

FINAL REPORT

Recovery of Native Plant Communities and Ecological Processes
Following Removal of Non-native, Invasive Ungulates from
Pacific Island Forests

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Supplementary Table 2. Field Nutrient Manipulation Experiment: Initial mean (± 1 SE) values for chemical elements across the three soil nutrient treatments in the *Dodonaea* shrubland. For all chemical elements no significant differences were found across treatments.

Supplementary Table 3. Field Nutrient Manipulation Experiment: Mean soil attributes (± 1 SE) in each soil nutrient treatment in the tropical wet forest. No significant differences among weeded and not weeded treatments were found for all soil attributes. Different letters denotes significant differences among soil nutrient treatments.

Supplementary Table 4. Field Nutrient Manipulation Experiment Mean soil attributes (± 1 SE) in each soil nutrient treatment in the *Dodonaea* shrubland. No significant differences among weeded and not weeded treatments were found for all soil attributes. Different letters denotes significant differences among soil nutrient treatments.

Supplemental Fig. 1. Carbon content of (a) live vegetation, (b) detritus, and (c) total ecosystem pools in paired pig present versus pig free plots across the wet forest chronosequence. No significant differences were present in pig removal versus pig present pairs.

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Supplemental Fig. 7. Carbon content of (a) live vegetation, (b) detritus, and (c) total ecosystem pools across the *Dodonaea* shrubland chronosequence. Letters denote significant differences.

List of Acronyms

ANOVA: Analysis of Variance

ASR: Area for species recovery

C: Carbon

Ca: Calcium

C:N: Carbon to Nitrogen ratio

CWD: Coarse Woody Debris

DBH: Diameter at Breast Height

DoD: Department of Defense

DST: Decision support tool

F_L : Annual litterfall

F_S : Soil-surface CO₂ efflux

K: Potassium

Mg: Magnesium

N: Nitrogen

NH₄⁺: Ammonium

NMS: Non-metric Multidimensional Scaling

NO₃⁻: Nitrate

NRO: Natural Resource Office

P: Phosphorus

PERMANOVA: Permutational Multivariate Analysis of Variance

PTA: Pōhakuloa Training Area

TBCF: Total belowground carbon flux

TDF: Tropical Dry Forest

TER-S threatened, endangered, and at-risk species

TWF: Tropical Wet Forest

SE: Standard Error

VWC: Volumetric Water Content

WSA: Water stable soil macro-aggregates

Key words

Disturbance, Invasive species, Hawaii, Nonnative ungulates, Soil nutrient manipulation, Restoration, Tropical ecosystems

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Abstract – RC - 2433

Objectives: Nonnative ungulates exert a large negative effect on native biodiversity and the structure and function of terrestrial ecosystems throughout the Pacific Island region. In Hawaii, removal of ungulates is broadly recognized as a critical first step in conserving native ecosystems and species, particularly threatened, endangered, and at-risk species (TER-S). To this end, land managers commonly fence and remove nonnative ungulates where conservation of native biodiversity is a priority. However, these actions are labor and cost intensive, and the long-term outcomes are not well quantified. Surprisingly little information exists on the magnitude and time frame of native plant recovery across different ecosystem types, the potential for nonnative plant invasions, or the response of critical, underlying ecological processes to nonnative ungulate removal. This study quantified the impacts of nonnative ungulate removal on the biodiversity, structure, and function of two major ecosystem types – tropical wet forest (TWF) and tropical dry forest (TDF) – found on DoD installations throughout the Pacific Island region. Specifically, we examined pathways and mechanisms through which ungulate removal impacts native and nonnative plant dynamics in four distinct ecosystem/plant community types. We also measured how ungulate removal affects key underlying ecological processes in three of these ecosystem types, focusing on ecosystem carbon (C) storage and flux, and soil nitrogen (N) cycling and availability. We then tested if manipulation of soil nutrients can be used as a management tool to favor native plants over nonnative, invasive plants in both greenhouse and field experiments. Finally, we initiated the development of a Decision Support Tool (DST) to assist land managers at the DoD Pōhakuloa Training Area to spatially prioritize land management decisions associated with TER-S throughout a large and complex landscape.

Technical Approach: The overall experimental design involved utilizing previously established management units where fences were constructed and nonnative feral ungulates removed at various time points in the past on the Island of Hawaii. In tropical montane wet forest, we utilized an existing ~20 year chronosequence of five feral pig removal units and adjacent feral pig present sites in Hawaii Volcanoes National Park and the Pu‘u Maka‘ala Natural Area Reserve (Cole and Litton 2014), and constructed a time-zero site to look at early impacts of nonnative ungulate removal in the Kahau‘alea Natural Area Reserve. In tropical dry ecosystems, we worked in three widespread vegetation types in the Pōhakuloa Training Area (PTA) – *Metrosideros* woodland, *Dodonaea* shrubland, and *Eragrostis* grassland – where the experimental design for each vegetation type consisted of a set of existing ungulate removal units established at different points in the past and adjacent areas with feral ungulates present. We conducted vegetation measurements in all four vegetation types and detailed ecological processes measurements in three of the vegetation types (excluding the *Eragrostis* grassland). We also established a greenhouse nutrient manipulation experiment to test how nutrient availability affects native vs. nonnative invasive plant growth and competition (the only Go/No Go Point in the project). The results of the greenhouse experiment were then used to inform the establishment of a field nutrient manipulation experiment in TWF and TDF where the response of vegetation and key ecological processes to nutrient availability was assessed. Finally, a Decision Support Tool (DST) was developed through a series of facilitated meetings with PTA land managers to generate a knowledge base and develop a logic model to enable spatially explicit prioritization of management activities in relation to TER-S.

Results: The response of vegetation to feral ungulate removal varied somewhat across plant communities in TWF and TDF, but general patterns were evident. First, ungulate removal is a key first step in conserving and promoting native plant communities. Second, nonnative invasive

plants also seem to benefit from ungulate removal, making their control an important aspect to consider when fencing and removing ungulates. Third, recovery of TER-S occurred with ungulate removal in all four ecosystem types studied, and recovery was highest where there was a population present at the time of fencing and ungulate removal. Finally, the rate of recovery varied substantially across the studied ecosystems, with the most rapid responses occurring in tropical wet forest and the slowest in the TDF ecosystems. TWF ecosystems have higher resource availability (e.g., precipitation) which likely explains the more rapid response to ungulate removal in this ecosystem type. In addition, the TDF sites were more heavily invaded by nonnative plants at the time of fencing and ungulate removal, which likely also resulted in a slower recovery.

The response of ecological processes to nonnative feral ungulate removal also varied somewhat across ecosystem types, but several common trends were evident. Overall, there was little impact of ungulate removal on ecosystem C storage and flux. The exception to this trend was increased belowground C cycling in TWF with nonnative feral pig removal, and an increase in fine detritus (i.e., fine fuels) in dry ecosystems following ungulate removal. Ungulate removal resulted in an increase in nitrogen mineralization (i.e., increased nitrogen cycling) in TWF and *Dodonaea* shrubland, but not in *Metrosideros* woodland. Similarly, inorganic nitrogen availability increased following nonnative ungulate removal in TWF and *Dodonaea* shrubland, but not in *Metrosideros* woodland. In general, feral ungulate removal led to increased nitrogen cycling and availability, and increased soil nitrogen availability persisted over time following ungulate removal.

Subsequent greenhouse and field experiments tested if this increase in nitrogen availability favors nonnative invasive plants over native plants. In the greenhouse experiment, we found that all but one native species showed very little response to increased nutrient availability. In contrast, all nonnative plants and one native shrub responded positively to nutrient availability by increasing growth and whole plant C gain with increasing nutrient levels. The field experiment had more variability and a weaker response to nutrient manipulation, but this was expected given that nutrient manipulations take longer to manifest under field conditions. Taken together with the ecological processes responses, our results strongly suggest that elevated soil nutrient supply following nonnative ungulate removal negatively affects native plants while benefiting nonnative invasive plants.

Three of five steps in the DST development process were carried out successfully under this project. Using facilitated sessions with active participation by PTA environmental staff, we identified the decision question (*What are the priority areas for management at PTA in regards to TER-S?*), and a suite of spatially explicit criteria to inform the answer to this question. We also identified and assembled the base-layer maps to guide the overall DST process. Remaining steps in the DST include developing a flexible user interface and creating a spatially explicit map of decision scores to guide final management prioritization.

Benefits: While nonnative ungulates degrade native vegetation and ecosystems, little prior work has been conducted to assess the response of vegetation and key underlying ecological processes to the increasingly common land management strategy of fencing and ungulate removal. The research conducted under this project provides insights into the effects of nonnative ungulate removal on plant communities and ecological processes on lands managed by DoD across the Pacific. In addition, we initiated a decision support framework for informing where management activities should be prioritized on the PTA landscape. As such, these results should be of direct utility for land managers on DoD and other facilities across the Pacific Island Region.

1. Objectives

Project #RC-2433 addressed focal areas 1 and 2 of RCSON-14-01 (*Recovery of Ecological Processes Impacted by Nonnative Invasive Species in the Pacific Islands*). Nonnative ungulates exert a large effect on native biodiversity and the structure and function of native ecosystems on islands throughout the Pacific region (Nogueira-Filho et al. 2009). In Hawaii, removal of ungulates is broadly recognized as a crucial first step in conserving native ecosystems, especially threatened, endangered, and at-risk species (TER-S). To this end, land managers, including those on DoD installations, fence and remove nonnative ungulates where conservation of native biodiversity is a priority. Critical to our research, these actions are labor and cost intensive, but the long-term outcomes are not well quantified. Surprisingly little information is available on the magnitude and time frame of native plant recovery following ungulate removal, the potential for nonnative plant invasions, or the response of critical, underlying ecological processes (Stohlgren et al. 1999b).

This project assessed how an increasingly common management action – fencing and removal of nonnative invasive ungulates – impacts long-term recovery dynamics in native vs. nonnative plant communities, and the ecological processes (carbon (C) and nitrogen (N) cycling) that at least partially underpin vegetation response. To address this, we explored similarities and divergences in ecological recovery following nonnative ungulate removal from several major ecosystem types in tropical wet forest (TWF) and tropical dry forest (TDF) which are found on DoD military installations throughout the Pacific Island region. Nonnative ungulate species differ by forest type, with TWF in Hawaii primarily impacted by feral pigs and TDF by feral goats and feral sheep. These differences in dominant ungulates are coupled with intrinsic differences in vegetation and resource availability across ecosystem types. To assess how shifts in nutrient cycling and availability following ungulate removal impact native vs. nonnative plant community dynamics and competitive tradeoffs, we tested how manipulation of soil nutrient availability, in both greenhouse and field experiments in representative wet and dry ecosystems, affects native vs. nonnative plant competitive dynamics to evaluate this approach as a potential management tool to restore native vegetation. Overall, we worked across chronosequences of feral ungulate removal in four distinct vegetation types occurring across TWF and TDF to examine the direction and magnitude of recovery in vegetation and ecological processes following ungulate removal, and to provide management recommendations based on observed ecosystem responses. This study addressed the following technical objectives and hypotheses:

Technical Objective 1: How does removal of nonnative ungulates affect the recovery of native plants vs. spread of nonnative invasive plants?

Technical Objective 3: What is the magnitude and direction of recovery in plant communities and ecological processes over time?

- H1: Nonnative ungulate removal will increase the abundance and diversity of both native and nonnative plants.
- H2: Native plant recovery will increase with time since ungulate removal.
- H3: Due to inherent differences in resource availability & prior degree of degradation, tropical dry forests will have relatively smaller responses to ungulate removal.

Technical Objective 2: How does removal of nonnative ungulates affect the ecological processes that underlie vegetation responses (C & N flux and storage)?

Technical Objective 3: What is the magnitude and direction of recovery in plant communities and ecological processes over time?

- H1: Nonnative ungulate removal will increase both above- and belowground C fluxes and storage.
- H2: Removal of nonnative ungulates will increase nitrogen cycling and decrease ecosystem loss of nitrogen (i.e., a more closed nitrogen cycle with higher nitrogen availability following ungulate removal).

Technical Objective 4: Can soil nutrient manipulations be used to alter native vs. nonnative plant competition to the benefit of native species?

- H1: While all plants will benefit from increased nutrient supply, nonnative, invasive plants will benefit more than natives from increased nutrient availability following ungulate removal. Native plants adapted to low nutrient conditions will show improved competitive advantage in relation to nonnative plants in response to decreased soil nutrient availability.

Technical Objective 5: What are the estimated costs of large-scale manipulations of nutrient availability?

- After consultation with environmental staff, this technical objective was altered to focus on the initial steps in creating a *Decision Support Tool* to prioritize management activities for TER-S across the highly heterogeneous PTA landscape.

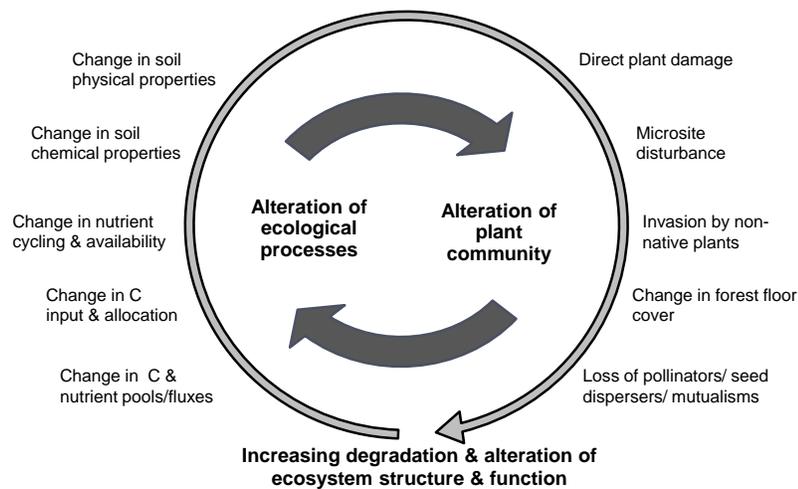


Fig. 1. Conceptual model for hypothesized changes in plant communities and ecological processes in the presence of nonnative feral ungulates.

These five technical objectives were addressed within a conceptual framework of the effects of nonnative ungulates on terrestrial ecosystems (Fig. 1). In this conceptual model, ungulates damage plants directly (e.g., herbivory and trampling) and indirectly (e.g., alteration to underlying ecological processes), while also creating microsite disturbances that facilitate invasion by nonnative invasive plants (Cole and Litton 2014). Ungulates also alter ecological processes such as soil physical and chemical properties that then result in subsequent changes in the cycling and storage of C and N. The impacts of feral ungulates on plant communities and ecological processes feedback on each other to maintain invaded systems in an altered ecological state or trajectory that persists for at least some time following nonnative ungulate removal.

2. Background

Non-native invasive ungulates dramatically alter ecosystem structure and function across a wide array of ecosystems through direct impacts on plant community structure, as well as indirect impacts on ecosystem processes (Campbell & Long 2009; Spear & Chown 2009; Peltzer et al. 2010). Although the detrimental impacts of non-native ungulates on plant communities have been documented globally (Nuñez et al. 2010), rates and even direction of ecosystem recovery following ungulate removal are poorly understood despite the significant costs associated with this management approach (Stohlgren et al. 1999a; Cole & Litton 2014). In addition, changes in key ecological processes associated with nonnative ungulates are potentially the most important long-term drivers of ecosystem change (Nuñez et al. 2010; Spear & Chown 2009). However, studies examining impacts on ecological processes have been rare (Siemann et al. 2009), and those that exist have often produced context-specific results (Tierney & Cushman 2006), at least partially because prior studies have focused on short temporal scales. Impacts are also likely to vary across distinct ecosystem types where important differences exist in plant communities, disturbance regimes, and resource availability (Stohlgren et al. 1999b), all of which influence what ungulates are present.

Non-native invasive ungulates impact ecosystems throughout the Pacific Island region, and large investments have gone into fencing and ungulate removal by land management agencies in conservation areas. In Hawaii, feral pigs occur in high densities in wet and mesic forests where they modify the forest understory (Cole et al. 2012; Cole & Litton 2014), facilitate the spread of non-native invasive plants (Diong 1982; Oduor et al. 2010), and have a large impact on key ecological processes. Similarly, in Hawaiian TDF, feral goats and sheep occur in high densities (Chynoweth et al. 2013) and reduce vegetation cover, abundance and diversity (Scowcroft & Giffin 1983; Scowcroft & Sakai 1983; Scowcroft & Conrad 1992).

2.1 Ungulate effects on plant community dynamics

Non-native ungulates can exert a large effect on native plant communities. The direct effects of ungulates on native vegetation in Hawaii have been documented in coastal communities (Williams 1990), mesic and wet forests (Spatz & Mueller-Dombois 1973; Aplet et al. 1991; Cole et al. 2012; Cole & Litton 2014), dry alpine woodlands (Giffin 1976; 1982; Scowcroft & Giffin 1983; Scowcroft and Conrad 1992), and dry forests (Blackmore & Vitousek 2000; Cabin et al. 2000). In almost all cases, non-native ungulates caused substantial decreases in native plant cover and richness. Feral pigs in Hawaii can extensively alter ground cover (Anderson & Stone 1993; Risch et al. 2010; Cole et al. 2012), reduce native plant cover and richness (e.g., Barrios-Garcia & Ballari 2012), and facilitate the establishment of non-native plants (Diong 1982; Siemann et al. 2009; Oduor et al. 2010, Fujinuma & Harrison 2012). Feral goats can extirpate preferred browse species and prevent recruitment of a broad range of native trees (Yocom 1967; Spatz and Mueller-Dombois 1973; Scowcroft & Griffin 1983). Although these short-term impacts have been relatively well quantified, plant community dynamics following ungulate removal over longer time periods are not well quantified.

Studies to date show widely varying patterns of recovery, likely due to differences in the extent of initial site degradation and/or the resilience of the given ecosystem. In most cases, ungulate removal results in positive gains in native vegetation. Removal of feral pigs led to increases in native species richness and cover in California coastal grassland (Corbin & D'Antonio 2004; Kotanen 2004; Tierney and Cushman 2006), Australian rainforest (Taylor et al. 2011), and Hawaiian TWF (Loh & Tunison 1999; Cole et al. 2012; Cole & Litton 2014).

Similarly, exclusion of feral goats (Scowcroft & Hobdy 1987) and sheep (Scowcroft & Griffin 1983) from Hawaiian TDF resulted in positive increases in native woody establishment.

However, recovery can be extremely slow or non-existent in some ecosystems (Stohlgren et al. 1999b). A nine-year study in TDF at PTA on Hawaii Island showed no change in the abundance of native vegetation following removal of a suite of ungulate herbivores (Kellner et al. 2011), and native woody species declined following exclusion of feral deer, pigs and goats from mesic forests on Kauai due to competition with non-native plants (Weller et al. 2011). The rate and extent of native plant recovery also varies among sites within ecosystems. Loh and Tunison (1999) and Cole et al. (2012) found that cover of herbaceous vegetation in Hawaiian TWF increased rapidly, within the first two years of feral pig removal, and then not appreciably in the following 16 years. Recovery of TER-S at the proposed chronosequence of sites in TWF occurred only at a few locations and was positively correlated with their presence at the time of ungulate removal (Cole & Litton 2014).

A major concern surrounding non-native ungulate removal is the potential for rapid proliferation of non-native plants released from top-down control. Removal of non-native ungulates can result in dramatic increases in non-native plant cover and richness (Zavaleta et al. 2001). This trend has also been documented at multiple locations in Hawaii (e.g., Blackmore and Vitousek 2000; Scowcroft & Conrad 1992; Cole et al. 2012), as well as within both of the proposed study ecosystems. Cole and Litton (2014) found that stem density of the non-native invasive tree *Psidium cattleianum* (strawberry guava) was 5x greater in ungulate-removal sites in TWF, and Kellner et al. (2011) reported increased non-native plant cover over a nine-year period following ungulate removal from TDF at PTA. Other studies have shown that ungulates promote invasive species such as strawberry guava through enhanced dispersal (Diong 1982; Warshauer et al. 1983; Nogueira-Filho et al. 2009).

Landscape scale management of ungulates has shown mixed results, and it remains unclear why some ecosystems and sites recover rapidly whereas others do not without intense management. In the worst case, costly management prescriptions are applied to improve native species condition, but the outcome is an alternate successional trajectory with novel assemblages of native and non-native plants. Although removal of non-native ungulates is clearly a critical first step for enabling recovery, numerous other variables can act to stress these systems and create multiple barriers to natural regeneration and restoration efforts (Weller et al. 2011). In particular, the degree of site degradation, presence of non-native plants, and the specific impacts of non-native ungulates (e.g., feral goats vs. pigs) are likely to vary across landscapes and over time. Underlying changes in soil nutrient availability may further reduce competitive ability of native plants (Ostertag & Verville 2002), while favoring non-native invasive plants (see below). To date, however, there has been little work comparing the outcomes of ungulate removal on native vs. non-native plant communities across ecosystems and over long periods of time. Understanding how ungulate removal affects plant communities will inform targeted management approaches in TWF and TDF ecosystems.

2.2 Ungulate effects on carbon and nitrogen cycling

Ecosystem C and nutrient cycling are critical underlying processes that are likely to be strongly influenced by ungulate presence, and their removal. Given the relationship between nutrient supply and plant diversity (Stohlgren et al. 1999b), impacted systems may remain altered for a significant time period after ungulate removal. The availability of N and other soil nutrients (e.g., P) is a key factor influencing plant community composition (Stohlgren et al.

1999b; Daehler 2003; Gross et al. 2005), and is also intimately associated with C cycling through ecological stoichiometric in photosynthesis and soil microbial dynamics (Sistla & Schimel 2012). Drivers of change in ecosystem C cycling include those factors that alter the input of C (i.e., photosynthesis), partitioning of the products of photosynthesis to production vs. respiration and above- vs. belowground, and losses of C via ecosystem respiration (Litton et al. 2007), all of which ultimately impact ecosystem C storage. The rate of soil nutrient cycling controls the availability of N and P for plant growth, and so strongly regulates plant C cycling (Binkley & Fischer 2010) and, therefore, plant community composition. As a result of evolutionary history, plant competitive dynamics are often tightly linked to a narrow range of N and P availability. If ungulate removal alters the availability of nutrients on short or long temporal scales, this would likely change competitive dynamics between native and non-native plants (Lake & Leishman 2004). Changes in C cycling do not occur independently of other nutrients because nutrients and C processes are tightly coupled. If non-native ungulate removal increases soil nutrient availability, increased ecosystem productivity and shifts in C partitioning to aboveground would be expected (Giardina et al. 2003; Litton et al. 2007). Alternatively, if ungulate removal increases ecosystem nutrient loss via leaching and soil trace gas efflux, reductions in ecosystem C input and shifts from above- to belowground C partitioning would be expected. However, very few studies have examined the impacts of ungulate removal on ecosystem C and nutrient cycling, and none have looked at the coupling of C, N and P across ecosystem types and over longer time scales.

2.3 Nutrient availability as a driver of plant community dynamics

Underlying soil processes play a large role in structuring plant communities (e.g. Hobbs & Henneke 1992). Increased nutrient availability, in particular, can facilitate non-native plant establishment and spread (Stohlgren et al. 1999b; Davis et al. 2000; Ostertag & Verville 2002) at the expense of native species that are less competitive under conditions of high resource availability (Vitousek & Walker 1987; Tilman 1990; Shea & Chesson 2002). In particular, elevated nutrient availability can favor invasions by fast-growing non-native plants adapted to high resource availability over slower-growing native species adapted to low resource availability (Chapin 1980; Blumenthal et al. 2003; Daehler 2003; Blumenthal 2009). However, all species typically benefit from higher resource availability (Funk & Vitousek 2007), and hot spots of nutrient availability can also be hot spots of native biodiversity (Stohlgren et al. 1999b). Further, some non-native invasive species grow well in low resource conditions (Lake & Leishman 2007). The simultaneous occurrence of both high native and non-native plant species diversity in locations of high nutrient availability (e.g. Stohlgren et al. 1999b) has been described as the 'Invasion Paradox' (Fridley et al. 2007). In these high diversity and high resource environments the loss of native species to herbivory can lead to accelerated invasion by non-native plants (Lake & Leishman 2007). Because of these complex interactions, manipulations of soil nutrients could be critical to understanding the competitive advantage of native vs. non-native plant species.

From biogeochemical theory (e.g., Vitousek 2004), we expect that productivity in dry ecosystems will be primarily limited by N availability and water, while productivity in wet ecosystems will be limited primarily by P availability. There is some evidence that P also exerts important controls in the TDF at PTA (S. Cordell, *pers. comm.*). Previous research suggests that invasive plants in both these ecosystems have high nutrient and water requirements, lower carbon assimilation per unit of N, and lower water use efficiencies (Funk & Vitousek 2007; Cavaleri & Sack 2010). In contrast, most native Hawaii plants display conservative resource use

traits including slow growth, low tissue nutrient concentration, and slow C assimilation (Funk & Vitousek 2007). Based on this, we predict that reductions of available N or P should exert a larger influence on non-native plants than native plants.

Carbon addition to soil has the effect of lowering plant-available nutrients. Increased C provides a substrate source for heterotrophic soil microbes that respond with increased biomass and activity (Morgan 1994). Microbes that are no longer C-limited immobilize available nutrients in the soil solution. As a result, measurements following C addition typically show significantly lower levels of inorganic nutrients (e.g., Morghan & Seastedt 1999; Blumenthal et al. 2003; Cione et al. 2002; Bleiler & Jackson 2007; Perry et al. 2010). Previous restoration studies have utilized high C:nutrient additions including sucrose, sawdust, and straw. Wood chips produced from removal of non-native invasive plants (e.g., strawberry guava) as part of control efforts may provide such a C addition, although this particular approach has not been tested.

3. Technical Approach

3.1 Establishment of TWF and TDF Experimental Design

To quantify the effects of nonnative ungulate removal on plant communities and ecological processes, we utilized existing management units that had been fenced and had ungulates removed over time. This approach consisted of six ungulate removal units in TWF located in Hawaii Volcanoes National Park, Kahauale‘a Natural Area Reserve, and the Pu‘u Maka‘ala Natural Area Reserve (Table 1; Fig. 1) representing a ~20 year chronosequence of feral ungulate removal (Fig. 2; see Cole and Litton (2014) for details).

Table 1. Established study sites for tropical wet forest on Hawaii Island. Each site consists of four 18 m radius circular plots inside and outside of each enclosure.

Site	Treatment	Size (ha)	MAP (mm)	MAT (°C)	Elev. (m)	Yrs since ungulate removal in 2009	†Soil Class	Pairing (pig removal / pig present)
Kahaualea*	Ungulate removal	108	3900	15.7	1139	0	Lithic Hapludands	Kah/Kah
Aku	Ungulate removal	117	3984	15.8	1143	8.5	Typic Hapludands	Aku/Aku
Koa	Ungulate removal	1024	3320	15.8	1158	16.5	Aquic Hapludands	Koa/Koa
Lava	Ungulate removal	152	2997	15.0	1311	6.5	Typic Hapludands	Lava/PMA
NLM	Ungulate removal	223	2938	14.8	1341	10.5	Typic Hapludands	NLM/PMA
Puu	Ungulate removal	240	2910	15.0	1295	18.5	Aquic Hapludands	Puu/Olaa
Kahaualea	Ungulate present		3900	15.7	1139	-	Lithic Hapludands	
Aku	Ungulate present		3903	15.6	1173	-	Typic Hapludands	
Koa	Ungulate present		3474	15.9	1143	-	Aquic Hapludands	
PMA	Ungulate present		2949	14.5	1372	-	Typic Hapludands	
Olaa	Ungulate present		3473	15.8	1158	-	Aquic Hapludands	

† NRCS survey (2010)

*Kah enclosure was also the site of the Field Nutrient Manipulation Study.

All of the wet forest study sites were located in areas of similar climate, vegetation, and substrate (Table 1; the one exception is the time zero site, which have an understory heavily dominated by a nonnative ginger species, *Hedychium gardnerianum*). Forest cover in all sites is classified as *Metrosideros polymorpha* (overstory tree)/ *Cibotium* spp. (mid-story tree fern) tropical montane wet forest (Wagner et al. 1999). We established paired sites inside and outside

of these six ungulate exclosures. All sites were established in 2009, with the exception of the time zero sites which were established in 2014. In addition to the sampling that occurred in the chronosequence plots, we conducted targeted sampling inside and outside of the 16.5 year old feral pig exclosure (targeted plot). Targeted plots were located both outside the fenced unit in areas with recent and heavy feral pig disturbance (e.g. dips and wallows) and inside the fenced unit in areas naturally protected from pig disturbance (i.e. between fallen trees or other natural barriers). The targeted plots were designed to estimate maximal differences in soil properties with feral pig removal.

In 2014, we established a similar series of plots inside and outside of existing ungulate exclosures in three major vegetation types in TDF at the Pōhakuloa Training Area on Hawaii Island: *Metrosideros* woodland, *Dodonaea* shrubland, and *Eragrostis* grassland (Table 2; Fig. 3). Study sites within each vegetation type are located in areas of similar climate, vegetation, and substrate (Table 2).

Table 2. Established study sites for tropical dry forest on Hawaii Island. Each site consists of four to seven 18 m radius circular plots inside and outside of each exclosure.

Site	Vegetation type	Treatment	# of plots [†]	MAP (mm)	Elev. (m)	Years since ungulates removed in 2014
Kipuka Kalawamauna West*	<i>Dodonaea</i> shrubland	Ungulate removal/Time zero	7	500	1600	0
Kipuka Kalawamauna East	<i>Dodonaea</i> shrubland	Ungulate removal	7	500	1600	8
MW-Control	<i>Metrosideros</i> woodland	Ungulate present	5	480	1705	-
MW-Time Zero	<i>Metrosideros</i> woodland	Time zero	4	480	1705	0
Kadua Koriaceae	<i>Metrosideros</i> woodland	Ungulate removal	5	480	1705	6
Kipuka Alala South	<i>Metrosideros</i> woodland	Ungulate removal	5	480	1705	8
Kipuka Alala North	<i>Metrosideros</i> woodland	Ungulate removal	5	480	1740	12
Kipuka Kapele	<i>Eragrostis</i> grassland	Ungulate removal	7	530	1750	30
Kipuka Ke'eKe'e	<i>Eragrostis</i> grassland	Ungulate present	7	530	1705	-

[†]Number of plots used in vegetation survey. All ecological process measurements are carried out in a randomly selected subset of 4 plots per site in *Dodonaea* shrubland and *Metrosideros* woodland.

* Kipuka Kalawamauna West exclosure was the site for the Field Nutrient Manipulation Study. The site was fenced and ungulates removed in 2016.

To quantify initial plant community composition and ecological processes immediately following ungulate removal, we constructed ‘time zero’ exclosures in both TDF and TWF (Tables 1 and 2). The TWF time zero site was constructed in collaboration with the State of Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife in a new 108-ha ungulate exclosure on similar substrate and in similar vegetation as the other TWF sites, but with a heavy invasion of nonnative ginger in the understory (Table 1). For TDF, we utilized two approaches to establish ‘time zero’ exclosures. First, in December 2014 we constructed a small exclosure (~50 × 50 m) in the *Metrosideros* woodland vegetation type (Fig. 3). Second, we utilized a large existing exclosure in *Dodonaea* shrubland from which ungulates were removed by PTA in 2014 that previously served as the ungulate present site in this vegetation type (Fig. 3).

As with our previous work in TWF (Cole and Litton 2014), we established four to seven 18-m-radius circular plots at each of the TDF sites in *Dodonaea* shrubland, *Metrosideros* woodland and in the time zero sites (Fig. 4). Because the original approach was created for forest, woodland and shrubland vegetation types, we used a modified design for *Eragrostis* grassland that is more relevant to that vegetation type. The oldest fenced sites (~30 years since ungulate removal) occur in *Eragrostis* grassland but in very steep terrain on the summit of Pu’u Kapele, a large cinder cone with little soil development. To reduce risk to personnel and make data collection feasible, we measured vegetation responses to ungulate removal using seven 100 × 2-m belt transects established along regularly spaced elevational contour lines around the summit cone of Pu’u Kapele. These transects were paired with seven transects on a nearby, unfenced cinder cone (Pu’u Ke’eke’e) characterized by similar substrate age and dominant vegetation (Fig. 4).

In 2016, we established the TDF part of the field nutrient manipulation study in the time zero exclosure in the *Dodonaea* shrubland (Fig. 3) near the chronosequence plots described above. We established the TWF part of the experiment in the time zero exclosure the Kahaualea Natural Area Reserve near the sites described above (Fig. 2).

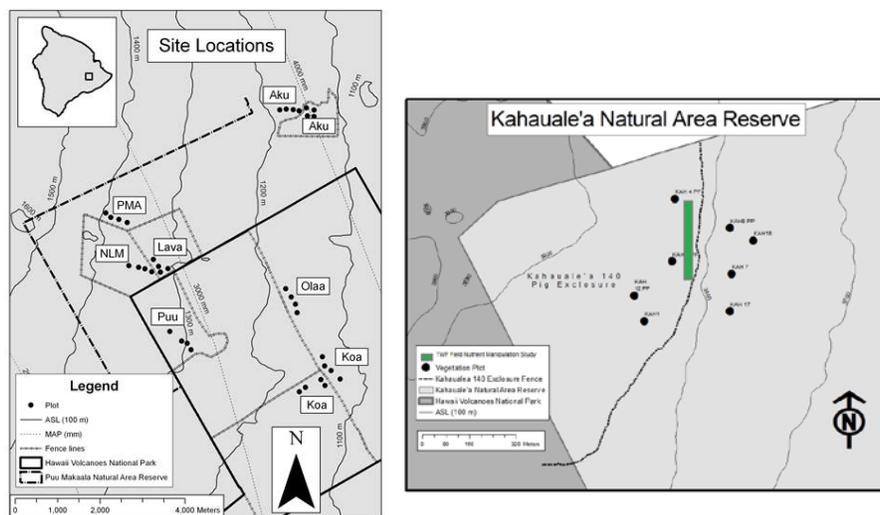


Fig. 2. Distribution of experimental sites across a chronosequence of feral ungulate removal units in tropical wet forest (left). The TWF time zero site and the Field Nutrient Manipulation study are located in the Kahaualea site (right).

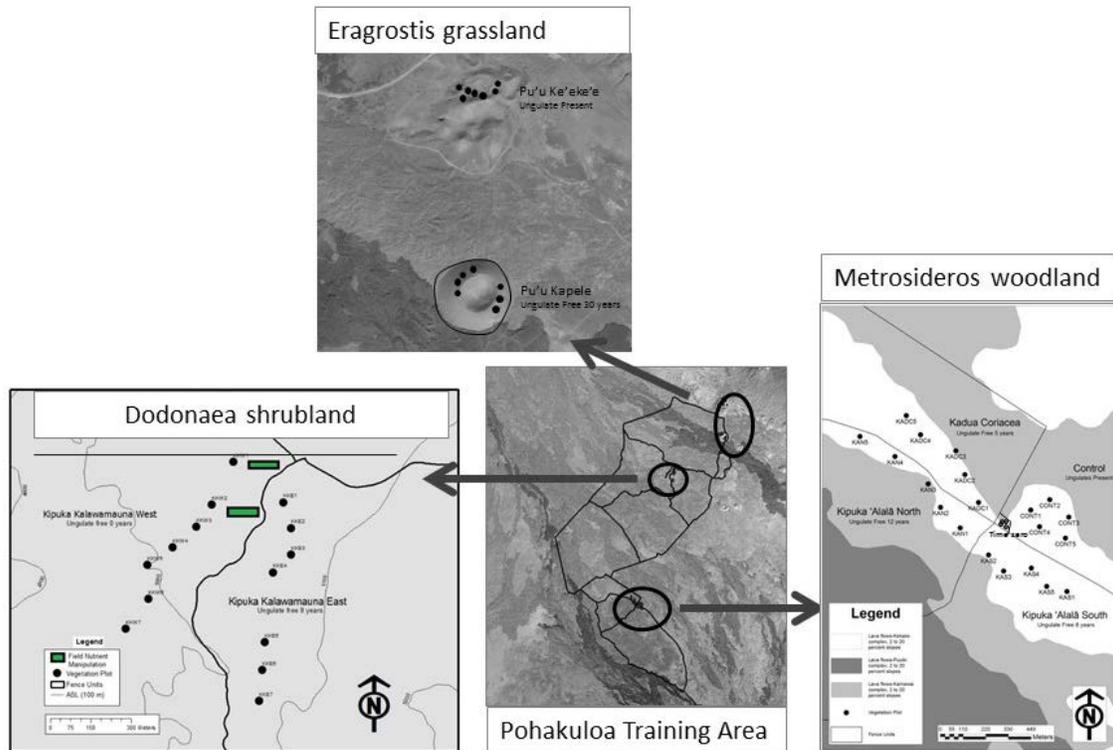


Fig. 3. Distribution of TDF experimental sites across a chronosequence of feral ungulate removal units. The Field Nutrient Manipulation study is located in the *Dodonaea* shrubland.

3.2 Vegetation Sampling

We conducted three vegetation surveys in each vegetation type: at the start of the study in Fall of 2014, and then in the Fall of 2016 and 2017. In addition to tracking change with time since ungulate removal, the surveys in the TDF occurred across years with very different levels of precipitation (Table 3).

Table 3. Mean annual precipitation (mm) at the three Tropical Dry Forest vegetation types from 2013-2017.

Year	2013	2014	2015	2016	2017	5-yr average
<i>Dodonaea</i> shrubland	77.0	287.8	414.3	414.0	352.5	309.0
<i>Eragrostis</i> grassland	194.3	181.4	388.9	267.7	232.4	252.9
<i>Metrosideros</i> woodland	228.6	430.2	742.9	399.5	299.5	420.1

Cooperative Climatological Data Summaries, Western Regional Climate Center, 2018. Web. 15 April 2018. <http://wrcc.dri.edu/climatedata/climsum/>

Vegetation surveys were adapted for each ecosystem type. In *Dodonaea* shrubland and *Metrosideros* woodland in TDF, we identified to species level and measured diameter at breast height (DBH) of all woody stems ≥ 10 cm DBH in the entire 18 m-radius plot (Fig. 4; Table 4). Woody stems ≥ 1 cm DBH were identified and measured in a 9 m-radius subplot (250 m²). We identified to species and measured the basal diameter of all shrub stems >1 cm basal diameter, and identified and counted all woody seedlings <1 cm basal diameter and >10 cm height in a 6 m-radius subplot (100 m²). Understory vegetation (herbaceous plants, grasses, and woody plants <1.3 m height) and cover of individual species were quantified using a modified Braun-Blanquet cover abundance scale in twenty 1 m² rectangular plots systematically distributed along two perpendicular 36 m transects oriented in cardinal directions (N-S and E-W) within the 18 m radius circular plots. We measured shrub cover by species and quantified ground cover (percent cover of rock, soil, litter, coarse woody debris, and bryophytes) along the two 18 m transects. In order to assess abundance of species of conservation interest (i.e., rare, threatened, endangered, or sensitive to disturbance), we identified and counted all individual plants along a 100 \times 2 m (200 m²) belt transect tangential to each 18 m-radius circular plot (Table 4).

In the *Eragrostis* grassland in TDF, we quantified shrub cover, identified plants to species level, counted shrub seedlings, measured cover of understory plants, and tallied plant species of conservation concern across 100 \times 2 m belt transects (Table 4).

In TWF sites, the initial sampling of vegetation (excluding the time zero sites), occurred in 2009-2010 following the methods described in Cole and Litton (2014), which were very similar to the measurements described above for shrubland and woodland sites in TDF (Fig. 4; Table 4). Differences in measurement between the TDF and TWF were due to differences in vegetation. In the entire 18 m-radius plot trees with diameter of > 20 cm were identified and measured. In addition to the woody stems measurement in the 9 m-radius plot (described above), woody stems ≤ 5 cm DBH and rooted ≤ 2 cm 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 plot 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 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 (Table 4). Understory vegetation, cover of individual species, ground cover, and abundance of conservation interest species was all measured the same for the TDF and TWF (Table 4). The measurements were taken in the time zero TWF sites in 2014, 2016, and 2017.

Table 4. Vegetation measurements taken in the chronosequence plots for each ecosystem.

Ecosystem	Measurement Area	Measurements	Measurement specifications
<i>Dodonaea</i> shrubland and <i>Metrosideros</i> woodland	18m radius plot	DBH	Woody sp \geq 10 cm DBH
	9m radius plot	DBH	Woody sp \geq 1 cm DBH
	6m radius plot	Basal diameter	shrub sp $>$ 1 cm basal diameter
	6m radius plot	Counts	woody sp $<$ 1 cm basal diameter and $>$ 10 cm height
	Twenty 1 m ² plots	Cover	-
	100 \times 2 m (200 m ²) belt transect	Count	Species of conservation interest
<i>Eragrostis</i> grassland	100 m transect	Shrub cover	First 75m
	Twenty 1 m ² plots	Herb cover	-
	1 \times 100 m transect	Count	Shrub and woody sp $<$ 1 cm basal diameter
	100 \times 2 m (200 m ²) belt transect	Count	Species of conservation interest
Tropical wet forest	18m radius plot	DBH	Woody sp $>$ 20cm DBH
	9m radius plot	DBH	Woody sp \geq 1 cm DBH
	9m radius plot	DBH	Woody sp \leq 5cm DBH & categorized as ground rooted (\leq 2 cm off the ground) or epiphytic (on a woody substrate \geq 10 cm above the soil surface)
	9m radius plot	Diameter	Ferns stem length \geq 50 cm
	9m radius plot	Count	Ferns stem length $<$ 50 cm; categorized as ‘sprouts’ or ‘independently established’
	6m radius plot	Count	Woody sp $<$ 1 cm dbh and \geq 10 cm in height; rooting location recorded
	Twenty 1 m ² plots	Cover	-
	100 \times 2 m (200 m ²) belt transect	Count	Species of conservation interest

3.2.1 Statistical analysis

Data from each of the dry ecosystem vegetation types (*Metrosideros* woodland, *Dodonaea* shrubland and *Eragrostis* grassland) were analyzed using Two-Way ANOVA across the three years of measurements and feral ungulate status (present vs. removed at various times). Data were transformed or ranked when necessary to meet assumptions of normality and homogeneity of variances. Statistical analyses were conducted using SPSS version 24 (IBM Corporation) at $\alpha = 0.05$. The standard error of the mean ($\pm 1SE$) are reported throughout.

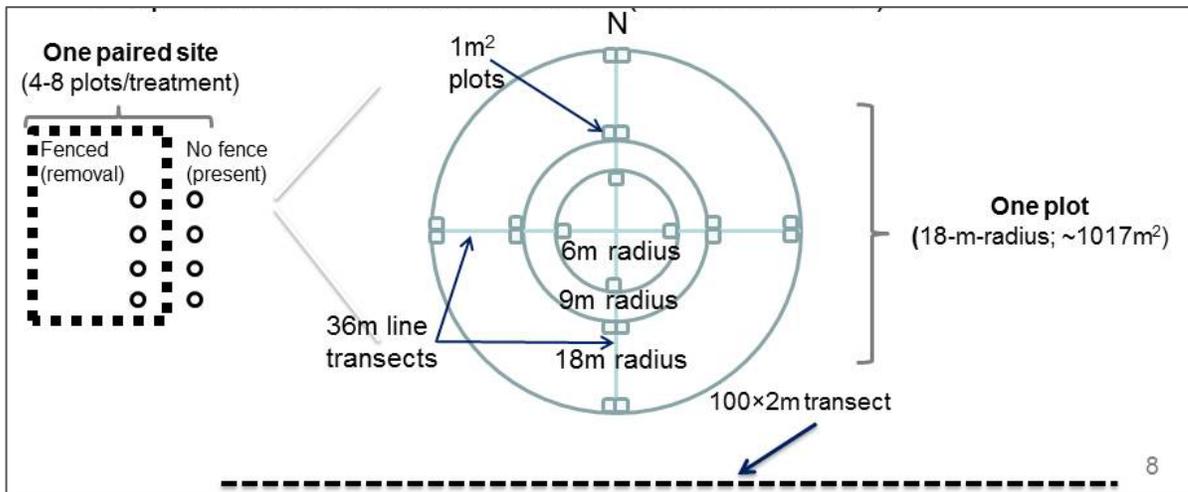


Fig. 4. Experimental design consisting of 4-8 plots per site in *Dodonaea* shrubland, *Metrosideros* woodland, and tropical wet forest. Plots consist of concentric circles of different areas in which specific measurements are taken (see text for details).

3.3 Ecological Processes Sampling

3.3.1 Soil physical properties

In June-July 2015, we sampled and processed soils from TDF for soil bulk density from the same cores described above for fine root biomass (samples were collected from 12 randomly located 3 cm diameter by 5cm deep cores in each plot). These samples were also analyzed for C and N content, extractable cations, and pH (Table 5). A wide suite of soil physical and chemical properties were assessed in TWF prior to the initiation of this study (Long et al. 2017; Table 5).

3.3.2 Ecosystem carbon pools and fluxes

In the *Dodonaea* shrubland and *Metrosideros* woodland sites, we quantified standing aboveground biomass of understory vegetation (herbaceous vegetation and grasses) in eight 0.5 m² clip plots per 18 m-radius plot one time in 2015 (see Fig. 4 above for design of circular plots; Table 5). Standing biomass was separated by species into live and dead components. Litter was collected in the same eight 0.5 m² quadrats per plot prior to standing biomass harvest. Coarse woody debris (CWD) was quantified along a single 100-m transect tangential to each plot, as

well as along two 18-m transects within each plot using a line-intercept technique modified for Hawaiian ecosystems (Iwashita et al. 2013). Fine root biomass was measured from twelve 3 cm diameter x 5 cm deep soil cores per plot. Biomass from clip plots and standing litter was dried to a constant weight at 70°C and was analyzed for C, and N content. These data were combined with measurements of standing and dead biomass of woody plants (DBH/basal diameter of trees and shrubs from Vegetation Sampling, above) and a combination of existing allometric equations and new equations developed for this project to estimate total above and below-ground biomass (Table 5).

We installed eight 0.2 m² litter traps in the *Dodonaea* shrubland, *Metrosideros* woodland, and TWF time zero plots in February 2015 and collected litter monthly for two years through January 2017 (this work was conducted in the other TWF sites over one year in 2010-2011; Table 5). All litter was dried to a constant weight at 70°C, and subsamples analyzed for C and N content.

In February 2015, we installed eight soil collars for soil surface CO₂ efflux measurements in each of four plots in the *Dodonaea* shrubland, *Metrosideros* woodland and the TWF time zero plots (this work was conducted in the remaining TWF sites in 2010-2011; Table 5). Larger 20 cm diameter collars were installed in TWF (following the protocol used in measurements of all established TWF sites), while 10 cm diameter collars were installed in TDF due to shallow and rocky soils. Soil-surface CO₂ efflux, soil temperature and soil volumetric water content were measured quarterly through the end of the study in 2017 on each soil collar with a LI-COR 8100 CO₂ gas analyzer in TWF and a LI-COR 6400 CO₂ gas analyzer in TDF (Table 5).

3.3.3 Nutrient Cycling and Availability

Rates of gross mineralization, nitrification, and immobilization were measured using ¹⁵N pool dilution methods modified from Hart et al. (1994a; 1994b). Four 5 cm diameter cores were collected from 0 to 5 cm in the soil, composited, and transported back to the laboratory (Table 5). Composite soils were then split into three portions, NH₄⁺ labeling, NO₃⁻ labeling, and a negative control (no N added, water only). Each was then labeled with an aqueous solution of 99% enriched ¹⁵N, and solution volumes were adjusted to minimize changes to percent soil water content by 1 to 2%. The amount of N was adjusted based on the amount of NH₄⁺ and NO₃⁻ in the soil. Immediately after homogenizing labeled soils, two replicate soil subsamples from each N treatment was extracted with 2M KCl (2:1 extractant: fresh soil ratio). These represented initial (t₀) samples. The two additional subsamples were extracted 12 h later and represented final (t_f) samples. Gross fluxes were then calculated using equations presented in Hart et al. (1994a; 1994b).

Availability of inorganic N (NO₃⁻-N and NH₄⁺-N) in soils was indexed using the ion-exchange resin bag method (Binkley & Matson 1983; Binkley & Hart 1989; Table 5). Because resins have the potential to mimic nutrient uptake by plants, they provide a useful measure of nutrient supply (Huang & Schoenau 1996), and resin-captured NO₃ has been shown to be highly correlated with both soil NO₃ concentrations and rates of net nitrification (Subler et al. 1995). Further, these measures of N provide a straightforward index of soil nutrient supply over time for comparison among experimental treatments, in addition to an absolute measure of nutrient pool sizes (Lajtha et al. 1999). Four resin-bag incubations were conducted at each study site and in each plot. Nylon mesh bags containing 10g of mixed bed cation-anion resin were placed at the litter layer-mineral soil interface within each plot. Resin bags were then incubated for 2-4 months. During

the incubation, controls bags were stored both in the field (in sealed plastic bags) and in the laboratory (refrigerator controls). Bags were collected at the end of the incubation, cleaned thoroughly with distilled water, and extracted with 100 mL of 2M KCl on a shaker table. Extracts were then analyzed calorimetrically with a Lachat QuickChem (Hach Co., Saskatoon, Canada) at the University of Hawaii – Hilo Analytical Laboratory.

To determine fluxes of N₂O from the soil, the same chambers used for the measurement of CO₂ fluxes were sealed and three 9 ml gas samples were sequentially taken through a septum port over a two-hour period and injected into previously evacuated gas-tight vials (Table 5). The vials were then transported back to the laboratory and analyzed for N₂O concentration on a gas chromatograph with an electron capture and flame ionization detector (Shimadzu Model 14A). Fluxes of N₂O were then calculated as the slope of the line describing the concentrations over time.

To measure annual N leaching, we utilized resin-based soil solution lysimeters (Table 5). Resin-based soil solution lysimeters allow for the calculation of annual leachate fluxes by isolating the resin from direct soil contact and quantifying the concentration of N in free percolating soil water. We installed one of these lysimeters in each site in the wet forest at a depth of 30 cm. A pit was excavated and the lysimeter installed laterally into the soil profile. Resins were collected after three months in the field, cleaned thoroughly with distilled water, and extracted with 100 mL of 2M KCl on a shaker table. Extracts were then analyzed calorimetrically with an AutoAnalyzer III (Pulse Instrumentation, Saskatoon, Canada). Due to concerns over unexploded ordinance in the dry forest sites, we used resin strips (PRSTM-probes Western Ag, Saskatoon, Saskatchewan Canada) for leachate measurements by placing strips horizontally at a depth of 10 cm. This method allows for the calculation of a mass per area of leaching (kg/ha) by using the area of resin probe window. Lysimeters were retrieved from the field after three months, rinsed with DI water, placed in plastic Ziploc bags and stored in the refrigerator until analysis.

□¹⁵N integrates all microbial and plant transformations of N so differences between treatments are indicative of changes in some aspect of the N cycle (Evans et al. 2001). Therefore, we monitored foliar and bulk soil □¹⁵N across all sites. Leaf and soil samples were collected from each plot, dried, and ground to a fine powder (Table 5). Samples were then transported to Cornell University, loaded into tin capsules and the isotopic composition determined using an isotope ratio mass spectrometer (Thermo Model Delta V) coupled to an elemental analyzer (Carlo Erba Model NC2500).

Table 5. Ecological processes measurements taken in the chronosequence plots for each ecosystem.

Ecosystem	Measurement Area	Measurements	Measurement specifications/notes
<i>Dodonaea</i> shrubland and <i>Metrosideros</i> woodland	Eight 0.5 m ² clip plots per 18 m-radius plot	Standing aboveground biomass	Used to created allometric equations to estimate biomass Analyzed for C and N
	Eight 0.5 m ² clip plots per 18 m-radius plot	Litter	Used to created allometric equations to estimate biomass Analyzed for C and N
	100 m transect + 2 18m transects within each plot	CWD	Used to created allometric equations to estimate biomass
	Twelve 3cm diameter x 5 cm deep soil cores per plot	Fine root biomass	Used to created allometric equations to estimate biomass
	Twelve 3cm diameter x 5 cm deep soil cores per plot	Bulk density	Analyzed for C and N, extractible cations, and pH
	Eight 0.2 m ² litter traps	Aboveground litterfall	Collected monthly for 2 years Subsamples analyzed for C and N
	Eight soil collars in four plots	Soil-surface CO ₂ efflux	Measured quarterly
	Eight soil collars in four plots	Soil temperature	Measured quarterly
	Eight soil collars in four plots	Soil volumetric water content	Measured quarterly
	Resin strips	Annual N leaching	
	All plots	Leaf and soil sampled	Analyzed for foliar and bulk soil $\delta^{15}\text{N}$ Analyzed using ¹⁵ N pool dilution methods to measure rates of gross mineralization, nitrification, and immobilization
	Four 5 cm diameter soil cores	Soil	
	Four resin-bag incubations in each plot	Inorganic soil N availability	Measured availability of inorganic NO ₃ ⁻ and NH ₄ ⁺

	Three 9 ml gas samples	N ₂ O flux	Used same chambers for measurement of CO ₂ fluxes
	-	Soil physical and chemical properties	*Assessed prior to the initiation of this study (Long et al. 2017) TWF time zero plots
	Eight 0.2 m ² litter traps	Aboveground litterfall	Collected monthly for 2 years Subsamples analyzed for C and N
	Eight soil collars in four plots	Soil-surface CO ₂ efflux	TWF time zero plots Measured quarterly
	Eight soil collars in four plots	Soil temperature	TWF time zero plots Measured quarterly
Tropical wet forest	Eight soil collars in four plots	Soil volumetric water content	TWF time zero plots Measured quarterly Analyzed using ¹⁵ N pool dilution methods to measure rates of gross mineralization, nitrification, and immobilization
	Four 5 cm diameter soil cores	Soil	Measured availability of inorganic NO ₃ ⁻ and NH ₄ ⁺
	Four resin-bag incubations in each plot	Inorganic soil N availability	Used same chambers for measurement of CO ₂ fluxes
	Three 9 ml gas samples	N ₂ O flux	Collected after three months in the field
	Lysimeters in each site	Annual N leaching	Analyzed for foliar and bulk soil □ ¹⁵ N
	All plots	Leaf and soil sampled	

3.3.4 Statistical analysis

Ecological process data were analyzed using One-Way ANOVAs. All ANOVA's were followed by Tukey's HSD *post hoc* tests. Data were transformed or ranked when necessary to meet assumptions of normality and homogeneity of variances. Statistical analyses were conducted using SPSS version 24 (IBM Corporation) at $\alpha = 0.05$.

3.4 Soil nutrient manipulations

We used both a greenhouse experiment and a field experiment to test how soil nutrient availability affects survival, growth, and competitive responses of representative native and

nonnative wet and dry ecosystem plants. The results from the greenhouse experiment were used to inform the experimental design of the field study.

3.4.1 Greenhouse experiment

This study was conducted at the Institute of Pacific Islands Forestry (IPIF) greenhouse facility in Hilo, HI (19°41'55.6"N 155°05'43.5"W), located on the windward side of the Island of Hawai'i at 109 m asl. Two parallel experiments (i.e. identical experiments for wet and dry ecosystems) were run from June 2014 to June 2015 using primarily common woody native and nonnative species, from both wet and dry ecosystems in Hawai'i. *Dodonaea viscosa* Jacq., *Metrosideros polymorpha* Gaud., and *Sophora chrysophylla* (Salisb.) Seem. were utilized as the common native woody species for the dry ecosystem, and *Acacia koa* A. Gray and *M. polymorpha* as the common woody native species for the wet ecosystem. *Cenchrus setaceus* (Forssk.) Chiov., a grass and the only non-woody plant in the study, and *Psidium cattleianum* Sabine were utilized as the common nonnative, invasive species for the dry and wet ecosystems, respectively. Species were selected based on the availability of seedlings, capacity for propagation, and dominance in each ecosystem type. Native species used are dominant woody canopy species of the ecosystems in which they are found. The nonnative invasive species utilized (a shrub/tree and a grass) typically invade understories of native ecosystems in Hawai'i and elsewhere, but over time can become canopy dominant through alterations in competition, regeneration and disturbance regimes. All seedlings were sourced from local nurseries except *P. cattleianum* and *C. setaceus* (Knauf 2016). *P. cattleianum* seedlings were collected from local stands surrounding IPIF. Live clumps of *C. setaceus* were collected from Saddle Road between Hilo and Kona, and separated into small individuals of a similar size. Once collected, both of these species were planted in standard potting soil approximately five weeks prior to the start of the study to promote establishment in the greenhouse.

Two-gallon pots were planted at a constant density of two plants per pot, and each species was planted in separate pots with a conspecific and the common invasive species from that ecosystem type. Each species combination was replicated eight times across five nutrient treatments. In June 2014, all seedlings were directly transplanted into pots representing one of five soil nutrient availability treatments: nutrient reduction high, nutrient reduction low, control, nutrient addition low, and nutrient addition high. Nutrient reductions were implemented with the application of carbon amendments. Based on recommendations from prior studies (Burke et al. 2013), we used a combination of sucrose, which produces a rapid but short-term effect, and sawdust, which produces a slower but long-term effect. Target C:N ratios were determined from an initial soil C:N of 13.5 to represent high (C:N ~35) and low (C:N ~20) levels of N immobilizations, and target C:N values were used to determine the quantity of sucrose and sawdust added to each treatment. Nutrient addition treatments were implemented using Apex 16-6-12 NPK slow-release fertilizer, following the manufacturer's recommendations for low and high fertilizer applications. All soil nutrient availability treatments were mixed into the soil prior to planting to create a homogenous mixture throughout each pot. In addition to the four soil nutrient treatments, a control treatment was used with no manipulation of soil nutrients. The dry ecosystem experiment ran for 6 months, and the wet ecosystem experiment for 1 year.

In order to quantify initial plant size, we measured the initial height and basal diameter of all woody species. *C. setaceus* clumps were separated into individual plants of similar size and the fresh weight of each plant taken prior to planting. Initial plant measurements (height, basal diameter, and canopy cover) for all species except *C. setaceus* individuals were conducted at the

time of planting to see if differences existed at the start of the study despite random assignment to treatments. Plant mortality was quantified weekly throughout the experiment (Table 6). Additionally, reproductive output (i.e., flowers and/or fruits on each individual plant) was recorded bi-monthly. At the end of each respective experiment, all plants were destructively harvested to obtain final belowground, aboveground and total biomass by drying plant material to a constant mass in a forced-air oven at 60° C (Table 6).

3.4.1.1 Statistical analysis

Linear regression models were used to analyze biomass response variables across the soil nutrient treatments for all plants combined and for each species separately. For all regression models, the mean initial soil C:N for a given nutrient treatment was used as a continuous independent variable. All tests were performed on the mean of each response variable for each species in a given nutrient treatment. Reproductive output and mortality were analyzed using a binary logistic regression. Data that did not meet model assumptions of homogeneity of variance were log transformed. Pots with any mortality were not used for data analysis outside of survival. Minitab 17.2.1 (Minitab Inc., State College, PA, USA) was used for all statistical analyses, and significance was determined at $\alpha=0.05$.

3.4.2 Field Nutrient Manipulation Experiment

The field nutrient manipulation study was carried out from January 2016 to September 2017 in *Dodonaea* shrubland and tropical wet forest. The *Dodonaea* shrubland plant community is largely composed of the native shrubs *D. viscosa* and *Chenopodium oahuense* and the native C₄ grass *Eragrostis atropioides* (Poaceae). The region is also heavily invaded by both the nonnative C₄ grass *Cenchrus setaceus* (fountain grass) and the invasive forb *Senecio madagascariensis* (fireweed). The study sites were initially fenced in 2009 and nonnative ungulates including feral goats and sheep were completely removed by 2015, approximately one year prior to the initiation of the study.

The TWF was comprised of the same native ecosystems as the chronosequence plots (see above), and nonnative plant species that are common in invaded forests including the nonnative N-fixing canopy tree, *Myrica faya*, a mid-canopy shrub, *Psidium cattelianum*, and an understory forb., *Hedychium gardnerianum*. The wet forest study sites were located in the Kahaualea Natural Areas Reserve in a 25 ha feral pig enclosure. The area was fenced in 2015 and nonnative feral pigs removed approximately one year prior to the initiation of the study.

We established 5 blocks within each ecosystem type and applied nutrient manipulation and weeding treatments within each block. Each block contained six 8 x 8-m plots with a fully factorial set of three nutrient treatments (control- no nutrient manipulation; carbon-carbon substrate added; and fertilizer- fertilizer added) and two weeding treatments (weeds- nonnative plants present and no weeds- nonnative plants removed; Fig. 5). Blocks within ecosystem types were separated from each other by at least 15m.

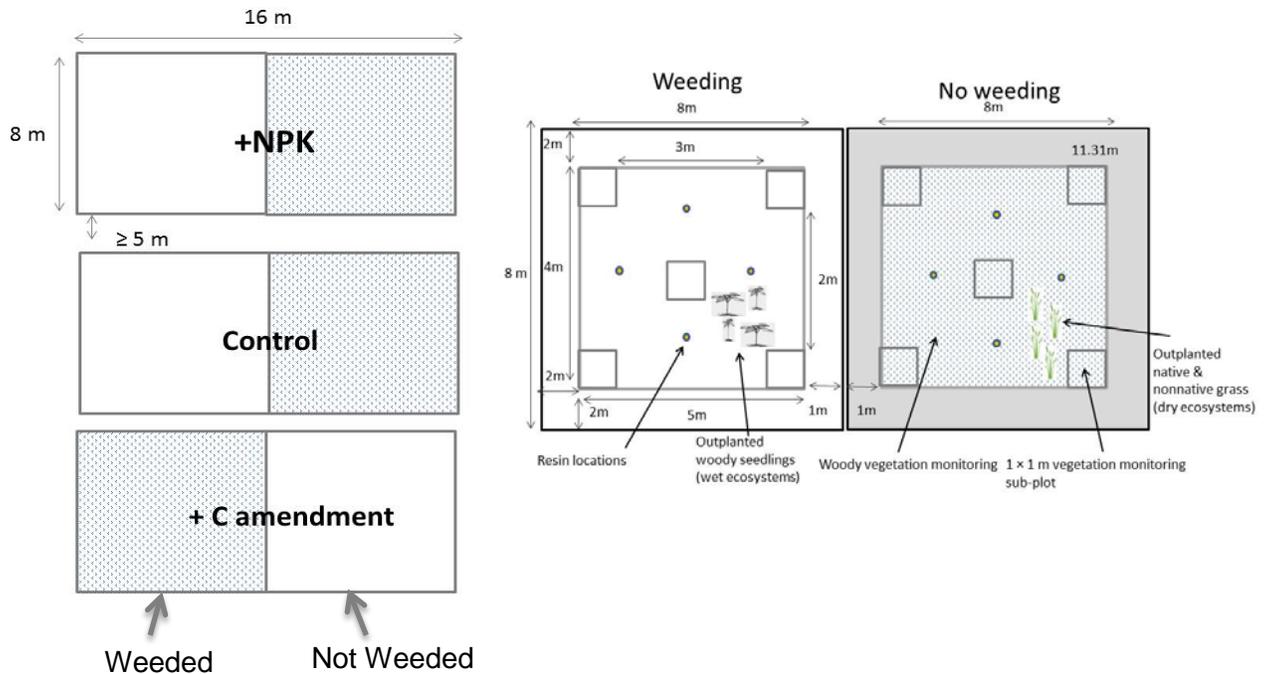


Fig. 5. One experimental block for the field nutrient manipulation experiment (left), which consisted on a weeded and not weeded plot for each soil nutrient manipulation. Within each ecosystem 5 blocks were established. Within each plot a series of vegetation and ecological processes measurements were taken (right).

Carbon amendments consisted of a combination of sucrose, which produces a rapid but short-term effect, and sawdust, which produces a slower but long-term effect on nutrient availability. At the initiation of the study in March 2016, we added 0.50 kg/m^2 sawdust and 0.25 kg/m^2 sucrose to all carbon plots in both ecosystems. The carbon addition treatment was repeated every 6 months in the same quantities as noted above of each type of substrate in October 2016 (sucrose only at both sites) and March 2017 (sucrose and sawdust to the wet forest sites and sucrose only at the *Dodonaea* shrubland sites). Sawdust was added only once at the *Dodonaea* shrubland sites as the first addition had not yet fully decomposed by the end of the first year. Apex 16-6-12 NPK slow-release fertilizer was applied to fertilizer plots in the amount recommended by the manufacturer (0.19 kg/m^2) on the same schedule as the carbon applications. Half of the plots (one carbon, control and fertilizer plot) were weeded (no weeds treatment) to remove all nonnative plants immediately prior to each of the nutrient manipulation applications. Half of the plots were not weeded (weeds treatment).

Rates of gross mineralization, nitrification, and immobilization were measured using ^{15}N pool dilution methods modified from Hart et al. (1994a; 1994b). On each sampling date, four 5 cm diameter cores were collected from 0 to 5 cm in the soil, composited, and transported back to the laboratory (Table 6). Composite soils were then split into three portions, NH_4^+ labeling, NO_3^- labeling, and a negative control (no N added, water only). Each was then labeled with an aqueous solution of 99% enriched ^{15}N , and solution volumes were adjusted to minimize changes to percent soil water content by 1 to 2%. The amount of N was adjusted based on the amount of NH_4^+ and NO_3^- in the soil. Immediately after homogenizing labeled soils, two replicate soil subsamples from each N treatment was extracted with 2M KCl (2:1 extractant: fresh soil ratio).

These represented initial (t_0) samples. The two additional subsamples were extracted 12 h later and represented final (t_f) samples. Gross fluxes were then calculated using equations presented in Hart et al. (1994a; 1994b).

Using similar methods to those used in the chronosequence study, availability of inorganic N ($\text{NO}_3^- \text{-N} + \text{NH}_4^+ \text{-N}$) in soils were indexed using ion-exchange resin bags (Table 6). Four resin-bag incubations were conducted at each study site and in each plot and repeated quarterly. Nylon mesh bags containing 10g of mixed bed cation-anion resin were placed at the litter layer-mineral soil interface. Resin bags were then incubated for 3 months. During the incubation, controls bags were stored both in the field (in sealed plastic bags) and in the laboratory (refrigerator controls). Bags were collected at the end of each incubation period, cleaned thoroughly with distilled water, and extracted with 100 mL of 2M KCl on a shaker table. Extracts were then analyzed calorimetrically with a Lachat QuickChem (Hach Co., Saskatoon, Canada) at the University of Hawaii – Hilo Analytical Laboratory.

To determine fluxes of N_2O from the soil, the same chambers used for the measurement of CO_2 fluxes were sealed and three 9 ml gas samples were sequentially taken through a septum port over a two-hour period and injected into previously evacuated gas-tight vials (Table 6). The vials were then transported back to the laboratory and analyzed for N_2O concentration on a gas chromatograph with an electron capture and flame ionization detector (Shimadzu Model 14A). Fluxes of N_2O were then calculated as the slope of the line describing the concentrations over time.

Similar to the chronosequence measurement, we monitored foliar and bulk soil $\delta^{15}\text{N}$ across all sites. Leaf and soil samples were collected from each plot, dried, and ground to a fine powder (Table 6). Samples were then transported to Cornell University, loaded into tin capsules and the isotopic composition determined using an isotope ratio mass spectrometer (Thermo Model Delta V) coupled to an elemental analyzer (Carlo Erba Model NC2500).

In order to test the effects of nutrient treatments on the growth of native and nonnative woody plants in TWF, we planted between 5-10 individuals of each of native *C. trigynum* and nonnative *P. cattelianum*. All seedlings were wildlings from the same age cohort and were collected from the area immediately surrounding the experimental sites. Initial seedling height and basal diameter were taken and each seedling was tagged and tracked for mortality and growth through the end of the study. After ~1.5 yrs, the planted seedlings were harvested including the roots, and dried and weighed to measure above- and below-ground biomass (Table 6).

In order to quantify changes in vegetation in the TDF, we established five 1×1m plots subplots in each 8×8 m plot. Cover of individual species was estimated in the subplots using a modified Braun-Blanquet cover-abundance scale (Table 6). To measure plant reproduction, we counted all inflorescences (herbs) and seed heads (grasses) by species. Measurements were repeated every 6 months through the end of the study. In the 8×8 m plot, all woody seedlings $\geq 10\text{cm}$ ht and $\leq 1\text{cm}$ DBH were identified to species, measured for basal diameter and height, tagged and tracked for survival and growth. All vegetation measurements were repeated every 6 months through the end of the study except for plant reproduction which was measured monthly (Table 6). We also planted grass seedlings of native *E. atropioides* and nonnative *C. setaceus* in the plots; however, seedlings had zero survival despite two planting efforts due to rodents digging up the seedlings and eating the roots in search of moisture.

3.4.2.1 Statistical analysis

All response variables were analyzed using either One-Way Randomized block ANOVA or Two-Way Randomized block ANOVA as appropriate. All ANOVA's were followed by Tukey's HSD *post hoc* tests. Data were transformed or ranked when necessary to meet assumptions of normality and homogeneity of variances. Statistical analyses were conducted using SPSS version 24 (IBM Corporation) at $\alpha = 0.05$.

Table 6. Nutrient manipulation experiment measurements taken in the greenhouse and field.

Experiment	Measurement Area	Measurement	Measurement specifications/notes
Greenhouse	All pots	Biomass	-
	All pots	Mortality	Checked weekly
	All pots	Reproduction	Checked bi-weekly for flowers and/or fruit on each plant
Field nutrient manipulation Tropical Dry Forest	Five 1×1m subplots in each 8×8 m plot	Cover	Measured every 6 months
	Five 1×1m subplots in each 8×8 m plot	Reproduction	Measured every 6 months Counted all inflorescences (herbs) and seed heads (grasses) by species
	All plots	Basal diameter	Woody seedlings ≥10cm ht and ≤1 cm DBH
	All plots	Height	Woody seedlings ≥10cm ht and ≤1 cm DBH
	All plots	Survival	Woody seedlings ≥10cm ht and ≤1 cm DBH
	Four 5 cm diameter soil cores	Soil	Analyzed using ¹⁵ N pool dilution methods to measure rates of gross mineralization, nitrification, and immobilization
	Three 9 ml gas samples	N ₂ O flux	Used same chambers for measurement of CO ₂ fluxes
	Four resin-bag incubations in each plot	Inorganic soil N availability	Measured availability of inorganic NO ₃ ⁻ and NH ₄ ⁺
	All plots	Leaf and soil sampled	Analyzed for foliar and bulk soil $\delta^{15}\text{N}$
	Field nutrient manipulation Tropical Wet Forest	All plots	Basal diameter
All plots		Height	Planted seedlings
All plots		Survival	Planted seedlings

All plots	Biomass	Planted seedlings
Four 5 cm diameter soil cores	Soil	Analyzed using ^{15}N pool dilution methods to measure rates of gross mineralization, nitrification, and immobilization
Three 9 ml gas samples	N_2O flux	Used same chambers for measurement of CO_2 fluxes
Four resin-bag incubations in each plot	Inorganic soil N availability	Measured availability of inorganic NO_3^- and NH_4^+
All plots	Leaf and soil sampled	Analyzed for foliar and bulk soil $\square^{15}\text{N}$

3.5 Decision Support Tool

Decision Support Tools (DST) are broadly defined as computer-based tools that incorporate: 1) a knowledge-base; 2) logic models representing the relationships and dependencies of the information within the knowledge-base in the context of the decision; and 3) a user interface that allows decision makers to manipulate criteria and/or desired outcomes, thereby assisting them in making informed judgments. The primary function of DST is to reduce the challenges inherent in processing large quantities of complex data to improve the quality of decision making, increase transparency and create reproducible decision processes while allowing flexibility from direct human interaction. Successful DSTs are developed and implemented when the stakeholders participate in the development process from the outset. In order to ensure the greatest likelihood of successful implementation of a DST for Pohakuloa Training Area (PTA), a facilitated user-driven process was stressed from the initial discussions.

The process for developing a DST for the PTA Natural Resource Office (NRO) was conducted through a series of facilitated meetings from March-November 2017. The first meeting introduced the DST concept and set the framework for developing the DST components, including the construction of a research question(s) to be answered by the DST, establishing the scope of study area and defining the study units. Subsequent meetings were held to develop the criteria needed to answer the research question, determine the availability of data layers to generate the knowledge-base and define the logic model. Meeting were facilitated by Heather Kimball and led by Lena Schnell PTA NRO Program Manager.

The PTA DST research question was based on the NRO's mandate to manage twenty threatened and endangered TER-S plant species, six of which are considered high priority for protection. Management methods include fencing, ungulate and rodent control, mechanical and chemical weed control and fire risk reduction. The goal of a DST developed for PTA, established by the PTA conservation staff as the stakeholders, was to determine priority areas to focus TER-S species management efforts as cost effectively as possible.

The process is ongoing with the key criteria defined and a draft logic model. The PTA conservation staff have produced or have access to most of the layers for the knowledge-base, though some need further processing before being incorporated into the logic model. With the

development of the remaining data layers, a preliminary DST decision score output layer can be produced for the PTA study area that can be used to determine priority areas for management.

4. Results

4.1 Vegetation Responses

The response of common native and nonnative invasive species to ungulate removal varied somewhat across ecosystems.

4.1.1 Tropical wet forest

Our results from the tropical wet forest, from both this study and earlier research (Cole et al. 2012, Cole and Litton 2014) show that species of conservation interest (TER-S) recover following ungulate removal, but they recover slowly and recovery is largely dependent on there being an existing population at the time of fencing and ungulate removal (Fig. 6a). Commonly occurring understory native woody plants recover quickly, within 6.5 years following removal of nonnative feral pigs (Fig. 6b) with no additional recovery over time.

Native and nonnative woody species rooted in mineral soil increased significantly following feral pig removal (Fig. 7, a,b). However, woody species growing epiphytically, both native and nonnative, do not increase following feral pig removal (Fig. 7, c,d). It is important to note that nonnative plant proliferation was only found to occur in TWF sites where a population had already established prior to fencing and ungulate removal.

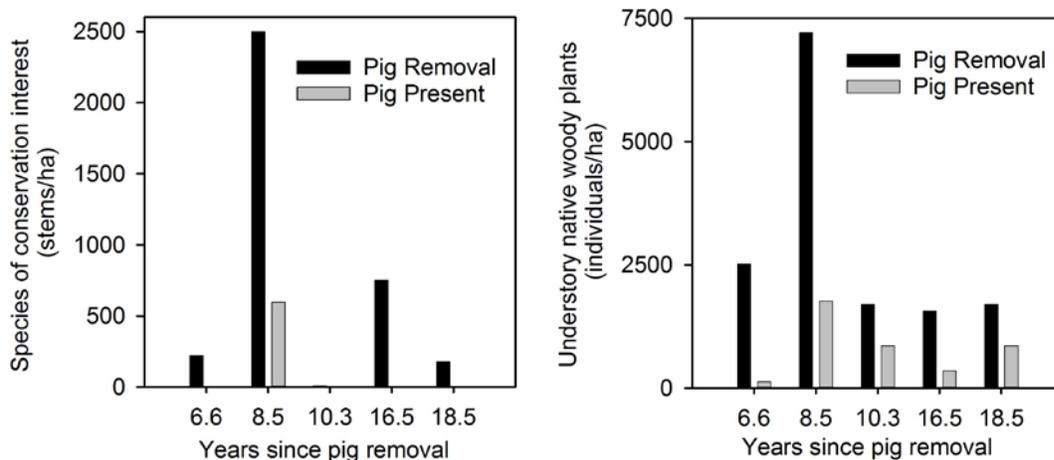


Fig. 6. Ungulate removal from tropical wet forest increased (a) plant species of conservation interest (TER-S), and (b) common understory native woody species (Cole & Litton, 2014).

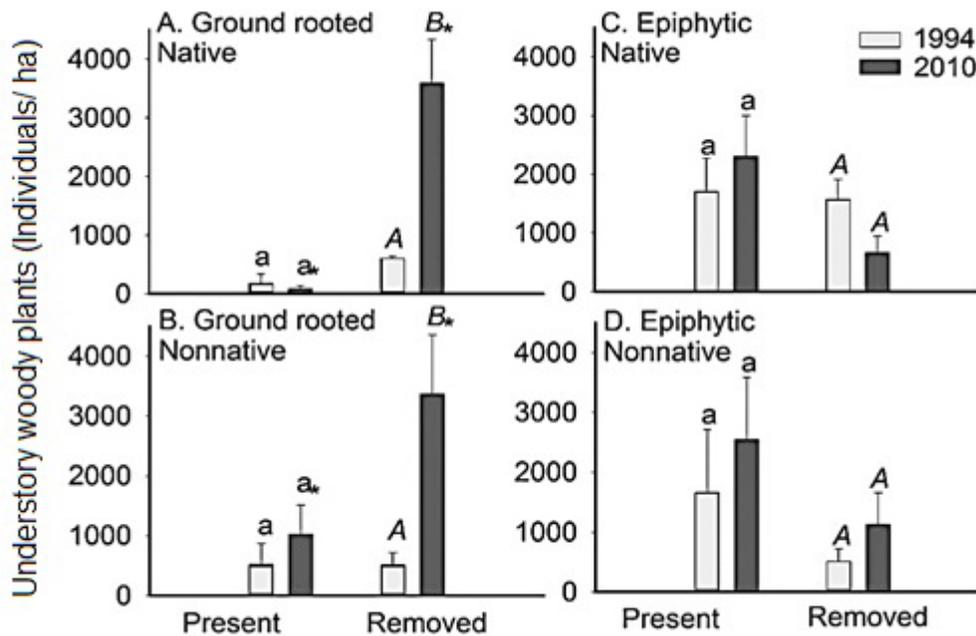


Fig. 7. Mean density of native and nonnative understory woody plants rooted in mineral soil (A-B; ground rooted) or on woody substrate (C-D; epiphytic) in ungulate removed and ungulate present treatments in 1994-2010. Different letters of the same case denote significant changes over time within a treatment. Asterisk indicate significance between treatments in a given year. (Cole et al 2012).

4.1.2 *Metrosideros* woodland

There were significant differences in nonnative herbaceous cover among survey years with cover being highest in the wetter 2014, largely due to cover of nonnative *Senecio madagascariensis* ($F = 68.8$, $p = 0.001$). There were no significant differences in nonnative herbaceous cover across ungulate removal plots of different ages ($F = 2.2$, $p = 0.091$) and there was no significant interaction between survey year and plot age ($F = 1.1$, $p = 0.354$) (Fig. 8a).

Similarly, native herbaceous cover varied significantly among survey years with cover being lowest in 2016, likely due to the drought conditions that year ($F = 19.2$, $p = 0.001$). There were no significant differences in native herbaceous cover across ungulate removal plots of different ages ($F = 0.6$, $p = 0.606$) and there was no significant interaction between survey year and plot age ($F = 1.2$, $P = 0.320$) (Fig. 8b).

Species of conservation interest (TER-S) varied significantly by both survey year ($F = 5.5$, $p = 0.007$) and ungulate removal plot age ($F = 26.3$, $p = 0.001$), and there was no significant interaction between survey year and time since ungulate removal ($F = 0.8$, $p = 0.569$). The number of individual plants increased with ungulate removal, and was lower in 2014 than in either of the subsequent surveys in 2016 and 2017, which were similar to each other. An increase in the density of individuals of conservation interest was significant and increased with time since ungulate removal (Fig. 8c). Basal area and the proportion of shrub cover did not differ with ungulate removal ($p > 0.05$ in all cases) (Fig. 9). Overall understory plant community composition did not differ among treatments (PERMANOVA: $F=1.1$, $P = 0.338$, data not shown).

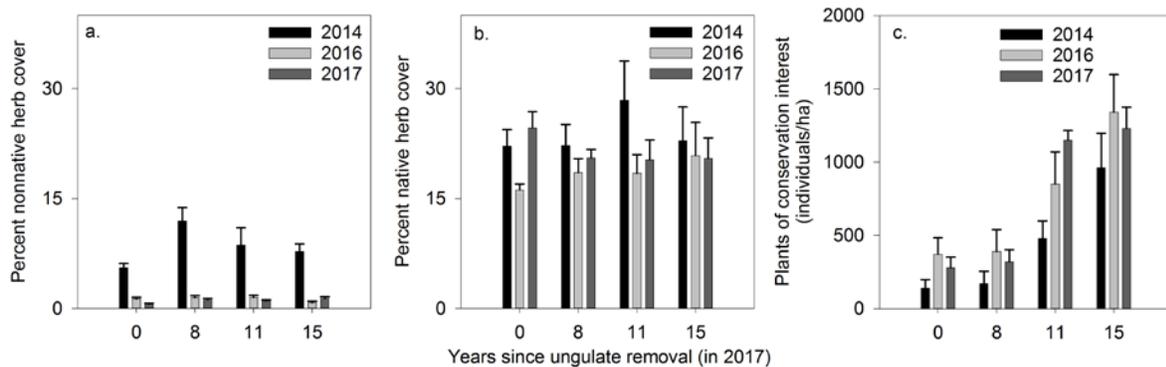


Fig. 8. Percent cover of nonnative herbs (a), percent cover of native herbs (b), and species of conservation interest (TER-S) (c) in different age ungulate present (i.e. time 0) and ungulate removal exclosures in surveys taken in 2014, 2016, and 2017 in *Metrosideros* woodland.

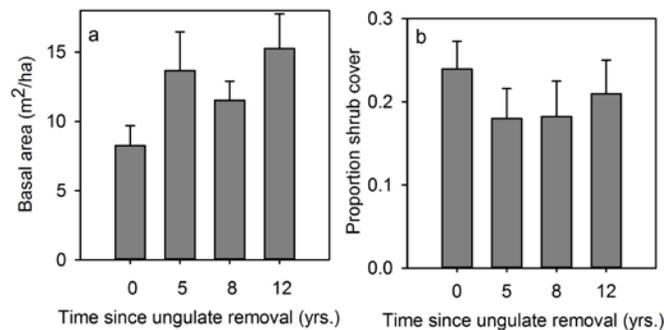


Fig. 9. Basal area and proportion of shrub cover across sites in *Metrosideros* woodland for ungulate present (i.e. time 0) and ungulate removal exclosures.

4.1.3 Dodonaea shrubland

There were differences in nonnative vegetation cover among survey years from 2014 to 2017 that likely corresponded to differences in precipitation across years ($F = 8.1$, $p = 0.001$). The percent nonnative herb cover was greatest in the wetter 2014, while cover was lowest in 2016 after a prolonged drought (Fig. 10a). There were no significant differences between ungulate removal plots of different ages ($F = 0.01$, $p = 0.953$), and there was no interaction between survey year and plot age.

Native vegetation varied by survey year ($F = 3.5$, $p = 0.0400$) but not by ungulate removal plot age ($F = 0.2$, $p = 0.833$). The percent of native vegetation cover was greater in 2017 compared to in 2014 in both the 2-year-old and 11-year-old ungulate removal sites (Fig. 10b). There was no interaction between survey year and plot age.

Species of conservation interest (TER-S) did not vary significantly among the three survey years ($F = 0.73$, $p = 0.487$). There was, however, a significant difference between sites of different ages with significantly greater numbers of TER-S in the older compared to the younger plot ($F = 9.1$, $p = 0.005$) (Fig. 10c). There was no interaction between survey year and plot age.

We found no significant differences in shrub stem density across plot ages ($p > 0.05$ in all cases; Fig. 11).

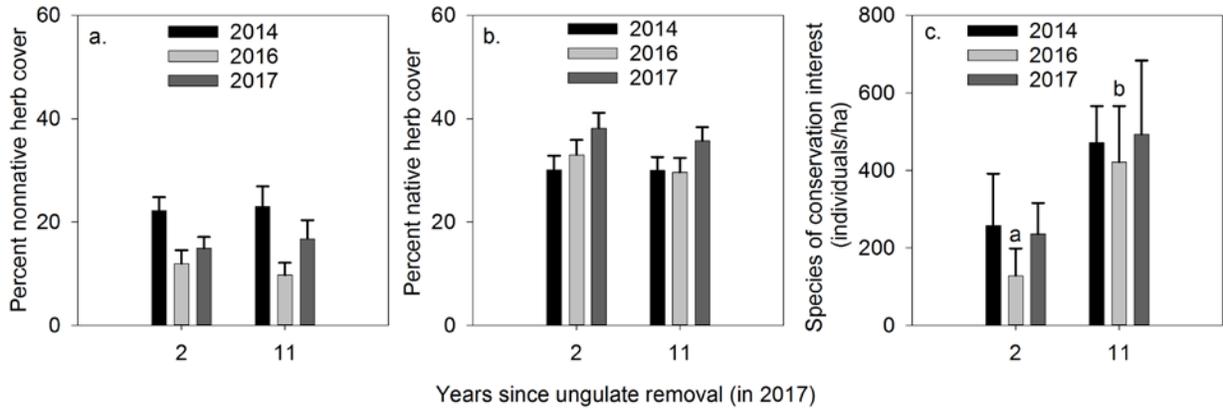


Fig. 10. Percent cover of nonnative herbs (a), percent cover of native herbs (b), and species of conservation interest (TER-S) (c) in different age ungulate removal exclosures in surveys taken in 2014, 2016, and 2017 in *Dodonaea* shrubland. Different letters denote significant differences in measurements within a given survey year.

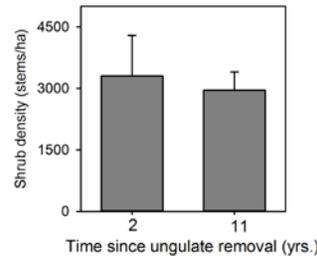


Fig. 11. Shrub stem density in *Dodonaea* shrubland across different age ungulate removal exclosures.

4.1.4 Eragrostis grassland

Nonnative herb cover varied across survey years ($F = 29.3$, $p = 0.001$) but not between ungulate-present and the 32-yr-old ungulate removal site ($F = 2.4$, $p = 0.134$). There was no significant interaction between survey year and ungulate removal treatment ($F = 2.6$, $p = 0.2$). Nonnative herb cover did vary among the three survey years however, with percent cover being highest in 2015 at the end of two years of high precipitation and lowest in 2016 during a prolonged drought (Fig. 12a).

Native herb cover did not vary significantly across survey years ($F = 0.7$, $p = 0.935$) but responded strongly and positively to ungulate removal ($F = 11.6$, $p = 0.002$). Nonnative herb cover was significantly greater in the 32-yr-old ungulate removal site compared to the ungulate-present site. There was no significant interaction between survey year and ungulate removal treatment ($F = 0.7$, $p = 0.499$) (Fig. 12b).

The number of individual plants of species of conservation concern (TER-S), were strikingly higher in the ungulate-removed site ($F = 3.7$, $p = 0.040$). There was no significant difference among survey years due to extremely high variability among survey plots (Fig. 12c).

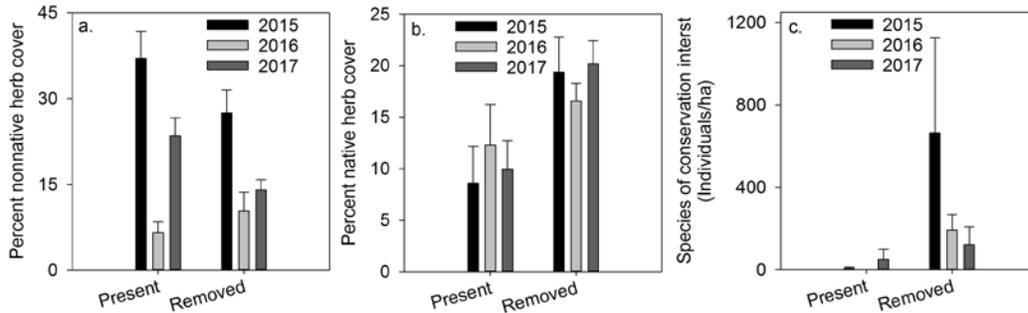


Fig. 12. Percent cover of nonnative herbs (a), percent cover of native herbs (b), and species of conservation interest (TER-S) (c) in a 32-yr-old ungulate removal site (age in 2017) and adjacent ungulate-present site in surveys taken in 2015, 2016, and 2017 in *Eragrostis* grassland.

4.2 Ecological Processes Responses

4.2.1 Tropical wet forest

4.2.1.1 Soil Physical Properties

In the chronosequence plots, feral pig removal decreased bulk density ($W = 14$, $P = 0.05$, $n = 5$; Fig. 12a, Table X), VWC ($W = 14$, $P = 0.05$, $n = 5$; Fig. 13b, Table X), and water-filled pore space ($W = 14$, $P = 0.05$, $n = 5$; Figure 13c, Table 7), while increasing soil porosity ($W = 14$, $P = 0.05$, $n = 5$; Fig. 13d, Table 7) Feral pig removal had no impact on: WSA ($W = 6$, $P = 0.39$, $n = 5$; Fig. 13e, Table 7).

In the targeted plots, feral pig removal reduced: VWC ($W = 138.5$, $P < 0.01$, $n = 10$; Fig. 13b) and water-filled pore space ($W = 143.0$, $P < 0.01$, $n = 10$; Fig. 13c, Table 7). Feral pig removal increased: WSA (52.3 ± 4.5 and 70.0 ± 3.2 %, respectively; $W = 69.0$, $P < 0.01$, $n = 10$; Fig. 13e). Feral pig removal had no impact on: bulk density ($W = 122.0$, $P = 0.11$, $n = 10$) and porosity ($W = 88.0$, $P = 0.11$, $n = 10$) (Fig. 13a,d, Table 7).

Table 7. Mean of various soil physical property variables in pig present and pig removal sites for chronosequence and targeted plots. For variables where there is no mean, feral pig removal had no impact.

Variable	Chronosequence Plots		Targeted Plots	
	Pig present	Pig removal	Pig present	Pig removal
Bulk density (g cm^{-3})	0.32 ± 0.06	0.23 ± 0.03	-	-
VWC (%)	66.6 ± 2.2	58.6 ± 5.0	79.0 ± 4.0	62.6 ± 2.5
Water-filled pore space (%)	76.4 ± 1.3	71.5 ± 3.0	79.0 ± 4.0	62.6 ± 2.5
Soil porosity (%)	88.0 ± 2.3	91.3 ± 0.9	-	-
WSA (%)	-	-	52.3 ± 4.5	70.0 ± 3.2

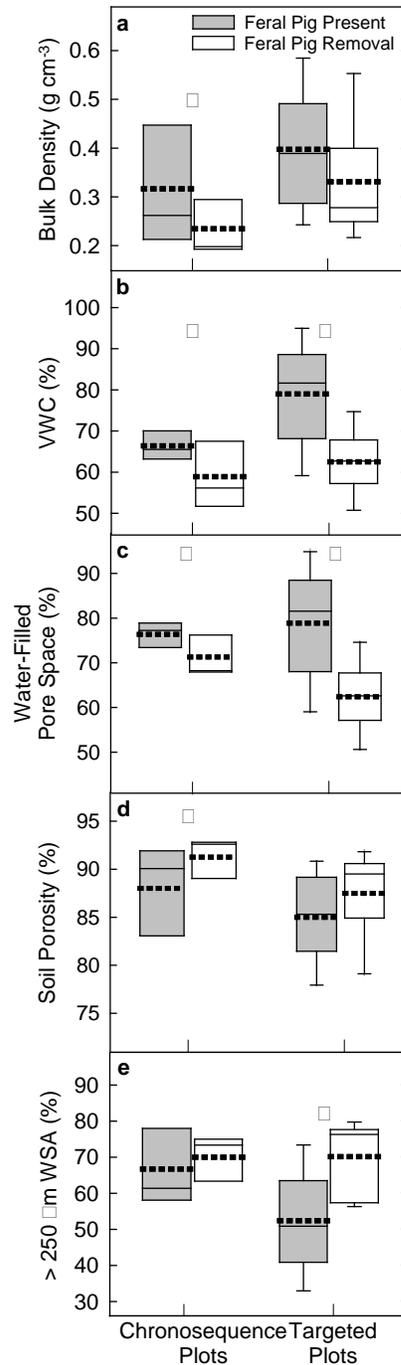


Fig. 13. Decreases in (a) bulk density in the chronosequence plots, and (b) volumetric water content, and (c) water-filled pore space in both the chronosequence and targeted plots following feral pig removal. Increases in (d) soil porosity in the chronosequence plots and (e) percent water stable soil macro-aggregates (WSA) in the targeted plots. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

4.2.1.2 Ecosystem Carbon Pools and Fluxes

No significant differences in C pools were found in paired feral pig present versus feral pig removal sites, including total ecosystem C, with the exception of 18.5 years of removal (Table 8, Supplemental Fig. 1). After 18.5 years of pig removal, aboveground tree fern C ($P < 0.01$, $t = 9.4$, $df = 3$), total aboveground C ($P = 0.04$, $t = 2.5$, $df = 7$), and litter C ($P < 0.01$, $t = 7.7$, $df = 3$) were larger than in the paired pig present sites. The majority of ecosystem C across the chronosequence in both pig removal and pig present sites was in detrital pools (Table 8). Soil carbon made up the largest portion of detrital pools (76% to 84%), followed by down CWD (13-20%), with litter and standing CWD comprising a small proportion (1-3% and $< 0.5\%$, respectively). Above- and belowground vegetation C only accounted for 2-3% and $< 0.5\%$ of total ecosystem C, respectively.

Table 8. Carbon content of above- and belowground live vegetation and detritus pools in paired pig present versus pig free plots across the wet forest chronosequence. Letters denote significant differences among the paired plots.

Pool	0 yr removal	6.6 yr removal	0 yr removal	8.5 yr removal	0 yr removal	10.3	0 yr removal	16.5 yr removal	0 yr removal	18.5 yr removal
Aboveground vegetation C										
Woody	7.5 (0.5)	7.1 (0.4)	13.3 (2.7)	11.7 (2.9)	7.5 (0.5)	7.6 (0.9)	5.2 (0.7)	8.1 (0.6)	8.9 (0.9)	6.7 (3.4)
Tree ferns	507.5 (6.6)	564.2 (13.2)	360.1 (5.6)	441.8 (6.8)	507.5 (6.6)	567.9 (10.7)	329.6 (9.3)	420.3 (12.4)	349.8 ^a (10.1)	575.1 ^b (8.7)
Total aboveground	515.0 (95.)	571.3 (112.7)	373.4 (59.6)	453.5 (68.8)	515.0 (95.0)	575.5 (109.2)	334.7 (64.4)	428.4 (85.7)	358.7 ^a (68.6)	581.9 ^b (108.8)
Belowground vegetation C										
Woody	1.5 (0.1)	1.5 (0.1)	2.7 (0.6)	2.4 (0.6)	1.5 (0.1)	1.6 (0.2)	1.1 (0.7)	1.7 (0.1)	1.8 (0.2)	1.4 (0.3)
Tree ferns	49.9 (2.1)	55.5 (8.6)	35.4 (1.5)	43.5 (2.3)	49.9 (2.1)	55.9 (5.7)	32.4 (4.2)	41.4 (7.6)	34.4 (5.0)	56.6 (3.7)
Total belowground	51.5 (9.2)	57.0 (11.0)	38.2 (5.6)	45.9 (6.6)	51.5 (9.2)	57.4 (10.6)	33.5 (6.2)	43.0 (8.3)	36.2 (6.6)	58.0 (10.7)
Detritus										
Down coarse woody debris	2183.0 (317.0)	2730.4 (150.4)	2388.2 (107.9)	2474.7 (317.8)	2183.0 (317.0)	2859.3 (261.9)	2442.3 (170.3)	2017.2 (170.3)	2130.6 (491.7)	3314.0 (222.1)
Litter layer	406.4 (53.2)	456.0 (31.8)	336.0 (42.6)	324.9 (39.9)	406.4 (53.2)	340.7 (34.4)	335.1 (29.6)	428.4 (27.3)	248.0 ^a (31.1)	538.0 ^b (28.6)
Standing coarse woody debris	0.4 (0.2)	0.8 (0.4)	0.4 (0.1)	0.9 (0.5)	0.4 (0.2)	0.1 (0.1)	0.2 (0.2)	0.1 (0.0)	0.2 (0.1)	0.8 (0.6)
Soil C	13785.8 (465.2)	12984.5 (529.4)	11172.9 (614.2)	11254.8 (761.4)	13785.8 (465.2)	11853.2 (393.2)	10939.0 (436.8)	10450.9 (468.8)	11666.4 (325.6)	12433.7 (517.2)
Total detritus	16375.6 (1465.7)	16171.6 (1500.6)	13897.4 (1258.9)	14055.3 (1194.1)	16375.6 (1465.7)	15053.3 (1302.3)	13716.6 (1208.1)	12896.6 (1100.3)	14045.1 (1241.2)	16286.4 (1450.5)
Total ecosystem C										
	16942.1 (804.0)	16799.9 (802.0)	14309.0 (604.5)	14554.8 (594.5)	16942.1 (712.6)	15686.2 (804.0)	14084.8 (660.1)	13368.0 (609.3)	14440.0 (683.4)	16926.2 (796.1)

Note: All pools are plot means and expressed in g C/m², and numbers in parentheses are 1 SE.

Across all study sites, feral pig removal increased annual soil CO₂ efflux (F_S) by 18%, from 1251.2 ± 89.6 to 1481.3 ± 78.5 g C m⁻² yr⁻¹ ($W = 14, P = 0.03; n = 5$) (Fig. 14b, Table 9). Feral pig removal increased annual total belowground carbon flux (TBCF) by 25%, from 916.3 ± 112.5 to 1143.4 ± 77.0 g C m⁻² yr⁻¹ ($W = 14, P = 0.05; n = 5$) (Fig. 14c, Table 9). Annual litterfall (F_L) ranged did not differ across all study sites ($W = 10, P = 0.30; n = 5$) (Fig. 14b, Table 9).

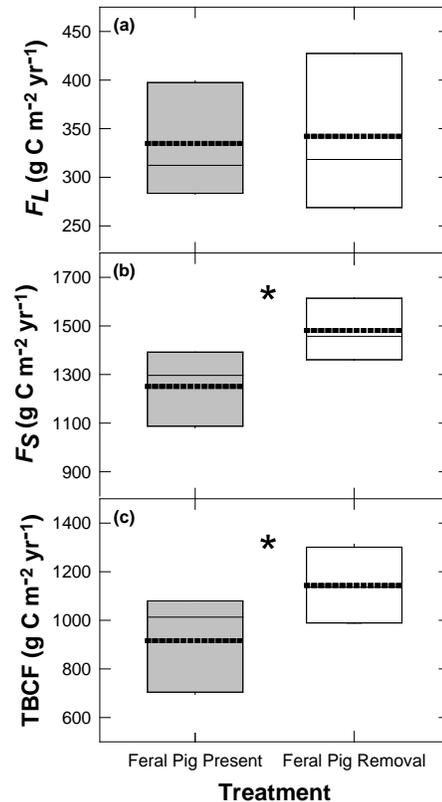


Fig. 14. Across the chronosequence of feral pig exclosures, feral pig removal did not impact (a) F_L , but significantly increased (b) F_S and (c) TBCF. Box plot whiskers are absent due to small sample size; dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

Table 9. Range of annual soil CO₂ efflux, TBCF, and litterfall in pig present and pig removal sites. Feral pig removal increased annual soil CO₂ efflux and TBCF significantly. Annual litterfall did not differ between pig present and removal sites.

Variable	Pig present range	Pig removal range
Soil CO ₂ efflux (g C m ⁻² yr ⁻¹)	906.9 ± 97.0 to 1392.3 ± 119.3	1274.3 ± 50.7 to 1761.1 ± 293.6
TBCF(g C m ⁻² yr ⁻¹)	480.2 ± 106.7 to 1374.9 ± 77.8	988.6 ± 79.4 to 1404.5 ± 300.4
Litterfall (g C m ⁻² yr ⁻¹)	254.7 ± 22.7 to 426.7 ± 24.0	253.3 ± 15.2 to 482.5 ± 65.3

The relative difference in F_S between paired treatments showed a significant positive linear relationship with time since feral pig removal ($F_{(1,3)} = 26.04$, $R^2 = 0.90$, $P = 0.02$; $n = 5$), increasing from a relative difference of 4% in the youngest enclosure (6.5 years since feral pig removal) to 62% in the oldest enclosure (18.5 years since feral pig removal) (Fig. 15d). TBCF also showed a significant positive linear relationship with time since feral pig removal ($F_{(1,3)} = 18.87$, $R^2 = 0.86$, $P = 0.02$, $n = 5$), increasing from 5% in the youngest enclosure to 106% in the oldest enclosure (Fig. 15f). There were no significant linear relationships between increasing time since feral pig removal and F_L ($F_{(1,3)} = 0.22$, $R^2 = 0.07$, $P = 0.67$, $n = 5$; Fig. 15e).

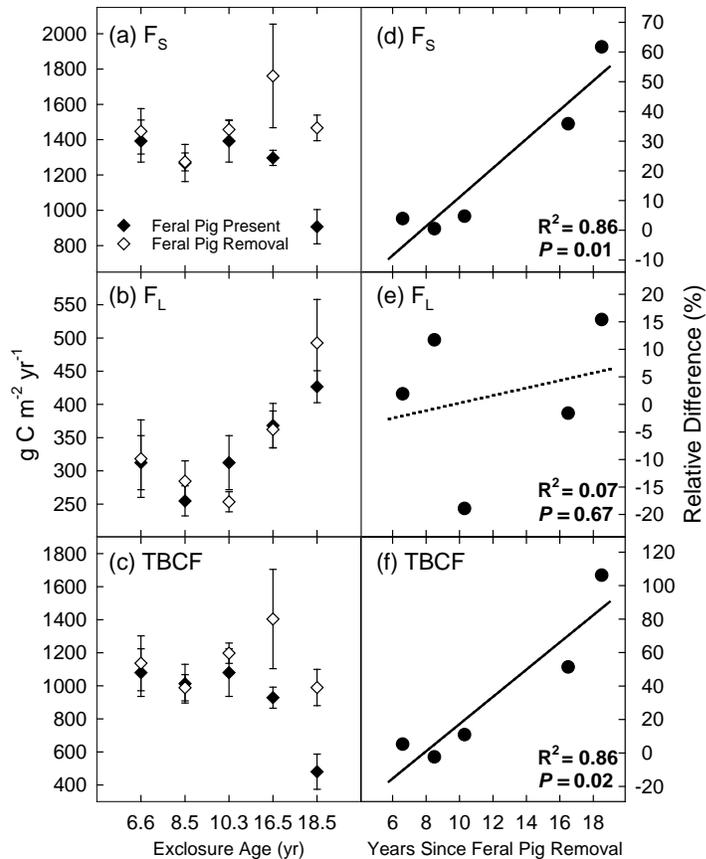


Fig. 15. Mean annual (a) F_S , (b) F_L , and (c) TBCF ($\text{g C m}^{-2} \text{ yr}^{-1}$) for paired sites across the chronosequence of five exclosures. Filled diamonds indicate values for feral pig present sites and open diamonds indicate values for feral pig removal sites. Error bars indicate SE. The relative difference (%) in (d) F_S and (f) TBCF had significant positive linear relationships with increasing time since feral pig removal ($\alpha = 0.10$). (e) F_L had no relationship with increasing time since feral pig removal. Relative difference is calculated as the % difference between means of paired sites: $[(\text{Feral Pig Removal} - \text{Feral Pig Present}) / \text{Feral Pig Present}] * 100$

4.2.1.3 Nutrient Cycling and Availability

In the chronosequence plots, feral pig removal increased extractable K, Ca, and Mg ($W = 15$, $P = 0.03$, $n = 5$; Fig. 16a-c, Table 10). Feral pig removal had no impact on: resin available NH_4^+ ($W = 4$, $P = 0.21$, $n = 5$), NO_3^- ($W = 6$, $P = 0.4$, $n = 5$), and total inorganic N ($W = 5$, $P = 0.30$, $n = 5$) (Fig. 17a-c, Table 10).

In the targeted plots, feral pig removal reduced extractable P ($W = 132.0$, $P = 0.05$, $n = 10$; Fig. 16d, Table 10). Feral pig removal reduced resin available NH_4^+ ($W = 88.0$, $P < 0.01$, $n = 10$) and increased resin available NO_3^- ($W = 380$, $P < 0.01$, $n = 10$) and total inorganic N ($W = 43.0$, $P = 0.03$, $n = 10$) (Fig. 17a-c, Table 10). Feral pig removal had no impact on: extractable K ($W = 103.0$, $P = 0.91$, $n = 10$), Ca ($W = 107.0$, $P = 0.91$, $n = 10$), and Mg ($W = 108.0$, $P = 0.85$, $n = 10$) (Fig. 16a-c).

Table 10. Mean of extractable K, CA, MP, P and resin available NH_4^+ , NO_3^- , and total inorganic N in pig present and pig removal sites for chronosequence and targeted plots. For variables where there is no mean, feral pig removal had no impact.

Nutrient	Chronosequence Plots		Targeted Plots	
	Pig present	Pig removal	Pig present	Pig removal
K ($\mu\text{g cm}^{-3}$)	135.8 \pm 27.1	206.6 \pm 28.6	-	-
Ca ($\mu\text{g cm}^{-3}$)	1729.1 \pm 92.7	2063.1 \pm 124.2	-	-
Mg ($\mu\text{g cm}^{-3}$)	350.4 \pm 13.8	435.5 \pm 19.7	-	-
P ($\mu\text{g cm}^{-3}$)	37.0 \pm 9.3	16.5 \pm 1.7	37.0 \pm 9.3	16.5 \pm 1.7
NH_4^+ ($\mu\text{g 10cm}^{-2}$ 4wk $^{-1}$)	-	-	5.0 \pm 1.2	0.9 \pm 0.2
NO_3^- ($\mu\text{g 10cm}^{-2}$ 4wk $^{-1}$)	-	-	9.3 \pm 3.1	100.1 \pm 43.4
Total inorganic N ($\mu\text{g 10cm}^{-2}$ 4wk $^{-1}$)	-	-	14.3 \pm 2.8	101.1 \pm 43.4

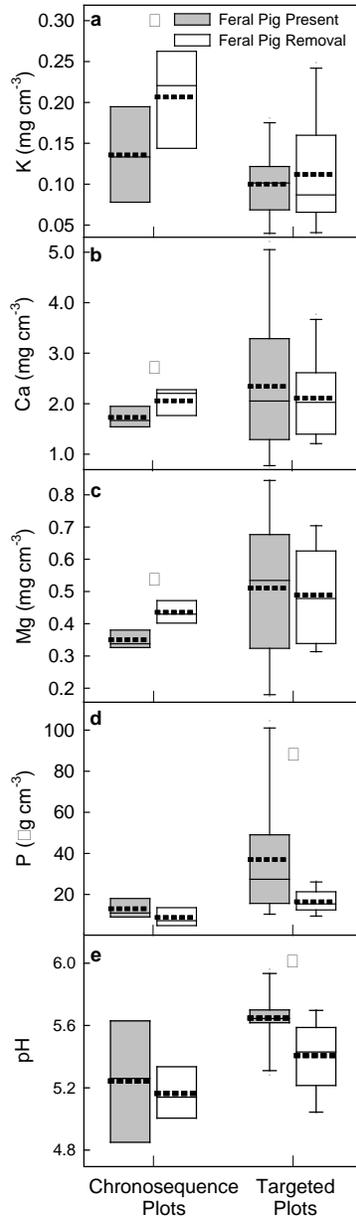


Fig. 16. Extractable (a) K, (b) Ca, and (c) Mg increased in the chronosequence plots, while (d) extractable P and (e) soil pH decreased in the targeted plots following feral pig removal. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

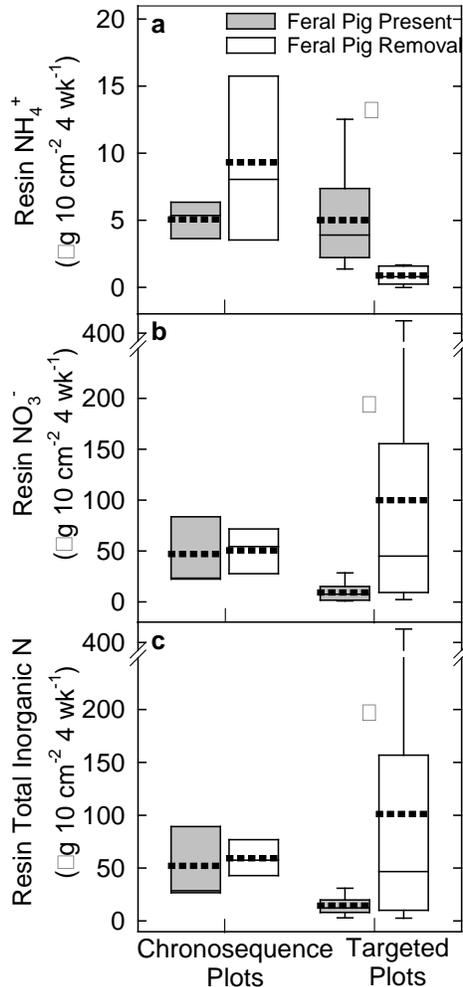


Fig. 17. Feral pig removal resulted in a significant decrease in (a) resin available NH_4^+ and significant increases in (b) resin available NO_3^- and (c) total resin available inorganic N in targeted plots. Whiskers indicate 10% and 90% values for the targeted plots (no whiskers are presented for chronosequence plots due to small sample size); dotted lines indicate mean and solid lines indicate median values; asterisks indicate significant differences ($\alpha = 0.10$)

Nutrient availability along the wet forest chronosequence was relatively constant, with no trend through time in control, treatment or the difference between the two ($r^2 < 0.01$, $p > 0.7$). However, pairwise comparisons at two and fifteen showed higher total available nitrogen in pig-present areas ($t=2.05$, $p < 0.01$ and $t=2.05$, $p < 0.01$, respectively) (Fig. 18).

Nitrogen losses across the wet forest chronosequence through leaching were consistent both along the wet forest chronosequence ($r^2 < 0.01$, $p > 0.8$) (Fig. 19) and between pig present and pig removed plots within a given point in the chronosequence. Rates of leaching were between 3-10 $\text{Kg N ha}^{-1} \text{ yr}^{-1}$ and highly variable among plots. Similarly, nitrogen losses through gaseous emission of N_2O ranged between 0.1 and 0.6 $\text{Kg N ha}^{-1} \text{ yr}^{-1}$ with no detectable trends with time or between pig present and pig removed sites (Fig. 20).

Across all wet-forest chronosequence plots, no strong patterns in gross mineralization or gross nitrification were observed (Fig. 21). There were no trends over time ($r^2 = 0.04$, $p = 0.3$)

and of the six paired chronosequence positions, two showed differences between pig present and pig removed plots with higher rates of mineralization in the pig removed plots; n year 15 of the chronosequence ($t=2.447$, $p=0.008$) and year 23 of the chronosequence ($t=5.23$, $p=0.0004$) (Fig. 21a). Similar to gross mineralization, gross nitrification showed no trends over time ($r^2=0.075$, $p=0.24$) and only one difference between pig present and pig removed plots. In the paired plots at two years after animal removal, gross nitrification was higher in the pig present plot ($t=2.776$, $p=0.05$) (Fig. 21b).

The two species of plant phytometers sampled across the wet forest chronosequence (*Broussaisia argute* and *Cibotium glaucum*) showed trends in both foliar nitrogen content and foliar nitrogen isotope ratio. *B. argute* exhibited both increasing foliar nitrogen content ($r^2=0.131$, $p<0.01$) and increasing foliar nitrogen isotope ratio ($r^2=0.078$, $p<0.01$) with time since feral animal removal (Fig. 22). *C. glaucum* showed a similar increasing trend in foliar isotope ratio ($r^2=0.0501$, $p=0.06$), but the reverse trend in foliar nitrogen content ($r^2=0.1249$, $p<0.01$) (Fig. 23).

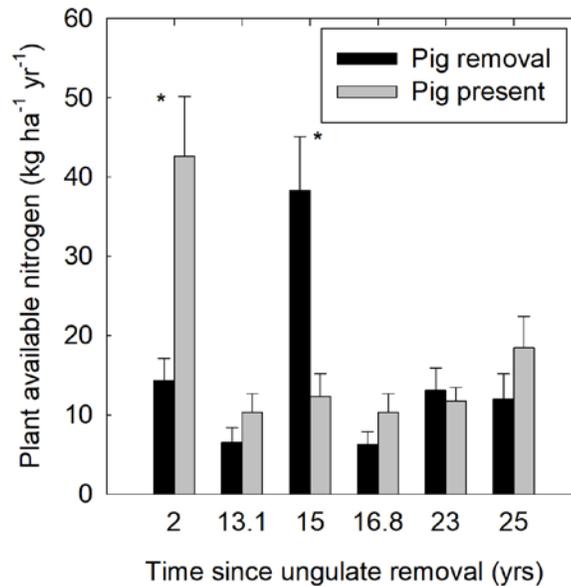


Fig. 18. Total available nitrogen in paired feral pig present and feral pig removed sites over the wet forest chronosequence. Asterisks indicate differences within a given pair.

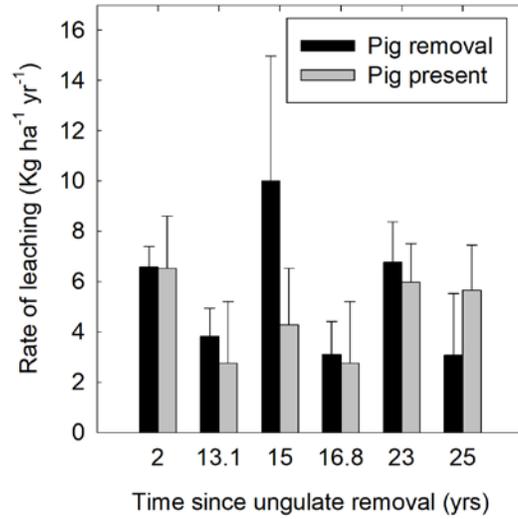


Fig. 19. Total leaching rates across the wet forest chronosequence. Rates varied between 3-10 Kg N ha⁻¹ yr⁻¹ and were variable among plots.

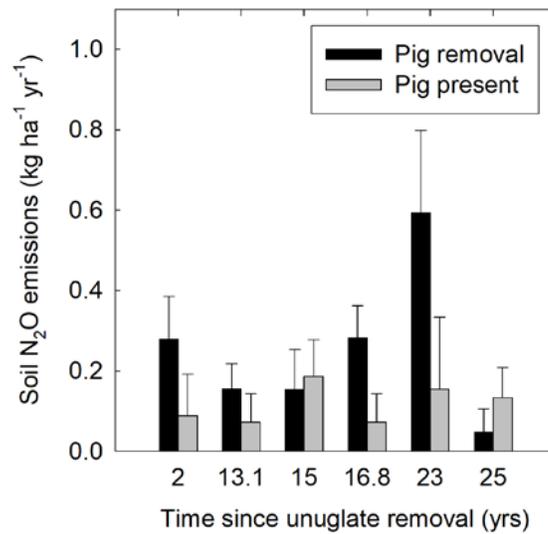


Fig. 20. Rates of nitrous oxide soil emission from all plots along the wet forest chronosequence. Emission rates ranged between 0.1 and 0.6 Kg N ha⁻¹ yr⁻¹, but did not predictably vary through time or between pig present and pig removed plots.

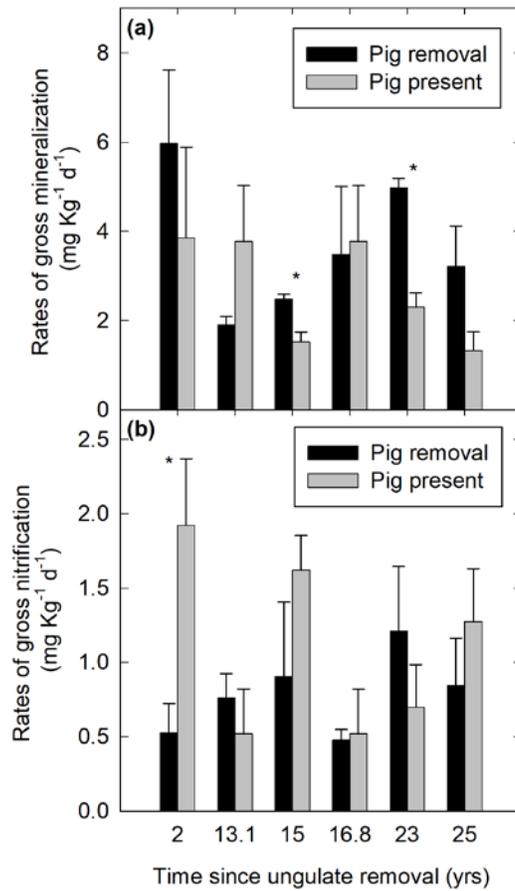


Fig. 21. Rates of a) gross mineralization and b) gross nitrification across all wet forest chronosequence sites.

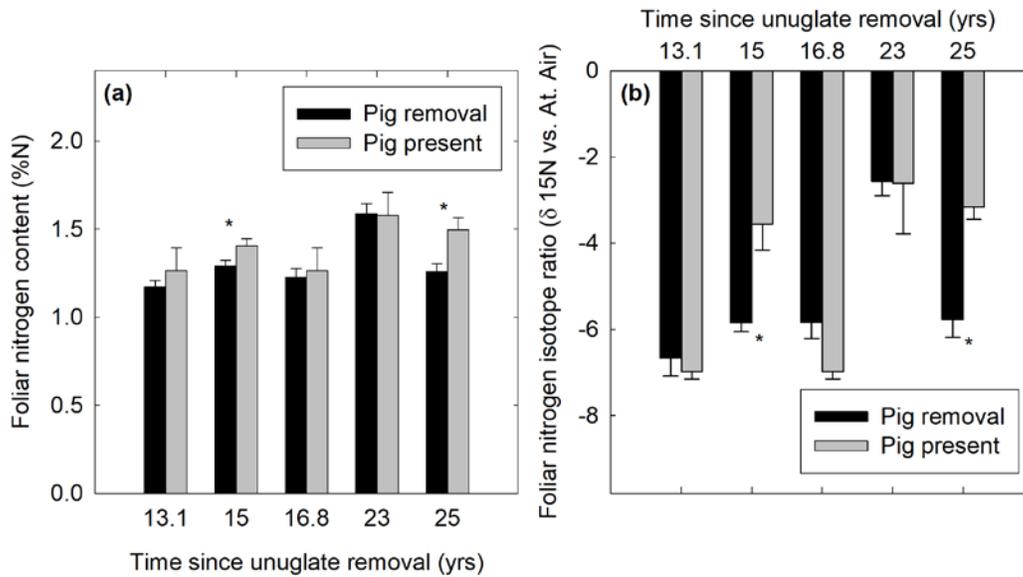


Fig. 22. Foliar nitrogen content and nitrogen isotope ratio in *Broussaisia argute* sampled from all plots within the wet-forest chronosequence.

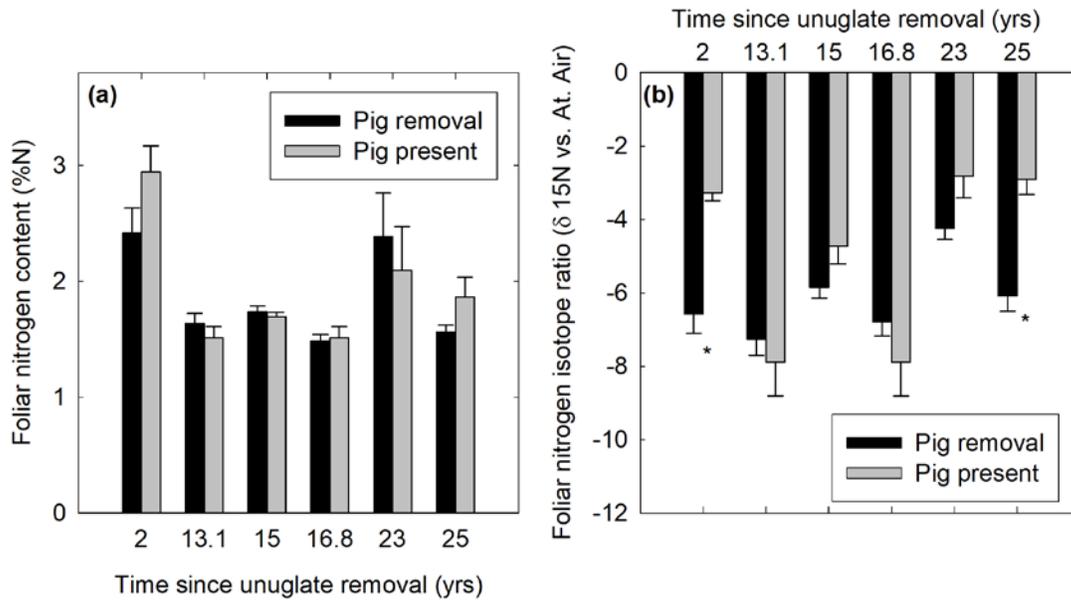


Fig. 23. Foliar nitrogen content and nitrogen isotope ratio in *Cibotium glaucum* sampled from all plots within the wet-forest chronosequence.

4.2.2 *Metrosideros* woodland.

4.2.2.1 Soil Physical Properties

In the chronosequence plots, feral ungulate removal had no impact on bulk density ($P=0.10$, $f=2.40$, $df=4$; Fig. 24).

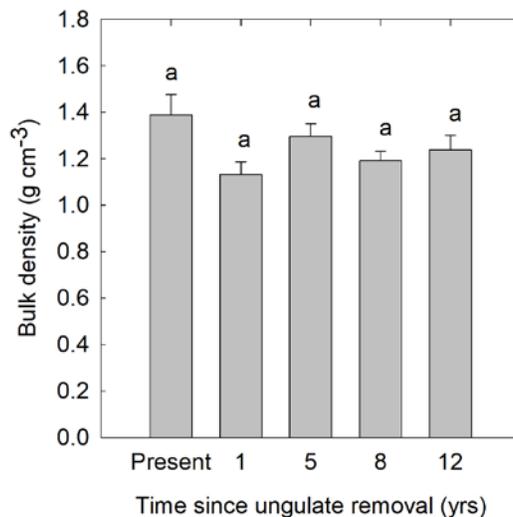


Fig. 24. Across the ungulate exclosure chronosequence in the *Metrosideros* woodland, ungulate removal did not impact bulk density. Different letters denote significant differences ($\alpha = 0.05$).

4.2.2.2 Ecosystem Carbon Pools and Fluxes

Species specific allometric equations were created for three common species found in both the *Metrosideros* woodland and *Dodonaea* shrubland using basal diameter measurements from the field to estimate leaf, wood, dead and total biomass (Table 11). A linear regression approach was used for *Dodonaea viscosa* and *Chenopodium oahuense*, as these models had the best fit for each species ($r^2=0.71-0.90$ and $r^2=0.61-0.92$, respectively; Supplemental Fig. 2 & 3). For *Styphelia tameiameia* a nonlinear quadratic approach was the best fit with $r^2=0.60-0.89$ (Supplemental Fig. 4). Models estimating dead wood generally had lower r^2 's, except for *C. oahuense*, whose model estimating foliage biomass has a slightly lower r^2 (Supplemental Fig. 5).

Table 11. Species specific allometric equations for species common in *Metrosideros* woodland and *Dodonaea* shrubland.

Species & Biomass Component	Equation	r^2
<i>D. viscosa</i>		
Live wood biomass	$\log(y)=1.198+2.215*\log(x)$	0.83
Dead wood biomass	$\log(y)=2.677*\log(x)$	0.71
Foliage biomass	$\log(y)=1.158+1.573*\log(x)$	0.74
Total Biomass	$\log(y)=1.510+2.142*\log(x)$	0.90
<i>C. oahuense</i>		
Live wood biomass	$\log(y)=1.456+2.167*\log(x)$	0.96
Dead wood biomass	$\log(y)=3.911*\log(x)$	0.65
Foliage biomass	$\log(y)=0.987+1.522*\log(x)$	0.61
Total Biomass	$\log(y)=1.618+2.322*\log(x)$	0.92
<i>S. tameiameia</i>		
Live wood biomass	$y=99.664+(-59.110*x)+(21.825*x^2)$	0.72
Dead wood biomass	$y=9.313+(-4.697*x)+(7.533*x^2)$	0.60
Foliage biomass	$y=-28.671+(27.881*x)+(2.119*x^2)$	0.72
Total Biomass	$y=142.858+(-94.223*x)+(38.571*x^2)$	0.89

Across the chronosequence, significant differences in carbon pools were only found in litter C ($P<0.01$, $f=8.7$, $df=4$) and total detritus C ($P=0.03$, $f=2.8$, $df=4$), with both increasing with ungulate removal (Table 12, Supplemental Fig. 6). Further, both litter C and detrital C were highest after ungulates had been removed for 12 years. Detrital C accounted for the majority of *Metrosideros* woodland ecosystem carbon (33% to 63%). Standing and down coarse debris C was the largest component of the detritus pool (26% to 51%), followed by litter C (24-38%). Above- and belowground vegetation C comprised (26% to 48%) and (10% to 18%), respectively. For both above- and belowground vegetation C, C from woody species made up the majority of the C pool.

Table 12. Carbon content of above- and belowground live vegetation and detritus pools across the *Metrosideros* woodland chronosequence. Letters denote significant differences among the paired plots.

Pool	Control	0 yr removal	5 yr removal	8 yr removal	12 yr removal
Aboveground vegetation C					
Woody	147.4 (39.1)	120.8 (35.7)	76.7 (7.6)	90.6 (21.8)	120.8 (21.7)
Herbaceous	2.3 (1.4)	4.9 (1.1)	6.8 (2.4)	6.6 (2.2)	9.7 (2.7)
Total aboveground	149.7 (0.7)	125.7 (0.9)	83.5 (1.5)	97.2(0.9)	130.6 (1.8)
Belowground vegetation C					
Woody	47.5 (12.6)	38.9 (11.5)	24.7 (2.4)	29.2 (7.0)	38.9 (7.0)
Herbaceous	10.3 (1.5)	9.4 (2.1)	18.6 (3.8)	9.9 (1.2)	11.4 (2.2)
Total belowground	57.7 (1.9)	48.3 (2.0)	43.3 (3.6)	39.1(1.7)	50.3 (2.1)
Detritus					
Litter layer	25.7 ^a (9.3)	46.1 ^a (7.7)	67.2 ^{ab} (11.5)	38.5 ^a (7.6)	99.0 ^b (11.8)
Standing & down coarse debris	51 (10.7)	26.3 (7.6)	75.0 (26.3)	74.8 (19.1)	163.3 (81.8)
Soil C	24.5 (1.3)	25 (2.0)	24.8 (2.1)	22.9 (2.8)	24.2 (1.2)
Total detritus	102.9 ^a (4.4)	97.4 ^{ab} (4.5)	174.0 ^{ab} (7.5)	148.8 ^{ab} (4.7)	315.4 ^b (21.2)
Total ecosystem C	310.4 (3.0)	271.4 (3.5)	300.8 (4.9)	285.1 (3.8)	496.2 (11.9)

Note: All pools are plot means and expressed in g C/m², and numbers in parentheses are 1 SE.

Across all study sites, ungulate removal did not impact annual F_L , F_s , or TBCF ($P > 0.05$; Fig. 25 – 28). Soil temperature and soil CO₂ efflux (F_s) averaged across five measurement times did not vary with time since ungulate removal ($P > 0.05$; Fig. 26). VWC was significantly higher 5 years following ungulate removal compared to ungulate present and 0 year ungulate removal sites ($P < 0.01$ $f=5.4$, $df=4$; Fig. 26). When soil temperature, VWC, and F_s were separated into wet and dry periods, all variables were higher under wet conditions ($P < 0.01$; Fig. 27), and no differences were found over time with ungulate removal for soil temperature or F_s ($P > 0.05$). VWC, in contrast, was highest after 5 years of ungulate removal in both the wet and dry periods ($P=0.03$, $f=3.7$, $df=4$ and $P < 0.01$, $f=7.0$, $df=4$, respectively), but remained fairly constant across the rest of the chronosequence.

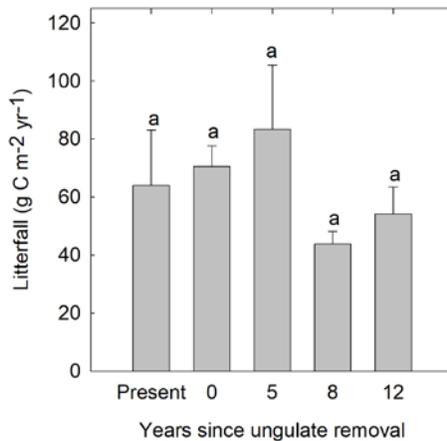


Fig. 25. Across the ungulate exclusion chronosequence in the *Metrosideros* woodland, ungulate removal did not impact litter. Letters denote significant differences ($\alpha = 0.05$).

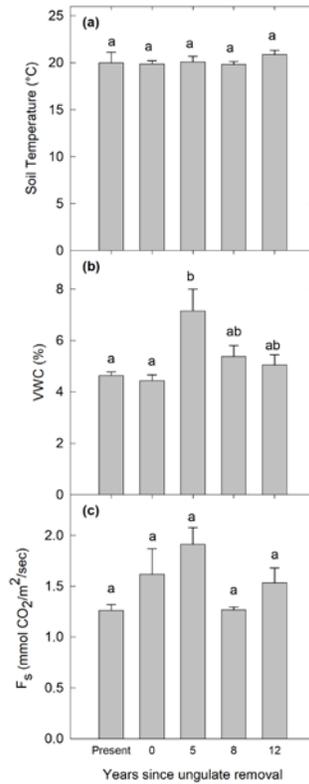


Fig. 26. Across the chronosequence of ungulate exclosures, in the *Metrosideros* woodland, feral ungulate removal did not impact (a) soil temperature and (c) F_s, but did significantly increase (b) VWC after 5 years of ungulate removal when compared to ungulate present and 0 year removal, when averaged over time. Letters denote significant differences ($\alpha = 0.05$).

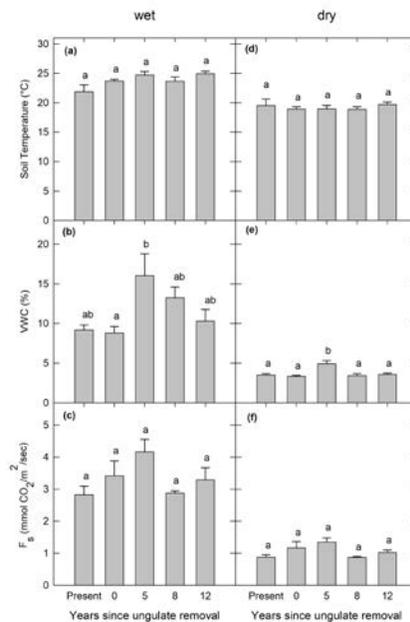


Fig. 27. Soil temperature, VWC, and F_s separated into wet (a-c) and dry (d-f) periods, in the *Metrosideros* woodland. All variables were significantly higher under wet conditions and no

differences were found over time with ungulate removal for (a & d) soil temperature and (c & f) F_s . After 5 years of ungulate removal, in both wet and dry periods, (b & e) VWC was highest. Letters denote significant differences ($\alpha = 0.05$).

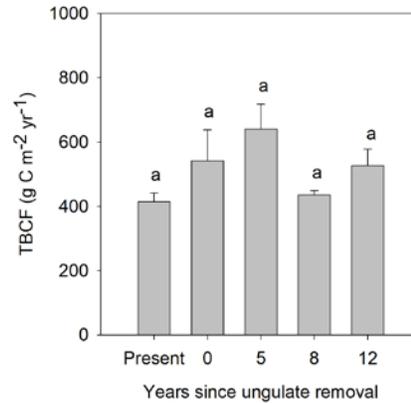


Fig. 28. Feral ungulate removal did not impact TBCF across the chronosequence, in the *Metrosideros* woodland. Letters denote significant differences ($\alpha = 0.05$).

4.2.2.3 Nutrient Cycling and Availability

Along the *Metrosideros* woodland chronosequence, there was no impact of the removal of feral ungulates on nitrogen availability ($r^2=0.006$ $p=0.52$) (Fig. 29). Available nitrogen ranged between 6 and 8 Kg N ha⁻¹ yr⁻¹ depending upon plot.

Nitrogen losses through leaching increased with time since feral ungulate removal ($r^2 = 0.260$, $p=0.02$) (Fig. 30). In contrast, gaseous losses as N₂O from soils decreased along this same chronosequence. However, this decrease was only apparent post irrigation ($r^2 = 0.215$, $p<0.001$) and not under dry soil conditions ($r^2 = 0.0069$, $p=0.5$) (Fig. 31).

Neither rates of gross mineralization ($r^2=0.0066$ $p=0.73$) or rates of gross nitrification ($r^2=0.1085$ $p=0.20$) changed with time since removal of feral ungulates (Fig. 32).

The phytometer plant (*Styphelia tasmaeiae*) sampled in all plots in the the *Metrosideros* woodland chronosequence showed an increase in foliar nitrogen ($r^2 = 0.097$, $p=0.01$) over time since removal of feral ungulates (Fig. 33). However, there was no observed relationship in foliar nitrogen isotope ratio ($r^2 = 0.0464$, $p=0.09$; Fig. 33).

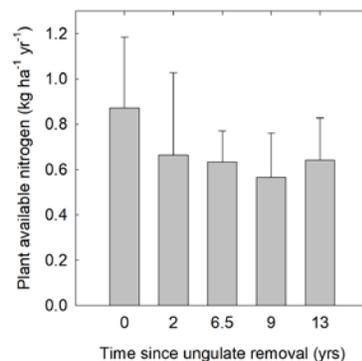


Fig. 29. Total nitrogen availability measured at all plots along the *Metrosideros* woodland chronosequence.

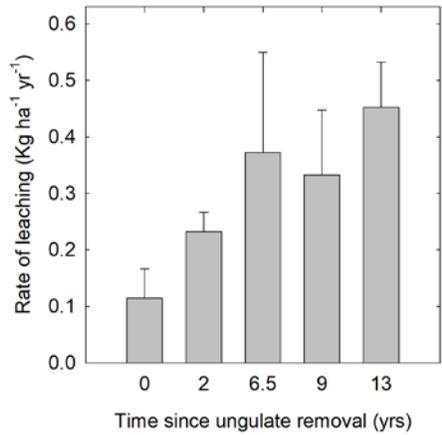


Fig. 30. Nitrogen losses due to leaching measured over time since feral ungulate removal. With time since ungulate removal there was a significant increase of leachate N.

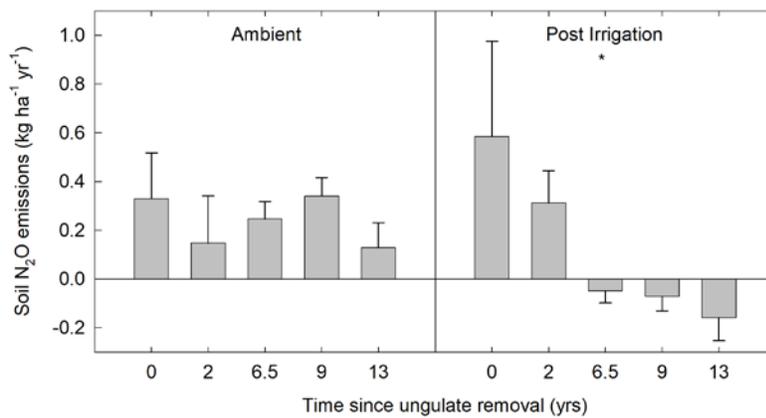


Fig. 31. Nitrogen losses due to emission of gaseous N₂O under a) ambient soil moisture, and b) twenty-four hours after a simulated rain event. Under post irrigation conditions loss of gaseous N₂O decreased with time since ungulate removal.

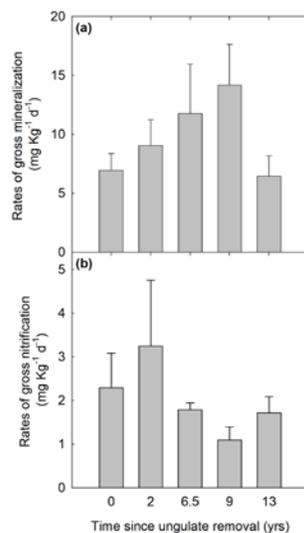


Fig. 32. Rates of a) gross mineralization and b) gross nitrification in all plots making up the *Metrosideros* woodland chronosequence.

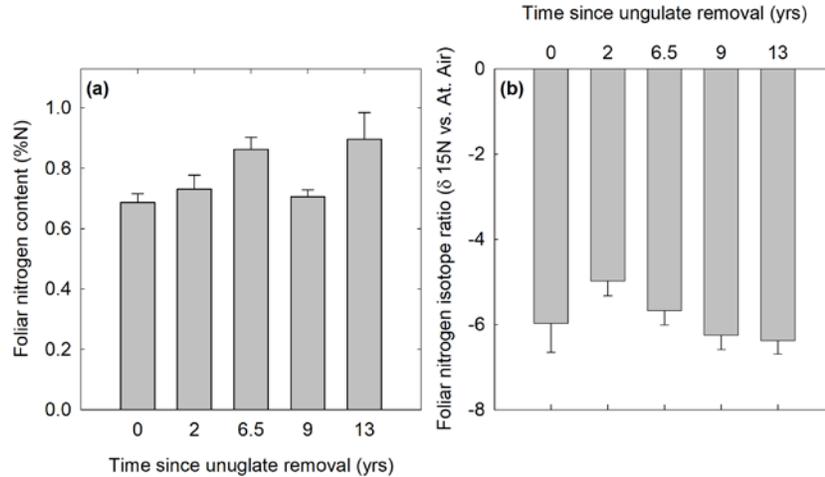


Fig. 33. Foliar a) nitrogen content, and b) foliar nitrogen isotope ratio in the phytometer plant (*Stypelia tamaeiae*) sampled in all plots along the *Metrosideros* woodland chronosequence.

4.2.3 Dodonaea shrubland

4.2.3.1 Soil Physical Properties

In the chronosequence plots, feral ungulate removal had no impact on bulk density ($P=0.45$, $t=-0.80$, $df=6$; Fig. 34)

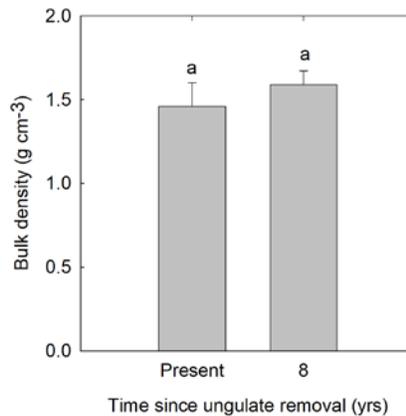


Fig. 34. Across the ungulate exclosure chronosequence, in the *Dodonaea* shrubland, ungulate removal did not impact bulk density. Letters denote significant differences ($\alpha = 0.05$).

4.2.3.2 Ecosystem Carbon Pools and Fluxes

Differences in carbon pools across the chronosequence were only found in belowground herbaceous vegetation C ($P<0.01$, $t=4.0$, $df=6$), which was larger with ungulates present (Table 13; Supplemental Fig. 7). The majority of *Dodonaea* shrubland ecosystem C across the chronosequence was in detritus C (52% to 59%). Litter C made up the largest portion of detrital pools (83%-89%), with standing and down coarse debris and soil C accounting for a smaller

proportion (9% to 15% and 4%-5%, respectively). Aboveground vegetation made up more of total ecosystem carbon (31-39%) than belowground vegetation (7%-8%).

Table 13. Carbon content of above- and belowground live vegetation and detritus pools across the *Dodonaea* shrubland chronosequence. Letters denote significant differences among the paired plots.

Pool	0 yr removal	8 yr removal
Aboveground vegetation C		
Woody	18.5 (4.7)	27.6 (5.2)
Herbaceous	132.2 (16.3)	131.0 (12.6)
Total aboveground	150.7 (18.3)	158.6 (16.6)
Belowground vegetation C		
Woody	19.7 (5.0)	29.3 (5.5)
Herbaceous	13.8 ^a (0.9)	6.6 ^b (1.5)
Total belowground	33.5 (3.3)	35.9 (4.9)
Detritus		
Litter layer	180.7 (46.8)	250.1 (36.4)
Standing & down coarse debris	19.5 (7.2)	46.6 (21.5)
Soil C	11.9 (2.5)	13.9 (0.9)
Total detritus	201.8 (2.4)	299.5 (7.5)
Total ecosystem C	384.1 (6.0)	501.3 (6.5)

Note: All pools are plot means and expressed in g C/m², and numbers in parentheses are 1 SE.

Across all study sites, ungulate removal did not impact annual F_L , F_s , or TBCF ($P > 0.05$; Fig. 35 – 38). Soil temperature, VWC, and soil CO_2 efflux (F_s) averaged across seven measurement times did not vary with time since ungulate removal ($P > 0.05$; Fig. 36). When soil temperature, VWC, and F_s were separated into wet and dry periods, all variable except soil temperature were higher under wet conditions ($P < 0.01$; Fig. 37), and no differences were found over time with ungulate removal for soil temperature or VWC ($P > 0.05$). F_s , in the wet data, was higher with ungulates present ($P = 0.002$, $t = -4.4$, $df = 3$), however, in the dry data no differences in F_s were present over years since ungulate removal.

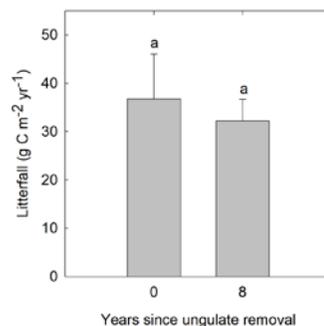


Fig. 35. Across the ungulate exclosure chronosequence, in the *Dodonaea* shrubland, ungulate removal did not impact litter. Letters denote significant differences ($\alpha = 0.05$).

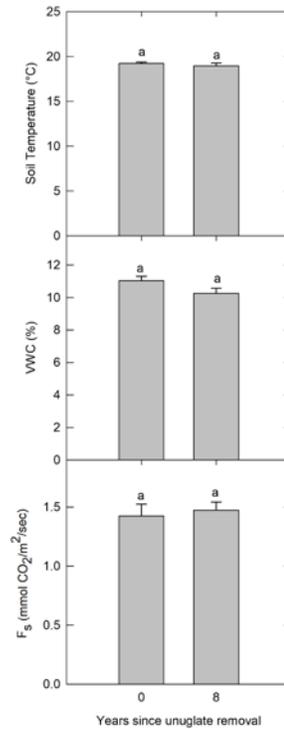


Fig. 36. Across the chronosequence of unguilate exclosures, in the *Dodonaea* shrubland, feral unguilate removal did not impact (a) soil temperature, (b) VWC and (c) F_s when averaged over time. Letters denote significant differences ($\alpha = 0.05$).

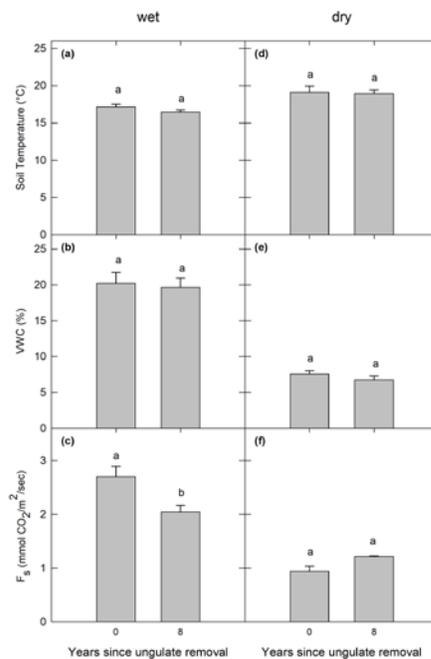


Fig. 37. Soil temperature, VWC, and F_s separated into wet (a-c) and dry (d-f) periods, in the *Dodonaea* shrubland. All variables were significantly higher under wet conditions and no differences were found over time with unguilate removal for (a & d) soil temperature, (b & e) VWC and (c & f) F_s, except (c) F_s in the wet period where F_s was higher with unguilates present.

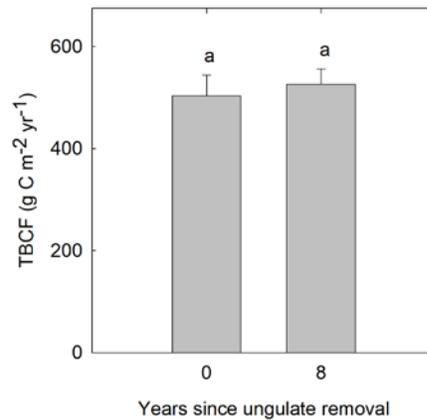


Fig. 38. Feral ungulate removal did not impact TBCF across the chronosequence, in the *Dodonaea* shrubland. Letters denote significant differences ($\alpha = 0.05$).

4.2.3.3 Nutrient Cycling and Availability

Along the *Dodonaea* shrubland chronosequence, there was no trend in nitrogen availability with time since removal of feral ungulates ($t=2.04$, $p=0.11$; Fig. 39). Losses of nitrogen along the chronosequence due to leaching did not change with removal of feral ungulates ($t=2.571$, $p=0.10$; Fig. 40). However, gaseous losses of soil emissions of N_2O increased after the removal of feral ungulates under both ambient ($t=2.060$, $p<0.001$; Fig. 40a) and irrigated ($t=2.060$, $p=0.02$; Fig. 41b) conditions.

Across the chronosequence, rates of gross mineralization did not change after the removal of feral ungulates ($t=2.45$, $p=0.32$; Fig. 42a). However, rates of gross nitrification decreased with time after the removal of feral ungulates ($t=2.571$, $p=0.03$; Fig. 42b).

The phytometer plant (*Dodonaea viscosa*) sampled in all plots in the *Dodonaea* shrubland chronosequence showed no change in foliar nitrogen ($t=2.047$, $p=0.36$; Fig. 43a) over time since removal of feral ungulates. However, there was a decrease in foliar nitrogen isotope ratio ($t=2.074$, $p<0.0001$; Fig. 43b).

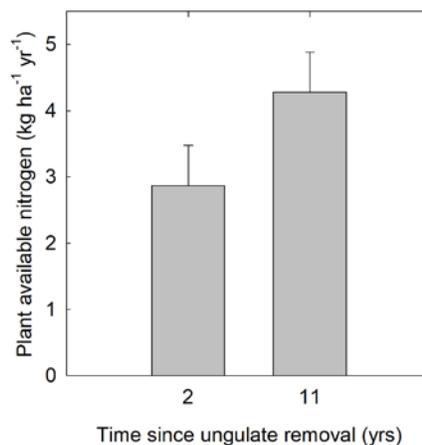


Fig. 39. Plant available nitrogen along the *Dodonaea* shrubland chronosequence.

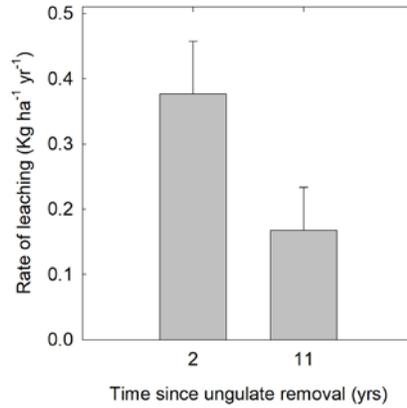


Fig. 40. Losses of nitrogen through leaching two and eleven years after the removal of feral ungulates.

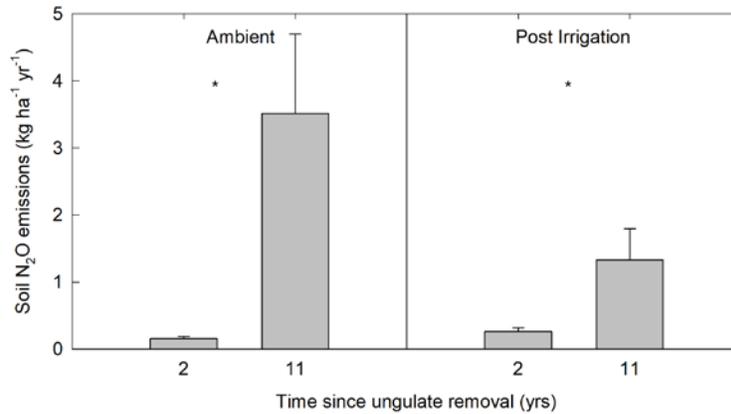


Fig. 41. Nitrogen losses from soil emissions of N₂O two and eleven years after the removal of feral ungulates. Emissions were measured under both a) ambient soil moisture, and b) after an artificial rain event.

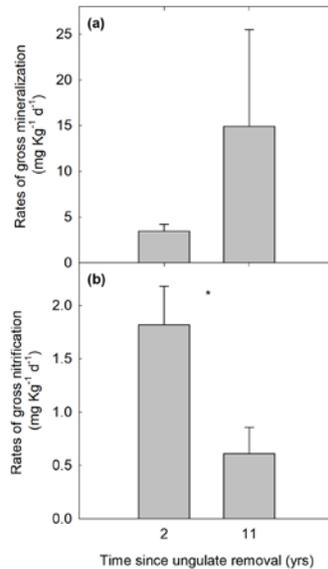


Fig. 42. Rates of a) gross mineralization of nitrogen and b) gross rates of nitrification sampled in all plots in the *Dodonaea* shrubland chronosequence.

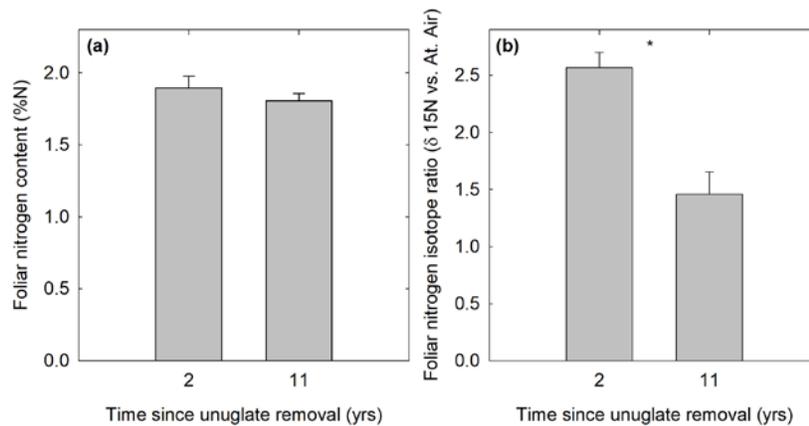


Fig. 43. Foliar nitrogen and foliar nitrogen isotope ratio in the phytometer plant (*Dodonaea viscosa*) sampled in all plots in the *Dodonaea* shrubland chronosequence.

4.3 Soil nutrient manipulation

4.3.1 Greenhouse

Nonnative, invasive species showed stronger growth responses to soil nutrient availability compared to native species. Total biomass of *P. cattleianum* increased by ~12% as soil nutrients increased (i.e., for every one unit decrease in C:N) in intraspecific competition ($F = 30.93$, $P < 0.01$, $r^2 = 0.48$, $n = 35$), compared to a ~15% increase in biomass as soil nutrients increased in interspecific competition ($F = 73.88$, $P < 0.01$, $r^2 = 0.59$, $n = 54$; Fig. 1c & 1d). *C. setaceus* total biomass also increased by ~12% in response to increased soil nutrient availability in intraspecific competition ($F = 35.34$, $P < 0.01$, $r^2 = 0.52$, $n = 35$), and ~8% in interspecific competition ($F = 32.36$, $P < 0.01$, $r^2 = 0.28$, $n = 87$; Fig. 44a & 44b).

Most native species (i.e., three of four) showed a more neutral growth response to soil nutrient availability compared to nonnative species. *A. koa* and *S. chrysophylla*, showed no significant change in total biomass in response to soil nutrient availability for either intra- or interspecific competition (Fig. 44). Additionally, excluding the treatment with complete mortality (i.e., wet ecosystem, nutrient addition low, target C:N = 10.4), *M. polymorpha* had a neutral growth response to soil nutrient availability. *M. polymorpha* experienced high mortality in nutrient addition treatments (see below) and, therefore, was not analyzed with all five nutrient treatments). *D. viscosa* biomass response to nutrient availability was in line with that seen for the invasive species, increasing approximately 8% as nutrients increased in intraspecific competition ($F = 61.43$, $P < 0.01$, $r^2 = 0.66$, $n = 34$), and increasing 11% as nutrients increased in interspecific competition ($F = 49.63$, $P < 0.01$, $r^2 = 0.60$, $n = 34$; Fig. 44a & 44b).

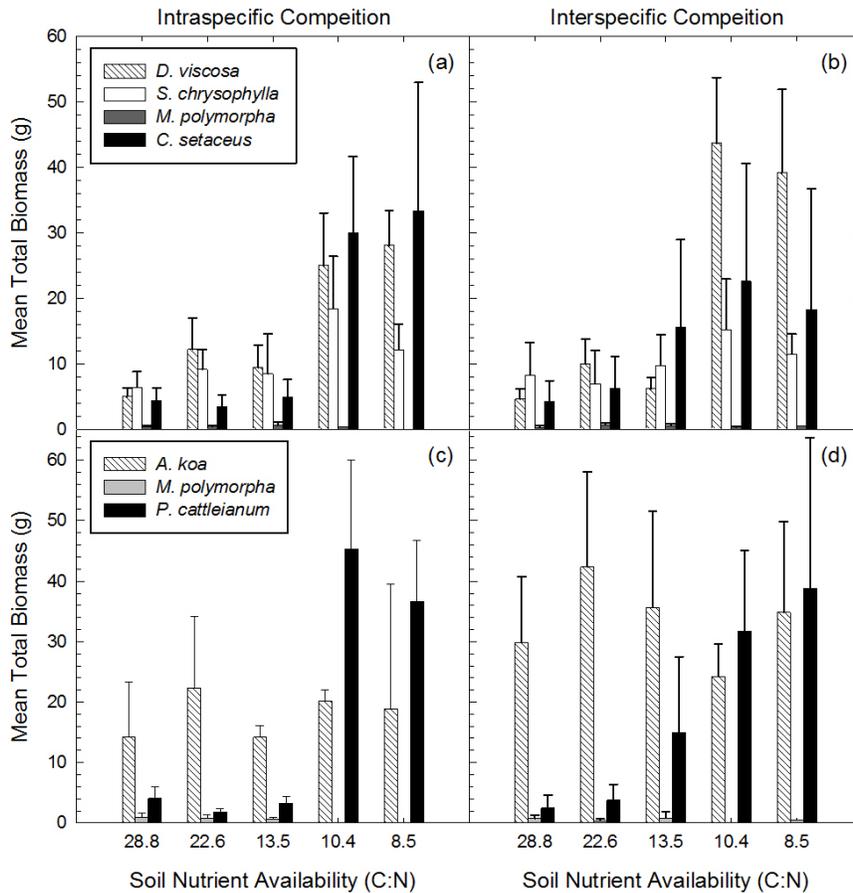


Fig. 44. Total biomass (mean + 1 S.D.) for species from the dry ecosystem (a & b) and wet ecosystem (c & d) across the five soil nutrient manipulation treatments in intraspecific and interspecific competition. For species in both intra and interspecific competition significant increases in biomass with increases in soil nutrient availability (i.e., C:N) are shown for both invasive species, *C. setaceus*, and *P. cattleianum*, and a single native species, *D. viscosa* ($P < 0.05$). No significant changes in biomass with varying soil nutrients for three of the four native species, *M. polymorpha*, *S. chrysophylla*, and *A. koa* ($P > 0.05$). Responses were analyzed using linear regression models and $\alpha=0.05$.

In addition to growth, soil nutrient availability affected the survival and reproduction of several species tested. *M. polymorpha* experienced significant mortality as soil nutrient availability increased ($P < 0.01$, $Chi-square = 98.28$, $r^2 = 0.45$), with up to 100% mortality in both nutrient addition treatments (Fig. 45). In the nutrient reduction and control treatments, mortality of *M. polymorpha* was much lower and ranged from 0 to 38% across both ecosystem types. Mortality of all other species was low and did not vary with soil nutrient availability treatments, ranging from 0 to 33% across species, treatments and ecosystem types. *C. setaceus* was the only species with reproductive output, and reproduction increased strongly with soil nutrient availability (to as high as 80% of individuals in the increased soil nutrient availability treatments ($P < 0.01$, $Chi-square = 73.87$, $r^2 = 0.37$; Fig. 46).

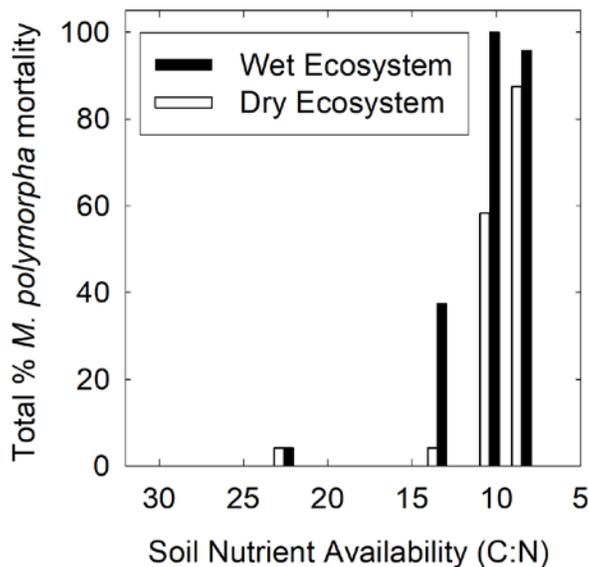


Fig. 45. Total percent mortality of *M. polymorpha* across all nutrient availabilities for both the wet and dry ecosystems. No mortality occurred in the high nutrient reduction treatments (C:N = 28.8) and complete mortality occurred in the nutrient addition low treatment for the wet ecosystem. Binary logistic regressions were applied for analysis and $\alpha=0.05$.

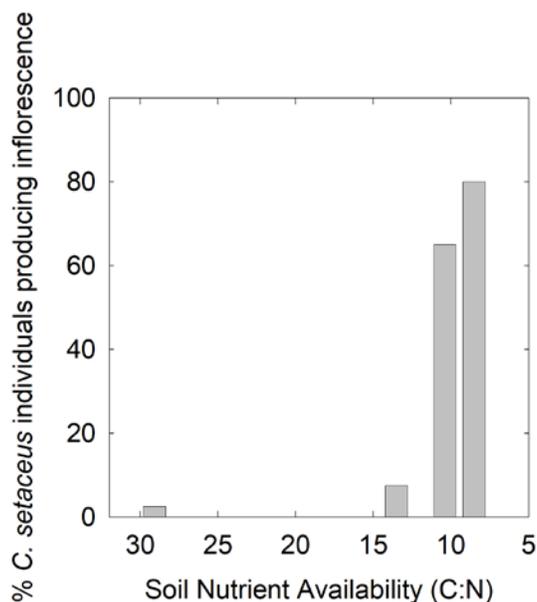


Fig. 46. Total percent of *C. setaceus* individuals that produced inflorescences. Reproductive output of the invasive grass species increased significantly as soil nutrient availability increased. Less than 3% of individuals produced inflorescences in the nutrient reduction treatments compared to 65% and more of individuals in the nutrient addition treatments. Binary logistic regressions were applied for analysis at $\alpha =0.05$.

4.3.2 Field Nutrient Manipulation Experiment

4.3.2.1 Soil Responses

Initial soil nutrients, prior to treatment applications, did not differ across any of the experimental plots within ecosystems in the TWF or the *Dodonaea* shrubland (Supplementary Table 1,2.). In the TWF, neither soil temperature or VWC varied significantly across nutrient or weeding treatments. Tropical wet forest soil CO₂ efflux was affected by nutrient but not weeding treatment. The fertilizer plots had higher soil CO₂ efflux compared to the control but not carbon treatment; control and carbon did not differ from each other (Supplementary Table 3). In the *Dodonaea* shrubland, mean soil temperature was higher in fertilizer treatments compared to both the carbon and control. *Dodonaea* shrubland VWC varied significantly by nutrient treatment; values were highest in the carbon, lowest in fertilizer and intermediate in control treatments but did not vary by weeding treatment (Supplementary Table 4).

Resin bag measurements taken at the start of the study, prior to nutrient manipulations applications, show no differences in soil across plots within ecosystems ($p < 0.5$ in all cases; Fig. 47). The nutrient additions had a large effect on plant available soil nitrogen in TWF sites ($F = 211.6$, $P < 0.001$). Weeding had no effect on N ($F = 0.6$, $p = 0.446$) and there was no significant interaction between nutrient treatment and weeding treatment ($F = 0.8$, $P = 0.717$). Carbon additions significantly decreased mean N (kg/ha/yr) compared to control while fertilizer significantly increased mean N compared to the carbon and control treatments (Fig. 47). Gaseous losses of nitrous oxide (N₂O in Kg N/ha/yr) in the tropical wet forest did not differ significantly across nutrient or weeding treatments (Fig. 48).

The results for nutrient addition in *Dodonaea* shrubland followed slightly different trends. Fertilizer addition had a large effect on plant available soil nitrogen ($F = 23.9$, $P < 0.001$), weeding had no effect on N ($F = 8$, $p = 0.377$) and there was no significant interaction between nutrient treatment and weeding treatment ($F = 0.3$, $P = 0.711$). However, carbon additions did not decrease mean available N (kg/ha/yr) compared to control during most of the time periods measured across the study. Fertilizer significantly increased mean plant available N compared to the carbon and control treatments as measured by the resin bags (Fig. 47).

Emissions of nitrous oxide did not differ significantly in either TWF or *Dodonaea* shrubland sites across nutrient or weeding treatments ($p > 0.5$ in all cases) (Fig. 48, 49). Foliar percent N and $\delta^{15}\text{N}$ of native and nonnative plants species did not differ significantly across the nutrient or weeding treatments in any of the four species tested across the two ecosystems ($P > 0.05$ in all cases; data not shown).

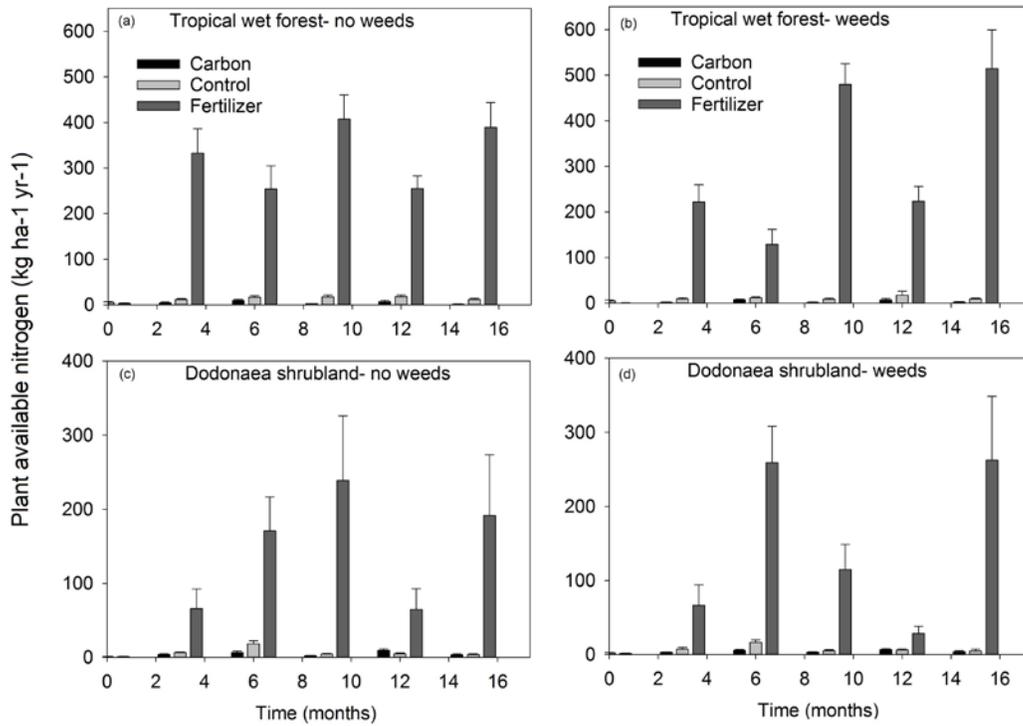


Fig. 47. Mean plant available nitrogen over the 18-month study in carbon, control and fertilizer treatments in tropical wet forest and in the dry *Dodonaea* Shrubland.

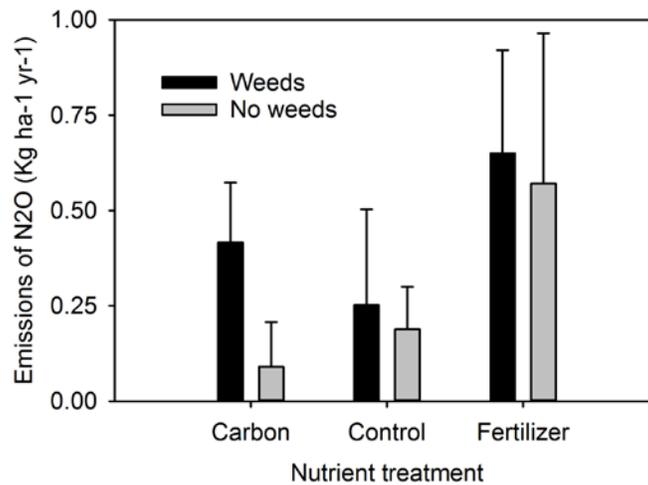


Fig. 48. Mean Kg N/ha/yr in nitrous oxide trace gas efflux across nutrient and weeding treatments in the tropical wet forest sites.

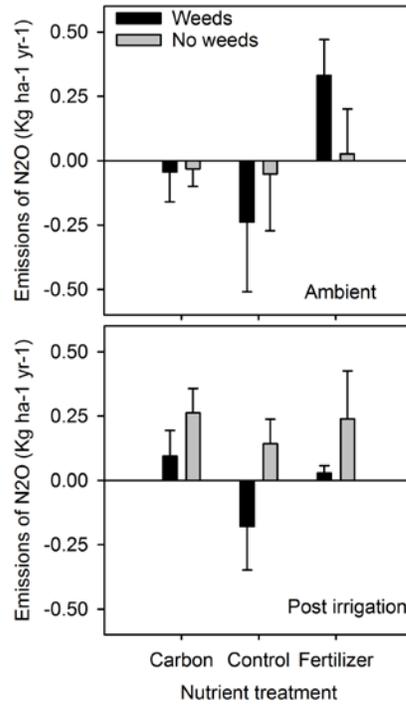


Fig. 49. Mean Kg N/ ha/yr in nitrous oxide trace gas efflux across nutrient, weeding, and watering (ambient and post-irrigation) treatments in the dry *Dodonaea* shrubland sites.

4.3.2.2 Tropical wet forest vegetation responses

The mean density of stems $\geq 1\text{m}$ in length of nonnative invasive *H. gardnerianum* (kahili ginger) across study sites in the TWF of Kahaulalea Natural Area Reserve was $3.2 \text{ stems/m}^2 \pm 0.6$. The initial estimated mean above-ground biomass ($0.81 \text{ kg/m}^2 \pm 0.1$) and mean below-ground biomass ($3.3 \text{ kg/m}^2 \pm 0.6$) did not differ significantly across the experimental plots ($F = 0.24$; $df = 2$; $p = 0.791$ and $F = 0.42$; $df = 2$; $p = 0.811$ respectively) prior to treatment application. Total mean estimated biomass after one year responded significantly to nutrient treatments ($F = 12.0$; $df = 2$; $p = 0.004$) with fertilizer treatments showing a large increase compared to both control and carbon (Fig. 50).

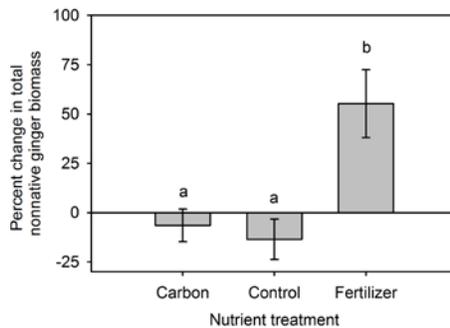


Fig. 50. The percent change in mean estimated biomass of nonnative *H. gardnerianum* in carbon, control and fertilizer treatments after one year. Different letters indicate significant differences across nutrient treatments.

Survival of planted native *C. trigynum* seedlings had overall percent survival of 46.7 ± 0.6 with exceptionally low survival (~3%) in the fertilizer plots where weeds were present. These seedlings were strongly negatively affected by fertilizer and the presence of weeds with both nutrient ($F = 7.4$; $df = 1$; $p = 0.004$) and weeding ($F = 9.0$; $df = 1$; $p = 0.007$) treatments being significant. There was no significant interaction ($F = 0.3$; $df = 2$; $p = 0.707$) (Fig. 51a). In contrast, planted nonnative *P. cattelianum* had overall high percent survival (84.7 ± 0.5) which did not vary significantly across all nutrient ($F = 0.3$; $df = 2$; $p = 0.805$) and weeding treatments ($F = 3.7$; $df = 2$; $p = 0.067$). The interaction was not significant ($F = 0.03$; $df = 2$; $p = 0.969$) (Fig. 51b).

The growth of planted *C. trigynum* seedlings was negatively affected by the presence of weeds but did not respond to nutrient treatment. Seedling percent change in height did not vary across nutrient treatments ($F = 0.02$; $df = 2$; $p = 0.979$) although weeding was significant ($F = 22.1$; $df = 2$; $p = 0.001$). There was no interaction ($F = 2.8$; $df = 2$; $p = 0.087$) (Fig. 51c). Nonnative *P. cattelianum* responded positively to both fertilizer and weed removal. Change in percent height varied significantly by nutrient ($F = 10.5$; $df = 2$; $p = 0.001$) and weeding treatment ($F = 7.1$; $df = 2$; $p = 0.015$) but there was no interaction ($F = 1.7$; $df = 2$; $p = 0.206$) (Fig 51d).

The root to shoot ratio of native *C. trigynum* was affected by weeding ($F = 8.2$; $df = 2$; $p = 0.015$) but not nutrient ($F = 2.5$; $df = 2$; $p = 0.120$) with no significant interaction ($F = 0.3$; $df = 1$; $p = 0.358$) (Fig. 51e). However, the lack of nutrient effect and interaction is likely due to the extremely low survival in fertilizer plots with weeds present, as there were not enough seedlings in this combination of treatments to include in the analysis. In contrast, *P. cattelianum* root to shoot ratio did not vary by weeding treatment ($F = 1.7$; $df = 2$; $p = 0.213$) but did respond to nutrients ($F = 6.6$; $df = 2$; $p = 0.006$) (Fig. 51f). There was no significant interaction ($F = 0.2$; $df = 1$; $p = 0.643$).

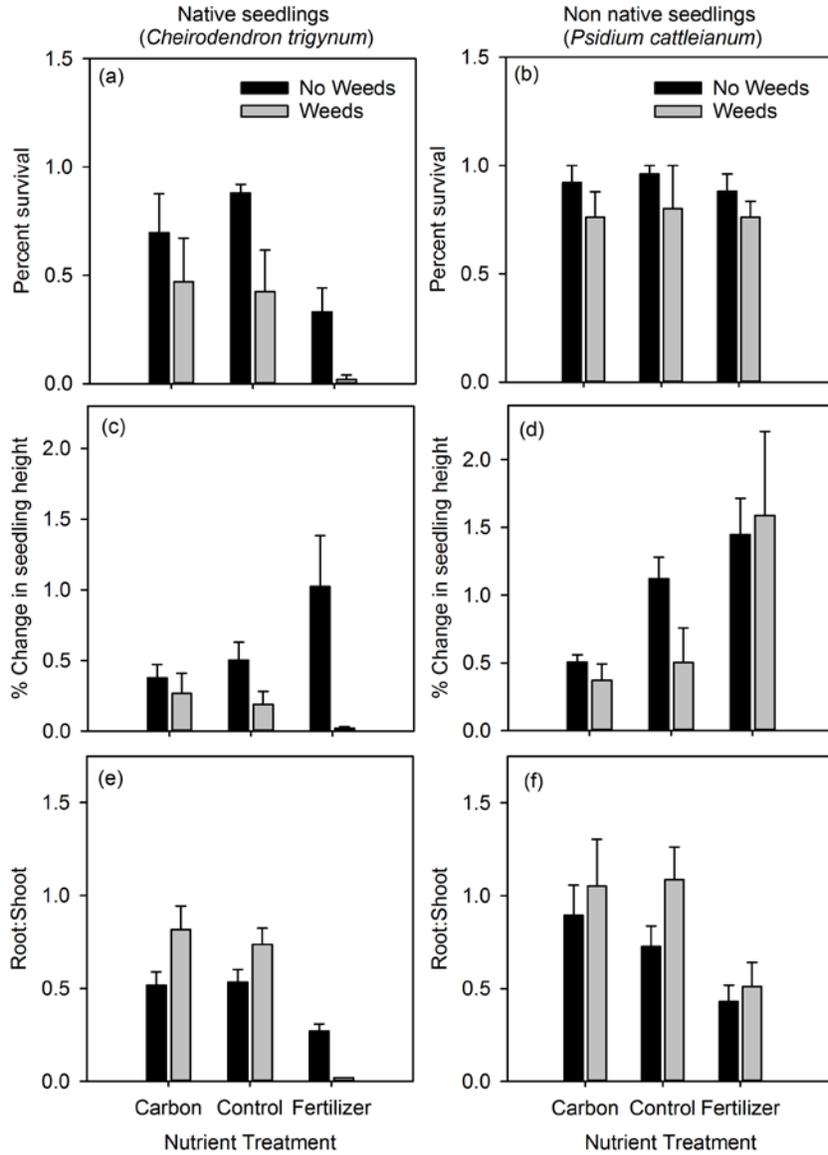


Fig. 51. Percent survival of native *C. trigynum* (a) and nonnative *P. cattleianum* (b) after 18 months of growth by nutrient and weeding treatments. Percent change in height of native *C. trigynum* (c) and nonnative *P. cattleianum* (d) after 18 months of growth by nutrient and weeding treatments. Root to shoot ratio of native *C. trigynum* (e) and nonnative *P. cattleianum* (f) after 18 months of growth by nutrient and weeding treatments. Different letter of the same case indicate significant differences across nutrient treatments. An asterisk (*) indicates a significant effect of weeding treatment.

4.3.2.3 Dodonaea shrubland vegetation responses

Initial measures prior to application of treatments showed similar percent total plant cover of native and nonnative plants across the experimental plots ($P > 0.05$). The native grass, *E. atropioides*, represented ~95% of total plant cover followed by the nonnative herb, *S. madagascariensis*, which represented ~4% of total plant cover.

The percent change in total native plant cover after one year did not show a significant response to either nutrient ($F = 0.1$; $df = 2$; $p = 0.902$) or weeding treatments ($F = 1.0$; $df = 2$; $p = 0.339$). Similarly, the percent change in the total nonnative vegetation cover did not show a response to nutrient treatment ($F = 2.2$; $df = 2$; $p = 0.170$) (Supplementary Table 4). There was, however, a strong response in reproductive output in the dominant native and nonnative species. The native grass, *E. atropioides*, had almost two orders of magnitude higher reproductive output in fertilizer treatments compared to carbon or control which did not differ from each other ($F = 17.9$; $df = 2$; $p < 0.001$). Weeding treatment was not significant ($F = 0.5$; $df = 2$; $p = 0.286$) no was there a significant interaction ($F = 0.2$; $df = 2$; $p = 0.622$) (Fig. 52a). The nonnative herb, *S. madagascariensis*, had a four-fold increase in reproductive output in fertilizer treatments compared to both carbon and control which did not differ from each other ($F = 6.9$; $df = 2$; $p = 0.004$) (Fig. 52b).

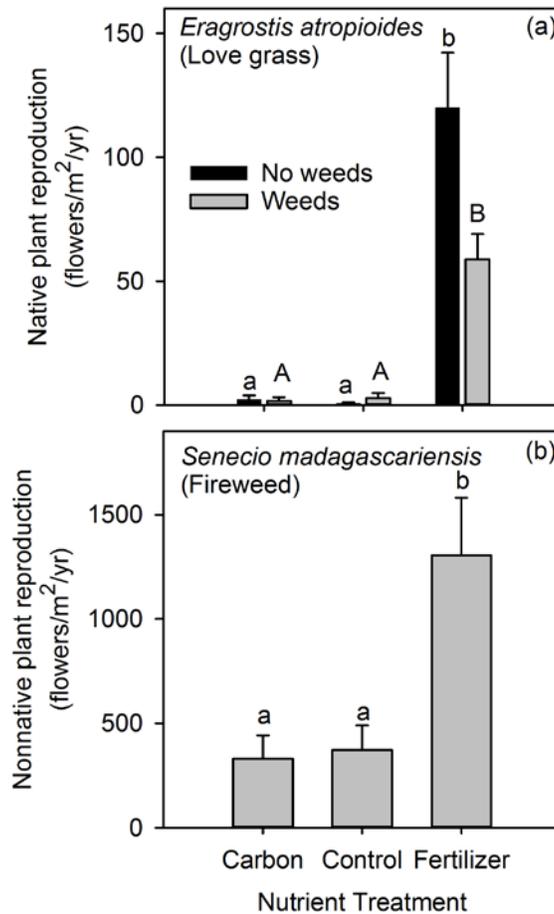


Fig. 52. Total reproductive output in native *E. atropioides* in Weeds and No weeds treatments across nutrient treatments (a). Total reproductive output in nonnative *S. madagascariensis* across nutrient treatments (b). Different letter of the same case indicate significant differences across nutrient treatments.

The native woody shrub *C. oahuense* had a significantly greater percent change in height in the fertilizer compared to carbon or control treatments which did not differ from each other (F

= 25.5; df = 2; p > 0.001). Weeding had no effect on seedling height (F = 3.2; df = 2; p = 0.0.82) and there was no interaction among treatments F = 1.3; df = 2; p = 0.286) (Fig. 53).

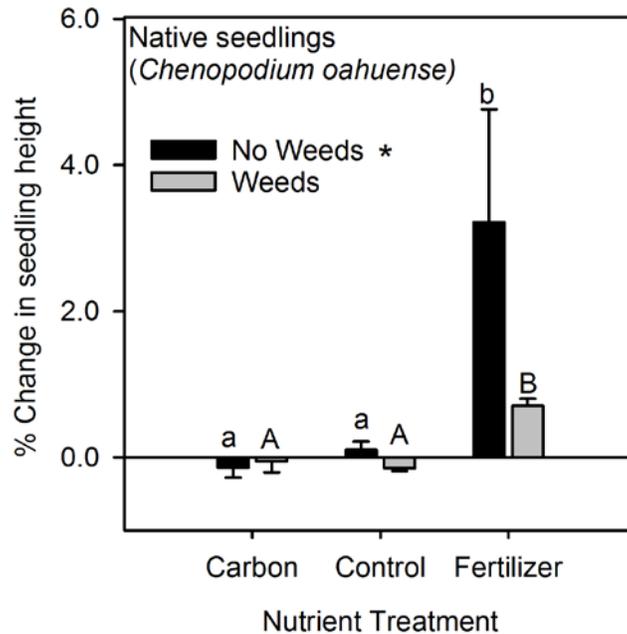


Fig. 53. Percent change in height of native *C. oahuense* after 18 months of growth by nutrient and weeding treatments. Different letter of the same case indicate significant differences across nutrient treatment. An asterisk (*) indicates a significant effect of weeding treatment.

4.4 Decision Support Tool

In the first meeting held at the PTA NRO, the conservation staff were provided with an overview of the DST process. This included stressing the value of a user driven, facilitated process for DST development and the value of the process to identify information gaps and develop a transparent logic-based decision-making process. The overview also covered methods for identifying and measuring criteria for the knowledge-base, establishing the logic model to relate criteria and options for developing a user interfaces for establishing priorities and producing desired reports. After the initial overview, the Office staff developed their primary DST Question: “What areas of the PTA training area should be designated as Area for Species Recovery (ASR) and have the highest priority for management efforts based on the PTA regulatory requirements and availability of funds?” This DST focused on mid-level T&E species, while excluding the six that were considered high priority as these would be targets for management regardless of other criteria. Objectives of the project were defined to include increasing overall efficiency of the program and the production of reports for funding request.

4.4.1 DST Criteria

The PTA conservation staff identified a preliminary list of criteria required to develop an answer to their research question (Tables 14,15 & 16). The PTA conservation staff refined and prioritized this initial list and determined which datasets were available for each criterion. Key criteria from the initial list were identified as: 1) Current Species Distribution; 2) Accessibility;

3) Fire Risk; 4) Percent Weed Cover; and 5) Habitat Quality. Based on the format and resolution of the datasets associated with the five key criteria it was determined that the final DST product would be based on 30X30 m pixel rasters.

Table 14. The four main criteria for the PTA DST, Kernel Density, Fire Risk, Accessibility and Percent weed cover, their sub layers and description.

Raster Layer	Sub Layers	Description
<i>Kernel Density Hot Spot Map (Current Species Distribution)</i>	Number of individuals	Based on Installation Wide Survey (IWS) - 5 years of point data
	Rarity in PTA	
	Proximity to other T & E species (both #of species and Individuals)	
<i>Fire Risk</i>	Vegetation Layer Map	Fuel Load - Converted ranked raster
	NDVI Fuel Load	Fuel Load - growth of vegetation
	Corridor map	Probability of ignition - Developed from combination of roads, trails, fuel break - segments will be ranked and buffered - converted to continuous/ranked raster
	Proximity to live fire area	Probability of ignition - Converted to ranked raster
<i>Accessibility-excluding heli-op areas</i>	Roads, Trails, Fence Lines	On Network - Polyline with travel speeds by segment
	Vegetation layer	Off network - Polygons with travel speeds assigned by vegetation class
	Geology layer	Off network - Based on travel speeds in barren areas based on different geology
	Slope	Off network - Slope raster from DEM
<i>Weed Cover</i>	% Weed Cover	From either Landsat based classification or vegetation map - proxy for labor and treatment costs

Table 15. Additional Criteria under consideration for the PTA DST

Criterion	Description
Existing management	NRO invested time to manage the area (Covered by % weed cover?)
Habitat Continuity	Continuous area covered by a population
Habitat Extent	Number of fuel cells where individual species exist
Habitat Quality	Vegetation cover, nonnative cover, etc.
Species Priority	Sub-Criteria will be necessary to rank priority (see Table 3)
Species Ranges	J. Price et al. used here for the total number of species
Species Ranges Under Future Climate	J. Price et al. used here for the total number of species
Suitability for Soil Amendment Treatment	C. Litton project results
Time ungulate-free	
Ungulates	Similar to fencing may want to have in case of fence breach
Wildlife Habitat Potential	
Fencing	ASRs are currently fenced putting this in as a place holder in case you want to track fence quality or age

Table 16. Sub-criteria for a possible Species Priority component to the PTA DST.

Criterion	Description
Number of individuals in PTA	Could also be ratio of PTA individual/state wide individuals
Number of individuals state wide	
Population trajectory	
Regeneration ability	
Number of fire cells where species is present	
Habitat Continuity	Used here for individual species
Habitat Suitability	Used here for individual species
Species Ranges	J. Price et al. used here range extent for individual species
Species Ranges Under Future Climate	J. Price et al. used here range extent for individual species

A kernel density hotspot analysis, developed by the PTA conservation staff, was chosen as the methodology to represent current species distribution and species priority. This density analysis was based on the combination of the Installation Wide Survey, which identifies existing plant

locations, rarity in PTA and proximity to other species. This layer replaced the species priority layer described in Table 10.

Accessibility will be measured by the calculation of overall travel time to each pixel in the study area using a protocol developed by Mark Wasser (UH Hilo). This method combines the ArcMap Network Analyst output of travel times for “On Network” travel on roads, trails and fence lines with “Off Network” travel times. Off Network travel times are calculated using vegetation cover, slope and substrate in barren areas. The output of the accessibility raster will be a continuous raster in units of time.

The fire risk layer will be developed by calculating fuel load (vegetation type classification and NDVI rasters) and probability of ignition. Probability of ignition will be developed from the combination of roads, trails, fuel break segments which will be ranked and buffered and then converted to a ranked raster. This will be then combined with a layer detailing proximity to the live fire areas. It has yet to be decided how these individual layers will be combined and if some of the layers will be given greater weight in the overall calculation of fire risk. The ranked raster output of the fire risk calculation will be compared to fire history data to assess the quality of the risk assessment calculation.

Current vegetation cover and percent weed cover dataset will be developed by using classified remotely sensed LANDSAT data, allowing for the most up-to-date measures. Management and labor costs are directly correlated to percent weed cover and accessibility. Including cost layers in the DST would result in double counting these factors, so the conservation staff removed the cost layers from the list of criteria.

The PTA conservation staff concluded that habitat quality would need to be determined on an individual species basis. Measurements for habitat quality (climate and substrate) are species specific so it is not possible to develop a uniform habitat quality for all species across the landscape. Habitat quality would also have to factor in the individual species distribution and a review of the species’ locations relative to fire cells in order to “spread the risk” of threats to the mid-level priority species. In the future, the product of the initial DST, which would determine overall priority areas for management, could be combined with habitat quality maps for each species to further refine the identification of management areas at the species level.

4.4.2 DST Logic Model

A simple logic model to connect criteria to each other and to the decision-making priorities of PTA conservation staff, drafted using ArcMap Model Builder, is shown below in Fig. 54. In Step 1 of this model, each of the rasters from the knowledge base are converted to generic units on a -1 to +1 scale. The kernel density analysis, accessibility and weed cover layers are all continuous and are converted with Raster Calculator to a uniform scale using a fuzzy-logic formula (Fig. 55) where variables A and B represent thresholds unique to each data layer. For example, using the fuzzy-logic formula with thresholds of 20% and 80% for weed cover, any pixel with a value for weed cover under 20% would be given a value of +1 (easy to manage), any values over 80% could be given a value of -1 (difficult to manage) and the values in between would be calculated relative to these thresholds (value of Y based on the slope between thresholds A and B). Fire risk is a ranked raster and is converted to the -1 to +1 using Reclassification based on the stakeholders’ determination of the relationship of rank to scale. The second step in the model is to calculate a decision score for each pixel in the study area by combining all four layers in Raster Calculator. It is in this step that the PTA staff can adjust the

relative weight of each input layer based on their priorities. If all input layers are weighted equally they are each multiplied by 0.25 and summed to create a decision score output. If staff view fire risk as a centrally important driving force on landscapes, then the DST than the multiplier for fire risk could be increased and the other criteria multipliers decreased. Once the data layers, thresholds for the fuzzy-logic formulas and priorities in step 2 have been set an output raster of decision scores can be generated. Using Zonal Statistics and the DST input layers in ArcMap, the PTA staff should be able to produce additional calculations of land area, travel times and labor and treatment cost for their selected area.

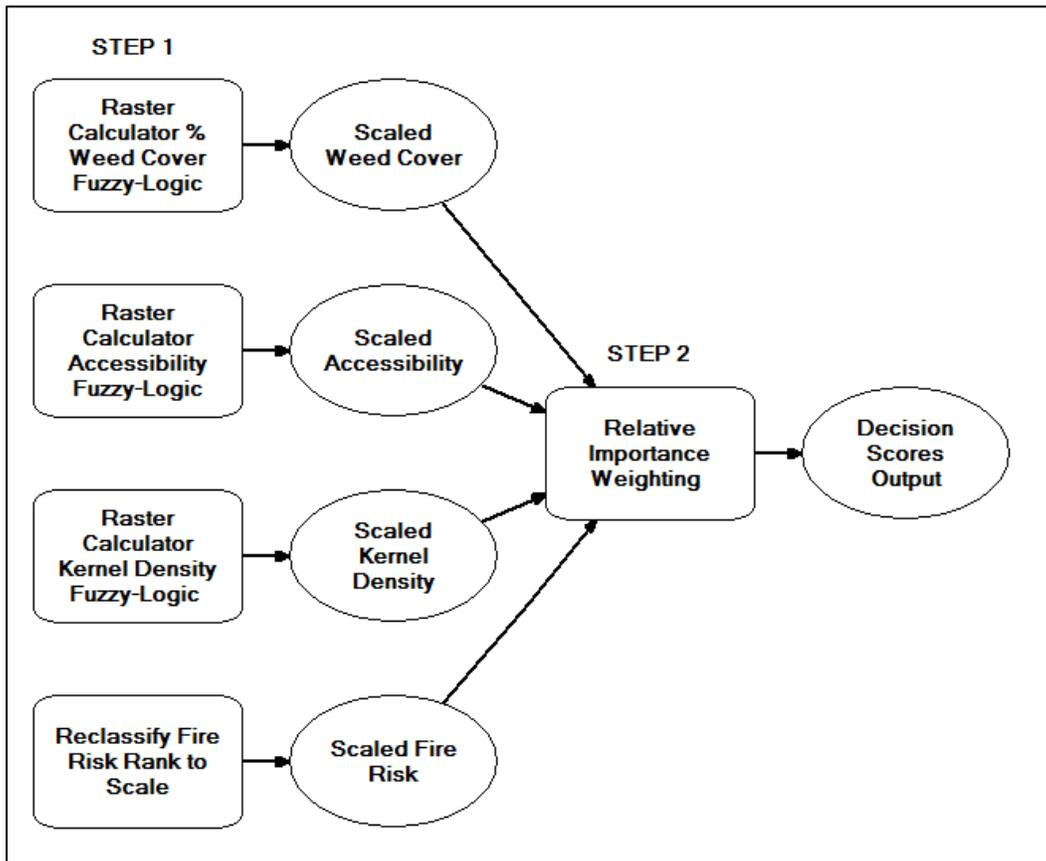


Fig. 54. Draft PTA DST logic model build in ArcMap with Model Builder. Step 1 converts input raster values to a unitless -1 to +1 scale. Step 2 weighs each input raster relative to the others and sums the values.

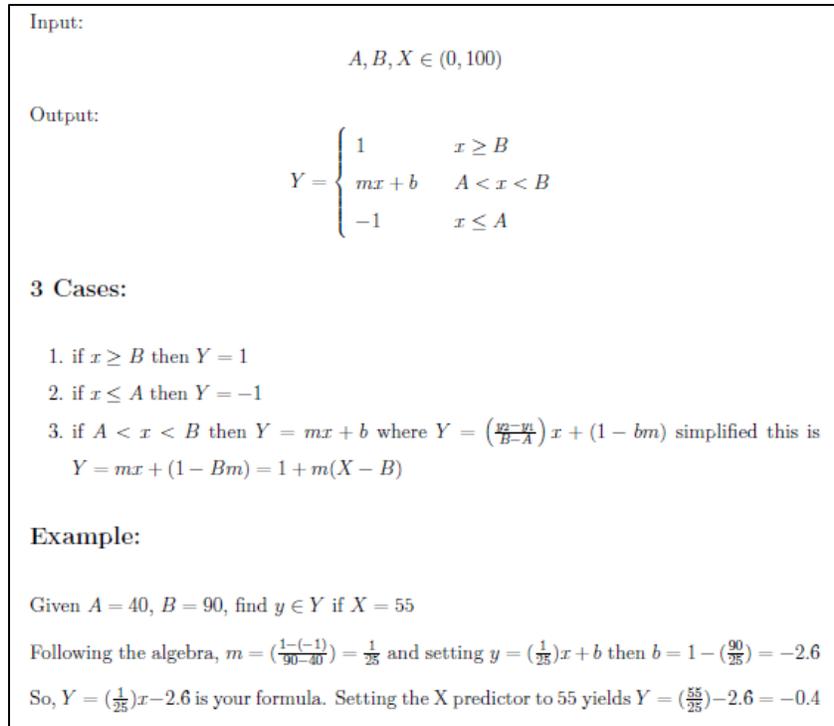


Fig. 55. Fuzzy-Logic formula for conversion of raster input values to a unitless -1 to +1 scale. A and B represent thresholds values for an individual rater input and X the input pixel value. The outputs are pixel values (Y) that fall within the -1 to +1 scale.

5. Discussion

5.1 Vegetation Responses

Based on this and other studies, the removal of nonnative ungulates is critical for the recovery of native plants, including both common species and those of conservation concern. However, the time frame and degree of recovery varied across ecosystems, likely as a result of the prior degree of degradation at the time of fencing and ungulate removal. For example, the tropical wet forest was significantly impacted by feral pigs but most of the disturbance was to the soil and understory, leaving the overstory largely intact. This forest had patches of significant nonnative plant invasions but also many areas that have remained relatively uninvaded. In the dry ecosystem vegetation types, the *Metrosideros* woodland was the least degraded. The *Dodonaea* shrubland, in turn, had extensive invasion by nonnative grasses and forbs prior to fencing and ungulate removal. The fenced area of the *Eragrostis* grassland was the oldest enclosure studied, and the adjacent unfenced area where ungulates were present was intensely degraded by the time of this study in 2014.

As a result in these differences in the degree of ecosystem degradation at the time of fencing and ungulate removal, vegetation recovery was more extensive and happened over a shorter time frame in the tropical wet forest compared to all of the dry ecosystem vegetation types. Commonly occurring native plants recovered within the first 6.5 years since feral pig removal. In addition, species of conservation interest increased after the removal of feral pigs, particularly if there was a population to start with at the time of exclusion. Species of conservation interest were almost entirely absent in pig-present areas. Many native species commonly thought to only grow only epiphytically (off the ground on trees or tree ferns) were found to flourish at ground level when feral pigs were removed. In addition to native plant recovery, nonnative invasive plants also increased when released from top-down disturbance by feral pigs.

In TDF, vegetation response in the *Metrosideros* woodland was slower, but also showed recovery following ungulate removal. None of the commonly occurring native or nonnative vegetation showed any change over the first 15 years of ungulate removal. However, we did find that species of conservation interest (TER-S) increased in abundance with time since ungulate removal. In *Dodonaea* shrubland, common native and nonnative species showed no significant changes over the eleven-year chronosequence used in this study. However, species of conservation interest increased slightly after the exclusion of feral animals. The *Eragrostis* grassland showed the most pronounced differences of the dry ecosystem vegetation types studied. Native herb cover was significantly greater in the ungulate removal sites compared to the adjacent ungulate present sites. The abundance of TER-S was also much higher in ungulate-removal sites.

5.2 Ecological Processes Responses

Impacts of feral ungulate removal on ecological processes in general took longer to manifest than vegetation, and were at least somewhat ecosystem dependent. Changes in C cycling were more extensive in the tropical wet forest compared to the dry ecosystem types studied. In the tropical wet forest, soil respiration (F_s) increased with feral pig removal and the relative difference between paired feral pig removal and feral pig present sites showed a strong, positive relationship with increasing time since feral pig removal. This results appears to be the result of decreased soil bulk density and soil VWC when feral pigs are removed, which resulted

in increased autotrophic and heterotrophic contributions to soil respiration (Long et al. 2017). Litterfall, an index of overall stand productivity, did not change with feral pig removal. Feral pig removal did have an effect on TBCF, which increased with feral pig removal as a result of increased soil respiration.

Total ecosystem C did vary with time since ungulate removal in TWF, however, aboveground tree fern C, total aboveground C, and litter C all increased after 18.5 years of ungulate removal. Soil respiration, litterfall, TBCF, and total ecosystem C in the *Metrosideros* woodland and *Dodonaea* shrubland did not vary with ungulate removal. In the *Metrosideros* woodland, litter C and total detrital C generally increased over time with ungulate removal, while in the *Dodonaea* shrubland belowground herbaceous C was the only component of total ecosystem C that changed with ungulate removal.

The results of this study suggest that in TWF, particularly in areas of intense ungulate activity, nitrogen availability increases with feral animal removal. In TDF, results were somewhat more variable. In *Dodonaea* shrubland, similar to TWF, at least some metrics suggested nitrogen availability increased with the removal of feral animals. However, this trend was completely absent in *Metrosideros* woodlands where soil development is limited by substrate and resource availability. The removal of feral ungulates had no impact on the primary nitrogen loss terms of leaching and gaseous loss of nitrous oxide (N₂O). However, our best proxy for nitrogen cycling (gross rates of mineralization) suggested at least modest increases in nitrogen cycling after the removal of feral animals in all of the ecosystem types examined. However, does this increase in nutrient availability provide an advantage to nonnative compared to native plants?

5.3 Soil nutrient manipulation

Soil nutrient manipulations have the potential to alter competitive dynamics between native and invasive species, particularly when natives and nonnatives employ different resource use strategies. In the greenhouse experiment, all species generally had greater biomass with increased soil nutrient availability, as would be expected. However, in most cases the invasive species were much more responsive to nutrient availability compared to the native species as a whole. For five of the six species tested our hypothesis was supported on that nonnative invasive plants benefited from increased nutrient availability and native plants showed competitive advantage in response to decreased nutrient availability. *D. viscosa*, was the single exception for native species in that it responded more similarly to the nonnative, invasive species.

The field nutrient manipulation experiment partially supported the hypothesis that native species would show an advantage in decreased nutrient availability and nonnatives will benefit from increased nutrients. In the TWF, native plants grew similarly across the nutrient treatments whereas, nonnative species growth increased significantly with increased soil nutrient availability. In the TDF, the percent cover of native and invasive herbaceous plants did not differ with soil nutrient manipulation treatments, but reproduction of dominant native and invasive species did. With increased soil nutrient availability reproduction of native species increased 2-fold, while nonnative species reproduction increased 4-fold.

However, we note that the strongest vegetation responses in the field study overall occurred in the increased fertility treatment, and not in the decreased fertility treatment. This is in part due to the scale of the response of soil nutrient availability to fertilization vs. C amendments. In the tropical wet forest, C amendments reduced plant available N to ~38% of N in the control treatment while the fertilizer addition increased N by ~2500% compared to the control. In the dry

ecosystem (*Dodonaea* shrubland), the carbon addition resulted in a weaker reduction in plant available N (62% of N available in control) which may explain the lack of significant plant responses to that treatment. The weaker response in the *Dodonaea* shrubland to the carbon addition is likely due to lower rates of incorporation of the added C into soils (Austin and Vitousek 2000). Slower rates of decomposition in the dryer ecosystem also suggest that the effect of nutrient reduction may play out over a longer time frame than measured in this study.

In a field restoration scenario, the desired response to carbon amendments is to favor native species by reducing the growth of invasive but not native species, or reducing growth in invasive species more than native species (Horn and Redente 1998, Alpert and Maron 2000, Paschke et al. 2000). The tradeoff, however, is that native species adapted to low resource availability are not as adapted to take advantage of increased resources (Vitousek et al. 1987, Hobbs and Huenneke 1996). In the greenhouse study, the majority of the native species (but not *D. viscosa*) grew similarly across all nutrient conditions while the nonnatives all showed strong and positive responses to increasing nutrient availability and negative responses to nutrient reduction. In the field study, the results were more mixed and were also affected by the weeding treatment which reduced competition with nonnative plants. In TWF, the native woody species, *C. trigynum*, grew more when there was more N available and weeds were removed. However, survival and growth were both strongly reduced in treatments where N was increased and weeds (nonnative plants) were present. Very similarly, the dry *Dodonaea* shrubland, the native woody species *C. oahuense*, grew significantly more in fertilizer treatments where weeds were removed compared to the control and carbon treatments. Nonnative plants generally prospered with increasing nutrients. For example, in the TWF, all nonnative species monitored had strong and positive growth responses across the gradient of increasing soil nutrients.

A particularly important finding was the negative impact of increased soil nutrients on survival of dominant native woody species, including *M. polymorpha* in the greenhouse and *C. trigynum* in the field study. A prior field study similarly found that growth and density of *M. polymorpha* seedlings were reduced with the addition of nutrients (Ostertag and Verville 2002). The results of this study suggest that elevated nutrient levels, such as those occurring with feral ungulate removal, will negatively affect population dynamics of keystone native species that appears to be adapted to low resource environments.

On the positive side for applied restoration scenarios were the effects of nutrient manipulation on reproduction rates. The ability of a species to reproduce is critical to its success as an invader (Bryson and Carter 2004). In the greenhouse experiment, flowering of nonnative grass was reduced to zero with soil nutrient availability, making C amendments a promising technique for this aggressive and prolific invader. In the field nutrient experiment, both native and invasive species reproduction increased with increased nutrient availability.

One of the most important hypothesis we set out to test was that nonnative ungulate removal would both increase carbon storage and flux, and increase nitrogen cycling and plant availability. This hypothesis was partially supported. Ungulate removal appears to have a limited influence on C cycling, although we did observe large changes in belowground carbon cycling in TWF and important changes in fine detritus with ungulate removal in TDF. In contrast, metrics of nitrogen cycling and availability increased in most ecosystems. So, in sum, our results suggest that feral ungulate removal results in an increase in nutrient availability for some period of time, depending upon the ecosystem.

Whether or not this increase in nutrient availability has a direct or indirect influence on the competition between native and nonnative plants was only partially answered by this study.

The greenhouse study strongly suggested that increased nutrient availability favored nonnative species in all cases except for one native species. Based only on the greenhouse study, a reasonable conclusion would be the manipulation of available nutrients is a viable and strong land-management strategy. However, our field studies reveal many of the challenges in operationalizing results from a highly controlled greenhouse experiment.

In the field, native and nonnative species in general benefitted from increased nutrient availability. Decreasing soil nutrient availability proved to be difficult within the timescales of this study in that it took many months for the C amendments to reduce nutrient availability. However, the overall observation was that nonnative plants respond positively to increased nutrients through increased growth and flowering. This response likely at least partially explains the difficulty in reintroducing native plants after feral animal removal in many ecosystems. Our results also highlight that simply classifying plants into native vs. invasive species can be too simplistic: some native plants respond well to nutrient addition while others are strongly resource conservative. Our results also suggest that adding C to reduce nutrients does not appear to negatively affect native plants while it can strongly reduce the reproduction of nonnative invasive species. Finally, our results also indicate that active weeding removal is important for the success of native species, particularly in disturbed environments where nutrients are likely to be elevated.

Decision Support Tool

The DST was successful, but needs continued support to be finalized. Critically, a DST is more likely to be successful if the process remains user driven, keeping the focus on stakeholder input driving the process rather than producing a specified end-product. Under the current user specifications, the DST will be produced from 30X30 meter rasters covering the entire PTA Installation using the following four criteria data layers: (i) Kernel Density Analysis; (ii) Fire Risk; (iii) Accessibility; and (iv) Percent Weed Cover. The continuous kernel density raster layer in relative units has been completed by the PTA staff. Percent weed cover will also be a continuous raster which will be created from a classification of remotely sensed LANDSAT data. The sub-layers to develop both the fire risk and accessibility are available but have yet to be processed into final form. Fire risk will be a ranked raster and accessibility will be a continuous raster in units of time. The PTA conservation staff will do a final review the remaining criteria from the initial list established by the group and determine if any additional criteria should be considered for integration into the DST at this time. Some of the initial criteria have already been determined to be covered by the four listed above. For example, labor costs are directly related to travel time and percent weed cover, so it does not need to be included as an additional layer. If any additional layers are determined to be critical to the DST and are not covered by the four main criteria an additional meeting will be required to evaluate how these criteria will be measured and the availability of any necessary data sets. The preliminary logic model has been drafted and can be utilized once the knowledge-base layers are completed. This would allow for the PTA conservation staff to generate decision scores based to their criteria to determine which area should be designated as Area for Species Recovery and have the highest priority for management. The advantage of a DST model is the ability to easily change the thresholds and importance weighting of each of the four data input layers, and then to be able to visualize different scenarios as expressed in decision scores for the study area. The PTA staff have the ability to adjust the priority scores directly in Model Builder, however, a user interface could be

built out to allow the NRO to adjust thresholds and priorities as needed based on funding and regulatory requirements, thus maximizing the Utility and flexibility of the PTA DST.

6. Conclusions and Implications for Future Research/Implementation

6.1 Vegetation responses

Our original hypotheses (in italics below) were partially supported.

- *Nonnative ungulate removal will increase the abundance and diversity of both native and nonnative plants.*
- *Native plant recovery will increase with time since ungulate removal.*
- *Due to inherent differences in resource availability & prior degree of degradation, tropical dry forests will have relatively smaller responses to ungulate removal.*

Species of conservation interest (TER-S) increased in all four ecosystems. Common native species recovered in two of the four ecosystems (TWF and *Eragrostis* grassland). Nonnative invasive plants only increased in abundance in one ecosystem (TWF), but this appears to be largely because they were already well-established at the time of fencing and ungulate removal. There were few trends in recovery over time of commonly occurring native species, although species of conservation interest did increase with time in three of four ecosystems studied. Overall, tropical dry forest ecosystems had relatively smaller and slower responses to ungulate removal than the TWF ecosystem.

The results of the vegetation surveys across the four different vegetation types in tropical wet and tropical dry forest lead to several major conclusions. First, ungulate removal is a key first step in conserving native plant communities, and TER-S in particular. Second, control of nonnative invasive plants is also critical and will be most effective if the ecosystem has not become extensively invaded at the time of fencing and ungulate removal. Third, recovery of species of conservation interest occurs only in ungulate removal areas, and is accelerated when there is an existing population present at the time of fencing and ungulate removal. Lacking a population at the time of fencing and ungulate removal, recovery may be slow or nonexistent and more intensive efforts such as propagation and outplanting may be necessary in order to reestablish TER-S populations. Finally, rate of recovery varied substantially across ecosystems with the most rapid responses occurring in tropical wet forest and the slowest in dry ecosystem types.

6.2 Ecological processes responses

Our original hypotheses (in italics below) were partially supported.

- *Nonnative ungulate removal will increase both above- and belowground C fluxes and storage.*
- *Removal of nonnative ungulates will increase nutrient cycling, decrease ecosystem loss of nutrients, and increase nutrient availability.*

Overall, there was only a minimal impact of ungulate removal on C storage and flux. The exception to this trend was increased belowground C cycling in TWF, and increased fine detritus in TDF. We observed increased N mineralization (i.e., increased nutrient cycling) in TWF and *Dodonaea* shrubland, but not *Metrosideros* woodland. Similarly, nutrient availability increased following nonnative ungulate removal in TWF and *Dodonaea* shrubland, but not *Metrosideros* woodland.

Our general conclusions are that disturbance caused by ungulates can lead to increased nutrient cycling and subsequent increases in nutrient availability following their removal. These increases in nutrient availability can persist over time following ungulate removal. Combined

with our other results, this suggests that disturbance to ecological processes caused by ungulates can favor nonnative plant invasions following ungulate removal.

6.3 Soil nutrient manipulation responses

Our original hypotheses (in italics below) were partially supported.

- *Nonnative, invasive plants will benefit from increased N availability following ungulate removal.*
- *Native plants adapted to low nutrient conditions will show improved competitive advantage in response to decreased plant-available N.*

The greenhouse nutrient manipulation experiment strongly supported these hypotheses. Nonnative plants showed strong growth responses to increased nutrient availability while all but one native plant had neutral responses. We found increased mortality of keystone native species in wet and dry ecosystems under elevated nutrient availability, and increased reproduction of nonnative invasive species. The field nutrient manipulation had similar but less pronounced trends. In addition, we found that weeding (removal of nonnative plants) had a strong positive effect on native species while the combination of increased nutrients and presences of weeds had the most deleterious effect on native plants. Overall, manipulation of nutrients as a restoration strategy holds promise in specific targeted situations but must be weighed against other options such as top-down control of nonnative plants.

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8. Appendices

A. Supporting data

Supplementary Table 1. Field Nutrient Manipulation Experiment: Initial mean (± 1 SE) values for chemical elements across the three soil nutrient treatments in the tropical wet forest. For all chemical elements no significant differences were found across treatments.

Tropical wet forest				
Treatment	Carbon	Control	Fertilizer	p, f, df
Phosphorus (mg/kg)	17.40 \pm 2.46	16.30 \pm 0.70	18.50 \pm 1.73	P=0.692, f=0.38, df=2
Potassium (mg/kg)	88.20 \pm 12.24	93.00 \pm 10.46	99.10 \pm 6.58	P=0.749, f=0.3-, df=2
Sulfur (mg/kg)	57.60 \pm 7.05	60.70 \pm 4.85	57.70 \pm 7.09	P=0.928, f=0.08, df=2
Calcium (mg/kg)	655.00 \pm 91.26	891.80 \pm 192.21	886.90 \pm 77.16	P=0.373, f=1.07, df=2
Magnesium (mg/kg)	198.80 \pm 38.06	222.80 \pm 47.70	215.70 \pm 29.03	P=0.906, f=0.10, df=2
Sodium (mg/kg)	41.80 \pm 4.31	46.60 \pm 4.18	51.50 \pm 4.26	P=0.3107, f=1.30, df=2
Zinc (mg/kg)	3.34 \pm 0.53	4.24 \pm 0.59	3.79 \pm 0.35	P=0.469, f=0.81, df=2
Iron (mg/kg)	571.00 \pm 59.96	630.60 \pm 42.16	651.20 \pm 92.50	P=0.696, f=0.37, df=2
Manganese (mg/kg)	28.80 \pm 3.48	38.80 \pm 6.18	28.80 \pm 3.38	P=0.239, f=1.50, df=2
Copper (mg/kg)	4.02 \pm 0.24	4.59 \pm 0.23	3.88 \pm 0.42	P=0.263, f=1.50, df=2
Boron (mg/kg)	0.78 \pm 0.07	0.90 \pm 0.06	0.84 \pm 0.09	P=0.564, f=0.60, df=2
Aluminum (mg/kg)	1652.00 \pm 117.02	1774 \pm 35.44	1592.00 \pm 163.35	P=0.554, f=0.62, df=2

Supplementary Table 2. Field Nutrient Manipulation Experiment: Initial mean (± 1 SE) values for chemical elements across the three soil nutrient treatments in the *Dodonaea* shrubland. For all chemical elements no significant differences were found across treatments.

<i>Dodonaea</i> shrubland				
Treatment	Carbon	Control	Fertilizer	P, f, df
Phosphorus (mg/kg)	57.60 \pm 3.93	55.30 \pm 17.40	69.00 \pm 14.23	P=0.739, f=0.31, df=2
Potassium (mg/kg)	641.60 \pm 31.42	665.20 \pm 35.52	766.60 \pm 120.93	P=0.479, f=0.78, df=2
Sulfur (mg/kg)	40.60 \pm 3.88	36.40 \pm 4.44	34.10 \pm 4.67	P=0.577, f=0.58, df=2
Calcium (mg/kg)	3622.00 \pm 290.06	4348.00 \pm 174.42	4749.00 \pm 440.82	P=0.078, f=3.17, df=2
Magnesium (mg/kg)	458.60 \pm 35.00	527.30 \pm 34.55	529.50 \pm 33.52	P=0.290, f=1.38, df=2
Sodium (mg/kg)	40.20 \pm 0.20	34.60 \pm 2.64	41.40 \pm 4.49	P=0.272, f=1.45, df=2
Zinc (mg/kg)	4.42 \pm 0.68	6.19 \pm 2.50	7.63 \pm 2.36	P=0.548, f=0.63, df=2
Iron (mg/kg)	207.00 \pm 10.16	201.60 \pm 32.05	202.90 \pm 22.82	P=0.986, f=0.14, df=2
Manganese (mg/kg)	13.80 \pm 1.66	14.10 \pm 4.48	15.70 \pm 3.59	P=0.917, f=0.09, df=2
Copper (mg/kg)	2.12 \pm 0.09	1.99 \pm 0.16	2.18 \pm 0.13	P=0.583, f=0.56, df=2
Boron (mg/kg)	1.08 \pm 0.08	1.28 \pm 0.07	1.36 \pm 0.13	P=0.160, f=2.141, df=2
Aluminum (mg/kg)	2882.00 \pm 60.78	2784.00 \pm 86.41	2843.00 \pm 107.71	P=0.732, f=0.32, df=2

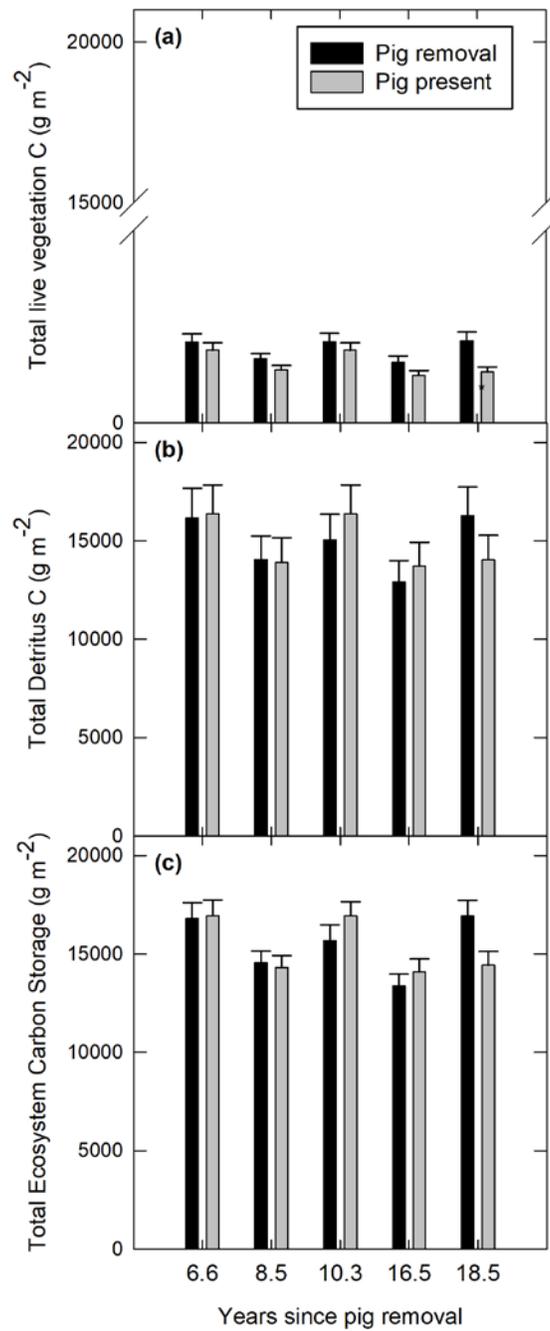
Supplementary Table 3. Field Nutrient Manipulation Experiment: Mean soil attributes (± 1 SE) in each soil nutrient treatment in the tropical wet forest . No significant differences among weeded and not weeded treatments were found for all soil attributes. Different letters denotes significant differences among soil nutrient treatments.

Tropical wet forest	Weeding Treatment	Carbon	Control	Fertilizer	Weeding treatment p, f, df	Soil nutrient treatment p, f, df
Soil CO2 Efflux	No weeds	2.93 \pm 0.18 ^{ab}	2.52 \pm 0.21 ^a	2.81 \pm 0.16 ^b	P=0.983, f=0.00, df=1	P=0.039, f=3.815, df=2
	Weeds	2.8 \pm 0.24 ^{ab}	2.19 \pm 0.21 ^a	3.23 \pm 0.23 ^b		
VWC	No weeds	42.68 \pm 1.24	44.25 \pm 1.35	42.58 \pm 1.16	P=0.725, f=0.128, df=1	P=0.066, f=3.123, df=2
	Weeds	46.20 \pm 1.00	44.03 \pm 1.21	40.52 \pm 1.58		
Soil Temperature	No weeds	16.81 \pm 0.29	16.83 \pm 0.32	16.65 \pm 0.25	P=0.084, f=3.308, df=1	P=0.969, f=0.032, df=2
	Weeds	16.58 \pm 0.24	16.50 \pm 0.22	16.68 \pm 0.25		

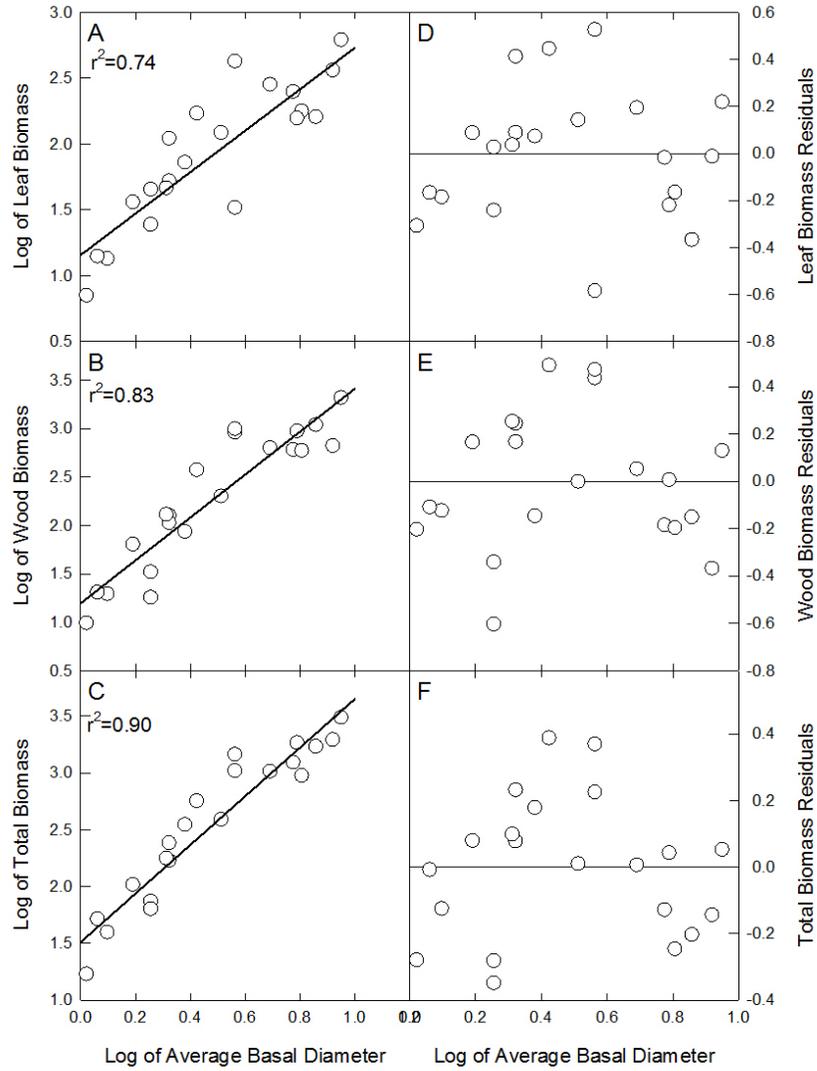
Supplementary Table 4. Field Nutrient Manipulation Experiment Mean soil attributes (± 1 SE) in each soil nutrient treatment in the *Dodonaea* shrubland . No significant differences among weeded and not weeded treatments were found for all soil attributes. Different letters denotes

significant differences among soil nutrient treatments.

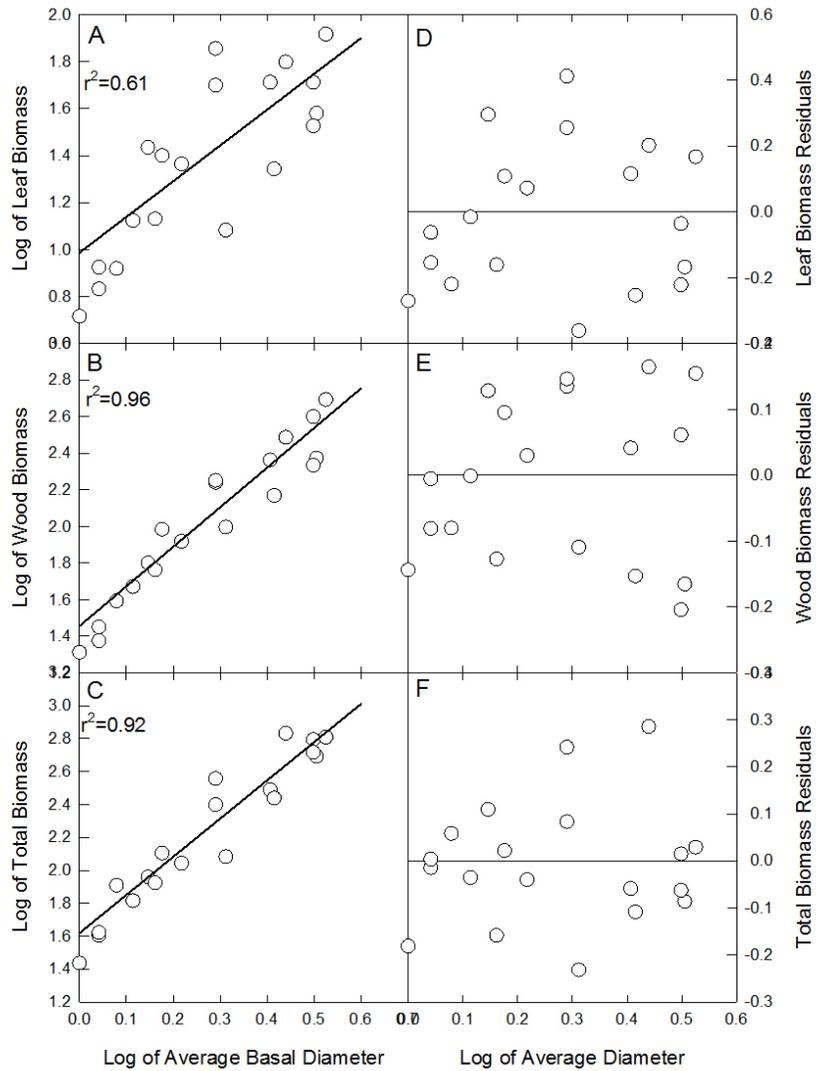
<i>Dodonaea</i> shrubland	Weeding Treatment	Carbon	Control	Fertilizer	Weeding treatment p, f, df	Soil nutrient treatment p, f, df
Soil CO2 Efflux	No weeds	1.95 ± 0.25	1.59 ± 0.13	1.63 ± 0.19	P=0.748, f=0.106, df=1	P=0.097,f=2.629, df=2
	Weeds	2.01 ± 0.24	1.76 ± 0.18	1.54 ± 0.24		
VWC	No weeds	10.27 ± 1.58 ^a	9.59 ± 1.37 ^b	4.20 ± 0.64 ^c	P=0.799, f=1.300, df=1	P=0.000, f=70.782, df=2
	Weeds	10.44 ± 1.89 ^a	8.35 ± 1.31 ^b	4.95 ± 0.88 ^c		
Soil Temperature	No weeds	18.81 ± 1.08 ^a	18.65 ± 1.05 ^a	19.80 ± 1.14 ^b	P=0.486, f=0.503, df=1	P=0.000, f=11.594, df=2
	Weeds	18.88 ± 1.04 ^a	18.25 ± 1.09 ^a	19.66 ± 1.17 ^b		



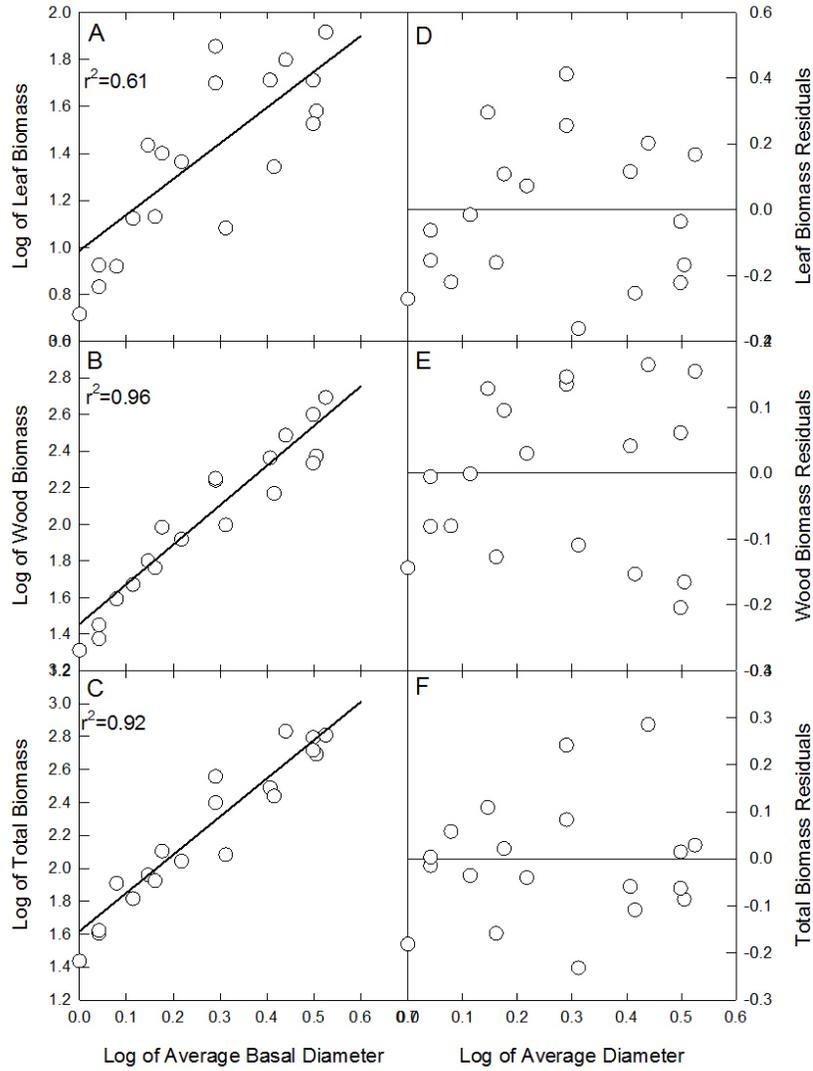
Supplemental Fig. 1. Carbon content of (a) live vegetation, (b) detritus, and (c) total ecosystem pools in paired pig present versus pig free plots across the wet forest chronosequence. No significant differences were present in pig removal versus pig present pairs.



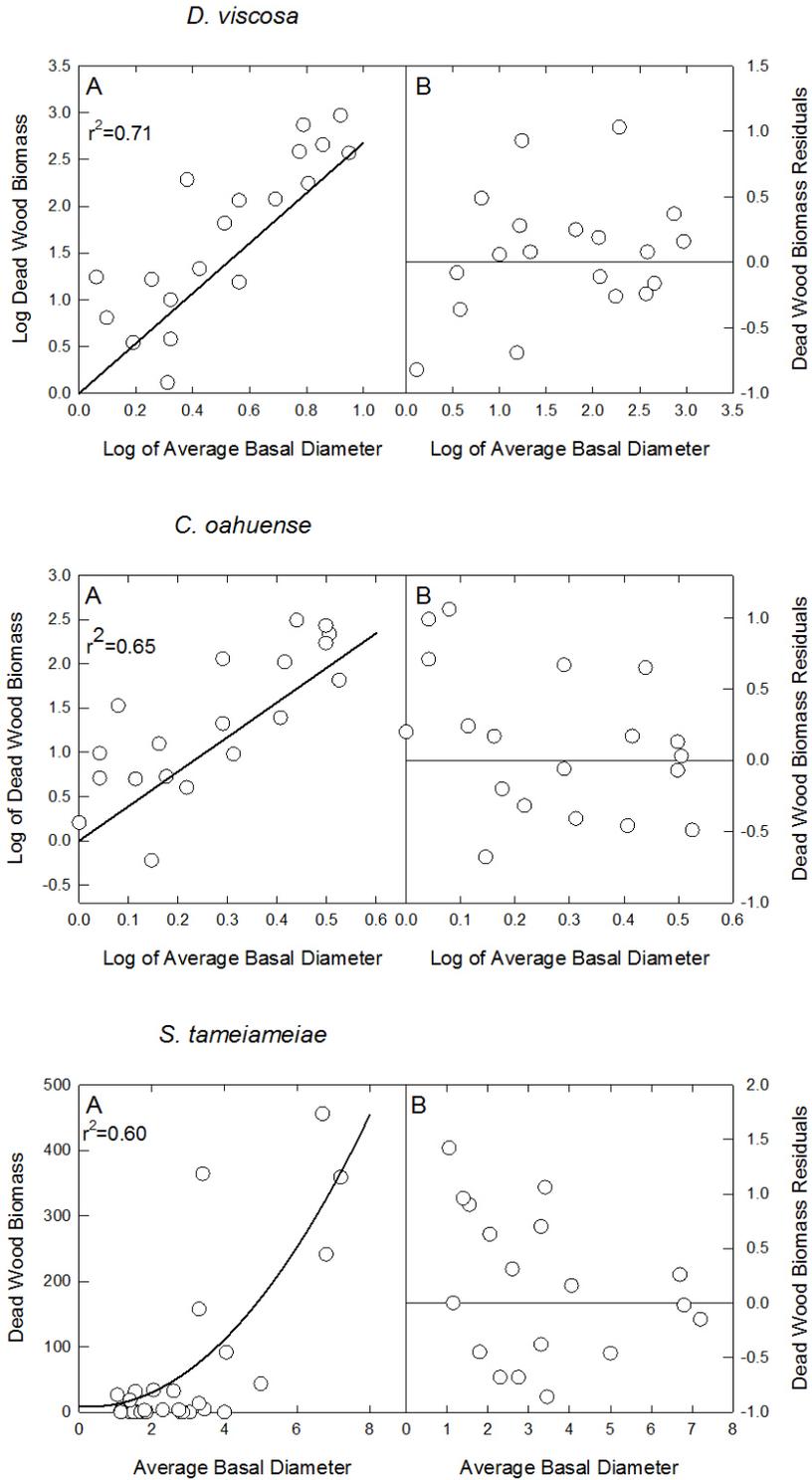
Supplemental Fig. 2. The relationship between (a) leaf biomass, (b) wood biomass, and (c) total biomass and basal diameter used to estimate live and dead aboveground biomass for *D. viscoa* and the associated (d-e) residual plots.



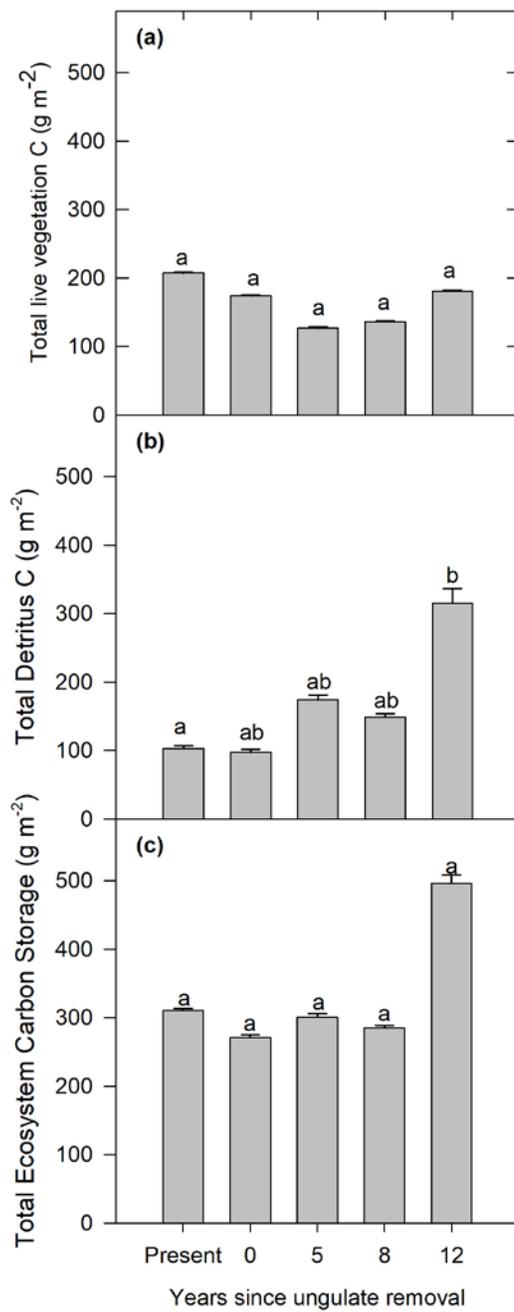
Supplemental Fig. 3. The relationship between (a) leaf biomass, (b) wood biomass, and (c) total biomass and basal diameter used to estimate live and dead aboveground biomass for *C. oahuense* and the associated (d-e) residual plots.



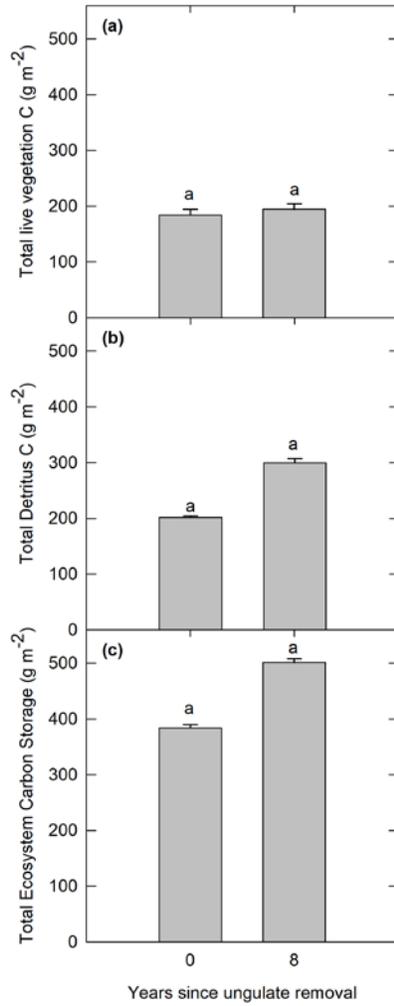
Supplemental Fig. 4. The relationship between (a) leaf biomass, (b) wood biomass, and (c) total biomass and basal diameter used to estimate live and dead aboveground biomass for *S. tameiameiae* and the associated (d-e) residual plots.



Supplemental Fig. 5. The relationship between (a) dead wood biomass and basal diameter and (b) the associated residual plots utilized in developing allometric equations for three common species in the *Metrosideros* woodland and *Dodonaea* shrubland.



Supplemental Fig. 6. Carbon content of (a) live vegetation, (b) detritus, and (c) total ecosystem pools across the *Metrosideros* woodland forest chronosequence. Letters denote significant differences.



Supplemental Fig. 7. Carbon content of (a) live vegetation, (b) detritus, and (c) total ecosystem pools across the *Dodonaea* shrubland chronosequence. Letters denote significant differences.

B. Publications and presentations to date

Publications: Published

1. Chynoweth, M.W., Lepczyk, C.A., Litton, C.M., Hess, S.C., Kellner, J.R., Cordell, S. 2015. Home range use and movement patterns of nonnative feral goats in a tropical island montane dry landscape. *PLoS ONE* 10, e0119231. doi:0119210.0111371/journalpone.0119231.
2. Knauf, A. 2016. Effects of soil nutrient availability on nonnative invasive and native plants in Hawaiian wet and dry ecosystems. M.S. Dissertation. University of Hawaii, Manoa, Honolulu, HI.
3. Long, M.S. 2017. Effects of feral pig removal on soil properties and belowground carbon cycling in native Hawaiian montane wet forests. M.S. Thesis. University of Hawaii at Manoa.
4. Long, M.S., Litton, C.M., Giardina C.P., Deenik, J., Cole, R.J., and Sparks, J.P. 2017. Impact of nonnative feral pig removal on soil structure and nutrient availability in Hawaiian tropical montane wet forests. *Biological Invasions* 19: 749-763.
5. Wehr, N.H., Hess, S.C., and Litton, C.M. 2018. Biology and Impacts of Pacific Islands Invasive Species. 14. *Sus scrofa*, the Feral Pig (Artiodactyla: Suidae). *Pacific Science* 72, 177-198.
6. Hess, S. C., Wehr, N. H. and Litton, C. M. In press. Ecology, Impacts, and Management in the Pacific Islands: Invasive Wild Pigs in North America. VerCauteren, K., Strickland, B., Beasely, J., & Mayer, J., Eds. CRC Press.

Publications: In preparation

1. Knauf, A., Litton, C.M., Cole, R.J., Sparks, J.P., Giardina C.P., and Gerow, K. Linking growth and physiological responses of native and nonnative, invasive plants to soil nutrient availability. *Ecological Applications*: In preparation.
2. Cole R.J., Litton C.M., Sparks J.P., & Giardina C.P. Vegetation response to removal of nonnative ungulates from three Hawaiian dry forest habitats. *Journal of Applied Ecology*: In preparation.
3. Litton, C.M., Sparks, J.P., Cole, R.C., and Giardina, C.P. Impact of nonnative ungulate removal on ecological processes in wet and dry tropical ecosystems. *Ecosystems*: In preparation.
4. Long, M.S., Litton, C.M., Cole, R.C., Giardina, C.P. Sparks, J.P., and Deenik, J. Impact of feral pig removal on soil carbon pools and fluxes in native Hawaiian tropical montane wet forest. *Soil Biology & Biochemistry*: In preparation.
5. Cole, R.J., Sparks, J.P., Knauf, A.E., Litton, C.M., Gerow, K.G., and Giardina C.P. Manipulating soil nutrients to restore invaded Hawaiian ecosystems. *Journal of Applied Ecology*: In preparation

Presentations: January 2015 – April 2018

1. Cole, R.J., Litton, C.M., Giardina, C.P., Knauf, A., Long, M. and Sparks, J.P. 2015. Ecosystem responses to fencing and removal of nonnative ungulates in Pacific Island forest. USDA Forest Service, Institute of Pacific Islands Forestry Seminar Series, Hilo, HI, 06/02/15.
2. Knauf, A., Litton, C., Cole, R., Giardina, C., and Sparks, J.P. 2015. Effects of soil nutrient availability on competitive dynamics between nonnative invasive and native species in Hawaiian tropical dry montane forests. College of Tropical Agriculture and Human Resources Student Research Symposium, University of Hawaii at Manoa, Honolulu, HI, 04/10/15.

3. Cole, R.J., Litton, C.M., Giardina, C.P., Long, M. and Sparks, J.P. 2015. Vegetation response across four Hawaiian ecosystems following removal of nonnative ungulates, Hawaii Ecosystems Annual Meeting, Hilo, HI, 07/09/15.
4. Knauf, A., Litton, C., Cole, R., Giardina, C., and Sparks, J.P. 2015. Effects of soil nutrient availability on competitive dynamics between nonnative invasive and native species in Hawaiian tropical dry montane forests. Hawaii Ecosystems Annual Meeting, Hilo, HI, 07/09/15.
5. Cole, R.J., Litton, C.M., Giardina, C.P., and Sparks, J.P. 2015. Vegetation response to removal of nonnative ungulates across Hawaiian tropical montane dry and wet ecosystems. 52nd Annual Meeting of the Association for Tropical Biology and Conservation, Honolulu, HI, 07/15/15.
6. Knauf, A., Litton, C., Cole, R., Giardina, C., and Sparks, J.P. 2015. Effects of soil nutrient availability on competitive dynamics between nonnative invasive and native species in Hawaiian tropical dry montane forests. 52nd Annual Meeting of the Association for Tropical Biology and Conservation, Honolulu, HI, 07/15/15.
7. Litton, C.M., Long, M., Cole, R.J., Sparks, J.P. and Giardina, C.P. 2015. Response of soil physical & chemical properties to removal of feral pigs from Hawaiian montane tropical wet forest. 52nd Annual Meeting of the Association for Tropical Biology and Conservation, Honolulu, HI, 07/15/15.
8. Sparks, J.P., Sparks, K.L., Cole, R.J., Long, M.S., Knauf, A., Litton, C.M., and Giardina C.P. 2015. What happens when the animals are gone? Investigating ecosystem function post the removal of nonnative ungulates. Ecology and Management of Alien Plant Invasions, Waikoloa Village, HI, 09/24/15.
9. Knauf, A., Litton, C.M., Cole, R., Giardina, C., and Sparks, J.P. 2015. Effect of soil nutrient availability on nonnative invasive vs. native plant growth. Ecology and Management of Alien Plant Invasions, Waikoloa Village, HI, 09/22/15.
10. Knauf, A., Litton, C., Cole, R., Giardina, C., and Sparks, J. 2015. Effect of soil nutrient availability on competitive dynamics between nonnative invasive and native plants in Hawaiian tropical dry montane ecosystems. Hawaii Conservation Conference, Hilo, HI, 08/05/15.
11. Cole, R., Litton, C., Stewart, M., Hamnett, R., Giardina, C., and Sparks, J. 2015. Vegetation responses across four Hawaiian ecosystems following removal of nonnative ungulates. Hawaii Conservation Conference, Hilo, HI, 08/05/15.
12. Cole, R.J. 2016. Restoration across diverse tropical ecosystems. Carbon Sequestration Potential of Restoration Conference. Piro Biological Station, Costa Rica, 02/07/16.
13. Sparks, J.P., Sparks, K.L., Cole, R.J., Long, M.S., Knauf, A., Litton, C.M., and Giardina C.P. 2016. What happens when the animals are gone? Investigating ecosystem function post the removal of nonnative ungulates. NREM Seminar Series, Honolulu, HI, 02/29/16.
14. Litton, C.M., Cole, R.J., Long, M.S., Knauf, A., Sparks, J.P., and Giardina C.P. 2016. Impacts of nonnative ungulate removal on vegetation and ecological processes: A tale of two sides of the fence. NREM Seminar Series, Kahului, HI, 03/18/16.
15. Knauf, A., Litton, C., Cole, R., Giardina, C., and Sparks, J. 2016. Effect of soil nutrient availability on nonnative invasive vs. native plant growth. College of Tropical Agriculture and Human Resources Student Research Symposium, Honolulu, HI, 04/09/16.

16. Cole, R.J. 2016. What happens after the animals are gone? Investigating recovery following removal of nonnative ungulates from Hawaiian ecosystems. Department of Environmental Sciences Seminar Series, Huxley College of the Environment, Bellingham, WA, 05/19/16.
17. Knauf, A., Litton, C.M., Cole, R.J., Giardina, C., and Sparks, J. 2016. Effects of soil nutrient availability on nonnative invasive and native species in Hawaiian wet and dry ecosystems. Ecological Society of America Annual Meeting, Ft. Lauderdale, FL, 08/09/16.
18. Santiago, M.Q., Knauf, A., Litton, C.M., Cole, R.J., and Sparks, J.P. 2016. Photosynthetic and biomass responses of native versus nonnative plants from Hawaiian wet forest under varying soil nutrient availabilities. Ecological Society of America Annual Meeting, Ft. Lauderdale, FL, 08/12/16.
19. Cole, R.J. 2017. Recuperación de ecosistemas nativos. University of Costa Rica Field Ecology Course. Las Cruces Biological Station, Costa Rica, 05/01/17.
20. Cole, R.J. 2017. After the animals are gone: Investigating recovery following removal of nonnative ungulates from Hawaiian ecosystems. Alma College Field Course, Las Cruces Biological Station, Costa Rica, 05/19/17.
21. Cole, R.J. 2017. After the animals are gone: Investigating recovery following removal of nonnative ungulates from Hawaiian ecosystems. R. Tropical Field Biology Graduate Course, Las Cruces Biological Station, Costa Rica, 06/26/17.
22. Litton, C.M., Knauf, A., Cole, R.J., Sparks, J.P. and Giardina, C.P. 2017. Manipulating soil nutrient availability to promote native species following nonnative ungulate removal. Hawaii Conservation Conference, Honolulu, HI, 07/20/17.
23. Litton, C. M., Cole, R. J., Giardina, C. P., and Sparks, J. P. . 2017. Recovery of vegetation and ecological processes following removal of nonnative ungulates from Pacific Island terrestrial ecosystems (Oral Presentation). SERDP and ESTCP Symposium, Washington, D.C., 11/28/17.
24. Litton, C. M., Cole, R. J., Giardina, C. P., Knauf, A., Long, M., Sparks, K., and Sparks, J. P. 2017. Recovery of native plant communities and ecological processes following removal of nonnative, invasive ungulates from Pacific Island forests (Poster Presentation). SERDP and ESTCP Symposium, Washington, D.C., 11/28/17.
25. Cole, R.J. 2018. After the animals are gone: Investigating recovery following removal of nonnative ungulates from Hawaiian ecosystems. Organization for Tropical Studies Graduate Biology Field Course, Las Cruces Biological Station, Costa Rica, 05/01/18.

