

Effects of invasive alien kahili ginger (*Hedychium gardnerianum*) on native plant species regeneration in a Hawaiian rainforest

V. Minden, J. D. Jacobi, S. Porembski & H. J. Boehmer

Abstract

Questions: Does the invasive alien *Hedychium gardnerianum* (1) replace native understory species, (2) suppress natural regeneration of native plant species, (3) increase the invasiveness of other non-native plants and (4) are native forests able to recover after removal of *H. gardnerianum*.

Location: A mature rainforest in Hawai'i Volcanoes National Park on the island of Hawai'i (about 1200 m a.s.l.; precipitation approximately 2770 mm yr⁻¹). Study sites included natural plots without effects of alien plants, ginger plots with a *H. gardnerianum*-dominated herb layer and cleared plots treated with herbicide to remove alien plants.

Methods: Counting mature trees, saplings and seedlings of native and alien plant species. Using non-parametric *H*-tests to compare impact of *H. gardnerianum* on the structure of different sites.

Results: Results confirmed the hypothesis that *H. gardnerianum* has negative effects on natural forest dynamics. Lower numbers of native tree seedlings and saplings were found on ginger-dominated plots. Furthermore, *H. gardnerianum* did not show negative effects on the invasive alien tree species *Psidium cattleianum*.

Conclusions: This study reveals that where dominance of *H. gardnerianum* persists, regeneration of the forest by native species will be inhibited. Furthermore, these areas might experience invasion by *P. cattleianum*,

resulting in displacement of native canopy species in the future, leading to a change in forest structure and loss of other species dependent on natural rainforest, such as endemic birds. However, if *H. gardnerianum* is removed the native Hawaiian forest is likely to regenerate and regain its natural structure.

Keywords: cohort dynamics; dieback; foundation species; Hawai'i; invasive species; long-term dynamics; *Metrosideros polymorpha*; montane rainforest; rainforest regeneration.

Nomenclature: Wagner et al. (1999).

Abbreviations: *N* = natural, *C* = cleared, *G* = ginger, HAVO = Hawai'i Volcanoes National Park.

Introduction

The Hawaiian Islands are famous for their unique flora and fauna. The remote location of the islands, with 3200 km distance to the nearest high-island group, and the resulting low rate of colonization have led to a native biota consisting almost entirely of endemic species (Loope & Mueller-Dombois 1989). However, over 4600 non-native plant species have been introduced over the last 200 years, of which 86 have become serious pests (Smith 1985; Staples & Cowie 2001). Numerous studies have documented the diverse effects of invasive plants on native ecosystems (Elton 1958; Stone et al. 1992; Cox 1999; Lockwood et al. 2008). These include, for example, changes in fire regimes, nutrient cycling and hydrology, degradation of terrestrial environments and alteration of species composition (Neser 1980; Cross 1982; Vitousek & Walker 1989; West et al. 1994; Williams & Meffe 1999; D'Antonio & Kark 2002).

A well known example of a problematic alien species in Hawai'i is *Hedychium gardnerianum*, a rhizomatous herb native to India's Himalaya region (Mitra 1958; Naik & Panigrahi 1961). *H. gardnerianum* has been introduced throughout the tropics and is invasive in many forest ecosystems (for a detailed list see CAB International 2005). It was brought to Hawai'i sometime before 1943 as an ornamental (Doty & Mueller-Dombois 1966; Wagner et al. 1999). The first individual in the wild was

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found in the 1950s on the island of Hawai'i, and today this species occupies an area of about 500 ha in Hawai'i Volcanoes National Park (hereafter abbreviated as HAVO; Smith 1985; Wester 1992; Stone & Pratt 1994). With a height of 1-2 m, it has ovate-elliptic leaves that are 20-45 cm long and 10-15 cm wide (Wagner et al. 1999). Inflorescences are erect and produce numerous seeds in late fall and winter (Wagner et al. 1999). Today, *H. gardnerianum* grows between 0 and 1700 m a.s.l. (Smith 1985). In its natural range, *H. gardnerianum* prefers open environments, but it is also found in forests and woodlands as an understory species (CAB International 2005). In Hawai'i it grows in semi-shade and full shade beneath the forest canopy.

The purpose of this study was to test (1) whether *H. gardnerianum* replaces native understory species, (2) if its presence suppresses the natural regeneration dynamics of native plant species in the montane rainforest, (3) if it increases the invasiveness of other alien plant species into the area and (4) whether native forests are able to recover from the impact of *H. gardnerianum*.

Materials and Methods

Study sites and plots

The study area is located at the east flank of Kilauea Volcano (island of Hawai'i) at an elevation of about 1200 m a.s.l. (19°25'08"N, 155°14'57"W). Annual rainfall is ca. 2770 mm and average temperature ranges between 11.4 and 20.6°C (Western Regional Climate Center 2007).

The natural vegetation of the area consists of a *Metrosideros polymorpha*-dominated rainforest. This species is dominant in Hawaiian rainforests, and is found from early stages of succession to mature forest (Drake & Mueller-Dombois 1993; Kitayama et al. 1995; Mueller-Dombois 2000). *M. polymorpha* forms even-aged stands. This cohort structure and subsequent cohort dynamics (including cohort senescence; Mueller-Dombois 1987) is based on a combination of biotic and abiotic factors that includes generic levels as well as volcanic disturbance and climatic triggers (Mueller-Dombois 1988; Boehmer 2005).

A distinct subcanopy tree layer mainly composed of native *Myrsine lessertiana*, *Coprosma ochracea*, and *Ilex anomala*, and a conspicuous tree fern layer dominated by *Cibotium glaucum* characterize Hawaiian montane rainforests at this elevation. Tree ferns create a microclimate of cool temperatures and

low light, in which shade-tolerant plant species occur (Mueller-Dombois 1987; Mueller-Dombois & Fosberg 1998; Mueller-Dombois 2000). Those include the natives *Astelia menziesiana*, *Isachne distichophylla*, and *Kadua centranthoides*, but also the invasive *H. gardnerianum* (Sheppard ex Ker.Gaw., Zingiberaceae), *Anemone hupehensis* var. *japonica*, *Kyllinga brevifolia* and *Rubus rosifolius*. However, as this paper focuses on woody species and herbs, abundances of tree fern species were not measured.

Kilauea volcano is still active; a series of eruptions in 1790 produced large amounts of tephra ("volcanic ash"). The so-called Keanakako'i Ash covered an area of 190 km², destroying major parts of the vegetation around the crater (Holcomb 1987; Mastin et al. 1999). Only tall, well-developed *Metrosideros* trees survived. In the study area, a tephra layer of about 30-40 cm thick overlays an older (300-400 years) pahoehoe lava flow (Vitousek et al. 1995).

Sampling design

Plots were established within an area of 2.8 km² (Fig. 1b). Fieldwork was conducted over a 4-month period beginning in April 2004. Three area types were compared. They included (1) natural plots (*N*; Fig. 2a), serving as control plots, with no or little impact of alien plants, partly owing to manual removal of alien species by HAVO-members; (2) ginger plots (*G*; Fig. 2b) with a *H. gardnerianum*-dominated herb layer; and (3) cleared plots (*C*; Fig. 2c), which were treated with herbicide applied on a large scale in order to remove alien plants, particularly *H. gardnerianum*. The treatment in the *C*-plots, which took place in summer 1998, consisted of cutting off epigeal sprouts manually before spraying with the herbicide Escort (methyl 2-[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)-amino]carbonyl]-amino]-sulfonyl] benzoate; Dow, Midland, MI, USA), which inhibits cell division in roots and shoots and is fatal for the plants (Harris et al. 1996). Five plots of 200 m² (10 m × 20 m) were sampled within each area type, resulting in a total of 15 plots (*N1-N5*, *C1-C5*, and *G1-G5*, Fig. 1b and c). The location of each plot was chosen randomly (stratified random sampling). Random numbers were generated and provided distance measures from one corner of a plot to the corner of the next plot.

Most of the study sites were established at ca. 1200 m a.s.l. (Table 1). The tight grouping of the sites with respect to elevation suggests minimal differences in precipitation. Differences between the area types, especially between *G* and *N* plots were considered

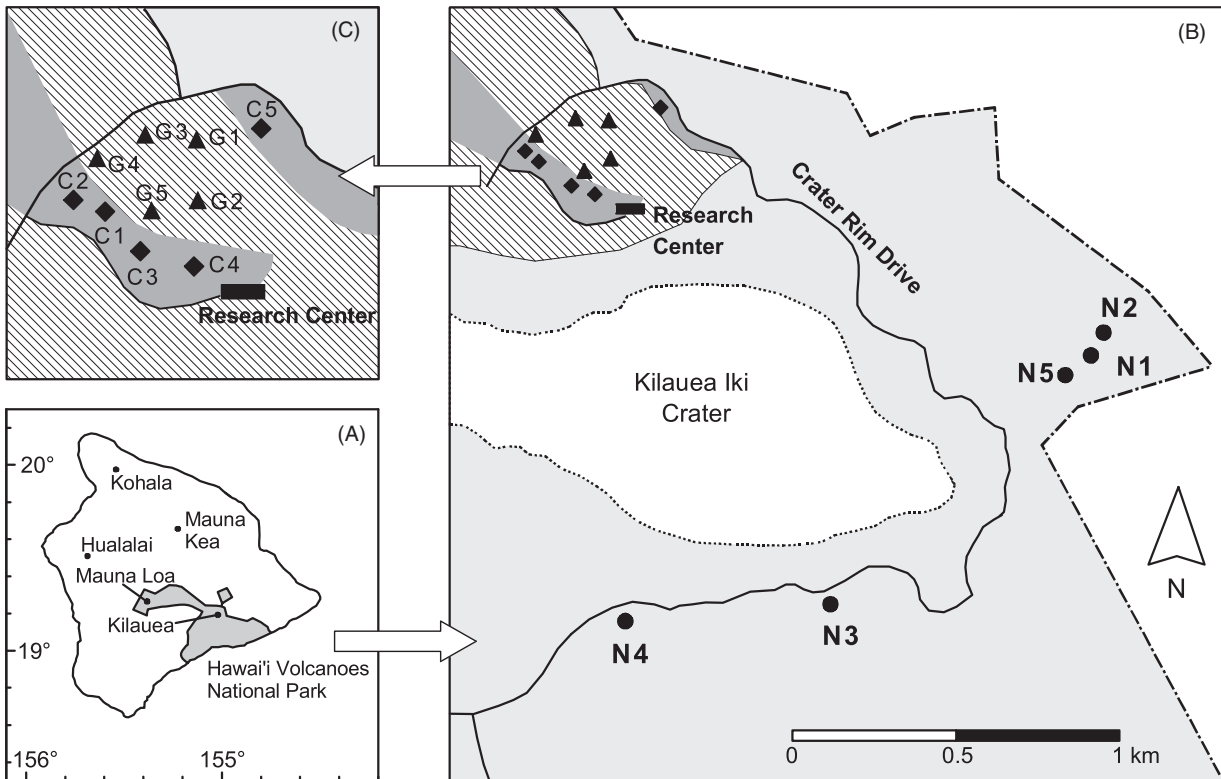


Fig. 1. (a) Island of Hawai'i; (b) Section of Hawai'i Volcanoes National Park showing the location of natural area types (N, 1-5); (c) Section showing the location of cleared (C, 1-5) and ginger plots (G, 1-5). Natural rainforest is indicated by light tinted background and cleared plots by dark tint; distribution of *Hedychium gardnerianum* in high abundances is indicated by shaded areas. Area sizes are roughly estimated and represent the distribution as of 2004.

necessary to ensure as little impact of alien species in the natural area types as possible. The natural area types were located up to a distance of 1.6 km away from the G and C plots. As is typical for a shield volcano, the inclination of the study area was not very steep, and always below 12°. Most of the plots had an east or south exposure. However, it is assumed that all of the plots received similar intensity and duration of solar radiation and rainfall.

Within each plot, forest stand structure was surveyed, by recording all seedlings, saplings and mature plants. The species identity and abundance was recorded for all trees taller than 5 m. All woody plants between 0.5 and 5 m in height were considered saplings, and plants 0.02-0.5 m tall were recorded as seedlings. All woody plant species and *H. gardnerianum* were included in the survey. Plant species nomenclature followed Wagner et al. (1999).

Data analysis

Counts of mature trees, saplings, and seedlings were compared between the three area types (N, C

and G). Data were first tested for normality with the Kolmogoroff-Smirnov test (Bortz et al. 1990). As most of the data were not normally distributed, the Kruskal-Wallis nonparametric *H*-test was applied for all data sets. This test provides an analysis of variance that compares different groups with regard to the ordinal variables. For significant overall effects, pair-wise comparisons were performed using the Mann-Whitney *U*-test (Mann & Whitney 1947) applying Bonferroni correction (Holm 1979) with $\alpha = 0.05/3 = 0.0166$. All statistical analyses were performed using SPSS (version 12.0; SPSS Inc., Chicago, IL, USA).

Results

The data on mature trees, saplings, and seedlings served separate functions. The purpose of the survey of mature trees was to compare the forest structure of the three area types, whereas the impact of *H. gardnerianum* on species composition and germination was assessed by surveying



Fig. 2. (a) Natural understory of a montane *Metrosideros*-dominated rainforest on the island of Hawai'i ("natural forest type"); (b) understory of a montane *Metrosideros* rainforest invaded by *Hedychium gardnerianum* ("ginger forest type"); (c) understory of a montane *Metrosideros* rainforest ("cleared forest type"). All photographs by Hans Juergen Boehmer.

Table 1. Table of header data taken for each plot (N1–5, C1–5, G1–5) including elevation above sea level with accompanied accuracy, coordinates for (true) North and West, inclination and exposure with the corresponding compass direction, and comments on the structure of the plot.

	Elevation (m)	Accuracy (m)	Position in grid		Inclination (°)	Exposure (°)	Orientation	Structure of plot
			N	W				
N1	1210	6.7	19°24'51"	155°14'17"	7	165	SSE	High in center
N2	1213	10.1	19°24'52"	155°14'17"	2	187	SSE	Uneven
N3	1212	25.3	19°24'30"	155°14'40"	10	1	N	Level
N4	1212	17.1	19°24'26"	155°14'58"	3	217	SW	High in center
N5	1197	11.9	19°24'50"	155°14'16"	3	48	NE	High in center
C1	1231	6.7	19°25'14"	155°15'04"	4	85	E	Level
C2	1230	6.7	19°25'16"	155°15'06"	1	338	NW	Uneven
C3	1203	10.4	19°25'13"	155°15'02"	3	100	ESE	Uneven
C4	1231	24.1	19°25'12"	155°15'00"	3	103	ESE	Uneven
C5	1231	10.7	19°25'22"	155°14'57"	4	120	SE	Depression in center
G1	1231	9.4	19°25'21"	155°14'59"	12	127	SE	Uneven
G2	1212	7.6	19°25'17"	155°14'59"	10	94	ESE	Uneven
G3	1218	3.8	19°25'20"	155°15'02"	9	35	NE	Uneven
G4	1219	10.1	19°25'18"	155°15'04"	5	93	ESE	Even
G5	1231	24.7	19°25'16"	155°15'03"	4	88	E	Even

saplings and seedlings. Another objective was to answer the question of whether the cleared area types are able to recover from the influence of invasive species.

Mature trees

Only *M. polymorpha* and *P. cattleianum* showed significant differences in their density between the

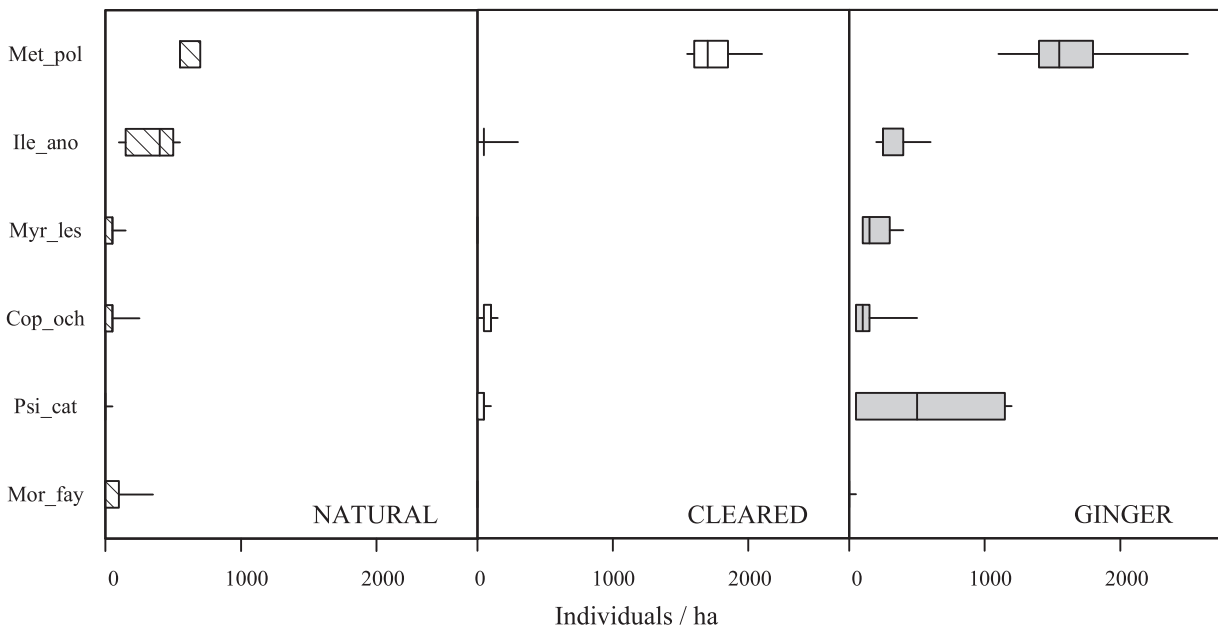


Fig. 3. Boxplots of the density of six tree species in the area types natural (*N*), cleared (*C*) and ginger (*G*). Boxes end at lower and upper quartile (25% and 75% of data; left and right, respectively), with the minimum and maximum values indicated by lines. For abbreviations see Table 2.

separate area types (Fig. 3, Table 2). *M. polymorpha* showed significant differences when comparing *N/C* and *N/G*. Abundances of *P. cattleianum* resulted in significant differences between *N* and *G* plots. *I. anomala*, *M. lessertiana*, *C. ochracea*, and *Morella faya* showed no significant differences between the area types, although abundances were highest in the *G* plots and lowest in the *C* plots.

Saplings

Figure 4 shows a graphical display of all species counted in the three area types (*N*, *C*, and *G*). The natural area types contained the largest overall number of individuals. Almost all important native species were present in this area type, but *Vaccinium reticulatum* was absent in the *N* plots, and occurred only with low number in the *C* plots. In the *G* plots few native species were found, whereas the non-native *P. cattleianum* was the most abundant species. For the sapling data, only *M. lessertiana* was normally distributed and therefore, all data on species composition were analysed using the non-parametric *H*- and *U*-tests. The results are listed in Table 2.

M. lessertiana, *Cheirodendron trigynum*, *V. reticulatum*, *Vaccinium calycinum*, *Psidium cattleianum* and *M. faya* did not show significant differences in their density in the three area types. The *H*-test of the remaining three species resulted in the rejection

of the null hypothesis, with $P < 0.016$. The subsequent *U*-test revealed that the abundance of *C. ochracea* was significantly different between *N* and *C* plots and *G* and *C* plots. *M. polymorpha* did not show significant differences in its abundances between *N* and *C* plots, but the *U*-test resulted in significant differences between the *G* plots and both *N* and *C* plots. The *U*-test for *I. anomala* revealed significant differences between *N* and *C* plots, as well as for *C* and *G* plots.

Seedlings

A total of 10 species was found in the seedlings category. Species number was equally high in the *N* and in the *C* plots (10 each), whereas only five different species were present in the *G* plots (Fig. 5).

The *C* plots showed higher numbers of individuals of *M. polymorpha*, *I. anomala*, *M. lessertiana*, *V. reticulatum*, *H. gardnerianum*, *P. cattleianum*, and *M. faya* compared to the *N*-plots (Fig. 5). The highest numbers of individuals of *C. ochracea*, *C. trigynum*, and *Vaccinium calycinum* were found in the *N*-plots. *P. cattleianum* was counted 121 times and *H. gardnerianum* 2918 times in the *G* plots, which is more than the sum of all seedlings, native and non-native, found in the *N* and *C* plots together.

The number of individuals of *M. lessertiana*, *C. trigynum*, *V. calycinum*, and *P. cattleianum* was

Table 2. List of species found as mature trees, saplings, and seedlings in natural (*N*), cleared (*C*) and ginger (*G*) plots, with abbreviation of species names and results of *H*-test and pair-wise comparisons with Mann-Whitney *U*-test applying Bonferroni correction ($\alpha = 0.016$). The right columns show heterogeneous sub-groups with same letters, significant differences are displayed by the use of dissimilar letters.

	Abbreviation	<i>H</i> -test (<i>P</i> -values)	N	C	G
Trees					
<i>Metrosideros polymorpha</i>	Met_pol	0.008	a	b	b
<i>Ilex anomala</i>	Ile_ano	0.048	-	-	-
<i>Myrsine lessertiana</i>	Myr_les	0.006	-	-	-
<i>Coprosma ochracea</i>	Cop_och	0.366	-	-	-
<i>Psidium cattleianum</i>	Psi_cat	0.021	a	ab	b
<i>Morella faya</i>	Mor_fay	0.266	-	-	-
Saplings					
<i>Metrosideros polymorpha</i>	Met_pol	0.008	a	a	b
<i>Ilex anomala</i>	Ile_ano	0.01	a	b	a
<i>Myrsine lessertiana</i>	Myr_les	0.142	-	-	-
<i>Coprosma ochracea</i>	Cop_och	0.004	a	b	a
<i>Cheiodendron trigynum</i>	Che_tri	0.099	-	-	-
<i>Vaccinium reticulatum</i>	Vac_ret	0.034	-	-	-
<i>Vaccinium calycinum</i>	Vac_cal	0.032	-	-	-
<i>Psidium cattleianum</i>	Psi_cat	0.465	-	-	-
<i>Morella faya</i>	Mor_fay	0.088	-	-	-
Seedlings					
<i>Metrosideros polymorpha</i>	Met_pol	0.007	a	a	b
<i>Ilex anomala</i>	Ile_ano	0.009	a	a	b
<i>Myrsine lessertiana</i>	Myr_les	0.021	-	-	-
<i>Coprosma ochracea</i>	Cop_och	0.007	a	a	b
<i>Cheiodendron trigynum</i>	Che_tri	0.037	-	-	-
<i>Vaccinium reticulatum</i>	Vac_ret	0.022	ab	a	b
<i>Vaccinium calycinum</i>	Vac_cal	0.114	-	-	-
<i>Hedychium gardnerianum</i>	Hed_gar	0.002	a	b	c
<i>Psidium cattleianum</i>	Psi_cat	0.715	-	-	-
<i>Morella faya</i>	Mor_fay	0.012	ab	a	b

not significantly different between the area types (Table 2). However, significant differences were determined between *N* and *G* plots and *C* and *G* plots for *M. polymorpha*, *I. anomala*, and *C. ochracea*. *V. reticulatum* and *M. faya* showed significant differences between *C* and *G* plots, and the number of seedlings of *H. gardnerianum* resulted in significant differences for all three area types.

Discussion

The lower seedling abundance indicates that *H. gardnerianum* negatively affects the germination of native species. Native species were found both in natural and cleared plots, mostly with an evenly distributed number of individuals. Conversely, gin-

ger plots lacked most of the native species, but in turn showed high abundances of *H. gardnerianum*. These results are comparable with those of Williams et al. (2003), who found lower woody seedling densities and species richness in dense *H. gardnerianum* stands (compared with areas with sparse coverage) in forests of New Zealand.

The conclusion that seedling germination and the establishment of native species is hindered under dense stands of *H. gardnerianum* is further demonstrated by the fact that, in the cleared study sites, native tree species seemed to benefit from the removal of the invasive plant and showed a potential for regeneration. However, cleared area types run the risk of being recolonized by *H. gardnerianum* from nearby populations, which could lead to the displacement of native species in the long term (Boehmer 2005; Fig. 6).

Evidence for the regeneration potential of the cleared plots is indicated by the high number of seedlings therein: some species such as *M. polymorpha*, *I. anomala*, *M. lessertiana*, and *V. reticulatum* seedlings were more abundant in the cleared area types than in the natural area types (Fig. 5). The increase in native tree seedlings could result from the favorable light and temperature conditions, which could be a result of the removal of *H. gardnerianum*. Asner & Vitousek (2005) showed that *H. gardnerianum* lowers available nitrogen; thus, clearing the invader increases available nitrogen, which might explain the rapid recovery of native seedling establishment in the Hawaiian rainforest. The high numbers of *V. reticulatum*, which normally is found in open, dry forests, indicate a change of light and temperature regime (Fig. 6).

As noted above, the establishment of *P. cattleianum* does not seem to be negatively influenced by *H. gardnerianum*, as this is the only species able to regenerate in the ginger plots. This was also observed by Huenneke (1997) in the context of leaf litter accumulation; as the ginger plots showed the greatest amounts of organic material, the high abundance of *P. cattleianum* saplings support her assumptions.

In the natural plots, all important native species were found as saplings, but there were no significant differences between the natural and cleared plots for *M. polymorpha* and *V. calycinum*. The remaining species varied in their occurrence. *V. reticulatum* has been observed to prefer open dry forests, whereas *V. calycinum* is most abundant in wet forests (Stone & Pratt 1994). However, *V. calycinum* occurred in the cleared area type to the same extent as in the natural plots. The potential of regeneration as

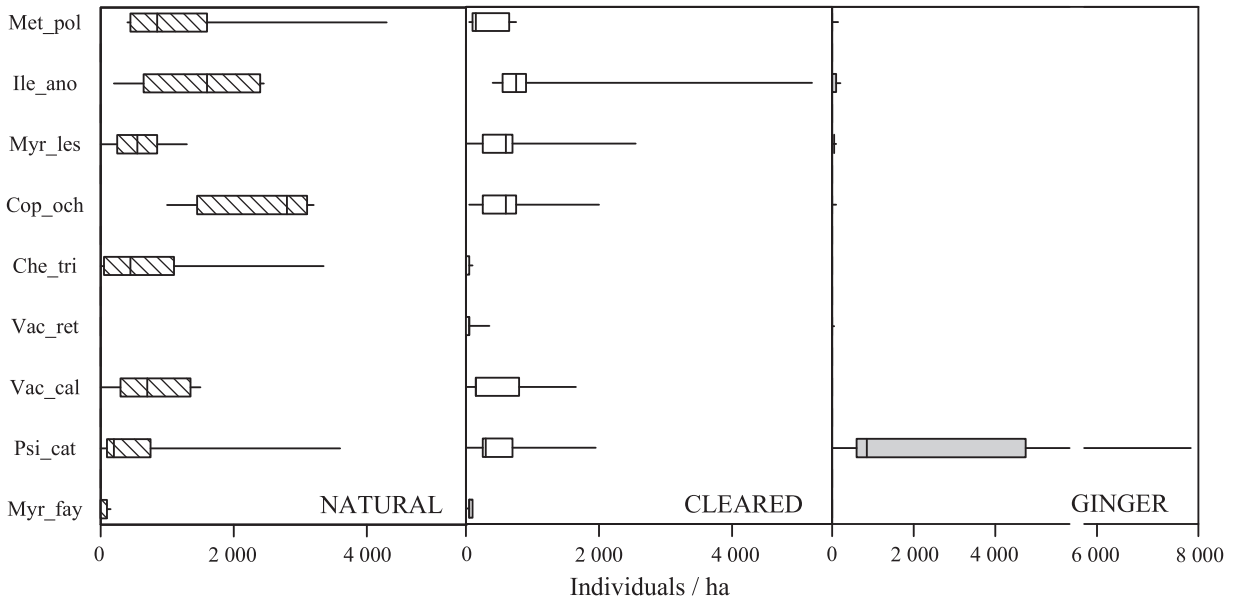


Fig. 4. Box plots of sapling density per ha for nine tree species in each of the area types (natural, cleared and ginger). For abbreviations see Table 2.

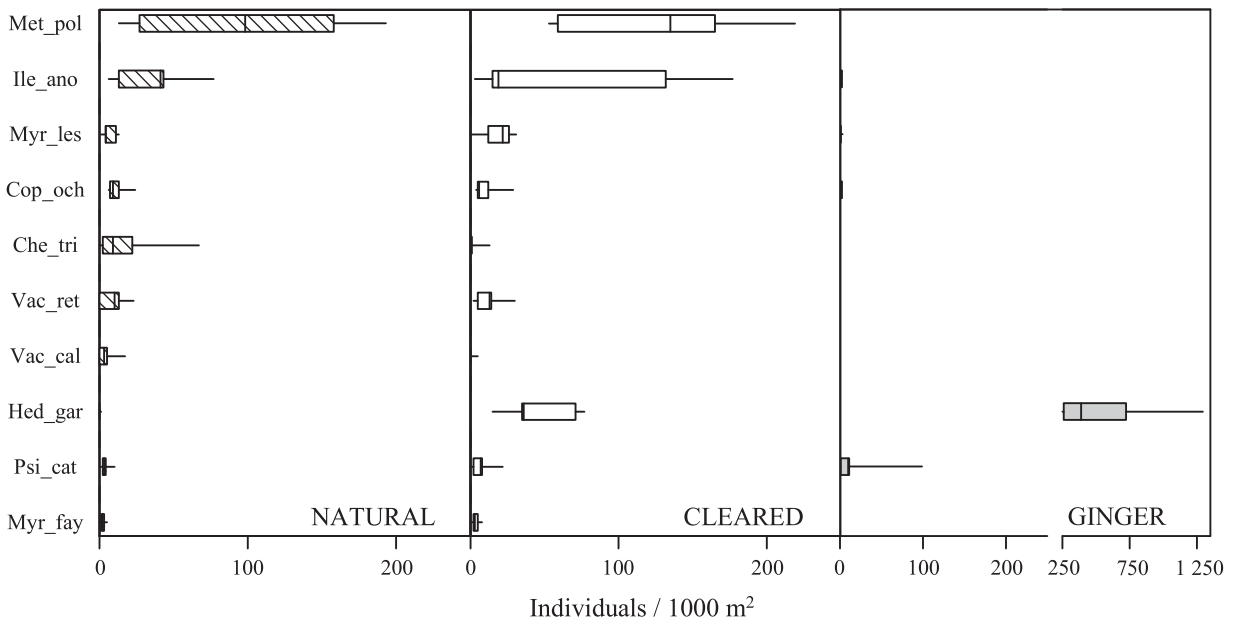


Fig. 5. Graph showing the distribution of seedling species in the three area types, N (natural) C (cleared) and G (ginger). The total individuals counted for the five plots that make up each area type are displayed. For abbreviations see Table 2.

measured by sapling abundance is clearly highest in the natural plots, second highest in the cleared plots and lowest in the ginger plots. The reason for the lower abundance of native saplings in the cleared plots could be the prior abundance of *H. gardnerianum*, which caused the suppression of germination and seedlings establishment in this area. In addition, the application of herbicide might have killed many of the smaller saplings.

It seems that conditions for sapling establishment were similar in all area types before invasion by *H. gardnerianum*, at least for *M. polymorpha*. Following *H. gardnerianum* invasion, the number of saplings decreased in ginger and cleared forest stands in comparison to natural sites. After removing alien species, the number of native plants increased again, implying possible regeneration of those study sites.

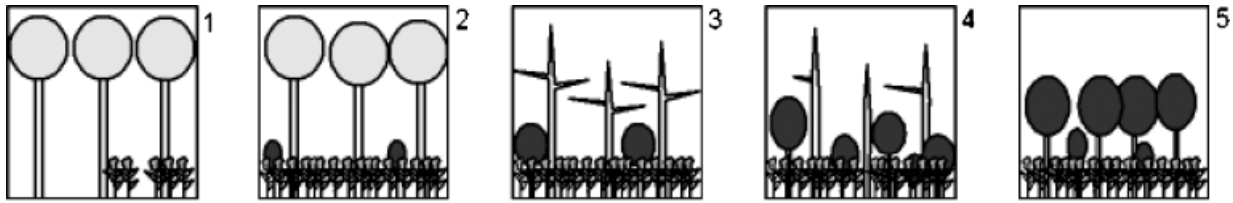


Fig. 6. Potential long-term effects of *Hedychium gardnerianum* on the native ecosystem. Beginning invasion of *H. gardnerianum* (1) and subsequent dominance in the understory of a montane rainforest dominated by *Metrosideros polymorpha* (2). Natural dieback of canopy forming tree species *M. polymorpha* without regeneration via gap-filling saplings (3), displacement of the dead canopy species by *Psidium cattleianum* (4) and establishment of a *Psidium*-forest with *Hedychium*-dominated understory (from Boehmer 2005).

According to Mueller-Dombois (1987) the first generation of mature *Metrosideros-Cibotium* forest does not have many saplings. Seedlings appear when moss-covered fallen logs accumulate over time (Burton 1982). A canopy opening event (owing to windthrow or dieback) is needed for *M. polymorpha* saplings to establish. The cleared area type experienced an “artificial” canopy opening by the removal of *H. gardnerianum*. In the ginger area types, the invasive plant itself acts as additional “canopy” and thereby suppresses the transition of seedlings to saplings. As long as this species persists in the area, sapling establishment cannot be expected.

It is presumed that the presence of *H. gardnerianum* could also increase the likelihood of other invasive species invading the area. The increased numbers of *P. cattleianum* in the ginger plots seems to affirm this hypothesis. This is the only tree species observed that is able to maintain itself in dense *H. gardnerianum* stands. Young trees of this species are already penetrating into the upper tree layers.

In the case of climate induced canopy decline (ohia dieback; Mueller-Dombois 1987; Auclair 1993) a substantial change of forest structure can be expected because of the lack of regeneration of native rain forest plants (including the foundation species *M. polymorpha*) in ginger-dominated forest stands. Instead, a new exotic rain forest type, dominated by two alien plant species, is likely to persist (Boehmer 2005; Fig. 5), thus causing a loss of ecosystem services provided by Hawaiian natural montane rainforest (Boehmer in press).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. *Metrosideros polymorpha* – flower of dominant tree species of Hawaiian rainforests; establishment of new seedlings and saplings and regeneration of rainforest by this species is threatened by invasive alien *Hedychium gardnerianum*.

Fig. S2. Ginger rainforest. Area cleared of *Hedychium gardnerianum* prior to application of herbicide in order to remove alien species

Fig. S3. Cleared rainforest. Formerly invaded part of rainforest by *Hedychium gardnerianum* 4 yr after clearing.

Fig. S4. Native rainforest. View into natural rainforest without impact of alien species. Tree fern layer and tree layer visible.

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