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Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i

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ABSTRACT

Ecological invasions are a major driver of global environmental change. When invasions are frequent and prolonged, exotic species can become dominant and ultimately create novel ecosystem types. These ecosystems are now widespread globally. Recent evidence from Puerto Rico suggests that exotic-dominated forests can provide suitable regeneration sites for native species and promote native species abundance, but this pattern has been little explored elsewhere. We surveyed 46 sites in Hawai'i to determine whether native species occurred in the understories of exotic-dominated forests. Native trees smaller than 10 cm in diameter were absent in 28 of the 46 sites and rare in the others. Natives were never the dominant understory species; in fact, they accounted for less than 10% of understory basal area at all but six sites, and less than 4% on average. Sites with native species in the understory tended to be on young lava substrate lacking human disturbance, and were mostly located close to intact, native-dominated forest stands. Even where we found some native species, however, most were survivors of past exotic encroachment into native forest, rather than products of active recolonization by native species. In contrast with successional trajectories in Puerto Rico, Hawaii's exotic-dominated forests can emerge, via invasion, without human disturbance and native Hawaiian plants are largely unable to colonize them once they appear. We suggest that a wide diversity of growth strategies among the exotic species on Hawai'i may limit the opportunities for native plants to colonize exotic-dominated forests.
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1. Introduction

Nearly all of Earth's ecosystems have been impacted to some extent by global environmental change, and ecological invasions are a primary agent of such change (Vitousek et al., 1997a,b). Most studies have focused on the invasion of exotic species into native-dominated, or intact ecosystems (e.g., citations in Mack et al., 2000). However, in areas where exotic species are numerous and persist over time, ecosystem dominance can shift from native to exotic species, effectively creating novel ecosystem types (i.e., variously called new, emerging, or no-analog ecosystems; Seabloom et al., 2003; Denslow and Hughes, 2004; Lugo, 2004; Wilkinson, 2004; Hobbs et al., 2006; Williams et al., 2007; Seastedt et al., 2008). Novel ecosystems are widespread, in some areas covering millions of hectares and becoming more regionally abundant than native ecosystems (Hobbs et al., 2006). In forests, examples exist in South Africa (Versfeld and van Wilgen, 1986), Hawai'i (Vitousek et al., 1987; Mueller-Dombois and Fosberg, 1998; Hughes and Denslow, 2005), Florida (Serbesoff-King, 2003), Argentina (Lichstein et al., 2004), Puerto Rico (Lugo and Helmer, 2004), Central Europe (Kowarik and Körner, 2005), and the Midwestern U.S. (Martin, 1999; Mascaro and Schnitzer, 2007). Novel forests are often ignored in ecological study and management due to their high incorporation of exotic species (Kowarik and Körner, 2005). However, the evidence to date suggests that they are dramatically increasing in abundance, thus warranting increased study (Hobbs et al., 2006).

A key area of uncertainty is whether novel forests will continue to provide ecosystem services, ranging from carbon storage and sequestration to the provision of habitat for native biodiversity (Fischlin et al., 2007). In the fynbos of South Africa, for example, an estimated 10 million ha of exotic pine, acacia, and eucalypt forests have increased transpiration and lowered the water table significantly (Macdonald, 2004; Moran et al., 2005). This interruption of ecosystem services has led the government to spend

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more than US $300 million on aggressive control programs, including biocontrol. In many degraded landscapes, however, novel forests can repair basic ecosystem services such as watershed integrity with little management investment (Ewel and Putz, 2004). The emergence of novel forests may also benefit some native species (Lugo, 1992; Lugo et al., 1993; Ewel et al., 1999; Zavaleta et al., 2001; Lugo and Helmer, 2004; Neilan et al., 2006). In Puerto Rico, Lugo (2004) reported that native species benefited from stand initiation by the exotic pioneer tree *Spathodea campanulata* (African tulip), colonizing these stands after 25 years and becoming co-dominant after 40 years. Without *Spathodea*, native species were less able to colonize disturbed sites after abandonment, where microsites were less favorable and native trees competed poorly with grasses and other herbaceous species. Citing Lugo (2004) as a key example, Ewel and Putz (2004) suggest that exotic tree species could be important tools in ecosystem restoration.

Like those in Puerto Rico, nearly all native Hawaiian ecosystems below ~500 m in elevation were altered or destroyed by centuries of agriculture and development (Mueller-Dombois and Fosberg, 1998; Woodcock, 2003; Lugo, 2004). Many of these areas have since been abandoned, and novel forests have emerged, ranging from monospecific, even-aged stands to diverse, structurally complex forests. Because novel Hawaiian forests have been poorly studied, however, it remains an open question whether they incorporate native species to any degree. Thus, we surveyed the novel forest communities on Hawai'i Island to determine whether native species occurred in their understories.

2. Methods

2.1. Study area

We surveyed 46 exotic-dominated forest sites on the windward side of Hawai'i Island (Fig. 1, Appendix A; see Mueller-Dombois and Fosberg, 1998; Wagner et al., 1999; Ziegler, 2002; Vitousek, 2004 for natural and ecological histories of the Hawaiian Islands). We selected the sites based on inspection of 1990 aerial photography at the Department of Forestry and Wildlife office in Hilo, HI. We considered a site to be exotic-dominated if exotic tree species appeared to constitute >2/3 of the canopy surface area. However, to prevent a possible bias, no site was excluded once selected, even if sampling revealed that exotic species made up <2/3 of the overstory basal area. Although we attempted to include sites from a wide geographic area, our site selection was not random; we were constrained to forests in public parks, forest reserves, and private land where owners were willing to permit access. Half of the sites (23/46) were in forest fragments <50 ha, while the remaining sites were in contiguous forests >50 ha. Within a given contiguous forest, 2–4 sites were placed in areas that differed by parent material age or dominant canopy tree species. The sites in fragments ranged from 10 to 100 m from the nearest forest edge, while those in contiguous forests ranged from 100 m to 1 km from the nearest edge. Fourteen of the sites were adjacent to stands of intact native forest (30%), while the remaining sites ranged from 200 to 4500 m away from native stands. Sites ranged in mean annual precipitation from 2000 to 4000 mm (follows Giambelluca et al., 1986; i.e., subtropical moist forest to

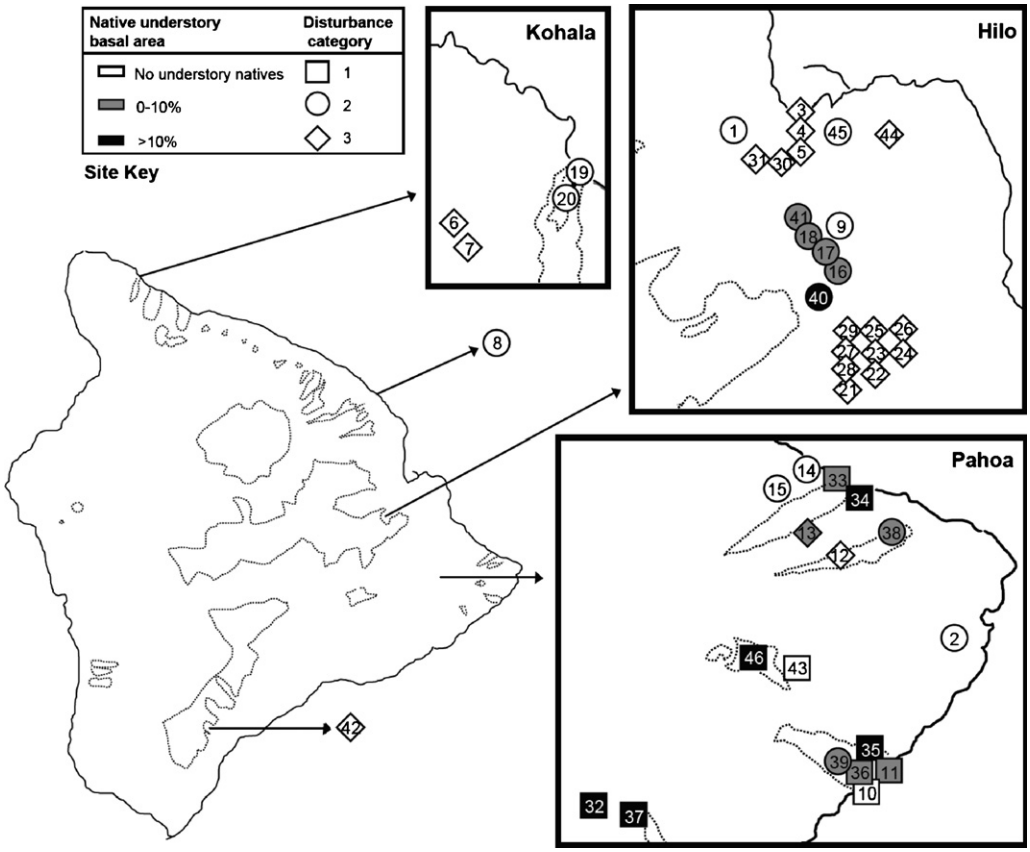

Fig. 1. Map of 46 lowland, exotic-dominated forest sites on the Island of Hawai'i. Site numbers are listed within each symbol (see Appendix A); shading and outline denote mean relative native understory basal area (% of m^2/ha averaged across all 46 sites) and disturbance category, respectively. Disturbance scored 1–3 (1 = undisturbed, 2 = canopy but not soil disturbance, 3 = soil disturbance), as described in the text. Dotted lines outline forest reserves. Two sites (9 and 42) had natives in the recruit layer (0–1.9 cm dbh), which was not included in understory basal area (2–9.9 cm dbh).

subtropical wet forest in the Holdridge life-zone system; Holdridge et al., 1971; Tosi et al., 2001; Price et al., 2007). Sites further ranged from 3 to 570 m in altitude, and thus were considered lowland forests. For 44 of the 46 sites, parent material was basaltic lava rock (either 'a'a, which is rough and blocky; or pahoehoe, which is smooth and ropy) and tephra from the Kilauea, Mauna Loa, and Mauna Kea volcanoes, ranging in age from 51 to 230,000 years since deposition (follows Wolfe and Morris, 1996). Due to weathering processes, these sites generally ranged from bare rock with patchy shallow soil to deep clay according to age (Vitousek, 2004). At two sites (19 and 20), parent material was sand transported by alluvial and marine activity.

We characterized the level of disturbance at each site based on site inspection, aerial photography, and discussion with property owners. Previous studies have utilized time since abandonment (e.g., Lugo and Helmer, 2004); however, we found that Hawaii's exotic-dominated forests are unique in that many have arisen without human disturbance (e.g., Hughes and Denslow, 2005), and thus we used a simple ordinal approach: (1) "undisturbed," for sites with no evidence of canopy or soil disturbance (i.e., sites that became dominated by exotic trees via invasion into intact native forest), (2) "light disturbance," for sites with evidence that a former native forest canopy was removed by humans but no evidence that the site was dozed or tilled, and (3) "major disturbance," for sites with historical evidence of agricultural activity or other evidence that the soil was dozed or tilled. Most sites in this category were farmed for sugar cane and had been abandoned for approximately 22 years at the time of sampling (21–29). Time since abandonment for the remaining sites in this category was unknown (3–7, 12, 13, 30, 31, 42, and 44), but appeared to be >22 years based on a higher mean basal area as compared to the abandoned cane sites (i.e., 34 m^2/ha vs. 23 m^2/ha; Appendix A).

2.2. Sampling methods

We combined three datasets collected using three different spatial approaches, including one dataset previously published by Hughes and Denslow (2005; sites 32, 35, and 37). In all cases, we measured all live and dead trees, lianas, tree ferns, palms, shrubs, and arborescent plants such as bananas using a nested sampling technique based on stem diameter. For all approaches, we differentiated among three size classes: (1) "overstory" stems ≥10 cm diameter at breast height (i.e., dbh; 1.3 m from the ground), (2) "understory" stems 2–9.9 cm dbh, and (3) "recruits" <2 cm dbh and >1.3 m in height. We measured overstory and understory stems to the nearest mm, and tallied all recruits. For all sites, we used nine 1 m × 1 m quadrats to quantify groundcover, woody seedling abundance, and light availability at the forest floor. For each quadrat, we recorded the single most abundant plant species, regardless of life form, estimated the total % cover of all plants ≤1.3 m height, measured light penetration using a concave densiometer (Model C, Forestry Suppliers, Inc.), and tallied all non-herbaceous "seedlings" (i.e., those stems ≤1.3 m in height). We excluded seedlings for which only cotyledons were present.

At 36 sites (1–31 and 42–46) sampled in 2006–2007, we measured all overstory and understory stems and tallied all recruits in a randomly selected 2 m × 80 m transect (0.016 ha total area). Within a 10-m radius subplots at 0, 40, and 80 m, we also measured all overstory stems (~0.1 ha total area). Nine groundcover quadrats were placed at 10-m intervals.

At six sites (33, 34, 36, 38, 39, and 41) sampled in 2006–2007, we randomly established 1–4 transects, and along these transects we placed a total of 10 permanent plots between 40 and 50 apart. A seventh site (40) was smaller and included only five plots. Plot number and spacing were constrained due to the shape of each forest and its underlying lava flow. Within each plot we established an 18-m radius circle wherein we measured all overstory stems ≥30 cm dbh (~1.0 ha total area). Inside a 9-m radius, we measured all overstory stems 10–29.9 cm dbh, and all understory stems (~0.25 ha total area). Inside a 6-m radius, we tallied all recruits (~0.1 ha total area). At each site, nine groundcover quadrats were distributed evenly over each site conterminous with the large plots.

At three sites (32, 35, and 37) sampled in 2001, Hughes and Denslow (2005) established 10 plots between 15 and 25 m apart, following the constraints on forest shape and lava flow extent described above. At each plot, all overstory and understory stems were measured within a 5.64-m radius circle (0.1 ha total area), and all recruits were tallied within a 2.82-m radius circle (0.025 ha total area). At each site, nine groundcover quadrats were distributed evenly over each site conterminous with the large plots 2007.

We attempted to identify all plants to species (nomenclature and nativity follow Wagner et al., 1999; Palmer, 2002), with the exception of grasses, which were not commonly encountered and are represented almost exclusively by exotic species at low elevations on Hawai'i (Mueller-Dombois and Fosberg, 1998). When identification could not be determined, we created morphospecies and collected voucher specimens and/or photographs for submission to Bishop Museum in Honolulu, HI (~1.9% of individuals). In a small number of cases, we were unable to collect a useful sample and these plants are labeled "unknown" (~0.09% of individuals). Based on our familiarity with the native flora, we do not believe any of our morphospecies or unknowns are native plants.

2.3. Data analysis

Because our study included datasets with differing sample areas among sites, we compared all basal area and density measurements on a per-area basis. We ranked the basal area of the overstory and understory species according to mean m^2/ha and the density of understory species and recruits by mean stems/ha among all 46 sites. In contrast, seedling and groundcover plant data were collected with equal sampling effort for each site, and thus we ranked seedlings by the number encountered and groundcover species by the number of quadrats dominated by each species.

3. Results

3.1. General characteristics of novel Hawaiian forests

The novel forests we sampled varied considerably in composition, although at most sites a single species constituted more than 50% of total basal area (Appendix A). Relative dominance among the most dominant species at each site ranged from 19 to 100%, with a mean of 63%. The highest dominance was typically attained by *Falcataria moluccana* (albizia; e.g., 98% at site 32) and *Casuarina equisetifolia* (ironwood; e.g., 95% at site 19), although several other species attained more than 50% dominance, including *Psidium cattleianum* (strawberry guava), *Cecropia obtusifolia* (trumpet tree), *Macaranga mappa* (bingabing), *Trema orientalis* (gunpowder tree), *Melochia umbellata*, and *Cocos nucifera* (coconut palm). Novel forests had many structural elements not present in native forests, due to their incorporation of exotic species with growth strategies that are new or uncommon on Hawai'i. These included hemi-epiphytes and stranglers (e.g., *Schefflera actinophylla* [octopus tree], *Clusia rosea*, and *Ficus microcarpa* [Chinese banyan]), and to a lesser

Table 1
Notable species encountered in the understory layer (2–9.9 cm diameter at breast height) of 46 lowland exotic-dominated forest sites on Hawai'i Island

Species	Mean relative BA	Mean relative density	Number of sites		
			Where most dominant	Where most abundant	Where occurred
Ten most dominant					
Psidium cattleianum	46.09	53.15	17	18	27
Macaranga mappa	10.68	8.56	4	5	13
Cecropia obtusifolia	7.59	4.72	5	6	23
Melochia umbellata	5.30	3.68	4	5	18
Melastoma candidum	2.97	3.97	0	0	8
Syzygium jambos	2.93	3.51	2	2	3
Falcataria moluccana	2.87	2.24	3	3	9
Casuarina equisetifolia	2.18	1.32	2	0	5
Psychotria hawaiiensis	**1.87**	**1.40**	**0**	**0**	**7**
Psidium guajava	1.27	1.20	1	0	10
All native species encountered					
P. hawaiiensis	1.87	1.40	0	0	7
Diospyros sandwicensis	1.13	0.72	0	0	4
Metrosideros polymorpha	0.96	0.60	0	0	6
Canthium odoratum	0.34	0.41	0	0	3
Cibotium glaucum	0.27	0.08	0	0	2
Cibotium menziesii	0.14	0.06	0	0	2
Pipturus albidus	0.13	0.26	0	0	1
Pandanus tectorius	0.07	0.02	0	0	2
Myrsine spp.	0.04	0.06	0	0	1
Wikstroemia spp.	0.01	0.02	0	0	2
Freycinetia arborea	0.01	0.04	0	0	2
Scaevola sp.	0.00	0.00	0	0	1

Relative basal area (% of m^2/ha) and relative density (% of stems/ha) were averaged for each species across all 46 sites. Remaining species are found in Appendix B. One native species among the 10 most dominant is highlighted in bold. Members of *Myrsine* and *Wikstroemia* are likely all *M. lessertiana* and *W. sandwicensis*, respectively, though both genera include cryptic congeners and we cannot discount the possibility that other species were included.

extent vines, lianas, and aroids (Appendices 1–3). Novel forests also lacked some structural elements common to Hawaiian forests, notably understory tree ferns (Palmer, 2002). Some sites included a minor component of escaped agricultural species, such as *Macadamia integrifolia* (Macadamia nut), *Musa* X *paradisiaca* (banana), and *Coffea arabica* (coffee), as well as escaped ornamentals (e.g., *Filicium decipiens* [fern tree]). We evaluated the species richness of novel forests by contrasting six of our sites (33, 34, 36, 38, 39, and 41) with six native forests sampled by Zimmerman et al. (2008; sites NAN, MKY, BRY, NAN47, MKO, NANO). Among these sites, where sampling methods and sample areas were identical and lava age was restricted to a range of 50 to ~1100 years, novel forest species richness was comparable to the native forests sampled by Zimmerman et al. (15.8 ± 2.7 vs. 13.7 ± 2.3, respectively).

3.2. Understory layer

We encountered 56 species among stems 2–9.9 cm dbh, which we defined as the understory layer, of which 12 were native (Table 1 and Fig. 2a). However, no native species was the most dominant understory species at any of the 46 sites. Mean native relative basal area in the understory was 3.7 ± 0.7%, while mean relative density was only 2.8 ± 1.0%. Eight exotic tree species were more dominant than any native, and only three native species ranked in the top 25 most dominant understory species overall (Fig. 2a). *P. cattleianum* was by far the most widespread and dominant understory tree in exotic forests, occurring at 27/46 sites and accounting for 48% of total basal area and 53% of total stem density in the understory layer. More than 11,000 of 22,000 measured living stems were *P. cattleianum*, and only 21 dead stems of this species were encountered. Despite its dominance, however, *P. cattleianum* was not ubiquitous in the understory of exotic forests. It was absent or uncommon at several disturbed sites with a history of agricultural activity, particularly those near Hilo and Keaau (Fig. 1).

3.3. Recruit layer

We encountered 64 species among stems 0–1.9 cm dbh and ≥1.3 m tall, which we defined as the recruit layer, of which 13 were native (Table 2 and Fig. 2b). These species included all 12 natives that were found in the understory layer, as well as *Perrottetia sandwicensis* (olomea), which is a small tree capable of reaching the understory. *P. cattleianum* was again the most abundant species in this layer, accounting for 63% of recruit stem density. However, several abundant species in this layer were unique from those of the understory. *Clidemia hirta* (Koster's curse) is a shrub that frequently invades native forest (DeWalt et al., 2004), and was particularly abundant in exotic forests, occurring at more sites than all other species except *P. cattleianaum*. Several species were extremely abundant in particular sites but not widespread. Morphospecies "kohala-1" and "hilo-3" are small trees, each found to be extremely dense at two particular sites (6, 7, and 30, 31, respectively), but absent in the 44 remaining sites. Likewise, *C. nucifera* was found only at three sites (14, 15, and 33), but reached 9900 stems/ha at site 15.

3.4. Seedlings

We encountered a total of 2687 woody seedlings, of which only 15 individuals were natives, representing just 3 out of 39 total species (Table 3 and Fig. 2c). *Psydrax odorata* (alahee) was the most abundant native seedling, found at two sites near the coast (11 and 35). We found one seedling each of *Psychotria hawaiiensis* (kopiko) and *Pipturus albidus* (mamake) at sites 40 and 31, respectively. *P. cattleianum* was also the most abundant species in the seedling layer overall, accounting for 29% of seedlings, as compared to 53% of stem density in the understory and 63% in the recruit layer.

3.5. Ground cover

Dominant ground cover species were overwhelmingly exotic (Table 4). Out of 63 species, only one native species was found to

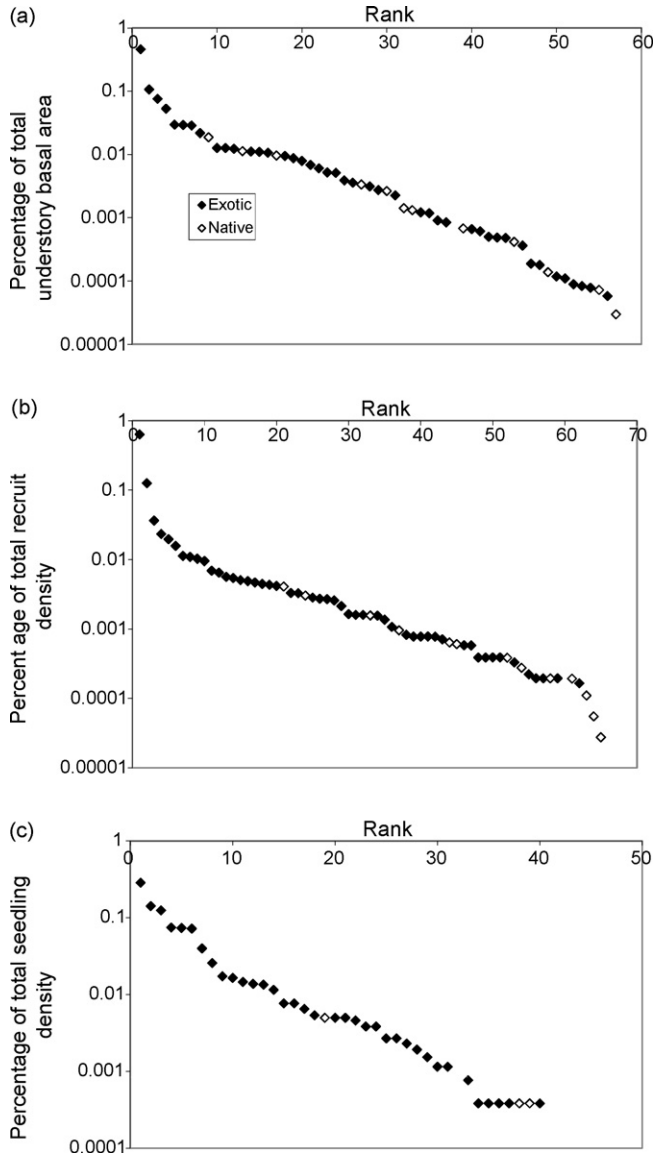

Fig. 2. (a) Rank abundance curve of 56 species encountered in the understory size class (2–9.9 cm dbh). Rank determined by the fraction of total basal area (m^2/ha; summed for all 46 sites) contributed by each species. (b) Rank abundance curve of 64 species encountered in the recruit size class (0–1.9 cm dbh). Rank determined by the fraction of total stem density (stems/ha; summed for all 46 sites) contributed by each species. (c) Rank abundance curve of 39 species encountered as seedlings ($\leq$1.3 m tall). Rank determined by the fraction of total seedling density (seedlings/ha; summed for all 46 sites) contributed by each species. A rank for unknowns is omitted at 38, 60, and 32, respectively. See Appendix B for species names.

dominate any groundcover plots (i.e., *Nephrolepis cordifolia* [native swordfern] at 2 of the 9 plots at site 41). *Oplismenus hirtellus* (basket grass), and the exotic swordfern, *Nephrolepis multiflora* were extremely abundant and collectively dominated 30% of groundcover plots.

4. Discussion

4.1. The scope of native regeneration in exotic-dominated forests

> "An ultimate and complete ascendancy of alien vegetation is but a matter of time alone.... Indigenous plants are helpless before the onslaught; the native forest, doomed, disintegrates and retreats sometimes even before the invaders have arrived." – F.E. Egler (1942; satirically relaying the views of an anonymous student on O'ahu).

The combination of our dataset with existing studies in lowland Hawai'i Island yields a clear picture of expanding regional dominance by exotic species. Exotic tree species are gradually replacing the last remnants of native-dominated forests (Hughes and Denslow, 2005; Zimmerman et al., 2008), and, according to our results, native species appear unable to recolonize areas already dominated by exotic species. In fact, we found that native plant regeneration in exotic-dominated forests on the wet side of Hawai'i Island was nearly absent. There were no native tree species <10 cm dbh at 28 of the 46 sites and native species were rare in the remaining sites. Native tree species accounted for less than 4% of the total understory basal area. Thus, it is highly unlikely that novel, exotic-dominated forests on Hawai'i promote the regeneration of native species, as was reported in Puerto Rico (Lugo and Helmer, 2004; Lugo, 2004).

Native species were present, although in very low abundance, in the understory of undisturbed sites on young lava substrate adjacent to intact native forests (e.g., 11, 32–37, and 46; Fig. 1; Appendix A). This is where natives under exotic canopies might be expected to have the best chance for establishment. However, the evidence suggests that understory natives at these sites are likely survivors of past exotic encroachment into native forest, rather than products of active recolonization by native species. All 10 undisturbed sites (i.e., those listed above plus sites 10 and 43, which do not have natives in the understory) are dominated by either *C. equisetifolia* or *F. moluccana,* two large N_2-fixing exotic tree species which, according to aerial photography and our own observation, are actively invading native forests without human disturbance. As invasion proceeds, *C. equisetifolia* and *F. moluccana* rapidly create a canopy over top of the slow-growing native *Metrosideros polymorpha* (ohia). Along three of these invasion fronts, natives *M. polymorpha* and *Diospyros sandwicensis* (lama) had diameter growth rates of approximately 0.5 and 1.4 mm/year, respectively, compared to 2.3 and 8.5 mm/year for the exotics *P. cattleianum* and *F. moluccana* (i.e., sites 32, 35, and 37; Hughes and Denslow [USFS], unpublished data 2003–2008). Beneath *F. moluccana* canopies at these sites, mortality of natives *D. sandwicensis* and *P. albidus* reached 11% per year but was less than 1% for *F. moluccana* and zero for *P. cattleianum*. In fact, among understory individuals at all 46 sites, standing dead stems were nearly 10 times more common for native than exotic species (Fig. 3). Most of these dead stems were *M. polymorpha* (84%), for which dead stems were actually more common than living stems at eight of the 16 sites where the species occurred. Collectively, the evidence suggests that many natives are being actively excluded by *C. equisetifolia* and *F. moluccana*, and thus the understory populations of these natives will likely decline rather than increase.

Our results differ from with those of Harrington and Ewel (1997), who examined understory colonization on Hawai'i Island beneath plantations of three naturalized exotic trees: *Fraxinus uhdei* (tropical ash), *Eucalyptus saligna* (Sydney blue gum), and *Flindersia brayleyana* (Queensland maple). The area of study was the Waiakea Timber Management Area (WTMA), which is very close to several of our own study sites (9, 16–18, 40, and 41). Beneath *F. uhdei*, the authors found high regeneration by natives *Cibotium glaucum* (hapuu) and *M. polymorpha*—the two most dominant components of native Hawaiian rainforests; however, the authors also found that the understories of *E. saligna* and *F. brayleyana* were dominated by exotic species, including *P. cattleianum*. Still, the reported abundance of natives was far higher than what we found in lowland forests.

Table 2
Notable species encountered in the recruit layer (<2 cm diameter at breast height and >1.3 m tall) of 46 lowland exotic-dominated forest sites on Hawai'i Island. Relative density (% of stems/ha) was averaged for each species across all 46 sites

Species	Mean relative density	Number of sites	
		Where most abundant	Where occurred
Ten most abundant			
P. cattleianum	63.57	20	30
Clidemia hirta	12.58	2	13
Cocos nucifera	3.64	2	3
Morph-kole-1	2.33	0	1
Melastoma septemnervium	1.97	0	11
Morph-kohala-1	1.57	2	2
Morph-hilo-3	1.13	1	2
Syzygium jambos	1.09	2	3
M. mappa	1.03	4	10
Morph-ship-2	0.95	3	6
All native species encountered			
Psydrax odorata	0.41	0	2
M. polymorpha	0.30	0	3
P. albidus	0.16	0	2
P. hawaiiensis	0.10	0	4
Myrsine spp.	0.06	0	3
Freycinetia arborea	0.06	0	1
P. tectorius	0.04	0	1
Wikstroemia spp.	0.03	0	1
C. glaucum	0.02	0	1
Scaevola sp.	0.02	0	1
D. sandwicensis	0.01	0	1
Perrottetia sandwicensis	0.01	0	1
Cibotium menziesii	0.00	0	1

Remaining species are found in Appendix B. No native species ranked among the 10 most abundant recruits.

Several site differences likely account for the disparity between our results and those of Harrington and Ewel (1997). The plantations examined in the latter study were at much higher elevation (~900 m), in wetter forest (~4800 mm), and effectively constituted an island of exotic-dominated forest surrounded by undisturbed native forest. When compared to the remainder of the WTMA, which ranges from 100 to 1000 m in elevation, native regeneration appears to be restricted to high elevation areas studied by Harrington and Ewel (1997). A wider forest inventory that considered understory dominance across the entire plantation area showed that exotics *P. cattleianum*, *M. umbellata*, and *T. orientalis* were the most common understory species below ~500 m (Constantinides and Cannarella, 1999). These authors concluded that *P. cattleianum* was continuing to advance to higher elevation, and that excluding *Cibotium* spp., native species were the most dominant understory species for only 3% of the management area.

While many native species will likely be lost from Hawaii's lowland forests, it is possible that some natives will continue to persist at the low abundances we found. The two best candidates may be *P. odorata* and *P. hawaiiensis*, which occurred in all four-size classes in novel forests (Appendix B). Both species are small to medium-sized understory trees, and using species-specific allometric relationships developed in Puna (Hughes, unpublished data), we have confirmed that each has reached the maximum height reported by Wagner et al. (1999), suggesting there are at least some reproductive individuals. In particular, *P. odorata* was probably never very abundant on the wet side of Hawai'i (Wagner et al., 1999), and its abundance in the novel forests we studied

Table 3
Notable species encountered in the seedling layer (woody stems ≤1.3 m tall) of 46 lowland exotic-dominated forest sites on Hawai'i Island

Species	Mean relative density	Number of sites	
		Where most abundant	Where occurred
Ten most abundant			
P. cattleianum	28.63	10	21
Syzygium jambos	14.22	2	4
F. moluccana	12.49	5	16
C. hirta	7.46	3	10
Swietenia mahagoni	7.38	2	4
Syzygium cumini	7.23	1	2
Clusia rosea	4.00	1	2
Rubus rosifolius	2.57	2	8
Morph-kole-1	1.73	0	1
Melastoma septemnervium	1.65	0	5
All native species encountered			
P. odorata	0.50	0	2
P. albidus	0.04	0	1
P. hawaiiensis	0.04	0	1

No native species ranked among the 10 most dominant seedlings. Relative density (% of seedlings/m^2) was averaged for each species across all 46 sites.

Table 4
Notable species encountered in the ground cover layer of 46 lowland exotic-dominated forest sites on Hawai'i Island

Species	Percentage of subplots dominated	Number of sites	
		Where most dominant	Where occurred
Ten most dominant			
Oplismenus hirtellus	17.15	7	28
Nephrolepis multiflora	12.32	8	12
P. cattleianum	10.39	5	17
C. hirta	5.07	4	5
Paederia foetida	4.83	3	9
Phymatosorus grossus	4.11	1	10
Setaria palmifolia	4.11	2	8
Christella dentata X *parasitica*	2.66	0	7
Syzygium jambos	2.42	1	3
Desmodium triflorum	2.17	2	4
All native species encountered			
Nephrolepis cordifolia	0.48	0	1

For each 1 m^2 quadrat, the species with the highest abundance <1.3 m in height was recorded. Nine ground cover quadrats were placed at each site, 414 in total. No native species ranked among the 10 most dominant ground cover species.

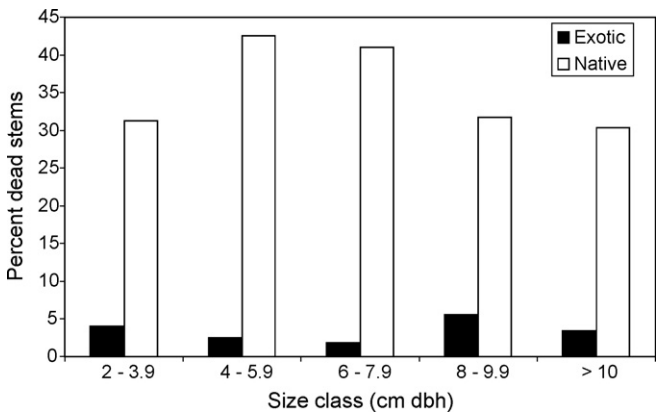

Fig. 3. Proportion of dead stems out of total stems by size class (i.e., mean stems/ha) in exotic-dominated forests in Hawai'i.

actually exceeds that in native forests adjacent to our sites (Zimmerman et al., 2008). *P. odorata* may perform better in forests dominated by exotic N_2-fixers, possibly benefiting from increased N availability, soil development, or shade. In contrast, *P. hawaiiensis* is far less abundant in novel forests compared to native forests in the region (Zimmerman et al., 2008). A third species, *Pandanus tectorius* (screwpine), may also be capable of colonizing novel forest understories. The species is a widespread canopy dominant of native forests, often exceeding the dominance of *M. polymorpha* and *D. sandwicensis* (Wagner et al., 1999; Zimmerman et al., 2008). While we found few small individuals of this species, it was encountered frequently as an overstory tree in novel forests, and at times it dominated large sections of the canopy (5 sites, ranked 32/55; Appendix B). Due to its palm-like growth form, *P. tectorius* probably escaped inclusion in our understory size class because its stem is rarely <10 cm dbh when first reaching 1.3 m in height.

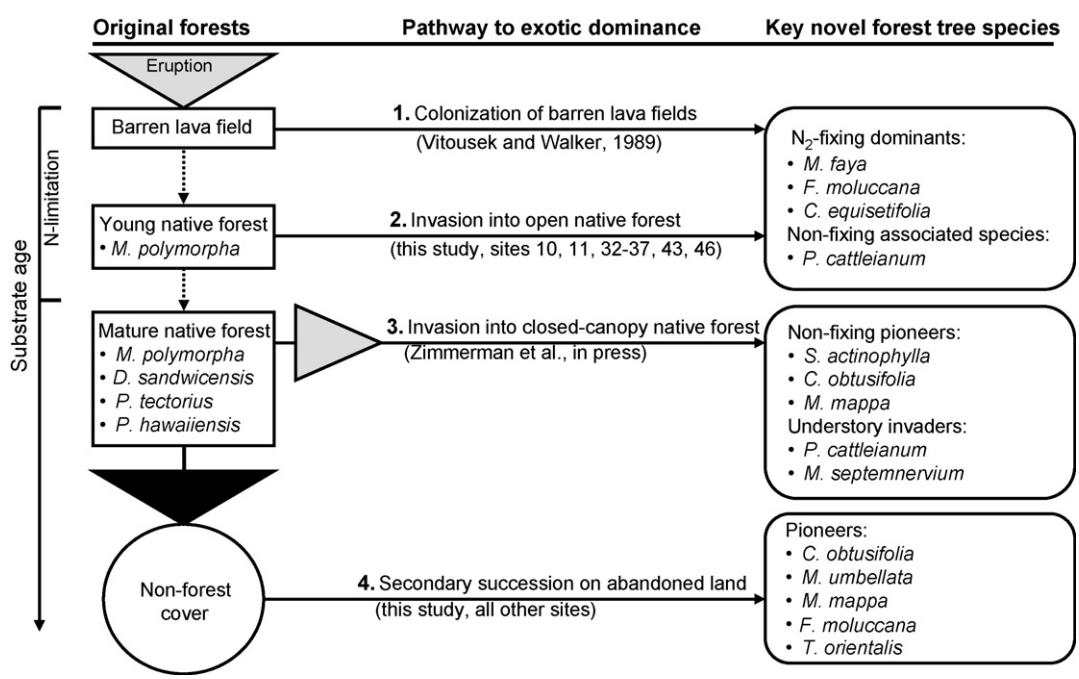

Fig. 4. Proposed pathways to exotic dominance on Hawai'i. Squares represent distinct native forest states, while dotted lines indicate the typical progression of native forest development (after Zimmerman et al., 2008). Gray triangles represent natural sources of disturbance, while a single black triangle represents human disturbance. Solid lines show four distinct pathways that can lead to exotic-dominated forests as described in the text.

4.2. Patterns of succession in new Hawaiian forests

We propose four possible successional pathways to exotic dominance on Hawai'i depending on the stage of native-dominated primary succession at which invasion occurs (Fig. 4): (1) exotic N_2-fixing trees may immediately colonize new lava or tephra substrate. In recent history, most new deposits have been colonized by *M. polymorpha*, but *Morella faya* (firetree) was the first tree to colonize some mid-elevation deposits (Vitousek and Walker, 1989), and both *F. moluccana* and *C. equisetifolia* are likely to do so at lower elevations if new deposits intersect their current populations. (2) Exotic N_2-fixing trees may invade open *M. polymorpha* forest. In our study, this pathway was accomplished by *F. moluccana* and *C. equisetifolia*, and *M. faya* does so at higher elevations (Vitousek et al., 1987; Vitousek and Walker, 1989; Hughes and Denslow, 2005). (3) Exotic non-fixing tree species may invade closed-canopy *M. polymorpha* forest. Historically, *M. polymorpha* retained a share of canopy dominance indefinitely (Vitousek, 2004), but its recruitment in the native forests studied by Zimmerman et al. (2008) is extremely low and negatively impacted by invasion. Except in areas where invasion is controlled by aggressive management, Zimmerman et al. (2008) found that the degree of exotic encroachment ranges from 10 to 50% of basal area. Succession toward exotic dominance is proceeding by a combination of gap filling by exotic pioneer species (e.g., *C. obtusifolia*, *M. mappa*, and *S. actinophylla*) and ubiquitous understory invasion by *P. cattleianum* and *M. septemnervium*. At one such site, Susan Cordell et al. (USFS; personal communication) found that only with the complete removal of exotic species biomass – a Herculean 50% of basal area! – did *M. polymorpha* successfully recruit even to seedling stage. (4) Exotic pioneers initiate secondary succession following agricultural abandonment. This pathway can be initiated by N_2-fixers and non-fixers, and occurs on substrates old enough to support agriculture (i.e., generally $>$1000 years old).

Once established, novel Hawaiian forests are clearly not easily colonized by native species, although we cannot discount the possibility that continued succession will lead to a greater abundance of native species. However, because native forests are undergoing succession *toward* dominance by exotic tree species, it seems unlikely that increased forest age will encourage a substantial recovery of native species. In contrast, Puerto Rico's novel forests gradually recover many native species with succession, leading to forest communities that typically include both exotic and native tree species in roughly equal abundance (Lugo, 2004). Lugo found that native species were present in all novel forests, and constituted about half of forest basal area after roughly 40 years of succession. Lugo also found that native species were highly diverse and often dominant in the understories of exotic tree plantations (Lugo, 1992, 1997).

A broader explanation for the contrast between Hawai'i, where exotics appear to monopolize new forests, and Puerto Rico, where natives readily return, may lie in the differences between the two floras. The native Hawaiian flora, having evolved in extreme isolation, is much more highly endemic than the Puerto Rican flora, a fact that has likely contributed to both the number of successful introductions on Hawai'i and the apparent competitive superiority of many exotic species (Egler, 1942; Denslow, 2003; Woodcock, 2003). Physiological and ecosystem-level studies suggest that species introductions on Hawai'i have expanded the diversity of growth strategies considerably beyond that present in the native flora (Vitousek et al., 1987; Pattison et al., 1998; Baruch and Goldstein, 1999; Hughes and Denslow, 2005; Funk and Vitousek, 2007). With enough diversity among the exotic plants (and/or lack of diversity among native plants; Denslow, 2003), there may not be a successional state that can be exploited by native species to recolonize novel forests, as is the case on Puerto Rico.

4.3. Management implications

We found that native species represent a very small, and probably decreasing share of understory plant diversity in novel Hawaiian forests, and therefore found no evidence to support the use of exotic tree species in restoration activities in which the goal is to promote native plant regeneration. The current approach of prioritizing the protection of mostly intact, native-dominated forests is clearly better suited to preserving native species. However, Hawai'i is a unique ecoregion, and our results should not dissuade others from exploring the approach elsewhere (e.g., Lugo, 2004).

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Appendix A

Summary characteristics for 46 lowland, exotic-dominated forest sites on Hawai'i Island. Elevation = m above sea level; lava age = years before present; disturbance scored 1–3 (1 = undisturbed, 2 = canopy but not soil disturbance, 3 = soil disturbance); MAP = mean annual precipitation (mm); distance = distance to nearest native-dominated forest (m or adjacent); type = contiguous area >50 ha (C) or fragment < 50 ha (F); openness = mean densiometer score (%); cover = mean plant cover in ground cover plots (%); basal area = site basal area (m^2/ha); relative native contribution = % basal area and % density in overstory (≥10 cm dbh), % basal area % density in understory (2–9.9 cm dbh), % density of recruits (0–1.9 cm dbh and >1.3 m height), and % density of seedlings (≤1.3 m height). Richness of stems as measured reflects stems >1.3 m in height (see Section 2)

Site	Elevation	Lava age	Disturbance	MAP	Distance	Type	Openness	Cover	Basal area	Richness of stems as measured	Seedling richness	Relative native contribution to:					
												Over. BA	Over. Den.	Und. BA	Und. Den.	Rec. Den.	Seed. Den.
1	82	15000	2	4000	900	F	5	53	63	9	6	0	0	0	0	0	0
2	61	300	2	2500	2100	F	2	32	32	7	1	0	0	0	0	0	0
3	3	1125	3	4000	3100	F	5	55	34	9	1	0	0	0	0	0	0
4	3	1125	3	4000	3000	F	2	39	34	11	4	<1	1	0	0	0	0
5	3	1125	3	4000	2700	F	4	57	37	11	3	0	0	0	0	0	0
6	427	175000	3	3000	1300	C	1	15	18	4	5	0	0	0	0	0	0
7	427	175000	3	3000	1300	C	2	16	89	5	2	0	0	0	0	0	0
8	6	157500	2	4000	4500	F	4	34	21	6	4	0	0	0	0	0	0
9	73	1125	2	4000	2850	F	1	3	54	12	3	16	8	0	0	<1	0
10	12	216	1	2500	Adj	F	1	27	40	7	3	0	0	0	0	0	0
11	18	216	1	2500	Adj	F	4	17	30	11	6	1	3	4	3	2	28
12	87	575	3	3000	Adj	C	8	64	18	5	1	0	0	0	0	0	0
13	73	1125	3	3000	Adj	C	15	64	13	7	2	59	60	6	2	<1	0
14	24	1125	2	3000	Adj	C	1	29	54	6	3	1	1	0	0	0	0
15	34	575	2	3000	Adj	C	4	7	53	6	2	<1	1	0	0	0	0
16	104	1125	2	4000	2400	C	1	7	67	10	4	1	4	2	3	<1	0
17	76	1125	2	4000	2700	F	1	21	51	20	9	8	9	3	2	<1	0
18	76	1125	2	4000	2700	F	2	11	66	15	7	0	0	6	3	0	0
19	12	5000	2	2000	2000	C	6	31	49	2	2	0	0	0	0	0	0
20	12	5000	2	2000	2000	C	3	17	46	3	3	0	0	0	0	0	0
21	134	7500	3	4000	4100	F	5	73	23	5	2	0	0	0	0	0	0
22	85	7500	3	4000	4300	F	8	77	23	8	3	0	0	0	0	0	0
23	91	7500	3	4000	4200	F	9	88	22	4	1	0	0	0	0	0	0
24	88	7500	3	4000	4300	F	27	93	15	8	0	0	0	0	0	0	0
25	91	7500	3	4000	4200	F	17	81	17	6	0	0	0	0	0	0	0
26	98	7500	3	4000	3900	C	3	74	28	4	1	0	0	0	0	0	0
27	91	7500	3	4000	3600	C	2	65	25	7	2	0	0	0	0	0	0
28	85	7500	3	4000	3600	C	3	26	28	5	3	0	0	0	0	0	0
29	113	7500	3	4000	4200	F	13	87	23	5	0	0	0	0	0	0	0
30	61	1125	3	4000	1300	F	4	30	38	19	10	0	0	0	0	0	0
31	67	1125	3	4000	1250	F	8	47	30	14	7	0	0	0	0	0	0
32	268	51	1	2000	Adj	C	1	44	33	7	5	0	0	11	21	39	<1
33	24	166	1	3000	Adj	C	2	33	42	14	2	0	0	3	2	0	0
34	24	166	1	3000	Adj	C	2	28	38	14	3	16	29	22	14	3	0
35	18	216	1	2500	Adj	C	1	14	21	10	4	3	17	12	12	8	<1
36	30	216	1	2500	Adj	C	3	23	22	11	4	1	5	9	5	0	0
37	274	300	1	2000	Adj	C	1	30	68	7	3	40	66	49	35	<1	2
38	37	575	2	3000	Adj	C	1	56	38	11	3	3	13	5	2	8	0
39	43	575	2	2500	Adj	C	5	36	33	16	1	8	6	<1	<1	2	0
40	114	1125	2	4000	2000	C	3	17	56	21	7	40	49	22	13	2	0
41	73	1125	2	4000	2800	F	1	6	41	29	6	10	7	1	1	<1	0
42	570	2250	3	2500	400	F	4	52	34	2	0	0	0	0	0	7	0
43	195	216	1	3500	400	C	2	20	74	8	2	<1	10	0	0	0	0
44	14	1125	3	4000	500	F	2	4	30	8	3	0	0	0	0	0	0
45	6	1125	2	4000	2500	F	1	4	38	8	3	1	3	0	0	0	0

Appendix A (*Continued*)

Site	Elevation	Lava age	Disturbance	MAP	Distance	Type	Openness	Cover	Basal area	Richness of stems as measured	Seedling richness	Relative native contribution to:					
												Over. BA	Over. Den.	Und. BA	Und. Den.	Rec. Den.	Seed. Den.
46	201	575	1	3500	200	C	1	26	45	6	3	0	0	15	10	0	0

Appendix B

Summary data for all species encountered in the overstory (≥10 cm dbh), understory (≥2 and <10 cm dbh), as recruits (<2 cm dbh and >1.3 m height), and as seedlings (<1.3 m height) for 46 lowland exotic-dominated forest sites on Hawai'i Island. Rankings determined by the relative percentage of each species' contribution to total basal area for overstory and understory, and total stem density for recruits and seedlings. Tied rankings were used here in contrast to those depicted in Fig. 2. Growth forms: (T) trees, (P) palms, (F) tree ferns, (S) shrubs, and (L) lianas. Native species are noted in bold. Members of *Myrsine* and *Wikstroemia* are nearly all *M. lessertiana* and *W. sandwicensis*, respectively, though both genera include cryptic congeners and we cannot discount the possibility that other species were included

Species	Family	Growth form	Number of sites where encountered:				Rank			
			Over.	Und.	Rec.	Seed.	Over.	Und.	Rec.	Seed.
Agathis robusta	Araucariaceae	T	1	0	0	0	33	-	-	-
Alectryon sp.	Sapindaceae	T	1	1	1	1	40	44	62	34
Aleurites moluccana	Euphorbiaceae	T	3	4	2	1	25	24	36	27
Archontophoenix alexandrae	Arecaceae	P	10	3	4	6	14	31	39	13
Ardisia elliptica	Myrsinaceae	T	0	0	1	0	–	–	48	–
Artrocarpus altilis	Moraceae	T	0	1	0	0	–	52	–	–
Carica papaya	Caricaceae	T	0	1	0	0	–	41	–	–
Casuarina equisetifolia	Casuarinaceae	T	9	5	3	0	2	8	42	–
Cecropia obtusifolia	Cecropiaceae	T	28	23	13	5	4	3	18	17
Cestrum nocturnum	Solanaceae	T	0	0	3	1	–	–	15	28
Cibotium glaucum	**Dicksoniaceae**	**F**	**5**	**2**	**1**	**0**	**20**	**30**	**56**	–
Cibotium menziesii	**Dicksoniaceae**	**F**	**2**	**2**	**1**	**0**	**21**	**32**	**65**	–
Cinnamomum sp.	Lauraceae	T	1	2	2	2	36	36	12	11
Citrus maxima	Rutaceae	T	1	0	0	0	49	–	–	–
Clidemia hirta	Melastomataceae	S	0	0	13	10	–	–	2	4
Clusia rosea	Clusiaceae	T	2	2	2	2	22	12	29	7
Cocos nucifera	Arecaceae	P	4	2	3	4	5	23	3	19
Coffea arabica	Rubiaceae	P	0	0	1	0	–	–	48	–
Cordyline fruticosa	Agavaceae	T	1	7	6	1	53	11	17	33
Desmodium cajanifolium	Fabaceae	S	0	0	4	3	–	–	13	19
Diospyros sandwicensis	**Ebenaceae**	**T**	**5**	**4**	**1**	**0**	**23**	**13**	**63**	–
Eucalyptus spp.	Myrtaceae	T	3	1	1	0	11	25	26	–
Falcataria moluccana	Fabaceae	T	16	9	8	16	1	7	19	3
Ficus microcarpa	Moraceae	T	10	6	4	0	6	19	27	–
Filicium decipiens	Sapindaceae	T	0	0	0	2	–	–	–	30
Flindersia brayleyana	Rutaceae	T	1	1	1	0	46	43	38	–
Freycinetia arborea	**Pandanaceae**	**L**	**0**	**2**	**1**	**0**	–	**55**	**45**	–
Heliocarpus popayanensis	Tiliaceae	T	5	2	2	2	19	21	47	25
Hibiscus tiliaceus	Malvaceae	T	1	1	1	1	28	16	22	34
Lantana camara	Verbenaceae	S	0	0	5	1	–	–	14	34
Livistona chinensis	Arecaceae	P	1	0	0	0	44	–	–	–
Macadamia integrifolia	Proteaceae	T	1	1	1	1	30	35	34	34
Macaranga mappa	Euphorbiaceae	T	10	13	10	4	17	2	9	15
Macaranga tanarius	Euphorbiaceae	T	0	2	2	0	–	40	46	–
Mangifera indica	Anacardiaceae	T	3	1	1	0	18	46	53	–
Melaleuca quinquenervia	Myrtaceae	T	1	0	0	0	27	–	–	–

Appendix B (*Continued*)

Species	Family	Growth form	Number of sites where encountered:				Rank			
			Over.	Und.	Rec.	Seed.	Over.	Und.	Rec.	Seed.
Melastoma septemnervium	Melastomataceae	T	2	8	11	5	50	5	5	10
Melastoma sanguineum	Melastomataceae	T	0	1	0	0	–	56	–	–
Melochia umbellata	Sterculiaceae	T	17	18	11	8	7	4	11	12
Metrosideros polymorpha	**Myrtaceae**	**T**	**12**	**6**	**3**	**0**	**12**	**17**	**24**	–
Miconia calvescens	Melastomataceae	T	0	0	3	2	–	–	39	25
Morinda citrifolia	Rubiaceae	T	1	5	5	2	54	22	16	29
Musa X *paradisiaca*	Musaceae	T	2	1	2	0	38	37	48	–
Myrsine spp.	Myrsinaceae	T	1	1	3	0	47	45	44	–
Olea europaea	Oleaceae	T	2	0	0	0	26	–	–	–
Pandanus tectorius	**Pandanaceae**	**T**	**5**	**2**	**1**	**0**	**32**	**39**	**52**	–
Perrottetia sandwicensis	**Celastraceae**	**T**	**0**	**0**	**1**	**0**	–	–	**64**	–
Persea americana	Lauraceae	T	3	1	3	0	24	47	32	–
Pipturus albidus	**Urticaceae**	**T**	**0**	**1**	**2**	**1**	–	**33**	**33**	**34**
Psidium cattleianum	Myrtaceae	T	18	27	30	21	15	1	1	1
Psidium guajava	Myrtaceae	T	7	10	8	3	29	10	25	14
Psychotria hawaiiensis	**Rubiaceae**	**T**	**3**	**7**	**4**	**1**	**31**	**9**	**37**	**34**
Psydrax odorata	**Rubiaceae**	**T**	**1**	**3**	**2**	**2**	**52**	**27**	**21**	**19**
Rubus rosifolius	Rosaceae	S	0	0	4	8	–	–	28	8
Scaevola sp.	**Goodeniaceae**	**T**	**0**	**1**	**1**	**0**	–	**57**	**61**	–
Schefflera actinophylla	Araliaceae	T	13	11	8	6	13	18	20	15
Schinus terebinthifolius	Anacardiaceae	T	0	2	0	0	–	42	–	–
Solanum sp.	Solanaceae	S	0	0	1	0	–	–	56	–
Spathodia campanulata	Bignoneaceae	T	11	9	6	7	10	15	23	23
Swietenia mahagoni	Meliaceae	T	3	1	2	4	8	54	55	5
Syzygium cumini	Myrtaceae	T	5	1	2	2	9	29	35	6
Syzygium jambos	Myrtaceae	T	3	3	3	4	16	6	8	2
Terminalia catappa	Combertaceae	T	1	1	1	1	37	28	39	34
Tetrazygia bicolor	Melastomataceae	T	0	4	4	1	–	26	30	30
Trema orientalis	Ulmaceae	T	21	7	4	0	3	20	43	–
Wikstroemia spp.	**Thymelaeaceae**	**T**	**1**	**2**	**1**	**0**	**55**	**49**	**54**	–
Morph–hilo-2		T	0	1	0	0	–	50	–	–
Morph-hilo-3		T	1	1	2	2	51	34	7	23
Morph-hilo-4		T	1	0	0	0	35	–	–	–
Morph-hilo-5		T	1	1	1	0	41	53	56	–
Morph-hilo-6		T	3	0	0	0	39	–	–	–
Morph-kohala-1		T	1	2	2	1	34	14	6	18
Morph-kole-1		L	0	0	1	1	–	–	4	9
Morph-pfr-1		T	1	0	0	0	48	–	–	–
Morph-pfr-2		T	1	0	0	0	45	–	–	–
Morph-pfr-3		T	1	0	0	0	43	–	–	–
Morph-ship-1		S	0	0	1	0	–	–	48	–
Morph-ship-2		S	0	0	6	0	–	–	10	–
Morph-waa-1		T	0	1	1	1	–	48	31	22
Morph-waa-2		L	0	1	0	0	–	51	–	–
Unknown		–	2	3	1	3	42	38	56	30

Appendix C

Summary data for species found to dominate ground cover quadrats in 46 lowland exotic-dominated forest sites on Hawai'i Island. Rank determined by the percentage of 414 total ground cover quadrats dominated by each species (nine 1 m^2 quadrats were placed at each site; the single most dominant species was recorded for each quadrat). Growth forms: (H) herbaceous plants and subshrubs, (T) trees, (P) palms, (F) ferns, (S) shrubs, (A) aroids, (G) grasses, (L) lianas, and (M) mosses. One native species is noted in bold

Species	Family	Growth form	Number of sites where encountered	Rank
Ageratina adenophora	Asteraceae	H	3	25
Ageratum conyzoides	Asteraceae	H	2	21
Ageratum sp.	Asteraceae	H	1	25
Alectryon sp.	Sapindaceae	T	1	44
Archontophoenix alexandrae	Arecaceae	P	1	44
Arthrostema ciliatum	Melastomataceae	H	1	25
Arundina graminifolia	Orchidaceae	H	1	44
Begonia hirtella	Begoniaceae	H	2	26
Blechnum appendiculatum	Blechnaceae	F	2	25
Cecropia obtusifolia	Cecropiaceae	T	1	44
Christella dentata X *parasitica*	Thelypteridaceae	F	7	8
Cinnamomum sp.	Lauraceae	T	2	15
Clidemia hirta	Melastomataceae	S	5	4
Clusia rosea	Clusiaceae	T	1	44
Cocos nucifera	Arecaceae	P	1	25
Cordyline fruticosa	Agavaceae	T	1	44
Deparia petersenii	Athyriaceae	F	1	21
Desmodium incanum	Fabaceae	H	1	21
Desmodium triflorum	Fabaceae	H	4	10
Dissotis rotundifolia	Melastomataceae	H	3	12
Epipremnum pinnatum	Araceae	A	2	15
Filicium decipiens	Sapindaceae	T	1	44
Hedychium sp.	Zingiberaceae	H	4	12
Hyptis pectinata	Lamiaceae	H	4	14
Justicia betonica	Acanthaceae	H	1	25
Kalanchoe pinnata	Crassulaceae	H	1	26
Macaranga mappa	Euphorbiaceae	T	3	15
Melastoma septemnervium	Melastomataceae	T	4	21
Miconia calvescens	Melastomataceae	T	1	44
Mimosa pudica	Fabaceae	H	1	44
Nephrolepis cordifolia	**Nephrolepidaceae**	**F**	**1**	**26**
Nephrolepis multiflora	Nephrolepidaceae	F	12	2
Oplismenus hirtellus	Poaceae	G	28	1
Paederia foetida	Rubiaceae	H	9	5
Phymatosorus grossus	Polypodiaceae	F	10	6
Pneumatopteris hudsoniana	Thelypteridaceae	F	1	44
Psidium cattleianum	Myrtaceae	T	17	3
Psidium guajava	Myrtaceae	T	2	26
Rubus rosifolius	Rosaceae	S	3	15
Schefflera actinophylla	Araliaceae	T	1	44
Setaria palmifolia	Poaceae	G	8	6
Spathodia campanulata	Bignoneaceae	T	2	26
Spathoglottis plicata	Orchidaceae	H	2	25
Spermacoce assurgens	Spermacoce	H	1	44
Sphagneticola trilobata	Asteraceae	H	3	15
Swietenia mahagoni	Meliaceae	T	1	26
Syngonium podophyllum	Araceae	A	1	44
Syzygium cumini	Myrtaceae	T	1	25
Syzygium jambos	Myrtaceae	T	3	9
Terminalia catappa	Combertaceae	T	1	26
Thunbergia fragrans	Acanthaceae	H	1	44

Appendix C (*Continued*)

Species	Family	Growth form	Number of sites where encountered	Rank
Trifolium sp.	Fabaceae	H	2	25
Viola sp.	Violaceae	H	1	44
Morph-hilo-1		L	1	44
Morph-kole-1		L	1	26
Morph-kohala-1		T	1	44
Morph-ship-3		H	1	44
Morph-ship-4		H	1	25
Morph-ship-5		H	1	44
Moss		M	1	44
Unknown		–	2	26
Unknown Araceae	Araceae	A	1	44
Unknown Poaceae	Poaceae	G	6	10
No cover		–	4	15

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