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RESEARCH ARTICLE

Restoration benefits of soil nutrient manipulation and weeding in invaded dry and wet tropical ecosystems in Hawai‘i

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Reducing soil nutrient availability has been proposed as a strategy to favor native vs. non-native invasive plant species and represents a potential alternative to traditional manual removal or chemical control methods. We implemented a field experiment in invaded dry and wet montane Hawaiian ecosystems to test responses of soil and dominant plant species to three soil nutrient treatments (Control = no nutrient manipulation; Carbon = C substrate added to reduce nutrients; Fertilizer = fertilizer added to increase nutrients) and two non-native plant treatments (Weeds removed; Weeds present) in a fully factorial experiment in each ecosystem over 18 months. Carbon amendments reduced soil inorganic nutrient availability by 60–70% in dry shrubland and 30–50% in wet forest. Fertilizer amendments increased soil inorganic nutrient availability by >20-fold. Altered nutrient availability did not impact gross mineralization or nitrification rates in either ecosystem. In dry shrubland, neither C amendments nor weed removal altered growth or reproduction, but fertilizer increased woody growth and forb/grass reproduction in both natives and non-natives. In wet forest, weed removal but not C amendments increased growth and survival of native woody seedlings, while fertilizer decreased native seedling survival and increased non-native woody seedling growth. Overall, growth and reproduction of native and non-natives responded similarly to altered nutrient availability, indicating that for the tropical ecosystems and species examined, manipulating nutrient availability does not favor native versus non-native invasive plants in the first 18 months. In contrast, weed removal had positive effects on native plant growth, likely mediated through changes in other resources.

Key words: carbon amendments, fertilization, nitrogen immobilization, plant reproduction, tropical montane dry shrubland, tropical montane wet forest

Implications for Practice

- Based on this 18-month study, C amendments have the ability to lower inorganic soil N availability in Hawaiian montane wet forest and montane dry shrubland. However, this had minimal impacts on native or non-native invasive plant survival, growth, or reproduction, and as such is likely not a useful short-term restoration strategy.
- As expected, fertilizer addition consistently enhanced growth of dominant native and non-native plant species. Further, there is evidence in this study that survival was reduced for several dominant wet forest native woody species with fertilization.
- Removal of non-native invasive plants enhanced growth and survival of dominant native species in wet forest, but not dry shrubland, suggesting that weed removal is a viable management strategy for restoration in some ecosystems.

Introduction

Non-native plant invasions represent a critical barrier to ecosystem restoration (D'Antonio & Meyerson 2002). Control of non-native invasive plants, most commonly carried out through manual or chemical methods, is both expensive and labor intensive, and alternative methods are needed to scale restoration efforts (Weidlich et al. 2020). One potential alternative is linked to factors enabling non-native plant invasions, specifically increased resource availability. The success of non-native invasive plants in native-dominated ecosystems has been attributed to a diverse range of mechanisms including, among others, competitive traits like fast growth and high reproductive output (Blumenthal 2005) and responsiveness to increased soil

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resource availability (Davis et al. 2000). Soil resource availability can be increased by natural and anthropogenic disturbances with substantial consequents for plant communities. Elevated soil nutrients have been found, in general, to favor fast-growing invasive species (i.e. resource exploitative) over slower-growing native species with higher resource use efficiency (i.e. resource conservative) (Burke & Grime 1996; Daehler 2003) across numerous ecosystems (Stohlgren et al. 1999), including tropical forests (Hobbs 1989; D'Antonio 1993; Ostertag & Verville 2002; Funk 2008; Ostertag et al. 2008). If dominant native and invasive species respond differently to varying resource availability, then, altering soil nutrients as a restoration strategy to favor native over non-native invasive species may be a viable approach to use in place of, or in combination with, common restoration strategies such as manual and chemical weed removal (Blumenthal et al. 2003; Corbin & D'Antonio 2009).

A common approach for reducing soil nutrient availability is the application of a metabolic substrate high in C relative to other elements (i.e. high C:N), such as sucrose, cellulose, or sawdust (Alpert 2010). Because soil microbes maintain a biomass C:N of approximately 8.5 (Cleveland & Liptzin 2007), metabolism of substrates with a higher C:N increases microbial demand for N which, in turn, results in microbial immobilization of inorganic N (ammonium; NH_4^+ and nitrate; NO_3^-) from soil that reduces N availability for plants (Alpert 2010). Although field studies show that C amendments can reduce soil nutrient availability (Alpert 2010; Perry et al. 2010; Burke et al. 2013), growth responses of native versus invasive plants vary across experiments. Some studies show C amendments effectively increase native plant growth and/or survival while decreasing non-native biomass (Zink & Allen 1998; Blumenthal et al. 2003; Perry et al. 2004; Prober et al. 2005; Eschen et al. 2006). Others show reduced growth of natives equal to or larger than non-native species (Morghan & Seastedt 1999; Monaco et al. 2003; Gendron & Wilson 2006). Drivers of this variation include: (i) species-level differences in responsiveness to nutrient availability (Blumenthal et al. 2003); (ii) magnitude of soil nutrient reduction (Blumenthal et al. 2003; Perry et al. 2010); (iii) suppression of nutrient availability that occurs over time periods longer than a given study (Alpert 2010); (iv) differences in baseline resource availability among ecosystems (Blumenthal et al. 2003); and/or (v) other factors limiting plant growth (e.g. water or light resources, Alpert 2010; Zink & Allen 1998).

Most prior research testing effects of nutrient manipulation on native versus non-native invasive plants comes from temperate ecosystems dominated by grasses and forbs. Studies demonstrating utility in lowering nutrient availability to reduce invasive biomass over native species biomass have been conducted with grass and herbaceous plants (Zink & Allen 1998; Blumenthal et al. 2003; Perry et al. 2004; Prober et al. 2005; Eschen et al. 2006). Far fewer studies have examined response of native and non-native invasive woody species to nutrient manipulation (Alpert 2010) or compared outcomes to common control methods like manual and chemical weed removal (Weidlich et al. 2020). In addition, we are not aware of any such field studies in tropical ecosystems despite the increasing vulnerability to invasion of these ecosystems globally (Döbert et al. 2018).

Carbon amendments in a restoration context will be most effective where native species are resource-conservative and invasive species are resource-exploitative. In a prior greenhouse experiment (Knauf et al. 2021) using woody tropical species from Hawai'i, we demonstrated that C amendments effectively altered competitive dynamics between native and non-native invasive species when resource use efficiencies of these groups differed. For example, the native N-fixing tree *Acacia koa* maintained relatively constant biomass over a broad range of nutrient availabilities while the biomass of the invasive non-native tree *Psidium cattleyanum* decreased by 10-fold at low compared to high soil nutrient availability. A field study in Hawaiian montane wet forest, in turn, found that fertilizer addition negatively impacted the growth of a dominant native tree (*Metrosideros polymorpha*), while increasing the density of the invasive understory species *Hedychium gardnerianum* (Ostertag & Verville 2002). Taken together, these studies support the idea that at least some native and non-native invasive plants respond differently to variation in soil nutrient availability. Testing how dominant native and non-native invasive plants respond to different levels of soil nutrient availability in the field will help address whether C amendments can support restoration efforts in invaded tropical ecosystems versus more traditional approaches such as manual or chemical control.

Globally, the most widely used control methods for non-native invasive plants are application of herbicide and non-chemical methods (e.g. manual removal of invasive plants) (Weidlich et al. 2020). These activities are cost and labor intensive, require long-term commitment of resources to maintain sites free of non-natives (Ostertag et al. 2009), and often have mixed success. For example, manual removal of invasive grass improved the growth of at least some native shrubs in degraded Hawaiian grassland (D'Antonio et al. 1998). However, 2 years of intensive removal of non-native biomass from Hawaiian wet forest had no effect on the growth of large, established native trees, perhaps due to the very slow growth and conservative resource use of dominant native overstory trees (*Metrosideros polymorpha* and *Diospyros sandwicensis*) (Ostertag et al. 2009). Despite these challenges, manual and chemical plant removal are currently the primary options for restoring invaded Hawaiian ecosystems.

In this study, we examined how altering soil nutrient availability, non-native plant removal, and their combination affect growth and reproduction of dominant native and non-native plants in both Hawaiian montane dry shrubland and wet forest ecosystems. We hypothesized that: (i) survival, growth, and reproduction of dominant native species would show little response to experimental manipulation of soil nutrient availability, whereas dominant non-native invasive species would respond strongly (Knauf et al. 2021); (ii) removal of non-native plants would positively affect growth of native species (D'Antonio et al. 1998), and (iii) native and non-native species growth responses would be larger in wet compared to dry ecosystems, where other limitations (e.g. water availability) may

exert strong limitations on plant growth. To test these hypotheses, we manipulated soil nutrient availability and non-native species cover in a fully factorial design over 18 months, and quantified soil nutrient availability and nutrient cycling metrics (mineralization, nitrification, and foliar chemistry) and dominant native and non-native plant species growth, cover, survival, and reproduction.

Methods

Study Site

The experiment was conducted from March 2016–September 2017 in tropical montane wet forest (hereafter, "wet forest") and tropical montane dry shrubland (hereafter, "dry shrubland") on the Island of Hawai'i. Dominant native species in the wet forest site include *Metrosideros polymorpha*, *Cheirodendron trigynum* (overstory trees), and *Cibotium* spp. (midstory tree fern) (Wagner et al. 1990). Dominant non-native trees include the mid-canopy tree *Psidium cattleyanum* (strawberry guava) and the N-fixing canopy tree *Morella faya* (fire tree). The understory is extensively invaded by the non-native forb *Hedychium gardnerianum* (kahili ginger) (Fig. 1). The wet forest study site is located within a fenced 25-ha unit in the Kahauale'a Natural Area Reserve (19°24′N, 155°8′W); the fence was built in 2015 and all non-native ungulates were removed approximately 1 year before the start of nutrient manipulations for this study. The site is located at 1,200 m a.s.l. with mean annual temperature of 15°C and mean annual precipitation of 3,985 mm with no distinct wet or dry seasons (Giambelluca et al. 2013). Soils are ashy, amorphic, isothermic Lithic Hapludands of the Puhimau series. These are shallow, moderately well-drained soils formed in volcanic ash over pāhoehoe lava. These ashy silt loam soils are relatively high in organic matter, with high base saturation in the O horizon, and are acidic with pH ranging from 4.3 in surface layers to 6.6 at depth (NRCS 2010). Preliminary measurements showed uniform overhead canopy cover across all plots (87–92%).

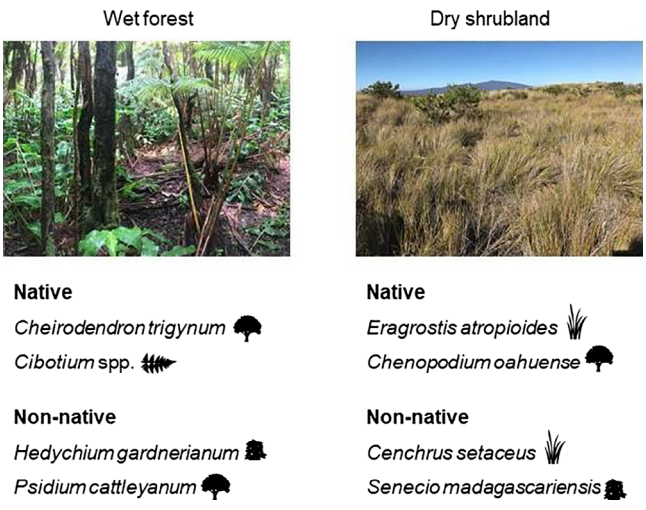

Figure 1. Montane wet tropical forest and montane dry shrubland in Hawai'i, with focal species for this study. Sites are heavily invaded by non-native plant species (e.g. kahili ginger (*Hedychium gardnerianum*) visible throughout the wet forest understory). Symbols indicate growth form: tree/shrub, fern, herb, or grass.

Dominant native woody species in dry shrubland include *Chenopodium oahuense* with sparsely occurring *Dodonaea viscosa*. The dominant native C_4 grass, *Eragrostis atropioides*, represented approximately 98% of native plant cover. Dominant non-native species include the forb *Senecio madagascariensis* (fireweed; >65% of non-native cover) and the C_4 grass *Cenchrus setaceus* (fountain grass; approximately 5% non-native plant cover) (Fig. 1). The study site was fenced in 2009 and non-native ungulates were removed approximately 1 year before the start of nutrient manipulations for this study. This study site is located in Pohakuloa Training Area (19°40′N, 155°20′W) at 1,500 m a.s.l. with 13°C mean annual temperature and 310 mm mean annual precipitation (Giambelluca et al. 2013). Soils are medial-skeletal, amorphic, isothermic Humic Haplustands of the Puu Pa series. These are deep, well-drained soils formed in basic volcanic ash in 'a'a lava. These relatively fertile, very fine sandy loam soils have high base saturation and are slightly acidic with pH ranging from 5.9 in surface soils to 6.6 at depth (NRCS 2010).

Treatment Design

Two non-native plant removal options (Weeds present = non-native plants present in the understory; Weeds removed = non-native plants removed from understory), three levels of nutrient manipulation (Control = no nutrient manipulation; Carbon = C substrate added; Fertilizer = fertilizer added) and their factorial combination (weeding × nutrient manipulation) were replicated across five blocks in each ecosystem type ($n = 5$). Each block contained six 8 × 8 m plots that received one of each of the six treatments. Blocks were separated by ≥15 m and plots within blocks were separated by 5 m.

Based on prior studies (Knauf et al. 2021; Burke et al. 2013), we used a combination of sucrose and wood sawdust for C amendments to immobilize nutrients on both shorter (sucrose) and longer (sawdust) time scales. Sucrose is immediately available to microbes and rapidly reduces nutrient availability, but because it is quickly metabolized the effects are short lived. Sawdust is a less accessible energy source for soil microbes resulting in longer-lasting effects on nutrient availability that are slower to develop (Burke et al. 2013). Sucrose was applied as table sugar and sawdust as a homogenized mixture of *Eucalyptus robusta* and *Acacia koa*. All sawdust was heat-treated to eliminate fungal pathogens prior to application. In March 2016, we added 0.5 kg/m^2 of sawdust and 0.25 kg/m^2 of sucrose to all Carbon treatment plots. To maintain low nutrient conditions over time, we also added 0.25 kg/m^2 of sucrose at 6 and 12 months (October 2016 and March 2017). At 12 months, we again applied sawdust (0.5 kg/m^2) to the wet forest site because the first application was no longer visible. In contrast, most sawdust remained on the soil surface in dry shrubland plots after 12 months, so re-application was deemed unnecessary.

For the fertilizer treatment, we applied Apex 16-6-12 NPK slow-release fertilizer pellets (Simplot Professional Products, Lathrop, CA) at the manufacturer-recommended rate for woody plants of 0.19 kg/m^2 (equal to 304 kg N ha^{-1} as ammonium nitrate, 49 kg P ha^{-1} as phosphate, and 189 kg K ha^{-1} as soluble potash). This fertilizer also includes Mg, S, Cu, Fe, Mn, Mo, and Zn at proportions ≤6%. Fertilizer amendments were added at the start of the study (March 2016) and repeated at 6 and 12 months at all sites.

In the Weeds present treatment, non-native plants were left undisturbed. In Weeds removed plots, non-native forbs and graminoid plants (but not trees) were removed immediately before the application of nutrient treatments. In the wet forest, we followed practices utilized by land managers in Hawai'i (Anderson & Gardner 1999), where stems of *H. gardnerianum* were cut and treated with a spot application of metsulfuron-methyl (Escort, Dupont, Wilmington, DE). In dry shrubland, non-native plants were hand removed. All weeding treatments were repeated at 12 months.

Soil Nutrient Availability and Cycling

Soil bulk density was measured at the start of the study in all blocks by collecting six 3 × 5 cm (15 cm^3) cores, passing soil through a 2 mm sieve, and drying at 105°C for 48 hours. Volumetric water content (VWC) and soil temperature were measured in each subplot bimonthly using a 10 cm Hydrosense soil moisture probe and thermocouple (Campbell Scientific, Logan, UT).

While soil manipulations should affect the availability of all nutrients, we focused measurements on N by assessing soil NO_3^- and NH_4^+ availability using the ion-exchange resin bag method (Binkley & Hart 1989). Previous studies have found N limitation to be typical in the relatively young tropical soils associated with our study sites, while P limitation is more prevalent on older soils (Vitousek 1997). At the initiation of nutrient manipulation (March 2016), four nylon mesh bags per plot containing 10 g of mixed bed cation-anion resin (Sigma Aldrich, St. Louis, MO) were placed at the litter layer-mineral soil interface, left for 3 months, and replaced quarterly. During incubations, control bags were stored both in the field (in sealed plastic bags) and laboratory (refrigerator controls). Upon collection, bags were cleaned with distilled water, then extracted by shaking with 100 mL 2 M KCl for 2 hours. Extracts were analyzed colorimetrically with a Lachat QuickChem (Hach Co., Saskatoon, Canada) at the University of Hawai'i at Hilo Analytical Laboratory.

We quantified soil gross mineralization and nitrification rates using the ^{15}N pool dilution method (modified from Hart et al. 1994a; Hart et al. 1994b). Four 5-cm diameter cores (0–5 cm depth) were collected, composited, and split into three treatments, receiving an aqueous solution of 99% enriched [$(^{15}NH_4)_2SO_4$, $K^{15}NO_3^-$] or deionized water (negative control). Solution volumes were adjusted to limit changes to percent soil water content by 1–2%. Label quantity was adjusted based on previous measures of NH_4^+ and NO_3^- concentrations in study plots. Immediately after homogenizing labeled soils, two replicate subsamples from each treatment were extracted in 2:1 2 M KCl. Two additional subsamples were extracted after 12 hours of incubation at room temperature. Inorganic N concentrations in extracts were quantified as described above. Diffusion filters were analyzed for $\delta^{15}N$ using a continuous-flow isotope ratio mass spectrometer (Model Delta V Advantage; Thermo-Scientific) at Cornell University Stable Isotope Laboratory. Control diffusions were run to account for N contamination by reagents. Gross fluxes were calculated using equations as per Hart et al. (1994a, 1994b). Nitrous oxide (N_2O) and CO_2 emissions from the soil surface were measured at one and three time points, respectively, throughout the experiment (Supplement S1).

We assessed foliar chemistry by harvesting three fully expanded leaves (most recent cohort) from three individuals of the dominant native and non-native plant species in each plot every 3 months. Sampled species included native tree fern *C. glaucum* and non-native *H. gardnerianum* in the wet forest, and native grass *E. atropioides* and non-native grass *C. setaceus* in the dry shrubland (all from Weeds present plots only). Samples were dried for 48 hours at 65°C, ground, and analyzed for total C, N, $\delta^{15}N$, and $\delta^{13}C$ as above.

Wet Forest Vegetation Measurements

To non-destructively quantify understory invasion in wet forest, above- and belowground biomass of the dominant invader (*H. gardnerianum*) was harvested and excavated from a set of twenty 1 × 1 m harvest plots located outside of the experimental blocks. Number and length of aboveground stems were recorded, and subsamples weighed, dried, and re-weighed for wet: dry. Belowground biomass was cleaned, weighed, and subsamples dried to estimate biomass per unit area. These data were used to generate an allometric equation to estimate belowground dry biomass from harvested aboveground wet biomass ($r^2 = 0.801$):

$$\text{Belowground biomass} = (4.565 \times \text{aboveground biomass}) - 0.620 \quad (1)$$

We then estimated the relationship between number and length of stems and aboveground dry biomass per unit area. To monitor change in non-native *H. gardnerianum* in Weeds present treatments, all aboveground stems were counted and measured at the time of application of nutrient amendments (March 2016) and 1 year later (in the same season); above- and belowground biomass were then estimated using the relationships described above.

To test effects of treatments on growth of dominant native and non-native woody plants, individual seedlings of the native *C. trigynum* and non-native *P. cattleyanum* from the same age cohort and size range (approximately 10–20 cm and 20–35 cm height, respectively) were transplanted into each treatment plot in May 2016, approximately 2 months after treatment application. These two species comprise >90% of the seedling population present at the time of the study based on preliminary surveys. We used transplanted seedlings due to naturally patchy

distributions (i.e. naturally established seedlings were not found in all treatment plots). A total of 150 *C. trigynum* (five per treatment plot) and 300 *P. cattleyanum* (10 per treatment plot) were transplanted. Initial height and basal diameter were recorded, and seedlings were tagged and tracked for mortality and growth for 18 months (October 2017), after which they were harvested, separated into above- and belowground biomass, dried, and weighed.

Dry Shrubland Vegetation Measurements

We quantified herbaceous vegetation growth and reproduction responses in dry shrubland in five 1 × 1 m subplots in each of the 8 × 8 m treatment plots. Because destructive harvesting of native plants is not allowed in this conservation area, we employed commonly used non-destructive estimators of growth. Cover of dominant forb and graminoid species was quantified using a modified Braun-Blanquet cover-abundance scale at the beginning of the study (March 2016) and 1 year later (in the same season). To measure reproduction of the dominant species (i.e. native grass *E. atropioides* and non-native grass *C. setaceus*), all inflorescences were counted monthly and tallied. Seedlings of *E. atropioides* and *C. setaceus* were transplanted into each 8 × 8 m plot (external to 1 × 1 m subplots) to assess growth responses to treatments. However, survival was 0% due to herbivory by rodents and/or birds. As such, we used naturally established seedlings of the dominant native shrub *C. oahuense* from the entire 8 × 8 m plot, where seedlings ≥10 cm height and ≤ 1 cm DBH were tagged and measured for basal diameter, height, and survival. Because the size and presence of this perennial woody species varies minimally seasonally, we made measurements at the start of the study and again after 18 months.

Data Analysis

Changes in *H. gardnerianum* biomass in wet forest and vegetation cover in dry shrubland were calculated as the difference between the first and second annual measurements from the same season. Outplanted woody seedling growth (height and basal diameter) was calculated as the percent change between time of planting and harvest. Preliminary analysis showed that seedling height was a better predictor of seedling biomass than basal diameter and was used for all calculations. Change in biomass of *H. gardnerianum* in wet forest and percent change in non-native vegetation cover and reproduction in dry shrubland were analyzed across nutrient manipulations in Weeds present plots using a one-way randomized block ANOVA. All responses of native vegetation and outplanted seedlings including change in percent height, percent survival, and root: shoot (wet forest), and survival and percent change in height of naturally occurring seedlings and herbaceous plant reproduction (dry shrubland), and foliar nutrients were compared across all treatments using a randomized block two-way ANOVA with interaction terms. Soil nutrient concentrations, temperature, and volumetric water content, which were measured repeatedly over time, were analyzed with mixed models using sampling date, weeding and nutrient treatments, and their interactions as fixed effects and plot as a random effect.

All data were transformed when necessary (i.e. Johnson's SI for foliar chemistry and soil N concentration data, and log transformation for vegetation responses) to meet assumptions of normality and homogeneity of variances. Analyses were followed by Tukey's HSD post hoc tests. Statistical analyses were conducted using SPSS v.24 (IBM Corporation) or JMP Pro v.13 (SAS Institute) and significance determined at $\alpha = 0.05$. Mean and standard error of the mean (± 1 SE) are reported throughout. Interactions between treatments were tested in all cases, but only reported where statistically significant. Degrees of freedom are $df = 1$ when testing for effects of weeding treatments and $df = 2$ for nutrient manipulation.

Results

Soil Nutrient Availability and Cycling

Neither nutrient manipulations nor weeding treatments affected soil temperature or moisture in wet forest. In contrast, in dry shrubland, fertilization in Weeds present and Weeds removed plots increased soil temperatures by 1.1–1.3°C and decreased soil VWC by approximately 50% compared with the control; weeding treatments had no effect on these variables (Table 1).

Table 1. Mean soil temperature and volumetric water content (VWC; ± 1SE) as a function of nutrient and weeding treatments in wet forest and dry shrubland in Hawai'i. Different letters denote significant differences among soil nutrient treatments. Weeding treatment and weeding nutrient interactions were not significant in any case ($p > 0.05$).

	Weeding Treatment	*Carbon*	*Control*	*Fertilizer*	*Soil Nutrient Treatment* p, f, df
Dry shrubland					
VWC (%)	Removed	10.3 ± 1.6 [a]	9.6 ± 1.4 [b]	4.2 ± 0.6[c]	$p < 0.0001$,
	Present	10.4 ± 1.9 [a]	8.4 ± 1.3[b]	5.0 ± 0.9[c]	$f = 70.78$, $df = 2$
Soil	Removed	18.8 ± 1.1 [a]	18.7 ± 1.1 [a]	19.8 ± 1.1 [b]	$p < 0.0001$,
Temperature (°C)	Present	18.9 ± 1.0 [a]	18.3 ± 1.0[l]	19.7 ± 1.2[b]	$f = 11.59$, $df = 2$
Wet forest					
VWC (%)	Removed	44.3 ± 1.4	42.7 ± 1.2	42.6 ± 1.2	$p < 0.066$,
	Present	44.0 ± 1.2	46.2 ± 1.0	40.5 ± 1.6	$f = 3.12$, $df = 2$
Soil	Removed	16.8 ± 0.3	16.8 ± 0.3	16.7 ± 0.3	$p < 0.969$,
Temperature (°C)	Present	16.5 ± 0.2	16.6 ± 0.2	16.7 ± 0.3	$f = 0.03$, $df = 2$

Carbon amendments in dry shrubland increased VWC by approximately 7–25% but had no effect on temperature (Table 1).

Nutrient manipulations, but not weeding treatments, impacted average resin-available soil NH_4^+ and NO_3^- concentrations in both ecosystems (Fig. 2). For all ecosystem types, nutrient manipulation effects on soil inorganic N were evident by the first re-sampling at 3 months following treatment application (Fig. S1). Fertilizer treatment strongly increased the availability of both NO_3^- and NH_4^+ regardless of ecosystem or weeding treatment (Wet; $f = 517.18$, $f = 245.37$, respectively. Dry: $f = 242.33$, $f = 99.98$, respectively; all $p < 0.001$). In wet forest, increases relative to pre-treatment level were

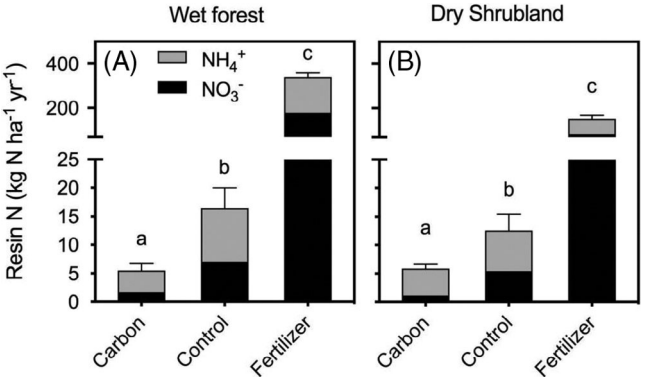

Figure 2. Effect of nutrient (carbon or NPK fertilizer) amendments on soil resin-available NH_4^+ and NO_3^- in (A) wet forest and (B) dry shrubland. Carbon amendments are designed to immobilize plant-available N, while fertilization is designed to increase total plant N availability. Lowercase letters indicate significant differences in total resin N (NH_4^+ and NO_3^-) between nutrient amendments. As weeding was not statistically significant in either ecosystem ($p > 0.05$), weeding treatments are combined into a single mean. Values are mean of 18 months of treatment amendments +1 SE ($n = 228$ per treatment and ecosystem). Sampling time-specific values are presented in (Fig. S1).

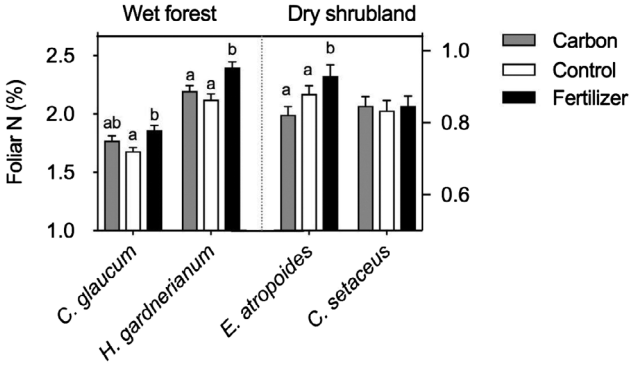

Figure 4. Foliar nitrogen content (%) for common wet forest species, native tree fern *Cibotium glaucum* and invasive forb *Hedychium gardnerianum* and dry shrubland species, native grass *Eragrostis atropioides* and invasive grass *Cenchrus setaceus* under nutrient manipulation treatments. Values are means of foliar N measured every 3 months from 3 to18 months after treatments were initiated, +1 SE. Different lowercase letters indicate significant differences between treatments.

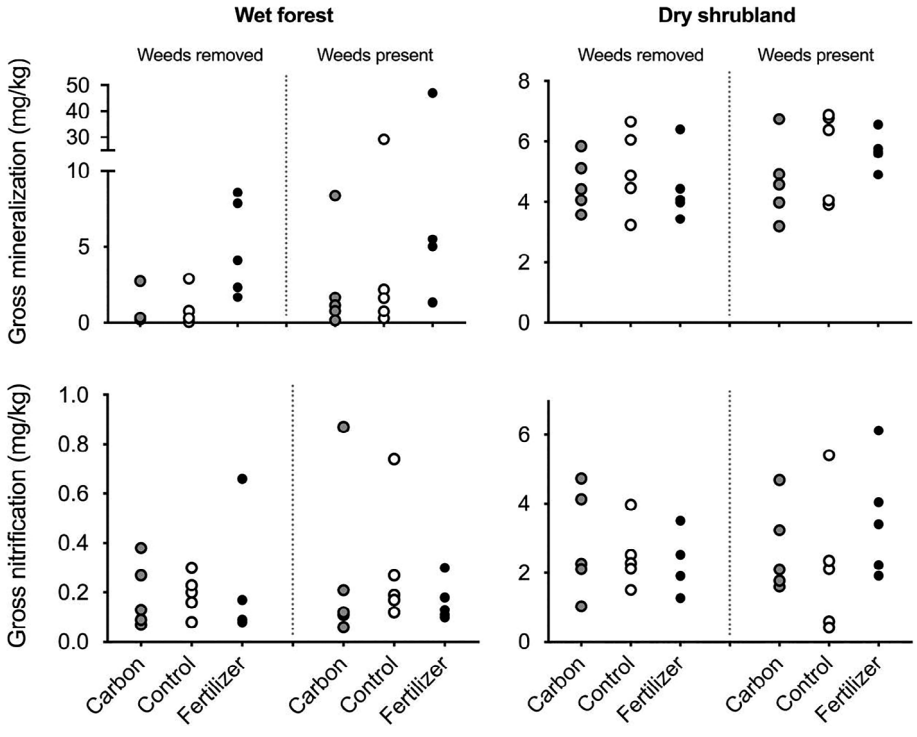

Figure 3. Gross mineralization and nitrification (mg/kg dry soil) in wet forest or dry shrubland soils treated with nutrient additions and weed removal. There are no significant treatment effects in either ecosystem ($p > 0.05$).

23–32-fold larger than that observed in the Control plots. In the dry shrubland, increases were approximately 20-fold larger for Fertilized compared with Control plots. The increases for both ecosystem types were split approximately evenly between NO_3^- and NH_4^+ (Fig. 2). Carbon amendments in wet forest significantly decreased total inorganic N (f = 1,057.7; $p < 0.001$) to between 30 and 50% of Control values, and this effect was more than twice as large for NO_3^- as for NH_4^+. Carbon amendments in dry shrubland also reduced total inorganic N to 60–70% of that observed in Control plots (f = 234.1; $p < 0.001$), with a 3-fold greater effect on NO_3^- compared with NH_4^+ (Fig. 2).

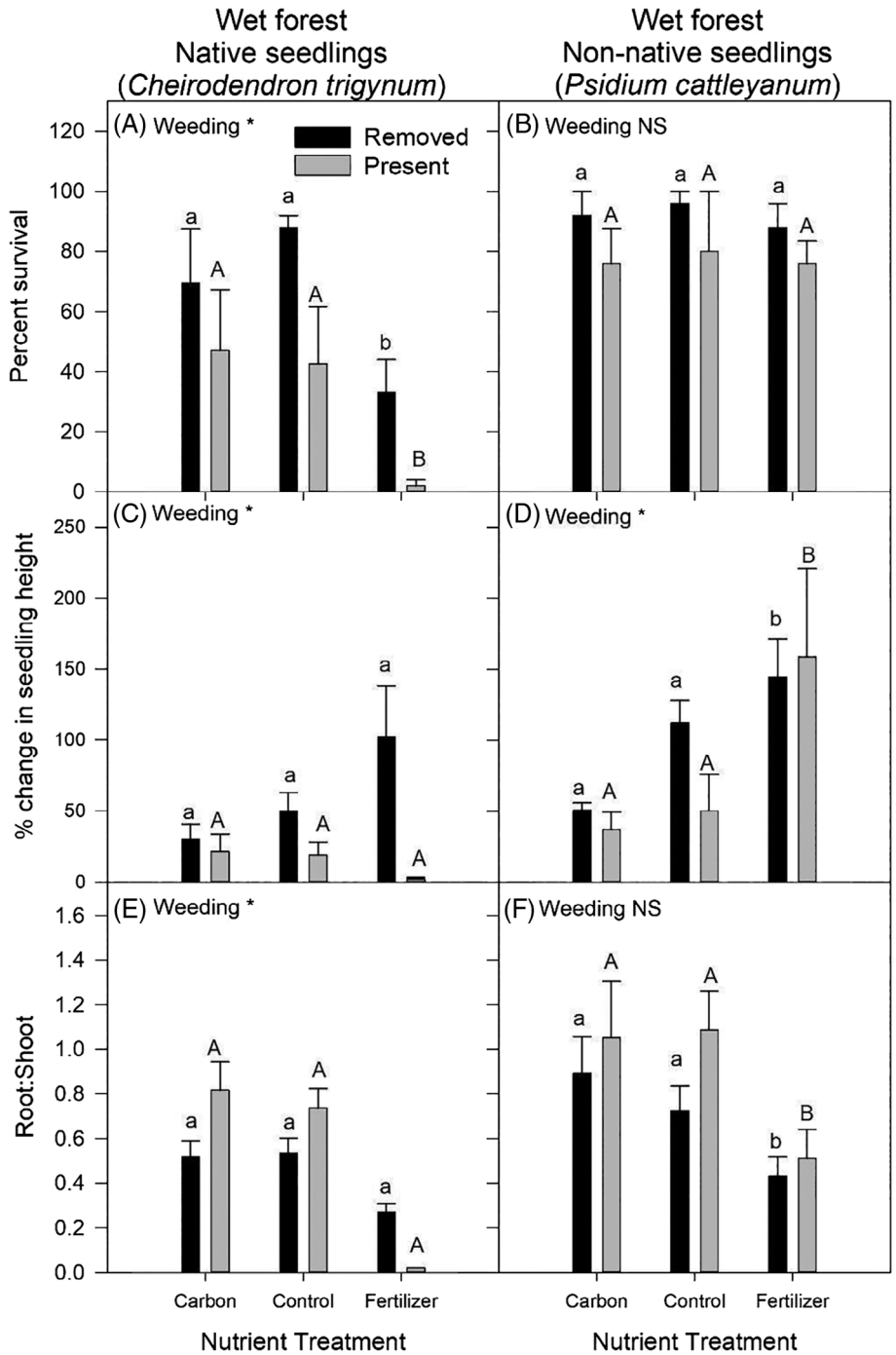

Figure 5. Percent survival (A, B), percent change in height (C, D) and root to shoot ratio (E, F) of planted native *Cheirodendron trigynum* and non-native *Psidium cattleyanum* woody seedlings after 18 months of nutrient and weed removal treatments in wet forest. Different letters of the same case indicate significant differences across nutrient treatments. An asterisk (*) indicates a significant effect of weeding treatment, NS = non-significant. Values are means +1 SE.

Changes in inorganic N were not accompanied by changes in gross mineralization or nitrification rates in either ecosystem (Fig. 3, $p > 0.05$ for all ecosystem/treatment/variable combinations). In both ecosystems, there was significant nutrient manipulation effect on soil N_2O fluxes, which increased with both Carbon and Fertilizer treatments (Table S1). Soil surface CO_2 efflux was unaffected by weeding treatments across both ecosystem types but decreased in dry shrubland and strongly increased in wet forest in response to increased soil nutrient availability.

In wet forest, increased soil N associated with the Fertilizer treatment increased foliar N concentrations in both invasive *H. gardnerianum* and the native tree fern *Cibotium* ($f = 6.3$; $p = 0.001$; Fig. 4). For *H. gardnerianum*, fertilization lowered foliar $\delta^{15}N$ ($f = 10.0$, $p = 0.001$). Carbon treatment had no effect on foliar nutrient concentrations or $\delta^{15}N$.

In dry shrubland, foliar N of the native grass *E. atropioides* increased in response to Fertilizer ($f = 6.5$; $p = 0.003$; Fig. 4) but not other treatments. Foliar nutrients in non-native *C. setaceus* did not respond to nutrient or weeding treatments (Fig. 4, all $p > 0.05$). Neither $\delta^{13}C$ nor foliar C varied in any species in response to any of the nutrient or weeding treatments ($p > 0.05$ for all ecosystem/species/treatment combinations).

Wet Forest Vegetation

The initial mean density of *H. gardnerianum* stems ≥1 m in length was 3.2 ± 0.6 stems/m^2, equal to 4.1 ± 0.7 kg/m^2 of total dry biomass (0.81 ± 0.13 and 3.3 ± 0.6 kg/m^2 above- and belowground, respectively). There was no significant difference across treatments ($p > 0.05$). After 1 year, total mean *H. gardnerianum* biomass responded significantly to nutrient treatments ($f = 12.0$; $p = 0.004$), with Fertilizer plots showing a > 60% increase compared to both control and carbon treatments, which did not differ from each other (Fig. S2).

Overall percent survival of transplanted native *C. trigynum* seedlings was 47 ± 1%, with low survival (approximately 3%) in the Fertilizer/Weeds present treatment. Seedling survival was strongly and negatively affected by fertilizer addition ($f = 7.4$; $p = 0.004$), but not C amendments. Weed removal increased *C. trigynum* survival by a factor of 1.5–2 ($f = 9.0$; $p = 0.007$; Fig. 5A), and also increased percentage height gain ($f = 22.1$; $p = 0.001$; Fig. 5C), while reducing root:shoot ($f = 8.2$; $p = 0.015$; Fig. 5E). *C. trigynum* percent height gain did not vary across nutrient manipulation treatments. However, the lack of treatment and interaction effects are likely due to low survival in the Fertilizer/Weeds present treatment, as there were not enough surviving seedlings in this combination of treatments to include in the analysis.

Survival of transplanted non-native *P. cattleyanum* was high (85 ± 1%) and did not differ across nutrient and weeding

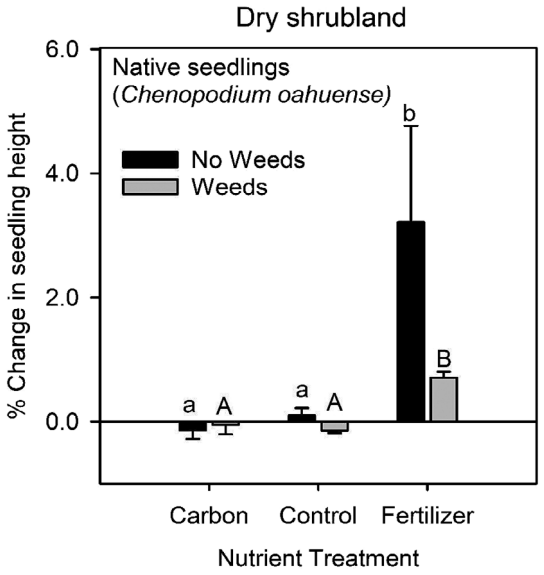

Figure 6. Percent change in height of native woody seedling *Chenopodium oahuense* after 18 months of growth under nutrient amendments and weed removal treatments. Different letters of the same case denote significant differences between nutrient treatments. An asterisk (*) indicates a significant effect of weeding treatment. Values are means +1 SE.

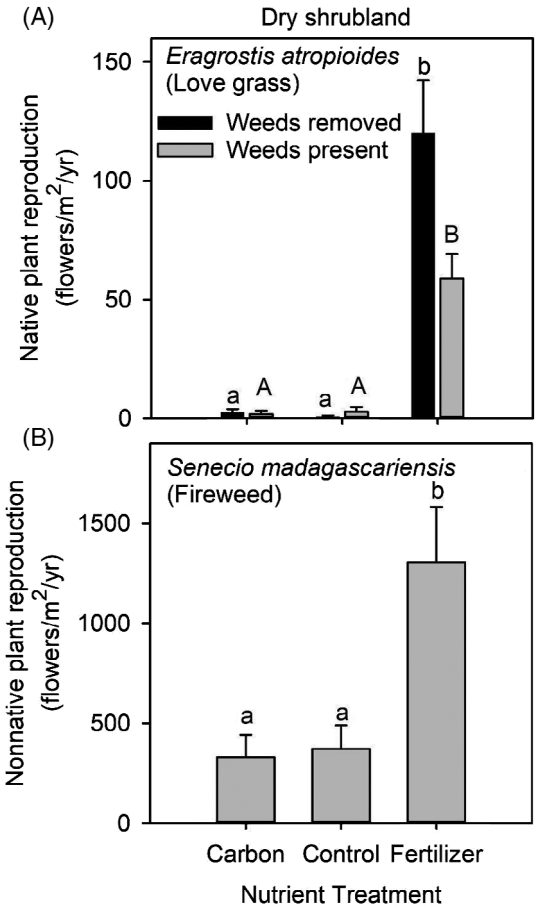

Figure 7. Total reproductive output of (A) native grass *Eragrostis atropioides* and (B) invasive forb *Senecio madagascariensis* under nutrient amendment and weeding treatments. Different letter of the same case indicates significant differences across nutrient treatments. There was no significant effect of weeding. Values are means +1 SE

treatments (Fig. 5B). Changes in percent height of *P. cattleyanum* were significantly affected by nutrient manipulation ($f = 10.5$; $p = 0.001$) and weeding ($f = 7.1$; $p = 0.015$) treatments with strong, positive response to fertilizer addition, and weeding (Fig. 5D). Root: shoot did not vary by weeding treatment but was significantly lower in Fertilizer treatments ($f = 6.6$; $p = 0.006$; Fig. 5F).

Dry Shrubland Vegetation

Naturally established seedlings of the native shrub *C. oahuense* showed a significant, positive growth response in terms of percent height increase to Fertilizer ($f = 25.5$; $p = 0.001$), but not to Carbon treatment (Fig. 6). Weeding treatments had no effect on seedling height.

Prior to treatment initiation, the native grass *E. atropioides* represented approximately 95% of total plant cover in dry shrubland plots followed by the non-native herb *S. madagascariensis* (approximately 4%). Neither species showed significant response in terms of percent cover to nutrient treatment (*S. madagascariensis*) treatments or nutrient and weeding treatments (*E. atropioides*) ($p > 0.05$). Similarly, the percent change in total native plant cover did not change significantly in response to nutrient or weeding treatments, nor did total percent non-native plant cover respond to nutrient treatments ($p > 0.05$).

Reproduction of dominant species was strongly favored by Fertilizer treatment, but not did not vary significantly across weeding treatments. Flowering of native *E. atropioides* increasing by two orders of magnitude in Fertilizer compared to Control and Carbon treatments, which did not differ from each other ($f = 17.9$; $p < 0.001$; Fig. 7A). Flowering of the non-native forb *S. madagascariensis* increased 4-fold in Fertilizer compared to Control plots, which did not differ from each other ($f = 6.9$; $p = 0.004$; Fig. 7B).

Discussion

Over 18 months, C amendments substantially reduced the availability of inorganic N in Hawaiian montane dry shrubland and wet forest soils, but this did not translate into increased metrics of N cycling or universal favorable growth responses of native versus non-native invasive species. While soil nutrient reduction via C amendments had no negative effects on dominant native or non-native plant survival, growth, or reproduction in either ecosystem, it did not confer positive advantages to natives over non-natives during the time frame of this study. In contrast, increasing soil nutrient availability through fertilization led to significant positive growth and reproductive responses of dominant non-native and native plant species in dry shrubland, and non-native invasives in the wet forest. Fertilizer also caused high seedling mortality of the common native wet forest tree species *C. trigynum*. Weed removal generally had positive effects on native plant growth and survival. These results support our first hypothesis that non-native invasive plants respond strongly to increased soil nutrient availability but do not demonstrate that reducing soil nutrients improves the competitive balance of native versus non-native plants.

The reasons for the apparent disconnect between strong growth reductions of non-native invasives in response to C amendment observed in a greenhouse setting (Knauf et al. 2021) and the field results reported here are not entirely clear. However, there are several potential explanations. First, while our field results showed that C amendments to Hawaiian dry shrubland and wet forest soils reduce the availability of inorganic N by up to 70%, the amendments did not decrease rates of N mineralization or nitrification and had minimal impacts on soil surface CO_2 efflux. This suggests that while the short-term immobilization of standing N stock increased, the C amendments do not ultimately impact the supply of new inorganic N by inducing persistent changes in the activity of the soil microbial community. In the greenhouse experiment, the C amendment was mixed uniformly through the soil profile while in field situations it was applied only to the soil surface and appeared to only have local effects that do not extend through the full soil profile occupied by established plant roots. This may partly explain why effects of field C amendments on soil N are often shown to subside within months of application (Alpert 2010; Perry et al. 2010; Burke et al. 2013).

Second, the timescale of this experiment may simply be too short to observe changes in the underlying soil nutrient biogeochemistry. Although other studies testing soil nutrient reductions have seen positive outcomes for native species within 1 year, these responses have been strongest in forb and graminoid-dominated temperate ecosystems (Prober et al. 2005; Eschen et al. 2006). Results from our greenhouse study, where plants were grown under highly favorable conditions, showed that three of the four native species tested benefited from nutrient reductions relative to the invasive species with which they were competing within 6–12 months (Knauf et al. 2021). It is possible that the current study did not confirm the greenhouse-based findings simply because it was not of a long enough duration to detect competitive benefits for native versus non-native species under field conditions.

Third, this study, and others like it, only examine a subset of species in any given community, which does not capture the extent to which all native and non-native species compete across a wider spectrum of conditions. For example, a study in an intensively managed *Eucalyptus* plantation on Hawai'i Island showed that nearly all colonizing individuals across a broad range of nutrient and light levels were non-native invasive species (Ostertag et al. 2008). While we are not able to differentiate among these possible mechanisms in the current study, the results suggest that surface C addition will have limited efficacy in tropical ecosystems with woody species within the first 18 months.

In contrast to the nutrient manipulations, the results support our second hypothesis that removal of invasive non-native plants positively affects native species growth. Specifically, we found improved native woody seedling growth in dry shrubland and increased survival and growth in wet forest. Invasive plant removal had little effect on soil nutrient availability or soil VWC in either ecosystem, or light levels in the dry shrubland (data not shown). As a result, the positive effects observed, particularly for the wet forest, are likely mediated by reduced

competition for light. *H. gardnerianum* exhibited a density of >3 stems/m^2 with stems achieving >1 m in height as measured at the time of removal, which would have greatly increased light levels for the target seedlings in weeded plots. Removal of invasive plants has been shown to increase native seedling germination and growth in other Hawaiian wet forests (Cordell et al. 2009).

Although we hypothesized that water limitations would exert stronger controls on plant growth than nutrients in the dry shrubland, we found no evidence for this. Growth and reproduction responded positively to fertilizer amendments even though they increased soil temperatures and reduced soil VWC by almost half but did not respond to C amendments even when they increased soil VWC by 7–25%. Leaf C stable isotopes also did not reflect differences in integrated stomatal conductance between treatments, which is suggestive of no difference in water limitation (Farquhar 1989).

Ultimately, several factors limit the usefulness of using nutrient manipulation for restoration. The timescale of influence may be too short to be feasible for land managers, or the differences in resource use efficiency between native and invasive species may simply not be strong enough to drive differential growth or survival responses. Given the diverse life forms and strategies of invasive species, with some invasives showing resource conservative strategies under low nutrient conditions (Funk & Vitousek 2007), this finding is perhaps not surprising. However, several studies have found support for a suite of more resource conservative traits of native Hawaiian species (e.g. lower leaf construction costs) compared to invasives (Baruch & Goldstein 1999, but see Ostertag et al. 2008), including our preliminary greenhouse study. This contrast among studies suggests that C amendments may be effective in some targeted ecosystems, or at appropriate timescales.

Some native and most invasive species showed strong positive biomass, height, and reproduction responses to fertilizer amendments in dry shrubland and wet forest, and there was increased foliar N in most species. This illustrates that both native and non-native plants can exploit resources under conditions of high resource availability, including native species that may be adapted to low resource availability (Hobbs & Huenneke 1992; Vitousek 1997). However, for the midstory dominant native wet forest tree *C. trigynum*, elevated soil nutrients had a pronounced negative effect on seedling survival. Although the nutrient concentrations that drove these effects are significantly higher (approximately 20-fold) than typically occur in these plots after feral ungulate disturbance (Long et al. 2017), this is still significant given that regeneration is a key aspect of restoration and a critical filter for invasive species success and community assembly. This finding is also consistent with previous observations that *M. polymorpha*, a dominant native overstory tree, showed greatly reduced growth and survival under high nutrient conditions in our greenhouse study (Knauf et al. 2021), as well as with fertilizer additions applied in situ in N-limited wet montane forests (Ostertag & Verville 2002). These results collectively support the idea that resource manipulation can have complex effects on ecosystems, with elevated nutrient supply negatively affecting some dominant native species adapted to low-resource environments.

We found that surface C amendments can reduce soil N standing stocks but are not effective in altering mineralization or nitrification over a timescale of 18 months. This resulted in limited influence of this management technique on competitive dynamics between native and non-native invasive species in Hawaiian montane dry shrubland and wet forest ecosystems. This highlights the need to combine screening experiments such as highly controlled greenhouse studies with field-based experiments testing restoration interventions over longer time periods. This may allow for the strategic application of C amendments to ecosystems with higher chance for success, or simply inform the longevity of the treatment application that is needed. Removal of non-native invasives provided positive outcomes for native wet forest woody seedlings in this study. Given that weed removal is highly labor intensive and requires continued, long-term maintenance (Ostertag et al. 2009), further research to develop effective restoration strategies for invaded ecosystems is needed.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Soil gas fluxes (N2O, and CO2, ± 1 SE) as a function of nutrient and weeding
767 treatments in wet forest and dry shrubland on Hawaii.
Figure S1. Total resin inorganic N ($NH4^+ + NO_3^-$).
Figure S2. Percent change in mean estimated biomass of non-native *Hedychium gardnerianum* 779 (kahili ginger).
Supplement S1. Supplementary methods.

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