Received: 15 November 2022 | Revised: 17 May 2023 | Accepted: 18 May 2023

DOI: 10.1002/eap.2894

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Functional trait-based restoration alters nutrient cycling and invasion rates in Hawaiian lowland wet forest

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Funding information
Hawaii Army National Guard Environmental Office; NSF, Grant/Award Number: 1754844; Strategic Environmental Research and Development Program, Grant/Award Number: RC2117

Handling Editor: Jennifer L. Funk

Abstract

Many degraded ecosystems have altered nutrient dynamics due to invaders' possessing a suite of traits that allow them to both outcompete native species and alter the environment. In ecosystems where invasive species have increased nutrient turnover rates, it can be difficult to reduce nutrient availability. This study examined whether a functional trait-based restoration approach involving the planting of species with conservative nutrient-use traits could slow rates of nutrient cycling and consequently reduce rates of invasion. We examined a functional trait restoration initiative in a heavily invaded lowland wet forest site in Hilo, Hawai'i. Native and introduced species were chosen to create four experimental hybrid forest communities, in comparison to the invaded forest, with a factorial design in which communities varied in rates of carbon turnover (slow or moderate [SLOW, MOD]), and in the relationship of species in trait space (redundant or complementary [RED, COMP]). After the first 5 years, we evaluated community-level outcomes related to nutrient cycling: carbon (C), nitrogen (N), and phosphorus (P) via litterfall, litter decomposition, and outplant productivity and rates of invasion. We found that (1) regardless of treatment, the experimental communities had low rates of nutrient cycling through litterfall relative to the invaded reference forest, (2) the MOD communities had greater nutrient release via litterfall than the SLOW communities, (3) introduced species had greater nutrient release than native species in the two MOD experimental communities, and (4) within treatments, there was a positive relationship between nutrient levels and outplant basal area, but outplant basal area was negatively associated with rates of invasion. The negative relationships among basal area and weed invasion, particularly for the two COMP treatments, suggest species existing in different parts of trait space may help confer some degree of invasion resistance. The diversification of trait space was facilitated by the use of introduced species, a new concept in Hawaiian forest management. Although challenges remain in endeavors to restore this heavily degraded ecosystem, this study provides evidence that functional trait-based restoration approaches using carefully crafted hybrid communities can reduce rates of nutrient cycling and invasion in order to reach management goals.

KEYWORDS
biological invasion, hybrid communities, introduced species, leaf litter decomposition, litterfall, native species, nutrient use, productivity, trait space

INTRODUCTION

In the field of restoration ecology, one of the most vexing issues is how to improve predictive assessments of which species are likely to survive and perform well, particularly in situations where invasive species are prevalent. This issue is not trivial due to the tremendous investment of time, money, and effort that goes into seeding and planting efforts. A recent trend in restoration ecology embraces a functional trait-based framework in which it is hypothesized that communities can be restored by using information about morphological and physiological traits of species and matching them to environmental conditions likely to yield high performance (Drenovsky & James, 2010; Funk et al., 2008). Functional trait-based restoration is an application of functional trait theory in which species are chosen for restoration treatments specifically based on their trait profiles (Carlucci et al., 2020). Integrating a trait-based approach in restoration planning can allow managers to target species-specific ecosystem services by selecting species with effect traits that strongly influence given ecosystem functions and support project goals (Suding et al., 2008). However, as this is a new approach, major challenges and uncertainties remain, such as how to choose species (Laughlin, 2014; Ostertag et al., 2015; Rayome et al., 2019; Wang et al., 2020), how to operationalize in a management setting (Merchant et al., 2023), and how to link community composition to specific and measurable ecosystem services (Carlucci et al., 2020; Kollmann et al., 2016).

One application where functional trait theory can be applied in a restoration context is the exclusion of invasive species through interspecific competition (Funk et al., 2008). A situational context where this concept can be applied is a deliberate introduction of species with specific trait values to counteract negative effects of invasive species on ecosystem functioning. For example, many invaded ecosystems have altered nutrient dynamics, and a frequent pattern in high-nutrient environments is that invaders have greater litterfall production and faster decomposition rates, which can occur when the invaders are nitrogen-fixing plants (e.g., Hughes & Denslow, 2005) and also when they are not (e.g., Gómez-Aparicio & Canham, 2008). In environments where nutrient cycling rates are high, two results often emerge: invasion of new plant species or functional types and an increase in the abundance of established invaders (e.g., Lake & Lieshman, 2004; Ostertag & Verville, 2002; Sardans et al., 2017). Because these are typically undesired outcomes, some kind of management strategy is usually sought after, but the reality is that it can be daunting to reverse the effects of nutrient enrichment (e.g., Isbell et al., 2013).

This study examined whether the intentional planting of species with conservative nutrient-use traits could slow rates of nutrient cycling in a highly nutrient-enriched environment and consequently reduce rates of invasion. An innovative experimental restoration project, *Liko Nā Pilina*, loosely translating to "budding new relationships," tested a functional trait-based approach by creating hybrid communities composed of both native Hawaiian species and nonnative yet noninvasive species (hereafter introduced). Unlike other studies that analyzed the relationships between traits and plant performance in restoration settings after the fact, this study is one of the first to use a technique that intentionally designed the functional diversity of a community a priori. The forest site where this study was conducted has some native canopy left, but it has been heavily invaded by species on the acquisitive end of the plant economics spectrum (Zimmerman et al., 2008). Nutrient cycling, plant regeneration, and the soil seedbank have been altered considerably by the invasion (Cordell et al., 2009; Ostertag et al., 2009), and previous attempts to remove invasive species have failed (Cordell et al., 2016). In short, without management this site will become entirely non-native-dominated (Zimmerman et al., 2008). The premise of the Liko Nā Pilina experiment was to transform a heavily invaded Hawaiian lowland wet forest into a more self-sustaining ecosystem with the acknowledgment from researchers and land managers that a completely native restoration would not be feasible (Cordell et al., 2016).

A key strategy of the experiment was to choose species based on their functional trait values to (1) produce canopy conditions that shade out invaders but allow for seedling regeneration of desired species and (2) decrease rates of nutrient turnover in litterfall to achieve slower rates of nutrient cycling. Species were carefully chosen with slow or moderate rates of nutrient turnover (Ostertag et al., 2015, 2020), and incorporating redundancy and complementarity in functional trait profiles into the experimental design served to test community assembly theory related to invasion resistance (Drenovsky & James, 2010; Funk et al., 2008; Hooper & Dukes, 2010). To establish the treatments, we chose a labor-intensive option of removing

invasive species and planting species with trait values on the nutrient-conservative end of the spectrum, rather than other known restoration methods, for several reasons. For instance, while removal of the upper 25–50 cm of topsoil has been successful in some grassland restoration efforts (Kardol et al., 2008; Klimkowska et al., 2007), this option would not have been feasible at the study site, nor at many of the remaining lowland wet forests on Hawai'i Island (Zimmerman et al., 2008), because this forest type occurs on young lava substrates with very little soil development. Carbon (C) addition is another method that has been applied in restoration to alter ratios of C and N, immobilize N, and reduce uptake (Török et al., 2011). This method has been used in a variety of restoration attempts to encourage native plant dominance (Corbin & D'Antonio, 2004; Kulmatiski, 2011), later successional species (Eschen et al., 2006), or shifts in community trait composition (Sandel et al., 2011). However, in several examples in Hawai'i, the addition of carbon was not successful. Cole et al. (2021) compared weed removal, NPK fertilizer addition, and C amendments (a combination of sucrose and wood sawdust), and it was found that weed removal in these forests was the only treatment that improved growth of native species (Cole et al., 2021). Similarly, Yelenik et al. (2017) added C and N and manipulated the abundance of an invasive grass in a subtropical woodland in Hawai'i. They found that C addition did not decrease soil N, nor did it improve growth or survival rates of species in restoration trials, but that grass removal was beneficial (Yelenik et al., 2017). In another experiment in montane wet forest that experienced years of monoculture under a native nitrogen-fixing tree, they found that the addition of *Metrosideros polymorpha* litter, a canopy tree with high C:N litter, did not reduce soil nitrogen or decrease the biomass of an invasive grass (Yelenik et al., 2021). Thus, given the evidence that nutrients were unlikely to be reduced through soil removal or amendments, we opted for a different strategy—removing competitors and rebuilding the forest canopy and understory using a functional trait approach.

In this study, we analyzed the nutrient dynamics via litterfall within the first 5 years of the four experimental treatments of this hybrid restoration experiment compared to invaded forest. We evaluated community-level outcomes related to nutrient cycling by measuring the following metrics: C, N, and P in litterfall, litter decomposition rates, outplant productivity, and density of nondesired species and person-hours to remove them. We sought to understand whether intentional planting could reduce levels of nutrient release and, if so, whether these reduced nutrient cycling rates could interact with the restored forest's productivity and rates of invasion. We posed the following research questions:

Q1.
   a. Are there differences in the quantity of nutrients (C, N, and P) being cycled via litterfall by hybrid forest in comparison to the invaded reference forest?
   b. Are there differences in the quantity of nutrients (C, N, and P) being released via litterfall among the four experimental hybrid forest communities?

Q2. Across the experimental hybrid forest communities, are the outplants of introduced species releasing more nutrients (C, N, and P) via litterfall than the outplants of native species?

Q3. Does the rate of nutrient (C, N, and P) release from litterfall correlate positively with the abundance of undesired weed species in the experimental hybrid forest communities?

METHODS

Research approach

The crux of the method is to develop experimental communities (treatments) with a suite of native and introduced species (see Ostertag et al. [2015] for details; Appendix S1: Table S1 for species list) to discourage colonization by the highly invasive species. Many of the introduced species chosen are canoe plants introduced by early Polynesian settlers (Whistler, 2009) that have been growing in the Hawaiian Islands for approximately 1000 years (Athens et al., 2014) and, thus, are considered naturalized. We chose these species based on their Hawai'i Pacific Weed Risk Assessment scores (Daehler et al., 2004) and observations of experts that had seen them growing in lowland wet forest habitats without invasive tendencies. The metrics of success being tracked in the experimental communities were related to slower rates of nutrient cycling, reduced rates of invasion, and increased natural regeneration.

Site description

The study site is located within a heavily degraded lowland (30 m above sea level) wet forest (mean annual rainfall 3347 mm/year; Giambelluca et al., 2013) at the Keaukaha Military Reservation (KMR, 19°42′15″°N, −155°2′40″°W) in Hilo, Hawai'i. In this forest, invasive species have almost completely excluded native Hawaiian flora in the understory, and they dominate the midstory. In time, and without intervention, this forest would most likely become devoid of all native plant species, as invasive tree species are also encroaching into the canopy (Zimmerman et al., 2008). Yet, due to the presence of

older endemic canopy dominants (*Metrosideros polymorpha* and *Diospyros sandwicensis*) and native subcanopy species (*Psychotria hawaiiensis*, *Myrsine lessertiana*, *Cibotium glaucum*, and *Pandanus tectorius*), this site has been the focus of research to experimentally test potential restoration strategies for nearly two decades.

Experimental design

The logic behind the experimental treatments has been described elsewhere (Ostertag et al., 2015, 2020). There are four experimental communities: slow carbon turnover redundant (SLOW RED), moderate carbon turnover redundant (MOD RED), slow carbon turnover complementary (SLOW COMP), and moderate carbon turnover complementary (MOD COMP), all of which had a constrained species richness ($n = 10$ per experimental community). The two SLOW treatments were selected specifically to have four core species with functional trait values related to a slower growth and turnover of tissues. The MOD treatments had four core species with trait values correlated with faster growth and turnover than the slow treatment, but those trait values were still much lower than is typically seen in the highly invasive species in this region. Thus, we expected that the SLOW and MOD treatments would have slower rates of nutrient cycling than the invaded forest. The two treatments RED and COMP were designed so that an additional six species would have trait values that were either similar or dissimilar to the four core species based on Euclidean distances in trait space (Ostertag et al., 2015). The experiment was a randomized block design ($n = 4$), and each block consisted of one reference (invaded forest) and the four experimental communities. Plot size was 20 × 20 m with a 5-m perimeter buffer. The plots were cleared of all nonnative species and planted in 2013. Monitoring of these experimental communities began in January 2014.

Nutrient cycling metrics

Litterfall was measured as an index of productivity. Litter screens (40 cm × 40 cm, 1 mm mesh size) were placed in the plots along diagonal and crossed transect lines ($n = 20$ per plot). Litter was collected monthly, bulked per plot, dried at 70°C for at least 48 h, and then weighed. Starting in 2016 we separated out litter from the outplant species and sorted and weighed each species in order to calculate species-specific productivity and overall outplant contribution to the plots. Nutrients in the litterfall of outplant species were determined by grinding material in a Wiley mill (40 mesh) and then processing samples with a Costech CE Elemental Analyzer (Costech ECS 4010; Valencia, CA, USA) to obtain the concentration of carbon (C) and nitrogen (N), and a Varian inductively coupled plasma spectrometer (Varian Vista-MPX inductively coupled plasma-optical emission spectrometry; Palo Alto, CA, USA) was used to obtain the concentration of P. All nutrient analyses were conducted at the University of Hawai'i at Hilo Analytical Laboratory.

We also examined the decomposition rate (mass loss) of each outplanted species, using litterfall collected in 2016. Litter bags with dimensions of 20 cm × 30 cm (area inside) were constructed of 1-mm-mesh fiberglass window screen, each filled with 5 g of litter. Bags were placed in another area of the forest used for past experiments (Kandert et al., 2021; Ostertag et al., 2009). Bags ($n = 10$ per time period per species) were collected at intervals of 4 and 12 months. Nonlitter items, such as roots and small rocks, were discarded prior to drying (70°C for 48 h) and weighing. Samples were ashed at 500°C for 5 h (Muffle furnace Thermolyne 1400; University of Hawai'i at Hilo Analytical Laboratory) to determine the percentage of organic material and mass were corrected accordingly. The proportion of mass loss was calculated at each time point.

For each species, we did not measure nutrient uptake but were able to determine nutrient release with a series of two calculations that combined litterfall rates, litter nutrient concentrations, and decomposition rates (mass loss %) per species. The series of equations used were as follows:

$$\text{Litterfall mass (g/plot)} \times (\text{C, N, or P}\,[\%]/100) = \text{C, N, or P in litterfall mass (g C, N, or P/plot)} \quad (1)$$

$$\text{C, N, or P in litterfall mass (g C, N, or P/plot)} \times (\text{Mass loss}\,[\%]/100) = \text{C, N, or P released from litterfall (g C, N, or P/plot)}. \quad (2)$$

These equations provided the nutrient release per species per plot, and for treatment comparisons, we added up values from all 10 species per plot.

Productivity and invasion metrics

In May 2014 all outplants were tagged and their locations within plots mapped using ArcPad on Allegro MX field computers. All stems at least 1.0 cm in diameter were measured at 1.3 m height (dbh) to calculate basal area at the individual and then plot level. All existing natives

and outplants were censused annually to monitor changes in survival and growth. Although the number of outplant individuals with a dbh ≥1.0 cm was minimal in 2014, 25% of outplants were recorded with a dbh by 2017. In using basal area/plot as a proxy for productivity, it should be noted that this metric is not inclusive for all outplants but rather the most productive as gauged by those reaching the 1.0-cm dbh threshold.

From the moment plots were originally cleared, it was necessary to hand weed at approximately 3- to 4-month intervals to sustain outplant growth. We removed all undesired recruits (any seedling or resprout that was not native or of a species outplanted in the experiment). After 2 years of plant community development, we were able to reduce weeding frequency to 6-month intervals. However, maintenance hours were still too high to consider the level of labor input feasible for extending this restoration method across larger landscapes. At this point we adjusted our management tactic slightly and decided to apply a foliar herbicide (Roundup Pro Concentrate; 1.5%) after hand weeding to the more persistent weed species (i.e., difficult to hand weed or fast germination rate after weeding) with the goal of reducing labor inputs to levels that would be feasible in larger landscapes. Stems that were too large to be managed by hand pulling were cut with loppers and treated with herbicide (30% Garlon 4 Ultra, mixed with 70% crop oil). At the start of 2016 and subsequent years, we began recording the number of weed species found in the plots, as well as the number of person-hours taken to weed a plot. These data were used to quantify invasion rates, as described in what follows.

Statistical analyses

JMP (version 11. SAS Institute Inc., Cary, NC, 1989–2019) was used for all statistical analyses. To determine whether the hybrid forests reduced nutrient cycling rates (Question [Q] 1a), we compared each nutrient (g C, N, and P/plot; see previously listed equations) released in litterfall between the invaded reference forest and the treatments (four experimental communities combined as one group) with a Welch ANOVA test. The Welch ANOVA was used because, although the ANOVA assumption of normality was achieved, the assumption of equal variances was not. To address whether there are differences in the quantity of nutrients (g C, N, and P/plot) being released via litterfall among the four experimental hybrid forest communities (Q 1b), we used a one-way ANOVA. Square-root transformations were used to achieve normality for all three response variables. Tukey's HSD were used in post hoc analyses.

To determine whether the outplants of introduced species released more nutrients (g C, N, and P/plot) via litterfall than the outplants of native species (Q 2), we conducted a two-way ANOVA with the treatment type as one factor, species type (introduced and native outplants) as the second factor, a two-way interaction of factors incorporated into the model, and nutrient (g C, N, and P/plot) released as the response variable. Normal distributions of all three response variables were achieved by performing cube-root transformations. Tukey's HSD were used in post hoc analyses of least-squares means. Nutrients (g C, N, and P/plot) released from litterfall were analyzed over a 3-year period (2016–2018) (Qs 1 and 2).

Lastly, to assess whether the rate of nutrient release from litterfall affects rates of invasion in the experimental hybrid forest communities (Q 3), a series of linear regressions were conducted. First, we used linear regression with the nutrient (g C, N, and P/plot) released as the factor (2016–2018 time period) and the invasion metrics (weed species [No.] and weeding hours [No.] over the following year, 2017–2019 time period) as the response variables. We also examined a two-part series of linear regressions: (1) the nutrient released (g C, N, and P/plot) as the factor and outplant basal area as the response variable, followed by (2) outplant basal area as the factor and the invasion metrics (weed species [No.] and weeding hours [No.]) as the response variable. Three years of data were combined into one analysis (2016–2018 nutrient factors; 2017–2019 following year response variables), and regressions were conducted for the treatments individually and combined as one experimental hybrid community.

RESULTS

Nutrient release in hybrid and reference forests

The experimental communities released lower amounts of nutrients via outplant litterfall than the invaded reference forest (Table 1). The average nutrients released for the experimental communities were approximately 17%, 13%, and 8% of that released in the invaded reference forest, for C, N, and P, respectively. The greater amount of nutrients released in the invaded reference forest, compared with the experimental communities, is due to a combination of higher litterfall rates, greater nutrient concentrations, and faster decomposition (Appendix S1: Table S1). Examining among the four hybrid community restoration treatments, we found that the MOD RED treatment consistently had the highest release of C ($F_{(3,16)} = 5.85$, $p = 0.0106$; Figure 1a), N ($F_{(3,16)} = 8.92$, $p = 0.0022$, Figure 1b), and P ($F_{(3,16)} = 8.02$, $p = 0.0034$,

TABLE 1 Nutrients (carbon, nitrogen, and phosphorus) released through litterfall compared between invaded reference forest and experimental hybrid forest communities (all four treatments combined).

Nutrient released through litterfall	Mean and SE	Invaded reference ($n = 4$)	Experimental community ($n = 16$)
Carbon (g C/plot)	Mean	84,424	14,255
	SE	11,833	2543
Nitrogen (g N/plot)	Mean	2473	311
	SE	450	61
Phosphorus (g P/plot)	Mean	179	14
	SE	33	3

Note: Statistics provided from a Welch Analysis of Variance for mean comparisons between the invaded forest and the experimental hybrid communities; carbon (g C/plot) F-ratio = 31.72, p-value = 0.0087, nitrogen (g N/plot) F ratio = 22.63, p-value = 0.0162, phosphorus (g P/plot) F-ratio = 24.66, p-value = 0.0152.

Figure 1c). The MOD COMP treatment was intermediate between the MOD RED and the two SLOW treatments—(SLOW COMP and SLOW RED)—across all nutrient comparisons. The greater amount of nutrients released was due to the MOD RED's having much higher litterfall rates than the other three treatments (Appendix S1: Table S1).

Nutrient release from introduced and native outplants

The two-way ANOVA models conducted for all three nutrients released from outplant litterfall indicated significant interactions between species type and experimental communities; therefore, the effect of species type was not consistent across the experimental communities. The full models explained 75% of the variation for C released ($F_{(7,32)} = 14.04$, $p < 0.001$), 81% for N released ($F_{(7,32)} = 19.50$, $p < 0.0001$), and 82% for P released ($F_{(7,32)} = 20.59$, $p < 0.0001$). Two prominent findings resulted from these analyses. First, introduced outplants had greater release, of all three elements, than native outplants in the two MOD treatments, but not in the two SLOW treatments (Figure 2a–c). Second, there is significantly greater release of all three elements from introduced outplants in the MOD RED experimental community compared with all species type and experimental community groups, with the exception of the introduced outplants in the MOD COMP experimental community, which released similar amounts of C and N from litterfall (Figure 2a–c).

Nutrient release and invasion

Nutrient release, plant growth (as determined by outplant basal area), and invasion were related to each other in contradictory ways that overall suggest that the litter nutrients could indirectly suppress weed regeneration. First, C, N, and P release all showed significant negative relationships to both invasion metrics (weed species [No.] and weeding hours [No.]) when analyzed across all treatments (Table 2)—an unexpected result suggesting increased nutrient release from the outplant litterfall did not lead to higher invasion rates. Examining these relationships within each treatment resulted in identifying the two COMP treatments as being the most significant influencers for the overall significant negative relationship (Table 2).

Yet the C, N, and P release showed significant positive relationships to plant growth (outplant basal area) when analyzed across all treatments (Table 3). Within-treatment comparisons yielded significant positive relationships, with the exceptions of N and P release × Outplant basal area in the SLOW RED treatment and C release × Outplant basal area in the MOD COMP treatment, which were nearly significant (i.e., $p < 0.10$) (Table 3; Figure 3a–c). Finally, outplant basal area showed significant negative relationships to both invasion metrics when analyzed across all treatments (Table 3). Within-treatment comparisons yielded significant negative relationships, with the exception of Outplant basal area × Weeding hours in the SLOW RED treatment (Table 3; Figure 3d,e). These results suggest that basal area growth might respond to nutrients, forming a canopy environment that can shade out unwanted invaders.

DISCUSSION

Removal of invaders is often the first approach used in restoration and management, yet it may not be sufficient to reduce future invasion if litter and soil nutrient pools experience legacy effects (Elgersma et al., 2011). In this study, we showed that with intentional planning to

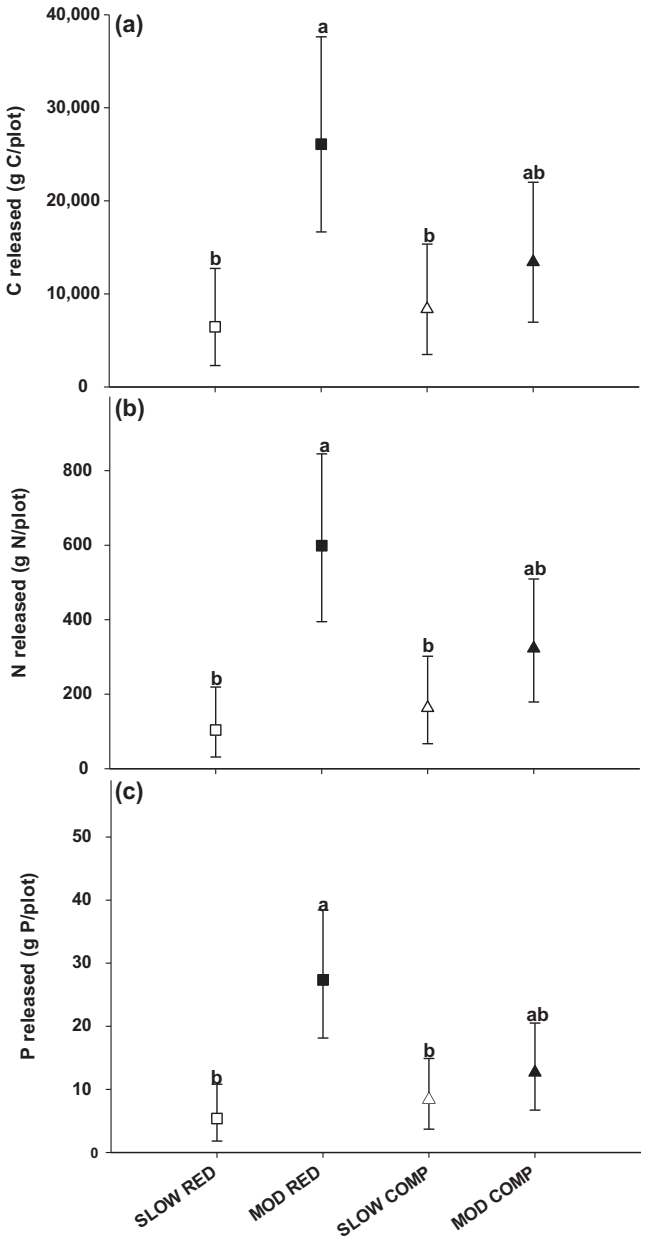

FIGURE 1 Carbon (a), nitrogen (b), and phosphorus (c) released from litterfall across the four experimental community treatments (SLOW RED, MOD RED, SLOW COMP, and MOD COMP). Values are back-transformed means ± 95% CIs. Letters indicate significant difference resulting from ANOVA followed by Tukey's comparisons test. MOD COMP, moderate carbon turnover complementary; MOD RED, moderate carbon turnover redundant; SLOW COMP, slow carbon turnover complementary; SLOW RED, slow carbon turnover redundant.

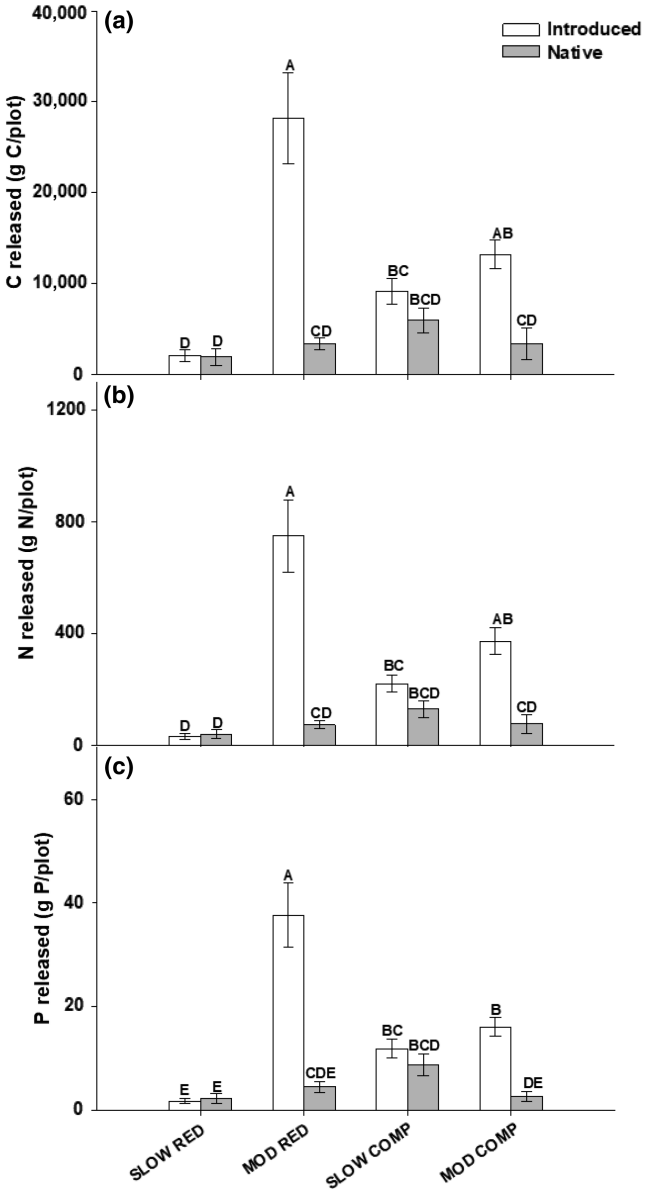

FIGURE 2 Carbon (a), nitrogen (b), and phosphorus (c) released from litterfall across the four experimental community treatments (SLOW RED, MOD RED, SLOW COMP, and MOD COMP) and separated between introduced (white bars) and native (gray bars) outplants. Values are means ± SE. Letters indicate significant difference across treatments resulting from a two-way ANOVA followed by Tukey's comparisons test of least-square means. MOD COMP, moderate carbon turnover complementary; MOD RED, moderate carbon turnover redundant; SLOW COMP, slow carbon turnover complementary; SLOW RED, slow carbon turnover redundant.

introduce species with functional traits on the slower end of the resource economics spectrum, communities can be built that have a much slower rate of nutrient cycling than the invaded forest. Remarkably, over a 5-year period, the rate of C, N, and P cycling through litterfall was reduced by more than 80%, and these experimental communities were effective in keeping out invaders. Because nutrient release from litter of these planted species was not correlated with higher rates of invasion (Table 2) but was correlated with increased basal area of the outplants (Table 3; Figure 3), a possible mechanism for decreased invasion is a change in abiotic conditions

TABLE 2 Statistical results from linear regressions to answer the question: Has increased nutrient release resulted in higher rates of invasion?

		Carbon released		Nitrogen released		Phosphorus released	
Treatment	Statistics	Weed species (No.)	Weeding hours (No.)	Weed species (No.)	Weeding hours (No.)	Weed species (No.)	Weeding hours (No.)
ALL	Adjusted R^2	**17**	**15**	**18**	**16**	**16**	**11**
	p-value	**0.0023**	**0.0004**	**0.0014**	**0.0025**	**0.0031**	**0.011**
	Slope (−/+)	**(−)**	**(−)**	**(−)**	**(−)**	**(−)**	**(−)**
SLOW RED	Adjusted R^2	6	9	8	8	9	5
	p-value	0.5387	0.8195	0.6708	0.6926	0.7799	0.4994
	Slope (−/+)	(−)	(+)	(−)	(+)	(−)	(+)
MOD RED	Adjusted R^2	22	12	**30**	18	21	10
	p-value	0.0679	0.1442	**0.0389**	0.0943	0.0745	0.1703
	Slope (−/+)	(−)	(−)	**(−)**	(−)	(−)	(−)
SLOW COMP	Adjusted R^2	**65**	**59**	**61**	**66**	**63**	**45**
	p-value	**0.0009**	**0.0022**	**0.0016**	**0.0008**	**0.0013**	**0.0098**
	Slope (−/+)	**(−)**	**(−)**	**(−)**	**(−)**	**(−)**	**(−)**
MOD COMP	Adjusted R^2	12	**29**	26	**35**	**34**	22
	p-value	0.143	**0.042**	0.052	**0.024**	**0.028**	0.069
	Slope (−/+)	(−)	**(−)**	(−)	**(−)**	**(−)**	(−)

Note: Regression with all treatments combined for all years ($n = 12$ per treatment), plus separate regressions for each treatment, with nutrients released as the factor and weed species (No.)/weeding hours (No.) as the response variables. Relevant statistics provided are adjusted R^2 (%), *p*-value, and direction of slope (−/+). Significant results highlighted by bold font.

Abbreviations: MOD COMP, moderate carbon turnover complementary; MOD RED, moderate carbon turnover redundant; SLOW COMP, slow carbon turnover complementary; SLOW RED, slow carbon turnover redundant.

(e.g., increased shade, lower nutrients). While this mechanism concurs with data from past studies (Cordell et al., 2009; Ostertag et al., 2009), it is also possible that the physical effect of the litter on the forest floor, or some kind of allelochemical effect of the litter, could have influenced the germination of invasive seedlings.

Manipulation of nutrient availability

Nutrient cycling is sometimes far more rapid in invaded forests compared with Hawai'i's remaining native forests (Allison & Vitousek, 2004; Hughes et al., 2014). From a restoration standpoint, the reduced rate of nutrient cycling through litterfall in this study is extremely encouraging because others have not found success in reducing nutrient availability in Hawaiian forests using high carbon amendments (Cole et al., 2021; Yelenik et al., 2017, 2021). The key innovation here is wholesale replacement and a remaking of the plant community using functional trait theory. Although the applications of functional trait-based restoration for recovering ecosystem services have been discussed (see review by Carlucci et al., 2020), this study provides some of the first evidence of its practice—demonstrating that careful and intentional restoration with purposely crafted functional trait profiles can lead to desired outcomes in terms of plant growth and species composition. Demonstrating a clear linkage between plant functional traits and ecological processes has been dubbed the "Holy Grail" in the ecological literature (Lavorel & Gamier, 2002; Suding & Goldstein, 2008). But as Funk et al. (2017) point out, the challenges in deciphering these complex relationships lies in choosing the "right" functional traits, considering intraspecific variation in traits, and scaling from trait data to community- and ecosystem-level processes. This study provides evidence that linkage to ecosystem processes is possible under certain simplified conditions, such as the restoration of relatively low species diversity forest, with a limited set of objectives.

Choosing which functional traits to manipulate to foil invaders is one of the most intractable issues and involves best guesses. In this study, we intuited that altering the cycling of the leaf litter could strongly redirect abiotic and biotic processes. The strong reduction in litter nutrient cycling, regardless of which hybrid community

TABLE 3 Statistical results from a two-step series of linear regressions to answer the questions: Has increased nutrient release resulted in higher rates of plant growth? If so, has higher rates of plant growth resulted in decreased rates of invasion?

		Outplant basal area (m^2/ha)			Outplant basal area (m^2/ha)	
Treatment	**Statistics**	**Carbon released**	**Nitrogen released**	**Phosphorus released**	**Weed species (No.)**	**Weeding hours (No.)**
ALL	Adjusted R^2	**67**	**68**	**75**	**34**	**27**
	p-value	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	Slope (−/+)	**(+)**	**(+)**	**(+)**	**(−)**	**(−)**
SLOW RED	Adjusted R^2	**30**	22	22	**40**	11
	p-value	**0.0381**	0.0681	0.0718	**0.0167**	0.1564
	Slope (−/+)	**(+)**	(+)	(+)	**(−)**	(−)
MOD RED	Adjusted R^2	**57**	**61**	**61**	**59**	**43**
	p-value	**0.0029**	**0.0017**	**0.0017**	**0.0022**	**0.0118**
	Slope (−/+)	**(+)**	**(+)**	**(+)**	**(−)**	**(−)**
SLOW COMP	Adjusted R^2	**63**	**63**	**60**	**68**	**67**
	p-value	**0.0013**	**0.0013**	**0.0019**	**0.0006**	**0.0006**
	Slope (−/+)	**(+)**	**(+)**	**(+)**	**(−)**	**(−)**
MOD COMP	Adjusted R^2	23	**40**	**54**	**86**	**47**
	p-value	0.067	**0.016**	**0.004**	**<0.0001**	**0.008**
	Slope (−/+)	(+)	**(+)**	**(+)**	**(−)**	**(−)**

Note: Regression with all treatments combined for all years ($n = 12$ per treatment), plus separate regressions for each treatment, with nutrients released as the factor and outplant basal area as the response variable, and outplant basal area as the factor and weed species (No.)/weeding hours (No.) as the response variables. Relevant statistics provided are adjusted R^2 (%), *p*-value, and direction of slope (−/+). Significant results highlighted by bold font.
Abbreviations: MOD COMP, moderate carbon turnover complementary; MOD RED, moderate carbon turnover redundant; SLOW COMP, slow carbon turnover complementary; SLOW RED, slow carbon turnover redundant.

composition was used, points to the promise of this technique and validates the concept of using effect traits to alter environmental conditions (Funk et al., 2008; Suding et al., 2008). However, the greater cycling of nutrients through the litter of invaders is not universal (e.g., Prescott & Zukswert, 2016), and, importantly, there are also good examples where invaders are effective at colonizing low-resource environments (Funk & Vitousek, 2007). A review of the literature shows that invaders can have trait values on both the resource-acquisitive and resource-conservative ends of the spectrum (Funk, 2013; van Kluenen et al., 2010) such that no set of invader characteristics fits all conditions. Instead, when practitioners apply the functional trait-based approach, they must think carefully about how the functional characteristics of species match environmental parameters rather than simply making assumptions based on the invasive/nonnative/native classification (Guerin et al., 2018; Yelenik et al., 2017). Given the generality and flexibility of the trait-based approach, its value should be tested in other ecosystems using a variety of restoration objectives (Rayome et al., 2019).

This type of restoration experiment should be examined over time because, due to the young age of the planted communities and with species not yet reaching maturity, it would be expected that litterfall quantities will increase substantially in years to come. In addition, the release of nutrients from the litter of outplanted species might be an underestimation because species that we intentionally chose for their low litter quality (high C-to-N and C-to-P ratios) could be immobilizing rather than releasing nutrients (Hobbie, 2015). Nonetheless, we argue that, given the success over this short 5-year time period in terms of both reduction of invasion and nutrient pools, functional trait-based restoration is a viable strategy for creating Hawaiian lowland wet forest communities.

Natives versus introduced species

The geographic isolation of the Hawaiian archipelago has resulted in disharmonic flora (Denslow, 2003; Simberloff, 1995), and, as a consequence, invasive species often outcompete the resource-conservative native species for critical resources (Baruch & Goldstein, 1999). Due to the conservative resource strategies of many Hawaiian native plants, it was hypothesized that outplants from the

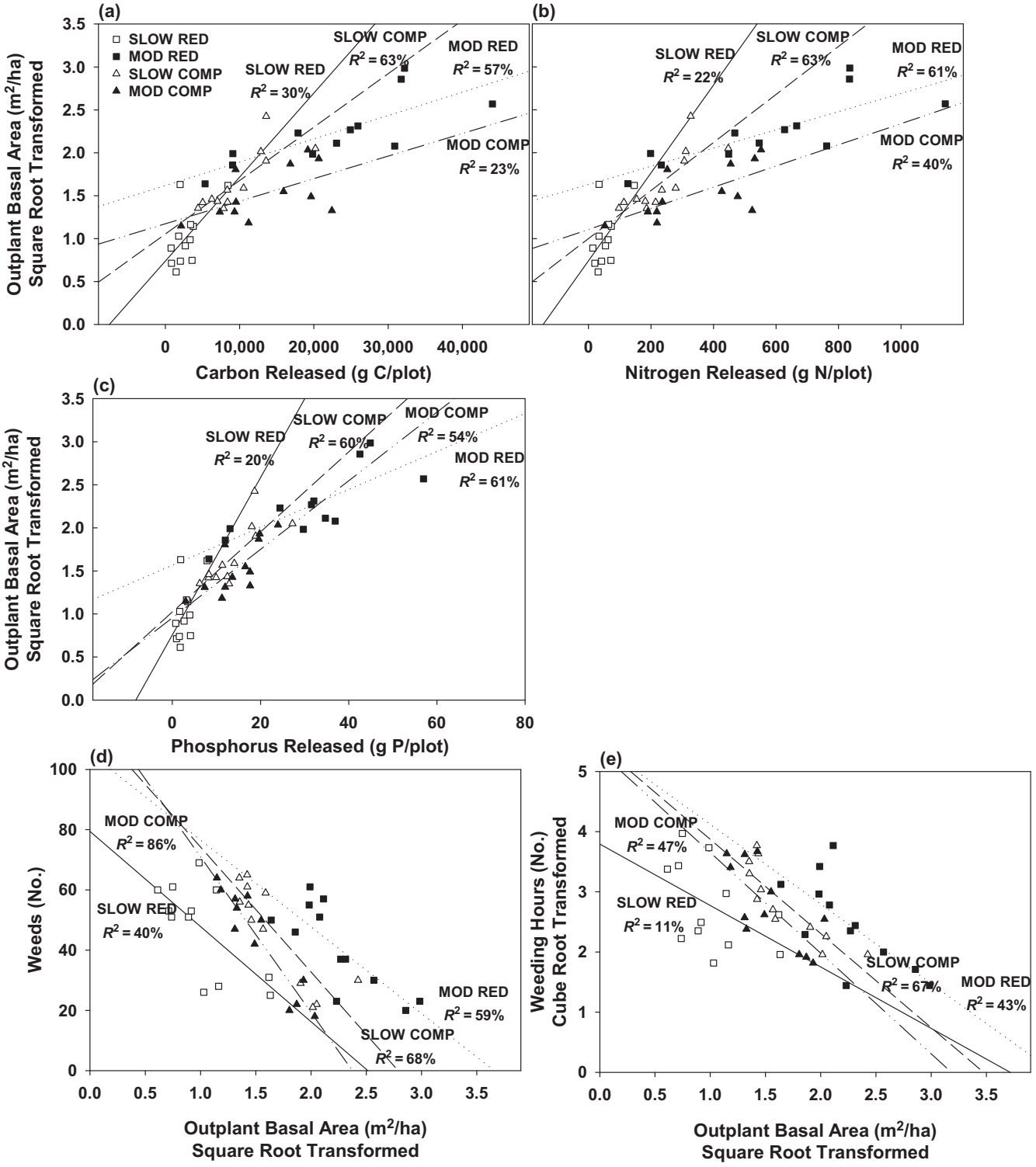

FIGURE 3 Linear regressions of (1) plant growth (outplant basal area) in response to carbon (a), nitrogen (b), and phosphorus (c) released from litterfall, and (2) invasion metrics (weed species [d]; weeding hours [e]) in response to plant growth (outplant basal area). Three years of data are presented with treatments represented by separate regression lines and adjusted R^2 values provided. MOD COMP, moderate carbon turnover complementary; MOD RED, moderate carbon turnover redundant; SLOW COMP, slow carbon turnover complementary; SLOW RED, slow carbon turnover redundant.

introduced species would have higher nutrient release than the native species (Q 2). This hypothesis was not supported across the board but varied by treatment, with introduced species having higher C, N, and P release only in the two MOD treatments (Figure 2). These two MOD communities have the same core species—chosen for

their ability to become the largest trees in the treatment—but it is noteworthy that the MOD RED community has a more pronounced difference in nutrients released (g C, N, and P/plot) between introduced and native species. Thus, it is likely that the trait values of the introduced COMP versus RED species also influence nutrient cycling.

What is unclear, however, is whether the differences in the amount of nutrients released of the introduced species between treatments are due simply to the sum of each individual species' traits or interactions that might occur among species during the decomposition process. Meta-analysis has shown that leaf litter mixtures do not always decompose in an additive manner (what would be predicted based on each species' initial mass; Gartner & Cardon, 2004) but often decompose in a nonadditive manner, either faster (synergistically) or slower (antagonistically) than expected. Litter mixtures that contain species more functionally dissimilar in physical and chemical traits are hypothesized to have synergistic effects (Lecerf et al., 2011; Schindler & Gessner, 2009). Based on this hypothesis and what is known about plant–soil feedbacks (Hobbie, 2015), the MOD COMP treatment would be predicted to have the highest level of nutrient release. Our results showed no difference between the MOD treatments, and we point out that a more detailed mechanistic analysis of decomposition rates is necessary if we are to understand how niche complementarity relates to nutrient cycling in this experiment.

Resistance to invasion

The most striking result in this study is the negative relationship between outplant basal area and metrics of invasion (Q 3; Table 3). In this study, we cannot tease apart the cause and effect, but this relationship is extremely promising from a restoration perspective. Indeed, the functional trait-based restoration approach allowed us to simultaneously manipulate canopy and nutrient characteristics. Further experimentation should be done to determine whether light becomes the primary driver of invasion when litterfall nutrient release is kept to low levels. The lower resource environment will not keep out all invaders (e.g., Funk & Vitousek, 2007), but at least at this 5-year time scale it appears promising.

Complementarity in trait space might be advantageous for keeping out invaders, a premise of the hypothesis of limiting similarity (Abrams, 1983). The negative relationships among basal area and weed invasion were stronger for the two COMP treatments and were not significant at all for the SLOW RED treatment (Table 3). Such a result supports the underlying premise that functional trait-based restoration can be used to provide some level of invasion resistance (Funk et al., 2008) because being in different parts of trait space reduces both competition and niche overlap, which may deter the establishment of invaders (Divísek et al., 2018). Yet it is clear within the Liko Nā Pilina experiment that there are tradeoffs between growth, reproduction, and invasion resistance, and these tradeoffs could easily be altered by unforeseen events (e.g., differential species effects of disturbance, disease or pest outbreaks). These 5-year results can be considered short-term, but the long-term outcomes may be quite different, highlighting the importance of balancing multiple management strategies during the species selection phase of a restoration project.

It is also important to highlight that outplant productivity does not explain all the variability observed in the invasion resistance metrics (Table 3), which leads us to question what other abiotic and/or biotic elements are influencing early invasion resistance in these experimental communities. For example, a generalized linear mixed model (GLMM) of weeding effort (No. person-hours) was best predicted by treatment, topography, outplant litterfall nutrients, and preexisting native canopy basal area (Ostertag et al., in preparation). Topography and preexisting native canopy basal area are two predictors that are not subsumed within the experimental design of the project (i.e., not controlled by species selection of the communities) and vary across the landscape, affecting native sapling distributions (Kandert et al., 2021). In addition, litterfall quantity could reduce invasion by acting like a weed mat, a commonly used practice in restoration (Nsikani et al., 2018; Sweeney et al., 2002), effectively reducing light availability to weed seedlings and creating a barrier to growth during the germination phase. An example of this occurrence can be found in Baker and Murray (2010), who found reduced emergence, height, survival, and establishment of *Pinus radiata* seedlings, an invasive species in Australian native eucalypt forests, with increasing depths of native leaf litter. While the data here cannot distinguish among mechanisms, it is clear that these four experimental communities have reduced nutrient release from litterfall and are successfully keeping out invaders.

Conclusions

A hybrid ecosystem restoration that uses introduced species is certainly not appropriate in all places or ecosystem types and requires care in its implementation. A primary motivation for adopting the hybrid restoration approach for Hawai'i's lowland wet forest was

research demonstrating that maintaining an all-native forest was not feasible due to time, labor, costs, and rates of invasion (Cordell et al., 2009, 2016; Ostertag et al., 2009). While there are some differences among the four experimental treatments, the most remarkable aspect of this study is how well all four hybrid communities had reduced litter nutrient cycling rates and lower numbers invasive plant species, demonstrating linkages between functional traits and ecosystem services. Although challenges remain, particularly in scaling up (e.g., collecting functional trait data, labor, and costs), this study is one of the first to demonstrate that manipulating the functional diversity of a forest ecosystem through targeted and purposeful planting is a viable strategy for forest management.

ACKNOWLEDGMENTS

Funding from the Strategic Environmental Research and Development Program (Project RC-2117) supported the original setup of the experiment and additional funding has come from National Science Foundation (NSF) 1754844 and the Hawai'i Army National Guard Environmental Office. We thank Craig Blaisdell, Kristine Barker, and staff at Keaukaha Military Reservation for facilitating the establishment of the Liko Nā Pilina project and for their continued support of the project. Nutrient analyses were conducted by Erik Johnson and Tara Holitzki at the UH Hilo Analytical Laboratory; they were supported in part by National Science Foundation Award No. EPS-0903833. We also thank the numerous interns, the University of Hawai'i at Hilo students, and volunteer individuals and groups that have come out in the field to assist in many aspects of project creation, maintenance, and monitoring.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ostertag et al., 2023) are available in Dryad: https://doi.org/10.5061/dryad.zkh1893d5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: DiManno, Nicole, Rebecca Ostertag, Amanda Uowolo, Amy Durham, Kaikea Blakemore, Susan Cordell, and Peter Vitousek. 2023. "Functional Trait-Based Restoration Alters Nutrient Cycling and Invasion Rates in Hawaiian Lowland Wet Forest." *Ecological Applications* e2894. https://doi.org/10.1002/eap.2894