

Invasion and management of alien *Hedychium gardnerianum* (kahili ginger, Zingiberaceae) alter plant species composition of a montane rainforest on the island of Hawai'i

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Abstract *Hedychium gardnerianum* is a major invader of native Hawaiian forests and suspected of smothering native understory species and preventing native tree seedlings' establishment. In this study, effects on species composition in six vegetation layers of a Hawaiian rainforest were examined (Tree Layer 1, Tree Layer 2, Fern-Shrub Layer, Herb Layer, Bryophyte–Herb Layer, and Bryophyte Layer). Three different area types were compared, which included (i) Natural area types with no influence of non-native species, (ii) Ginger area types with a *Hedychium gardnerianum* dominated herb layer, and (iii) Cleared area types, which were treated with herbicide to remove alien species in 1998.

Species composition sampled in 2004 of the upper three vegetation layers (Tree Layer 1, Tree Layer 2, and Fern-Shrub Layer) differed little. The lower three vegetation layers (Herb Layer, Bryophyte–Herb Layer, and Bryophyte Layer) showed highly significant differences. Species composition in the Ginger area types showed notable abundances of non-native *Psidium cattleianum*, but low coverage of native species. In the area freed of *Hedychium gardnerianum* (Cleared area types), native species are regenerating, although it still reveals signs of disturbance. If this area is managed to prevent reinvasion, then it is likely to regain a natural forest structure.

Keywords Hawai'i · Hawaiian rainforest · *Hedychium gardnerianum* · Invasive alien species · *Psidium cattleianum* · Principal Component Analysis

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Introduction

The alteration of ecosystems in terms of providing land to yield goods and services is considered the main impact of human domination on earth (Vitousek et al. 1997). The second leading threat for ecosystems and species conservation is biological invasion, a widespread component of global change. Oceanic islands are especially susceptible to biological invasions, as most of them have evolved in total

biogeographical isolation (Office of Technology Assessment 1993). Here, invasive species can alter ecosystem structure, function, biodiversity, and species composition to a greater extent than on continental land masses (Cross 1982; Vitousek 1986; Vitousek et al. 1987; Vitousek and Walker 1989).

Native ecosystems are influenced by alien species in various ways. False Acacia (*Robinia pseudoacacia*) introduced to Europe in the seventeenth century causes nitrogen soil enrichment due to symbioses with nutrient-fixing bacteria of the genus *Rhizobium*. In turn, fast growing species outcompete those with slow growth rates, which leads to a displacement of the former flora (Hoffmann 1961; Jurko 1963; Boehmer et al. 2001). *Spartina anglica* has been used worldwide as an agent for coastal protection and stabilization as well as for land reclamation. Its invasion and spread leads to the exclusion of native plants such as *Zostera* and *Salicornia* species. It also leads to the loss of feeding habitats for wildfowl and waders (Kowarik 2003). Similarly, *Hakea sericea*, a native of Australia, is growing taller than native plant species in the fynbos region of South Africa. It forms a larger and denser canopy and increases evapotranspiration, which eventually decreases the amount of water draining out of the region (Neser 1980).

In Hawaiian rainforests, a prominent invasive species suspected of changing species composition is *Hedygium gardnerianum* (kahili ginger, Zingiberaceae) (Wagner et al. 1999; Williams et al. 2003). *Hedygium gardnerianum* can form dense colonies in native forests, which results in a reduction of native plants in lower vegetation layers and in a significant decline in tree-seedling establishment. *H. gardnerianum* was found to form the dominant understory species in some parts of the native rainforest on the island of Hawai'i, under which native tree species were not able to regenerate. The potential of *H. gardnerianum* to alter species composition is compounded by the non-native tree species *Psidium cattleianum*, which is, in contrast to native tree species, able to establish in low light conditions (Huenneke and Vitousek 1990). As canopy species gradually die back due to natural determination, gaps are not filled by native species (Boehmer 2005), but instead, by *P. cattleianum*, which leads to the establishment of a forest dominated by two invasive species. The combination of these two invasive species might ultimately lead to a displacement of

native forests. This alteration of both the function and structure of the forest could cause forest stands to even completely disappear (Williams et al. 2003).

This study focuses on the effects of *H. gardnerianum* on plant species composition in a montane rainforest on the island of Hawai'i. Three types of forest are considered stratified by the herb layer characteristic “absence of *H. gardnerianum*”, “dominance of *H. gardnerianum*”, and “treatment with herbicide” to remove former dominance of *H. gardnerianum*. Specifically, three questions are addressed: (i) Do the upper vegetation layers not influenced by *H. gardnerianum* differ in species composition; (ii) How does the dominance of *H. gardnerianum* affect the lower vegetation layers; and (iii) How does removal of *H. gardnerianum* influence species composition?

Methods

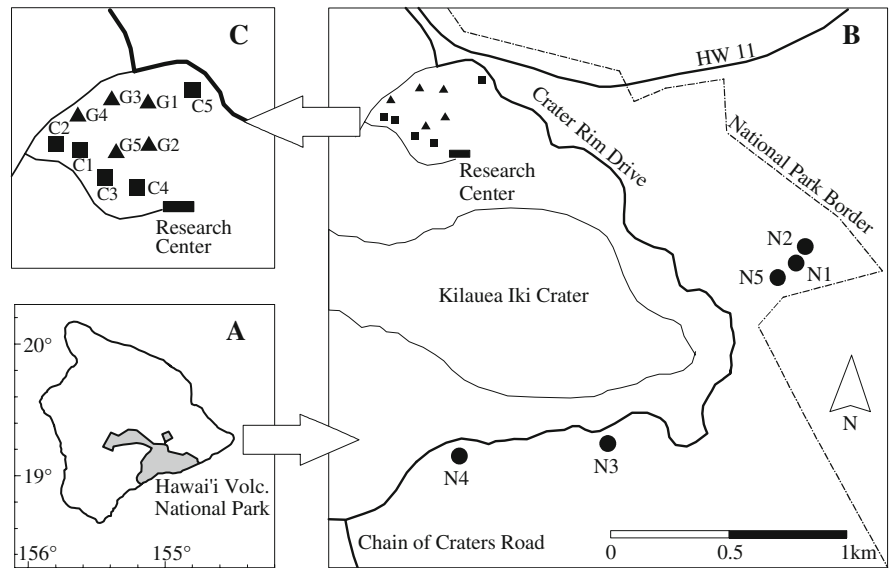
Study area

The study area was located on the southeast side on the island of Hawai'i in Hawai'i Volcanoes National Park (hereafter called HAVO, Fig. 1a). The study sites were situated near Kilauea crater along Crater Rim Drive in an area of 2.8 km² (Fig. 1b).

Based on the data from 1949 to 2004, the study area has a mean annual temperature of 16.1°C and receives a total rainfall of approximately 2,770 mm per year (Western Regional Climate Center 2009). The temperature remains relatively constant during the year and monthly precipitation consistently stays above 120 mm. However, there is a distinct rainy season from November to April, with a monthly rainfall of 280–340 mm. The study area, at an elevation of between 1,197 and 1,231 m above sea level, receives gentle trade winds from the northeast and frequently experiences heavy and low cloud cover.

Kilauea volcano is still active; frequent eruptions produce tephra (“volcanic ash”) and lava flows. The impacts of a 1790 eruption affecting the study area were considerable. More than 75,000,000 m³ of ash were deposited over an area of 190 km² (Mastin et al. 1999). This ash eruption caused the death of almost all the vegetation around the crater. Only single, well-developed trees survived. Ash deposition around the

Fig. 1 **a** Location of Hawai'i Volcanoes National Park; **b** position of survey sites; **c** enlargement of the location of C- and G-plots. *N* natural rainforest, *G* rainforest with Ginger, *C* cleared rainforest (compare text)



crater is at least 15 cm thick and, east of Kilauea Crater, it reaches depths of about 30–40 cm, where it overlays an older (300–400 years) Pahoehoe lava flow (Vitousek et al. 1995).

Montane rainforest on the island of Hawai'i occurs from 300 to 2,200 m above sea level (Mueller-Dombois 2000a; Stone and Pratt 1994). Its structure can be characterized by six layers. The most important native canopy species in the study area is *Metrosideros polymorpha*. It is among the first tree species to colonize young lava flows and forms a monodominant canopy in primary succession (Tree Layer 1 (TL1), Fig. 2) (Mueller-Dombois 2000a). A second tree layer (TL2) follows the upper canopy. It comprises native species, such as *Ilex anomala*, *Myrsine lessertiana*, *Coprosma ochracea*, as well as exotic species such as *Psidium cattleianum* and *Morella faya*. Hawai'i's montane rainforest is also characterized by the existence of a distinct tree fern layer [Fern-Shrub Layer (FSL)], made up mainly of *Cibotium glaucum*, *Sadleria pallida*, and *S. cyatheoides*. Underneath the three dense upper layers, shade-tolerant plants, such as endemic *Astelia menziesiana*, *Isachne distichophylla*, or *Kadua centranthoides*, constitute the Herb Layer (HL). This layer is also influenced by invasive species, such as *Anemone hupehensis* var. *japonica*, *Kyllinga brevifolia*, *Hedychium gardnerianum*, and *Rubus rosifolius*. The Bryophyte–Herb Layer (BHL) consists of small seedlings of tree and tree fern species, such as

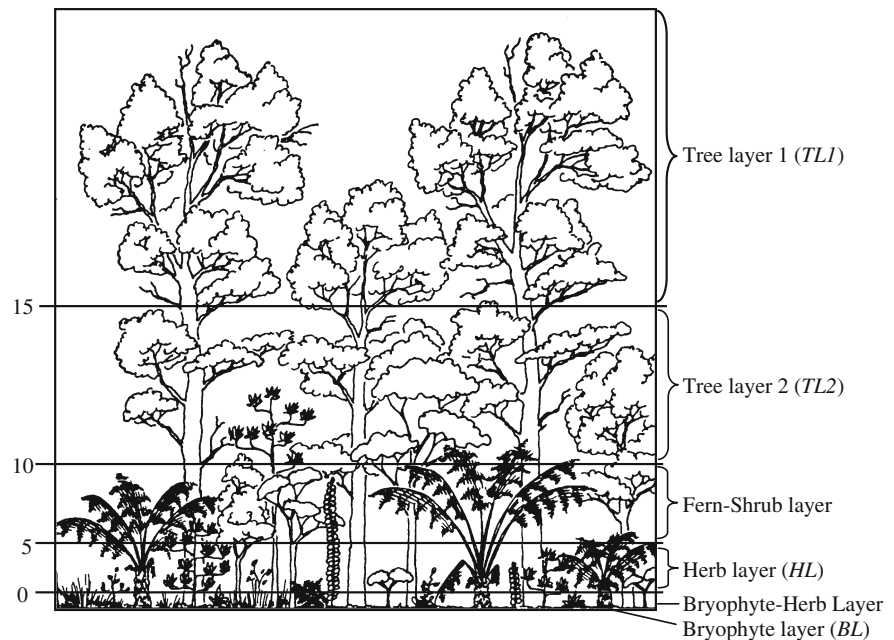
Metrosideros polymorpha, *Ilex anomala*, *Myrsine lessertiana*, *Cibotium glaucum*, *C. chamissoi*, *Sadleria pallida*, and *Sadleria cyatheoides*. Finally, moss mats and moss covered logs form the Bryophyte Layer (BL) lowest to the ground. The presence of the Bryophyte Layer is of major importance for the successful germination of native woody species (Burton and Mueller-Dombois 1984; Medeiros et al. 1993; Mueller-Dombois et al. 1981; Santiago 2000).

Study species and management treatment

Hedychium gardnerianum is native to the Himalayan region of India (Naik and Panigrahi 1961). Today, it is listed as introduced in the Cook Islands (Space and Flynn 2002), New Caledonia (MacKee 1994), The Federated States of Micronesia (Fosberg et al. 1987), and Fiji-Islands (Smith 1979). It is designated as invasive in New Zealand (Williams et al. 2003), Madeira (Cronk and Fuller 1995), La Réunion (Macdonald et al. 1991), Jamaica (Grubb and Tanner 1976), South Africa and Azores (Cronk and Fuller 1995), and the Hawaiian islands (Anderson and Gardner 1999; Wagner et al. 1999; Wester 1992).

Hedychium gardnerianum was brought to Hawai'i as an ornamental some time before 1943. The first individual in the wild was found in the 1950s on the island of Hawai'i, and today, the species occupies an area of about 500 ha in HAVO (Smith 1985; Stone and Pratt 1994; Wester 1992).

Fig. 2 Schematic cross section of a montane rainforest with six designated vegetation layers. TL1: >10 m; TL2: 5–10 m; FSL: 2–5 m; HL: 0.1–2 m; BHL: <10 cm; BL: Bryophytes only. Illustration based on Schaal (1993)



Hedychium gardnerianum is a rhizomatous herb with ovate–elliptic leaves that grows to a height of 1–2 m. Inflorescences are erect and produce numerous seeds in late fall and winter (Wagner et al. 1999). Seeds are dispersed by exotic birds, which enable the plant to reach remote forests (Stone and Pratt 1994). Owing to the formation of partially large rhizomes, the species is capable of distinctive vegetational growth. On Hawai'i, *H. gardnerianum* grows in wet habitats between sea level and 1,700 m above the sea (Smith 1985). Although it prefers open, well-lighted environments, it can also sustain itself in partial and full shade beneath the forest canopy.

In summer of 1998, the species was removed from certain parts of HAVO by the use of Escort® [(methyl 2-[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)-amino]carbonyl]-amino]-sulfonyl] benzoate)] with a concentration of 1.5 g/l. The herbicide was applied aerially after epigeal sprouts had been cut down. It is absorbed by the plants through roots and foliage, and inhibits cell division in roots and shoots, which leads to rapid wilting and death. Escort® might cause environmental damage, such as soil leaching and ground water contamination and might possibly affect non-target native species (Harris et al. 1996).

Sampling design

Three area types of montane rainforest were stratified in the field to compare the vegetation composition of forests on the basis of presence or absence of *H. gardnerianum* (Fig. 1b, c).

1. *Natural rainforest* (N): The first area type consisted of natural rainforest where impacts of *H. gardnerianum* were not observed. In addition, N showed a low impact of other alien plants, a distinctive canopy as well as an established tree fern layer (Mueller-Dombois 2000a). In the study area, N represents the most natural stage of forest, and it is treated as a control in this study.
2. *Rainforest with Ginger* (G): This area type consisted of rainforest as described for N, with the distinction that *H. gardnerianum* occurred with an abundance of 75–100% coverage.
3. *Cleared rainforest* (C): The third area type had been characterized by a formerly high abundance of *H. gardnerianum*, as described for G, until it was treated with Escort® to remove alien plants. This area type was recovering from both the influence of *H. gardnerianum* and the effect of the applied herbicide.

Species composition of the upper three layers (TL1, TL2, and FSL) was observed with respect to the effect of *H. gardnerianum* on species composition in layers that are not under the immediate impact of the alien plant species. As *H. gardnerianum* is most abundant in the Herb Layer (HL), it was assumed that its effects would be the highest here, as well as in the layers below the HL [Bryophyte–Herb Layer (BHL) and Bryophyte Layer (BL)]. Finally, species composition in the Cleared area types, as compared to Natural and Ginger area types provided a basis for observing the capacity of the rainforest for regeneration after the impact of alien plants had been removed.

For each area type, five permanent marked plots were established (N1-5, C1-5, and G1-5, see Fig. 1b and c). Each plot comprised an area of 200 m² (10 × 20 m), for which the location was chosen on random *x*- and *y*-coordinates. In order to reduce the effects of interference, the distance between plots, as well as from any road or street, had to be at least 20 m. As the herbicide was applied selectively, the C-plots had to be established within an area of limited size, which happened to be adjacent to the area of the highest abundance of *H. gardnerianum*, in which the G-plots were established. The N-plots, selected for a lack of disturbance by invasive species, were located further from the areas with the highest abundance of *H. gardnerianum*.

For each vegetation layer (Fig. 2), every species occurring in each plot was listed and its cover was estimated using the Braun-Blanquet cover scale. In addition, the total cover of each layer was estimated. Flowering plant species, ferns and fern-allies, and bryophytes were identified according to Wagner et al. (1999), Palmer (2003) and Staples et al. (2004), respectively. Plants that could only be assigned by their genus were listed with an attached species.

Statistical analysis

Principal component analysis was conducted (PCA, Canoco for Windows 4.51) to ordinate the data set of the six vegetation layers. The non-metric Braun-Blanquet scaling was converted to a metric scale as proposed by van der Maarel (1979) (Table 1). For the Braun-Blanquet term “*r*” the conversion coefficient 0.02 was chosen, according to the ratio of the other terms. Detrended correspondence analysis

Table 1 Braun-Blanquet scaling with corresponding degree of coverage (Dierschke 1994) and transformed metric scaling (van der Maarel 1979)

Braun-Blanquet	Cover range	Transformed cover value
<i>r</i>	1–2 individuals	0.02
+	<1%	0.1
1	1–5%	2.5
2m	Many, but <5%	5
2a	5–12.5%	8.75
2b	12.5–25%	18.75
3	25–50%	37.5
4	50–75%	62.5
5	75–100%	87.5

(DCA, Canoco for Windows, 4.51) revealed a linear response for four out of the six data sets (maximum length of gradient in standard deviation units (SD): TL1 = 1.245 SD; TL2 = 2.176 SD; FSL = 2.529 SD; BL = 1.783 SD). Thus, calculation of PCA was suitable in this case (ter Braak and Šmilauer 2002). For HL and BHL, for which gradients of 3.061 SD and 3.826 SD were calculated, the unimodal method would also have been appropriate. However, it was decided to use linear methods for all the data sets to achieve uniformity within the analysis (Lepš and Šmilauer 2003). Data were log-transformed ($\log(x + 1)$), to raise the influence of the subordinate species as compared with the dominant species (Lepš and Šmilauer 2003), and centered by species. Scaling was focused on “inter-sample distances” and species scores were not post-transformed.

In order to test for significant differences between the area types N, C, and G, a redundancy analysis (RDA, Canoco for Windows 4.51) was conducted, followed by a Monte-Carlo permutation test (*P*-value = 0.05). The nominal variable vegetation type was coded as a dummy variable (0–1 matrix), in which three dummy variables represented the three area types, and this matrix was entered as environmental variable in RDA. As the results of this global test do not inform about specific differences between area types, RDA of sub-data sets (N vs. C, N vs. G, and C vs. G) were performed to test for significance between each area type. Subsequently, the results of this multiple comparison were ranged in significant groups. The internal *P*-value of the

multiple comparison was set on 0.0166, following the Bonferroni-correction (Holm 1979), in which the P -value results from α/k ($\alpha = 0.05$; $k =$ number of combinations, here—3).

Results

A high amount of floristic variability of each of the six data sets was explained by the first two PCA axes (cumulative percentage of explained floristic variability: 56.3% (BHL)–90.8% (BL); Table 2). This can be explained by the low species number of some of the considered data sets (Appendix) and the resulting low number of dimensions of ordination spaces.

The species composition of TL1, dominated by *Metrosideros polymorpha* (Appendix), was not significantly different between area types, although they were differentiated along the second PCA axis (Fig. 3a; Table 2). For TL2 and FSL, significant differences in species composition between area types occurred, but these were not associated with the occurrence of *H. gardnerianum*, as evidenced by the fact that N-plots did not differ from G- and C-plots for TL2, and G-plots were similar to both C- and N-plots for FSL (Fig. 3b, c; Table 2). In contrast, species composition of the three lower vegetation layers (HL, BHL, and BL) showed clear differences between area types, (P -values: 0.001), with the exception of G- and C-plots for BL (Table 2). These differences led to a directed differentiation of area types along the first PCA axis of all the three of the lower vegetation layers in the order G-, C-, and N-plots for HL and BHL (Fig. 3d, e), as well as a separation of G- and C-plots from N-plots for BL (Fig. 3f).

Discussion

Do vegetation layers not influenced by *H. gardnerianum* differ in species composition?

Species composition in TL1 did not differ significantly between the area types. The most dominant tree species was *Metrosideros polymorpha*. Other species, such as *Ilex anomala* and *Myrsine lessertiana* occurred only to minimal extents, which reflects the typical composition of the upper canopy of Hawai'i's montane rainforest (Mueller-Dombois 2000b). Differences for TL2 and FSL occurred, but the discrepancies in species composition appear more likely caused by a local increase in abundance of species rather than by the presence of *H. gardnerianum*.

The vegetation in the entire study area developed largely under similar conditions in the 200 years since the eruption of the Kilauea volcano in 1790. In terms of primary succession, *Metrosideros* trees colonized young lava flows and formed the canopy of the mature forest (Mueller-Dombois 2000a). As the studied rainforest stands have the same age, the structure of the canopy, especially of TL1, is very similar. It is therefore reasonable for this study to use the Natural area type as a control for evaluating Ginger and Cleared area types.

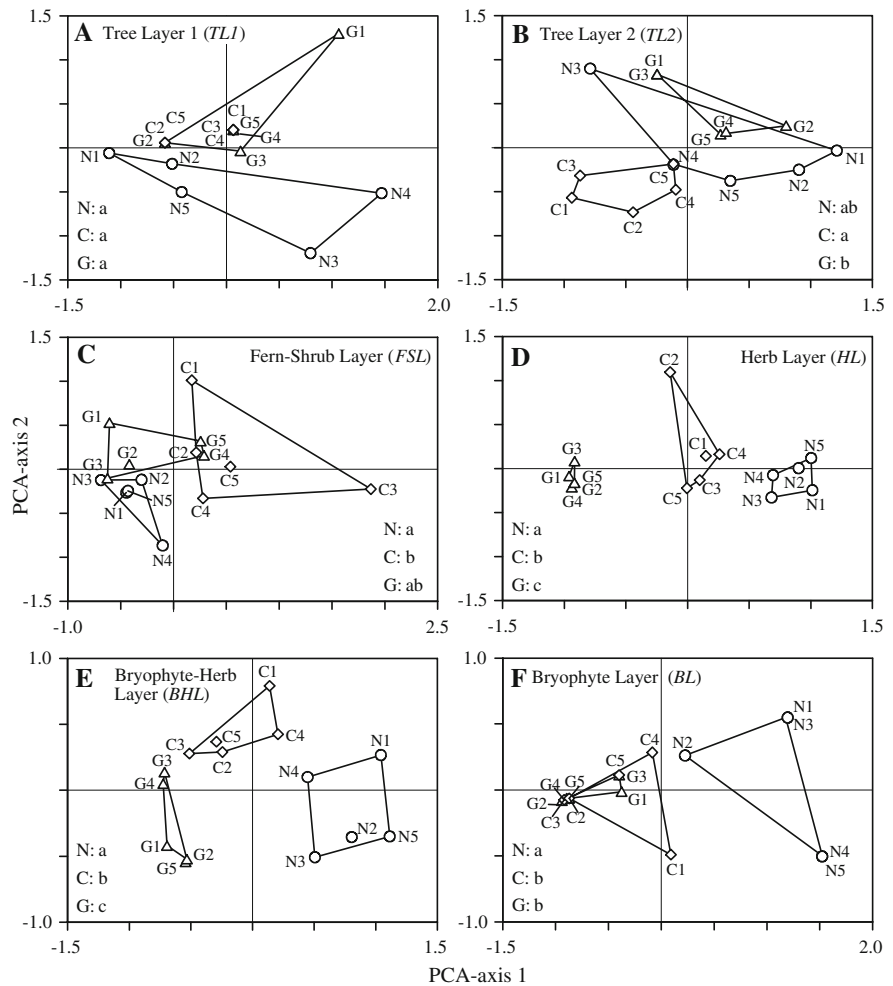
Although *H. gardnerianum* appears not to affect the species composition of the upper vegetation layers in the study area, an effect of *H. gardnerianum* on these layers was detected by Asner and Vitousek (2005). They observed decreased foliar nitrogen concentrations of overstory *Metrosideros* trees in dense stands of *H. gardnerianum* in Hawaiian montane rainforests.

Table 2 Variance of species data according to the first four PCA axes and significance levels of pairwise comparison of area types for six vegetation layers (for abbreviations, compare Fig. 2 and text)

Area type	Cumulative percentage variance of species data				Significance level		
	Axe 1	Axe 2	Axe 3	Axe 4	N ~ C	N ~ G	C ~ G
TL1	44.3	70.2	91.2	99.9	0.1014	0.1599	0.4665
TL2	38.8	64.1	82.7	89.9	0.0631	0.0270	0.0142
FSL	39.8	56.8	68.6	78.6	0.0001	0.2555	0.0573
HL	54.9	65.7	74.9	80.9	0.0001	0.0001	0.0001
BHL	39.9	56.3	69.6	80.4	0.0001	0.0001	0.0001
BL	80.5	90.8	95.6	99.4	0.0001	0.0001	0.5573

Significant differences were achieved with $P < 0.016$

Fig. 3 a–f Sample scores of the first and second PCA axes based on species abundance for six vegetation layers (TL1, TL2, FSL, HL, BHL, and BL; compare Fig. 2). Plots of each area types (C, G, and N; compare text) are enclosed by envelopes. Values of explained floristic variability of the axes is given in Table 2. Significant differences between area types are marked by *small letters* ($P = 0.016$)



Canopy chemistry (particularly nitrogen concentration) is highly correlated with rates of plant productivity and nutrient use efficiency, decomposition, and nutrient availability in the soil (Field and Mooney 1986; Vitousek 2004). Though not observable in our study, the demonstrated impact of *H. gardnerianum* on canopy chemistry might affect the vigor of mature trees, which could lead to an increased susceptibility of the forest to climatic perturbations. Thus, over the long term, *H. gardnerianum* might lead to an observable change in species composition by spurring die back.

How does the dominance of *H. gardnerianum* influence lower vegetation layers?

The lower three vegetation layers exhibited the strong influence of *H. gardnerianum*. The difference in species composition between Natural and Ginger area

types was highly significant, especially due to the high abundance of *H. gardnerianum* (HL and BHL) and the virtual absence of other species (HL, BHL, and BL) in Ginger plots (Appendix). In contrast, species number and abundance were found to be high in the Natural areas of the montane rainforest. Conditions there are more favorable for the growth of native species.

However, even in a mature, undisturbed montane rainforest, there are barriers to seedling growth for major native species. *Metrosideros polymorpha*, for example, has characteristically vulnerable seeds that present a risk to the species' survival. The seeds are 3 mm long and 0.2–0.4 mm wide (Corn 1972) and range in weight from 57 µg in filled seeds (embryo-containing) to 47 µg in unfilled (embryo-lacking) seeds (Drake 1992). Owing to their small size, *Metrosideros polymorpha* seeds contain only limited

resources, and their seed coat is thin (Burton 1982). They do not form a soil seed bank, nor do they need a dormancy break, but germinate rapidly (Corn 1979). The seeds mainly rely on moss-covered fallen logs for germination, as the environment they provide is incubating and retains moisture (Mueller-Dombois et al. 1981; Burton and Mueller-Dombois 1984; Medeiros et al. 1993; Santiago 2000). *Metrosideros polymorpha* seeds are so fragile, that Burton and Mueller-Dombois (1984) determined their highest survival rates to be 5–45% under full irradiance, and characterized *M. polymorpha* as a small-gap specialist.

The distinctiveness in species composition in Ginger type areas can be explained both by the deficiency of moss species and by decreased amount of light reaching the ground, both of which result from the abundance of *H. gardnerianum*. Therefore, germination is reduced indirectly through the presence of *H. gardnerianum*. The importance of canopy opening for the development from seedlings into saplings has been pointed out by Mueller-Dombois (1987). In the *Hedychium*-dominated sites, the invader acts similar to a canopy species by reducing light availability and negatively impacting saplings' establishment. Even seedlings that can successfully establish themselves are inhibited in their development into the next life stage by the dense cover of *H. gardnerianum*.

In contrast to mosses and native woody species, *H. gardnerianum* and *Psidium cattleianum* can be found in great abundance in Ginger area types. Adult *Hedychium* plants appear not only to create favorable germination sites for their own offspring, but to encourage the abundance of *P. cattleianum* as well. This alien tree species has numerous competitive advantages over native species. For example, its fruits attract rooting feral pigs that may enhance the tree's spread (Huenneke and Vitousek 1990). Furthermore, whereas *M. polymorpha* seedlings are often damaged by falling fronds of the native tree fern *Cibotium* (Drake and Pratt 2001), *P. cattleianum* did not show increased mortality (Huenneke and Vitousek 1990). In addition, its tolerance of heavy leaf litter, the ability to grow in the deep shade of other species, and allelopathic effects, which inhibit the growth of other plants, may contribute to its ability to establish under *H. gardnerianum* stands (Huenneke and Vitousek 1990; Smith 1985; Wagner et al. 1999). The relative

importance of the factors contributing to the abundance of both *H. gardnerianum* and *P. cattleianum* in the G-plots (e.g., ability to tolerate low light conditions, increased seed input), could not be determined in this study and needs further research.

In this study, the Ginger area types clearly reflect the negative influence of *H. gardnerianum* on species composition in lower vegetation layers. The impact is apparent in the reduction of species richness of native species and the favoring of a few alien species. The findings of this study corroborate those of Williams et al. (2003), who found lower species richness on dense ginger stands in forests in New Zealand.

How does removal of *H. gardnerianum* influence species composition?

The species composition of Cleared area types was similar to Ginger area types for the BL, indicating that moss species have a low regeneration potential after the removal of *H. gardnerianum*. This is presumably because Ginger type areas are better insulated and higher in temperature, as compared to Natural area types. Also, the applied herbicide could have affected the bryophyte mats. However, for HL and BHL, the removal of *H. gardnerianum* appears to initiate a development from highly degraded Ginger area types toward Natural area types. This is indicated by the fact that Cleared area types have an intermediary position between the others with respect to species composition (Fig. 3d, e). A large number of native species was observed in Cleared area types, but with low abundance. A central factor affecting this low abundance might be the degraded Bryophyte layer, which plays a vital role in regeneration (see discussion above). It is possible that an increase in native species abundance, even in the early stages, may enhance moss regeneration and in turn favor the regeneration of native woody species.

This study shows that the removal of *H. gardnerianum* has positive effects on species composition and stand regeneration in the lower vegetation layers. The regeneration of *Ilex anomala* and the predominant tree species *Metrosideros polymorpha* is especially significant. On the other hand, the problematic alien species *H. gardnerianum* and *Psidium cattleianum* also regenerate well in Cleared area types. Thus, these species should be removed to initiate the regeneration of native species, as shown by D'Antonio et al. (1998).

They found increased abundances of native woody species in areas in which invasive grass species were removed, concluding that management to remove and keep out invasive grasses will result in increased densities of native shrubs in the submontane zone on the island of Hawai'i.

The application of herbicide to remove *H. gardnerianum* and other invasive plant species may be justified for the initial control of dominant stands of *H. gardnerianum*, but its repeated application may be inappropriate given the global effects of herbicides on non-target species (Anderson and Gardner 1999; Harris et al. 1996). Alternative methods for control of this species should be pursued in the long term.

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Appendix

See Table 3.

Table 3 Species abundance according to the Braun-Blanquet scaling (Table 1), species number and total vegetation cover (%) in six vegetation layers for three area types (N, C, and G; compare text)

Plot No.	N1	N2	N3	N4	N5	C1	C2	C3	C4	C5	G1	G2	G3	G4	G5	Origin
Total number of species	30	34	39	44	42	38	33	24	29	27	21	24	18	15	19	
Tree Layer 1 (%)	70	50	25	40	20	60	65	65	60	70	60	60	40	60	60	
<i>Metrosideros polymorpha</i>	4	3	2a	3	2b	4	4	4	4	4	4	4	3	4	4	n
<i>Ilex anomala</i>	2a	1	–	–	1	–	1	–	–	1	–	1	–	–	–	n
<i>Morella faya</i>	–	–	1	2a	–	–	–	–	–	–	–	–	–	–	–	a
<i>Myrsine lessertiana</i>	–	–	–	1	–	–	–	–	–	–	2a	–	–	–	–	n
<i>Psidium cattleianum</i>	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	a
Species count	2	2	2	3	2	1	2	1	1	2	3	2	1	1	1	
Tree Layer 2 (%)	10	10	35	10	10	6	10	10	10	8	10	10	20	15	15	
<i>Metrosideros polymorpha</i>	–	–	2a	1	1	2a	2a	1	2a	1	1	+	1	1	1	n
<i>Ilex anomala</i>	2a	1	1	1	1	–	+	–	1	1	1	1	1	1	1	n
<i>Coprosma ochracea</i>	–	–	1	1	r	1	–	2a	–	1	1	r	1	–	r	n
<i>Myrsine lessertiana</i>	–	r	1	–	–	–	–	–	–	–	1	r	1	1	1	n
<i>Psidium cattleianum</i>	–	–	1	–	–	–	–	–	–	r	1	1	1	r	r	a
<i>Morella faya</i>	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	a
<i>Dicranopteris linearis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	n
<i>Pipturus albidus</i>	–	r	–	–	–	–	–	–	–	–	–	–	–	–	–	n
Species count	1	3	6	3	3	2	2	2	2	4	5	5	5	5	5	
Fern-Shrub Layer (%)	70	50	90	60	80	20	20	20	25	7	60	40	60	20	10	
<i>Cibotium glaucum</i>	4	3	5	3	4	2a	2a	1	2b	2a	4	3	4	2b	2a	n
<i>Myrsine lessertiana</i>	+	1	r	1	–	–	–	–	r	–	–	1	1	+	–	n
<i>Metrosideros polymorpha</i>	+	+	1	1	–	–	1	–	–	–	–	r	–	–	r	n
<i>Ilex anomala</i>	1	+	–	1	1	–	–	–	1	1	–	1	–	–	–	n
<i>Coprosma ochracea</i>	–	+	–	1	r	r	–	2b	1	–	–	–	–	–	–	n
<i>Psidium cattleianum</i>	–	–	1	r	–	r	–	–	–	–	1	+	1	–	–	a
<i>Vaccinium calycinum</i>	–	–	–	r	r	r	R	+	–	–	1	–	–	–	r	n
<i>Cibotium chamissoi</i>	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	n
<i>Dicranopteris linearis</i>	–	–	–	–	–	–	–	2a	–	1	–	–	–	1	–	n

Table 3 continued

Plot No.	N1	N2	N3	N4	N5	C1	C2	C3	C4	C5	G1	G2	G3	G4	G5	Origin
Total number of species	30	34	39	44	42	38	33	24	29	27	21	24	18	15	19	
<i>Sadleria cyatheoides</i>	–	–	–	–	–	2a	–	–	–	–	1	1	–	–	–	n
<i>Cheirodendron trigynum</i>	–	–	–	–	r	–	–	–	–	–	–	–	–	–	–	n
<i>Sadleria pallida</i>	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	n
Species count	4	5	4	8	5	5	3	4	4	4	4	6	3	3	3	
Herb Layer (%)	20	15	10	15	30	30	25	10	15	15	95	95	95	95	95	
<i>Hedychium gardnerianum</i>	–	–	–	–	–	1	2a	1	1	2a	5	5	5	5	5	a
<i>Coprosma ochracea</i>	1	+	1	+	1	1	+	+	1	1	–	–	–	–	–	n
<i>Ilex anomala</i>	+	1	+	+	+	+	+	+	1	–	–	–	–	–	–	n
<i>Psidium cattleianum</i>	–	–	2m	+	–	–	–	+	r	+	1	r	1	–	–	a
<i>Isachne distichophylla</i>	1	1	+	+	1	+	1	–	1	–	–	–	–	–	–	n
<i>Vaccinium calycinum</i>	+	1	–	+	1	+	1	+	–	–	–	–	1	–	–	n
<i>Myrsine lessertiana</i>	+	+	–	+	–	+	1	+	1	–	–	–	–	–	–	n
<i>Astelia menziesiana</i>	–	–	–	1	–	1	1	+	–	1	–	r	–	–	r	n
<i>Rubus rosifolius</i>	–	+	–	+	+	+	+	2a	–	+	–	–	–	–	–	a
<i>Sadleria pallida</i>	2b	2a	1	1	2a	–	–	–	–	1	–	–	–	–	–	n
<i>Vaccinium reticulatum</i>	+	–	+	–	+	+	+	–	r	–	–	–	–	–	–	n
<i>Machaerina angustifolia</i>	–	–	–	+	+	+	1	–	+	–	–	–	–	–	–	n
<i>Sadleria cyatheoides</i>	–	–	–	–	–	1	1	–	r	–	1	–	–	r	–	n
<i>Lycopodium cernuum</i>	+	–	–	–	r	+	1	–	–	+	–	–	–	–	–	n
<i>Cibotium glaucum</i>	–	–	–	–	1	–	1	–	–	–	–	r	1	–	–	n
<i>Kyllinga brevifolia</i>	–	–	–	–	–	+	+	1	+	–	–	–	–	–	–	a
<i>Morella faya</i>	–	–	r	–	r	–	+	–	r	–	–	–	–	–	–	a
<i>Spathoglottis plicata</i>	–	r	–	+	r	r	–	–	–	–	–	–	–	–	–	a
<i>Dicranopteris linearis</i>	–	–	–	+	–	+	–	–	–	1	–	–	–	1	–	n
<i>Uncinia uncinata</i>	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	n
<i>Ehrharta stipoides</i>	–	–	+	1	1	–	–	–	–	–	–	–	–	–	–	a
<i>Myrsine lessertiana</i>	–	–	–	–	+	+	–	–	–	–	+	–	–	–	–	n
<i>Cheirodendron trigynum</i>	+	+	–	–	+	–	–	–	–	–	–	–	–	–	–	n
<i>Metrosideros polymorpha</i>	+	+	–	–	1	–	–	–	–	–	–	–	–	–	–	n
<i>Hedyotis cantranthoides</i>	–	–	–	–	r	+	+	–	–	–	–	–	–	–	–	n
<i>Anemone hupehensis</i>	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	a
<i>Psilotum complanatum</i>	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	n
<i>Thelypteris</i> sp.	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	
<i>Elaphoglossum paleaceum</i>	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	n
<i>Fragaria vesca</i>	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	a
<i>Dryopteris wallichiana</i>	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	n
<i>Hypericum parvulum</i>	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	a
Species count	10	11	11	17	17	18	17	9	12	8	4	5	4	3	2	
Bryophyte–Herb Layer (%)	10	6	5	7	8	4	1	2	3	5	1	<1	1	<1	1	
<i>Hex anomala</i>	2m	2m	1	1	2m	1	1	+	2m	2m	–	–	–	–	+	n
<i>Hedychium gardnerianum</i>	r	–	–	–	–	2m	2m	2m	1	2m	2m	2m	2m	2m	2m	a
<i>Psidium cattleianum</i>	–	–	2m	+	–	+	2m	–	+	1	2m	+	–	1	r	a
<i>Metrosideros polymorpha</i>	2m	2m	1	1	2m	2m	1	+	2m	+	–	–	–	–	–	n

Table 3 continued

Plot No.	N1	N2	N3	N4	N5	C1	C2	C3	C4	C5	G1	G2	G3	G4	G5	Origin
Total number of species	30	34	39	44	42	38	33	24	29	27	21	24	18	15	19	
<i>Cheirodendron trigynum</i>	1	+	+	<i>r</i>	1	–	–	<i>r</i>	–	–	–	–	<i>r</i>	–	–	<i>n</i>
<i>Morella faya</i>	–	<i>r</i>	+	+	+	<i>r</i>	–	–	<i>r</i>	<i>r</i>	–	–	–	–	–	<i>a</i>
<i>Mecodium recurvum</i>	+	2m	2m	–	2m	–	–	–	–	–	1	2m	–	–	2m	<i>n</i>
<i>Coprosma ochracea</i>	1	+	1	1	2m	–	–	–	–	–	–	+	–	–	–	<i>n</i>
<i>Vaccinium reticulatum</i>	+	+	+	–	1	–	+	–	+	–	–	–	–	–	–	<i>n</i>
<i>Hypericum parvulum</i>	–	–	1	–	2m	2m	–	2m	–	1	–	–	–	–	–	<i>a</i>
<i>Rubus rosifolius</i>	–	–	–	+	–	–	–	+	+	+	–	–	–	–	–	<i>a</i>
<i>Myrsine lesseriana</i>	1	+	–	–	+	1	–	–	–	–	–	–	–	–	–	<i>n</i>
<i>Ehrharta stipoides</i>	2m	2m	–	–	–	–	–	–	–	–	–	–	–	–	–	<i>a</i>
<i>Coprosma ochracea</i>	–	–	–	–	–	1	–	–	–	–	–	–	–	–	<i>r</i>	<i>n</i>
<i>Elaphoglossum paleaceum</i>	–	–	<i>r</i>	–	–	–	–	–	–	–	–	–	–	–	–	<i>n</i>
<i>Lepisorus thunbergianus</i>	–	–	<i>r</i>	–	–	–	–	–	–	–	–	–	–	–	–	<i>n</i>
<i>Uncinia uncinata</i>	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	<i>n</i>
<i>Vaccinium calycinum</i>	–	–	–	<i>r</i>	–	–	–	–	–	–	–	–	–	–	–	<i>n</i>
<i>Dryopteris wallichiana</i>	–	–	–	–	<i>r</i>	–	–	–	–	–	–	–	–	–	–	<i>n</i>
<i>Psilotum complanatum</i>	–	–	–	–	–	–	–	–	–	–	–	–	2m	–	–	<i>n</i>
Species count	9	9	12	8	10	8	5	6	7	7	3	4	3	2	5	
Bryophyte Layer (%)																
<i>Rhizogonium spiniforme</i>	2a	1	2a	2a	2a	1	+	+	1	1	1	+	1	–	+	<i>n</i>
<i>Telaranea</i> sp.	2a	1	2a	2a	2a	1	+	+	1	1	–	+	1	+	+	
<i>Leucobryum gracile</i>	2a	1	2a	2a	2a	–	+	–	1	–	–	+	–	–	+	<i>n</i>
<i>Bazzania</i> sp.	2a	1	2a	2a	2a	1	+	–	–	–	1	–	–	–	+	
<i>Dicranum speirophyllum</i>	–	–	–	2a	2a	1	–	–	–	–	–	–	–	–	–	<i>n</i>
Species count	4	4	4	5	5	4	4	2	3	2	2	3	2	1	4	

Classification of species with regard to their origin: *n* native, *a* alien

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