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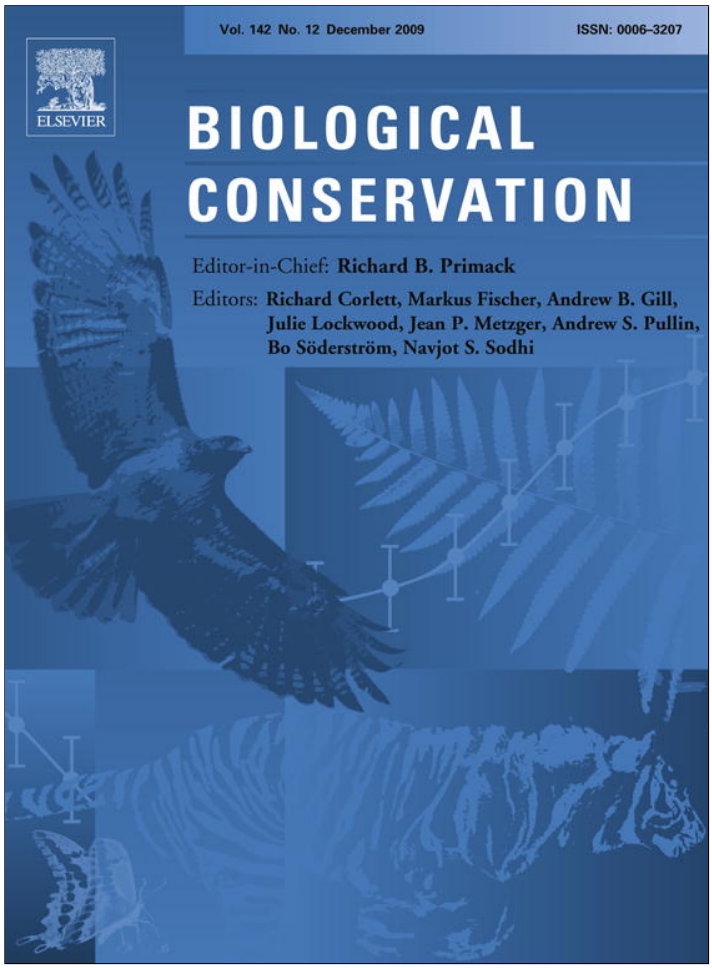

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Biological Conservation 142 (2009) 2997–3004

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest

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ARTICLE INFO

Article history:
Received 23 January 2009
Received in revised form 24 July 2009
Accepted 30 July 2009
Available online 25 August 2009

Keywords:
Germination
Melastoma
Metrosideros
Non-native species
Seed bank
Seed rain

ABSTRACT

Many tropical island forest ecosystems are dominated by non-native plant species and lack native species regeneration in the understorey. Comparison of replicated control and removal plots offers an opportunity to examine not only invasive species impacts but also the restoration potential of native species. In lowland Hawaiian wet forests little is known about native species seed dynamics, recruitment requirements, or the effects of management. In a heavily invaded lowland wet forest, we examined the relationship between seed presence and seedling establishment in control and removal plots. Non-native species were competitively superior because they had higher germination percentages and dominated the seed bank; only seven out of 33,375 seedlings were native. In contrast, the seed rain contained native seed, but native seedling recruitment was almost exclusively limited to removal plots, suggesting that optimum establishment conditions are not met in the presence of a dense mid-storey of non-native species. Non-native species dominance was altered and biomass significantly decreased over time resulting in a reduced weeding effort (12.38–0.77 g day^{-1}). We suggest that with opening of the canopy through non-native species removal and subsequent weeding, it may be possible to reduce the seed bank enough to skew the regeneration potential towards native species. Our results suggest that germination success and lack of a seed bank are the main bottlenecks for native species. We conclude that without invasive species control, future regeneration of Hawaiian lowland wet forests is likely to be almost entirely non-native.

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1. Introduction

Invasive species impact many processes in forested ecosystems including: light acquisition (Levine et al., 2003; Reinhart et al., 2006), microclimate (Holl, 1999), carbon and nutrient cycling (D'Antonio and Corbin, 2003; Gomez-Aparicio and Canham, 2008), and seed dynamics (Holmes and Cowling, 1997; Holl et al., 2000). The relative importance of the impact of these processes depends on a number of factors including the vulnerability and resilience of native ecosystems (Levine and D'Antonio, 1999; Slocum and Mendelssohn, 2008), geographic location or human development patterns, historical land use, biodiversity and size of native systems, and resource availability (Rejmánek and Richardson, 1996; Lonsdale, 1999; Mack et al., 2000; Montserrat et al., 2007; Westphal et al., 2008).

Colonization by non-native species can strongly influence regeneration and successional patterns. Understanding regeneration requires an examination of seed rain, seed banks, seed germination, and seedling dynamics. These attributes of a species' life history can show key differences between species, which ultimately might be exploited in designing restoration strategies. For example, at Kealakomo, Hawaii, while vegetation and the seed rain were moderately similar to each other, the seed bank bore little similarity to the seed rain, and even less to the vegetation. While the seed rain was dominated by native species, the seed bank was dominated by non-native species, an unfavorable result for the long-term survival of this native forest (Drake, 1998). Similarly, in South Africa, resource competition from a non-native species (*Acacia saligna*) ultimately reduced the fecundity and seed set of native species leading to a gradual attrition of native seeds in the soil (Holmes and Cowling, 1997). These examples show how

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0006-3207/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.biocon.2009.07.033

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prolific seed production or seed banks can eventually lead to a dominance of non-native species. Although this dynamic is dependent on many factors (Holl, 1999; Holl et al., 2000) it is likely that if a species is more competitive in seed production, seed longevity, germination, or seedling establishment, a change in successional patterns is likely.

Removal experiments can be a powerful method to study seed dynamics and regeneration. Eradication via invasive species removal has the potential to eliminate non-native seed rain and perhaps alter the seed bank. For example, removal of invasive species can increase native seedling densities and diversity (Biggerstaff and Beck, 2007). On the other hand, the result of higher native seedling densities is not guaranteed after removal, due to continued seed pressure of invasives via the seed bank and dispersal (Adams and Galatowitsch, 2008), as well as legacy effects from invasion (e.g., higher nutrient levels) that may favor non-native species (Ehrenfeld, 2003).

Little is known about most native Hawaiian species seed dynamics and recruitment strategies and less is known how non-native species management will impact these dynamics. The geographic isolation and geologic origins of Hawaii have resulted in a disharmonic flora with few fast growing pioneer species. The accidental and deliberate introduction of non-native species has led to numerous examples of forest degradation and native species declines (Vitousek, 1986; D'Antonio and Vitousek, 1992; Cox, 1999; Denslow, 2003; Zimmerman et al., 2008). Furthermore, it is generally recognized that the plant species in the Hawaiian Islands suffer from seed predation by non-native animals (Cabin et al., 2000), loss of the seed bank from non-native ungulates (Scowcroft and Giffin, 1983), and loss of dispersers and pollinators (Loope and Mueller-Dombois, 1989). To examine the relationship between seed presence and the establishment of native and non-native species, four control and four non-native species removal plots have been created in an invaded Hawaiian lowland wet forest. This study is part of a larger project examining the effects of invasive species removal on forest dynamics and is the only manipulative removal experiment in this unique forest type (Ostertag et al., 2009). Specifically, we ask does non-native species removal affect the spatial and temporal dynamics of seeds, and seedling regeneration. We predicted non-native species would have greater abundances in the seed rain and in the seed bank, as well as higher germination rates and seedling establishment. Our removal plots were a way to assess the ability of native species to reproduce and regenerate after the reduction of competition and subsequent changes in resource availability (Wong, 2006; Ostertag et al., 2009). We hypothesized that removal plots would contain relatively more native seeds in the seed rain and seed bank, leading to greater establishment of native seedlings.

2. Materials and methods

2.1. Study area

The study was conducted in the Hawaiian archipelago which is comprised of eight principal high islands in the Pacific Ocean and are volcanic in lithologic composition (Mueller-Dombois and Fosberg, 1998). The study site is located in the southern portion of the Keaukaha Military Reservation (KMR) immediately south of the Hilo Airport on the eastern coast of Hawaii Island (Fig. 1). It is about 30 m in elevation and is situated on a 750–1500 year old 'a'ā lava flow. Rainfall, as determined by gages at Hilo Airport, averages 3280 mm yr^{-1}. A portion of the forest (43.3 ha) was fenced in 2002 to exclude pigs (19°42.15N, 155°2.40W). The site is classified as lowland wet forest (LWF), based on the definitions of >2500 mm precipitation at 1000 m and >3000 mm at sea level

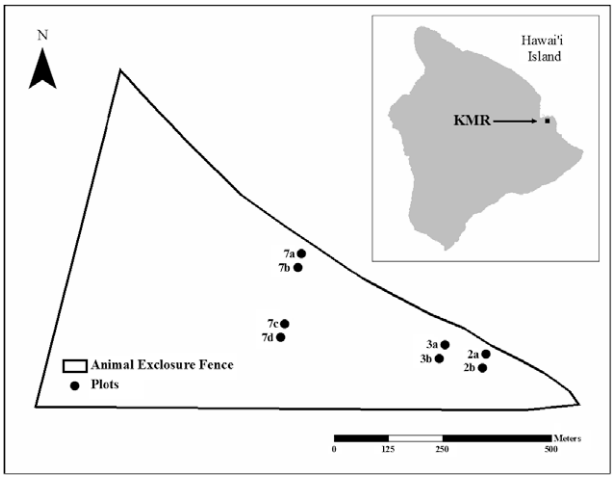

Fig. 1. Map of Keaukaha Military Reservation study area, showing location within the Hawai'i Island (inset), and within the site, the location of our eight study paired control and removal plots.

(Price et al., 2007), and on the vegetation descriptions of Gagné and Cuddihy (1999) .

The KMR site is dominated by *Metrosideros polymorpha* (Myrtaceae) and *Diospyros sandwicensis* (Ebenaceae) in the overstorey, and various shrubs, small trees, and ferns (e.g., *Pandanus tectorius*, *Alyxia oliviformis*, and *Psychotria hawaiiensis*) in the mid-storey and understorey; this *Metrosideros – Diospyros* forest community is currently found only on the eastern side of the island of Hawai'i (Gagné and Cuddihy, 1999). Numerous non-native species have invaded these forests throughout their range, most notably the trees strawberry guava (*Psidium cattleianum*), bingabing (*Macaranga mappa*), *Melastoma septemnervium*, *Falcataria moluccana*, and the shrub *Clidemia hirta* (Zimmerman et al., 2008). An inventory at this site showed that for woody species the basal area of stems $\geqslant$2.0 cm DBH was 19.8 m^2 ha^{-1} for native species and 16.4 m^2 ha^{-1} for woody non-native species, with a density of 1591 native stems ha^{-1} and 17199 non-native stems ha^{-1} (Zimmerman et al., 2008). Although the overstorey remains largely native, younger individuals in the forest are mainly non-native, and without intervention non-native species will soon dominate this forest.

2.2. Experimental design

Four pairs of 10 m × 10 m control and removal plots were set up within the exclosure fence along three permanent transects at the KMR site. Control plots were located approximately 20 m away from removal plots. We chose areas of forest with closed canopy and similar stem density for each pair of plots. In April–June 2004 all non-native species were removed, leaving only seedlings and adult forms of the native species. With the exception of *Pandanus tectorius,* few to no native mid-storey species are present in this forest. To minimize potential edge effects, non-native species were also cleared from a 2.5 m perimeter buffer around the removal plots. Trees were removed by hand or saws and cut stumps were immediately dosed with a triclopyr-based herbicide (Garlon 4, Dow AgroSciences LLC). This basal bark treatment was effective as <0.5% of the stems resprouted. Herbaceous vegetation and small shrubs were hand pulled. Information on biomass removed and characteristics of the adult tree community can be found in Ostertag et al. (2009). Previous work has shown that resource availability is different in the removal plots than controls. Light transmittance data collected at 1 m height in each plot

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showed that the invaded forest averaged 2%, with many areas less than 1%, while the removal plots averaged 21% (Wong, 2006). Other factors associated with canopy opening were increased air and afternoon soil temperatures, decreased humidity, lower leaf area indices, and reduced litterfall mass and nutrient inputs (Ostertag et al., 2009).

2.3. Seed rain

Sixteen seed rain traps were used per plot, eight in the middle of the plot (spaced approximately 1–2 m apart) and eight along two of the plot edges (approximately 2 m apart). The design followed Cottrell (2004) for situations where seed predators might be problematic; at our site we suspected that introduced rodents and ants may eat seeds. Each trap consists of a bag (~6 × 13 cm) taped or velcroed to a polyethylene funnel with a 19.37 cm diameter mouth. This equates to a 0.029 m^2 trap area. The seed collecting bag was placed inside of a pvc pipe (~20 cm long) and the funnel was then attached to the pipe by wire. The seed trap was attached to rebar and pounded into the ground so that the funnel was approximately 40 cm above the ground. Seed bags were collected approximately once a week. We modified the seed collecting bag slightly each year-during 2005 we used fiberglass window screening (1 mm holes) but switched to monofilament polyester silkscreen (53 μm mesh size) in 2006 and 2007 to better capture small seeds. In addition, the length of collection time was 28 days in 2005, 35 in 2006, and 22 in 2007, all of which occurred during the months of June and July. We present all data as number of seeds day^{-1}. Seeds were identified and counted using a Leica dissecting microscope at 100× magnification.

2.4. Seed bank

Sixteen samples per plot were taken in June within 1 m of established seed traps using a 6 cm diameter × 10 cm deep corer. Our focus on the seed rain in the summer was to address the potential of native seed inputs as a source for native recruitment. We are less confident about the magnitude (i.e., if seeds were collected throughout the year). Our shadehouse methodology varied slightly by year as we attempted to perfect germination conditions. In 2005 and 2006, each soil core was spread across a prepared 13 cm × 20 cm plastic tray that contained ~1 cm layer of sterilized potting soil and placed in a greenhouse located in Hilo, Hawaii. The shadehouse is exposed to natural light and has a mean annual temperature of approximately 25 °C. The trays had a set watering regime (5 min day^{-1} in 2005; 3 min day^{-1} in 2006) but also received supplemental hand watering when necessary to help prevent them from drying out. In 2007 each soil core was combined with 1 cup each of sterilized vermiculite and perlite and spread into a section, 6.4 × 5.1 cm, of a 53.3 × 20.3 cm seed tray (4 sections each–4 trays per plot). Trays were watered for 2 min day^{-1}.

In all years, two to six control trays containing only sterilized potting soil (to account for potential seed or spore rain from the greenhouse) were dispersed among the trays containing the soil cores. No seedlings germinated from the sterilized soil controls. Trays were placed in a randomized block design (a total of 16 blocks) and blocks were rotated at least once. Seedlings that could be identified upon the appearance of the first true leaves were counted and then removed. Unidentifiable seedlings with true leaves were marked with a colored toothpick until they could be identified. The seed bank was followed for four weeks in 2005, for 30 weeks in 2006 and 33 weeks in 2007. We discovered that spores of fern species germinate much later than other species and therefore ran our sampling longer in 2006 and 2007; for comparison sake we present data with and without ferns.

2.5. Seed germination in shadehouse

To better understand the optimum conditions for seed germination, in 2007 we conducted a shadehouse germination experiment. We chose six non-native and three native species that were represented in the seed rain and seed bank. One of the native species chosen, *Pipturus albidus*, is not currently found in the forest but was discovered in the seed bank. This species is an endemic shrub to small tree and is common in disturbed, high light environments. We designed shade structures (48 cm wide, 91 cm long, 61 cm high) out of PVC and shadecloth. Light treatments were determined based on the light levels in the field (Wong 2006) and were low light (~95–99% light blocked), medium light (~55–60% light blocked) and high light control (~1–5% light blocked) that contained no shade cloth and represented ambient shadehouse conditions. Light levels were determined using quantum sensors (Li-190, Li-COR Inc. Lincoln NE). Seeds of all nine species were collected from the field site (except for *Pipturus*), cleaned, air-dried and then placed in petri dishes on moistened sterilized sand. We randomly placed 50 seeds of each species in five Petri dishes. Germination was measured for 15 weeks and three times each week the number of newly-emerged seedlings was recorded and seedlings discarded.

2.6. Seedling census in field plots

In April 2008, approximately 4 years after initial and continued non-native species removal from field plots, we surveyed the native seedling and sapling community. In each plot, we set up two parallel transects that were 5 m apart, sampling a 1m^2 plot every other meter along a transect. In each plot all native plants were counted by height category (0–5 cm, 5–10 cm, 10–30 cm, 30–100 cm).

2.7. Weeding of emergent biomass

We conducted regular (three times a year) weedings of field plots, with the first one occurring one month after initial removal of non-native species. All non-native species were pulled up by their roots and weighed after drying for a minimum of 48 h at 70 °C. Biomass was separated by species for the first three weedings; these data are presented here. The data are expressed as g day^{-1} to account for the fact that intervals between weedings were not identical.

2.8. Data analysis

Statistical and power analyses was executed using JMP Version 6 (SAS Institute, 2005). Equal variances were confirmed before analysis and log transformed if unequal. Although removal and control plots were paired when we set up the experiment, we did not analyze the data as a block design because of a lot of variation in species composition among all plots (Ostertag et al., 2009). There were some slight methodological differences in the seed rain and seed bank studies between years, but we tested for this by using year as a factor in our analyses ($n = 24$; 2 treatments × 4 replicates × 3 years). Two-way ANOVA tests were carried out to determine differences in the total number of native and non-native species found in the seed rain and seed bank between treatments and among years. We used Sørensen's Similarity Index to analyze species overlap between the seed rain and seed bank and Czekanowski's Similarity Index to analyze overlap in abundance. We present data as significant if $p \leqslant 0.05$ and we present the power for each analysis regardless of the p value to give the reader a sense of the statistical robustness of our comparisons.

For the seed germination experiment, due to the presence of zeroes, variances were unequal between species. We therefore

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analyzed each species separately with a one-way ANOVA, using Tukey's test for multiple comparisons. There was no need to analyze the seedling survey or weeding biomass statistically due to lack of presence in control plots.

3. Results

3.1. Seed rain and seed bank

Removal plots had greater numbers of seed rain of natives in all years ($F_{1,18}$ = 4.6, p = 0.045, power = 0.53; Fig. 2) but there was no difference among years (power = 0.09) or a significant interaction between time and treatment (power = 0.27; Fig. 2). For non-native species neither the treatment (power = 0.45) or time (power = 0.27) factors were significant. These results suggest that non-native seeds are being dispersed into the removal plots and that the different methods used to capture seeds did not likely influence seed number.

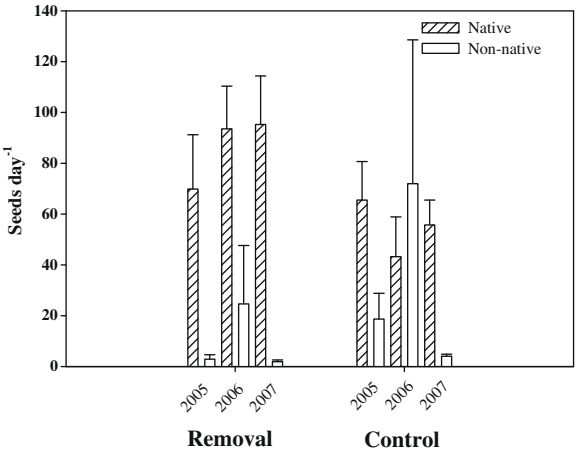

Fig. 2. Seed rain falling into all plots measured for approximately one month during three different years. Native seed rain generally is greater than non-native seed rain due to the prolific production of the wind-dispersed canopy tree, *Metrosideros polymorpha*. Values represent average and SE (n = 4 plots).

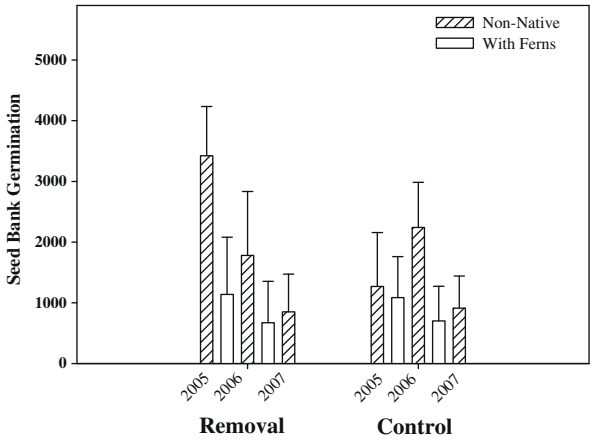

Fig. 3. Total number of seedlings germinating from seeds stored in the soil (seed bank). Samples were collected from all treatment plots using a soil corer in three different years. In 2005, the experiment was not run long enough to allow ferns to germinate, as they generally germinated after the other species. The data are therefore presented as all non-natives but ferns and an additional column for ferns that germinated from the seed bank for 2006 and 2007. Values are average and SE (n = 4 plots).

For the seed bank only seven native seedlings germinated out of a 3-year total of 33,375; all were *Pipturus albidus*, a species

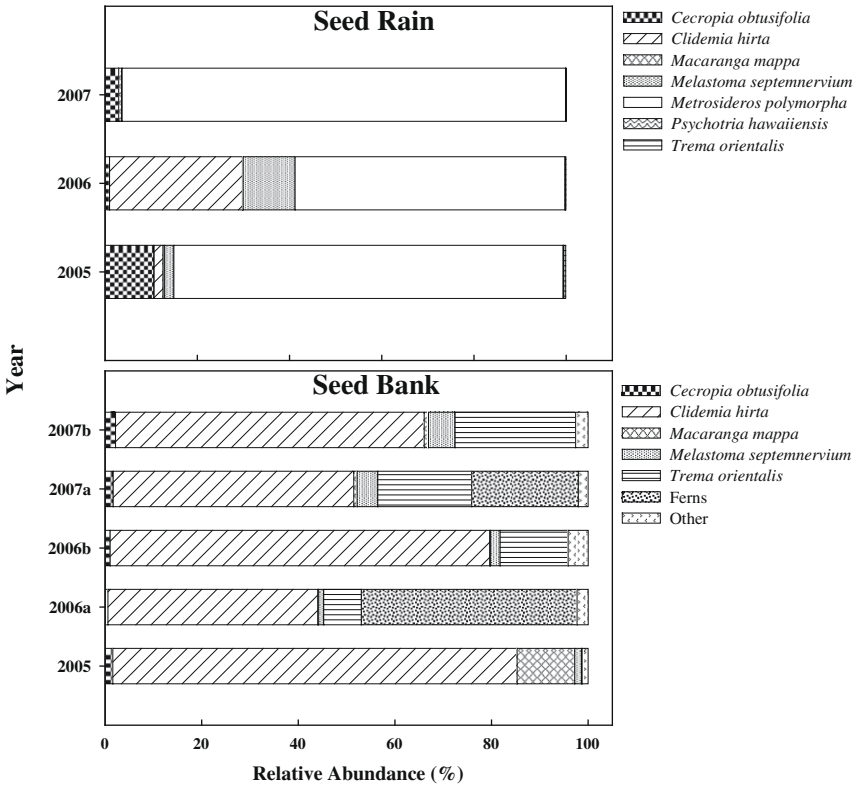

Fig. 4. Relative abundance of species found in the seed rain and the seed bank, sampled annually in all treatment plots for three years. For the seed bank, data are presented with (a) and without (b) fern germinants, which tended to germinate later than other species and were not measured in 2005. The other category includes all less common species.

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Table 1
List of species found in seed traps and seed bank soil cores. Values represent the total number of seeds found in all eight plots. For life forms: H, herb; S, shrub; T, tree; F, fern; G, graminoid; V, vine; O, orchid. Non-native species are in bold and the ones we consider invasive based on their stem density or cover have an asterisk.

	Seed rain			Seed bank			Life form	Family
	2005	2006	2007	2005	2006	2007		
Ageratum conyzoides					7		H	Asteraceae
Alstonia scholaris	10	11					T	Apocynaceae
Begonia hirtella					1		H	Begoniaceae
Blechnum appendiculatum*					67	14	F	Blechnaceae
Buddleja madagascariensis					267	6	H	Buddlejaceae
Cecropia obtusifolia*	1898	319	404	163	95	120	T	Cecropiaceae
Christella parasitica*					6727	1450	T	Thelypteridaceae
Clidemia hirta*	360	9426	2	8547	7004	3516	S	Melastomataceae
Crassocephalum crepidioides					1		H	Asteraceae
Cyperus rotundus				3	15	1	G	Cyperaceae
Dioscorea pentaphylla				9			V	Dioscoreaceae
Falcataria moluccana					7	1	T	Fabaceae
Galium divaricatum					1		H	Rubiaceae
Macaranga mappa*	57	43	95	1217	10	49	T	Euphorbiaceae
Melastoma septemnervium*	359	3689	7	144	179	303	T	Melastomataceae
Metrosideros polymorpha	15,133	19,144	13,286				T	Myrtaceae
Nephrolepis spp.*					8	28	F	Nephrolepidaceae
Oplismenus hirtellus				1	1		G	Poaceae
Paederia foetida		1					V	Rubiaceae
Paspalum conjugatum				1	1		G	Poaceae
Phymatosorus grossus					7		F	Polypodiaceae
Pipturus albidus					7		T	Urticaceae
Pityrogramma calomelanos*					380	67	F	Pteridaceae
Pluchea indica				8	31		H	Asteraceae
Psidium cattleianum*					1		T	Myrtaceae
Psychotria hawaiiensis	30	10	3				T	Rubiaceae
Rubus rosifolius				3	21	128	H	Rosaceae
Spathoglottis plicata				2	1		O	Orchidaceae
Trema orientalis*	70	42	24	14	1253	1373	T	Ulmaceae
Unknown		18		100	8	7		

currently not found in this forest. Neither factor (treatment and time, power = 0.05 and 0.23, respectively) nor the interaction (power = 0.05) significantly affected non-native seeds. The results suggest that the non-native seeds in the seed bank are evenly distributed in the forest (Fig. 3), and that differential methodology between years was not influential.

The species composition of the seed rain and seed bank was dramatically different (Fig. 4), mainly because the seed rain is predominantly the native *Metrosideros*, whereas the seed bank is mainly *Clidemia*, *Trema*, and ferns. Species' abundances were highly variable by year (Table 1). Species overlap between the seed rain and seed bank was 41.3% but the similarity in abundances was 83.7%, largely due to the quantity of *Clidemia*.

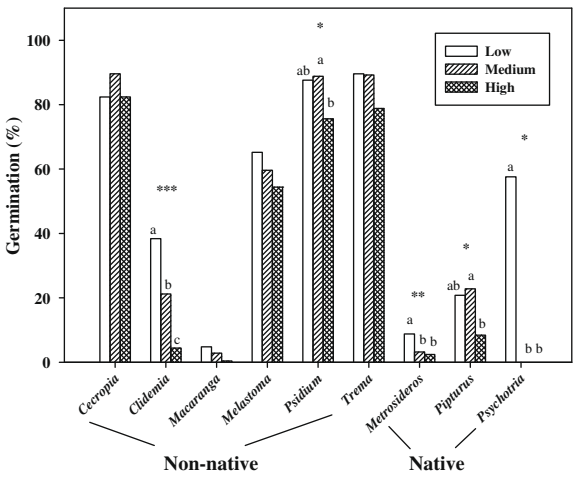

Fig. 5. Germination of seeds in petri dishes under three different light treatments. The experiment was run on six non-native and three native species. Within a species, significant differences are represented by asterisks ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$) and letters represent treatment differences.

3.2. Seed germination in shadehouse

Five species showed significant differences among light treatments. Of the native species, *Metrosideros* did best in low light conditions ($F_{2,12} = 7.9$, $p = 0.007$, power = 0.89), and *Psychotria* only germinated under low light ($F_{2,12} = 6.0$, $p = 0.016$, power = 0.78). *Pipturus* was also capable of germinating under low light conditions ($F_{2,12} = 5.5$, $p = 0.021$, power = 0.74; Fig. 5). Four non-native species (*Cecropia, Macaranga, Melastoma*, and *Trema*) showed no difference in germination percentage among light treatments, indicating that they would be successful under both invaded and removal conditions. *Clidemia* germination was lowered under high light ($F_{2,12} = 18.6$, $p = 0.0002$, power = 1.0), and the same was true for *Psidium* ($F_{2,12} = 4.9$, $p = 0.023$, power = 0.69).

3.3. Seedling census and weed management in field plots

Native species regeneration was very low in the control plots (<10% than found in removal plots) (Table 2), and the only species that was found to regenerate in this amount of shade was *Psycho-*

Table 2
Total number of native seedlings and saplings found in all four plots per treatment (80 m^2 area).

	Removal	Control
Alyxia oliviformis (Apocynaceae)	0	1
Metrosideros polymorpha (Myrtaceae)	115	0
Psychotria hawaiiensis (Rubiaceae)	330	34

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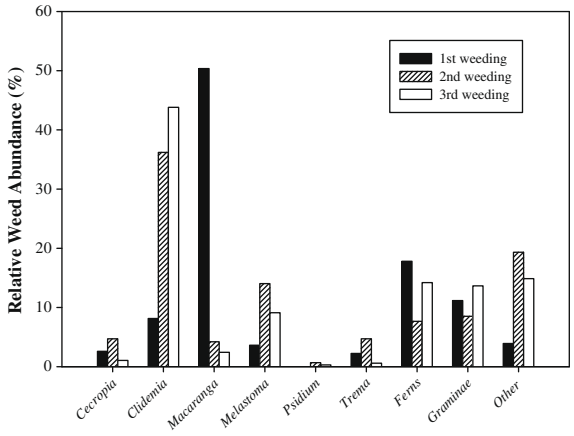

Fig. 6. Relative abundance of weed biomass establishing in the four removal plots, over the course of three weedings. The figure describes both total abundance and shows the shift in species composition over time. The plots were established between April–June 2004. The first weeding was conducted in January–February 2005; the second in September–November 2005; and the third in July–November 2006.

tria. However, in removal plots this species has 10 times more establishment than in the heavily-shaded control plots. *Metrosideros* seedlings and saplings were only found in the removal plots and we noted that no seedlings were found until more than a year after removal. Most of the plants of all species were quite small: 29.4% were 0–5 cm tall, 39.0% were 5–10 cm, 27.3% were 10–30 cm, and 4.4% were 30–100 cm.

There was a large difference in both the total biomass and relative abundance of species between weedings. The first weeding yielded 12.38 g day^{-1} of biomass, which dropped to 0.77 g day^{-1} (Ostertag et al., 2009) by the third weeding. The first weeding was dominated by *Macaranga* but this species was not very important by the second and third weedings, in which *Clidemia* dominated (Fig. 6).

4. Discussions and conclusions

Native and non-native species were clearly different in many of their regeneration dynamics and seed traits, and our study demonstrates mechanisms by which species are successful. In the long-term, invasion by non-native species represents an ecological threat to the integrity of the Hawaiian lowland wet forest as they have altered the structure (Zimmerman et al., 2008) and functioning of this forest (Ostertag et al., 2009); therefore, an ecological return to pre-colonization by non-native species is not a realistic approach. In addition, most of the dispersers are non-native birds (Foster and Robinson, 2007) or mammals.

4.1. Seed dynamics and regeneration in invaded forest

The current low-light environment of the invaded forest favors the non-native species because of the differential regeneration limitations of the native and non-native species. Although the specific reasons why the dominant species are successful vary among species (Table 3), germination appears to be a key factor given that most native and non-native species can germinate under low light (Fig. 5). However, we did not adjust the red / far red threshold in this experiment which may not accurately portray species with photoblastic germination dynamics. *Macaranga* is the only species that did not germinate well, and its low levels in the seed rain, but strong presence in the seed bank suggests that it requires disturbance. Our results for *Psidium* agree with those from previous studies done on this species in Hawaii (Uowolo and Denslow, 2008), in which a limited seed bank and high germination percentages were found.

While in many other geographic areas native and non-native species can be equally competitive in regeneration and growth (e.g., (Horvitz et al., 1998), in Hawaii this is often not the case due to a limited pool of native species and a set of resource-use traits that are generally conservative (Pattison et al., 1998; Stratton and Goldstein, 2001; Daehler, 2003; DeWalt and Hamrick, 2004; Litton et al., 2006; Funk and Vitousek, 2007). These traits include slow growth rates, low foliar nutrients and long-lived leaves. Our study shows that the native species are at a disadvantage due to poor recruitment success in the invaded forest, shown by the absence of seedlings (Table 2). This recruitment failure is not due to lack of seed rain, or the ability to germinate under low light conditions. However, the non-native species have a higher overall germination rate than the natives and completely dominate the seed bank. Drake (1998) suggests that the small wind dispersed seeds of *Metrosideros* do not form a long lived seed bank and while year round seed production allows for consistent seed availability following disturbance, seedling establishment depends on the nature of the post disturbance environment. In contrast to our results, *Metrosideros* has been shown to require high light conditions for germination (Burton, 1982; Burton and Mueller-Dombois, 1984) and growth, whether it occurs as the pioneer species on a recent lava flow or as a dominant species in late succesional forests (Stemmermann, 1983; Mueller-Dombois, 1992a, b; Mueller-Dombois, 1994, 2000). It is also notable that no seedlings or seeds of *Diospyros*, the other native canopy dominant were found. We conclude that future regeneration at our study site and similar LWF in Hawaii will be almost entirely non-native.

4.2. Effects of invasive species manipulation

Comparison of replicated control and removal plots offers an opportunity to examine the efficacy of invasive species impacts

Table 3
Regeneration characteristics of the major non-native and native species under low light conditions (present closed canopy) and under high light conditions (canopy opening through biomass removal).

Species	Regeneration capacity		Reasons
	Closed canopies	Open canopies	
Non-native			
Cecropia obtusifolia	High	High	High germination rate, moderate seed rain
Clidemia hirta	High	High	Large seed bank, moderate germination rate in low light, moderate seed rain
Macaranga mappa	High	High	Large seed bank in year 1
Melastoma septemnervium	High	High	High germination rate, moderate seed rain
Psidium cattleianum	High	High	High germination rate
Trema orientalis	High	High	High germination rate, moderate seed bank
Native			
Metrosideros polymorpha	None	High	No seed bank and low germination rate but high seed rain
Psychotria hawaiiensis	Low	Moderate	Moderate germination rate but no seed bank and limited seed rain

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and restoration potential (D'Antonio and Chambers, 2006). Increasing light availability via invasive species removal appears to be a viable option for encouraging native species. Only one native species, *Pipturus albidus*, a species currently not found in this forest germinated in the seed bank study. This finding is interesting because *P. albidus* possesses traditional r-selected life history traits with small widely dispersed seeds and generally establishes in disturbed high light environments (Wagner et al., 1999). Because the native species were not generally found in the seed bank, seed sources must come from the seed rain. Removal plots had higher amounts of seed rain of *Metrosideros* during our short survey period, which suggests that canopy opening may lead to greater allocation to reproduction. Similar results were found with other native species where invasive understory plants were removed (Litton et al., 2006). It is also possible that the presence of non-native species in the control plots may inhibit seed fall into the traps. In addition removal plots had greater seedling establishment of *Metrosideros* and *Psychotria* than control plots (Table 2).

The disturbance of canopy opening and weed pulling also stimulates establishment of non-native species, due to their strong presence in the seed bank (Figs. 3 and 6). This conclusion was echoed by work in another Hawaiian forest where the seed rain was predominately native, but the seed bank was comprised of 67% non-native seeds (Drake, 1998). Such an outcome may have been reduced if we did a partial canopy removal or slowly killed the trees via girdling, as was noted by Loh and Daehler (2007), where native seeding success was highest in plots where trees were girdled rather than removed.

Uncertainties about understorey light levels of LWF before human presence complicates the canopy opening question, but we suggest that these forests are at a higher density than historically because light levels for *Metrosideros*-dominated wet forest range from 5–10% (Burton and Mueller-Dombois, 1984; Pattison et al., 1998), while the invaded forests averaged 2% (Wong, 2006). Other microclimatic factors associated with canopy opening may also favor non-native species over natives. Granted, although removal plots may lead to soil disturbance and affect microclimate and nutrient availability (Biggerstaff and Beck, 2007), they are appropriate for this ecosystem type, in which pristine uninvaded areas are non-existent (Zavaleta et al., 2001; Díaz et al., 2003). Given that we saw no native *Metrosideros* seedlings establish until 1 year after removal, it is unlikely they are benefiting from a short-term treatment artifact.

Species-specific patterns after canopy opening are worth elaborating, as they offer clues to the mechanisms by which species are likely to be strong competitors. Initially after removal, *Macaranga* dominates, as seen both by its abundance in the seed bank the first year (Table 1), and its establishment (Fig. 6); this strategy is similar to a "seed-bank robber" as defined by (Horvitz et al., 1998). *Clidemia* largely replaces *Macaranga* as the most important weed at later time points due to later observations of emergence. This species has been demonstrated in Hawaii to invade and grow well under low light conditions in contrast to it's native range where its presence is restricted to open pastures and disturbed areas (DeWalt et al., 2004). Although these species shifts are noteworthy, and will affect competitive interactions among species, the weeding effort did decrease over time. We suggest that with continued invasive species removal, it may be possible to alter the seed bank enough to encourage native regeneration. Additional data on seed longevity and dispersal efficiency of the non-native species will supplement knowledge on how to reduce the seed bank over time. Because invaders in this ecosystem are trees, and some with potentially long-lived seeds, the impacts of invasion may be greater than when dealing with short-lived species (Panetta and Sparkes, 2001; Cacho et al., 2006).

4.3. The future structure of Hawaiian lowland wet forests

Hawaiian lowland wet forests will likely shift to non-native species dominance due to lack of regeneration of native trees (Zimmerman et al., 2008). Consequences of this altered composition will likely affect habitats and food resources for native Hawaiian birds, which only recently have been seen in LWF (Spiegel et al., 2006), after developing some form of decreased sensitivity to avian malaria (Woodworth et al., 2005). We recommend non-native species removal to encourage natural regeneration, with supplemental native species planting as an additional strategy. However, a consequence of canopy opening will be increased establishment of non-native species due to their complete dominance in the seed bank. Our research suggests that large scale disturbance of non-native understory dominated Hawaiian lowland wet forests without follow up invasive species removal may actually promote the spread and further success of invasive species. In addition, small-scale studies do not always translate to the landscape scale, if new non-native species invade the larger disturbed areas (Ogden and Rejmánek, 2005). To promote native species dominance or a trajectory towards a functionally native ecosystem, a smaller-scale intensive effort is likely to be more effective in highly threatened ecosystems such as Hawaiian LWF; without it, this ecosystem is very likely to become a new stable state of non-native trees.

Acknowledgements

This research was funded and facilitated through NSF EPSCoR Awards 0237065 and 0554657, NSF REU 0139379, NSF TCUP 0223040, NSF CAREER 0546868 and The USDA Forest Service, Institute of Pacific Islands Forestry. For student support we thank L. Canale, K. Gunderson, S. Juvik, D. Kapp, H.E. Perry, C. Perez-Frayne, D. Price, and S. Ziegler-Chong. Access to field sites was provided by the Hawaii Army National Guard Environmental Office (Col. O. Peterson), and C. Blaisdell, C. Thurkins, and Major Lindsey facilitated this research at Keaukaha Military Reservation. We also thank C. Thurkins for her guidance and hard work and the numerous volunteers who assisted in plot creation. We thank all of those who helped us in the field, A. Skipper, K. Publico, and J. Enoka. C. Baskin and K. Holl provided helpful comments. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of NSF.

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