



## Patterns of Primary Succession of Native and Introduced Plants in Lowland Wet Forests in Eastern Hawai'i

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### ABSTRACT

The majority of Hawai'i's lowland wet forests no longer exist, with many of the last remaining patches found on the eastern, windward sides of the largest islands. To better understand successional patterns and invasion in these native systems, we quantified basal area (BA) and densities of woody species and understory cover at nine sites in the Puna district on the Island of Hawai'i, representing age gradients of native stand development on both 'a'ā and pāhoehoe lava flows. On both flow types, BA of native species increased (from 5 to 50 m<sup>2</sup>/ha) and stem densities decreased (from 3700 to 2600 stems/ha) with increasing stand/flow age. Both native and introduced species compositions diverged between substrate types on older flows. We found that lowland wet native forests remain at least partially intact in several locations, but their functional and compositional integrity is increasingly compromised by invasion of nonnative species, such as *Psidium cattleianum* and *Melastoma candidum*, which become more common at sites greater than 300-yr old. This time period may represent a threshold, after which abiotic environmental conditions no longer constrain recruitment of introduced species. On older flows, nonnative stem densities swamped those of native species by an order of magnitude, with nonnative stems (height > 1.3 m) achieving densities as high as 18,000 stems/ha. In addition, all stands lacked recruitment of native woody species in the understory, suggesting that without management, the native components of these forests may soon no longer be self-sustaining.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

**Key words:** ecosystem development; invasive species; *Melastoma candidum*; *Metrosideros polymorpha*; *Psidium cattleianum*.

DESPITE THE PREVALENCE OF NONNATIVE SPECIES THROUGHOUT Hawai'i (Wagner *et al.* 1999), not all of Hawai'i's diverse ecosystems have been invaded by nonnative species to the same degree (Mueller-Dombois & Fosberg 1998). It has been demonstrated elsewhere that the relative susceptibility of a given ecosystem to invasion by introduced flora is, at least in part, due to resource availability (Huenneke *et al.* 1990, Stohlgren *et al.* 1999, Davis & Pelsor 2001, Daehler 2003). In Hawai'i, previous studies have demonstrated that biologically available nitrogen (N) is exceedingly low on young lava flows undergoing initial stages of primary succession (Vitousek *et al.* 1993). Available N accumulates with increasing lava flow age (Vitousek *et al.* 1992, Hughes & Denslow 2005), but in a relatively gradual manner constrained by the absence of native Hawaiian N-fixing plant species during early stages of primary succession. Under such conditions, invasibility should be constrained or moderated by low N availability, and prior research has shown that increasing N supply on these young lava flows, either through fertilization or N fixation by nonnative trees, increases abundance of nonnative species (Vitousek & Walker 1989, Ostertag & Verville 2002, Hughes & Denslow 2005).

In addition, tropical lowland wet forest ecosystems on islands are often characterized by a lower species richness—a disharmonic flora—that leads to 'open niches' as compared to continental systems (Simberloff 1995, DeWalt *et al.* 2004, Denslow & DeWalt 2006). A case in point, the native flora of the Hawaiian Islands is highly endemic (89%), yet it is also correspondingly disharmonic, *i.e.*, it lacks several major floral groups as compared to mainland ecosys-

tems (Kitayama & Mueller-Dombois 1992, Wagner *et al.* 1999). This disharmonic flora has been subjected to a remarkable number of nonnative species introductions (Skolmen 1960, Loope & Mueller-Dombois 1989), which has led to a situation in which the number of naturalized, nonnative species present in the Hawaiian flora is roughly equivalent to the number of native species (Wagner *et al.* 1999).

However, despite the prevalence of introduced species in Hawai'i, many questions remain regarding patterns of invasion in native-dominated lowland wet forests undergoing primary succession, particularly in the absence of nonnative N-fixing species. These forests seem to be balancing between two opposing factors. On early successional lava flows, strong N limitation likely leads to low invasibility, instead favoring colonization by native species adapted to low-nutrient conditions. Simultaneously, these native-dominated lowland forest ecosystems, composed of a potentially disharmonic flora, face an abundance of potential invasive species—a situation expected to lead to high invasibility. Specifically, then, how do these two forces—nutrient limitation during early succession and a disharmonic native flora during latter succession—interact within the context of primary succession in lowland wet environments of Hawai'i?

While several studies in Hawai'i have investigated similar questions, most have emphasized succession dominated by native vegetation (Atkinson 1970, Drake & Mueller-Dombois 1993, Aplet & Vitousek 1994, Kitayama *et al.* 1995, Aplet *et al.* 1998, Vitousek 2004), and these studies typically have taken place at higher montane elevations. In addition, although numerous studies have documented the patterns and impacts of nonnative plant invasions in Hawai'i (*e.g.*, Vitousek & Walker 1989, Huenneke &

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Vitousek 1990, Hughes *et al.* 1991, D'Antonio & Mack 2001), few have documented and explicitly emphasized the nature and extent of invasion along successional gradients (but see Aplet & Vitousek 1994, Aplet *et al.* 1998). Successional patterns in lowland wet forests in Hawai'i have received little attention primarily because so little of this ecosystem type remains in existence; most were deforested and converted to agriculture (Kirch 1985, Burney *et al.* 2001, Ziegler 2002). However, remnant patches of native lowland wet forest, which span a large range of successional states, can still be found on the Island of Hawai'i, primarily due to the existence of young (< 750 yr) lava substrates that are unsuitable for agriculture. Consequently, the current state of these remnant lowland wet forests is not well documented or understood, particularly with regard to the degree to which they have been altered by introduced species.

The objectives of this study were to assess the composition, structure, and diversity of lowland wet forests found in the eastern portion of the Island of Hawai'i. We were particularly interested in exploring interactions between successional stage (*i.e.*, early, mid-, or late-successional) and patterns or degrees of invasion. We explored these interactions by quantifying characteristics of forest composition and forest structure across a range of lava flow ages and substrate types. In this paper, we present analyses of species composition, diversity, size class distributions, and degree of nonnative species dominance in relation to these successional factors. In doing so, we highlight the importance of lowland forests as reservoirs of native biodiversity as well as the nature and pattern of nonnative species invasions within a landscape increasingly fragmented by agricultural and residential development.

## METHODS

**SITE DESCRIPTION.**—A series of nine sites on a broad range of available lava flow ages and substrate types on Kilauea Volcano in eastern Hawai'i (Trusdell *et al.* 2005) were selected to provide a census of some of the best remaining examples of remnant native-dominated wet lowland forest (Fig. 1). We define wet as > 2500 mm precipitation at 1000 m and > 3000 mm at sea level delineated using geographic information systems (J. P. Price *et al.* 2007). The 213-yr-old and *ca* 650-yr-old Malama Kī sites (Table 1) could also be classified as moist mesic (< 3000 mm rain at sea level), but precise rainfall data are scarce for that area, and the site is likely near the high end of the moist mesic category. Lowland was defined as < 800 m based on Gagné and Cuddihy (1999) and Price (2004); the upper elevations of this zone correspond with a peak in native species richness across the Hawaiian Islands (Price 2004), which is due to both climatic and anthropogenic factors. Pāhoehoe substrate is characterized as smooth, with a ropy texture and frequent cracks that occur during cooling. In comparison, 'a'ā lava flows are characterized by the rough, jagged, 'clinker' rubble that results from their lower temperature and higher viscosity. 'A'ā and pāhoehoe differ primarily with respect to texture, surface area, and weathering rate, but not chemistry (Macdonald *et al.* 1983), while ash substrates, which overlay either pāhoehoe or 'a'ā, have been shown to increase N availability (Kitayama *et al.* 1995).

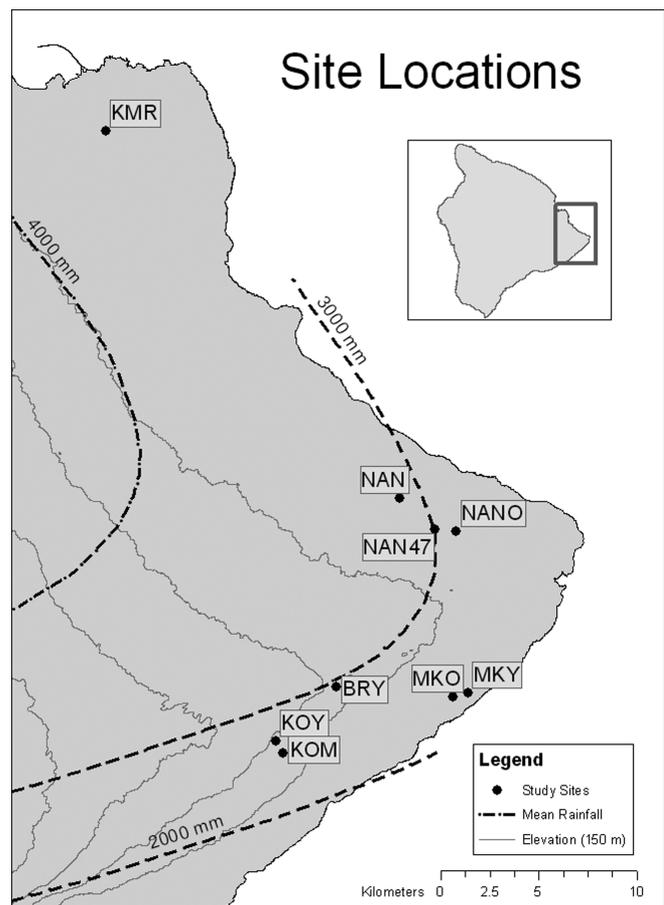


FIGURE 1. Study site locations on the Island of Hawai'i.

**VEGETATION SAMPLING.**—Transects were established at each site, and along each transect a minimum of ten circular plots were established. Intervals between plots were constant within each site, but the length of the fixed intervals varied (from 50 to 100 m) across sites due to limitations imposed by the particular size and extent of each underlying flow. Within these constraints, transects ranged in length from 500 to 1000 m. Vegetation components were sampled using a nested design. In the largest sampling area (*i.e.*, 18-m-radius circular plot), all trees with a diameter  $\geq$  30 cm were identified to species and their diameter at breast height was recorded (dbh; *ca* 1.3 m). In a smaller (9-m radius) concentric plot, trees  $\geq$  2 cm but < 30 cm diameter were identified to species and measured (dbh). All trees < 2 cm diameter but > 1.3 m in height were identified to species and tallied in a third concentric plot of 6 m in radius. Stems were considered to be located within each plot if they were rooted in each plot. Only stems with orientation at breast height > 45 degrees to the vertical were measured; this reduced over-representation of decumbent stems with one or more branches sprouting upward. For trees and shrubs with caespitose growth forms (*i.e.*, having multiple trunks below breast height) the basal areas for each of the trunks (> 45 degrees to the vertical) were calculated, and these were then combined to give the basal area for that individual. A

TABLE 1. Description of the study sites. Substrate age derived from Trusdell et al. (2005).

Site	Code	No. of plots	Latitude (N)	Longitude (E)	Approx. Elevation (m)	Precip. range (mm)	Lava type	Flow age (yr)
Keauohana forest reserve	KOY	10	19°25'21"	154°57'19"	300	2500–3000	'A'a	51
Nānāwale forest reserve	NAN	11	19°32'09"	154°53'47"	75	3000–3500	'A'a	163
Malama Ki forest reserve	MKY	10	19°26'45"	154°51'44"	30	2500–3000	Pāhoehoe	213
Keauohana forest reserve	KOM	10	19°25'02"	154°57'05"	260	2500–3000	'A'a	200–400
Pu'u Kali'u	BRY	13	19°26'52"	154°55'34"	275	2500–3000	Pāhoehoe w/ ash	500
Nānāwale forest reserve	NAN47	10	19°31'18"	154°52'45"	85	3000	'A'a	400–750
Malama Ki forest reserve	MKO	10	19°26'39"	154°52'09"	45	2500–3000	Pāhoehoe	500–800
Keaukaha military reservation	KMR	10	19°42'14"	155°02'30"	15	3300	'A'a	750–1500
Nānāwale forest reserve	NANO	10	19°31'14"	154°52'07"	85	2500–3000	Pāhoehoe	750–1500

unique feature in Hawaiian forests is the presence of tree ferns in the *Cibotium* and *Sadleria* genera. Due to their relatively uniform 'trunk' size from the ground to the apical meristem, tree ferns were measured either at breast height if the individuals were sufficiently tall, or were measured at a height below the hanging frond debris along the trunk. *Cibotium* and *Sadleria* individuals were considered to be above breast height if their fronds reached above 1.3 m—even if their 'trunk' did not. This is justified by the large influence, in terms of shade and litter inputs, that these individuals have on the subcanopy light environment. Site values for basal area ( $\text{m}^2/\text{ha}$ ) and stem density (stems/ha) are given as the mean of all nested plots located within each respective site.

At the two Keauohana sites (KOY and KOM), a slightly different methodology was used because woody species data were previously collected by Hughes and Denslow (2005) using a similar nested circular plot design. At these sites, all stems  $\geq 2\text{-cm}$  dbh within a 5.64-m radius (*i.e.*, a plot area of  $100\text{ m}^2$ ) had their dbh measured and were identified to species. In a concentric subplot of 2.82 m (area =  $25\text{ m}^2$ ), woody stems  $< 2\text{-cm}$  dbh were identified to species and tallied. To compare plots of various sizes, data were extrapolated and compared on a hectare basis.

Understory cover was considered to be herbaceous vegetation as well as woody individuals  $< 1.3\text{ m}$  in height; it was sampled within four  $1\text{-m}^2$  quadrats located in the four cardinal directions (S, E, N, W) at 3, 6, 9, and 12 m, respectively, from the center point of each circular plot. Each quadrat was subdivided into  $10 \times 10\text{ cm}$  squares, and the type of vegetation or substrate directly beneath each of the inner 81 points was identified following the point-quadrat method as described in Mueller-Dombois and Ellenberg (1974). At each point, only the uppermost species below a height of 1.3 m was recorded. If no species were present, then the type of ground cover at that point was recorded. These point-counts were tallied to provide an estimate of understory cover.

**DATA ANALYSIS.**—Importance values (IV) were calculated for each aspect of the study. To account for differences in the area of concentric woody species sample plots, plot-level values were extrapolated

to a hectare basis and these data were used for all further comparison and analysis. For woody stems  $\geq 2\text{-cm}$  dbh, IV was defined as the sum of relative dominance, abundance, and frequency. For woody saplings (dbh  $< 2\text{ cm}$ , height  $> 1.3\text{ m}$ ), IV was defined as the sum of relative abundance and frequency as basal area data were not collected for this class of stems. An overall IV for each woody species was defined as the sum of these two. Understory cover point-counts were converted to percent cover and averaged across samples at each plot. IV were calculated as the sum of relative cover and relative frequency.

Statistical estimators for species richness and diversity index values were calculated using EstimateS 7.5 software (Colwell 2005). For all computations where randomization of runs was required, a default of 50 runs was used without replacement. As not all sites were sampled in an identical fashion, the nonparametric Chao2 incidence-based richness estimator (Chao 1987, Colwell & Coddington 1994) was calculated with log-linear 95 percent confidence intervals based on a standard of ten plots to estimate the richness at each site. Fisher's alpha index of diversity was also calculated (EstimateS 7.5) based on both woody species and tree ferns. This index was chosen because it is relatively unaffected by differences in sample size (Hayek & Buzas 1997, Magurran 2004).

Multivariate ordination was employed to aid in visualizing the similarities and differences between study sites, based on the IV of the species assemblages that were present at each site. Ordination analyses were done using PC-ORD version 4.39 software (McCune & Mefford 1999). Global NMS (nonmetric multidimensional scaling) based on Sørensen (Bray-Curtis) distance was selected as an ordination method based on its strength with nonnormal, discontinuous, or nonparametric data sets, and its minimal set of necessary assumptions (Kenkel & Orloci 1986, Bradfield & Kenkel 1987, Clarke 1993, McCune & Grace 2002). For both understory cover and woody species ordinations, a three-dimensional solution was chosen by following the standard protocol described by McCune and Mefford (1999).

Regression analyses were conducted with Intercooled Stata version 8.0 for OS X (StataCorp 2003) and SigmaPlot version 8.0 for Windows (SPSS 2002).

## RESULTS

**WOODY VEGETATION.**—Including both woody species and tree ferns, we identified 43 species across the nine sites, with 24 species being the maximum number estimated to occur at any one site (Table S1). On substrates older than *ca* 300 yr, richness of both introduced and native species increased (Table S1), but no significant patterns in diversity were found with substrate age. Values for Fisher's alpha index of diversity ranged from 0.08 to 1.07 (Table S1). *Metrosideros polymorpha*, a native tree, was the only species common to all nine sites (Table S2), and this species had high IV at all sites. The most widespread introduced species present was *Psidium cattleianum*, which became prevalent on substrates older than 200 yr.

Total basal area ranged from 2.4 m<sup>2</sup>/ha to 54.7 m<sup>2</sup>/ha (Table S3). Native species basal area values were greater than those for introduced species across all sites, with the largest values (54.3 m<sup>2</sup>/ha and 46.0 m<sup>2</sup>/ha) occurring at the intermediate-aged sites (Figs. 2 and 3A). Introduced species basal area increased with substrate age ( $R^2 = 0.71$ ,  $F_{1,7} = 16.9$ ,  $P < 0.005$ ), while native species basal area did not show a linear relationship with substrate age ( $P = 0.48$ ). *Metrosideros polymorpha* was a large component of basal area across all sites, with *P. tectorius* becoming important at the oldest pāhoehoe sites (Table S3).

While introduced species densities increased with substrate age from 0 to >17,000 individuals/ha ( $R^2 = 0.96$ ,  $F_{1,7} = 155$ ,  $P < 0.001$ ), native densities were comparatively constant (1870–3697

individuals/ha) across all sites and were less significantly correlated with substrate age ( $R^2 = 0.40$ ,  $F_{1,7} = 4.7$ ,  $P = 0.07$ ). Increased abundances of introduced species were most evident at the oldest 'ā'ā and pāhoehoe sites (Fig. 3B). *Psidium cattleianum* and *Melastoma candidum* were consistently the largest contributors at all sites. *Metrosideros polymorpha* was virtually the sole contributor to native stem densities at young sites (Table S4).

Distribution of trees among size classes also differed among sites. Native species accounted for most of the largest stems at all sites (Fig. 2). At young sites (< 400 yr), native species, primarily *M. polymorpha*, accounted for nearly all of the stem density and stand basal area (Fig. 2A–D and Table S2). At sites older than 400 yr, densities of nonnative saplings were greater than densities of native saplings, and these differences were amplified with increasing lava flow age (Fig. 2E–I; Table S4).

NMS based on species IV (stress value = 1.19, Monte Carlo  $P < 0.05$ ) showed separation between sites of different substrate ages (Fig. 4A, B; age vs. Dim3  $R^2 = 0.92$ ). On the older sites (> 400-yr old), species assemblages on 'ā'ā and pāhoehoe substrates tended to diverge from one another. Of the most abundant introduced species, *P. cattleianum* was more closely associated with older pāhoehoe substrates and *M. candidum* was more closely associated with older 'ā'ā sites.

**UNDERSTORY COVER.**—We identified 57 different understory species across the nine sites, with estimated species richness values ranging from 6 to 30 species per site (Table S1 and S5). On the sites

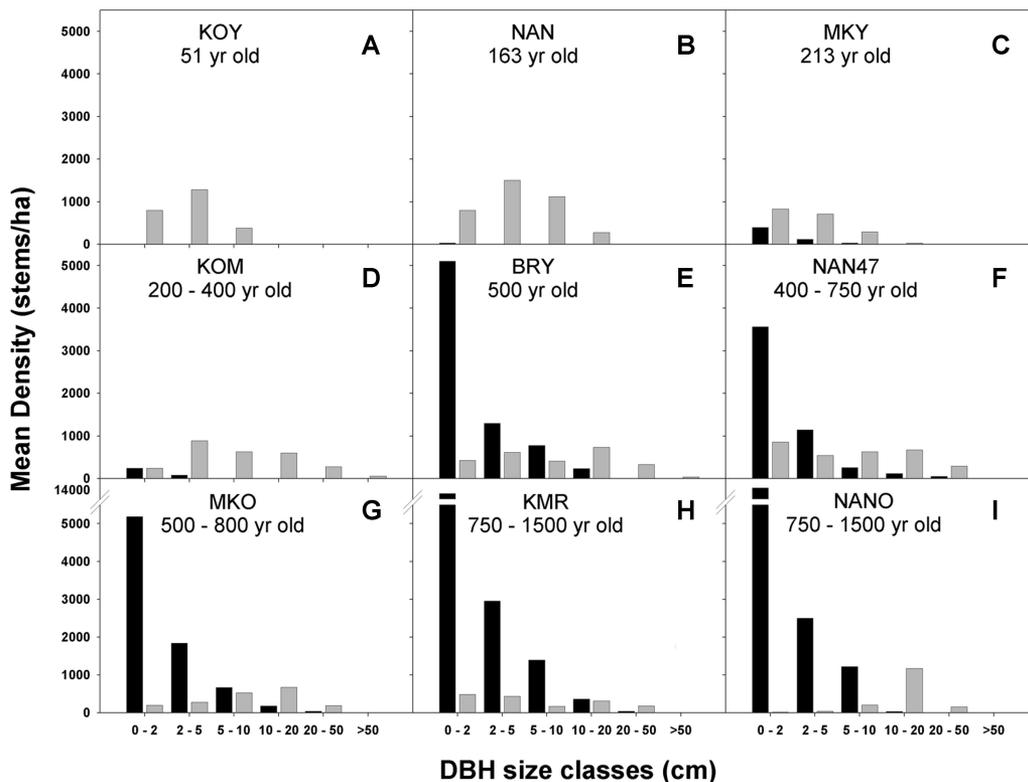


FIGURE 2. Woody species dbh size class histograms, arranged in order by substrate age. Black bars are for introduced species and gray bars are for native species.

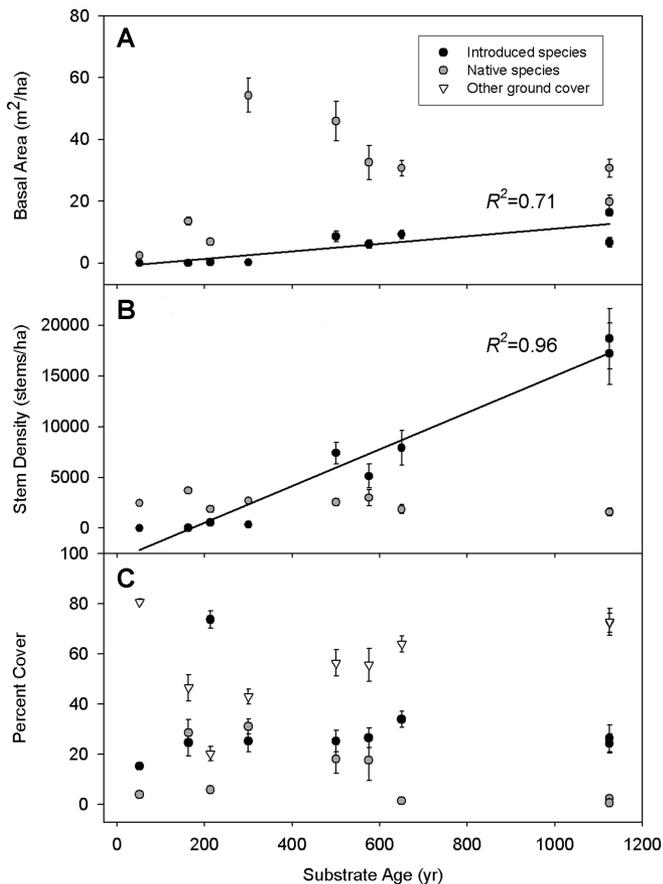


FIGURE 3. Plots consist of mean values across sites (mean  $\pm$  SE) versus substrate age for (A) woody basal area, (B) woody density, and (C) understory percent coverage. Substrate age values represent the midpoint of the substrate age range at each site. Significant linear regressions are included for both introduced species basal area ( $F_{1,7} = 16.9$ ,  $P < 0.005$ ) and introduced species densities ( $F_{1,7} = 155$ ,  $P < 0.001$ ). None of the other variables showed significant linear relationships with substrate age ( $P > 0.05$ ).

older than 400 yr, total percent cover of native understory species ranged from 0.7 to 18.2 percent; introduced understory species cover on these same sites ranged from 24.4 to 34 percent (Fig. 3C). Native woody species contributed relatively little (0.1–1.1%) to average percent cover values at any of the mid- to late-successional sites older than 400 yr. In contrast, introduced woody seedlings were more common (4.2–12.2%) components of understory cover on these latter successional sites. Using NMS based on understory species IV (stress value  $< 0.0005$ , Monte Carlo  $P < 0.005$ ) the sites showed separation based on substrate age (Fig. 4C, D, age vs. Dim1  $R^2 = 0.77$ ). Separation based on substrate type was not as pronounced as with the woody species.

## DISCUSSION

The lowland wet forest sites studied here exhibited several general stages of native forest composition and structure with respect to sub-

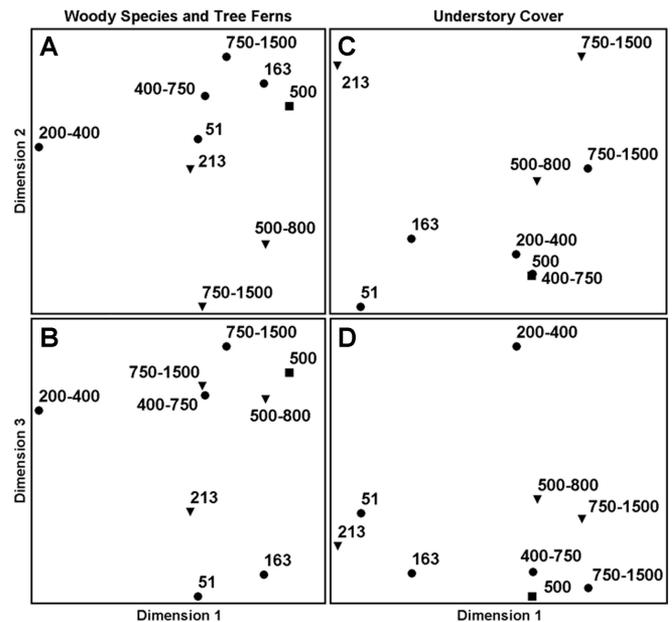


FIGURE 4. Three-dimensional NMS plots of woody species and tree fern importance values (A, B, stress value = 1.19, Monte Carlo  $P < 0.05$ ) and of understory cover (C, D; stress value  $< 0.0005$ , Monte Carlo  $P < 0.005$ ). Symbols represent substrate type, and labels are approximate site ages. Triangles represent sites with pāhoehoe substrates, circles represent sites with 'a'ā substrates, and squares represent sites with pāhoehoe-ash substrates.

strate age, and were consistent with patterns of primary succession in wet montane and dry ecosystems of Hawai'i (Aplet & Vitousek 1994, Kitayama *et al.* 1995, Aplet *et al.* 1998, Vitousek 2004), as well as with previous work examining succession in these lowland wet forests (Atkinson 1970). The younger sites (*ca*  $< 200$ -yr old) were distinguished by having lower species richness values and were composed primarily of stands of *M. polymorpha*, a native tree. While this tree was an important component of woody vegetation across all sites, it was particularly dominant on the youngest sites; this is attributable to its ability to colonize recently extruded nutrient-poor lava substrates (Mueller-Dombois & Fosberg 1998, Mueller-Dombois 2000). This initial, nearly monotypic *M. polymorpha*-dominated phase gradually grades into a more diverse, compositionally complex phase on 200- to 700-yr-old lava flows. As this is happening, other native woody species (*e.g.*, *Diospyros*, *Pandanus*, and *Psychotria*) establish beneath and within a *M. polymorpha* overstory that is generally decreasing in density as it increases in stature. A third phase of native forest succession is characterized by declining densities and basal area of *M. polymorpha* and increasing dominance by aforementioned mid- to late-successional native woody species.

**SUBSTRATE TYPE.**—Our results indicate that in addition to substrate age, substrate type (*e.g.*, pāhoehoe, 'a'ā, and ash) seemed to have influence on successional patterns. Atkinson (1970) found no such trends between 'a'ā and pāhoehoe, but his study focused on a smaller substrate age range and dealt primarily with native species trends,

perhaps because of a lower presence of introduced species at that time. In this study, we noted differences between latter-successional native species assemblages growing on pāhoehoe flows, which were characterized by *P. tectorius* and *M. polymorpha*, and those growing on 'a'ā flows, which were distinguished by the presence of *D. sandwicensis* and *M. polymorpha*. Similar patterns were seen for the introduced species, with larger observed presence of *P. cattleianum* on older pāhoehoe substrates and of *M. candidum* on older 'a'ā substrates. We do not currently understand the cause of this pattern.

**INTRODUCED SPECIES.**—The rapid influx and colonization of introduced species has been shown to be capable of affecting successional patterns of lowland wet forests (Hughes & Denslow 2005). Atkinson (1970) observed that *Psidium guajava*, *Pluchea odorata* (now *Pluchea symphytifolia*), and *Melastoma malabathricum* (now *M. candidum*) were the most abundant introduced species at the time of his study, although they were not a significant component of the forests at that time. Of these, *Pluchea symphytifolia* was not observed in any of the plots in our study. In the forest stands we studied, *P. cattleianum* and *M. candidum* were by far the most prevalent introduced species. While these and other introduced species were quite prevalent during latter-successional stages, they were relatively scarce in forests younger than 300 yr. At these earlier successional sites, the introduced grasses *Andropogon virginicum* and *Schizachyrium condensatum* were an exception to this trend, likely taking advantage of high light availability, and perhaps displacing less-prolific native colonizers.

Previous studies have shown that older sites are more invulnerable because of, among other reasons, greater resource availability (Ostertag & Verville 2002, Hughes & Denslow 2005). It may be that 200–300 yr of soil and forest development in these lowland wet forests represent a successional threshold. This threshold may denote a transition in native-dominated systems from the primarily abiotic constraints on ecosystem succession, which have often been observed on early primary successional lava flows (Vitousek *et al.* 1983, 1993), to one in which nutrient limitation no longer poses as strict a restraint to either native or introduced species. In concordance with our results, Hughes and Denslow (2005) found that the substrate age at which *P. cattleianum* began to appear across sites was *ca* 300 yr in the absence of the facilitative effect of the N-fixing species *Falcataria moluccana*.

**THE FUTURE OF THESE FORESTS.**—Of concern is the fact that native species, particularly *M. polymorpha*, showed very little recruitment on the mid- to oldest-aged sites. As *M. polymorpha* is relatively shade intolerant and slow growing, its presence on older substrates may be limited to individuals from the originally colonizing cohort, as evidenced by the similar basal areas exhibited by practically all individuals within each site. Ongoing studies of *M. polymorpha* productivity in a subset of the lowland wet forests studied here indicate relatively slow incremental growth rates of 0.7 and 2.0 mm/yr on 200- to 400-yr-old and 51-yr-old lava substrates, respectively (R. F. Hughes, pers. obs.). *Metrosideros polymorpha* also exhibits a characteristic cycle of canopy dieback whereby whole stand cohorts undergo concurrent senescence. In the past, the gaps formed as

these slow growing native overstory trees senesced would likely have promoted suitable conditions for subsequent native regeneration. Currently, such gaps likely favor the establishment and proliferation of introduced species capable of fast growth and appropriation of gap-induced pulses of limiting resources.

Our results show that, in terms of both basal area and density, young introduced saplings and herbaceous species dominate the understory of these forests on all substrate types, even while an older, larger, native overstory canopy remains intact, especially on sites older than 300 yr. As such, the future of these forests is uncertain. In 1970, Atkinson observed that whenever the canopy of these lowland wet forests was opened—by cutting, fire, or animals—introduced species rapidly invaded the disturbed area. He predicted then that the future of these forests would be characterized by invasion into these areas by *Psidium* and other introduced species. Hughes and Denslow (2005) have shown that disturbance is not a necessary precursor to invasion by *Falcataria*, and have quantified the drastic changes this species can cause in native ecosystems. Although different in nature, the long-term impacts of introduced species such as *P. cattleianum* and *M. candidum* will likely prove just as detrimental to the integrity of these native ecosystems. *Falcataria*, N-fixing and dominant in the overstory, has a 'top-down' effect on the ecosystems it invades, increasing N availability and decreasing light availability for native overstory dominants. Our results suggest that, in contrast, where subcanopy woody invaders such as *P. cattleianum* and *M. candidum* attain sufficient densities, they have the potential to constrain native plant recruitment—likely through resource competition—and thus have the capacity to profoundly alter the future successional trajectories of these lowland forests, even while a relatively intact native overstory remains in place.

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## SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: [www.blackwell-synergy.com/loi/btp](http://www.blackwell-synergy.com/loi/btp)

Table S1. *Vegetation structure summary showing the components of both woody and understory vegetation at each site.*

Table S2. *Woody species and sapling importance value table.*

Table S3. *Woody and tree fern basal area per hectare of the most common native and introduced plants.*

Table S4. *Woody and tree fern density per hectare of the most common native and introduced plants.*

Table S5. *Understory species importance value table.*

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