b_1 \neq b_2$) at

$$\text{Age} = 10^{\frac{a_1 - a_2}{b_2 - b_1}}.$$

We used estimated slopes and intercepts to generate the estimated point at which the two lines converged, and also generated 95% confidence intervals for each function to determine a lower and upper bound for our convergence estimates. ANCOVA analyses were conducted in JMP (2007), while the confidence interval analyses were conducted in SAS (SAS Institute 2008).

RESULTS

Community properties

The emergence of novel tropical forests on Hawai'i Island is associated with large changes in community composition, species richness, and diversity. We found that regional increases in net tree richness (i.e., native plus introduced species; Fig. 1) in novel forests translated to increases in local net tree diversity along a successional gradient (Fig. 2). Novel forests had more tree species (ANCOVA $F_{1,13} = 7.26$, $P = 0.0184$; Fig. 2a, Table 2), and had higher diversity of large trees (i.e., Shannon's diversity indexed by relative basal area, $F_{1,13} = 20.21$, $P = 0.0006$; Fig. 2d). The increases in local tree species richness were driven by both a greater richness of introduced tree species ($F_{1,13} = 15.86$, $P = 0.0016$; Fig. 2c) and the lack of a significant decline in richness of native tree species ($F_{1,13} = 2.38$, $P = 0.1465$; Fig. 2b). A significant or marginally significant (i.e., $P < 0.1$) effect of substrate age was evident for all community metrics, such that both tree richness and diversity in novel and native forests increased with increasing substrate age (Table 2, Fig. 2).

Aboveground biomass pools and fluxes

Aboveground biomass was highly variable, and did not differ significantly between novel and native forests ($F_{1,13} = 2.35$, $P = 0.1493$; Fig. 3a, Table 2). Fluxes in aboveground litterfall, AGB increment, and ANPP were all significantly higher in novel forests, but significant interactions between forest type and substrate age indicated that these differences did not extend to the oldest substrates (Fig. 3b–d). Using confidence interval analysis, we found that these significant differences extended to at least 500-year-old substrates for litterfall, 330-year-old substrates for AGB increment, and 540-year-old-substrates for ANPP (Table 3). For novel

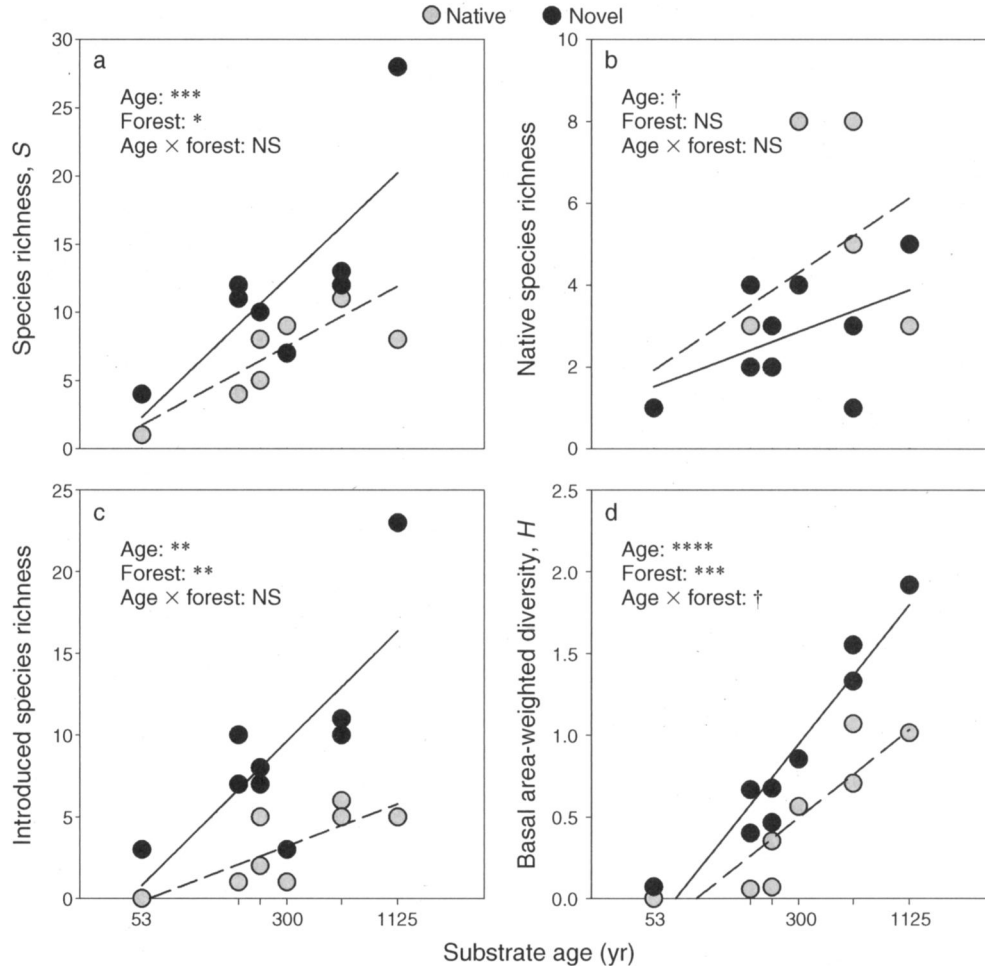


FIG. 2. Assessments of (a) species richness (stems ≥ 2 cm in diameter), (b) native species richness, (c) introduced species richness and (d) Shannon's diversity indexed by relative basal area in nine novel (solid line) forests dominated by introduced species compared to eight native forests (dashed line). Sites are found on a primary successional matrix of lava flows in lower Puna, Hawai'i Island. Significance levels reflect results of analysis of covariance, with substrate age (i.e., age) as the covariate (log-transformed to provide normality) and forest type as a fixed factor.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; † $P < 0.1$; NS, not significant.

forests on substrates 300 years old or younger (i.e., those dominated by N_2 -fixing tree species), litterfall, AGB increment, and ANPP averaged $>200\%$ higher than in native forests (Table 2).

N and P turnover and efficiency of use

We found strong differences in nutrient cycling and nutrient-use efficiencies between novel and native forests (Table 2; Fig. 4). Available soil N was two- to five-times higher in novel vs. native forests ($F_{1,13} = 15.25$, $P = 0.0018$; Fig. 4a). Litterfall N mass was also higher in novel forests ($F_{1,13} = 29.50$, $P = 0.0001$; Fig. 4c), but there was a significant interaction between forest type and substrate age ($F_{1,13} = 6.98$, $P = 0.0203$); confidence interval analysis suggested that the significant difference extended to 430-year-old substrates (Table 3). Litter-cycled N averaged $>700\%$ higher in novel forests on substrates 300 years old and younger relative to native

forests (Table 2). Available soil P did not differ significantly between novel and native forests ($F_{1,13} = 3.32$, $P = 0.0917$; Fig. 4b); however, litterfall P mass was significantly higher in novel forests ($F_{1,13} = 6.98$, $P = 0.0203$; Fig. 4d).

Nitrogen-use efficiency was significantly lower in novel vs. native forests ($F_{1,13} = 31.54$, $P = <0.0001$; Fig. 4d), with a significant interaction between forest type and age ($F_{1,13} = 6.96$, $P = 0.0204$; Fig. 4d). Confidence interval analysis revealed that novel forests had lower NUE until a substrate age of at least 410 years (Table 3). PUE was significantly lower in novel forests ($F_{1,13} = 7.10$, $P = 0.0195$; Fig. 4e). Lower nutrient-use efficiencies in novel forests reflect a combination of greater N and P losses to litter and greater storage of N and P to wood. We found that the native dominant *Metrosideros* had much lower wood N content than all of the introduced species (Fig. 5). The lowest wood N

TABLE 2. Summary of ANCOVA results comparing community and functional properties between novel and native-dominated forests on Hawai'i Island.

Parameter	Forest type		Age		Type × age		Mean difference from native forests (%)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	≤300 yr	>300 yr
Community properties								
Richness (<i>S</i>)	7.26	0.0184	19.82	0.0007	1.50	0.2422	67	66
Native species richness	2.38	0.1465	4.11	0.0637	0.33	0.5780	-26	-44
Introduced species richness	15.86	0.0016	15.18	0.0018	3.06	0.1066	252	175
Shannon's diversity, <i>H</i>	20.21	0.0006	87.31	<0.0001	4.48	0.0543	151	72
Matter pools and fluxes								
AGB (Mg/ha)	2.35	0.1493	1.42	0.2548	3.02	0.1060	137	-25
Litterfall (kg·m ⁻² ·yr ⁻¹)	37.58	<0.0001	3.57	0.0814	13.54	0.0028	214	23
AGB increment (Mg·ha ⁻¹ ·yr ⁻¹)	13.51	0.0028	0.05	0.8188	6.86	0.0213	238	-2
ANPP (kg·m ⁻² ·yr ⁻¹)	44.59	<0.0001	1.41	0.2564	18.24	0.0009	222	15
N and P turnover and efficiency of use								
Resin-capture N (μg·g ⁻¹ ·d ⁻¹)	15.25	0.0018	1.58	0.2313	3.58	0.0808	511	217
Resin-capture P (μg·g ⁻¹ ·d ⁻¹)	3.32	0.0917	0.30	0.5937	1.41	0.2566	176	120
Litterfall N mass (g N·m ⁻² ·yr ⁻¹)	29.50	0.0001	0.94	0.3492	6.98	0.0203	716	115
Litterfall P mass (g P·m ⁻² ·yr ⁻¹)	12.04	0.0041	0.41	0.5317	1.37	0.2632	338	117
NUE (gdw/g N)	31.54	<0.0001	3.15	0.0992	6.96	0.0204	-68	-41
PUE (gdw/g P)	7.10	0.0195	2.77	0.1200	1.45	0.2498	-36	-36
Belowground properties								
Belowground C (Mg/ha)	6.84	0.0213	16.30	0.0014	2.22	0.1599	116	11
Belowground N (Mg/ha)	7.01	0.0201	16.88	0.0012	0.56	0.4664	136	41
Litter C:N	39.54	<0.0001	0.32	0.5816	5.99	0.2940	-45	-33
Root C:N	29.48	0.0001	0.19	0.6682	3.71	0.0761	-47	-31
Soil C:N	0.38	0.5474	1.73	0.2109	0.02	0.8968	-6	-24

Notes: Abbreviations are: AGB, aboveground biomass; ANPP, aboveground net primary productivity; NUE, nitrogen-use efficiency; PUE, phosphorous-use efficiency; and gdm, grams dry mass. Degrees of freedom for all *F* values are 1, 13. Results significant at *P* < 0.05 are shown in boldface.

content for an introduced species was three times higher than the wood N content for *Metrosideros*, and it also had lower wood P content than all but a few introduced species (*Falcataria* was a notable exception; Fig. 5). Because *Metrosideros* is the most dominant native species in all the native sites, the very low rate of N and P storage to wood tissue contributed to a much higher NUE and PUE compared to the novel forests, particularly on the youngest sites that are almost completely dominated by *Metrosideros*.

Belowground properties

Belowground carbon ($F_{1,13} = 16.3026$, $P = 0.0014$; Table 2, Fig. 6a) and nitrogen stocks ($F_{1,13} = 16.8833$, $P = 0.0012$; Fig. 6b) each increased significantly with increasing substrate age in both novel and native forests, and novel forests had higher belowground carbon ($F_{1,13} = 6.8446$, $P = 0.0213$) and nitrogen stocks ($F_{1,13} = 7.0135$, $P = 0.0201$) stocks at a given substrate age. Belowground pools in novel forests were generally more N rich than those in native forests. Litter C:N ratios (i.e., higher N content in belowground organic matter) were much lower in novel compared to native forests ($F_{1,13} = 39.5385$, $P < 0.0001$; Fig. 7a). Root organic matter pools also had lower C:N ratios in novel forests ($F_{1,13} = 29.4811$, $P < 0.0001$, Fig. 7b). Soil C:N ratios did not differ significantly between novel and native forests ($F_{1,13} = 0.3817$, $P = 0.5474$; Fig. 7c).

DISCUSSION

Changing composition, diversity, and ecosystem function

We found strong support for the hypothesis that introduced species increase net species richness and local diversity for trees ≥ 2 cm diameter in lowland tropical forests on Hawai'i Island. (i.e., native plus introduced species; Fig. 2a, d). Our findings suggest that this local area is following regional patterns of increasing plant species richness due to introduced species in which successful introductions exceed extinctions (Sax 2002, Sax and Gaines 2003, 2008).

Globally high rates of introduction and low rates of extinction may be influenced by an extinction lag (Barnosky et al. 2011). Although none of the native tree species considered here are presently at risk of extinction, several lines of evidence suggest that their declining abundance in lowland forests is likely to continue. For example, the novel forests studied here had very low abundances of native tree species (~8% of basal area), and previous studies in these and similar forests suggest that native species are generally declining in abundance (Mascaro et al. 2008). Native species such as *M. polymorpha*, *D. sandwicensis*, and *M. lessertiana*, while still present at many of the novel forest sites considered here, experience dramatic decreases in growth rates and increased mortality following colonization by the introduced species *F. moluccana* and *P.*

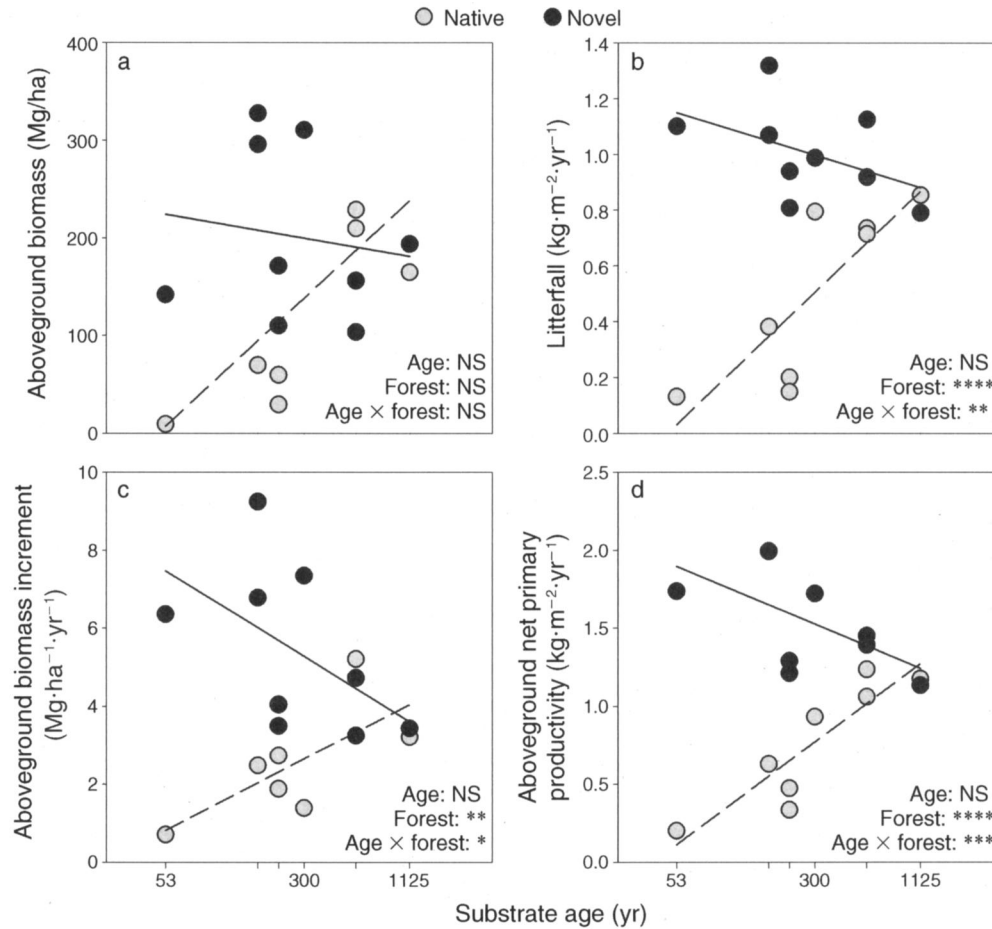


FIG. 3. Aboveground ecosystem properties and processes, including (a) aboveground biomass (AGB), (b) litterfall (leaves + stems <1 cm diameter), (c) AGB increment, (d) aboveground net primary productivity calculated as the sum of litterfall and AGB increment, in nine novel (solid line) forests dominated by introduced species compared to eight native forests (dashed line). Sites are found on a primary successional matrix of lava flows in lower Puna, Hawai'i Island. Significance levels reflect results of analysis of covariance, with substrate age (i.e., age) as the covariate (log-transformed to provide normality) and forest type as a fixed factor. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS, not significant.

cattleianum (among others) and are likely to be extirpated from lowland forests (Hughes and Denslow 2005, Ostertag et al. 2009). While some native species will continue to decline, tree diversity may remain higher in novel vs. native forests if novel forests retain a minimal number of native species or continue to acquire introduced species. At least two native species (*P. odorata* and *P. hawaiiensis*) are able to complete their life cycle beneath the canopies of introduced trees, and persist in one region that has been dominated by introduced trees for 80 years (Mascaro 2011). Introduced species are also continually spreading in the Hilo and Puna districts, and thus, novel forests may continue to increase in tree diversity (Little and Skolmen 1989, Mueller-Dombois 2008).

We found strong support for our second hypothesis that ecosystem function in novel forests would meet or exceed levels found in native forests in terms of aboveground biomass and productivity (sensu Naeem et al. 1994, Tilman et al. 2001), nutrient turnover (as

measured here by soil-available N and P and that cycled through litter; sensu Naeem et al. 1994), and belowground carbon storage (sensu Tilman et al. 2001). All significant changes in ecosystem functional properties

TABLE 3. Estimated intersection (age in years since lava flow formation) of native and novel forest trendlines in several ecosystem parameters.

Variable	Age of equality (yr)	95% CI	
		Lower	Upper
Litterfall ($\text{kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	1168	504	2708
AGB increment ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	932	334	2600
ANPP ($\text{kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	1070	541	2113
Litterfall N mass ($\text{g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	1633	429	6218
NUE (gdm/g N)	1738	413	7309

Notes: The lower bound may be viewed as the earliest age along the primary successional gradient in lowland Hawaii at which native and novel forests converge on a given ecosystem property. Abbreviations are: AGB, aboveground biomass; ANPP, aboveground net primary productivity; NUE, nitrogen-use efficiency; and gdm, grams dry mass.

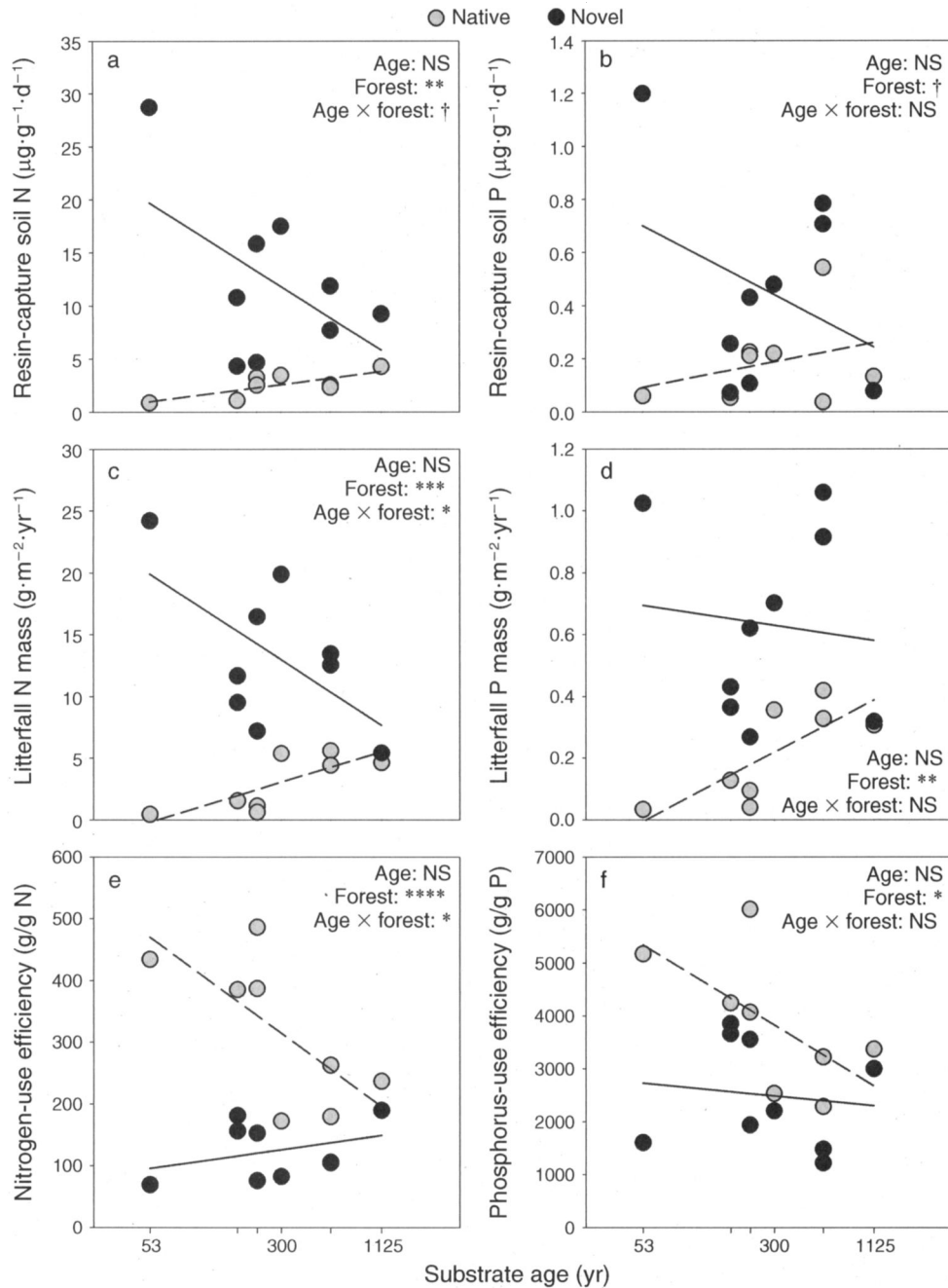


FIG. 4. Nutrient availability and efficiency of nutrient use, as assessed by (a) resin-capture soil N, (b) resin-capture soil P, (c) litterfall N mass, (d) litterfall P mass, (e) aboveground N-use efficiency (estimated as g dry aboveground production per unit N lost to litterfall or stored to wood), (f) aboveground P-use efficiency, in nine novel (solid line) forests dominated by introduced species compared to eight native forests (dashed line). Sites are found on a primary successional matrix of lava flows in lower Puna, Hawai'i Island. Significance levels reflect results of analysis of covariance, with substrate age (i.e., age) as the covariate (log-transformed to provide normality) and forest type as a fixed factor.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; † $P < 0.1$; NS, not significant.

increased with the increase in tree species richness and diversity in novel forests. The magnitude of diversity change was narrowest on younger lava flows where the changes in function were the greatest (e.g., compare Fig. 2d and Fig. 3d); this conforms with the theoretical prediction of the biodiversity–ecosystem function par-

adigm (and empirical evidence) that the greatest changes in function as driven by diversity occur at diversity levels closest to zero (as evidenced by the steeply asymptotic relationships between function and diversity; e.g., Tilman et al. 1997b, Wardle 2002, Schnitzer et al. 2011).

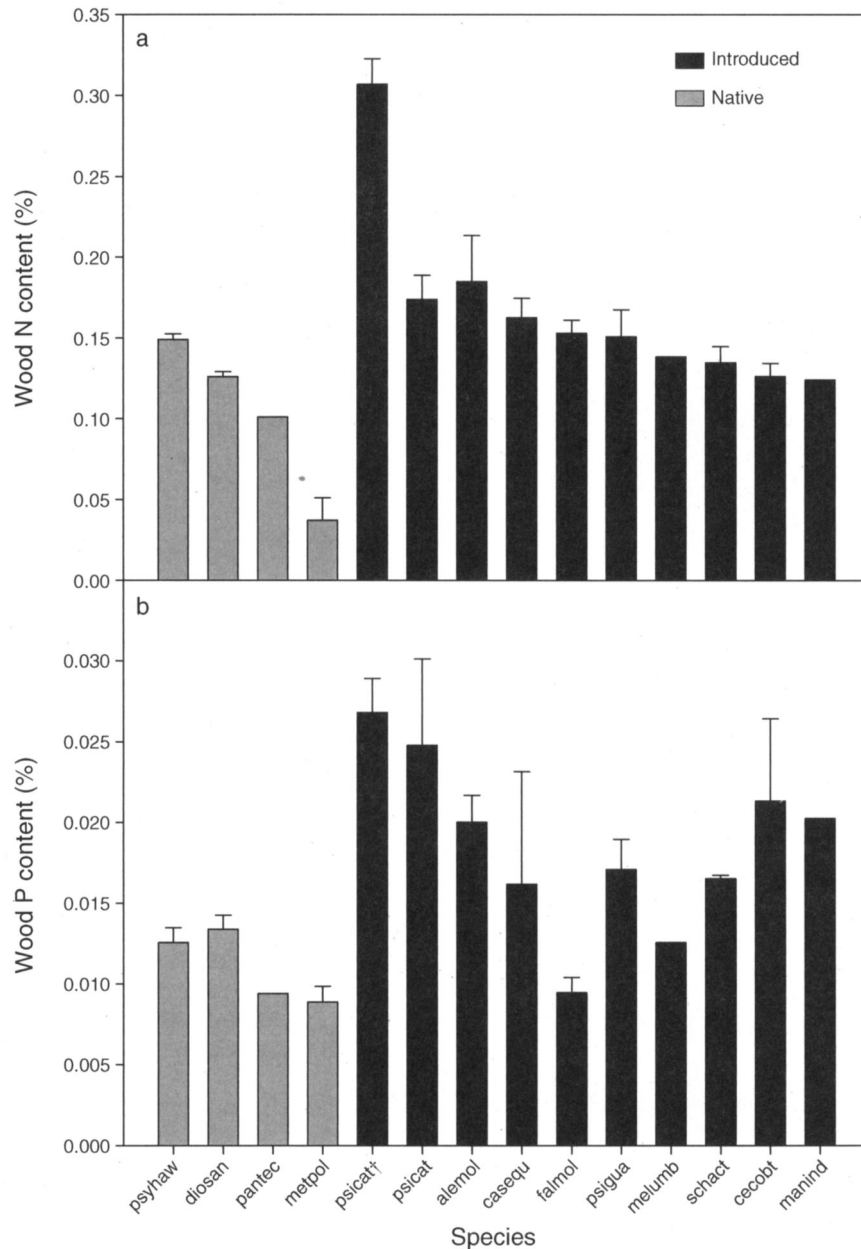


FIG. 5. (a) Wood nitrogen (N) and (b) phosphorus (P) content for four common native species and nine common introduced species in native and novel forest sites in lowland tropical forest on Hawai'i Island. Wood N content in *Psidium cattleianum* varied between sites dominated by introduced N₂-fixing species (psicatt†) and those without N₂-fixing species present (psicat). Standard error bars reflect variation among sites. For dominant species (see Table 1), 10 separate trees were composited to create one sample at a site; for other species, three trees were used. Abbreviations are: psychaw, *Psychotria hawaiiensis*; diosan, *Diospyros sandwicensis*; pantec, *Pandanus tectorius*; metpol, *Metrosideros polymorpha*; alemol, *Aluettia moluccana*; casequ, *Casuarina equisetifolia*; falmol, *Falcataria moluccana*; psigua, *Psidium guajava*; melumb, *Melochia umbellata*; schact, *Schefflera actinophylla*; cecobt, *Cecropia obtusifolia*; and manind, *Mangifera indica*.

We also found strong support for our third hypothesis that functional changes would be greater in novel ecosystems dominated by N₂-fixing tree species than in novel ecosystems dominated by non-fixing tree species. Hawai'i has few native N₂-fixing tree species at low elevations, none of which is capable of dominating the canopy, while introduced N₂-fixing tree species thrive in

Hawaii's N-limited basaltic lava flows. Significant interactions between forest type and substrate age indicated that increases in productivity and several other ecosystem properties and processes steadily declined with increasing substrate age. In no case did these significant differences extend to 575-year-old substrates, where we first find novel forests dominated

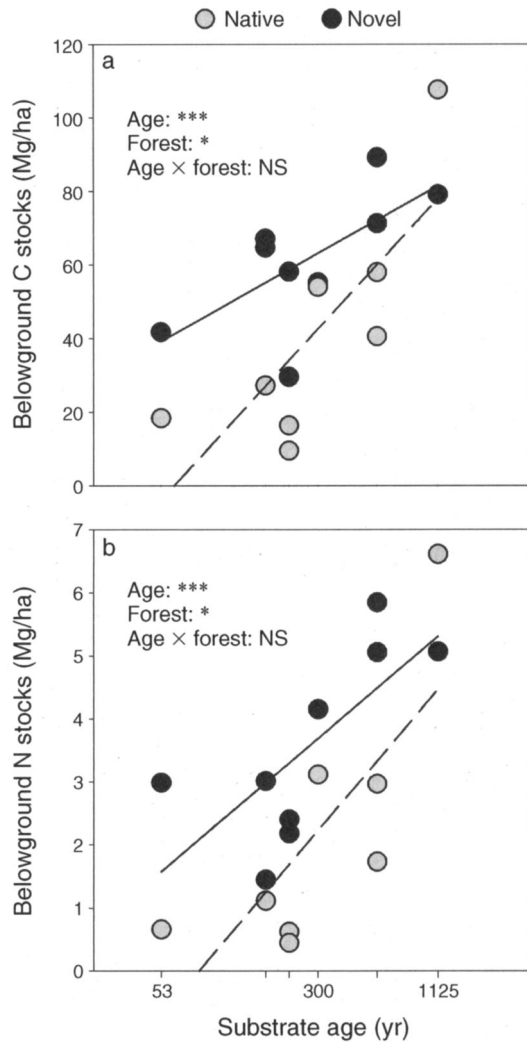


FIG. 6. Belowground (a) carbon and (b) nitrogen stocks in eight native (dashed line) and nine novel, exotic-dominated sites along a primary successional gradient of increasing substrate age in lowland tropical forests in the districts of Hilo and Puna, Hawai'i Island. Significance levels reflect results of analysis of covariance, with substrate age (i.e., age) as the covariate (log-transformed to provide normality) and forest type as a fixed factor.

* $P < 0.05$; *** $P < 0.001$; NS, not significant.

by non- N_2 -fixing species (lower bound, 95% confidence interval; Table 2). Thus, the changes in ecosystem function brought on by the compositional shift from historically dominant native species to introduced species was overwhelmingly influenced by the functional traits of those introduced species.

Binkley et al. (2004) noted that shifting species functional traits can drive increases in productivity by either increasing the availability of resources (through total inputs or turnover rates), or by increasing the efficiency of resource use; the evidence presented here supports the former. In novel forests, productivity

increases as driven by changing species composition are partly the result of increased N inputs in the N-limited environment, and may also be related to increased N and P turnover in these systems. Rock-derived P, in particular, may become increasingly available due to higher metabolic activity in novel forests, in turn, increasing weathering of primary minerals at these sites (Hughes and Denslow 2005).

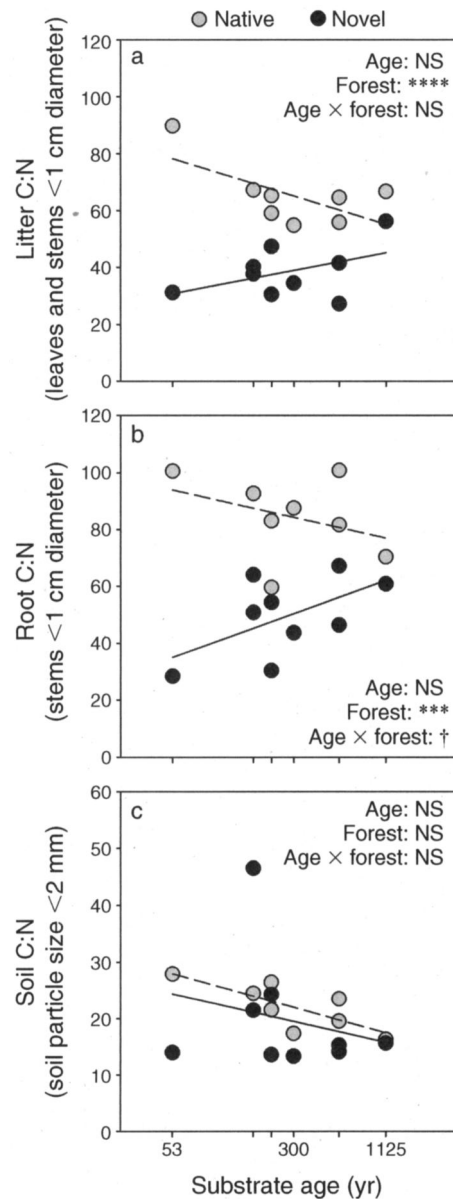


FIG. 7. C:N ratios within belowground pools of (a) litter, (b) roots, and (c) soil in eight native (dashed line) and nine novel, exotic-dominated (solid line) tropical forest sites along a primary successional gradient of increasing substrate age in lowland Hawai'i Island. Significance levels reflect results of analysis of covariance, with substrate age (i.e., age) as the covariate (log-transformed to provide normality) and forest type as a fixed factor.

*** $P < 0.001$; **** $P < 0.0001$; † $P < 0.1$; NS, not significant.

Furthermore, although increased nutrient-use efficiency may be a strategy employed by some introduced species in nutrient-limited environments (Funk and Vitousek 2007), we found that novel forest NUE and PUE were generally lower than in native forests.

Our estimates of NUE and PUE depend on two important assumptions. First, we assumed a universal leaf mass ratio for all stems (follows Enquist and Niklas 2002), although this parameter varies by species. For adult trees, however, where nearly all of wood increment occurs, the wood fraction of AGB predicted by this equation is >99%, and thus increasing or decreasing it slightly has a nominal influence on the value of the divisor in our nutrient-use efficiency estimations (i.e., nutrients lost to litter or stored to wood); the influence is particularly low relative to the different productivity levels at the sites (Fig. 3d), and differences in wood chemistry between native and introduced species (Fig. 4). Second, we did not consider nutrient residence time, which is an important factor in nutrient-use efficiency (Berendse and Aerts 1987, Laungani and Knops 2009). However, *Metrosideros* has a relatively long leaf life span compared to other tropical tree species (particularly relative to many of the introduced species considered here; Reich et al. 1992, Cordell et al. 2001), and therefore accounting for nutrient residence time would likely increase (rather than decrease) the disparity between native and novel forest nutrient-use efficiencies. Thus, the interpretation that novel forests have lower nutrient-use efficiencies than native forests should be robust to these assumptions.

Our study is one of the few to detect a strong influence of introduced species on belowground carbon storage. In this case, novel forests had higher belowground carbon stocks than native forests, although the increase was an order of magnitude higher on young substrates where novel forests were dominated by introduced N₂-fixing tree species. A previous review found that introduced N₂-fixing trees typically increase belowground carbon storage, while introduced non-N₂-fixing trees can cause the loss of belowground carbon (Ehrenfeld 2003). On Hawai'i, G. P. Asner and R. A. Martin (*personal communication*) have found that forest ecosystems dominated by introduced *Psidium* had higher soil respiration and net ecosystem respiration than ecosystems dominated by native *Metrosideros*, with a possible negative influence on belowground stocks, though this has yet to be quantified. Similarly, Litton et al. (2008) found that grass invasion in drier ecosystems on Hawai'i Island greatly increased soil CO₂ efflux, though belowground carbon pools are as yet unaltered.

The increase of belowground carbon due to colonization by introduced species with higher aboveground biomass and production may be a consistent feature of primary successional systems (e.g., Vitousek and Walker 1989, Titus and Tsuyuzaki 2003, Walker and del Moral 2003, Titus 2009). Compared to older soils (where high

biomass species introduction can reduce belowground carbon stocks; Jackson et al. 2002), primary successional environments have less (if any) long-lived carbon pools to lose. In our study area, for example, Hughes and Uowolo (2006), and R. F. Hughes and A. Uowolo (*unpublished data*) found that decomposition of a wide variety of litter types with varying qualities (i.e., various C:N and C:lignin ratios) proceeded much more rapidly at sites dominated by introduced *Falcataria* than sites dominated by native *Metrosideros*. Despite this, we observed an increase in belowground carbon storage in novel forests (Fig. 6), suggesting that the increase in organic matter fluxes into the soil overcame any increases in losses due to higher decomposition. Indeed, the increases in belowground carbon and nitrogen storage that we observed occurred alongside N enrichment of organic matter in belowground pools (Fig. 7), which might be predicted to increase decomposition rates.

Mechanisms for the diversity effect

Although our study was comparative rather than experimental, it is useful to consider why our results agree with the predictions of the biodiversity–ecosystem function paradigm. There are two non-mutually exclusive mechanisms that are purported to cause a positive effect of diversity on ecosystem function: (1) the selection effect, which suggests that when a greater number of species are present in a community (as “selected” in the case of manipulative experimental plots; Huston 1997, Fargione et al. 2007), there will be a higher probability that intrinsically productive species are present; and (2) niche complementarity, whereby species in diverse communities achieve a greater overall uptake of resources (Tilman et al. 1997b).

First, the increases in productivity we observed are ultimately dependent on a regional-scale selection effect. As the size of Hawaii's flora increases, the probability that highly productive and competitive plant species will colonize its various communities is increasing: in our study, the introduction of symbiotic N₂-fixing tree species allowed for higher productivity than is found in native forests that lack these plant functional types. Several studies, including this one, show that these introduced N₂-fixing tree species are particularly well suited to the strongly N-limited primary successional environments in lower Puna (Vitousek et al. 1987, Vitousek and Walker 1989, Hughes and Denslow 2005). Other plant functional types are becoming more prevalent in Hawaii due to the sampling of the global flora, including a dramatic increase in the diversity of large tree species, some of which dominate the novel forests we studied (Fig. 1), combined with a broad increase in the diversity of leaf chemistries and physiological strategies (Baruch and Goldstein 1999). Collectively, the addition of introduced species to the depauperate Hawaiian flora is increasing the breadth of plant functional traits.

There is also evidence for positive species interactions among introduced species (e.g., facilitation), which provide a potential mechanism for the diversity–productivity effect found in manipulative biodiversity experiments (Fargione et al. 2007). In our study area, when introduced N₂-fixing tree species colonize N-limited areas, the growth of one introduced tree species increases (i.e., *Psidium cattleianum*; Hughes and Denslow 2005). This was also documented by Vitousek et al. (1987) for N fixed by the introduced *Morella faya* in nearby Volcanoes National Park. This pattern is consistent with “overyielding” as observed in manipulative biodiversity experiments in which higher production of biomass by a species in high-diversity plots is observed compared to lower production by the same species in monoculture (HilleRisLambers et al. 2004). Biodiversity manipulations have found that the presence of N₂-fixing plant species is by far the strongest driver of overyielding by non-N₂-fixing species (Tilman et al. 2001, Spehn et al. 2005). Thus, both the selection and complementarity effects may partially explain our results.

Wilsey et al. (2009) demonstrated experimentally that the selection effect was stronger in novel than native grassland communities, while niche complementarity was weaker, and the results of our comparative study are compatible with this finding. In our novel sites on young substrates, the relative production by N₂-fixing species is overwhelmingly responsible for the observed increases in productivity, while the contribution of *Psidium* by complementarity is a small, though measurable factor (i.e., consider the relative dominance of *Psidium* in conjunction with its RGR; Appendices E and I). That diversity–productivity mechanisms in novel communities would be primarily driven by the selection effect fits the evolutionary naiveté expected for novel communities (Wilkinson 2004).

Implications

As noted previously, the biodiversity–ecosystem function paradigm has frequently been invoked in cases of diversity declines due to extinction, but has rarely been invoked in cases of diversity increases due to introduced species. Yet, the emergence of novel ecosystems is the synthetic outcome of changes in species richness and diversity operating at multiple spatial scales (Wardle et al. 2011), and this suggests that diversity increases are at least as important to consider in the context of the functional effects of biodiversity as diversity losses (sensu Naeem 2002). We have highlighted local diversity increases in lowland tropical forests on Hawai'i Island, but whether local diversity increases or decreases generally as novel ecosystems emerge is unknown. While regional trends in plant species richness increases are consistent across islands and mainlands (Sax and Gaines 2003), Hawaiian forests may be more prone to local diversity increases than mainland forests due to their depauperate flora (Mueller-Dombois 2008).

In temperate forests in Wisconsin, for example, local declines in plant richness occur in spite of regional plant richness increases (Rooney and Waller 2008). We may also expect different patterns in non-forest ecosystems; for instance, Wilsey et al. (2011) found that novel mainland grasslands in Texas, USA, tended to have lower species diversity than did native grasslands. In this case, as with many novel grasslands across the United States, the sites had a legacy of nutrient enrichment that has been shown experimentally to lead to diversity declines (Tilman 1987). Additionally, constraints imposed by ecosystem structure and nutrient availability may limit or enhance the role of diversity. On Hawai'i, for example, introduced grass species may result in the transformation of a forest to a grassland, with implications for ecosystem function that have little to do with diversity (Hughes et al. 1991, D'Antonio and Vitousek 1992, Litton et al. 2006). By contrast, in this comparative study, as in several experimental tests (e.g., Tilman et al. 2001, Spehn et al. 2002), high N limitation created an environment in which the addition of N₂-fixing species had an enhanced effect on ecosystem function. Given the complexities of diversity change (Wardle et al. 2011), future monitoring will be essential to determining how diversity changes lead to functional outcomes.

Our results highlight a strong disconnect between the conservation interest in protecting the functioning (biogeochemistry) and services (human welfare benefits) provided by ecosystems, and the theoretical architecture often used to support that conservation interest. The biodiversity–ecosystem function paradigm has been developed and tested in a quantitative and directional sense, i.e., wherein a decline in productivity or nutrient turnover constitutes “impairment” of ecosystem function (sensu Naeem et al. 1994). In the policy and conservation arena, however, a qualitative value is often placed on ecosystem function, in which any *change*, regardless of direction, is deemed to be impairment (Thompson and Starzomski 2007). Hawai'i is a perfect example: The increases in (or maintenance of) productivity caused by introduced species in lower Puna are considered by most to be a form of degradation and impairment. Many of the functional changes caused by novel forests are detrimental to native species (e.g., by changing habitat conditions; Hughes and Denslow 2005, but see Lugo 2004), and some may be directly detrimental to human welfare, such as increased nitrogen loading from N₂-fixing forests. The novel forest ecosystems that we studied provide little habitat for native species, including native birds and insects that are found nowhere else on Earth, and their continued proliferation is interrupting cultural resources provided by native species (Ziegler 2002). Srivastava and Vellend (2005) highlighted this incongruence between theory and application and concluded that, for the reasons mentioned here, the biodiversity–ecosystem function paradigm may be accurate, but may not always be relevant to conservation.

On the other hand, insofar as productivity, carbon storage, and nutrient turnover are functional elements of ecosystems that provide the supporting services of nature (*sensu* Fischlin et al. 2007), the fact that they are provided by introduced rather than native species should not impugn their value (e.g., Schlaepfer et al. 2011). Where native ecosystems have long been absent, novel ecosystems clearly provide services, including degraded land reclamation, watershed protection, and carbon storage and sequestration, and can do so without any management investment (Ewel and Putz 2004). For example, novel forests, savannas, and grasslands are now so abundant in Hawaii that they are likely responsible for nearly all ecosystem functioning below 500 m in elevation (Mueller-Dombois and Fosberg 1998). In landscapes where native ecosystems are totally absent, the utilization of novel ecosystems for the basic biogeochemical processes of nature should be considered. In matrix landscapes with residual native ecosystems, a cost–benefit consideration should be made by considering risks to native ecosystems from nearby novel ecosystem propagule pressure (Simberloff 2009). In our experience, the presence of novel forests in matrix landscapes in lowland Hawaii is accelerating the decline in native forests. This contrasts with other habitats in which novel ecosystems promote native species abundances after human land degradation (Lugo 2004).

Over the long term, the proliferation of novel ecosystems will likely be the primary way that the biosphere reacts to human modification of lands (Ellis and Ramankutty 2008, Hobbs et al. 2009, Lugo 2009). These transformations are reminiscent of previous reorganizations of communities that have occurred throughout Earth's history in response to various upheavals (e.g., Behrensmeier et al. 1992, Vermeij 2005), although they differ in rate and scope (Jackson 2006). As communities disassemble due to human manipulation, new communities will assemble in their place, incorporating native and introduced species in various proportions depending on local patterns (e.g., contrast Puerto Rico and Hawaii; Lugo and Helmer 2004, Mascaro et al. 2008). In this way, the simplest of functional roles provided by biological diversity (productivity, carbon accumulation, and nutrient turnover)—those that provide for Earth's life support systems (Naeem et al. 1999)—will continue.

ACKNOWLEDGMENTS

We thank A. Uowolo, G. Sanchez, K. Nelson-Kaula, N. Crabbe, M. Kaeske, J. Brown, R. McDowell, and C. McFadden for laboratory and field assistance; P. Hart, K. Carlson, N. Zimmerman, S. Cordell, and other USFS-IPIF and USGS-BRD personnel for contributing vegetation data; and J. Baldwin for assisting in analyses. The collection of below-ground data was made possible by the University of Hawai'i Pacific Internship Program for Exploring Science. G. Asner, R. Laungani, K. McElligott, and two anonymous reviewers commented on a previous draft of the manuscript, which also benefited from insightful discussion with A. Lugo, J. Kellner, C. Farrior, E. Marris, R. MacKenzie, C. Giardina, T. Varga, N.

Lasca, J. Karron, and E. Young, as well as participants of a workshop on novel ecosystems at the Ecological Society of America meeting in Milwaukee, Wisconsin, in 2008. This research was supported by a National Science Foundation Graduate Research Fellowship to J. Mascaro, a Doctoral Dissertation Improvement Grant to S. A. Schnitzer, R. F. Hughes, and J. Mascaro (DEB-0808498), a University of Wisconsin–Milwaukee (UWM) Golda Meir Library Scholar Award to J. Mascaro, and a UWM Graduate Fellowship to J. Mascaro. Additional funding and logistical support was provided by the USDA Forest Service Institute for Pacific Islands Forestry.

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SUPPLEMENTAL MATERIAL

Appendix A

Map of 17 site locations (*Ecological Archives* M082-009-A1).

Appendix B

Relative density of all stems at eight native sites (*Ecological Archives* M082-009-A2).

Appendix C

Relative dominance of all stems at eight native sites (*Ecological Archives* M082-009-A3).

Appendix D

Relative density of all stems at nine novel sites (*Ecological Archives* M082-009-A4).

Appendix E

Relative dominance of all stems at nine novel sites (*Ecological Archives* M082-009-A5).

Appendix F

Allometric equations used to estimate aboveground biomass (*Ecological Archives* M082-009-A6).

Appendix G

Species-specific assignment of allometric equations and wood density values (*Ecological Archives* M082-009-A7).

Appendix H

Relative growth rates at eight native sites (*Ecological Archives* M082-009-A8).

Appendix I

Relative growth rates at nine novel sites (*Ecological Archives* M082-009-A9).

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.rs7b0>