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Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest

Rebecca J. Cole · Creighton M. Litton

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Abstract Globally, non-native ungulates threaten native biodiversity, alter biotic and abiotic factors regulating ecological processes, and incur significant economic costs via herbivory, rooting, and trampling. Removal of non-native ungulates is an increasingly common and crucial first step in conserving and restoring native forests. However, removal is often controversial and there is currently little information on plant community responses to this management action. Here, we examine the response of native and non-native understory vegetation in paired sites inside and outside of exclosures across a 6.5–18.5 year chronosequence of feral pig (*Sus scrofa*) removal from canopy-intact Hawaiian tropical montane wet forest. Stem density and cover of native plants, species richness of ground-rooted native woody plants, and abundance of native plants of conservation interest were all significantly higher where feral pigs had been removed. Similarly, the area of exposed soil was substantially lower and cover of litter and bryophytes was greater with feral pig removal. Spatial patterns of recruitment were also strongly affected. Whereas epiphytic establishment was similar between treatments, the density of ground-rooted woody plants was four times higher with feral pig removal. Abundance of invasive non-native plants also increased at sites where they had established prior to feral pig removal. We found no patterns in any of the measured variables with time, suggesting that commonly occurring species recover within 6.5 years of feral pig removal. Recovery of species of conservation interest, however, was highly site specific and limited to areas that possessed remnant populations at the time of removal, indicating that some species take much longer (>18.5 years) to recover. Feral pig removal is the first and most crucial step for conservation of native forests in this area, but subsequent management should also include control of non-native invasive plants and outplanting native species of conservation interest that fail to recruit naturally.

Keywords Disturbance · Non-native invasive ungulates · Restoration · *Sus scrofa* · Tropical montane wet forest

R. J. Cole (✉)
Institute of Arctic and Alpine Research, University of Colorado at Boulder, Boulder, CO 80303, USA
e-mail: cole.rebeccaj@gmail.com

R. J. Cole · C. M. Litton (✉)
Department of Natural Resources and Environmental Management, University of Hawaii at Manoa, Honolulu, HI 96822, USA
e-mail: litton@hawaii.edu

Introduction

Globally, non-native invasions threaten native biodiversity, alter biotic and abiotic factors that regulate ecological processes, and incur significant economic costs worldwide (D'Antonio and Vitousek 1992; Mack et al. 2000; Mooney and Hobbs 2000). Ecosystem degradation by non-native ungulates, in particular, is a global problem with multiple avenues of ecological degradation (Vitousek 1990; Didham et al. 2005; Nuñez et al. 2010). In addition to direct impacts from herbivory, non-native ungulates can alter vegetation by changing disturbance regimes via trampling and rooting activities. For example, feral goats, sheep, and pigs substantially increase the area of exposed soil and subsequent soil erosion in both tropical and temperate ecosystems (Scowcroft and Hobdy 1987; Anderson and Stone 1993; Siemann et al. 2009; Cole et al. 2012). Non-native ungulates can also have dramatic impacts on the structure of plant communities through selective herbivory and alteration of competitive dynamics between native and non-native plants (Cushman et al. 2004; Oduor et al. 2010). Introduction of deer, feral goats, and sheep have all led to extensive changes in vegetation cover and widespread loss of native plant species (e.g. Courchamp et al. 2003). Moreover, non-native ungulate invasions are frequently associated with subsequent invasion by non-native plants across a broad range of ecosystems (e.g. Parker et al. 2006). Non-native ungulates can also alter trophic interactions; changes in soil micro- and macrofaunal communities have been found in association with feral goats and deer in New Zealand (Wardle et al. 2001), and feral pigs in Australia (Taylor et al. 2011). Collectively, non-native ungulate invasions can lead to complex changes in ecosystem structure and function, with legacies that may persist over long periods of time after their removal from the ecosystem (e.g. Zavaleta et al. 2001). As removal of non-native ungulates becomes more common worldwide for protection of native plant communities, it becomes increasingly important to document the efficacy of this management approach.

Feral pigs (*Sus scrofa*) are an increasingly widespread non-native ungulate that has invaded terrestrial ecosystems on six continents and many oceanic islands (Nuñez et al. 2010; Barrios-Garcia and Ballari 2012). Feral pigs affect native ecosystems directly via rooting, trampling, and browsing of above- and belowground plant material, and indirectly by facilitating non-native plant invasions (Ickes et al. 2001; Spear and Chown 2009) and altering soil processes (Risch et al. 2010). Disturbance by feral pigs can be far greater than background levels of disturbance to which native vegetation is evolutionarily adapted, particularly on islands. For example, a single feral pig is capable of disturbing up to 200 m^2/day of forest soil surface (Anderson and Stone 1993). These disturbances have potentially long-term consequences for plant regeneration (Lipscomb 1989; Mitchell et al. 2007; Webber et al. 2010), forest structure (Busby et al. 2010; Cole et al. 2012), and ecosystem biogeochemistry (Siemann et al. 2009).

The greatest immediate impacts of feral pigs, as with most other non-native ungulates, are reduction and alteration of vegetation cover (Barrios-Garcia and Ballari 2012). Feral pig activity has been found to substantially decrease vegetation cover and species richness across a diverse range of ecosystems, including deciduous forests in the southern Appalachians (Bratton 1975), subalpine grasslands in Australia (Hone 2002), arid shrublands in Argentina (Cuevas et al. 2010), and wet Hawaiian forests (Cole et al. 2012). Feral pig disturbance can also facilitate non-native species establishment (Diong 1982; Siemann et al. 2009; Oduor et al. 2010). Several studies have reported increased non-native plant abundance in association with feral pig activity (e.g. Singer et al. 1984; Aplet et al. 1991; Kotanen 1995; Milton et al. 1997; Cushman et al. 2004; Tierney and Cushman 2006; Dovrat et al. 2012). For example, feral pig incursions into native forest in peninsular Malaysia are associated with establishment of a non-native, invasive shrub (Fujinuma and Harrison 2012). In addition, removal of non-native ungulates can also result in rapid increases in non-native plant abundance in at least some ecosystems due to release from top-down control (Eckhardt 1972; Zavaleta et al. 2001; Cole et al. 2012). Disturbance by feral pigs also has the potential to alter patterns of regeneration and lead to long-term changes in plant community structure. For example, the relative importance of clonal regeneration (sprouting) increased in feral pig-impacted Hawaiian wet forests due to damage to seedlings (Busby et al. 2010). Although feral pig impacts on plant communities have been increasingly documented throughout their global range, far less is known about the resilience of plant communities following management activities to remove non-native ungulates (Barrios-Garcia and Ballari 2012).

Island ecosystems that evolved in the absence of large mammals are likely to be particularly vulnerable to disturbance by non-native ungulates (Courchamp et al. 2003). Along with feral goats, sheep, and cows (Scowcroft and Giffin 1983; Scowcroft and Hobdy 1987; Scowcroft and Conrad 1992), feral pigs have negatively impacted almost every plant community in the Hawaiian Islands (Jacobi 1981; Anderson and Stone 1993; Nogueira-Filho et al. 2009), and today are considered to be one of the primary threats to remnant native wet forests. Polynesian settlers initially introduced a domesticated form of the Asiatic pig (*Sus scrofa vittautus*) and European explorers later released the undomesticated wild boar (*Sus scrofa scrofa*). These animals are thought to have since interbred to become widespread throughout the Hawaiian Islands (Nogueira-Filho et al. 2009). The predominant approach for actively conserving and restoring ecosystems in Hawaii and elsewhere impacted by feral pigs and other non-native ungulates is fencing and removal of these animals. However, because feral pigs are valued culturally and for subsistence and recreational hunting, fencing and removal remain highly controversial in many areas throughout the world (see Cole et al. 2012).

Prior studies examining the impacts of feral pigs and their removal on Hawaiian forests suggest that some common native species increase in cover within a few years of fencing and feral pig removal (Loh and Tunison 1999; Cole et al. 2012). On the other hand, there is little current evidence that plants of conservation concern in these ecosystems are recovering following removal of feral pigs (Cole et al. 2012). The vast majority of existing studies that examined forest recovery in Hawaii following feral pig control have either been conducted at the same site (Loh and Tunison 1999; Busby et al. 2010; Cole et al. 2012), lacked a control, or utilized small experimental exclosures which lead to concerns over the confounding influence of edge effects (reviews: Loope and Scowcroft 1985; Nogueira-Filho et al. 2009). Studies using large fenced exclosures and documenting plant succession over time exist (e.g., Loope et al. 1991, Medeiros et al. 1991, Pratt et al. 1999) but have been published in non-peer reviewed literature, limiting their accessibility to management and research communities (but see Cole et al. 2012). As a result, up-to-date ecological information on the spatial and temporal impacts of feral pig removal on native forest dynamics is currently needed to guide policy and management decisions.

The objective of this study was to examine the response of native and non-native understory plant communities to removal of feral pigs from large, native canopy-intact management units established over ~20 years to inform current management approaches. Specifically, this research: (1) assessed how native and non-native understory species density and richness responded to feral pig removal; and (2) determined whether understory vegetation communities in fenced and unfenced sites follow similar successional trajectories. We hypothesized, based on prior studies inside and outside of Hawaii (e.g. Loh and Tunison 1999; Tierney and Cushman 2006; Siemann et al. 2009; Cole et al. 2012), that native understory vegetation density and richness would respond positively over time to feral pig removal. To address this hypothesis, we compared forest understory vegetation in paired plots (inside and outside of existing exclosures) across a 18.5 year chronosequence of feral pig removal units in a ~2,000 ha area of contiguous Hawaiian tropical montane wet forest.

Methods

Study system

The study was conducted from May to September 2010 in five paired sites inside and outside of large ungulate exclosures in canopy-intact native montane wet forest in Hawaii Volcanoes National Park and Puu Makaala Natural Area Reserve on the Island of Hawaii (Fig. 1). The ungulate exclosures (i.e., fenced exclosures where non-native ungulates were eradicated) were constructed between 1989 and 2000. All exclosures were constructed within contiguous forest and the placement of fence lines were determined by cost and feasibility, rather than by pre-existing differences in vegetation (J. T. Tunison, R. H. Loh, and I. Cole, pers comm.). Although feral cattle and sheep occur in some wet forests in Hawaii, feral pigs are the only ungulates known to occur in the study area in appreciable numbers (I. Cole and R. H. Loh pers. com). Following fencing, intensive feral pig removal efforts occurred over a 1–2 year period during which the majority of animals were removed from the exclosures, with remnant individuals removed within the subsequent 1–2 years (S. Hess and C. Cole, pers. com.). Exclosure ages were determined by the year in which all remaining individuals were removed from

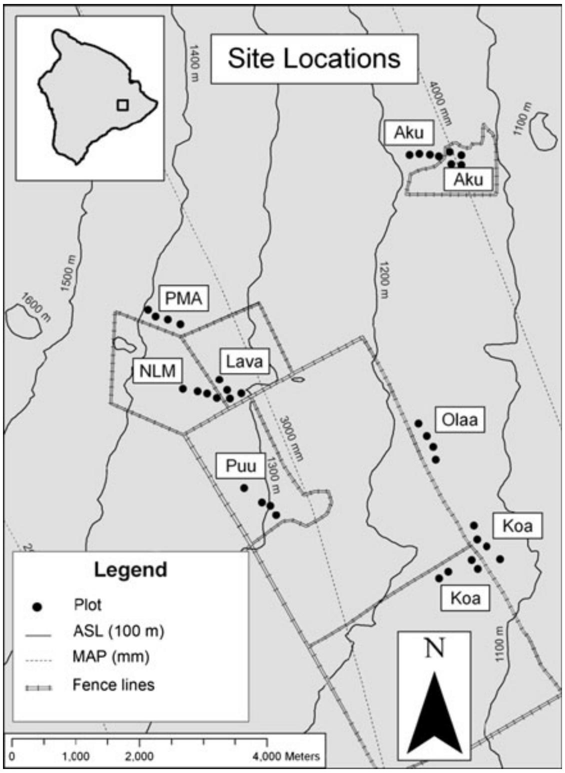

Fig. 1 Study site locations inside and outside of feral pig management units on the windward slope of Mauna Loa Volcano, Island of Hawaii

the management unit. Surrounding unfenced forests have never been managed for feral pigs outside of limited recreational hunting. Feral pig densities have been estimated at 12.5 pigs/km^2 in nearby, similar wet forest on the Island of Hawaii (Hess et al. 2007), and at 4.8–30.7 pigs/km^2 on the Island of Maui (Diong 1982; Anderson and Stone 1993).

All study sites are located in areas of similar climate, vegetation, and substrate (Table 1). Sites range in elevation from 1,140 to 1,370 m a.s.l., mean annual temperature is 14.4–15.9 °C, and mean annual precipitation is 2,910–3,985 mm with no distinct seasonality (Giambelluca et al. 2013). Forests in the study area are classified as *Metrosideros polymorpha* (overstory tree)/*Cibotium* spp. (midstory tree fern) tropical montane wet forest (Wagner et al. 1990). Overstory vegetation is exclusively native and dominated by *M. polymorpha*, with less frequent individuals of *Ilex anomala*, *Cheirodendron trigynum*, *Perrottetia sandwicensis*, and *Coprosma* sp. The subcanopy is dominated by native tree ferns (*Cibotium* spp.). Four of the paired sites had low levels of invasion by non-native plant species at the time of feral pig removal (I. Cole and R. H. Loh, pers. com), while one pair of sites (Koa management unit) had areas of heavier invasion by *Psidium cattleianum, Hedychium gardnerianum,* and *Setaria palmifolia* (Loh and Tunison 1999).

Study design

We used a paired feral pig removal/feral pig present design to assess the effects of feral pig removal, and changes over time since removal, on forest understory plant communities. We established paired sites inside and outside of five ungulate exclosures that had been fenced and cleared of feral pigs at different times, representing a 6.5–18.5 year chronosequence of feral pig removal. One site was established inside of each of the five exclosures and an adjacent site was established outside of each exclosure with one exception: a single feral pig present site served as the control for two feral pig removal sites due to the close proximity of the three sites (Table 1; Fig. 1). Within each site, four circular sampling plots (1,018-m^2; 18-m-radius) were established ≥40 m from each other and >70 m from existing fences. Measurements from two separate studies taken shortly after the time of initial fencing at the Koa site showed similar vegetation composition in feral pig removal versus feral pig present areas (Loh and Tunison 1999; Cole et al. 2012).

Vegetation sampling

We sampled vegetation in each of the four plots at each site using a nested design. In the largest sampling area (i.e., entire 18-m-radius circular plot) trees with diameter >20 cm were identified to species and diameter at breast height (dbh, ca 1.3 m) was measured. In a smaller (9-m-radius) concentric plot, woody stems ≥1 cm dbh were identified to species and dbh measured. Woody stems ≤5 cm dbh and rooted ≤2 m off the ground were categorized as ground-rooted (originating in mineral soil) or epiphytic (originating on a woody substrate ≥10 cm above the soil surface). Tree fern stem diameters were also measured within the 9-m-radius plots for all individuals having a stem length ≥50 cm. Tree ferns with live stem length <50 cm were counted and categorized as 'sprouts' or 'independently established'. We counted live tree ferns that had fallen (were

Table 1 Study site characteristics in feral pig present and feral pig removal sites in Hawaiian tropical montane wet forest on the Island of Hawaii

Site	Treatment	Size (ha)	MAP (mm)	MAT (°C)	Elev. (m)	Fenced (year)	Years since all feral pigs removed[a]	Soil class[b]	Pairing (pig removal/ pig present)
Aku	Pig removal	117	3,984	15.8	1,143	2000	8.5	Typic Hapludands	Aku/Aku
Koa	Pig removal	1,024	3,320	15.8	1,158	1989	16.5	Aquic Hapludands	Koa/Koa
Lava	Pig removal	152	2,997	15.0	1,311	1992	6.6	Typic Hapludands	Lava/PMA
NLM	Pig removal	223	2,938	14.8	1,341	1992	10.3	Typic Hapludands	NLM/PMA
Puu	Pig removal	240	2,910	15.0	1,295	1989	18.5	Aquic Hapludands	Puu/Olaa
Aku	Pig present		3,903	15.6	1,173			Typic Hapludands	
Koa	Pig present		3,474	15.9	1,143			Aquic Hapludands	
PMA	Pig present		2,949	14.5	1,372			Typic Hapludands	
Olaa	Pig present		3,473	15.8	1,158			Aquic Hapludands	

[a] Years of recovery since all feral pigs were removed are based on a sampling time in this study beginning in June 2010

[b] NRCS survey (2010)

prone on the ground). In a third concentric plot of 6 m radius, small woody plants and seedlings <1 cm dbh and ≥10 cm in height were identified to species, counted, and rooting location recorded as described above.

Understory vegetation (herbaceous plants, grasses, and woody plants <1.3 m height) and cover of individual species was measured using a modified Braun-Blanquet cover-abundance scale in twenty 1-m^2 rectangular plots systematically distributed along two perpendicular 18-m transects oriented in cardinal directions (N–S and E-W) within the 18-m-radius circular plots. We recorded stem density and percent cover of selected native species considered to be of conservation interest (i.e., rare and of conservation concern in this ecosystem and/or highly susceptible to disturbance by large herbivores; "Appendix"). We characterized forest floor cover (bryophyte, bare ground, leaf litter, coarse woody debris) along two 18-m perpendicular transects. Finally, we recorded percent overstory cover (measured at 1 m above the soil surface) at four points 9 m from the plot center in four cardinal directions using a spherical densiometer.

Statistical analysis

Values for all measurements are presented as the mean of all plots located within each respective site. Each pair of sites was considered to be a replicate ($n = 5$). We calculated importance values (IV) for woody species, including tree ferns, and understory vegetation. For woody species, IV was defined as the sum of the relative dominance, abundance, and frequency. For understory vegetation, IV was calculated as the sum of relative cover and relative frequency. Nonmetric multidimensional scaling (NMS) ordination based on the Bray-Curtis similarity index of the IV values of the species assemblages was used to examine differences in community structure between treatments (feral pig present vs. removal). This ordination method was selected based on its strength with nonnormal, discontinuous, and nonparametric data sets, and its minimal set of necessary assumptions (Bradfield and Kenkel 1987; Clarke 1993; McCune and Grace 2002). For all ordinations, a two-dimensional solution was chosen by following the standard protocol described by McCune and Mefford (1999). We used the joint plot overlay function to analyze the direction and strength of correlations between the ordination axes and measures of environmental variables (elevation, mean annual precipitation, mean annual temperature, and soil series) in order to examine their relationships with plant community composition. Because elevation and temperature were strongly correlated ($R^2 > 0.98$, $P < 0.0001$), we included only elevation in the final analysis (Fig. 2).

Statistical estimators for species richness were calculated for woody species plus tree ferns (>5 cm dbh), epiphytic and ground-rooted saplings (≥1 to 5 cm dbh), and epiphytic and ground-rooted small woody plants and seedlings ($\geq$10 cm in height and <1 cm dbh) across all four plots in each site using EstimateS (Colwell 2007). We estimated species richness for understory vegetation cover by converting presence/absence data in each of the twenty 1-m^2 subplots into frequency data for each plot. We selected the nonparametric Chao 2 incidence-based richness estimator with log-linear 95 % CIs and the incidence-based coverage estimator (ICE) (Chao 1987), based on a standard of four plots at each site. For all computations where randomization of runs was required, a default of 50 runs was used without replacement.

To test for effects of time since feral pig removal on each vegetation and ground-cover variable, we ran linear regressions of the difference between paired sites versus time since feral pig removal. These analyses showed no significant relationships over time for any measurement ($R^2 < 0.06$; $P > 0.22$ in all cases). We then used either a paired *t* test for normally distributed data or a Wilcoxon sign-ranked test for non parametric data to compare vegetation and ground-cover variables between treatments (feral pig present vs. feral pig removal). We used linear regression to test if total percent cover of understory vegetation, seedling and sapling stem density, or ground cover variables showed a relationship with percent canopy cover. Data were log or arcsine square-root transformed when necessary to meet assumptions of normality and homogeneity of variances (Zar 1996). Statistical analyses were conducted using Systat 13 (Systat Software, Chicago, Illinois, U.S.A.) at $\alpha = 0.05$. We report means ± 1 standard error (SE) throughout.

Results

Species composition and cover

Seventy-seven species were encountered across all sites, including 32 woody species, 31 ferns, tree ferns, and fern allies, nine herbaceous species, and five graminoids ("Appendix"). We identified 12 native species that we considered to be of conservation interest and 10 non-natives ("Appendix"). The vast majority of non-natives (95 %) occurred in four of nine sites, were exclusively found in the understory, and comprised <0.1 % of stems >1 cm and <5 cm dbh. Dominant non-natives included *S. palmifolia* (58 % of total non-native cover; found predominantly in Koa and Olaa feral pig present sites), *Cyperus haspan* (23 % of total non-native cover; found predominantly in Aku feral pig removal site) and *H.*

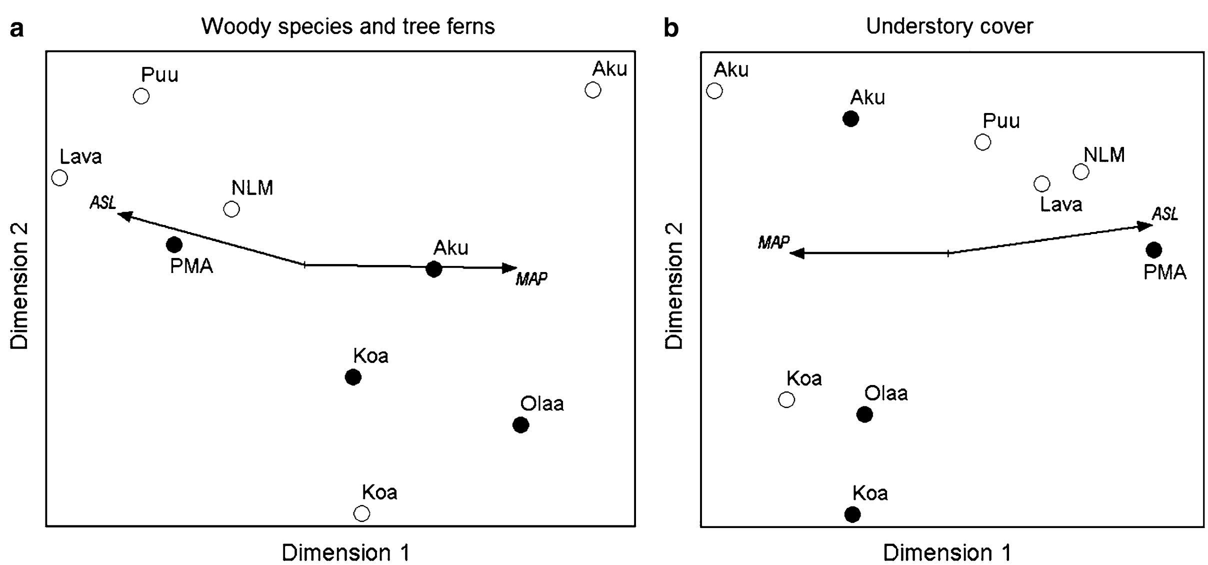

Fig. 2 Two-dimensional Nonmetric multidimensional scaling plots of woody species and tree fern importance values (**a**, stress value = 4.97, Monte Carlo $P < 0.012$) and of understory cover (**b**, stress value = 4.00, Monte Carlo $P < 0.028$). The *open symbols* represent feral pig removal sites and the *solid symbols* represent feral pig present sites. Joint plot overlay depicts two environmental variables, elevation (ASL) and mean annual precipitation (MAP)

gardnerianum (14 % of total non-native cover; found predominantly in Koa feral pig present and feral pig removal sites). *Psidium cattleianum* was the most abundant non-native woody species, but it was almost exclusively restricted (97 % of total *P. cattleianum* cover) to the Koa sites where it comprised 32 % of all small woody plants and seedlings ($\geq$10 cm height and <1 cm dbh), and was found in nine-fold higher densities in feral pig removal compared to feral pig present plots.

Stand density ranged from 2,527 to 4,052 stems/ha and basal area ranged 77.3–122.0 m^2/ha across all sites, and neither of these metrics varied significantly with treatment (paired t test, $t = 0.214$, $P = 0.841$ and $t = -2.43$, $P = 0.072$, respectively). Nonmetric multidimensional scaling of woody species and tree ferns based on species IV (stress value = 4.97, Monte Carlo $P < 0.012$) showed separation between sites based on MAP (MAP vs. Dim1, $R^2 = 0.805$) and elevation (ASL vs. Dim1, $R^2 = 0.679$), but not between treatments, soil types, or time since feral pig removal (Fig. 2a.). These trends were driven exclusively by the two most dominant woody species, *C. glaucum* and *M. polymorpha*. The *Cibotium glaucum* IV was positively correlated with increasing elevation and negatively correlated with increasing MAP ($R^2 = 0.89$, F = 30.8, $P < 0.001$). The opposite was true for *M. polymorpha*, which showed a moderate negative correlation of IV with elevation and a positive correlation with MAP ($R^2 = 0.62$, F = 4.9, $P = 0.057$) (Fig. 2b). Similarly, NMS of understory cover showed separation based on species IV values (stress value = 4.00, $P = 0.028$). Understory cover at the sites separated by MAP (MAP vs. Dim1, $R^2 = 0.719$) and elevation (ASL vs. Dim1, $R^2 = 0.964$), but not between treatments, soil types, or over time (Fig. 2b).

Forest floor cover varied significantly between feral pig removal and feral pig present sites (Fig. 3). Bryophyte cover was higher in feral pig removal sites (Wilcoxon sign-ranked test, $P = 0.043$), as was the proportion of forest floor covered with litter ($t > 3.78$, $P = 0.019$). The proportion of bare ground was more than tenfold greater in feral pig present sites ($t > 11.9$, $P < 0.0001$). Coarse woody debris cover did not vary among treatments ($t = -0.564$, $P = 0.603$). Mean percent overstory canopy cover (measured at 1 m above the soil surface) was marginally greater in feral pig removal (76.7 ± 0.2) versus present (71.8 ± 0.2) sites ($t = 2.80$, $P = 0.0490$).

Understory vegetation

Total understory cover was 45 % greater in feral pig removal compared to feral pig present sites ($t > 6.07$, $P = 0.004$), and this pattern was also true for component categories of understory plants including native ferns ($t > 4.75$, $P = 0.009$), species of conservation interest ($t > 3.81$, $P = 0.019$), and native herbs plus native small woody plants < 1.3 m height ($t > 3.79$, $P = 0.023$). Overall, non-native cover was very low and localized, and did not vary between treatments (Wilcoxon sign-ranked test, $P = 0.724$; Table 2). Total understory species richness was higher in feral pig removal compared to feral pig present sites in four of five pairs of sites, but did not differ statistically by treatment for either of the richness estimators used (Wilcoxon sign-ranked test, $P > 0.345$ in each case; Table 3).

The total stem density of small woody plants and seedlings ($\geq$ 10 cm in height and < 1 cm dbh) did not differ between treatments ($t = 0.769$, P = 0.485), averaging 6,592 (±1,824) in pig-removal and 4,470 (±1,434) in pig-present sites. There were substantial differences, however, when rooting location was considered (Table 2). Stem density of ground-rooted small woody plants and seedlings was more than four-fold greater in feral pig removal sites than feral pig present sites ($t > 5.45$, $P = 0.005$). This pattern was most notable for two species, *Coprosma ochrace* and

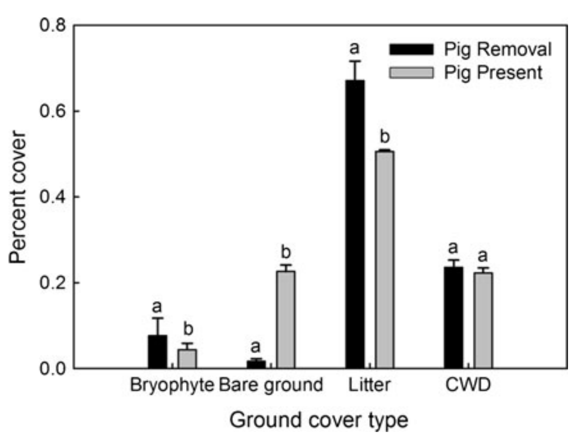

Fig. 3 Mean percent cover (±1 SE) of each ground cover category including bryophyte, bare ground, litter, and coarse woody debris (CWD), in feral pig removal and feral pig present treatments. *Different letters* in each category denote significant differences between treatments

Table 2 (1) Percent cover of understory vegetation for native ferns, native herbaceous species, species of conservation interest (CI), non-natives, and total cover; (2) stem density (stems/ha) of all ground-rooted and epiphytic small woody plants and seedlings (<1 cm dbh and >10 cm height) and the five most commonly occurring species in each category; (3) stem density of all ground-rooted and epiphytic saplings (≥1 to <5 cm dbh) and the five most commonly occurring species in each category; and (iv) stem density of small, sprouting, and fallen tree ferns. Different letters denote significant differences between treatments for a given variable. Different letters denote significant differences between treatments for a given variable. Values are means (±1 SE)

Vegetation type	Pig removal	Pig present
Understory cover (%)		
Total cover	24.8 ± 1.2[a]	13.7 ± 1.0[b]
Native ferns	18.1 ± 2.5[a]	9.1 ± 0.4[b]
Native herbs, woody plants <1.3 m height, and grasses	5.2 ± 1.2[a]	2.4 ± 0.6[b]
CI	0.63 ± 0.2[a]	0.11 ± 0.08[b]
Non-natives	1.5 ± 1.0[a]	2.2 ± 1.7[a]
Small woody plant and seedling density (stems/ha)		
Ground-rooted		
Total	3,850.7 ± 1,421.2[a]	915.1 ± 345.5[b]
Coprosma ochracea	1,320.3 ± 404.1	150.1 ± 78.5
Broussaisia arguta	867.0 ± 524.6	242.9 ± 123.3
Cyrtandra spp.*	313.5 ± 276.0	75.1 ± 75.1
Psidium cattleianum	322.4 ± 316.9	35.3 ± 35.3
Psychotria hawaiiensis	145.7 ± 113.8	66.2 ± 66.2
Epiphytic		
Total	2,741.0 ± 645.0[a]	3,554.4 ± 1,402.6[a]
Vaccinium calycinum	861.1 ± 411.3	1,815.0 ± 1,025.9
Cheirodendron trigynum	468.1 ± 108.7	627.1 ± 155.0
Metrosideros polymorpha	428.4 ± 246.2	189.9 ± 85.4
Coprosma ochracea	348.9 ± 78.8	331.2 ± 84.4
Ilex anomala	185.5 ± 87.7	273.8 ± 158.9
Sapling density (stems/ha)		
Ground-rooted		
Total	653.5 ± 333.8[a]	394.5 ± 77.1[a]
Broussaisia arguta	363.5 ± 234.0	113.9 ± 49.7
Perrottetia sandwicensis	74.6 ± 57.1	37.3 ± 24.1
Metrosideros polymorpha	35.2 ± 12.6	80.6 ± 30.7
Psychotria hawaiiensis	41.3 ± 34.4	41.2 ± 38.9
Coprosma ochracea	55.0 ± 34.4	11.8 ± 7.2
Epiphytic		
Total	147.2 ± 36.5[a]	182.5 ± 28.2[a]
Broussaisia arguta	31.4 ± 11.4	13.7 ± 9.1
Ilex anomala	37.3 ± 13.6	53.0 ± 15.4
Metrosideros polymorpha	17.6 ± 10.8	49.1 ± 29.6
Cheirodendron trigynum	9.8 ± 3.1	33.4 ± 9.1
Psychotria hawaiiensis	15.7 ± 13.4	3.9 ± 2.4
Tree fern density (stems/ha)		
Young	1,110.0 ± 149.4[a]	1,182.7 ± 7[a]
Sprouting	618.9 ± 82.4[a]	444.0 ± 77.4[b]
Fallen	422.3 ± 55.5[a]	422.4 ± 85.8[a]

* The *Cyrtandra* genus in Hawaii is notoriously difficult to separate into species due to hybridization (Wagner et al. 1990), therefore, *Cyrtandra paludosa* and *Cyrtandra lysiosepala* were combined into one category

Broussaisia arguta, which tend to grow predominantly in mineral soil (ground-rooted) (Table 2). Species richness indices were significantly higher for ground-rooted small woody plants and seedlings in feral pig removal compared to feral pig present sites (Wilcoxon sign-ranked test, $P < 0.043$ in each case; Table 3). In contrast, there were no differences between treatments in stem density (Wilcoxon sign-ranked test,

Table 3 Species richness estimators, the incidence-based richness estimator (Chao 2) with 95 % confidence intervals in parenthesis and the incidence-based coverage estimator (ICE) with mean values (±1 SE). Species richness estimators are shown for each vegetation category in feral pig removal and feral pig present treatments. Values with different letters in the same case are significantly different between treatments

Vegetation type	Pig removal		Pig present	
	Chao 2	ICE	Chao 2	ICE
Understory cover	32.60 (32.4–55.8)[a]	39.16 (6.6)[A]	29.60 (28.7–60.0)[a]	37.76 (2.8)[A]
Ground-rooted small woody plants and seedlings	18.71 (10.3–37.0)[a]	19.02 (3.9)[A]	7.85 (7.2–30.1)[b]	8.83 (2.3)[B]
Epiphytic small woody plants and seedlings	15.58 (10.2–34.5)[a]	15.69 (3.0)[A]	13.35 (8.7–30.0)[a]	12.96 (1.8)[A]
Ground-rooted saplings	8.53 (5.6–19.9)[a]	10.14 (3.1)[A]	10.59 (4.8–17.8)[a]	21.94 (13.7)[A]
Epiphytic saplings	10.57 (4.4–21.2)[a]	21.94 (13.7)[A]	6.90 (4.2–16.7)[a]	10.39 (1.58)[A]
Woody species and tree ferns	15.00 (10.5–35.2)[a]	15.17 (3.6)[A]	10.29 (8.1–25.2)[a]	12.31 (1.27)[A]

$P = 0.500$) or species richness indices (Wilcoxon sign-ranked test, $P > 0.104$ in each case) of epiphytically rooted plants. The number of small and live fallen tree ferns were similar between treatments (Wilcoxon sign-ranked test, $P = 0.686$ and $P = 0.892$, respectively) but there were 32 % more sprouting tree ferns in feral pig removal sites (Wilcoxon sign-ranked test, $P = 0.043$; Table 2).

There were no differences in the total number of ground-rooted or epiphytic saplings (≥1 to 5 cm dbh) between treatments (Wilcoxon sign-ranked test, $P > 0.685$), and the majority (69 %) of woody plants in this size range were found rooted in mineral soil (Table 2). In addition, species richness of saplings did not vary between treatments (Wilcoxon sign-ranked test, $P = 0.505$; Table 3). However, the stem densities of species of conservation interest, including all small woody plants, seedlings and saplings (≥10 cm height to <5 cm dbh), were significantly higher in feral pig removal sites (Wilcoxon sign-ranked test, $P = 0.043$). This was true for both ground-rooted and epiphytic plants (Wilcoxon sign-ranked test, $P < 0.043$ in both cases), although the majority (73 %) of individual plants of conservation interest were found to be rooted in the mineral soil (Fig. 4a). The distribution of species of conservation interest was markedly different between treatments (Fig. 4b). At least one individual was found in each of the five feral pig removal sites, while no individuals were found in three of the four feral pig present sites.

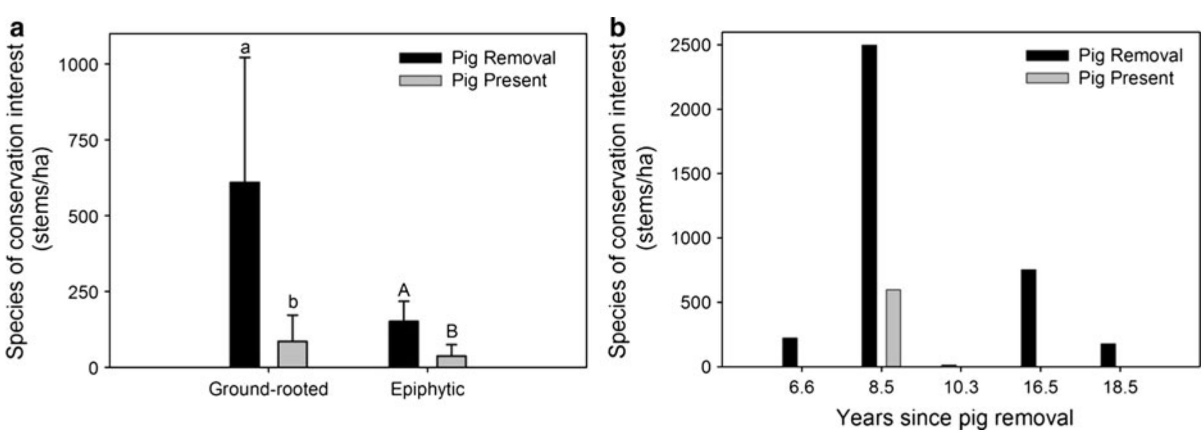

Fig. 4 **a** Mean stem densities (±1 SE) of epiphytic and ground-rooted woody species of conservation interest, including small woody plants and seedlings (<1 cm dbh and >10 cm height) and saplings (≥1 to <5 cm dbh) in feral pig removal and feral pig present treatments. **b** Variability in stem density of all small woody plants, seedlings and saplings of conservation interest across the chronosequence of feral pig removal sites. *Different letters* of the same case denote significant differences between treatments

Discussion

The results of this study point to several major patterns in understory plant community dynamics following feral pig removal from canopy-intact Hawaiian tropical montane wet forests, and contribute to a growing body of knowledge on the impacts of non-native ungulates on plant communities. First, in support of our hypothesis, the cover and abundance of native plants in the understory increased significantly with feral pig removal. Second, species richness of ground-rooted small woody plants and seedlings increased with feral pig removal. These two results indicate that feral pig disturbance strongly suppresses establishment of many native Hawaiian species, particularly those that are adapted to establish at ground level (i.e., in mineral soil). Third, our results support previous studies showing that feral pig removal extensively alters forest floor cover by decreasing the amount of disturbed soil and increasing the area of soil covered by bryophytes and litter. Fourth, in contrast to our original hypothesis, these overall patterns existed regardless of the amount of time that feral pigs had been removed, suggesting that common native species recover relatively quickly (within 6.5 years) following feral pig removal. Finally, we found that patterns of non-native species invasion and the recovery of species of conservation interest varied greatly across sites, with both increasing where they were present at the time of feral pig removal. Overall, these results indicate that management priorities following non-native ungulate removal should be based on local site conditions and, in many cases, will need to include control of non-native plants and outplanting of native species of conservation interest.

Understory plants

Removal of feral pigs had substantial positive effects on native understory vegetation. Both the percent cover and the abundance of small woody plants and seedlings rooted in mineral soil were markedly higher in feral pig removal versus feral pig present sites. The number of small sprouting tree ferns was also higher, likely due to reduced foraging and damage by feral pigs (Murphy 2013). These results support a growing number of studies from diverse ecosystems globally demonstrating positive responses of native vegetation to removal of feral pigs. For example, exclusion of feral pigs from Australian lowland rainforest (Mitchell et al. 2007; Taylor et al. 2011), Malysian rainforest (Ickes et al. 2001), and Texan mixed pine-hardwood forest (Siemann et al. 2009) led to increased understory native vegetation cover and/or seedling densities. Vegetation responses in small exclosures across a range of ecosystem types in Hawaii also showed that native plant cover remained constant or increased following control of feral pigs (Loope and Scowcroft 1985) and feral goats and cattle (Stone et al. 1992; Hess et al. 2010), with relatively less recovery in dry compared to wet ecosystems. Because only one pair of sites in our study had appreciable levels of non-native plant cover, we were unable to test if feral pigs promote non-native invasions. However, we found nine-fold higher stem density of the non-native tree *P. cattleianum* at the single feral pig present versus removal sites where this highly invasive species had established prior to fencing. This result is in line with an earlier study (Cole et al. 2012) showing that *P. cattleianum* responds positively to release from top-down control by feral pigs, and several other studies in Hawaii showing that non-native grasses and herbs increase in cover following removal of non-native herbivores in mesic and dry forests (Loope and Scowcroft 1985; Kellner et al. 2011), and in wet forest (Scowcroft and Hobdy 1987; Loh and Tunison 1999; Hess et al. 2010). Collectively, this research indicates the need for rapid and aggressive control of non-native invasive plants coupled with removal of feral pigs and other non-native ungulates as part of restoration and conservation efforts in these forests.

Native species of conservation interest showed a significant and positive response to the removal of feral pigs. Individual plants in this group were found only at one of four pig-present sites, whereas they were found in all five pig-removal sites. Recovery of plants of conservation interest was greatest for stems rooted in mineral soil, although there was also a trend of increasing incidence of these species growing epiphytically. These results contrast with several previous studies which found significant increases only in commonly occurring plant species following feral pig removal from wet Hawaiian forest (Loh and Tunison 1999; Busby et al. 2010; Cole et al. 2012). Although it is possible that there were more individual plants of conservation interest in the pig removal areas at the time of fencing at some sites, data from two different surveys near our study area conducted at the time of fencing and feral pig removal show that initial densities of plants of conservation interest were homogeneous and very low on both sides of the fence (Loh and Tunison 1999; Cole et al. 2012). Our results strongly suggest that feral pig removal allows some degree of regeneration for these species, particularly at less degraded sites.

Species richness of small native woody plants and seedlings was higher in feral pig removal compared to feral pig present sites, but only for ground-rooted plants. There was no significant difference in species richness in the herbaceous layer, although richness was greater in four of five feral pig removal sites. This is the first study to our knowledge demonstrating a positive response in species richness to feral pig removal in wet Hawaiian forests. However, native species richness has been found to increase following control of feral pigs in other ecosystems globally, including native bunch grass in California costal grasslands (Corbin and D'Antonio 2004; Kotanen 2004; Tierney and Cushman 2006), woody plants in Malaysian rainforest (Ickes et al. 2001) and herbaceous ground cover in the southeastern United States (Bratton 1975).

Of particular interest was the apparent effect of feral pigs on spatial patterns of recruitment. In contrast to large differences in ground-rooted plants, there were no significant treatment differences in the overall number of small woody plants and seedlings growing epiphytically. Moreover, the most commonly occurring species of ground-rooted and epiphytic seedlings differed, suggesting that feral pig disturbance leads to substantial long-term impacts on forest structure and species composition. The most frequently recorded plants rooted at ground level, including *C. ochracea* and *B. arguta*, were rarely found growing epiphytically and, as a result, occurred in much reduced densities with feral pigs (<18 % of total stems of these species were found in feral pig present sites). Although epiphytic establishment of tree and shrub species is common in Hawaiian wet forests, including common species such as *M. polymorpha*, *C. trigynum*, *I. anomala*, and *V. calycinum*, it is quite possible that the current structure of these forests reflects long-term effects (100+ years) of feral pig disturbance. At least one study has shown that feral pig disturbance alters spatial patterns of woody seedlings on the forest floor, leading to a more clumped distribution of a common subcanopy tree in Australian rainforest (Webber et al. 2010). Longer-term studies where feral pigs have been removed from Hawaiian tropical montane wet forest will contribute to understanding how feral pigs, as an exotic disturbance, modify spatial and temporal patterns of vegetation structure.

Forest floor cover

Similar to previous studies across a range of ecosystems (e.g., Campbell and Long 2009; Taylor et al. 2011), we found that feral pigs extensively alter the forest floor by increasing the area of exposed soil and decreasing litter cover. This is the first study, however, to document an increase in bryophyte cover following feral pig removal in wet Hawaiian forests. This finding is in contrast to one prior study showing a marginally non-significant decrease in bryophyte cover over a 16-year period following removal of feral cows and most feral pigs (Hess et al. 2010). Although the bryophyte layer is thought to be an important site for seed germination and establishment of some species (Iwashita 2012; Santiago 2000) there has been little research on the role of the bryophyte layer in seedling establishment, and such research would improve understanding of forest floor disturbance by non-native ungulates on plant community structure in these forests. The increase in area of exposed soil, mixing of litter into the soil, and deposition of urine and feces by feral pigs is also likely to impact soil physical, chemical and biological properties (Campbell and Long 2009; Spear and Chown 2009), which would also be expected to impact plant community dynamics. For example, rooting by feral pigs has been shown to reduce invertebrate macrofauna in soil and litter (Pavlov and Edwards 1995; Taylor et al. 2011), which play a key role in decomposition and nutrient cycling in wet tropical forests (Gonzales and Seastedt 2001). Additional research on direct and indirect effects of feral pigs on soil biogeochemistry and ecosystem function would provide valuable information for management of feral-pig impacted ecosystems.

Rates of recovery

Although there were clear differences in understory vegetation between treatments, the relative degree of recovery varied among sites and showed no relationship with time since feral pig removal. There are several possible reasons why we did not detect any consistent patterns over time across the chronosequence of sites. First, feral-pig activity is spatially and temporally patchy, and time since last disturbance may have differed across study sites. Second, the initial level of degradation almost certainly varied among sites at the time of fencing due to differences in extant and historical pig population densities, as well as other disturbances, contributing to at least somewhat different floristic composition at the time of feral pig removal. Third, it is possible that the majority of vegetation recovery occurred within 6.5 years since feral pig removal, which was the youngest removal site in this study. We feel that our data best support this last explanation. Trends reported in two previous studies in close proximity to our sites indicate that this is true for commonly occurring native understory plants. Loh and Tunison (1999) and Cole et al. (2012) found that cover of herbaceous vegetation increased rapidly within the first 2 years of feral pig removal, and not appreciably in the following 16 years.

Overall, we believe that our data support the concept of multiple factors affecting the rate and type of regeneration following non-native ungulate removal. Commonly occurring species in the understory appear to regenerate rapidly, in <6.5 years of cessation of feral pig disturbance. Recovery of more rare and disturbance intolerant species is most likely dependent on their presence/abundance at the time of feral pig removal, as well as the initial degree of site degradation. For example, prior studies in Hawaii suggest that recovery of even commonly occurring species is slower on more heavily degraded sites (Loope and Scowcroft 1985; Hess et al. 2010). Due to the loss of many native pollinators and seed dispersers (Foster and Robinson 2007) coupled with seed predation by rats (Shiels and Drake 2011), long range seed dispersal and natural recruitment of species of conservation interest is likely to be minimal, as observed in the current study and by Cole et al. (2012) over 16 years following feral pig removal. Recovery of species of conservation interest may, therefore, take much more than 18.5 years at highly degraded sites.

Conclusions

Feral pigs strongly reduced the cover and abundance of native plants adapted to grow at ground level in mineral soil, and reduced species richness of small woody plants and seedlings in Hawaiian tropical montane wet forest. Following removal of feral pigs from this system, commonly occurring plant species recover relatively quickly, within 6.5 years. Because feral pigs have the greatest impact on plants adapted to grow in mineral soil, rather than epiphytically, feral pig disturbance likely alters forest structure over time, as suggested by the differences found in this study in dominant ground-rooted and epiphytic seedlings and small woody plants. Species of conservation interest (i.e., of conservation concern in this ecosystem and/or highly susceptible to disturbance by large herbivores) showed a large and positive increase following feral pig removal. However, regeneration of these species was variable across the larger study area and negligible at one site, indicating that active outplanting at degraded sites is necessary to restore and conserve these species in areas where they do not exist at the time of ungulate removal. We found higher stem density and cover of the non-native shrub *P. cattleianum* in the one feral pig removal site where it had established prior to fencing, most likely due to release from top-down control by feral pigs. At a regional level, our results show that fencing and feral pig eradication is the first and most critical step towards recovery of native plant communities in tropical wet forests. Beyond this, management approaches should be adapted to local site conditions and, when necessary, include aggressive control of non-native invasive plants and outplanting of native species that fail to recruit naturally.

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Appendix

See Table 4.

Table 4 All native and non-native plant species occurring across the chronosequence of feral pig removal and feral pig present sites on the Island of Hawaii

Family	Genus species	Common name	Life form	Origin
Fabaceae	*Acacia koa* A. Gray	Koa	Tree	Endemic
Grammitidaceae	*Adenophorus tripinnatifidus*		Fern	Endemic
Apocynaceae	*Alixia oliviformis Gaud.*	Maile	Shrub	Indigenous
Aspleniaceae	*Asplenium lobulatum Mett.*		Fern	Indigenous
Asteliaceae	*Astelia menziesiana* Sm.	Pa‘iniu	Herb	Endemic
Athyriaceae	*Athyrium microphyllum* (Sm.) Alston	‘Ākōlea	Fern	Endemic
Hydrangeaceae	*Broussaisia arguta* Gaudich.	Kanawao	Shrub	Endemic
Hymenophyllaceae	*Callistopteris baldwinii (D. C. Eaton) Copel.*		Fern	Endemic
Cyperaceae	*Carex* sp.		Grass	Indigenous
Araliaceae	*Cheirodendron trigynum* (Gaudich.) A. Heller	‘Ōlapa	Tree	Endemic
Dicksoniaceae	*Cibotium chamissoi* Kaulf.	Hāpu‘u	Tree fern	Endemic
Dicksoniaceae	*Cibotium glaucum* (Sm.) Hook. & Arn.	Hāpu‘u pulu	Tree fern	Endemic
Dicksoniaceae	*Cibotium menziesii* Hook.	Hāpu‘u ‘i‘i	Tree fern	Endemic
Campanulaceae	*Clermontia hawaiiensis* (Hillebr.) Rock*		Shrub	Indigenous
Campanulaceae	*Clermontia parviflora* Gaudich spp. ex A. Gray*	‘Ōhā wai	Shrub	Endemic
Pteridaceae	*Coniogramme pilosa* (Brack.) Hieron.	Lo‘ulu	Fern	Endemic
Rubiaceae	*Coprosma ochracea* W. R. B. Oliv.	Pilo	Shrub	Endemic
Dryopteridaceae	*Ctenitis latifrons* (Brack.) Copel.		Fern	Endemic
Campanulaceae	*Cyanea floribunda* E. Wimm.*	‘Akū	Shrub	Endemic
Campanulaceae	*Cyanea pilosa* A. Gray subsp*		Shrub	Endmeic
Campanulaceae	*Cyanea tritomantha A. Gray**		Shrub	Endmeic
Campanulaceae	*Cyanea tritomantha A. Gray**		Shrub	Endemic
Cyperaceae	*Cyperus haspan* L.		Grass	Exotic
Cyperaceae	*Cyperus* sp.		Sedge	Indigenous
Gesneriaceae	*Cyrtandra lysiosepala* (A. Gray) C. B. Clarke*		Herb	Endemic
Gesneriaceae	*Cyrtandra paludosa* Gaudich.*		Herb	Endemic
Gesneriaceae	*Cyrtandra platyphylla* A. Gray*		Herb	Endemic
Athyriaceae	*Deparia petersenii* (Kunze) M. Kato		Fern	Exotic
Gleicheniaceae	*Dicranopteris linearis* (Burm. f.) Underw.	Uluhe	Fern	Endemic
Athyriaceae	*Diplazium sandwichianum* (C. Presl) Diels	Hō‘i‘o	Fern	Endemic
Dryopteridaceae	*Dryopteris fusco-atra* (Hillebr.) W. J. Rob. var. fusco-atra		Fern	Endemic
Dryopteridaceae	*Dryopteris glabra* sp.		Fern	Endemic
Poaceae	*Ehrharta stipoides* Labill.		Grass	Exotic
Lomariopsidaceae	*Elaphoglossum paleaceum* (Hook. & Grev.) Sledge	Māku‘e	Fern	Indigenous
Lomariopsidaceae	*Elaphoglossum parvisquameum* Skottsb.		Fern	Endemic
Pandanaceae	*Freycinetia arborea* Gaudich.	‘Ie‘i.e.	Herb	Indigenous
Grammitidaceae	*Grammitis hookeri* (Brack.) Copel.		Fern	Indigenous
Grammitidaceae	*Grammitis tenella* Kaulf.	Kolokolo	Fern	Endemic
Zingiberaceae	*Hedychium gardnerianum* Sheppard ex Ker Gawl.		Herb	Exotic
Clusiaceae	*Hypericum mutilum* L.	Kakili ginger	Herb	Exotic
Aquifoliaceae	*Ilex anomala* Hook. & Arn.	Kāwa‘u	Tree	Indigenous
Rubiaceae	*Kadua affinis* DC.	Manono	Tree	Endemic

Table 4 continued

Family	Genus species	Common name	Life form	Origin
Loganiaceae	*Labordia hedyosmifolia* Baill.		Tree	Endemic
Hymenophyllaceae	*Mecodium recurvum* (Gaudich.) Copel.	Ohia ku	Fern	Endemic
Rutaceae	*Melicope clusiifolia* (A. Gray) T. G. Hartley & B. C. Stone		Tree	Endemic
Rutaceae	*Melicope radiata* (H. St. John) T. G.Hartley & B.C. Stone		Tree	Endemic
Myrtaceae	*Metrosideros polymorpha* Gaudich.	‘Ōhi‘a lehua	Tree	Endemic
Dennstaedtiaceae	*Microlepia strigosa* (Thunb.) C. Presl	Palapalai	Fern	Indigenous
Myrsinaceae	*Myrsine lessertiana* A. DC.	Kōlea lau nui	Tree	Endemic
Nephrolepidaceae	*Nephrolepis exaltata* (L.) Schott	Kupukupu	Fern	Endemic
Solanaceae	*Nothocestrum longifolium* A. Gray		Tree	Endemic
Dryopteridaceae	*Nothoperanema rubiginosa* (Brack.) AR Sm. & DD Palmer	None	Fern	Endemic
Passifloraceae	*Passiflora mollissima* (Kunth) L.H. Bailey	Banana poka	Liana	Exotic
Piperaceae	*Peperomia* spp.	‘Ala‘ala wai nui	Herb	Endemic
Celastraceae	*Perrottetia sandwicensis* A. Gray	Olomea	Tree	Endemic
Urticaceae	*Pipturus albidus* (Hook. & Arn.) A. Gray	Māmaki	Tree	Endemic
Rutaceae	*Platydesma spathulata* (A. Gray) B. C. Stone		Shrub	Endemic
Thelypteridaceae	*Pneumatopteris sandwicensis* (Brack.) Holttum	Hō‘i‘o kula	Fern	Endemic
Polypodiaceae	*Polypodium pellucidum* Kaulf.		Fern	Endemic
Arecaceae	*Pritchardia* sp.	Lou’lu	Palm	Endemic
Myrtaceae	*Psidium cattleianum* Sabine	Strawberry guava	Shrub	Exotic
Psilotaceae	*Psilotum complanatum* Sw.		Fern Ally	Indigenous
Psilotaceae	*Psilotum nudum* (L.) P. Beauv.		Fern Ally	Endemic
Rubiaceae	*Psychotria hawaiiensis* (A. Gray) Fosberg	Kōpiko ‘ula	Tree	Endemic
Rosaceae	*Rubus ellipticus* Sm.	Yellow Himalayan raspberry	Shrub	Exotic
Rosaceae	*Rubus hawaiensis* A. Gray	‘Ākala	Shrub	Endemic
Rosaceae	*Rubus rosafolius* Sm.		Shrub	Exotic
Blechnaceae	*Sadleria pallida* (Blechnaceae) (amau)		Tree Fern	Endemic
Poaceae	*Setaria palmifolia* (J. König) Stapf	Palm grass	Grass	Exotic
Hymenophyllaceae	*Sphaerocionium lanceolatum* (Hook. & Arn.) Copel.		Fern	Endemic
Hymenophyllaceae	*Sphaerocionium obtusum* (Hook. & Arn.) Copel.	Palai lau li’i	Fern	Endemic
Lamiaceae	*Stenogyne calaminthoides* A. Gray*		Herb	Endemic
Urticaceae	*Touchardia latifolia* Gaudich*		Shrub	Endemic
Campanulaceae	*Trematolobelia grandifolia* (Rock) O. Deg.*		Shrub	Endemic
Ericaceae	*Vaccinium calycinum* Sm.	‘Ōhelo kau lā‘au	Shrub	Endemic
Hymenophyllaceae	*Vandenboschia* calycinum (Gaudich.) Copel.		Fern	Endemic
Hymenophyllaceae	*Vandenboschia davallioides* (Gaudich.) Copel.		Fern	Endemic

An asterisk (*) identifies a species occurring in experimental sites that is considered to be of conservation interest in Hawaiian tropical montane wet forests

References

Anderson SJ, Stone CP (1993) Snaring to control feral pigs *Sus scrofa* in a remote Hawaiian Rainforest. Biol Conserv 63:195–201

Aplet GH, Anderson SJ, Stone CP (1991) Association between feral pigs disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. Vegetatio 95:55–62

Barrios-Garcia M, Ballari S (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biol Invasions 14:2283–2300

Bradfield GE, Kenkel NC (1987) Nonlinear ordination using flexible shortest-path adjustment of ecological distances. Ecology 68:750–753

Bratton SP (1975) Effect of European wild boar, *Sus scrofa*, on gray beech forest in Great Smoky Mountains. Ecology 56:1356–1366

Busby PE, Vitousek P, Dirzo R (2010) Prevalence of tree regeneration by sprouting and seeding along a rainfall gradient in Hawai'i. Biotropica 42:80–86

Campbell TA, Long DB (2009) Feral swine damage and damage management in forested ecosystems. For Ecol Manag 257:2319–2326

Chao A (1987) Estimating the population-size for capture recapture data with unequal catchability. Biometrics 43:783–791

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. Aust J Ecol 18:117

Cole RJ, Litton CM, Koontz MJ, Loh RK (2012) Vegetation recovery 16 years after feral pig removal from a wet Hawaiian forest. Biotropica 44(4):463–471

Colwell RK (2007) EstimateS (Version 8.0.0). Retrieved from Available at http://viceroy.eeb.uconn.edu/estimates, on 3 Jan 2008

Corbin JD, D'Antonio CM (2004) Effects of exotic species on soil nitrogen cycling: implications for restoration. Weed Technol 18:1464–1467

Courchamp F, Chapuis JL, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. Biol Rev 78:347–383

Cuevas MF, Novillo A, Campos C, Dacar MA, Ojeda RA (2010) Food habits and impact of rooting behaviour of the invasive wild boar, Sus scrofa, in a protected area of the Monte Desert, Argentina. J Arid Environ 74:1582–1585

Cushman JH, Tierney T, Hinds JM (2004) Variable effects of feral pig disturbances on native and exotic plants in a California grassland. Ecol Appl 14:1746–1756

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. Ann Rev Ecol Syst 23:63–87

Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474

Diong CH (1982) Population biology and management of the feral pig (*Sus scrofa*) in Kipahulu Valley, Maui. Dissertation, University of Hawaii

Dovrat G, Perevolotsky A, Ne'eman G (2012) Wild boars as seed dispersal agents of exotic plants from agricultural lands to conservation areas. J Arid Environ 78:49–54

Eckhardt RC (1972) Introduced plants and animals in the Galapagos Islands. Bioscience 22:585–590

Foster JT, Robinson SK (2007) Introduced birds and the fate of Hawaiian rainforests. Conserv Biol 21:1248–1257

Fujinuma J, Harrison RD (2012) Wild pigs (*Sus scrofa*) mediate large-scale edge effects in a lowland tropical rainforest in Peninsular Malaysia. PLoS ONE 7(5):e37321. doi:10.1371/journal.pone.0037321

Giambelluca TW, Chen Q, Frazier AG, Price JP, Chen YL, Chu PS, Eischeid JK, Delparte DM (2013) Online Rainfall Atlas of Hawaii. Bull Am Meteorol Soc 94:313–316

Gonzales G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82:955–964

Hess SC, Jeffrey J, Ball DL, Babich L, Bailey JK (2007) Efficacy of feral pig removals at Hakalau Forest National Wildlife Refuge. Trans W Sect Wildl 42:53–67

Hess SC, Jeffrey JJ, Pratt LW, Ball DL (2010) Effects of ungulate management on vegetation at Hakalau Forest National Wildlife Refuge, Hawai'i Island. Pac Conserv Biol 16:144–150

Hone J (2002) Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. Biol Conserv 105:231–242

Ickes K, Dewalt SJ, Appanah S (2001) Effects of native pigs (*Sus scrofa*) on woody understory vegetation in a Malaysian lowland rain forest. J Trop Ecol 17:191–206

Iwashita DK (2012) Role of coarse woody debris in carbon storage and seedling establishment in Hawaiian tropical montane wet forest. Master's Thesis, University of Hawaii

Jacobi JD (1981) Vegetation changes in a subalpine grassland in Hawaii following disturbance by feral pigs. Technical Report 41. Cooperative National Park Resources Studies Unit, University of Hawaii

Kellner JR, Asner GP, Kinney KM, Loarie SR, Knapp DE, Kennedy-Bowdoin T, Questad EJ, Cordell S, Thaxton JM (2011) Remote analysis of biological invasion and the impact of enemy release. Ecol Appl 21:2094–2104

Kotanen PM (1995) Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian costal prairie. Ecography 18:190–199

Kotanen PM (2004) Revegetation following soil disturbance and invasion in a Californian meadow: a 10-year history of recovery. Biol Invasions 6:245–254

Lipscomb DJ (1989) Impacts of feral hogs on longleaf pine regeneration. South J Appl For 13:177–181

Loh RK and Tunison JT (1999) Vegetation recovery following pig removal in Olaa-koa rainforest unit, Hawaii Volcanoes National Park. Pacific Cooperative Studies Unit 123, University of Hawaii

Loope LL, Medeiros AC, Gagne BH (1991) Studies in the montane bog following protection from feral pig rooting. Technical Report 77. Cooperative National Park Resources, Studies Unit University of Hawaii, Honolulu, Hawaii

Loope LL, Scowcroft PG (1985) Vegetation response within exclosures in Hawaii: a review. In: Stone CP, Scott JM (eds) Hawaii's terrestrial ecosystems: preservation and management. University of Hawaii Press, Honolulu, pp 377–402

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach
McCune B and Mefford MJ (1999) Multivariate analysis of ecological data v. 4.39. MjM Software, Gleneden Beach
Medeiros AC, Loope LL, Gagne BH (1991) Degradation of vegetation in two montane bogs: 1982-1988. Technical Report 78. Cooperative National Park Resources, Studies Unit University of Hawaii, Honolulu, Hawaii
Milton SJ, Dean WRJ, Klotz S (1997) Effects of small-scale animal disturbances on plant assemblages of set-aside land in central Germany. J Veg Sci 8:45–54
Mitchell J, Dorney W, Mayer R, McIlroy J (2007) Spatial and temporal patterns of feral pig diggings in rainforests of north Queensland. Wildl Res 34:597–602
Mooney HA, Hobbs RJ (2000) Invasive species in a changing world. Island Press, Washington
Murphy M, Inman-Narahari F, Ostertag R, Litton CM (2013) Invasive feral pigs impact native tree ferns and woody seedlings in Hawaiian forest. Biol Invasions (in press)
Nogueira-Filho SLG, Nogueira SSC, Fragoso JMV (2009) Ecological impacts of feral pigs in the Hawaiian Islands. Biodivers Conserv 18:3677–3683
NRCS (2010) Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. http://websoilsurvey.nrcs.usda.gov/. Accessed 10 May 2012
Nuñez M, Bailey J, Schweitzer J (2010) Population, community and ecosystem effects of exotic herbivores: a growing global concern. Biol Invasions 12:297–301
Oduor AMO, Gomez JM, Strauss SY (2010) Exotic vertebrate and invertebrate herbivores differ in their impacts on native and exotic plants: a meta-analysis. Biol Invasions 12:407–419
Parker JD, Burkepile DE, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461
Pavlov P, Edwards PC (1995) Feral pig ecology in Cape Tribulation National Park, north Queensland, Australia. J Mt Ecol 3:141–151
Pratt LW, Abbott LL, Palumbo DK (1999) Vegetation above a feral pig fence in rain forests of Kilauea's East Rift, Hawaii Volcanoes National Park. Technical Report 124. Cooperative National Park Resources, Studies Unit University of Hawaii, Honolulu, Hawaii
Risch AC, Wirthner S, Busse MD, Page-Dumroese DS, Schutz M (2010) Grubbing by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. Oecologia 164:773–784
Santiago LS (2000) Use of coarse woody debris by the plant community of a Hawaiian montane cloud forest. Biotropica 32:633–641
Scowcroft PG, Conrad CE (1992) Alien and native plant response to release from feral sheep browsing on Mauna Kea. In: Stone CP, Smith CW, Tunison JT (eds) Alien plant invasions in native ecosystems of Hawaii: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, pp 625–664
Scowcroft PG, Giffin JG (1983) Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J Range Manag 36:638–645
Scowcroft PG, Hobdy R (1987) Recovery of goat-damaged vegetation in an insular tropical montane forest. Biotropica 19:208–214
Shiels AB, Drake DR (2011) Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii? Biol Invasions 13:883–894
Siemann E, Carrillo JA, Gabler CA, Zipp R, Rogers WE (2009) Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. For Ecol Manag 258:546–553
Singer FJ, Swank WT, Clebsch EEC (1984) Effects of wild pig rooting in a deciduous forest. J Wildl Manag 48:464–473
Spear D, Chown SL (2009) Non-indigenous ungulates as a threat to biodiversity. J Zool 279:1–17
Stone CP, Cuddihy LW, Tunison JT (1992) Responses of Hawaiian ecosystems to removal of feral pigs and goats. In: Stone CP, Smith CW, Tunison JT (eds) Alien plant invasions in native ecosystems of Hawaii: management and research. Cooperative National Park Resources Study Unit, University of Hawaii, Honolulu, Hawaii, pp 666–704
Taylor DL, Leung LKP, Gordon IJ (2011) The impact of feral pigs (*Sus Scrofa*) on an Australian lowland tropical rainforest. Wildl Res 38:437–445
Tierney TA, Cushman JH (2006) Temporal changes in native and exotic vegetation and soil characteristics following disturbances by feral pigs in a California grassland. Biol Invasions 8:1073–1089
Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57:7–13
Wagner WL, Herbst DR, Sohmer SH (1990) Manual of the flowering plants of Hawaii. University of Hawaii Press, Honolulu
Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecol Monogr 71:587–614
Webber BL, Norton BA, Woodrow IE (2010) Disturbance affects spatial patterning and stand structure of a tropical rainforest tree. Austr Ecol 35:423–434
Zar JH (1996) Biostatistical analysis. Prentice Hall, Upper Saddle River
Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol 16:454–459