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Technical Report 182

A preliminary study of effects of feral pig density on native Hawaiian montane rainforest vegetation

April 2012

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PCSU is a cooperative program between the University of Hawai`i and U.S. National Park Service, Cooperative Ecological Studies Unit.

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Recommended Citation:
Scheffler, P.Y., L.W. Pratt, D. Foote, and K.N. Magnacca. 2012. A preliminary study of effects of feral pig density on native Hawaiian montane rainforest vegetation. Technical Report No. 182. Pacific Cooperative Studies Unit, University of Hawai`i, Honolulu, Hawai`i. 43 pp.

Key words:
Feral pigs, *Sus scrofa*, montane wet forests, feral ungulate exclosures

Place key words:
Olaa Forest, Hawaii Volcanoes National Park, Puu Makaala Natural Area Reserve, Hawaii

About this technical report series:

This technical report series began in 1973 with the formation of the Cooperative National Park Resources Studies Unit at the University of Hawai'i at Mānoa. In 2000, it continued under the Pacific Cooperative Studies Unit (PCSU). The series currently is supported by the PCSU and the Hawai'i-Pacific Islands Cooperative Ecosystem Studies Unit (HPI CESU).

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

This study aimed to examine the effects of different levels of pig density on native Hawaiian forest vegetation. Pig sign was measured across four pig management units in the ʻŌlaʻa Forest from 1998 through 2004 and pig density estimated based upon pig activity. Six paired vegetation monitoring plots were established in the units, each pair straddling a pig fence. Percent cover and species richness of understory vegetation, ground cover, alien species, and preferred pig forage plants were measured in 1997 and 2003 and compared with pig density estimates. Rainfall and hunting effort and success by management personnel were also tracked over the study period. Vegetation monitoring found a higher percentage of native plants in pig-free or low-pig areas compared to those with medium or high pig densities, with no significant change in the percent native plant species between the first and second monitoring periods. Differences between plots were strongly affected by location, with a higher percentage of native plants in western plots, where pig damage has historically been lower. Expansion of this survey with more plots would help improve the statistical power to detect differences in vegetation caused by pigs. Because of the limited vegetation sampling in this study, the results must be viewed as descriptive. We compare the vegetation within 30 × 30 m plots across three thresholds of historical pig density and show how pig densities can change in unanticipated directions within management units. While these results cannot be extrapolated to area-wide effects of pig activity, these data do contribute to a growing body of information on the impacts of feral pigs on Hawaiian plant communities.

INTRODUCTION

Hawaiʻi, the world's most isolated archipelago, is known for its high levels of biodiversity and endemism; approximately 90% of the terrestrial species are endemic to the state (Allison 2003). Radiations leading to the evolution of scores of species from a single or few initial introductions are common. Examples include endemic *Drosophila* and cerambycid beetles, each with over 100 endemic species (Foote and Carson 1995,, Gressitt and Davis 1972), drepanid finches with over 50 species (Steadman 1995), and lobelioids (Rock 1919), most notably the endemic genus *Cyanea* (Givnish et al. 1995).

However, much of Hawaiʻi's biodiversity is imperiled by anthropogenic introductions of species which have become invasive, competing with natives and destroying habitat. Introduced species can substantially affect ecosystems either directly or indirectly by catalyzing trophic cascades that alter the function of entire plant communities (Croll et al. 2005). Weedy plant species such as *Morella faya* from the Azores, kahili ginger (*Hedychium gardnerianum*) from Nepal, and strawberry guava (*Psidium cattleianum*) from Brazil invade native forests and outcompete endemic species. Introduced insects such as the western yellowjacket (*Vespula pensylvanica*), mosquitoes (*Culex*, *Aedes*, etc.), and exotic fruit flies (e.g. *Bactrocera cucurbitae*, *B. dorsalis*, and *Ceratitis capitata*) disrupt native forest systems and agriculture (Stone & Scott, 1985). Introduced bird species now outnumber natives in lowland Hawaiian habitats (e.g. Reynolds et al. 2003). Alien mammals (e.g., rats [*Rattus* spp.], mongoose [*Herpestes auropunctatus*] and feral pigs [*Sus scrofa*]) disrupt local food chains and ecosystems.

Feral pigs are among the most problematic introductions to Hawaiian ecosystems. The first pigs were brought to the Hawaiian islands by Polynesian voyagers more than 1500 years ago (Kirch 1985). These pigs, small domesticated stock that were mostly contained in villages, are closely related to New Guinea pigs (Larson et al. 2005). When Captain James Cook arrived in the islands in 1778, he released several species of mammals, including English domestic pigs (Tomich 1986) that quickly established and became feral. The role of feral pigs in forest modification has been recognized since the early 1900's (Tomich 1986).

Feral pigs are known to disrupt ecosystems around the world. Pigs have been introduced to the Galàpagos Islands (Coblentz and Baber 1987), the Channel Islands of California (Moody and Jones 2000, Roemer et al. 2002), the barrier islands of Mississippi (Baron 1982), across the continental U.S. (Gabor and Hellgren 2000, Kotanen 1995, Mayer and Brisbin 1991), South America (Simberloff et al. 2003), New Zealand (Cuthbert 2002), and Australia (Hone 2002; Hone 1995, Hone and Stone 1989, Pech and McIlroy 1990).

In Hawaiʻi, feral pigs can be considered ecosystem engineers (Jones et al. 1997) due to the changes they catalyze in Hawaiian ecosystems. They root and trample soils, disrupting soil microarthropod communities (Vtorov 1993), leading to potential seedling mortality (Drake and Pratt 2001), and to reduced plant species richness (Hone 2002). Feral pigs also eat or otherwise destroy native vegetation (Diong 1982, Stone 1985); cause changes in soil chemistry (Singer et al. 1984, Vitousek 1986); act as dispersal agents and create habitat for exotic plants (Aplet et al. 1991, Diong 1982, Giffin 1978, Huenneke and Vitousek 1990, La Rosa 1984, Warshauer et al. 1983). They also create mosquito breeding habitat (Ahumada et al. 2004, LaPointe et al. 2012) by knocking over and hollowing out troughs in native tree ferns and making rain-filled wallows.

The implications of these last two activities are particularly relevant to Hawaiian forests. Once established, many exotic plants become difficult to control, out-competing natives and changing the composition of the forest (Stone et al. 1992). Mosquitoes are responsible for spreading avian malaria (van Riper and van Riper 1985, LaPointe et al. 2012) and avian pox (van Riper et al. 2002), diseases to which most native Hawaiian birds have little resistance, potentially leading to the extinction of many native passerines (Warner 1968, LaPointe et al. 2012).

Eradication of feral pigs from forested areas is most effective when areas are fenced into smaller management units (Stone et al. 1991). This has been accomplished for several areas in Hawaiʻi (Katahira et al. 1993, Stone and Holt 1990), and results in the eventual re-establishment of many native plant species (Higashino and Stone 1984, Loh and Tunison 1999). Complete eradication is difficult to achieve and is usually attempted within fenced exclosures through a combination of systematic hunting and trapping (Anderson and Stone 1993).

In some accessible areas, public hunting has the potential to reduce local pig populations to low levels (Stone 1985), but the effect of low density pig populations on native ecosystems is unknown. Typically, studies of pig impacts on native vegetation have involved comparisons of pig free areas to those with relatively high pig densities (e.g. Cole et al. 2011, Hess et al. 2011). In this study, we present a preliminary examination of the relationship between feral pig density and Hawaiian montane wet forest community structure and composition. Our goal was to begin to gain an understanding of the effect of low-density pig populations on native ecosystems.

STUDY SITE AND METHODS

Study Site

The study was conducted in the ʻŌlaʻa Forest of Hawaiʻi Volcanoes National Park (HAVO) and the adjoining Puʻu Makaʻala Natural Area Reserve (NAR) (Figure 1). This area is on Mauna Loa volcano at an elevation of approximately 1,150 m and experiences 2,000–4,000 mm rainfall per year with no distinct dry season (Giambelluca et al. 1986). Mean annual temperature is 16–17° C with little variation throughout the year (Juvik et al. 1998). Vegetation is characterized as ʻŌhiʻa/Hāpuʼu (*Metrosideros/Cibotium*) Tree Fern Forest, a montane wet forest dominated by tree ferns, especially *C. glaucum* (Gagné and Cuddihy 1999). ʻŌlaʻa Forest soils are composed of relatively recent (~2,000 years old) ash overlying older flows (J. P. Lockwood and F. Trusdell, personal communication 2005). Soils are classified as Kīloa extremely stony muck and Piʻihonua silty clay loam series (Typic Hydrandept, Riley and Vitousek 1995). In comparison to many Hawaiian montane forests, the soils and vegetation in this region are nutrient rich (Riley and Vitousek 1995).

ʻŌlaʻa Forest study sites were chosen in consultation with HAVO resource management staff (RM) so that they contained areas with historically low and high densities of feral pigs combined with areas that had been managed inside fenced exclosures to be pig-free (cf. Anderson and Stone 1994). The ʻŌlaʻa Forest is subject to varying levels of pig control and management. Puʻu Makaʻala NAR (Unit A) is located at the end of a paved road. At the onset of the study, the NAR was open to public pig hunting and hunting pressure was high in the lower (readily accessible) portion of the NAR. However, four years into our study, in January 2001, the area was closed to public hunting, and NARS personnel began an eradication program. The ʻŌlaʻa Forest is divided into five management units. This study was conducted in two fenced units, the Puʻu Unit (Unit B) and the New Unit (Unit C), and an unfenced area of approximately 1,700 ha to the east of the Unit C (Unit D). Unit B is a 240 ha exclosure that was fenced in 1985; all pigs were eradicated by 1986 (Anderson and Stone 1994). Thus, the area was pig-free for the duration of the study and had been so for over 10 years prior to the onset of the study. Unit C was unfenced at the onset of this study, but fences were established in late 1997, creating a 769 ha exclosure. Pig control efforts by HAVO RM began in 2000 and are ongoing in this area. Records are kept by HAVO RM personnel on the number of pigs removed and hours expended on hunting. Unit D is accessible only by foot and is located several hours hike from the nearest road; pig density in this area is high and there is no active management of feral pigs in this unit. The four management units span a mild elevation gradient with a decrease (approximately 250 m) in elevation from the top of Unit A to the bottom of Unit D.

Pig Activity Monitoring

Pig activity monitoring was conducted following the methods of Anderson and Stone (1994); frequency of digging, plant feeding, scat, tracks, trails, and other sign were recorded in three age classes: fresh, intermediate, and old. Pig activity was monitored along four permanent west-east running USGS/NPS transects. These transects were established from a random starting point in the first kilometer of the ‘Ōla‘a Forest boundary and were spaced at 400 m intervals. Transects in Unit A were 660 m and those in Unit B were 1,200 m long. In Unit C transects were 1,200 m long prior to the establishment of the new exclosure fence in 1998 and were extended across the unit for a total length of approximately 2,000 m. In Unit D transects extend 1,000 m into the unit. Signs of pig activity occurring in a 5 m wide band (2.5 m to either side of the transect) were recorded at 10 m intervals along these transects. Pig activity was monitored in Unit C from 1993-2004, in Unit A and D from 1998-2004, and in Unit B from 1999-2003 (Table 1). Because Unit B exhibited no pig activity during the monitoring period, density was assumed to be zero for the purpose of analysis in years when field data were not recorded in this unit (1997, 1998 and 2004). For units in which pig activity was not monitored at the onset of the study, we used the 1998 activity indices as an approximation of 1997 activity levels.

Vegetation Monitoring

The design for monitoring vegetation used in this study was developed by plant ecologist Patrick Dunn and his staff at The Nature Conservancy (TNC) Hawaii so that comparisons could be made between TNC study sites on Molokai and the ‘Ōla‘a Forest in HAVO. Six paired 30 × 30 m vegetation monitoring plots were established between Transects 4 and 5. Plots were situated 30 m on either side of fencelines (Figure 1). Ground cover, preferred forage species, and invasive alien species were measured twice in these plots: once at the beginning of the study (1997) and a second time in 2003.

Ground Cover

Cover of all understory species, bare soil, and litter was measured in three strata (ground level, 0–1 and 1–2 m) using point-intercept methods. Four 25 m transects were established in each of the six plots (with endpoints 2.5 m from the plot boundary) and data were taken at stations located at 25 cm intervals along these transects. A vertical rod was placed at each station and a point was recorded for each plant touching the rod within each of the three strata. Thus, from 0–1 and 1–2 m, it was possible to have multiple points but at the ground level, a single point was recorded.

Preferred Forage

The abundance (i.e. number) and size of species known to be preferred forage for pigs (*Astelia menziesiana*, *Cibotium* spp., *Sadleria* spp., *Cyrtandra* spp., *Cyanea* spp., and *Clermontia* spp.) were measured in 1997 and 2003. These species were counted in a subplot that was one quarter of the entire vegetation plot. The quarter was randomly chosen at the first plot, and all subsequent plots had preferred forage plants monitored in the same quarter. Height for all species except *Astelia* was measured using a 5m tape; general dimensions of *Astelia* were measured to give an approximate area of individual plants. Measurements of tree ferns were made from the fern growing tip along the height or length of the tree fern trunk to the ground.

Alien Species

The percent cover of invasive alien species was estimated along four transects within each plot (see Ground Cover section) using Braun-Blanquet cover classes (Mueller-Dombois and Ellenberg 1974). Percent cover of all alien species was estimated at 5-m intervals along each transect (six 5 × 5 m quadrats per transect).

Rainfall

Daily rainfall was measured at the corner of Kīlauea and Haunani roads in Volcano Village, about 7.5 km from the lower edge of Unit A.

Data Analysis

All data were analyzed using Systat 11.00.01 (Systat Software, Inc. 2004). Data were tested for normality before analysis and when possible, values with non-normal distributions were transformed to achieve normality. Transformed data were then back-transformed for presentation in the results. Data for which transformation did not result in a normal distribution were analyzed using nonparametric statistics.

The ‘Ōla‘a Forest exhibits a strong natural east-west gradient in vegetation, with the proportion of alien species increasing and natives decreasing from west to east. For example, Unit B, the pig-free exclosure, was purposely located in an area with some of the most intact native vegetation in the ‘Ōla‘a Forest (Tim Tunison, personal communication 2012), but the east and west sides differ substantially (see Figure 6b). Because observed pig activity outside of exclosures increased from west to east, vegetation data were compared in paired plots rather than being grouped by pig density. That is, Plots 1 and 2 were compared to one another, as were Plots 3 and 4 and Plots 5 and 6 using *t*-tests for normally distributed data (either transformed or untransformed) and Mann-Whitney U-tests for data that meet the assumptions of a parametric model. Prior to conducting *t*-tests, data were tested for equality using Levene's test and pooled variance was used for those values with equal variance. Because of the small sample size and correspondingly high potential for Type II error, Bonferroni corrections were not applied to these data.

Pig Activity

Pig density was estimated from the arcsine-transformed frequency of fresh digging, using the following ‘Ōla‘a Forest model: $y = 0.62 + 16.98x$, where y is pig density and x is frequency (arcsine-transformed) of fresh digging. This model had the highest correlation between frequency of sign and reconstructed pig density for the ‘Ōla‘a Forest, although the range of error from the model is large, between ±4.8 and ±5.1 pigs/km^2 (Anderson and Stone 1994). There have been attempts to more accurately model pig activity (e.g. Sweetapple and Nugent 2000) but, at present, despite its limitations, the Anderson and Stone model remains the most widely used method for assessing pig populations in Hawaii (Hess et al 2010).

The ‘Ōla‘a Forest model was determined based on values from areas where pig density ranged from 1–6.5 pigs/km^2, and it is unknown if the relationship of the variables continues in a linear fashion beyond these values (Anderson and Stone 1994). For example, areas with no sign of fresh pig activity are calculated as having 0.62 pigs/km^2 even though they may be obviously pig-free; in addition, the model becomes saturated at 27.3 pigs/km^2. Because of the large range of error and the difficulty in predicting large and small population sizes, we have divided pig density into four classes based on the accurate portions of the model (Table 2).

The hours spent hunting and the number of pigs removed by HAVO RM from Unit C were compared across years (mid-2000 through 2004) by ANOVA with post-hoc comparisons using Tukey's HSD. Correlations between the monthly number of hunting hours and the number of pigs caught were compared using the Sørensen Similarity Index (C_N). This index ranges from 0 (no association between the variables) to 1 (perfectly correlated variables) and can be either positive (an increase in one variable is associated with an increase in the other) or negative (an increase in one variable is associated with a decrease in the other). The number of pigs caught per hour hunting (per year), hunting success (monthly) and rainfall were also compared to estimated pig densities using this index.

Ground Cover

Species were grouped into life forms for analysis (Table 4). Cover, as measured by the mean of the total number of points for each life form along each transect in each of the three strata, was compared between the paired plots and between years using *t*-tests or Mann-Whitney U-tests. The percent occurrence of the life form groups was compared at the different strata using ANOVA tests on log (Y + 1)-transformed values.

Species richness, R, was calculated for each plot (R = the number of species present, not including lichens or bryophytes) for the total number of species, the number of alien species, and the number of native species. The percent native species was calculated from these values. The differences in percent native species were compared by year at different pig density and location using a Kruskal-Wallis test.

Preferred Forage

The average height of the most common preferred forage species was compared across paired plots and within plots across the two sampling years using two-sample *t*-tests on transformed data (*Cibotium glaucum* was fourth-root transformed, *Clermontia parviflora* and *Sadleria pallida* were square root transformed). Species richness and the total abundance of preferred forage plants were calculated for each sampling area and sampling year and compared using a chi-square test. Diversity of preferred forage was calculated using both Simpson's (Simpson 1949) and Shannon's (Shannon and Weaver 1949) indices. Both these indices are based on proportional species abundance but the Simpson's index is more influenced by common species (Magurran 1988).

Alien Species

Frequency (the number of occupied 5 × 5 m quadrats on the transect divided by the total number of quadrats per transect) was calculated for each species. Braun-Blanquet cover classes were converted to their mean values according to the following scale (Mueller-Dombois and Ellenberg 1974):

B-B Class	Cover-range (%)	Mean cover-range (%)
+	<1	0.1
1	1–5	2.5
2	5–25	15.0
3	25–50	37.5
4	50–75	62.5
5	75–100	87.5

An area-wide cover was determined for each species (area-wide cover = the sum of the mean cover range values/the total number of quadrats). The total area-wide cover and frequency of alien species were calculated from the individual species values and these values were compared across the paired plots and across sampling years using Mann-Whitney U-tests for frequency and two-sample *t*-tests on square-root transformed total area-wide cover values. Alien species with an average area-wide cover of greater than 0.50 or average frequency of greater than 0.10 in any plot were examined graphically.

RESULTS

Pig Density

Pig density, in general, increased over the course of the survey period (Figure 2). At the onset of the study, Unit D had significantly higher pig populations than any of the other units, followed by Unit C (Kruskal-Wallis, 1998-2000, P always ≤ 0.001). By 2001, the density of pigs in Unit C had risen to a level indistinguishable from Unit D but still distinct from Unit A (Kruskal-Wallis, $P \leq 0.001$); by 2002, only Unit B had a significantly different pig density from the other units (Kruskall-Wallis, 2002: $P = 0.017$; 2003: $P = 0.011$) . Pig activity during the years that vegetation was monitored (1997 and 2003) fell into all four density classes: pig-free, low, medium, and high (Table 3). In 1997 all four classes were represented: by 2003 areas were either pig-free (Unit B) or high density (Units A, C, D).

Hunting Effort and Catch

The average monthly effort (hours of hunting) of the NPS hunting crew in Unit C increased over the course of the study (ANOVA, $F_{4, 52} = 8.379$, $P \leq 0.001$) and the number of pigs caught was generally higher in later years (ANOVA, $F_{4, 52} = 3.700$, $P = 0.010$, Figure 3). The number of hunting hours was correlated with the number of pigs caught ($C_N = 0.68$); however, the success rate of pig removal was significantly higher in the first year of hunting (Figure 4, ANOVA $F_{4, 51} = 6.241$, $P < 0.001$). Average pig density was not correlated with either the number of pigs caught per year ($C_N = -0.30$) or monthly hunting success ($C_N = -0.10$).

Rainfall

Yearly rainfall during the vegetation monitoring phase (1997-2003) of the study ranged from 2,682 mm (in 2003) to 4,206 mm (in 2001) with a mean of 3,448 (SE = 205.5) mm per year (Figure 5). There was little correlation between rainfall and pig density in any given year, although pig density did appear to slightly decline with increased rainfall (mean C_N across all units = -0.50, range: -0.14 [Unit D] to -0.66 [Unit A]; Figure 5).

Vegetation Monitoring

Although there was a significantly higher percentage of native plants in the areas with little to no pigs (Figure 6a), the eastern plots had substantially fewer native species (as a percent of the all species), regardless of pig density (Figure 6b). Even in the pig-free unit (Unit B, Plots 2 and 3) there was a geographical trend along the east-west gradient.

Ground Cover

There were a total of 65 species of plants, plus bryophytes and lichens (not identified to species), bare soil, and litter. Plants were grouped into ten life form types; with the addition of bare soil and litter, there were twelve "life forms" represented (Table 4). Litter was the only "life form" with a normal distribution; tree ferns were normalized by square-root transforming and the remainder of the life form groups was analyzed with non-parametric statistics.

Seven of the twelve life form groups exhibited differences between the paired plots (Tables 5-7). Plots 1 and 2 differed only in tree fern cover in 1997 (Table 5). In 1997, Plot 2 had almost twice the cover of tall (1-2 m) tree ferns that Plot 1 had. Over the six-year study, tall tree fern cover increased in Plot 1 and remained the same in Plot 2. Plots 3 and 4 differed in native shrubs and trees and native terrestrial ferns in both years, tree ferns in 1997, and soil in 2003. Cover of native shrubs/trees was much greater in Plot 3 (pig-free) in both 1997 and 2003 than in Plot 4. By contrast, native terrestrial ferns had higher cover in Plot 4 than Plot 3 in 1997, but by 2003 terrestrial fern cover had increased 8-fold in Plot 3 and was greater than that of Plot 4 (Table 6). Plots 5 and 6 differed in native herbs in 1997, alien shrubs and trees in both years, and litter in 2003 (Table 7).

All twelve groups showed an affinity for a particular level of the forest as follows; 1) Bare soil and litter occurred almost exclusively at the substrate-level; 2) bryophytes were nearly absent above 1 m height; 3) native shrubs-and-trees, alien shrubs-and-trees, alien herbs (mostly vines), and tree ferns were all more common in the upper strata (> 1 m). Epiphytic ferns, alien-and-native terrestrial ferns and native herbs were most common in the middle (0-1 m) strata (Table 8).

Most of the life form groups occurred at high frequency along the transects. Bryophytes, native shrubs/trees, herbs, and ferns (both terrestrial and tree ferns) were ubiquitous across the landscape. Litter was found on a mean (SE) of 97.9 (2.1)% of the transects, epiphytic ferns on 91.7 (5.6)%, alien herbs on 68.8 (12.0)%, alien ferns on 58.3 (13.2)%, bare soil on 70.8 (10.6)%, alien shrubs and trees on 50.0 (10.2)%, and lichen on 6.3 (4.5)% of the transects. There were no significant trends in frequency based on either unit or year.

Native species comprised between 69 and 100% of the species found in each plot with a mean of 89% (SE = 1.348); the differences in native species seem to be particularly influenced by the geography of the site with a greater percentage of natives in the western plots, including those in the pig-free exclosure (Figure 6b). There were no statistical differences between the paired plots or within plots between years.

Preferred Forage

Eleven known preferred forage species were encountered in the four units. Species richness per plot ranged from 2-5 species and abundance ranged from 45-166 individuals (Table 9). There were no differences in species richness between the paired plots in either year, but the abundance of preferred forage plants was higher in 1997 in Plot 3 than 4 (χ^2 = 5.15, P = 0.023) and in Plot 6 than 5 (χ^2 = 3.97, P = 0.046) in the same year (Table 10). Plot 4 had significantly more preferred forage plants in 2003 than 1997 (χ^2 = 8.82, P = 0.003) and Plot 6 had significantly fewer (χ^2 = 3.97, P = 0.046, Table 10).

Height of preferred forage plants was variable across all the plots. Because the majority of the preferred forage species were relatively rare and three species (*Cibotium glaucum*, *Clermontia parviflora*, and *Sadleria pallida*) comprised over 96% of all the preferred forage individuals (87%, 8% and 1%, respectively), the remainder of the analyses will be conducted exclusively with these species. Differences in height between the plots were mostly non-significant. However, in 1997, the *C. glaucum* tree ferns were significantly larger in Plot 6 (mean [SE] = 1.30 [0.47]) than Plot 5 (1.25 [0.49], t = -2.64, P = 0.010, back-transformed values, Figure 7). *Cibotium glaucum* were larger in Plot 5 in 2003 (1.32 [0.48]) than in 1997 (1.25 [0.49], t = -3.18, P = 0.002). There were significantly more *C. glaucum* in Plot 1 (χ^2 = 5.34, P = 0.021) and Plot 4 (χ^2 = 11.25, P $\leq$ 0.001) in 2003 than 1997, but not in any of the other plots. *Clermontia parviflora* had a sporadic distribution (Table 9); they were absent in Plots 1-3 and in Plot 5 in 2003. They differed significantly between Plots 5 and 6 in 1997 (Plot 6: 2.56 [0.70], Plot 5: 1.67 [0.72], t = -2.90, P = 0.020, back-transformed values). Like *C. parviflora*, *S. pallida* ferns were rare in the plots (Table 9); there were no significant differences in its occurrence in the plots pairs in which the fern did occur.

Alien Plants

Twenty-three alien plant species were encountered during the study (Table 11). Over the two years combined, alien species occurred in 8% of the area surveyed (SE = 0.027) and comprised an average of 4.2% (SE = 0.65) of the cover (Table 12). The most common alien species, *Passiflora tarminiana*, occurred in nearly 50% of the surveyed area and made up 1.4% of the overall cover (one-third of the alien species cover), although other species were more locally common (e.g., *Setaria palmifolia* comprised up to 14% of the cover on individual transects). Alien species were more common and alien species richness was greater in the eastern units than in those farther to the west (Figure 8).

Frequency and area-wide cover of alien species followed similar trends and were strongly associated with geographic variation. There were few measurable differences between paired plots. In 1997, Plot 2 (mean [SE] = 0.49 [0.04]) had a higher overall frequency of alien species than Plot 1 (0.08 [0.08], Mann-Whitney U-test, P = 0.022) and in 2003 Plot 6 (frequency: 1.00 [0.00], area-wide cover 1.79 [0.31]) had a higher overall frequency (Mann-Whitney U-test, P = 0.040) but lower overall area-wide cover (t = 2.60, P = 0.040) than Plot 5 (frequency: 0.87 [0.04], density: 4.87 [0.14]). Alien plant frequency significantly decreased (Mann-Whitney U-test, P = 0.04) from 1997 (1.00 [0.00]) to 2003 (0.87 [0.04]) in Plot 5; during this period, alien plant cover also decreased in both Plots 5 (from 10.78 [0.55] to 4.87 [0.14], P = 0.041) and 6 (from 11.97 [0.24] to 1.79 [0.31], P = 0.001).

Anemone hupehensis, *Passiflora tarminiana*, *Rubus ellipticus*, and *Setaria palmifolia* were the most locally common weed species (mean area-wide cover [SE] across all plots: 0.96 [0.34], 1.42 [0.35], 0.62 [0.21], 1.02 [0.37], respectively). The distribution of these species was highly variable (Figure 9), but strongly influenced by geography; they were absent from the western plots. All species except *P. tarminiana* (which was greatest in Plots 3 and 4) reached their maximum cover in Plots 5 or 6. *Anemone hupehensis*, *Deparia petersenii*, *Erechtites valerianifolia*, *Juncus polyanthemos*, *P. tarminiana*, *Persicaria punctata*, *Plantago major*, *R. ellipticus*, and *S. palmifolia* all occurred on over 10% of at least one of the six plots (mean frequency [SE] across all plots: 0.32 [0.06], 0.38 [0.05], 0.06 [0.02], 0.08 [0.02], 0.46 [0.06], 0.04 [0.01], 0.03 [0.01], 0.22 [0.03], 0.13 [0.03], respectively). Like cover, frequency of alien species was highly variable among the plots (Figure 10). Although not locally common, many alien species occurred throughout the study area.

DISCUSSION

The goal of this study was to monitor vegetation change over time, contrasting areas with historically low versus high densities of feral pigs. This study was designed in consultation with plant ecologists at TNC and HAVO resource managers with the expectation that we would continue to observe low pig density in Unit A due to continued hunting pressure. However, four years into the study, on January 1, 2001, Unit A was closed to public hunting and remained closed throughout the remainder of the study. NARS personnel began pig-eradication efforts soon after the area was closed, but these measures were concentrated in portions of the Puʻu Makaʻala NAR that were not covered by this study (L. Hadway, personal communication 2005). In the areas where we recorded pig activity (the extreme eastern section of the NAR unit adjacent to the ʻŌlaʻa Forest), pig density doubled in the year following the initiation of removal efforts, continued to rise dramatically into 2002, and remained elevated for the duration of our study (Figure 2). Taken on its own, this rise in pig density would seem to indicate that public hunting may maintain low pig populations in accessible areas. Alternatively, the increase in density in Unit A may have been caused by ingress of pigs from adjacent NARS land on which management actions increased. However, there was a concomitant rise in pig populations in all units with pigs, making it impossible to determine the role of hunting in changing pig density in Unit A. Unit C, which was expected to exhibit a steady decline in pig populations due to organized pig control efforts during the study, increased approximately three-fold between the 2000 and 2001 monitoring periods. This regional increase in pig density does not appear to be due to any of the factors we measured, but suggests large year-to-year variation in reproductive success.

Yearly rainfall was not correlated with pig density. However, indirect effects of rainfall on food resources and its impact on pig densities were not examined and warrant further attention. Pig density also was not significantly correlated with hunting pressure in Unit C, although this may be an artifact of the small number of overlapping observations (only nine) and regional increases in pig populations discussed above. It is possible that increases in pig density in Unit C were due to insufficient hunting pressure. If continued hunting did not remove pigs at a rate greater than the reproductive potential, the population could have experienced a net increase in numbers. Furthermore, population cycles in animal numbers can be due to complex interactions of extrinsic factors, including disease and food availability (Korpimäki et al. 2004). Extended monitoring of pig populations in ʻŌlaʻa and Puʻu Makaʻala may allow better understanding of the population cycles of feral pigs and the factors which drive them.

Because of the limited sampling (no replication of plots within the units of different pig density) in this study, the results of the vegetation study must be viewed with caution. The statistics used simply compare the vegetation of one 30 × 30 m plot with another and cannot be used to extrapolate to the entire unit. Nevertheless, these results are suggestive of the effects of pigs on vegetation and we hope that they will inspire larger-scale studies of the effects of pig density on Hawaiian plants and forests.

Vegetation was comprised of a higher percentage of native species in the plots with fewer pigs, and this may be due to long-term differences in pig densities reflecting greater hunter access from the west (Figure 6). This portion of the ‘Ōla‘a Forest is intersected by Wright Road and has been used by public hunters for more than 50 years. The higher proportion of native species in the plots closer to the road may reflect a long history of pigs being kept at lower densities due to hunting pressure. Alternatively, variation in the amount of native species present may be due to natural environmental gradient that we did not examine. It would be interesting to add long-term pig exclosures in the eastern-most (D) unit to examine possible recovery of vegetation after removing pigs from this high-density area. A similar exclosure in a nearby koa kipuka with historically high pig densities exhibited a dramatic response to pig removal among native woody species (e.g. Coprosma sp.) after 16 years (Cole et al. 2012)

Only seven of the life form groups exhibited significant differences between the paired plots in 1997 and in 2003 (Tables 5-7). Native herbs and exposed soil both increased with increasing pig density: native herbs were more common in Plot 6 (high pig density) than Plot 5 (medium pig density) in 1997, and exposed soil was more prevalent in 2003 in Plot 4 (medium pig density) than in Plots 3 (pig-free). Increases in exposed soil with higher pig density have been widely reported in Hawaii and elsewhere (Hess et al 2010, Cole et al. 2012) since pigs are known to disturb soil when rooting for earthworms and other invertebrates (Cooray and Mueller-Dombois 1981). The species that comprise the “native herb” life form are the lily, *Astelia,* several species of *Peperomia,* and the sedge *Uncinia uncinata*. Although there is little reason to expect that *Astelia* and *Peperomia* would increase with pig density, it is not surprising that *Uncinia*, an indigenous sedge, would prefer the more open habitat created by high densities of pigs. During our surveys, we observed no evidence of pig feeding on the coarse, sharp-edged leaves of *Uncinia*. In addition, because *Uncinia* seeds cling to animal hair, skin, or feathers (Carlquist 1980), it is possible that pig populations are actually dispersing this sedge species.

Native shrubs and trees decreased as pig activity increased: in both years there were more native shrubs and trees in the pig-free Plot 3 than in Plot 4, which ranged from medium pig density in 1997 to high in 2003. Such woody species are likely accidental victims of pig digging and trampling, rather than favored foods (Cooray and Mueller-Dombois 1981, Diong 1982). Initially, native terrestrial ferns were more common in the plot with medium density (Plot 4, 1997) than in a pig-free plot (Plot 3), but by 2003, when pig density had increased dramatically in Plot 4, they were significantly less common than in pig-free Plot 3. Similar results of increases in terrestrial ferns after pig removal have been noted in previous studies in HAVO and at higher elevations in Hakalau National Wildlife Refuge (Loh and Tunison 1999, Pratt et al. 1999, Cole et al. 2012, Hess et al. 2011). In 1997, tree ferns were less common in Plot 1 (very low pig density) than in pig-free Plot 2, but they were more common in Plot 4 (medium density) than in Plot 3 (pig-free), indicating that there was perhaps something other than pig density affecting their numbers in these plots. Alien shrubs and trees were significantly more common in Plot 5 (medium-high pig density) than in Plot 6 (high pig density) in both years and their presence may be due to historical factors rather than current pig density. Litter only differed between Plots 5 and 6 (both high pig density in 2003), and it is unlikely that pig density was actually responsible for this difference. Overall, two life form groups exhibited significant differences between paired plots with the same pig density (both high), three groups were different between pig-free areas and areas with medium pig density, four groups between pig-free and high density areas, and a single group between pig-free and very low density pig populations. These comparisons suggest that the level at which pigs begin to cause measurable changes in common elements of vegetation probably lies somewhere in the medium density class, at least when contrasted with areas that have been pig-free for less than two decades. It is important to note that although we have chosen to use the term "medium density," this density class actually represents rather small pig populations: 1.1-6 pigs per km^2.

Most of the life form groups were quite common across the landscape, with mean frequencies well above 50%. This lack of a large range of variability suggests that frequency is probably not the best metric to use on grouped data such as these life forms. Likewise, the height of preferred forage plants, for the most part, was not measurably different between areas of different pig activity, although there were non-significant trends towards larger individuals in pig-free areas. The only significant differences occurred at the beginning of the study between Plots 5 and 6, both of which had relatively high pig density. Because *C. glaucum*, the most abundant of the preferred forage species, grows relatively slowly -- at a rate less than 6.5 cm/year in the ʻŌlaʻa Forest (Walker and Aplet 1994), it is possible that the time frame of this study was not sufficient to measure recovery from damage caused by pigs to this and related tree ferns.

Cibotium glaucum exhibited both recruitment and growth in most plots over the study period (Figure 7), but there was no clear pattern related to pig density. Mean height may not be a useful metric for *Cibotium* because it masks the relative contribution of very small and large individual tree ferns to the diet of feral pigs. The latter are typically the size class encountered along transects with obvious signs of pig feeding while the smallest ferns may be consumed whole or uprooted (cf. Diong 1982, Stone 1985). Results from other studies in montane rainforest of HAVO suggest that increased cover or abundance of small tree ferns (*Cibotium* spp.) occurs with reduction or elimination of feral pigs (Pratt et al. 1999, Cole et al. 2012).

Alien species were relatively uncommon throughout the ʻŌlaʻa Forest as indicated by the alien species study and the few species found in the ground cover study. It was rare to see alien species at high density, especially in the westernmost plots (Figure 8), but alien plants, both invasive and relatively innocuous species, did occur throughout the study area (Figure 10). Few of the alien species seemed to show a trend with relation to pig density. *Anemone hupehensis* was the one exception to this, occurring more frequently and more densely in areas with higher densities of pigs (Figures 9 and 10). *Anemone hupehensis* is common in disturbed areas (Duncan 1999) and it is likely that this species benefits from the ground disturbance associated with pigs. The presence of pigs affects individual species of alien plants in different ways (Aplet et al. 1991), so it is not surprising to see various responses in this study. Many of these species that increased at higher pig activity levels were likely to be either dispersed by pigs or adapted to the disturbed exposed soil created by pig rooting. *Passiflora tarminiana*, a species that is known to be primarily dispersed by pigs (Diong 1982, Giffin 1978, La Rosa 1984) and to decrease after the removal of pigs (Loh and Tunison 1999), occurred relatively frequently in all areas east of Plot 2. The high occurrence of this species in pig-free areas may be due to historic populations of pigs in the area: once banana poka has established, its survival rate is high and it is long-lived

(La Rosa 1984). Banana poka is dispersed locally by birds like kalij pheasant (*Lophura leucomelana*) (Warshauer et al. 1983), although passage of banana poka seeds through the kalij digestive tract does not appear to enhance germination (K. Postelli, personal communication, 2005).

CONCLUSIONS

The plant communities we measured within our study plots with low pig densities (1–6 pigs/km^2) could not be distinguished from those with higher numbers of pigs when each was compared to adjacent pig-free areas. However, the lack of replication of plant-monitoring plots means that the results from this study should be viewed as descriptive. Furthermore, this study focused only on common, easily measured elements of the Hawaiian rainforest vegetation; important components such as rare plants and associated insects and forest birds were not addressed in this study. Other factors that affected our study were that the pig-free unit had been pig free for a relatively short period (since 1988) and it is unknown how historic populations of pigs may have influenced the vegetation present today. It is likely (especially with the observed variation in pig populations) that the six-year period of this study was not sufficient to record long-term changes in vegetation.

Several recommendations for future management, continued monitoring, and further studies of the impacts of pigs arise from our observations. Replication of this study with additional vegetation plots would help improve the statistical power to detect more subtle differences in vegetation caused by pigs that may lead to significant impacts on the long-term health of forests. Increased removal of pigs with snaring in addition to hunting in the remote areas, such as Unit C, is likely to reduce pig populations further (Anderson and Stone 1993), particularly if hunting alone cannot reduce populations at a rate greater than the reproductive potential local pig populations (cf. Hess et al. 2011). Ideally, removed pigs should be aged through dentition; the resulting data may elucidate whether the hunting practices before and during our study actually caused a shift to a younger, more fecund population.

Finally, comparing trajectories of change in Hawaiian rainforests following the removal of feral pigs requires a commitment to long-term research. Pigs have been a component of Hawaiian ecosystems for more than one thousand years (Tomich 1986, Nogueira-Filho et al. 2009), yet most vegetation studies such as this one evaluate only two time points over relatively short intervals (Loope & Scowcroft 1985, but see Cole et al. 2012). Given the pattern of public hunting, the current adaptive management of feral pigs and changes in local pig density reported here, it is clear that studies measuring the conservation gains of feral pig suppression and ungulate removal will benefit from a multi-decadal approach.

ACKNOWLEDGMENTS

We would like to thank the many interns and technicians who monitored pig sign in both good and bad weather, entered the data, and performed data quality control measures, especially M. Montgomery, K. Camp, K. Schlappa and I. Stout. V. Doan created the map of the ‘Ōla‘a Forest and K. Schlappa assisted with compiling map coordinates. We are grateful to J. Bush for providing the rainfall data. J. Faford graciously shared the HAVO Resources Management pig hunting data. We thank T. Tunison, R. Loh, and the rest of the Resources Management staff at

Hawaiʻi Volcanoes National Park. Helpful comments on the manuscript were provided by K. Magnacca, K. Schlappa, G. Schuurman, J. Yoshioka, and two anonymous reviewers. Funding was provided by a grant from the Mellon Foundation (administered by The Nature Conservancy) and the Invasive Species Program of the U.S. Geological Survey. Additional support was provided by the National Park Service Inventory and Monitoring Program and the Pacific Cooperative Studies Unit, University of Hawaiʻi at Mānoa. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Table 1. Pig activity monitoring schedule for Pu‘u Maka‘ala NAR (Unit A) and ‘Ōla‘a Forest (Units B-D), Hawai‘i. Shaded areas are periods during which pig activity was monitored. Vegetation monitoring was conducted in 1997 and 2003.

Year	Month	Unit A	Unit B	Unit C	Unit D
1993	January/February			■	
	May/June			■	
	August			■	
	November			■	
1994	May/June			■	
1996	February			■	
1997	May/June			■	
1998	January			■	
	June			■	
	August	■		■	■
	October				
	December	■		■	■
1999	February/March	■	■	■	■
	June	■	■	■	■
2000	January/February	■	■	■	■
	May	■	■	■	■
	August/September	■	■	■	■
	November/December	■	■	■	■
2001	March	■	■	■	■
	July	■	■	■	■
2002	January	■	■	■	■
2003	June	■	■	■	■
2004	August/September	■		■	■

Table 2. Pig activity classes based on estimated pig density.

Estimated pig density (pigs/km^2)	*Density class*	*Relationship to model*
0.62	Zero (pig-free)	Lowest possible value
≤ 1.0	Low	Below accurate estimates
1.1-6.0	Medium	Within the range of accuracy
> 6.1	High	Above the range of accuracy

Table 3. Pig density classes encountered during vegetation monitoring in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawai‘i.

Year	*Area*	*Calculated density (pigs/km^2)*	*Density class*
1997	A*	0.98	Low
	B†	0.62	Zero
	C	6.01	Medium
	D*	11.76	High
2004	A	12.92	High
	B#	0.62	Zero
	C	12.45	High
	D	16.31	High

* estimated from 1998 values
† estimated from 1999 values
# estimated from 2003 values

Table 4. Species and life form group for plants encountered in Pu‘u Maka‘ala and ‘Ōla‘a Forest as part of the ground cover survey.

Group	**Status**	**Species**
Bryophytes	Predominantly native	Not identified to species
Lichen	Native	Not identified to species
Litter	N/A	
Soil	N/A	
Epiphytic ferns	Native	*Asplenium lobulatum* *A. polyodon* *Elaphoglossum paleaceum* *Grammitis hookeri* *Mecodium recurvum* *Polypodium pellucidum* var. *pellucidum* *Sphaerocionium lanceolatum*
Native terrestrial ferns	Native	*Athyrium microphyllum* *Coniogramme pilosa* *Dicranopteris linearis* *Diplazium sandwichianum* *Dryopteris fusco-atra* *Dr. glabra* *Dr. unidentata* var. *paleacea* *Dr. wallichiana* *Lycopodiella cernua* *Marattia douglasii* *Microlepia strigosa* *Nothoperanema rubiginosa* *Pneumatopteris sandwicensis* *Pseudophegopteris keraudreniana* *Pteris excelsa* *Vandenboschia davallioides*
Tree ferns	Native	*Cibotium glaucum* *C. menziesii* *Sadleria pallida* *S. souleytiana*
Alien terrestrial ferns	Alien	*Deparia petersenii*

Table 4. (continued). Species and life form group for plants encountered in Pu‘u Maka‘ala and ‘Ōla‘a Forest as part of the ground cover survey.

Group	Status	Species
Native shrub/tree	Native	*Alyxia oliviformis* *Broussaisia argutus* *Cheirodendron trigynum* *Clermontia parviflora* *Coprosma granadensis* *Co.* spp. *(Co. ochracea, Co. pubens)* *Cyanea floribunda* *Cya. pilosa* subsp. *longipedunculata* *Cyrtanda lysiosepala* *Cyr. platyphylla* *Cyr.* hybrid spp. *Freycinetia arborea* *Hedyotis terminalis* *Melicope clusiifolia* *Meterosideros polymorpha* *Myrsine lessertiana* *Perrottetia sandwicensis* *Pipturus albidus* *Psychotria hawaiiensis* *Rubus hawaiiensis* *Stenogyne calaminthoides* *Vaccinium calycinum*
Alien shrub/tree	Alien	*Rubus ellipticus* var. *obcordatus* *R. rosifolius*
Native terrestrial herbs	Native	*Astelia menziesiana* *Peperomia* spp. *Uncinia uncinata*
Alien terrestrial herbs/grasses	Alien	*Anenome hupehensis* var. *japonica* *Cardamine flexuosa* *Cyperus haspan* *Erechtites valerianifolia* *Hypericum mutilum* *Juncus polyanthemos* *Passiflora tarminiana* *Paspalum urvillei* *Persicaria punctata* *Setaria palmifolia*

Table 5. Mean cover and 95% CI for tree ferns (the only significantly different life form group) in Plots 1 and 2 in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawai‘i. Differences significant at the $\alpha = 0.05$ level are in bold text. Data are back-transformed values from square root transformation analyzed with two-sample t-tests.

Year	*Strata*	*Plot 1*			*Plot 2*			*t-statistic*	*P-value*
		Mean	**U CI**	**L CI**	**Mean**	**U CI**	**L CI**		
1997	Substrate	14.59	20.78	9.49	9.06	23.13	1.45	1.33	0.232
	0-1m	10.24	16.93	5.24	13.25	20.88	7.33	-1.07	0.327
	1-2m	22.28	39.19	10.14	35.64	42.39	29.52	-3.73	**0.002**
2003	Substrate	17.98	18.48	5.39	22.94	33.73	14.22		†
	0-1m	22.0	35.15	11.59	19.89	38.13	7.52		†
	1-2m	28.09	51.65	8.68	35.64	54.89	20.53	-0.57	0.597

† insufficient data to perform test

Table 6. Mean cover, with standard error (SE) or 95% Upper (U CI) and Lower (L CI) Confidence Intervals, in Plots 3 and 4 for the four life form groups that differ in these plots (data from ‘Ōla‘a Forest, Hawai‘i). Differences significant at the α = 0.05 level are in bold text. Tree fern data are back-transformed values from square root transformation and were analyzed with two-sample t-tests, all other values were analyzed with Mann-Whitney U-tests.

				Plot 3			***Plot 4***			
Life form	***Year***	***Strata***	**Mean**	**(SE) U CI**	**L CI**	**Mean**	**(SE) U CI**	**L CI**	***t - statistic***	***P-value***
Native Shrubs & Trees	1997	Substrate	0.25	(0.25)		0				0.317
		0-1m	11.25	(1.32)		4.0	(1.0)			**0.017**
		1-2m	10.5	(3.66)		2.5	(0.96)			0.081
	2003	Substrate	1.0	(0.71)		0.5	(0.5)			0.508
		0-1m	9.0	(2.04)		6.5	(1.85)			0.564
		1-2m	10.0	(1.41)		3.25	(0.85)			**0.020**
Soil	1997	Substrate	1.67	(0.33)		18.25	(2.36)			†
		0-1m	0			0				†
		1-2m	0			0				†
	2003	Substrate	1.67	(0.67)		18.25	(2.35)			**0.031**
		0-1m	0			0				†
		1-2m	0			0				†
Native Terrestrial Ferns	1997	Substrate	0.25	(0.25)		0				0.317
		0-1m	7.25	(2.46)		19	(2.25)			**0.020**
		1-2m	0			0.5	(0.29)			0.134
	2003	Substrate	0.25	(0.25)		0				0.317
		0-1m	58.75	(3.84)		19	(2.35)			**0.021**
		1-2m	5.0	(1.47)		0.5	(0.29)			**0.019**
Tree Ferns	1997	Substrate	4.06	19.41	-0.14	6.73	15.37	1.61	-0.68	0.525
		0-1m	4.80	11.76	0.90	7.63	19.99	1.11	-0.87	0.420
		1-2m	26.93	32.55	21.83	37.20	50.61	25.85	-2.54	**0.044**
	2003	Substrate	26.09	39.48	15.47	15.30	32.56	4.48	1.78	0.126
		0-1m	17.40	34.40	6.14	9.67	17.32	4.24	1.70	0.141
		1-2m	30.17	35.89	24.96	28.68	49.32	13.59	0.25	0.809

† insufficient data to perform test

Table 7. Mean cover (with standard error, SE) for three life form groups which differed between Plots 5 and 6 in ‘Ōla‘a Forest, Hawai‘i. Differences significant at the α = 0.05 level are in bold text. Litter were analyzed with t-tests, all other values were analyzed with Mann-Whitney U-tests.

Life form	***Year***	***Strata***	***Plot 5* Mean (SE)**	***Plot 6* Mean (SE)**	***t -statistic***	***P-value***
Litter	1997	Substrate	63.5 (8.19)	61.25 (5.12)	0.47	0.658
		0-1m	0	0		
		1-2m	0	0		
	2003	Substrate	63.25 (6.29)	81 (7.55)	-3.41	**0.019**
		0-1m	0	0		
		1-2m	0	0		
Alien Shrubs & Trees	1997	Substrate	0	0		
		0-1m	0.25 (0.25)	0.25 (0.25)		1.000
		1-2m	2 (0.82)	0		**0.046**
	2003	Substrate	0	0		
		0-1m	1.0 (0.41)	0		**0.046**
		1-2m	1.25 (0.95)	0		0.131
Native Herbs	1997	Substrate	0	0		
		0-1m	2.75 (0.75)	11.5 (1.32)		**0.020**
		1-2m	0	0		
	2003	Substrate	0	0		
		0-1m	3.25 (1.03)	6 (2.04)		0.237
		1-2m	0	0.5 (0.29)		0.127

Table 8. Mean cover and 95% Confidence Intervals (CI) for nine vegetative life forms, soil, and litter at three forest height levels in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawaii. Groups with significant differences at the P ≤0.05 level are in bold text.

Life form	*Level in Forest*	*Mean*	*Lower 95% CI*	*Upper 95%CI*	*F value*	*p-value*
Bryophytes	Substrate	12.060	10.428	13.925		
	0-1m	5.247	3.611	7.464	$87.008_{[2,132]}$	**<0.001**
	1-2m	0.189	0.003	0.409		
Epiphytic Ferns	Substrate	0.015	-0.015	0.044		
	0-1m	1.632	1.127	2.257	$40.377_{[2,132]}$	**<0.001**
	1-2m	0.115	0.002	0.242		
Litter	Substrate	62.098	51.548	74.767		
	0-1m	0.013	-0.013	0.040	$1264.258_{[2,132]}$	**<0.001**
	1-2m	0.457	-0.018	0.114		
Alien Shrubs & Trees	Substrate	0	0	0		
	0-1m	0.172	0.033	0.329	$2.953_{[2,132]}$	0.056
	1-2m	0.278	0.029	0.587		
Native Shrubs & Trees	Substrate	0.209	0.086	0.347		
	0-1m	7.951	6.277	10.010	$70.845_{[2,132]}$	**<0.001**
	1-2m	9.501	6.558	13.591		
Soil	Substrate	3.181	1.979	4.866		
	0-1m	0	0	0	$85.383_{[2,132]}$	**<0.001**
	1-2m	0	0	0		
Alien Terrestrial Ferns	Substrate	0	0	0		
	0-1m	0.892	0.525	1.347	$14.901_{[2,132]}$	**<0.001**
	1-2m	0.023	-0.022	0.070		
Native Terrestrial Ferns	Substrate	0.053	-0.009	0.119		
	0-1m	38.563	32.709	45.434	$195.416_{[2,132]}$	**<0.001**
	1-2m	3.090	1.868	4.832		
Alien Herbs	Substrate	0.015	-0.015	0.044		
	0-1m	2.472	1.389	4.048	$12.167_{[2,132]}$	**<0.001**
	1-2m	1.104	0.531	1.891		
Native Herbs	Substrate	0.090	-0.037	0.234		
	0-1m	52.285	28.265	96.018	$85.465_{[2,132]}$	**<0.001**
	1-2m	0.235	-0.033	0.577		
Tree Ferns	Substrate	7.298	5.349	9.845		
	0-1m	14.963	11.517	19.358	$69.531_{[2,132]}$	**<0.001**
	1-2m	67.523	60.123	75.818		

Table 9. Abundance of plant species per plot known to be preferred forage for feral pigs in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest.

Year	***Plot***	***Unit***	***Cibotium glaucum***	***Ci. chamissoi***	***Ci. menziesii***	***Clermontia parviflora***	***Cl. sp.***	***Cyanea floribunda***	***Cya. pilosa***	***Cyrtandra lysiosepala***	***Cyr. platyphylla***	***Sadleria pallida***	***Trematolobelia grandifolia***
1997	1	A	123	0	0	0	0	0	0	0	6	1	0
1997	2	B	126	0	0	0	0	0	1	1	1	26	0
1997	3	B	52	2	0	0	2	1	0	1	0	0	0
1997	4	C	25	0	0	2	0	0	0	1	0	8	0
1997	5	C	38	0	1	6	0	0	0	0	0	0	0
1997	6	D	57	1	3	4	0	0	0	0	2	0	1
2003	1	A	162	0	1	0	0	0	0	0	1	1	0
2003	2	B	122	0	0	0	0	0	0	0	0	37	0
2003	3	B	72	0	1	0	1	1	0	2	0	0	0
2003	4	C	55	0	0	1	0	0	0	2	0	8	0
2003	5	C	50	0	2	0	0	0	0	0	0	0	0
2003	6	D	42	0	1	2	0	0	0	0	0	0	0
Total			**924**	**3**	**9**	**15**	**3**	**2**	**4**	**7**	**10**	**81**	**1**

Table 10. Species richness (R), abundance (N), and diversity (Shannon's [H] and the reciprocal Simpson's [1/D]) of the eleven species known to be preferred forage for pigs in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawai‘i.

Year	*Plot*	*Unit*	*R*	*N*	*H*	*1/D*
1997	1	A	4	150	0.23	1.11
	2	B	5	155	0.50	1.45
	3	B	5	58	0.47	1.24
	4	C	4	36	0.85	1.87
	5	C	3	45	0.50	1.37
	6	D	5	66	0.56	1.33
2003	1	A	4	166	0.14	1.05
	2	B	4	163	0.66	1.63
	3	B	5	77	0.33	1.14
	4	C	4	66	0.58	1.41
	5	C	2	52	0.16	1.08
	6	D	3	45	0.29	1.15

Table 11. Scientific and common names of the 23 alien species found in the study area of Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest.

Species	***Common name***
Ageratina riparia	pāmakani
Anemone hupehensis var. *japonica*	Japanese anemone
Cardamine flexuosa	bittercress
Crassocephalum crepidioides	no common name
Cuphea carthagenensis	tarweed
Cyperus haspan	umbrella sedge
Deparia petersenii	no common name
Drymaria cordata var. *pacifica*	pipili
Ehrharta stipoides	meadow ricegrass
Erechtites valerianifolia	fireweed
Hypericum mutilum	St. John’s wort
Juncus polyanthemos	rush
Ludwigia palustris	primrose willow, kāmole
Passiflora tarminiana	banana poka
Paspalum urvillei	Vasey grass
Persicaria punctata	knotweed
Plantago major	common plantain, laukahi
Psidium cattleianum	strawberry guava, waiawī
Rubus ellipticus var. *obcordatus*	yellow Himalayan raspberry
Rubus rosifolius	thimbleberry
Setaria palmifolia	palmgrass
Setaria parviflora	yellow foxtail grass
Veronica serpyllifolia	thyme-leaved speedwell

Table 12. Frequency and area-wide cover (determined from Braun-Blanquet methods) of alien species in Puʻu Makaʻala NAR and ʻŌlaʻa Forest, Hawaiʻi. Values in parentheses are standard error (SE). Asterisks (*) indicate values of less than 0.01.

Year	***Plot***	***Species***	***Mean Frequency***	***Mean Density***
1997	1 (Unit A)	*Rubus rosifolius*	0.08 (0.08)	0.01 (0.01)
	2 (Unit B)	*Cyperus haspan*	0.08 (0.05)	0.01 (0.01)
		Deparia petersenii	0.08 (0.05)	0.01 (0.01)
		Drymaria cordata var. pacifica	0.08 (0.05)	0.63 (0.62)
		Erechtites valerianifolia	0.04 (0.04)	0.10 (0.10)
		Passiflora tarminiana	0.33 (0.12)	0.33 (0.01)
	3 (Unit B)	*Deparia petersenii*	0.37 (0.08)	0.14 (0.10)
		Erechtites valerianifolia	0.17 (0.17)	0.02 (0.02)
		Juncus polyanthemos	0.04 (0.04)	*
		Passiflora tarminiana	0.92 (0.05)	4.94 (1.08)
		Persicaria punctata	0.04 (0.04)	*
		Rubus ellipticus	0.08 (0.05)	0.01 (0.01)
		Rubus rosifolius	0.04 (0.04)	*
	4 (Unit C)	*Anemone hupehensis*	0.29 (0.04)	0.75 (0.72)
		Cardamine flexuosa	0.08 (0.05)	0.01 (0.01)
		Crassocephalum crepidioides	0.04 (0.04)	*
		Deparia petersenii	0.25 (0.05)	0.03 (0.01)
		Erechtites valerianifolia	0.29 (0.11)	0.13 (0.11)
		Hypericum mutilum	0.12 (0.08)	0.01 (0.01)
		Passiflora tarminiana	1.00 (0.00)	4.81 (1.81)
		Persicaria punctata	0.04 (0.04)	*
		Plantago major	0.12 (0.08)	0.01 (0.01)
		Rubus ellipticus	0.29 (0.11)	0.03 (0.01)
		Rubus rosifolius	0.17 (0.12)	0.02 (0.01)
	5 (Unit C)	*Ageratina riparia*	0.08 (0.05)	0.01 (0.01)
		Anemone hupehensis	0.92 (0.05)	3.05 (1.25)
		Cardamine flexuosa	0.08 (0.05)	0.01 (0.01)
		Cuphea carthagenensis	0.04 (0.04)	*
		Deparia petersenii	0.83 (0.17)	0.08 (0.02)
		Drymaria cordata	0.04 (0.04)	*
		Ehrharta stipoides	0.04 (0.04)	*
		Hypericum mutilum	0.12 (0.08)	0.01 (0.01)
		Juncus polyanthemos	0.25 (0.16)	0.03 (0.02)
		Ludwigia palustris	0.04 (0.04)	*
		Passiflora tarminiana	0.46 (0.21)	0.05 (0.02)
		Persicaria punctata	0.25 (0.05)	0.03 (0.01)
		Psidium cattleianum	0.04 (0.04)	*
		Rubus ellipticus	0.54 (0.04)	2.64 (1.02)
		Setaria palmifolia	0.58 (0.17)	5.28 (3.27)
		Setaria parviflora	0.21 (0.13)	0.02 (0.01)

Table 12. (continued) Frequency and area-wide cover (determined from Braun-Blanquet methods) of alien species in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawai‘i. Values in parentheses are standard error (SE). Asterisks (*) indicate values of less than 0.01.

Year	*Plot*	*Species*	*Mean Frequency*	*Mean Density*
	6 (Unit D)	*Anemone hupehensis*	0.96 (0.04)	7.20 (1.55)
		Deparia petersenii	1.00 (0.00)	0.10 (0.00)
		Hypericum mutilum	0.08 (0.05)	0.01 (0.01)
		Juncus polyanthemos	0.33 (0.07)	0.03 (0.01)
		Ludwigia palustris	0.04 (0.04)	*
		Passiflora tarminiana	0.29 (0.04)	0.03 (*)
		Paspalum urvillei	0.08 (0.08)	0.01 (0.01)
		Rubus ellipticus	0.25 (0.08)	0.03 (0.01)
		Setaria palmifolia	0.21 (0.04)	4.75 (0.77)
2003	1 (Unit A)	*Rubus ellipticus*	0.12 (0.08)	0.01 (0.01)
	2 (Unit B)	*Cyperus haspan*	0.12 (0.08)	0.11 (0.11)
		Passiflora tarminiana	0.08 (0.08)	0.01 (0.01)
		Veronica serpyllifolia	0.04 (0.04)	0.10 (0.10)
	3 (Unit B)	*Anemone hupehensis*	0.04 (0.04)	*
		Deparia petersenii	0.37 (0.11)	0.04 (0.01)
		Erechtites valerianifolia	0.04 (0.04)	*
		Juncus polyanthemos	0.12 (0.08)	0.01 (0.01)
		Passiflora tarminiana	0.92 (0.05)	3.70 (1.11)
		Plantago major	0.13 (0.04)	0.01 (*)
		Rubus ellipticus	0.37 (0.08)	0.66 (0.63)
	4 (Unit C)	*Anemone hupehensis*	0.33 (0.12)	0.03 (0.01)
		Cardamine flexuosa	0.04 (0.04)	*
		Cuphea carthagenensis	0.04 (0.04)	*
		Deparia petersenii	0.13 (0.04)	0.01 (*)
		Erechtites valerianifolia	0.17 (0.10)	0.01 (0.01)
		Hypericum mutilum	0.04 (0.04)	*
		Ludwigia palustris	0.04 (0.04)	*
		Passiflora tarminiana	1.00 (0.00)	3.28 (1.11)
		Persicaria punctata	0.08 (0.08)	0.01 (0.01)
		Plantago major	0.12 (0.08)	0.01 (0.01)
		Psidium cattleianum	0.04 (0.04)	*
		Rubus ellipticus	0.37 (0.11)	0.76 (0.60)
		Rubus rosifolius	0.08 (0.08)	0.01 (0.01)
	5 (Unit C)	*Ageratina riparia*	0.12 (0.08)	0.01 (0.01)
		Anemone hupehensis	0.33 (0.12)	0.03 (0.01)
		Deparia petersenii	0.79 (0.04)	0.08 (*)
		Juncus polyanthemos	0.13 (0.04)	0.01 (*)
		Passiflora tarminiana	0.29 (0.11)	0.13 (0.10)
		Rubus ellipticus	0.42 (0.05)	3.34 (1.30)
		Setaria palmifolia	0.33 (0.07)	0.75 (0.73)
		Setaria parviflora	0.21 (0.13)	0.63 (0.63)
	6 (Unit D)	*Ageratina riparia*	0.08 (0.05)	0.01 (0.01)
		Anemone hupehensis	0.96 (0.04)	0.40 (0.19)
		Deparia petersenii	0.71 (0.11)	0.07 (0.10)
		Ehrharta stipoides	0.17 (0.12)	0.02 (0.01)
		Juncus polyanthemos	0.04 (0.04)	*
		Passiflora tarminiana	0.25 (0.08)	0.03 (0.01)
		Rubus ellipticus	0.12 (0.08)	0.01 (0.01)
		Setaria palmifolia	0.41 (0.08)	1.48 (0.62)

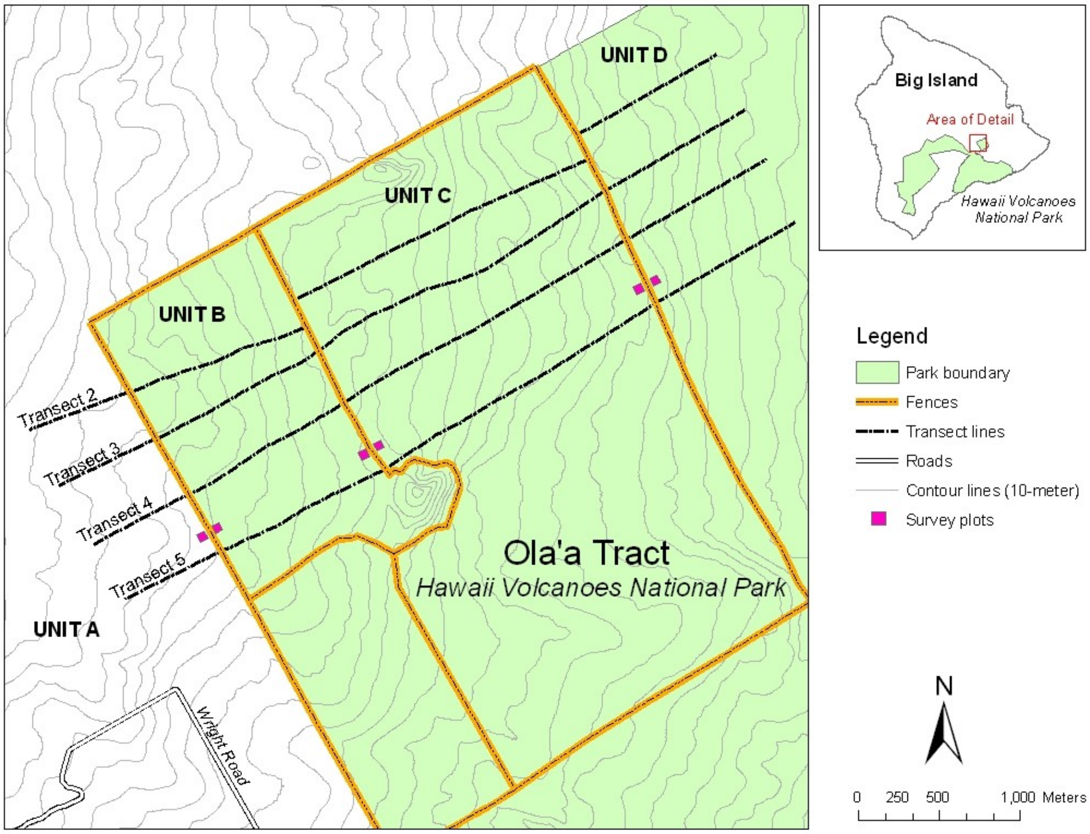

Figure 1. Study area: Pu‘u Maka‘ala Natural Area Reserve (unshaded including Unit A) and ‘Ōla‘a Forest (or “Olaa Tract” sensu historical literature and park maps, shaded area including Units B, C and D), Hawai‘i Volcanoes National Park, Hawai‘i Island (or “Big Island”) accessed by Wright Road (also called Amaumau Road). Survey plots are numbered from west to east, 1–6 starting in Unit A. Coordinates for fenceline intersection points 30 m from each plot are: Plots 1 & 2, Unit A/B fenceline (19°29'36.03"N 155°15'55.73"W), plots 3 & 4, B/C fenceline (19°29'57.91"N 155°15'21.48"W), plots 5 & 6 C/D fenceline (19°30'27.08"N 155°14'24.27"W).

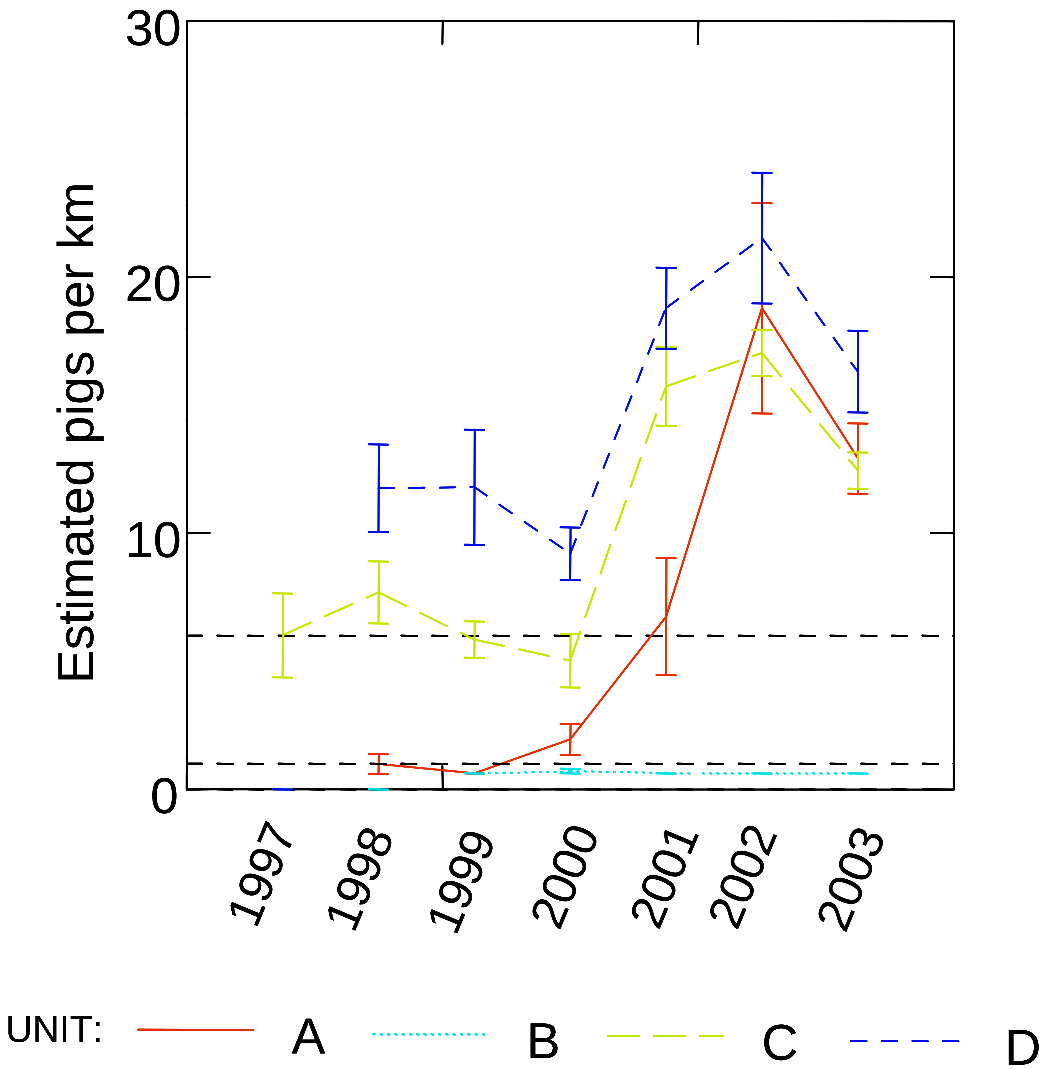

Figure 2. Estimated pig population densities from 1997 to 2003 in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest (Hawai‘i Volcanoes National Park), Hawai‘i. Lines are the mean value of four transects per unit; error bars represent standard error of the mean. The horizontal lines at 1 and 6 pigs/km^2 indicate the range of values for which the model was calculated; above or below these lines, the model may no longer be accurate.

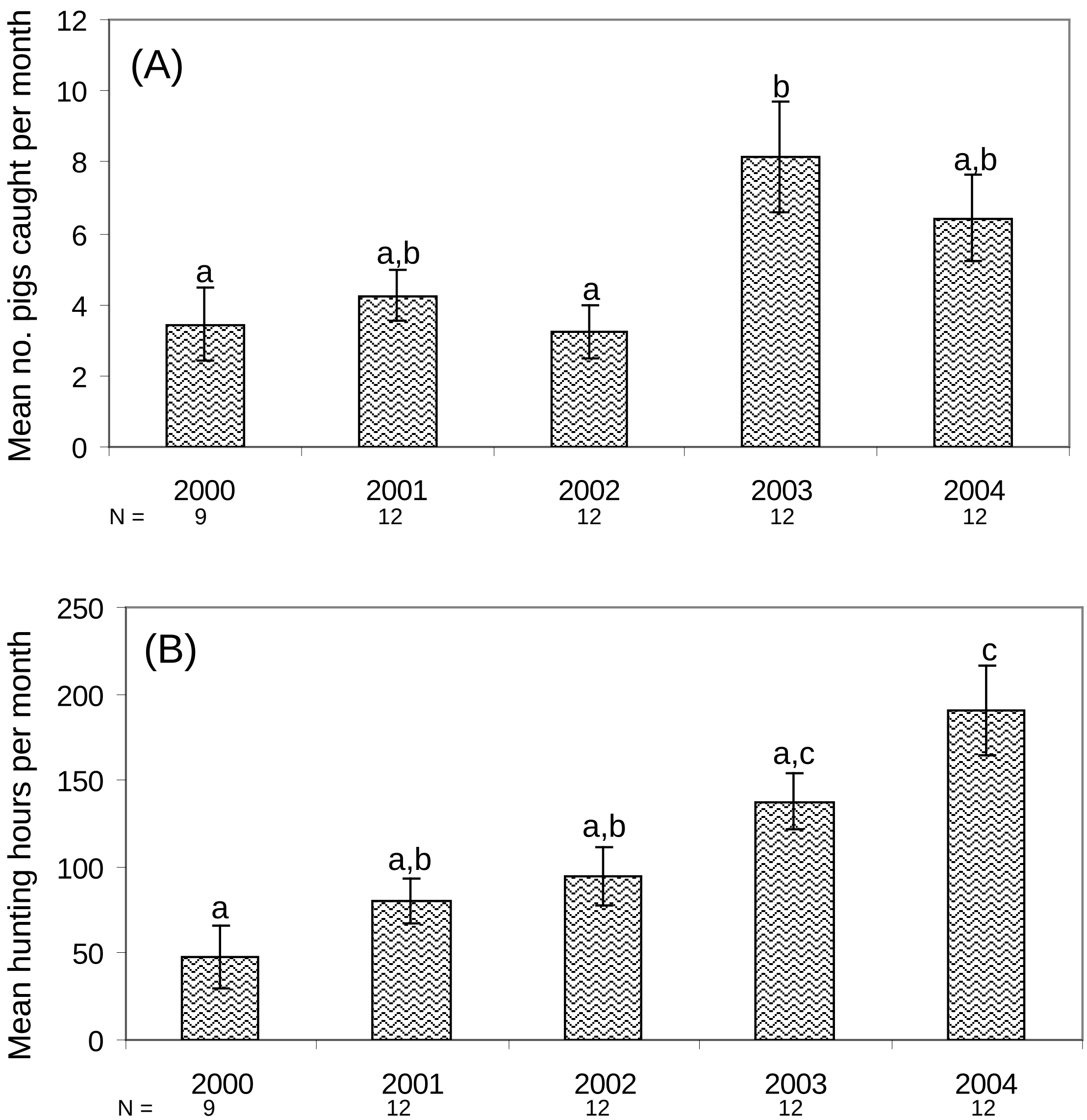

Figure 3. (A) Mean number of pigs taken per month by year, (B) mean number of hunting hours per month by year in Unit C, ʻŌlaʻa Forest, Hawaiʻi Volcanoes National Park. Error bars represent standard error of the mean; letters above the bars indicate significant groupings according to Tukey's HSD at α 0.05.

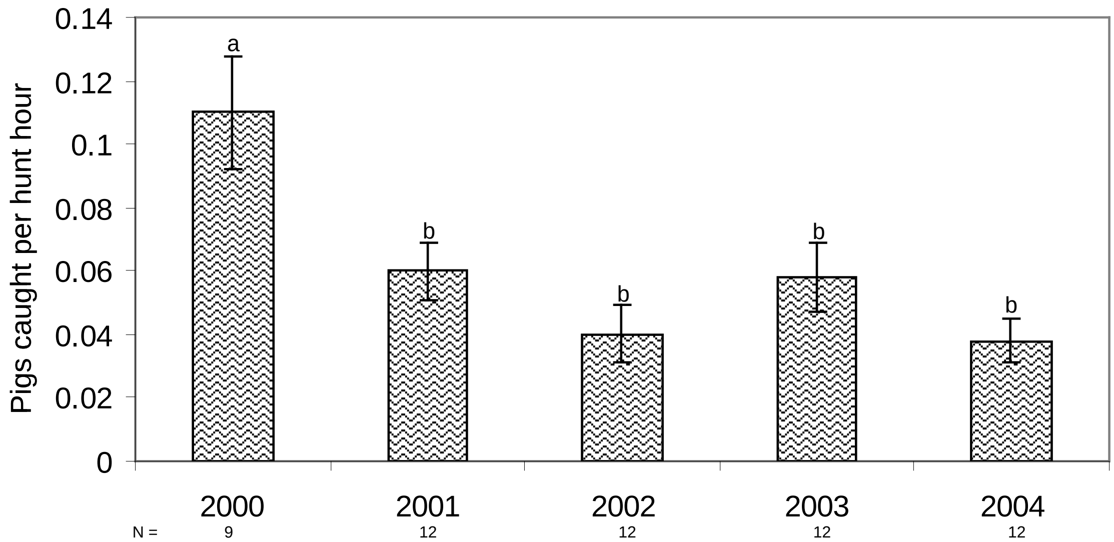

Figure 4. Hunting success by the Resources Management pig hunting crew in Unit C, ‘Ōla‘a Forest. Error bars represent standard error of the mean and the letters above the bars indicate significant groupings as calculated by Tukey’s HSD at $\alpha = 0.05$.

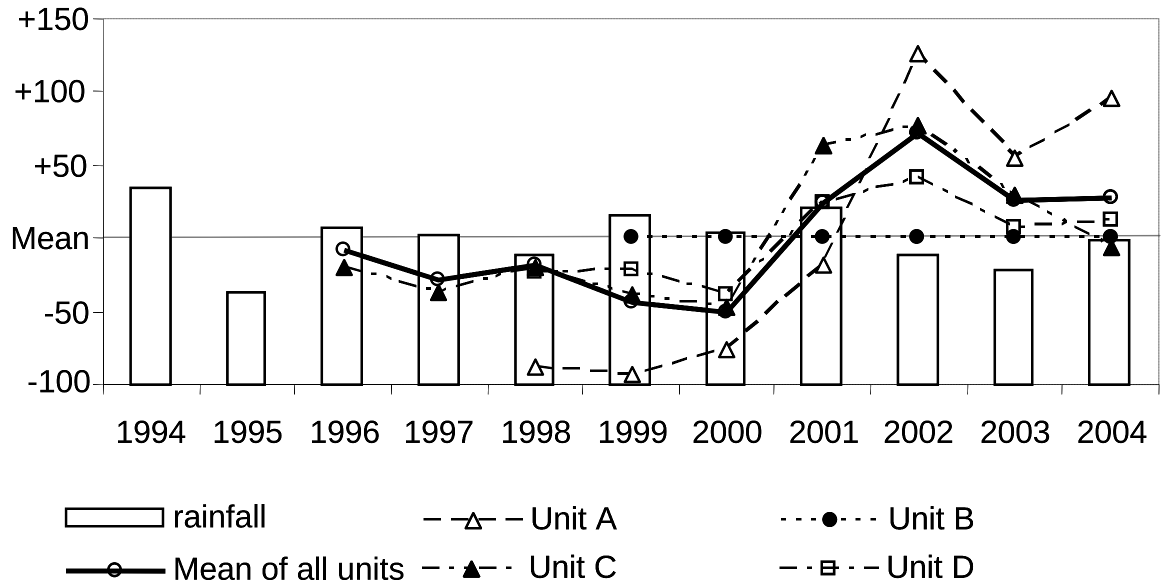

Figure 5. Comparison between normalized rainfall and pig density in the ‘Ōla‘a Forest, Hawai‘i. Bars are rainfall as a percentage of the mean rainfall (shown as a light-colored line) over an 11 year period; lines are pig density as a percent of the mean pig density during the monitoring period (7 years for Unit A, 6 years for Unit B, 10 years for Unit C, and 7 years for Unit D); the heavy line shows the percent change from the mean density of all units combined.

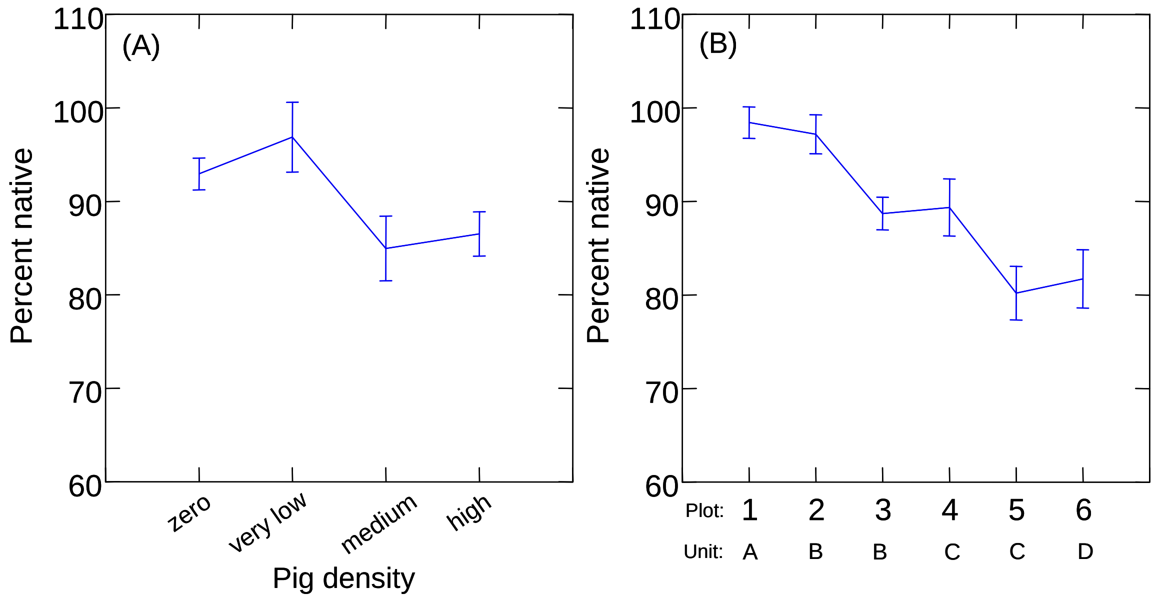

Figure 6. Mean percent of native plants found in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest. (A) The native plants as a percent of all plants (mean values) found at different pig density (zero = pig free, very low = <1 pig/km^2, medium = 1–6 pigs/km^2, high = 6+ pigs/km^2); (B) the percent of native species found at each plot. Plots are geographically sequential with Plot 1 the furthest west and Plot 6 the farthest east.

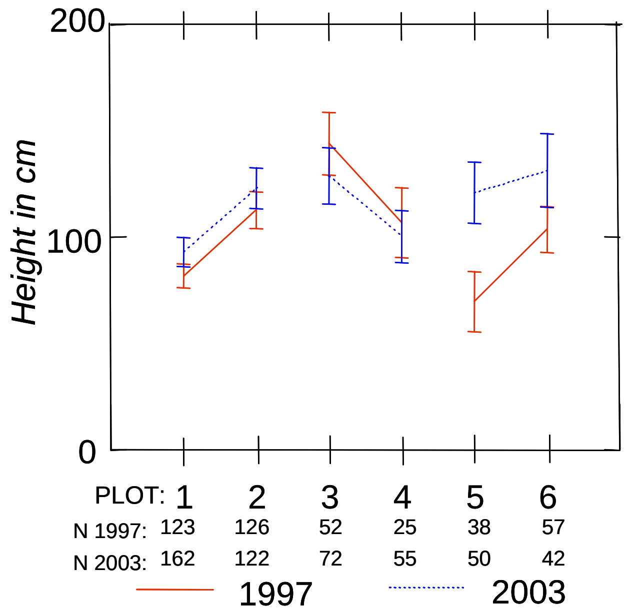

Figure 7. Height of *Cibotium glaucum* in four different pig management units in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawai‘i. Height is mean height in centimeters and error bars represent standard error. The total number of individuals for each year (N) is presented below the x-axis.

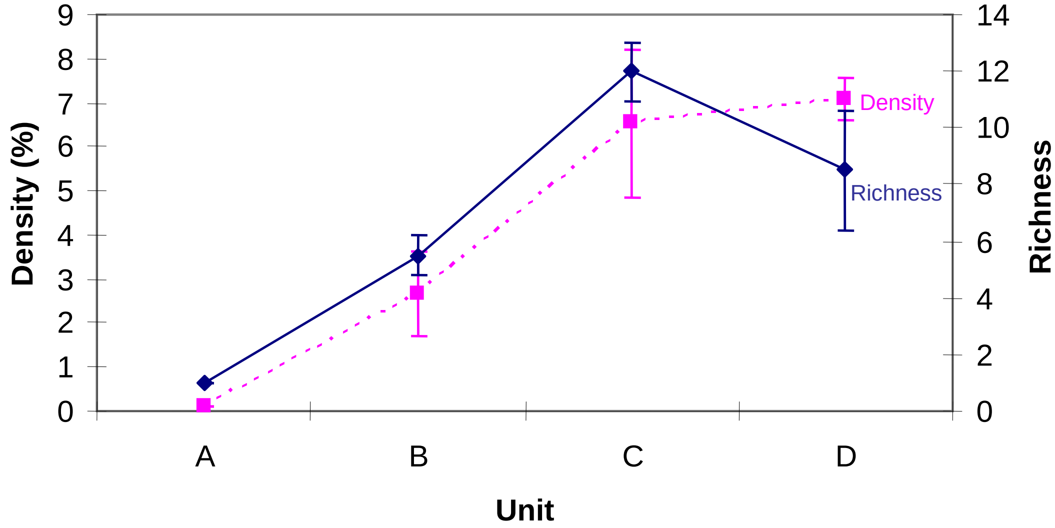

Figure 8. Total change in mean density of alien species (as a percent of total plant cover) and mean species richness for the four units in Puʻu Makaʻala NAR and ʻŌlaʻa Forest. Bars represent standard error of the mean.

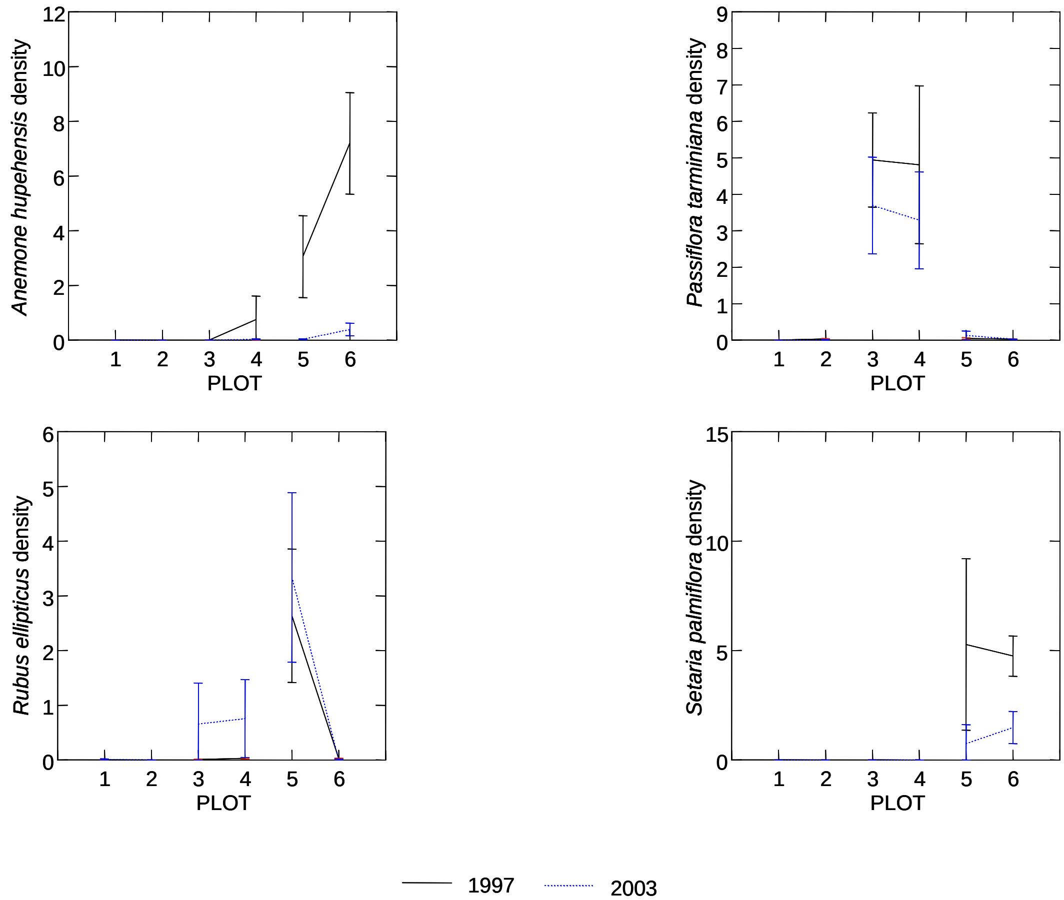

Figure 9. Mean density of the four most common weed species in Pu‘u Maka‘ala NAR and ‘Ōla‘a Forest, Hawai‘i. Error bars represent the standard error of the mean.

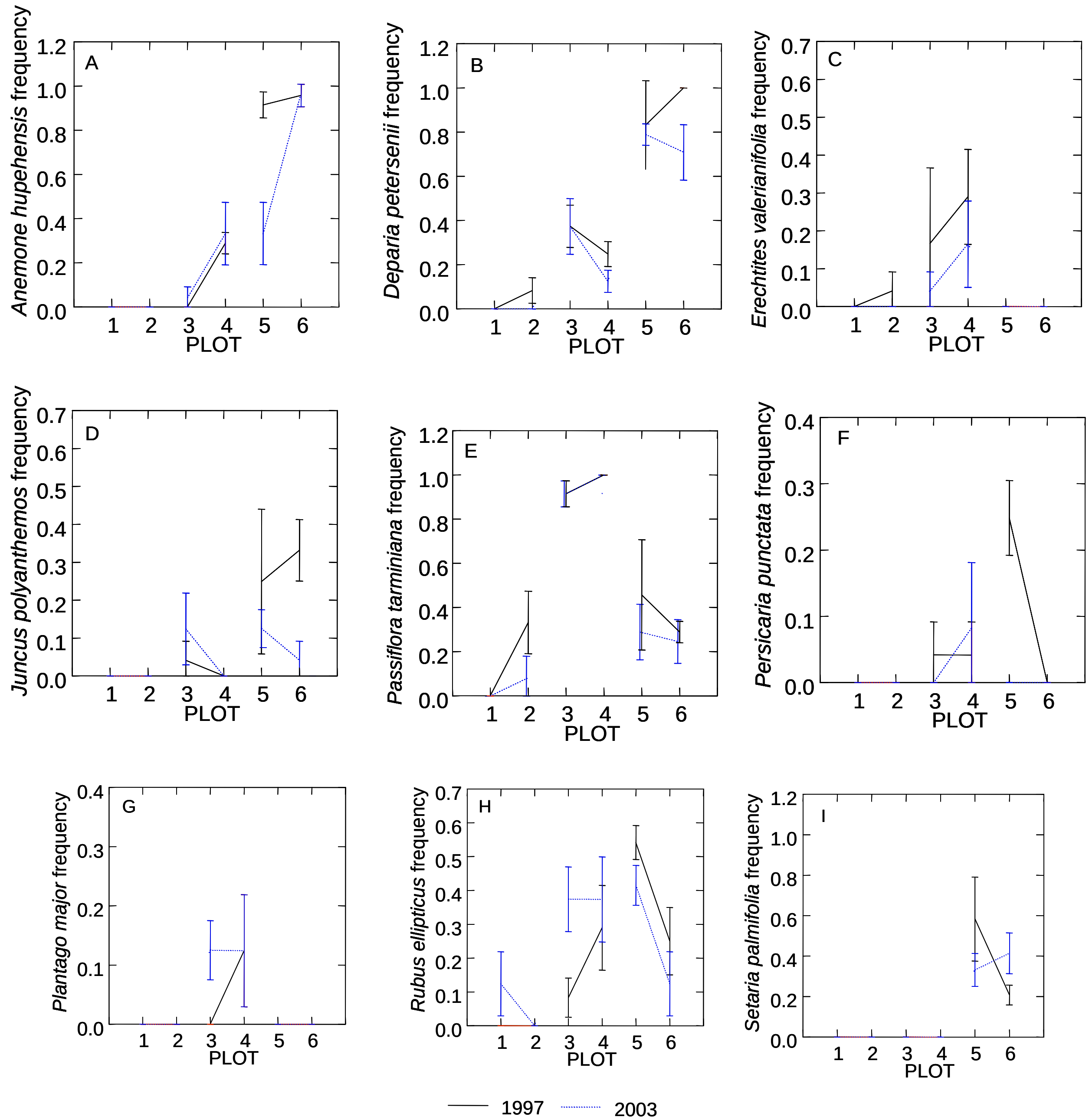

Figure 10. Mean frequency of nine of the most common weed species in Pu'u Maka'ala NAR and 'Ōla'a Forest, Hawai'i. Error bars represent the standard error of the mean.