BIOTROPICA 0(0): 1–9 2012 10.1111/j.1744-7429.2011.00841.x

Vegetation Recovery 16 Years after Feral Pig Removal from a Wet Hawaiian Forest

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ABSTRACT

Nonnative ungulates can alter the structure and function of forest ecosystems. Feral pigs in particular pose a substantial threat to native plant communities throughout their global range. Hawaiian forests are exceptionally vulnerable to feral pig activity because native vegetation evolved in the absence of large mammalian herbivores. A common approach for conserving and restoring forests in Hawaii is fencing and removal of feral pigs. The extent of native plant community recovery and nonnative plant invasion following pig removal, however, is largely unknown. Our objective was to quantify changes in native and nonnative understory vegetation over a 16 yr period in adjacent fenced (pig-free) vs. unfenced (pig-present) Hawaiian montane wet forest. Native and nonnative understory vegetation responded strongly to feral pig removal. Density of native woody plants rooted in mineral soil increased sixfold in pig-free sites over 16 yr, whereas establishment was almost exclusively restricted to epiphytes in pig-present sites. Stem density of young tree ferns increased significantly (51.2%) in pig-free, but not pig-present sites. Herbaceous cover decreased over time in pig-present sites (67.9%). In both treatments, number of species remained constant and native woody plant establishment was limited to commonly occurring species. The nonnative invasive shrub, *Psidium cattleianum*, responded positively to release from pig disturbance with a fivefold increase in density in pig-free sites. These results suggest that while common native understory plants recover within 16 yr of pig removal, control of nonnative plants and outplanting of rarer native species are necessary components of sustainable conservation and restoration efforts in these forests.

Key words: disturbance; feral ungulates; nonnative invasive species; *Psidium cattleianum*; *Sus scrofa*; tropical montane wet forest.

The introduction of nonnative ungulates can alter the structure and function of terrestrial ecosystems and poses a substantial threat to native plant communities via herbivory and increased levels of disturbance (*e.g.*, Vitousek 1990, D'Antonio & Vitousek 1992, Didham *et al.* 2005). Nonnative feral pigs (*Sus scrofa*; wild boar) have a considerable impact on forest ecosystems globally (Campbell & Long 2009, Siemann *et al.* 2009, Spear & Chown 2009). In the United States alone, they are thought to be a greater extinction threat to native species than any other single species aside from humans (Gurevitch & Padilla 2004). Feral pigs affect ecosystems primarily through rooting, trampling, browsing of above and belowground plant material, and presumably by facilitating nonnative plant invasions (Ickes *et al.* 2001, Spear & Chown 2009). Rooting by pigs can be extensive—a single animal can disturb up to 200 m^2/day of rain forest soil surface (Anderson & Stone 1993), with potentially large consequences for soil processes (Siemann *et al.* 2009), plant regeneration patterns, and competitive dynamics.

The impacts of feral pigs on plant communities have been documented in a wide array of habitats globally. In Malaysian rain forest where pigs are native, increasing pig population densities due to human encroachment substantially reduced recruitment and growth of woody seedlings (Ickes *et al.* 2001). Measurements inside experimental exclosures showed a marked increase in species richness, density, and height of woody seedlings within 2 yr (Ickes *et al.* 2001). Exclusion of nonnative feral pigs from mixed pine–hardwood forests in Texas led to increased diversity of woody understory plants over 7 yr (Siemann *et al.* 2009). Bratton (1975) reported a sharp decrease in the cover of herbaceous species in pig-invaded areas of deciduous forest in the southern Appalachians compared to areas where feral pig populations had not yet established. Likewise, increasing feral pig population densities and rooting activity resulted in diminished plant species richness in southeastern Australia (Hone 2002), and reduction in herbaceous species cover in arid shrubland in Argentina (Cuevas *et al.* 2010).

Feral pigs might also promote the occurrence and spread of nonnative plants (Diong 1982, Siemann *et al.* 2009, Oduor *et al.* 2010). In the Hawaiian Islands, feral pigs readily disperse the seeds of highly invasive species such as *Psidium cattleianum* (strawberry guava) (Diong 1982), and increased densities of nonnative plants have been reported in association with soil disturbance caused by feral pigs (Aplet *et al.* 1991). Disturbance by pigs may also alter patterns of regeneration. For example, Busby *et al.* (2010) found that clonal regeneration (sprouting) became more important than seedling establishment in feral pig-impacted wet forests in Hawaii due to the negative impacts on seedlings.

The effects of feral pigs on native plant communities are of particular conservation concern in island habitats that evolved in the absence of large mammalian herbivores (Courchamp *et al.* 2003). Feral pigs have impacted almost every plant community in the Hawaiian Islands (Jacobi 1981, Anderson & Stone 1993, Nogueira-Filho *et al.* 2009) and are considered to be one of the

Received 24 April 2011; revision accepted 1 September 2011.

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primary threats to Hawaiian wet forests today. The predominant approach for active conservation and restoration in Hawaiian wet forests is fencing and removal of feral pigs, along with the removal of other nonnative ungulates (*e.g.*, feral cattle, deer, and goats) and plants where needed. Despite the need for conservation and restoration of these forests, there is little information on patterns of native plant recovery or the effects of reduced disturbance with feral pig removal on native and nonnative plant dynamics over time following this management approach.

Although excluding feral pigs can have a positive effect on native vegetation (Loh & Tunison 1999, Ickes *et al.* 2001, Busby *et al.* 2010), it may also lead to unexpected changes in community structure. In several cases, removal of nonnative ungulates has been shown to release invasive plants from top-down control, resulting in dramatic increases in nonnative plant species richness and abundance, particularly on islands (Eckhardt 1972, Zavaleta *et al.* 2001). All of the studies that have documented increases in nonnative plants following nonnative ungulate exclusion, however, have focused on herbivores that disturb native communities primarily via browsing (*e.g.*, goats and cattle). In Hawaiian wet forests, epiphytic establishment of woody and herbaceous plants is common. Yet, because information on forest stand structure prior to pig disturbance is lacking and previous studies have focused on plant establishment at ground level, little is known about spatial patterns of recruitment (*i.e.*, epiphytic vs. mineral soil establishment) following pig removal.

In this study, we present long-term measurements of native and nonnative plant dynamics following the fencing and removal of feral pigs, a common management approach in conservation areas in the Hawaiian Islands and elsewhere. It is relevant to note that feral pig management in Hawaii occurs within a complex arena of social and conservation values, which have often been in conflict (Adler 1995, Maguire 2004). Today, feral pigs are viewed differently in Hawaii by biologists, native Hawaiian communities, and local communities (Adler 1995, Maguire 2004). The ecological consensus is that feral pigs are detrimental to native Hawaiian ecosystems, which has justified their removal from select conservation areas, most notably on the Island of Hawaii. Feral pigs, however, are simultaneously viewed as an important cultural element to native Hawaiians and as game for local hunters. As a result, tensions between these disparate stakeholder groups have historically been high. A conspicuous gap in this ongoing debate is rigorous measurement of the ecological impacts of feral pigs in Hawaiian forest. The majority of exclosure studies on the Hawaiian Islands have either lacked a comparison with pig-present areas, been carried out over relatively short time scales (≤ 8 yr), or utilized small experimental exclosures leading to concerns over the confounding influence of edge effects (reviews: Loope & Scowcroft 1985, Nogueira-Filho *et al.* 2009). The few studies using large fenced exclosures and documenting plant succession over time (*e.g.,* Loope *et al.* 1991, Medeiros *et al.* 1991, Pratt *et al.* 1999) have been published in nonpeer reviewed literature limiting their accessibility to management and research communities. The current study, the first to our knowledge to include long-term measurements in adjacent control areas where pigs were not removed, endeavors to provide information useful to management decisions on public lands in Hawaii and elsewhere throughout the tropics.

The objective of this study was to quantify how fencing and removal of feral pigs affect native and nonnative understory plant dynamics in canopy-intact Hawaiian tropical montane wet forest. We conducted the study over a 16-yr period in adjacent fenced (pig free) and unfenced (pig present) sites to measure changes in understory vegetation that occurred between and within treatments over time. Specifically, we: (1) compared density and cover of native and nonnative understory plants in the presence and absence of feral pigs; and (2) examined how pigs modify spatial patterns of recruitment by monitoring establishment of plants growing epiphytically and in the mineral soil.

METHODS

STUDY AREA.—The study was conducted in the Olaa-Koa rain forest unit of Hawaii Volcanoes National Park (HAVO) (19°28′22″ N, 155°15′00″ W), a 1024 ha management unit on the east slope of Mauna Loa at 1100–1200 m asl The forest is classified as Ohia/(*Metrosideros polymorpha*; overstory tree)/Hapuu (*Cibotium glaucum*; midstory tree fern) tropical montane wet forest (Wagner *et al.* 1990). Mean annual temperature is 15.7°C and mean annual precipitation is 3500 mm with no distinct seasonality (Giambelluca *et al.* 1986). Substrate is tephra-derived Hapludands consisting of deep, moderately well drained soils formed over basic lava (NRCS 2010). A pig-proof exclosure was constructed in 1989 around the entire management unit. Feral pigs were removed over the following three and half years, and the final individual was removed in 1994 (Loh & Tunison 1999). The surrounding unfenced forest has never been managed for feral pigs outside of recreational hunting, and there has been no management of invasive plants in the study plots or the surrounding area. Although no feral pig population studies have been done in the Olaa-Koa management unit, feral pig densities have been estimated at 12.5 pigs/km^2 in similar, nearby wet forest on the Island of Hawaii (Hess *et al.* 2006), and at 4.8–30.7 pigs/km^2 on the Island of Maui (Diong 1982, Anderson & Stone 1993).

Overstory vegetation in the study area is exclusively native and dominated by *M. polymorpha* and *Acacia koa*, along with less frequent individuals of *Ilex anomala*, *Cheirodendron trigynum*, *Perrottetia sandwicensis*, and *Coprosma* sp. The subcanopy is dominated by three native tree ferns (*Cibotium* sp.) with a variety of native shrub, fern, and herbaceous species composing the understory. A 1998 vegetation survey in the Olaa-Koa management unit (~1.5 km from the site of the current study) indicated that several nonnative plants, including *P. cattleianum* (strawberry guava) and *Setaria palmifolia* (palm grass), were present in low densities in the understory (Loh & Tunison 1999).

VEGETATION SAMPLING.—In 1994, a total of ten 20 × 50-m paired plots were established along the northeast perimeter of the Olaa-Koa unit. Five plots were established within the fenced exclosure (pig-free) and five in the surrounding unfenced area (pig-present). Plot pairs were placed at ~150-m intervals along the fence line starting from a randomly selected point, and pig-free and pig-present plots within a given pair were separated by ~30 m on either side of the fence. The vegetation was sampled in May–June 1994 and 16 yr later in April–May 2010. Because feral pig population density decreased over a three and a half year removal period it is possible that some vegetation recovery had occurred in fenced plots by the time of our initial 1994 measurements.

During both sampling periods, we quantified native and nonnative understory vegetation in each plot by measuring the density of understory woody plants (defined as all tree seedlings, saplings, and shrubs >10 cm height and <5 cm diamater at breast height [dbh at 1.3 m]) and herbaceous cover in a 10 × 10 m sub-plot. These subplots were consistently located on the southwest corner of the larger plots. For density, all understory woody plants rooted ≤ 2 m above the soil surface were identified to species and counted and the rooting location of each woody plant was quantified as either ground-rooted (originating in mineral soil) or epiphytic (originating ≥ 10 cm above soil surface on woody substrate). Herbaceous cover (≤ 2 m above the soil surface) was quantified using a point-intercept method along five 10 m transects spaced 2 m apart, where a pole was lowered vertically at 20 cm intervals and species touching the pole were recorded. In 1994, if no vegetation was intercepted by the pole, the ground cover type (bryophyte, litter, or bare soil) was recorded. In 2010, ground cover type was recorded at all points, regardless of plant cover, to better assess differences in ground disturbance between pig-free and pig-present sites.

To characterize overstory vegetation, all trees ≥ 5 cm dbh and all tree ferns were measured in the same 10 × 10 m sub-plots used for the understory vegetation and in an adjacent 10 × 10 m area to the southeast (200 m^2 total per plot). Each stem was identified to species and categorized into dbh size classes (5–9.9, 10–19.9, 20–29.9 cm, etc.). Because tree ferns often have decumbent growth, we measured stem length instead of dbh as length is a better estimate of plant size, and presumably age. Tree ferns were identified to species and stem length categorized into size classes (<50, 50–99.9, 100–149.9 cm, etc.). Dominant canopy species including *A. koa* and *M. polymorpha* trees ≥ 10 cm dbh were counted and placed into size classes as described above for the entire 20 × 50 m plot. Percent canopy cover was also quantified in each plot in 2010 using a spherical densiometer.

Statistical analyses.—Each plot within a treatment was considered a replicate (N = 5). Repeated measures Analysis of Variance (rmANOVA) was used to test whether total number of species, proportion of cover of native and nonnative herbs, number of young tree ferns (<50 cm length), and density of native and nonnative understory woody plants, either ground-rooted or epiphytic, had changed over time and as a factor of pig removal. Sampling period was considered as the repeated effect with treatment as the other main effect. *Post hoc* comparisons of means were carried out using paired t-tests. When there was a significant interaction between sampling period and treatment (time × treatment), changes over time within treatments and differences between treatments within sampling periods were analyzed using a paired t-test.

Because we lumped larger trees (≥ 5 cm dbh) and tree ferns (>50 cm) into size classes and the focus of the study was to assess changes in the understory where feral pigs are likely to have the greatest impact, we used these data only to compare forest structure between treatments within sampling periods, and not across time. Total estimated basal area of trees and total tree fern length were compared using paired t-tests or, where applicable, Wilcoxon sign-ranked tests for non-parametric data. Because of differences in methodology for ground cover measurements between sampling years, this metric was compared across treatments within each sampling period using paired t-tests, and not across time. Data were log or square-root transformed when necessary to meet assumptions of homogeneity of variance (Zar 1996). Statistical analyses were conducted using Systat 13 (Systat Software, Chicago, Illinois, U.S.A.) at $\alpha = 0.05$. Mean values with one standard error (SE) are reported throughout.

In addition, statistical estimators of species richness were calculated for understory woody plants in each treatment using EstimateS 8.20 software (Colwell 2007). We calculated the nonparametric Chao 2 incidence-based richness estimator with log-linear 95% CIs and the incidence-based coverage estimator (ICE) (Chao 1987, Colwell & Coddington 1994). These estimators are appropriate for quantifying species richness data from relatively small samples (ICE) and small grain size (Chao 2) (Brose *et al.* 2003, Hortal *et al.* 2006). The default of 50 randomization runs was used without replacement (Colwell 2007).

RESULTS

Species richness and ground and canopy cover.—A total of 40 species was found across all plots, including 15 native herbs and ferns, 18 native woody species (including tree ferns), three nonnative woody species, and four nonnative herbs, ferns, and grasses (Table S1). The total number of native and nonnative species did not differ by treatment or sampling period (Table 1). There was nearly complete overlap of species between treatments and over time with two exceptions: a nonnative fern (*Athyriopsis japonica*) and a nonnative herb (*Cardamine cordata*) were both present with low proportion of cover (< 0.02) in 1994 and were absent in 2010. Species richness of understory woody plants decreased moderately over time in both treatments with the greatest negative change occurring in the pig-present sites (Table 2). *Psidium cattleianum*, the most commonly occurring nonnative woody species, was present in four of five plots in both treatments in 1994, and in all plots in both treatments in 2010. *Setaria palmifolia* remained confined to one plot in the pig-free treatment during both sampling periods, but invaded an additional pig-present plot by 2010 (total of four plots in pig-present site by 2010).

The proportion of forest floor covered by litter was similar in both treatments in 1994 but was significantly higher in pig-free sites in 2010 (Table 3; P < 0.046). In contrast, the proportion of

TABLE 1. *Repeated measures ANOVA of the effect of treatment (pig-free vs. pigs-present) and time (sampling periods in 1994 and 2010) on native and nonnative vegetation. Significant results are shown in bold.*

	Treatment		Time		Treatment × Time	
Factor	F	P	F	P	F	P
Number of species	0.530	0.487	3.52	0.097	0.88	0.775
Small tree fern density	0.135	0.723	12.76	**0.007**	3.59	0.095
Proportion herbaceous plant cover						
Native herbs	7.50	**0.026**	6.58	**0.003**	2.24	0.173
Nonnative herbs	3.10	0.116	1.07	0.330	6.43	**0.035**
Understory woody plant density						
Total native woody plants	2.60	0.146	4.55	0.066	1.71	0.228
Total nonnative woody plants	0.006	0.942	17.21	**0.003**	3.20	1.112
Ground-rooted native	26.85	0.001	14.09	0.006	16.11	**0.004**
Ground-rooted nonnative	2.82	0.132	13.02	0.007	6.41	**0.035**
Epiphytic native	4.33	0.070	0.400	0.544	2.45	0.156
Epiphytic nonnative	1.87	0.209	1.77	0.220	0.36	0.565

TABLE 2. *Species richness estimators, incidence-based coverage estimator (ICE) and Chao 2, for tree seedlings and shrubs in pig-present and pig-free plots. For ICE, standard deviations are in parentheses. For Chao 2, 95% CI are in parentheses. Chao 2 estimators were calculated using the bias-corrected method (Colwell 2007).*

Year	Treatment	ICE	Chao 2
1994	Pig-present	20.5 (3.4)	17.9 (13.2–39.4)
1994	Pig-free	19.0 (4.7)	16.9 (12.7–36.7)
2010	Pig-present	13.6 (2.3)	13.0 (9.61–31.5)
2010	Pig-free	15.1 (1.8)	14.2 (10.6–33.0)

bare ground was substantially greater where pigs were present in both 1994 and 2010 (Table 3; $P < 0.006$ in each case). Bryophyte cover was similar between pig-free and pig-present sites during each sampling period (Table 2; $P > 0.803$). Total basal area of trees ≥ 5 cm ranged from 22.3 m^2 to 39.0 m^2/ha and did not differ between treatments in either the 1994 or 2010 sampling periods ($t < 1.14$, $P > 0.317$ in each case). Canopy cover ranged from 92.6 to 96.4 percent and was consistent across treatments.

UNDERSTORY WOODY VEGETATION.—The total density (ind./ha) of native understory woody plants was similar between treatments in both 1994 (1880.0 ± 621 pig-present; 2170.0 ± 306 pig-free) and 2010 (2380.0 ± 667 pig-present; 4250.0 ± 840 pig-free) although there was a marginally significant increase over time in the pig-free treatment (Table 1). When rooting location was taken into account, however, there was a strong time × treatment interaction for native ground-rooted woody plants (Table 1). In 1994, there was no significant difference between treatments. By 2010, however, density of native ground-rooted woody plants was six times higher in pig-free compared to pig-present sites and density in the pig-free treatment had increased significantly over time (Fig. 1A; $P < 0.008$). This pattern was particularly evident in the density of the most commonly occurring native species, *Coprosma ochracea*, which was virtually absent from the pig-present treatment (40.0 ± 2.4 in 1994; 0.0 ± 0.0 in 2010) but increased substantially in density in the pig-free treatment from 1994 (320.0 ± 74) to

TABLE 3. *Proportion cover of total native and nonnative herbaceous plants, cover of the most dominant non-woody native and nonnative species, and ground cover in pig-present vs. pig-free plots in 1994 and 2010. Values are means ± 1 SE in parenthesis. Values with the same letter are not significantly different between treatments within sampling years (*P *< 0.05). Significant changes within treatments over time are indicated by asterisks.*

Year	1994		2010	
Treatment	Pig-present	Pig-free	Pig-present	Pig-free
Vegetation type				
Native	0.20 (0.04)[a]*	0.33 (0.08)[a]	0.05 (0.02)[A]*	0.24 (0.04)[B]
Diplazium sandwichianum	0.06 (0.03)	0.06 (0.09)	0.01 (0.01)	0.01 (0.14)
Nothoperanema rubiginosa	0.07 (0.03)	0.06 (0.04)	0.03 (0.01)	0.07 (0.02)
Peperomia spp.	0.01 (0.00)	0.02 (0.01)	0.01 (0.00)	0.03 (0.01)
Nonnative	0.04 (0.01)[a]*	0.08 (0.03)[a]	0.12 (0.01)[A]*	0.04 (0.01)[B]
Setaria palmifolia	0.02 (0.01)	0.01 (0.01)	0.07 (0.02)	0.01 (0.01)
Ground cover type[1]				
Bare ground	0.26 (0.02)[a]	0.02 (0.01)[b]	0.32 (0.12)[A]	0.01 (0.00)[B]
Litter	0.64 (0.02)[a]	0.89 (0.02)[a]	0.53 (0.10)[A]	0.89 (0.02)[B]
Bryophyte	0.10 (0.02)[a]	0.9 (0.02)[a]	0.15 (0.03)[A]	0.10 (0.02)[A]

[1]Mean proportion of cover of vegetation types are compared both over time and between treatments in each sampling period (1994 and 2010). Proportion of ground cover types are compared only between treatments within each sampling period (see Methods).

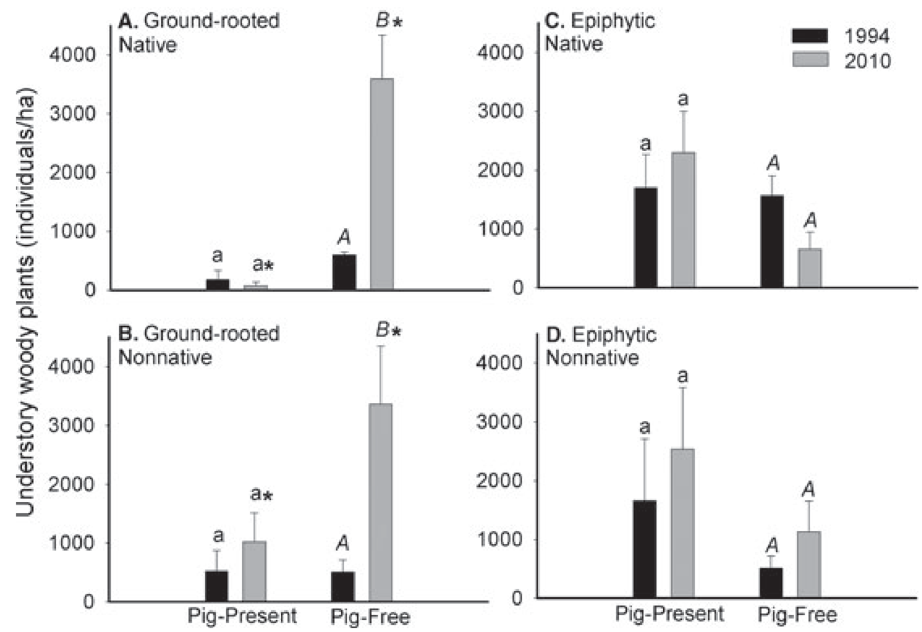

FIGURE 1. Mean density of native and nonnative understory woody plants rooted at ground level (A–B; ground-rooted) or >10 cm above the soil surface on woody substrate (C–D; epiphytic) in pig-present vs. pig-free treatments in 1994 and 2010. Different letters of the same case denote significant changes over time within a treatment. Asterisks indicate significant differences between treatments in a given year. Error bars represent one standard error.

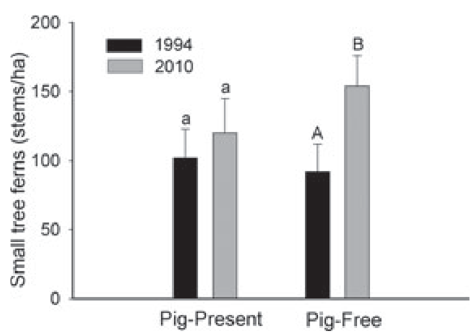

FIGURE 2. Mean density of small tree ferns (stem length <0.5 m) in pig-present vs. pig-free treatments in 1994 and 2010. Different letters of the same case denote significant changes over time within a treatment. Error bars represent one standard error.

2010 (1880.0 ± 658). We also found that density of small tree ferns (*Cibotium* sp. <50 cm length) increased significantly between sampling periods in the pig-free treatment, with no other differences in tree fern length between treatments or over time (Table 1; Fig. 2).

Nonnative understory woody plants followed a similar pattern as natives. Total density (ind./ha) of plants was comparable between treatments in both sampling periods but there was a significant increase in density in pig-free treatment over time (Table 1). There was also a significant time × treatment interaction for nonnative ground-rooted woody plants (Table 1; Fig. 1B). Density of nonnatives increased in pig-free ($P < 0.010$) but not pig-present sites over time. The vast majority of this increase was due to *P. cattleianum* which comprised ~74 percent of all nonnative woody plants in 2010. In contrast, there were no significant differences in the number of epiphytic native or nonnative understory woody plants across treatments or over time (Table 1; Fig. 1C and D).

Herbaceous vegetation.—The proportion of cover of native herbaceous vegetation varied by treatment and over time (Tables 1 and 3). Although native herbaceous cover was similar between treatments in 1994 ($P > 0.344$), it was significantly higher in the pig-free compared to the pig-present treatment in 2010 ($P > 0.024$). Overall native herbaceous cover decreased over time from 1994 to 2011 and this difference was primarily due to a decrease in the pig-present plots between sampling periods ($P < 0.048$). There was a significant interaction between sampling time and treatment for nonnative herbaceous cover (Table 1). Nonnative cover increased substantially in the pig-present treatment between sampling periods ($P < 0.042$) (Table 3).

DISCUSSION

The results of this study lead to several conclusions regarding temporal changes in the understory of Hawaiian tropical montane wet forest plant communities in the first 16 yr following the removal of nonnative feral pigs. First, native woody plants establish readily at ground level (*i.e.*, in mineral soil) within two decades of pig removal, whereas ground-rooted plants are rare where pigs are present and native regeneration is almost exclusively restricted to epiphytic establishment. Second, nonnative woody species already present at the time of feral pig removal, particularly *P. cattleianum*, respond positively (*i.e.*, increase in density) to release from disturbance by feral pigs. Third, as seen in previous studies, feral pigs have a substantial impact on forest floor cover by increasing the area of exposed soil and decreasing the area of soil covered by litter. Finally, these results indicate that while some native Hawaiian understory species recover rapidly following removal of feral pigs, subsequent control of nonnative invasive plants is a critical component of sustainable restoration and conservation efforts.

NATIVE SPECIES.—The effect of feral pig exclusion on native understory vegetation was considerable. First, we found that understory woody plants showed striking differences in establishment between treatments and over time, particularly when separated by ground-rooted vs. epiphytic establishment. Ground-rooted plants showed a large, positive response to pig removal with a sixfold increase in density between 1994 and 2010. Other studies in wet Hawaiian forest and elsewhere have reported similar increases in recruitment of native woody vegetation following removal of feral pigs. For example, Loh and Tunison (1999) recorded a flush of seedlings and saplings of subcanopy native trees 3 yr after pig removal and Busby *et al.* (2010) found that the density and basal area of tree seedlings was higher in 15 yr pig exclosures compared to pig-present forests. A study in Malaysian rain forest, where pigs are native but have increased in density, documented an increase in woody stem density only 2 yr after exclosures were built (Ickes *et al.* 2001). Because most previous studies of feral pigs have focused on plants growing at ground level, there is little information on how feral pigs may affect overall forest structure where epiphytic growth is common. We found no differences in the number of seedlings growing epiphytically across treatments or time. This is perhaps not surprising given that the most immediate impact of feral pigs on plants growing epiphytically would likely occur when large host plants, such as tree ferns, are damaged. Our results suggest that in addition to strongly reducing establishment of woody plants in mineral soil, feral pigs may alter forest structure by favoring species capable of germinating and establishing epiphytically.

Second, we found that although overall cover of native herbaceous vegetation was comparable among treatments when pigs were first removed, it was substantially higher in the pig-free sites after 16 yr. Unlike the trend observed in woody plants, however, this treatment difference was primarily due to a decrease in native herbaceous cover in the pig-present sites over time, rather than an increase in pig-free sites. In contrast to our findings, Loh and Tunison (1999) reported that understory herbs showed a positive increase in the first 2 yr following fencing, although percent cover of these plants remained similar over the subsequent 5 yr. There are several possible explanations for the decrease we observed in native plant cover in the pig-present sites. Ongoing feral pig activity, or greater population densities, may have caused additional degradation, creating increasingly unfavorable conditions for native understory plants. For example, a study in deciduous forest in southeastern United States reported that herbaceous ground cover was reduced from nearly 100 percent to 2–15 percent cover and that total number of plant species was greatly reduced in the plots where levels of pig disturbance were highest (Bratton 1975). Additionally, the increase in nonnative, invasive plant cover that we documented in pig-present sites (see below) may have increased competition to the detriment of native herbaceous species.

Third, we found few differences in species richness of understory woody plants or in the total number of species present in pig-free vs. pig-present sites. While our results demonstrate that some native species are resilient, here and in previous studies in Hawaiian forests (Scowcroft & Giffin 1983, Loh & Tunison 1999, Busby *et al.* 2010), the patterns of understory recovery were dominated by a few common understory species (*e.g.*, *Coprosma* spp, *Peperomia* spp, *Diplazium sandwichianum*, and *Nothoperanema rubiginosa*) and tree ferns (*Cibotium* sp.). Understory plants of conservation interest in the region were either absent or rare in our study area. The only two species found, *Cyanea pilosa* and *Clermontia parviflora*, were represented by only 1–2 total individuals. The response of vegetation to pig disturbance and removal can be influenced by many factors including initial species composition prior to pig removal and degree of degradation from pig activity (Jacobi 1981, Tunison *et al.* 1994). Whereas it is difficult to determine the extent of species of conservation concern that were historically present in the Olaa-Koa unit, populations at the time of fencing were extremely low, as documented by Loh and Tunison (1999), and we did not find any measurable recovery over time. In addition to impacts of feral pigs, recruitment of rarer species is likely to be limited by lack of seed dispersal due to the loss of native frugivores (Foster & Robinson 2007) and seed predation by rats (Shiels & Drake 2011). These results indicate that following fencing, outplanting may be necessary for restoration and conservation of rarer species in highly impacted forest understories.

NONNATIVE PLANTS.—The two dominant, nonnative plants at these study sites had strong but opposite responses to pig removal. Mirroring the pattern in native understory woody plants, there was a substantial increase in the total density (epiphytic and ground rooted) of nonnative woody plants, predominantly *P. cattleianum*, in the pig-free plots. The trend was strongest for plants rooted at ground level. Although initial densities of ground-rooted *P. cattleianum* were similar, this species increased more than fivefold in pig-free sites whereas density remained constant in pig-present sites. This pattern suggests that release from continued pig disturbance facilitates establishment by nonnative species once they have invaded an area, while continued disturbance by pigs appears to act as a top-down control to limit their spread. This does not, however, suggest that pigs are a viable management tool for controlling nonnative plant invasions, as the initial disturbance by pigs likely explains their presence in the first place (Diong 1982, Nogueira-Filho *et al.* 2009). As our data show, the cover of nonnative herbaceous plants was highest in the pig-present sites and cover in that treatment increased substantially over time. This was largely due to the invasive grass, *S. palmifolia*, which, in contrast to *P. cattleianum*, had established in dense patches in four of five sites in the pig-present treatment by 2010 but remained confined to a single site on the pig-free side. Similarly, an earlier study in HAVO showed that *S. palmifolia* was frequently found in conjunction with soil disturbance caused by feral pigs (Aplet *et al.* 1991) and this species is known to invade disturbed sites throughout Hawaii (Smith 1985, Wagner *et al.* 1990).

Our results concur with a growing number of studies in Hawaii and beyond. Feral pigs have been shown to disperse invasive plants (*e.g.*, *P. cattleianum*) by consuming fruit and depositing the seeds in their feces (Diong 1982, Cuddihy & Stone 1990) and to facilitate spread of invasive plants that are tolerant of high disturbance levels (Siemann *et al.* 2009). Multiple studies have also shown that once established, nonnative herbaceous weeds, grasses, and woody species can increase in cover following removal of feral ungulates (*e.g.*, Scowcroft & Hobdy 1987, Aplet *et al.* 1991, Scowcroft & Conrad 1992, Tunison *et al.* 1994, Zavaleta *et al.* 2001), presumably as a result of release from top-down control. One study on San Cristobal Island in the Galapagos showed a dramatic spread of the nonnative *Psidium guajava* in pastures following removal of feral cows (Eckhardt 1972). The apparent release of *P. cattleianum* from top-down control in the current study strongly suggests that continued monitoring and management of nonnative plants, particularly at sites where these species are present prior to pig removal, is critical for sustainable conservation and restoration efforts in this ecosystem.

Soil disturbance.—Similar to prior studies in other ecosystems (Campbell & Long 2009, Siemann *et al.* 2009), we found that the percent of forest floor covered by litter increased and the area of exposed soil decreased when feral pigs were removed from a Hawaiian tropical montane wet forest. The increased soil exposure and disturbance that occurs with pig activity is thought to increase erosion and sedimentation (Vitousek 1986, Stone & Loope 1987, Nogueira-Filho *et al.* 2009, Pejchar & Mooney 2009, Dunkell *et al.* 2011). Moreover, rooting by feral pigs, incorporation of litter into mineral soils, and deposition of feces and urine are likely to substantially impact soil physical, chemical, and biological properties (Campbell & Long 2009, Spear & Chown 2009). Additional research on the impacts of feral pigs, and their removal, on soil biogeochemistry, erosion, and water quality would provide valuable information for management of these forest ecosystems, and increased understanding of the impacts of feral pigs on native ecosystems beyond plant communities.

CONCLUSIONS

Overall, our results demonstrate that removal of nonnative feral pigs is a critical first step in the conservation and restoration of Hawaiian wet forests. Feral pigs have the greatest impact on understory plants rooted in the mineral soil, and following removal of pigs some of these species recover over a relatively short time without further management. We found little evidence, however, that species of conservation interest were recovering, perhaps due to lack of seed sources, disrupted dispersal mechanisms, or site degradation. Moreover, the total cover of native herbaceous plants decreased in sites where pigs were present for an additional 16 yr. *Psidium cattleianum* also responded positively to pig removal, with the number of plants rooted in the mineral soil increasing substantially over time. These results suggest that following feral pig removal, control of nonnative invasive plants and outplanting of native species that fail to recruit naturally into these degraded forest understories are essential components of efforts to conserve and restore native Hawaiian montane wet forests.

From a management perspective, feral pig removal is clearly warranted to promote the conservation and restoration of native Hawaiian forests. The recommendations contained herein do not, however, consider the important cultural aspects of nonnative feral pigs in Hawaii. While management for pigs may be warranted in select game management areas for social and cultural benefits of island residents, a much more concerted effort is needed to remove feral pigs from conservation areas throughout the Hawaiian islands, including the allocation of resources necessary to keep conservation areas free of feral pigs in the future and to combat the invasive plants that proliferate with feral pig disturbance and continue to impact native plant communities long after feral pigs are removed.

ACKNOWLEDGMENTS

Funding for this study was provided by the USDA-NIFA Tropical and Subtropical Agriculture Research (TSTAR) Program (Award 2009-34135-20101 to C. M. Litton) and the College of Tropical Agriculture and Human Resources at the University of Hawaii at Manoa (USDA CSREES-HAW00132H to C. M. Litton). We thank Hawaii Volcanoes National Park for supporting this work. M. Long and K. Kaneshiro provided valuable assistance with field data collection. Dr. J. B. Friday provided logistical support, Dr. K. G. Gerow provided guidance on statistical analyses, and Dr. C. P. Giardina and two anonymous reviewers made helpful comments to earlier drafts of this manuscript.

SUPPORTING INFORMATION

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

TABLE S1. *Native and nonnative plants occurring in pig-present and pig-free treatments over the 16 yr course of the study.*

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