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Impact of nonnative feral pig removal on soil structure and nutrient availability in Hawaiian tropical montane wet forests

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Abstract Conservation and restoration of ecosystems impacted by nonnative ungulates increasingly involves their removal and exclusion. While the influence of nonnative ungulate removal on plant communities is commonly monitored, impacts on underlying ecological processes are seldom quantified. Here we examined how nonnative feral pig (*Sus scrofa*) removal from Hawaiian tropical montane wet forests affects soil physical and chemical properties. Unique to this study, measurements were taken in paired sites inside and outside of five feral pig removal units representing a ~20 year, highly constrained chronosequence where other potentially confounding variables are held constant. Additional targeted measurements were taken inside and outside of a single exclosure in areas characterized by 'low' versus 'high' feral pig activity. Overall, nonnative feral pig removal increased stable soil aggregates and porosity, and decreased bulk density, water-filled pore space, and soil moisture content. Further, feral pig removal increased soil nutrient regeneration as evidenced by increased extractable cations, increased resin available NO_3^- and total inorganic N, and enriched foliar $\delta^{15}N$. Increasing time since feral pig removal was positively related to net nitrification and total net inorganic N mineralization, and negatively related to pH and net ammonification. Results from both the chronosequence and targeted sampling were consistent in direction and support a central role of feral pig removal in modifying soil physical and chemical properties. Changes in soil properties following ungulate removal coincided with large increases in understory vegetation cover, highlighting the need to better understand aboveground-belowground linkages following nonnative ungulate removal.

Keywords Chronosequence · Ecological restoration · Nonnative ungulates · Soil physical and chemical properties · *Sus scrofa*

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Introduction

Nonnative species invasions impact ecosystem function and the provisioning of goods and services globally (Vitousek et al. 1996; Mack and D'Antonio 1998; Mack et al. 2000; Ehrenfeld 2003; Didham et al. 2005; Peltzer et al. 2010), and so burden local and

national economies (Pimentel et al. 2000; Pejchar and Mooney 2009). Nonnative ungulates can be particularly destructive, resulting in the local extirpation of native taxa and facilitation of nonnative plant invasions (Campbell and Long 2009; Spear and Chown 2009; Nuñez et al. 2009; Oduor et al. 2010), and transmission of soil-borne pathogens, parasites and zoonotic diseases (Barrios-Garcia and Ballari 2012; Krull et al. 2013; Li et al. 2013). Consequently, control of nonnative ungulates is broadly viewed as a critical first step in the conservation and restoration of native ecosystems globally (Courchamp et al. 2003; Spear and Chown 2009).

Ungulates in general can alter soil organic matter (SOM) mineralization and the availability of nutrients via excreta, alterations in the litter layer, and physical fragmentation of organic matter during foraging and rooting activities (Hobbs 1996; Frank et al. 2000; Siemann et al. 2009; Palacio et al. 2013). In addition, ungulates have been shown to compact soils (Vtorov 1993), reduce soil aggregate stability (Beever et al. 2006), and disrupt soil structure, all of which play an important role in controlling the cycling and availability of soil nutrients (Brady and Weil 2010). European wild boars (*Sus scrofa*)—or 'feral pigs' in areas where they are nonnative—are thought to have particularly strong impacts on soils due to their rooting habit. However most existing research has focused on how these animals alter the structure and diversity of plant communities, with little information on how they impact soil properties (Spear and Chown 2009; Barrios-Garcia and Ballari 2012). Moreover, findings from the few existing studies that have examined the impacts of feral pigs on soils have largely been inconsistent.

In studies conducted in their home range, wild boar disturbance in Spanish alpine grasslands decreased soil moisture, carbon:nitrogen (C:N), ammonium (NH_4^+) and extractable Na, Mg, and Ca in soil solution, while increasing bulk density, total N, and nitrate (NO_3^-) (Bueno et al. 2013). In the Netherlands, wild boar rooting did not affect SOM (Bruinderink and Hazebroek 1996), while in Switzerland wild boars increased SOM and decreased inorganic N availability (Wirthner et al. 2012). In their introduced range, feral pig impacts on SOM and nutrient availability have also been variable across studies. Feral pig disturbance decreased bulk density in Tennessee deciduous forests (Singer et al. 1984), while bulk density decreased

within seven years of feral pig removal from a native Hawaiian montane wet forest (Vtorov 1993). In both cases, soil disturbance by feral pigs decreased soil faunal diversity and abundance (Singer et al. 1984; Vtorov 1993). In turn, SOM decomposition, cation exchange capacity and soil acidity increased with feral pig disturbance in high elevation beech gaps (Lacki and Lancia 1983), while feral pig removal had no effect on N mineralization or pH under oak canopies and grasslands on Santa Cruz Island (Moody and Jones 2000). In Texas mixed pine-hardwood forest, feral pig disturbance lowered soil C:N, presumably due to accelerated N mineralization (Siemann et al. 2009). Feral pig disturbance also increased N mineralization in deciduous forest (Singer et al. 1984), but had no significant impact in a coastal California grassland (Cushman et al. 2004). Inconsistent effects of wild boar and feral pigs could be an artifact of sampling scheme, statistical methods, or the natural heterogeneity of ecological systems (Davidson and Hewitt 2014). In addition, lack of consistent results across disparate studies may reflect underlying differences in the ecosystems studied in terms of initial soil properties, degree of degradation by ungulates, and/or feral pig population dynamics.

Despite inconsistencies in their impacts across studies, feral pigs are considered to be a destructive ungulate on all continents except Antarctica, with particularly large impacts on oceanic islands (Barrios-Garcia and Ballari 2012). In Hawaii in the late 18th century, European explorers and settlers released European wild boar that subsequently interbred with domesticated Asiatic pigs (*Sus scrofa vittautus*) introduced by Polynesian settlers in prior centuries to create the feral pig populations that exist today (Nogueira-Filho et al. 2009; Linderholm et al. 2016). Biodiversity conservation and ecological restoration in feral pig-impacted areas in Hawaii, and throughout the world, has increasingly relied on creating feral pig-free management areas via fencing and ungulate removal (Scowcroft and Hobdy 1987; Stone et al. 1992; Hess and Jacobi 2011; Cole and Litton 2014).

Within fenced management units from which feral pigs have been removed, common native and nonnative vegetation typically increase in density and abundance, with limited recruitment of rarer species (Stone et al. 1992; Tanentzap et al. 2009; Weller et al. 2011; Cole and Litton 2014), highlighting that fencing

and nonnative ungulate removal alone are often insufficient to achieve overall management objectives (Stone et al. 1992; Cole et al. 2012; Nuttle et al. 2014; Cole and Litton 2014). Soil alteration by nonnative ungulates may at least partially explain why vegetation recovery following ungulate removal can be site-specific, or dominated by nonnative plants (Siemann et al. 2009; Stritar et al. 2010; Barrios-Garcia and Ballari 2012; Kardol et al. 2014). Conversely, a lack of response in vegetation to ungulate removal may indicate few changes to soil properties given the strong linkages between above- and belowground communities (Wardle et al. 2004). However, this topic has received very little attention in the scientific literature, particularly in the context of nonnative ungulates (Campbell and Long 2009; Spear and Chown 2009; Kardol et al. 2014; Cole and Litton 2014).

To this end, we utilized a highly constrained, long-term chronosequence of feral pig removal units on Hawaii Island to examine how ungulate removal influences soil physical properties and biogeochemical processes. It was previously reported that native understory plant density, plant species richness, and the presence of ground-rooted woody plants were higher where feral pigs had been removed from this system. The change in vegetation with feral pig removal occurred concurrently with an increase in forest floor litter and bryophyte cover, and a corresponding decrease in exposed soil (Cole et al. 2012; Cole and Litton 2014). Here, we examine the impacts of feral pig removal on soil structure and nutrient availability by measuring a suite of soil physical and chemical properties across the chronosequence (chronosequence plots). In addition, we compared soil structure and nutrient availability inside and outside of the second oldest exclosure with targeted sampling (targeted plots) in areas with recent and heavy feral pig disturbance (i.e., digs and wallows) versus areas with historically low disturbance (i.e., areas between fallen trees or other natural barriers). Because feral pig removal increased understory vegetation and forest floor cover (Cole and Litton 2014), we hypothesized that removal would decrease bulk density while increasing soil aggregation and soil nutrient availability. We also hypothesized that changes in soil structure and nutrient availability would increase with time since feral pig removal as understory vegetation recovered. Finally, we expected

the direction of change with feral pig removal to be consistent between chronosequence and targeted plots, but that the magnitude of change would be greater in targeted plots characterized by higher and more recent feral pig activity.

Methods

Study sites

This study was conducted between August 2010 and December 2012 using plots established by Cole and Litton (2014) along a chronosequence of five feral pig exclosure units ranging from 6.6 to 18.5 years since removal on the East flank of Mauna Loa Volcano on the Island of Hawaii (Fig. 1). Estimated feral pig densities in surrounding forest are 0.6–16.3 animals/km^2 (Scheffler et al. 2012). All study plots are located between 1140 and 1370 m.a.s.l. Mean annual temperature and precipitation across all plots are 14.4–15.9 °C and 2910–3985 mm, respectively, with little seasonality (Giambelluca et al. 2013, 2014). Plots are located on 2000–10,000 year-old, tephra-derived Andisols of two closely related series: Eheuiki (medial, ferrihydritic, isothermic Typic Hydrudands) and Puaulu (medial over ashy, aniso, ferrihydritic over amorphic, isothermic Aquic Hapludands) (NRCS 2010). These soil series are characterized by deep, moderately well drained soils formed in basic volcanic ash deposited over basic lava with slopes of 2–5% (NRCS 2010). All plots are located in *Metrosideros polymorpha* (overstory tree)/*Cibotium* spp. (midstory tree fern) tropical montane wet forest (Wagner et al. 1990), with exclusively native canopy vegetation (Cole and Litton 2014).

Sampling occurred along the chronosequence (chronosequence plots) in pairs of plots established inside and outside of each fenced unit, with each plot consisting of four circular 9 m radius (256 m^2) replicate sub-plots located >70 m from fence lines and >140 m from each other (Fig. 1). We also conducted targeted sampling inside and outside of the 16.5 year-old feral pig exclosure (targeted plots) in ten 6 m^2 plots located along 150 m transects both outside the fenced unit in areas with recent and heavy feral pig disturbance (e.g., digs and wallows) and inside the fenced unit in areas naturally protected from feral pig disturbance (i.e., between fallen trees or other

Fig. 1 Study site locations inside and outside of five feral pig exclosures representing an 18.5 year chronosequence of feral pig removal units on the East slope of Mauna Loa Volcano, Island of Hawaii. Paired chronosequence study sites are labeled by years since feral pig removal (R) versus feral pig presence (P)
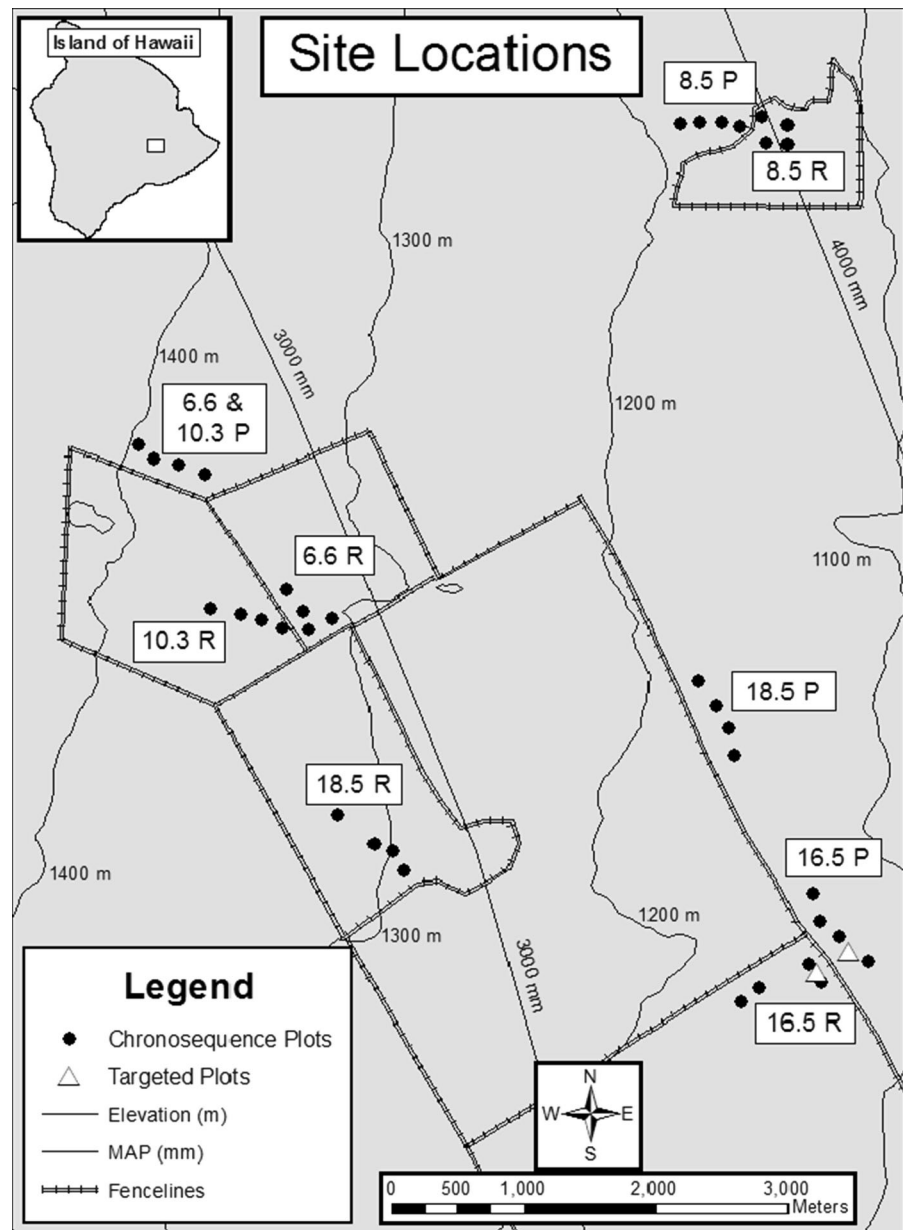
natural barriers) (Fig. 1). The targeted plots were designed to estimate maximal differences in soil properties with feral pig removal.

Soil sampling and analyses

In both chronosequence and targeted sampling plots, we collected soil cores to quantify the following variables: bulk density, porosity, water-filled pore space, water-stable soil macro-aggregates (>250 μm; WSA), resin available inorganic N (NO_3^- and NH_4^+), net N mineralization (NO_3^- and NH_4^+), pH, extractable nutrients (P, K, Ca, and Mg), mineral soil organic carbon (SOC) and soil organic nitrogen (SON), and hot water soluble C (i.e., labile SOC). We also measured soil volumetric water content (VWC) in each plot, and foliar $\delta^{15}N$ of the three dominant species in the overstory and midstory in the chronosequence plots as an index of soil nutrient cycling and availability (Craine et al. 2009). Over four consecutive days

characterized by constant weather, ten 5.1 cm diameter × 10 cm deep soil cores were collected from each chronosequence sub-plot and three soil cores were collected within each targeted sampling plot. The soil core locations were evenly distributed within the chronosequence sub-plots, and randomly established in each targeted plot. Soil cores were composited by sub-plot for chronosequence plots, transported to a refrigerator in coolers, and processed within 48 h of collection. Roots and rocks >0.6 cm were removed from each composited sample, and soils were weighed and homogenized for analyses.

The allophone and imogolite dominated Andisols of our study system are characterized by aluminum-humus complexes that promote strong stable aggregates (Nanzyo 2002; Perret and Dorel 2006). As these soils dry, their colloidal fraction irreversibly solidifies into pseudo-sands that cannot be rewetted (Nanzyo 2002; Perret and Dorel 2006). Consequently, all analyses were determined on fresh soil samples, except for SOC, SON and bulk density which were determined on oven-dried samples.

To determine SOC and SON content, homogenized sub-samples of field-moist soil were oven-dried at 70 °C to a constant mass and passed through a #10 (2 mm mesh) sieve. A representative sub-sample was ball-milled, passed through a #40 (0.5 mm mesh) sieve, and analyzed for SOC and SON content with a Costech Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA) at the University of Hawaii at Hilo Analytical Laboratory (UHHAL) in Hilo, HI. Bulk density (g cm^{-3}) was determined after oven-drying two weighed sub-samples of field-moist soil to a constant mass at 105 °C ($\sim$24 h), averaging the percent water lost across the two samples, and estimating the 105 °C dry weight equivalent of the bulk soil collection:

$$BD = \left(DW_{sample105}\right)/V_{core} \tag{1}$$

where $DW_{sample105}$ is the average 105 °C dry weight of the bulk sample and V_{core} is the total volume of the bulk sample.

Soil porosity (%) was calculated using a particle density of 2.65 g cm^{-3} (Soil Survey Staff 2014), which was then used to calculate water-filled pore space (%) (Soil Survey Staff 2014). Water stable macro-aggregates (WSA) >250 μm were quantified using the wet-sieving procedure from the USDA NRCS Soil Quality Test Kit (2001). Pseudo-sands

formed by aluminum-humus complexes in Andisols resist standard dispersion methods (Silva et al. 2015) and preclude quantifying sand content in WSA. As a result, $\sim$14 g of homogenized field-moist soil was placed onto a 250 μm sieve that was moved vertically 1.5 cm in DI water at 30 cycles per min for 3 min. Material >250 μm was oven-dried at 105 °C for 24 h and weighed. A second $\sim$12 g sub-sample was weighed, dried at 105 °C for 24 h and reweighed to determine gravimetric water content and calculate the dry weight of the field-moist sieved sample. WSA was then calculated as:

$$\% \ WSA = M_{WS}/M_{dry} * 100 \tag{2}$$

where M_{WS} is the dry mass of WSA (g) and M_{dry} is the dry weight of the sample prior to sieving.

Soil VWC was measured with a Hydrosense CS620 Water Content Sensor (Campbell Scientific, Logan, UT) with 12 cm probes. In each chronosequence sub-plot, sampling occurred at twelve evenly distributed locations throughout the plot. In each targeted plot, sampling occurred at eight randomly selected locations throughout the plot.

Resin available inorganic nitrogen (NO_3^- and NH_4^+; μg N 10 cm^{-2} 4 weeks^{-1}) was estimated with a 4-week deployment of Plant Root Simulator (PRS) Probes (Western Ag Innovations, Saskatchewan, Canada). In each chronosequence sub-plot, eight pairs of probes (one NO_3^- and one NH_4^+ probe per pair) were evenly distributed throughout the plot. In each targeted sampling plot, four pairs of probes were installed at four randomly selected locations. Foliar $\delta^{15}N$ was quantified as an index of the cycling and availability of soil N in the chronosequence plots using recently expanded sunlit leaves from three individuals each of *Cibotium glaucum* (tree fern), *Cheirodendron trigynum* (mid-canopy tree) and *M. polymorpha* (canopy tree) in each plot. These three species comprise >95% of stand basal area across all study sites (Cole and Litton 2014). Foliage samples were oven-dried at 70 °C, ball-milled to pass through a #60 sieve (0.25 mm mesh), and analyzed for $\delta^{15}N$ on an isotope ratio mass spectrometer (Model DeltaV, Thermo Environmental) at the Cornell University Stable Isotope Laboratory, Ithaca, NY.

Net N mineralization (N_{MIN}) was determined with a 2 M KCl extraction following a 30 days laboratory aerobic incubation at room temperature with soil moisture held at field capacity. Extracts were analyzed

for NH_4^+ and NO_3^- concentrations using an AutoAnalyzer (Pulse Instrumentation, Labtronics) at the UHHAL. The labile C pool was estimated via hot-water extraction described in Ghani et al. (2003) with the omission of the initial extraction of 20 °C water soluble C. Extracted labile C (μg C mL^{-1}) was quantified on a Shimadzu TOC-V Total Organic Carbon Analyzer (Shimadzu Scientific Instruments, Columbia, MD) at the UHHAL.

Soil pH, and extractable soil P, K, Ca, and Mg were determined at the University of Hawaii at Manoa Agricultural Diagnostics Service Center, Honolulu, HI. Extractable P was quantified with the Modified-Truog method and colorimetric analysis with an autoanalyzer, while K, Ca and Mg were determined via ammonium acetate extraction and atomic absorption spectrophotometer (Hue et al. 2000). Extractable nutrients are reported as volumetric concentrations to include any differences in soil bulk density with feral pig removal.

Statistical analyses

For chronosequence sampling the exclosure was the unit of replication, and for targeted sampling the individual plot was the unit of replication. The effect of time since feral pig removal on each soil property across the chronosequence ($n = 5$) was assessed with linear regression analyses of time since removal versus the percent relative difference between paired plots:

$$[(\text{Feral pig removal} - \text{Feral pig present})/$$
$$\text{Feral pig present}] \times 100 \qquad (3)$$

To determine if feral pig removal had a significant effect across the entire chronosequence, one-sided Wilcoxon signed-rank tests, which do not assume normally distributed data, were conducted on ranked differences between mean values in each pair of plots ($n = 5$), where plot mean values were an average of each soil property across four sub-plots/plot.

Results from the targeted plots were also determined to be non-normally distributed (Anderson–Darling tests on bootstrapped treatment means; 2000 iterations; $P < 0.05$) with satisfactory homogeneity of variance (non-parametric Levene's test; $P > 0.10$). Therefore, the effect of feral pig removal in the targeted plots was analyzed using one-sided non-parametric Mann–Whitney U tests ($n = 10$). All

statistical analyses were conducted using Minitab 16 statistical software (State College, PA) at $\alpha = 0.10$ due to small sample sizes. We report means $\pm$ 1 standard error (S.E.) throughout for both chronosequence and targeted plot results.

Results

Increasing time since feral pig removal from the chronosequence plots was negatively and linearly related to soil pH ($F_{(1,3)} = 16.74$, $r^2 = 0.85$, $P = 0.03$) and net ammonification ($F_{(1,3)} = 95.34$, $r^2 = 0.97$; $P < 0.01$; Fig. 2a). In addition, increasing time since feral pig removal was positively and
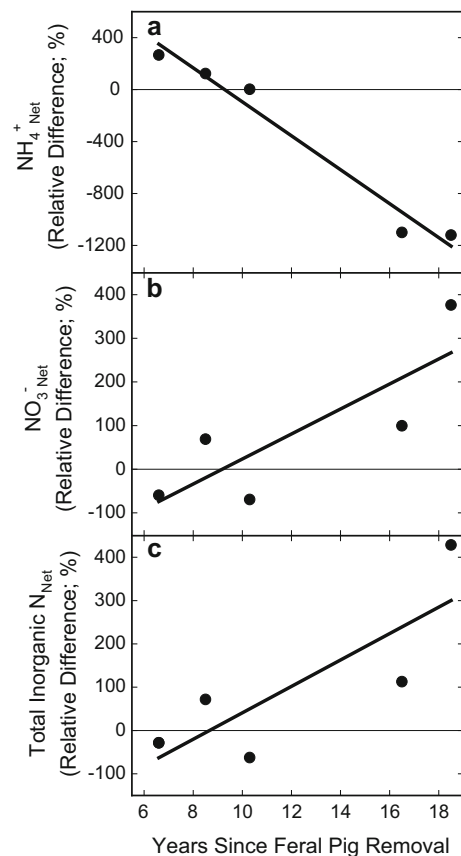
Fig. 2 The relative difference in **a** net ammonification ($NH_4^+{}_{Net}$) between paired feral pig removal and feral pig present sites was negatively related to increasing time since feral pig removal across the chronosequence plots, while the relative differences in **b** net nitrification ($NO_3^-{}_{Net}$) and **c** total net inorganic N mineralization (Total Inorganic N$_{Net}$) were positively related to increasing time since feral pig removal
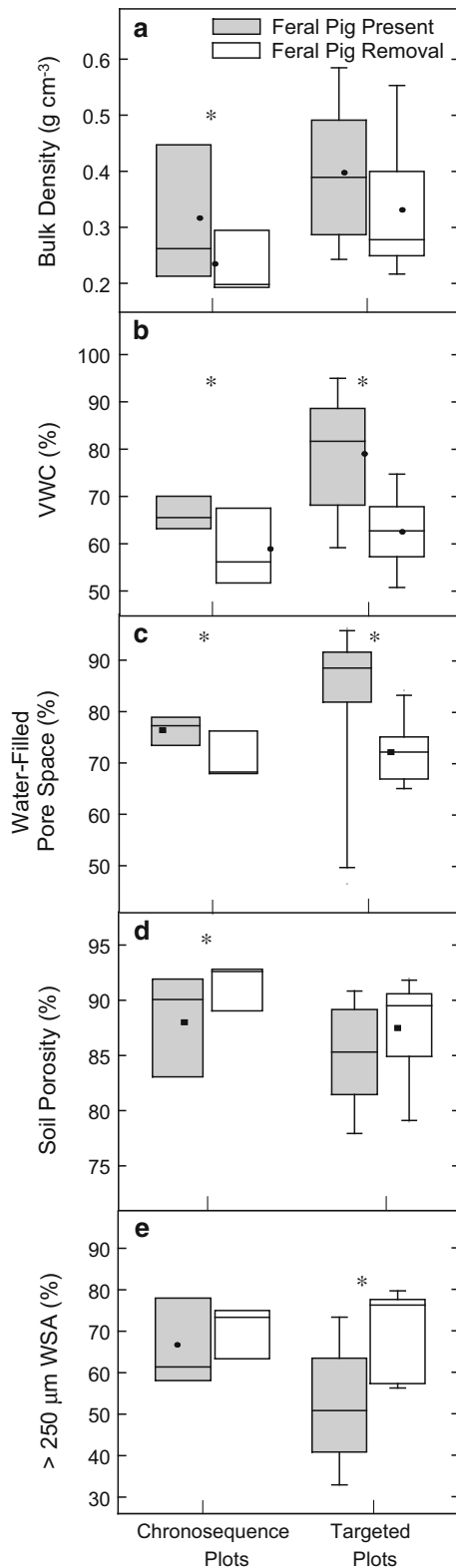
Fig. 3 Feral pig removal decreased **a** bulk density and **b** volumetric water content in the chronosequence plots, and decreased **c** water-filled pore space in both the chronosequence and targeted plots; and increased **d** soil porosity in the chronosequence plots and **e** percent water-stable soil macro-aggregates (WSA) in the targeted plots. *Whiskers* indicate the 10 and 90% percentiles (no whiskers for chronosequence plots due to small sample size); *dotted lines* indicate mean and *solid lines* indicate median values; *asterisks* indicate significant differences ($\alpha = 0.10$)

linearly related to net nitrification and total inorganic N mineralization ($F_{(1,3)} = 6.21$, $r^2 = 0.67$, $P = 0.08$ and $F_{(1,3)} = 5.73$, $r^2 = 0.66$, $P = 0.10$, respectively; Fig. 2b, c). Increasing time since feral pig removal had no significant effect on any other measured soil property in the chronosequence plots ($r^2 < 0.60$; $P > 0.12$).

Overall in the chronosequence plots, feral pig removal decreased bulk density by an average of 28% ($W = 14$, $P = 0.05$; $n = 5$; Fig. 3a), VWC by 12% ($W = 14$, $P = 0.05$; $n = 5$; Fig. 3b), and water-filled pore space by 6% ($W = 14$, $P = 0.05$; $n = 5$; Fig. 3c). In contrast, feral pig removal increased soil porosity by 4% ($W = 14$, $P = 0.05$; $n = 5$; Fig. 3d), extractable K by 52%, extractable Ca by 19%, and extractable Mg by 24% ($W = 15$, $P = 0.03$; $n = 5$; Fig. 4a–c). Moreover, feral pig removal enriched *C. trigynum* foliar $\delta^{15}N$ ($W = 13$, $P = 0.09$; $n = 5$), but had no impact on foliar $\delta^{15}N$ in *M. polymorpha* ($W = 8$, $P = 0.50$; $n = 5$) or *C. glaucum* ($W = 12$, $P = 0.14$; $n = 5$) (Fig. 5). Feral pig removal in the chronosequence plots had no significant impact on WSA ($W = 6$, $P = 0.39$; $n = 5$; Fig. 3e); SOC ($W = 10$, $P = 0.79$; $n = 5$), SON ($W = 12$, $P = 0.91$; $n = 5$) or labile C ($W = 3$, $P = 0.14$; $n = 5$) (Fig. 6a–c); or % N ($W = 3$, $P = 0.14$; $n = 5$), % C ($W = 3$, $P = 0.14$; $n = 5$), or C:N ($W = 7$, $P = 0.50$; $n = 5$) (Fig. 7a–c). Finally, there were no effects of feral pig removal on extractable P ($W = 13$, $P = 0.94$; $n = 5$) or pH ($W = 8$, $P = 0.61$; $n = 5$) (Fig. 4d, e); resin available NH_4^+ ($W = 4$, $P = 0.21$; $n = 5$), NO_3^- ($W = 6$, $P = 0.4$; $n = 5$), or total inorganic N ($W = 5$, $P = 0.30$; $n = 5$) (Fig. 8a–c); or $N_{(MIN)}$ ($W = 5$, $P = 0.3$; $n = 5$).

In the targeted plots, removal of feral pigs reduced VWC by 21% ($W = 138.5$, $P < 0.01$; $n = 10$; Fig. 3b); water-filled pore space by 14%
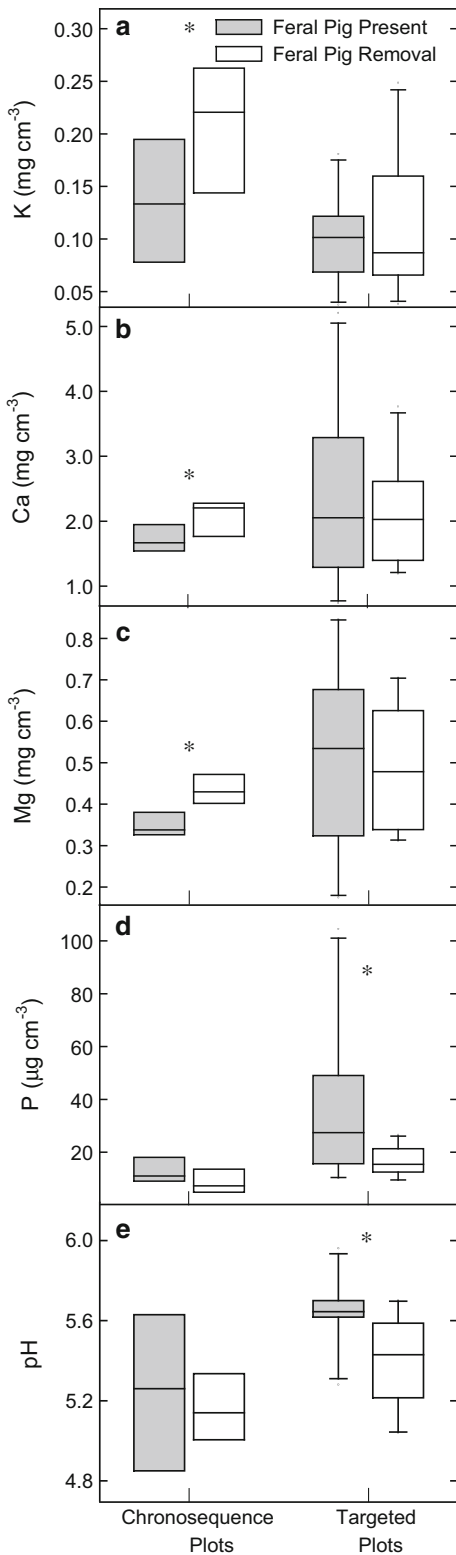
Fig. 4 Feral pig removal increased extractable **a** K, **b** Ca, and **c** Mg in the chronosequence plots, and decreased extractable **d** P and **e** soil pH in the targeted plots. *Whiskers* indicate the 10 and 90% percentiles (no whiskers for chronosequence plots due to small sample size); *dotted lines* indicate mean and *solid lines* indicate median values; *asterisks* indicate significant differences ($\alpha = 0.10$)

($W = 143.0$, $P < 0.01$; $n = 10$; Fig. 3c); SOC by 12% ($W = 105.0$, $P = 0.07$; $n = 10$; Fig. 6a); SON by 17% ($W = 128.0$, $P = 0.04$; $n = 10$; Fig. 6b); extractable P by 55% ($W = 132.0$, $P = 0.05$; $n = 10$; Fig. 4d); and soil pH by 4% ($W = 136.5$, $P < 0.01$; $n = 10$; Fig. 4e). In turn, removal of feral pig disturbance increased WSA by 34% ($W = 69.0$, $P < 0.01$; $n = 10$; Fig. 3e); labile C by 35% ($W = 81.5$, $P = 0.04$; $n = 10$; Fig. 6c); and C:N by 6% ($W = 82.0$, $P = 0.04$; $n = 10$; Fig. 7c). Feral pig removal in the targeted plots also reduced resin available NH_4^+ by 82% ($W = 88.0$, $P < 0.01$; $n = 10$), but increased resin available NO_3^- by almost an order of magnitude ($W = 380$, $P < 0.01$; $n = 10$) and total inorganic N by >200% ($W = 43.0$, $P = 0.03$; $n = 10$) (Fig. 8a–c). Feral pig removal in the targeted plots had no significant impact on bulk density ($W = 122.0$, $P = 0.11$; $n = 10$) or porosity ($W = 88.0$, P $= 0.11$; $n = 10$) (Fig. 3a–d); extractable K ($W = 103.0$, $P = 0.91$; $n = 10$), Ca ($W = 107.0$, $P = 0.91$; $n = 10$), or Mg ($W = 108.0$, $P = 0.85$; $n = 10$) (Fig. 4a-c); % N ($W = 105.0$, $P = 0.50$; $n = 10$) or % C ($W = 100.0$, $P = 0.73$; $n = 10$) (Fig. 7a-b); or $N_{(MIN)}$ ($W = 98.0$, $P = 0.31$; $n = 10$).

Discussion

Soil physical properties

The observed changes in soils following feral pig removal support the hypothesis that this common management approach alters key soil physical properties. Taken together, observed changes in soil properties with feral pig removal represent increased overall soil function and productivity. Lower bulk density and increased soil porosity promote root activity by decreasing soil resistance and increasing
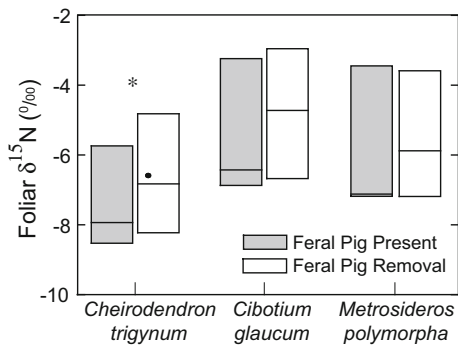
Fig. 5 *Cheirodendron trigynum* foliar $\delta^{15}N$ was significantly enriched following feral pig removal, while *Cibotium glaucum* and *Metrosideros polymorpha* foliar $\delta^{15}N$ were enriched but not significantly different following removal. *Dotted lines* indicate mean and *solid lines* indicate median values; *asterisks* indicate significant differences ($\alpha = 0.10$)

aeration. Increased water stable aggregates reduce soil bulk density, promote water infiltration and percolation, and increase resistance to soil erosion (Amezketa, 1999). Increased soil nutrient regeneration increases stand-level productivity and alters carbon partitioning where nutrients are limiting to primary production (Litton et al. 2007).

Soil aggregates are stabilized by a combination of factors including exchangeable cations, SOM and the labile C pool (Amezketa 1999), as well as plant roots and symbionts, soil fauna, and soil moisture (Bronick and Lal 2005). In Andisols, where soil aggregates are dominated by aluminum-humus complexes and high SOM content (Nanzyo 2002), increases in labile C and extractable cations, especially divalent Ca^{2+}, promotes flocculation and cementation of cation/particle structure to form more stable soil aggregates (Brady and Weil 2010). In this study, feral pig removal in the chronosequence plots increased extractable Ca, K, and Mg by 19, 52, and 24%, respectively, which likely contributed to enhanced WSA. In the targeted plots, feral pig removal increased labile C by 35%, which also likely contributed to the 34% increase in WSA > 250 μm (Ghani et al. 2003; Tisdale and Oades 1982), which is the aggregate size class most vulnerable to physical disturbance (Seybold and Herrick 2001). The digging, rooting and wallowing action of feral pigs appears to physically destroy soil aggregates which, in turn, could expose physically protected SOM to microbial oxidation.

The observed changes in soil physical properties with feral pig removal align with results reported in a
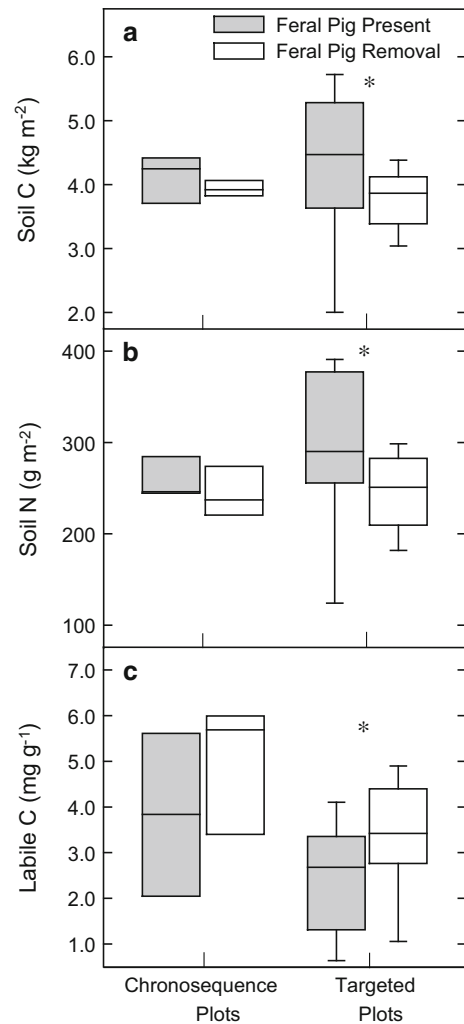

Fig. 6 a Mineral soil organic C and **b** N increased and **c** labile C decreased with feral pig removal in the targeted plots. *Whiskers* indicate the 10 and 90% percentiles (no whiskers for chronosequence plots due to small sample size); *dotted lines* indicate mean and *solid lines* indicate median values; *asterisks* indicate significant differences ($\alpha = 0.10$)

previous study where soil bulk density decreased after seven years of feral pig removal from montane wet forests in Hawaii (Vtorov 1993). Similarly, in alpine grasslands of the Spanish Pyrenees, soil bulk density showed large increases in areas affected by wild boar rooting activity (Bueno et al. 2013). On the other hand, a recent study in the Argentinian Patagonia showed that feral pig disturbance caused a decrease in bulk density (Barrios-García et al. 2014). These conflicting results may be attributed in part to the very short term presence of feral pigs in the Argentinian study
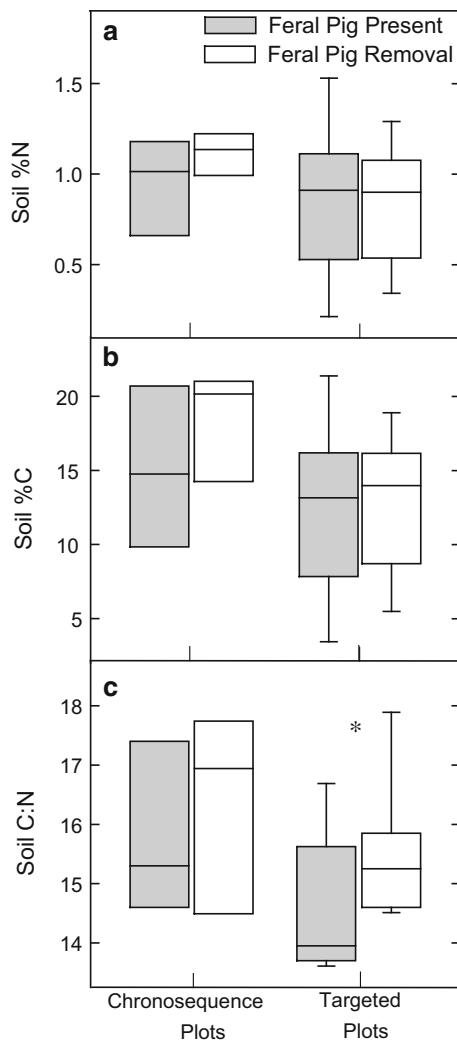
Fig. 7 Feral pig removal did not impact soil **a** % N or **b** % C in the chronosequence or targeted plots, but did increase **c** C:N in the targeted plots. *Whiskers* indicate the 10 and 90% percentiles (no whiskers for chronosequence plots due to small sample size); *dotted lines* indicate mean and *solid lines* indicate median values; *asterisks* indicate significant differences ($\alpha = 0.10$)

Fig. 8 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 the 10 and 90% percentiles (no whiskers for chronosequence plots due to small sample size); *dotted lines* indicate mean and *solid lines* indicate median values; *asterisks* indicate significant differences ($\alpha = 0.10$)

(~ 12 years). Several studies have reported increases in volumetric water content in soils affected by pig activity similar to our study (Mohr et al. 2005; Macci et al. 2012; Bueno et al. 2013). Feral pig impact on soil aggregation has been less well studied, but a study in Italian forests and olive groves found that water stable aggregation decreased significantly in soils where a grubbing treatment was imposed to mimic wild boar disturbance (Macci et al. 2012). Overall, the observed reductions in bulk density, VWC and water-
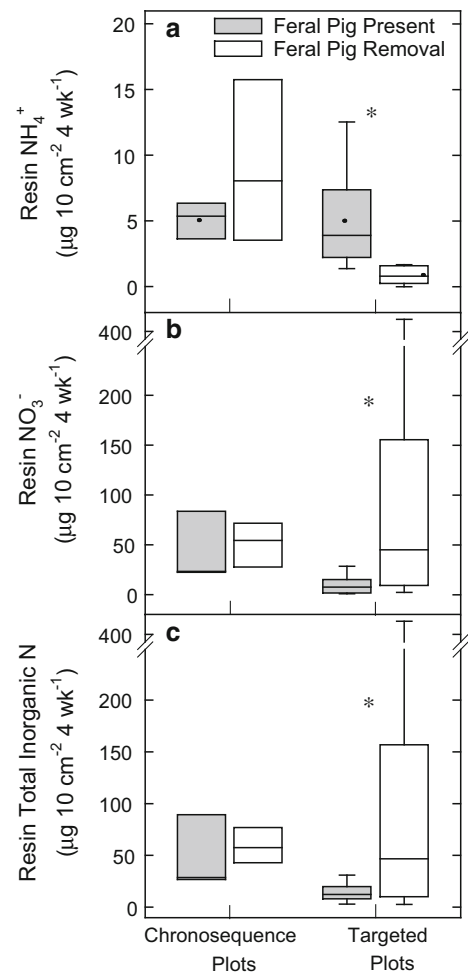
filled pore space, and increase in porosity, following feral pig removal in this study suggest an increase in soil aeration and oxygen diffusion with likely stimulation of soil microbial activity and nutrient regeneration (Schuur et al. 2001; Schuur and Matson 2001).

Soil nutrient availability

Soil nutrient availability is a critical driver of ecosystem productivity. Across the chronosequence plots,

feral pig removal increased extractable Ca, K, and Mg and enriched foliar $\delta^{15}N$ for one of the three studied species, while in the targeted plots feral pig removal increased resin available NO_3^- and total inorganic N. However, tropical ecosystems are often limited or co-limited by P availability, and we found that extractable P was lower with feral pig removal in the targeted plots. Lower extractable P concentrations with feral pig removal could result from a loss of P input from feral pig activity, accelerated P fixation by Andisols rich in amorphous Al and Fe oxides with decreased pH and lower SOM, and/or increased P uptake by recovering understory vegetation.

The measured increase in NO_3^- availability in the soils where feral pigs were removed suggests that nitrifying soil microbes are capitalizing on increased porosity, decreased water-filled pore space and a greater supply of labile C. Similar to the impacts of feral pig disturbance in this current study, grazing by large herbivores on clay soils in salt marshes in the Netherlands increased soil moisture, reduced redox potential, and reduced N mineralization rates (Schrama et al. 2012). Lower NO_3^- with feral pig disturbance could also result from elevated soil VWC and water-filled pore space, along with reduced porosity, as these soils have low hydraulic resistance and can readily leach NO_3^- (Lohse and Matson 2005). Elevated nitrification rates in soils following feral pig removal was reflected in enriched *C. trigynum* foliar $\delta^{15}N$, as increased N cycling rates create a more open N cycle and enriched soil $\delta^{15}N$ for plant uptake (Evans 2001).

Our results contrast previously reported increases in soil nutrient availability with both wild boar and feral pig disturbances. For example, in cool and dry hardwood forests of Switzerland with SOM-poor and sandy-loam textured soils, wild boar rooting and mixing of soil stimulated microbial activity, enhanced SOM decomposition, and increased soil %C and %N (Wirthner et al. 2012). In pine-hardwood forests in Texas, rooting and mixing of soil by feral pigs increased soil nutrient availability via soil aeration and accelerated SOM decomposition and N mineralization (Siemann et al. 2009). In our study in warm and wet Andisols with high SOM, feral pig disturbance increased VWC and water-filled pore space which likely inhibited aerobic production and availability of soil nutrients and soil gas exchange (Schuur et al. 2001; Schuur and Matson 2001).

Recovery of soils and vegetation

Understanding the linkages between observed changes in soil structure and nutrient availability with feral pig removal seen in this study and observed increases in the density and abundance of understory plants seen in prior studies (Cole et al. 2012; Cole and Litton 2014; Murphy et al. 2014) represents an important area of future research (Wardle et al. 2004). A resurgence of soil fauna following feral pig removal was previously documented in this same forest type (Vtorov 1993), which likely contributed to accelerated SOM decomposition, N mineralization and cation availability, and also an increase in soil aggregate stability. Recovering vegetation is likely capitalizing on increased nutrient availability, further increasing soil aggregate stability via fine root and hyphal growth. It is also likely that alterations in plant communities are at least partially driving observed changes in soil properties. Above- and belowground communities have been shown to be mutualistic drivers via both positive and negative feedbacks (Wardle et al. 2004).

In line with the idea of strong linkages between above- and belowground components for ecosystem recovery, vegetative recovery across the chronosequence plots was not restricted to native species. Stem density of the nonnative and highly invasive *Psidium cattleianum* increased as much as five fold following feral pig removal in the sites where it was present at the time of fencing, likely as a result of the release of top-down control by feral pigs (Cole et al. 2012; Cole and Litton 2014). The combination of alterations in soil structure and nutrient availability with increasing nonnative plant establishment following feral pig removal highlights that underlying soil processes likely play an important role in determining the competitive dynamics between native and nonnative plants, and supports the fluctuating resource availability hypothesis of invasibility (Davis et al. 2000). The spread of nonnative plants after feral pig removal in this chronosequence and with ungulate removal elsewhere in Hawaii (Scowcroft and Hobdy 1987; Stone et al. 1992; Cabin et al. 2000; Thaxton et al. 2010; Kellner et al. 2011; Weller et al. 2011) highlights the need for active vegetation management following fencing and nonnative ungulate removal, as well as the opportunity to explore how changes in underlying soil properties and processes influence competitive dynamics between native and nonnative plants.

Data limitations

Across the chronosequence, statistical analyses revealed no difference in several soil properties. Insufficient power to detect responses to feral pig removal may reflect the spatially heterogeneous nature of soils and/or feral pig activity. It is also possible that 20 years is not long enough to observe impacts of feral pig removal on some soil properties, as soil processes play out over temporal scales of hours to millennia (Bardgett et al. 2005). This was the primary reason for our targeted sampling scheme, which generally displayed patterns similar in direction but stronger in magnitude than the chronosequence sampling. Feral pig disturbance varies based on availability of food sources (Diong 1982; Anderson and Stone 1994; Lincoln 2014) and soil moisture and texture (Caley 1993; Elledge et al. 2012), and this could limit detectability of their impacts in observational studies with randomly located plots such as ours (Siemann et al. 2009). Despite these issues, we found general agreement for the results from the chronosequence and targeted sampling, and significant impacts of feral pig removal on a suite of soil physical and chemical properties.

Because we relied on existing exclosures, the chronosequence portion of the study was limited by small sample size ($n = 5$), requiring a conservative Wilcoxon Signed-Rank test to reduce the likelihood of Type II errors. We addressed this by establishing four sub-plots per plot to better capture heterogeneity of soil properties and feral pig disturbance within a given time period of removal (see Davidson and Hewitt 2014). While more sub-plots within each plot does not increase the overall sample size, it should diminish the effect of outliers.

Conclusions

This study documented that feral pig removal from tropical montane wet forests impacts a suite of soil physical and chemical properties, with an overall increase in soil structure and nutrient availability. Specifically, results showed that feral pig removal increased extractable cations, labile C, WSA, porosity, resin available NO_3^-, and foliar $\delta^{15}N$, while decreasing extractable P, bulk density, VWC, water-filled pore space, resin available NH_4^+, and pH.

Additionally, increasing time since feral pig removal decreased ammonification and increased nitrification rates. These results suggest that enhanced growth and abundance of both native and nonnative vegetation following nonnative ungulate removal (Cole et al. 2012; Cole and Litton 2014) may at least partially be the result of alterations to underlying soil properties that persist for some time period following their removal. Given the strong links between aboveground and belowground components observed in this study, we suggest that potential soil mediated responses by vegetation to nonnative ungulate removal requires greater study across a range of sites.

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