

# Patterns and consequences of re-invasion into a Hawaiian dry forest restoration

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**Abstract** The restoration of native plant diversity may be an effective tool for weed control, but its use has not been tested in the heavily invaded Hawaiian dry forest ecosystem. In addition, the ecological mechanisms by which invasive plants may cause declines in native plant diversity are generally not well understood. We examined invasion resistance and the relationships between invasion and declines in native plant diversity at local scales in a Hawaiian dry forest restoration by experimentally removing non-native species, planting native species, manipulating resources and environmental conditions, and allowing non-native species to re-invade. We found higher invasion rates in habitats that supported the most native species, suggesting that similar mechanisms may regulate the distribution of both native and

invasive species. *Pennisetum setaceum*, a dominant invasive perennial grass, was associated with native plant mortality and declines in native diversity. Although invasion rates were greatest in more favorable habitats, the association of invasion with native species loss was significant only in lower quality habitats, suggesting that environmental conditions may regulate competitive interactions between native and invasive species. We found that native woody plant restoration is not an effective tool for weed control in this community, and that invasion may result in declines in native diversity. Our study provides a caveat to previous suggestions that invasion impacts on native diversity will be greatest in the most diverse plant communities. At local scales in some communities it may also be effective to control invasive species in sensitive areas with low resource availability instead of, or in addition to, areas with high biodiversity.

**Keywords** Limiting similarity · Plant diversity · Local extinction · *Pennisetum setaceum* · *Cenchrus setaceus*

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## Introduction

Abiotic or biotic filters may increase invasion resistance in restored plant communities (D'Antonio and Meyerson 2002; Funk et al. 2008). Abiotic conditions such as water availability can be altered to reduce the

likelihood of invasion, and properties of restored plant communities can be altered to increase biotic resistance to invasion. Increasing the diversity of restored communities may enhance biotic resistance to invasion, because a negative relationship between native and non-native diversity is often observed at small spatial scales. More diverse native communities can draw down resources below levels required by invasive species through either niche complementarity or a sampling effect (Brown and Peet 2003; Davies et al. 2005; Dukes 2001; Fargione et al. 2003; Fridley et al. 2007; Levine and D'Antonio 1999; Levine et al. 2003). Therefore, it is thought that restoring native plant diversity should inhibit re-invasion into managed ecosystems, however, there have been few experimental tests of the importance of this diversity-invasibility mechanism in the context of ecological restoration (Bakker and Wilson 2004; Emer and Fonseca 2011; Middleton et al. 2010; Quinn and Holt 2009).

Understanding how to prioritize funding for invasive species control is an additional challenge for managing invaded ecosystems, and priorities should be placed on species with a large ecological impact and the ability to be controlled (D'Antonio and Meyerson 2002). A large body of work demonstrates that invasive plant species reduce the performance of native species through competition for resources (e.g., D'Antonio and Mahall 1991; HilleRisLambers et al. 2010; MacDougall and Turkington 2005; Mack et al. 2001); however, these competitive interactions are rarely linked to actual declines in native species diversity and may not pose a significant threat to the conservation of biodiversity (Davis et al. 2011; Gurevitch and Padilla 2004; Sax and Gaines 2008). There are also many studies identifying dramatic changes to ecosystem processes as a result of plant invasions, including altered fire regimes, nutrient cycling, and hydrology (reviewed by Levine et al. 2003). However, the effect of these impacts on community processes has received little attention except for the case of altered fire regimes, which have the potential to replace native woody communities with non-native grasslands (D'Antonio and Vitousek 1992; Levine et al. 2003). A better understanding of how (or whether) invasive plants affect native plant diversity will enhance our ability to prioritize invasive plant management programs.

When considering the effect of invasion on native biodiversity, the possible outcome will be no effect, a

positive effect (e.g., through facilitation), or a negative effect (species decline). Many observational studies in remnant native or semi-natural communities have documented lower native plant species diversity with increasing levels of invasion at small spatial scales, but it is not clear from these studies whether invasive species exclude native species from colonizing a community or cause a decline in native diversity through the mortality of native species (Brown and Peet 2003; Fridley et al. 2007; Gaertner et al. 2009; Hejda et al. 2009; Levine et al. 2003; Pysek and Pysek 1995; Stohlgren et al. 1999). Fewer studies have experimentally examined the mechanistic links between invasion and native diversity declines (Gooden et al. 2009; Yurkonis and Meiners 2004; Yurkonis et al. 2005), and so far none have found a reduction in diversity due to increased mortality and local extinction (but see Dilleuth et al. 2009; Williams and Crone 2006; Yurkonis et al. 2005). A better understanding of how invasive species alter native biodiversity in managed ecosystems will help determine which management activities will have the greatest impact on preventing invasion-caused declines in biodiversity.

Here, we investigate the relationship between abiotic conditions, native diversity, and re-invasion in a tropical dry forest in Hawaii following restoration activities. Hawaiian tropical dry forests are a model system for studying relationships between invasion, resource availability, and native diversity declines due to their high levels of invasion, extreme water limitation, and the susceptibility of Hawaiian endemic species to extinction (Cordell and Sandquist 2008; Vitousek 1990). Invasion by grasses such as African fountain grass, *Pennisetum setaceum* (Forssk.) Chiov. (*Cenchrus setaceus* (Forssk.) Morrone), and subsequent fires are largely responsible for the destruction of over 90 % of the original Hawaiian dry forests, causing them to become one of the most endangered ecosystems in the world (Allen 2000; Bruegmann 1996; D'Antonio and Vitousek 1992; Gillespie et al. 2011; Mehrhoff 1993). There is substantial evidence showing that invasive grasses compete with native species for limiting resources in this ecosystem (Cordell and Sandquist 2008; D'Antonio et al. 1998; Funk and Vitousek 2007; Goergen and Daehler 2002; Mack et al. 2001); however, competition with grasses has not yet been linked to native extinction or declines in native diversity. We expect that if invasion can

cause extinction through competition, Hawaiian dry forests are likely to show this effect.

We examined the patterns and consequences of re-invasion into a dry forest restoration experiment in Hawaii. Like most restoration studies, the original experiment was designed to examine the effect of non-native species removal and abiotic manipulations on the growth and survival of planted native species, and experimental manipulations led to measurable differences in soil water potential that were associated with differences in plant performance and survival 2 years after initiation of restoration (Thaxton et al. 2011). Longer term monitoring is absent from many restoration studies, but is essential for understanding the effect of restoration on community and ecosystem processes that take longer to develop (e.g., changes to soil quality and nutrients, regeneration of planted species, etc.). Here, we evaluate the effect of our restoration treatments on invasion resistance, an ecosystem property that is critical to the long-term management success of this ecosystem. We report results 5 years after the restoration treatments ended and after a time period when non-native species were allowed to recolonize the experiment, which allowed us to examine re-invasion into plots with different histories of environmental treatments and different levels of restored plant species diversity. This experimental design allows us to test the following questions: (1) How do historical environmental conditions or the diversity of native species provide resistance to invasion? (2) How does invasion influence native diversity and plant mortality? (3) How do environmental conditions regulate the relationship between invasion and native diversity declines?

## Methods

### Study site

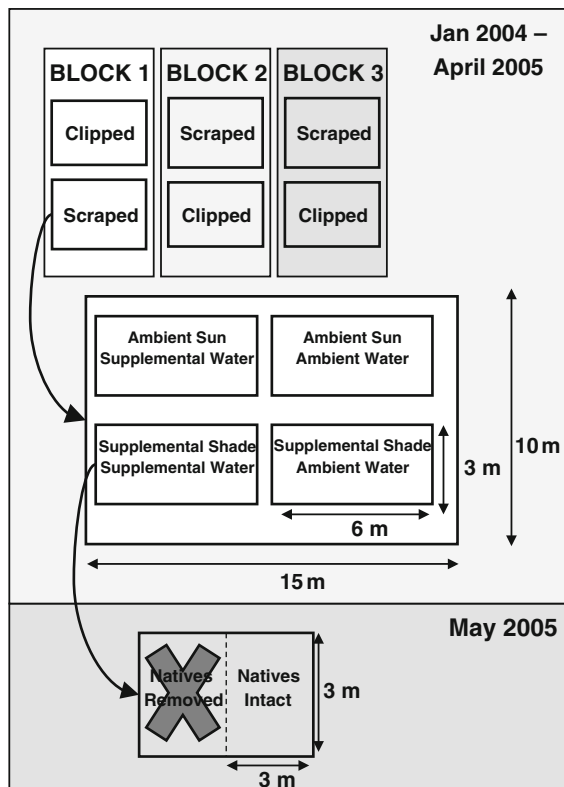
We conducted our study at the Kaupulehu Dry Forest Preserve, located at approximately 600 m elevation on the leeward side of the island of Hawaii (19°46′05″N, 155°56′19″W). Kaupulehu is managed for conservation and has been protected from non-native ungulates and fire for at least 10 years (Cabin et al. 2000). The tree canopies of forests are dominated by *Diospyros sandwicensis*. The understory and treeless grasslands are dominated by invasive African fountain grass

(*Pennisetum setaceum*). The preserve is located on a recent 1,500–3,000 year old a‘a flow and receives 500–750 mm average annual rainfall (Giambelluca et al. 1986). Dry forests like Kaupulehu that occur on young, poorly-developed lava substrates are characterized by a sparse canopy and high barren substrate cover ranging from 35 to 59 % on average (Kellner et al. 2011).

### Experimental design

We examined changes in native and non-native species abundance and diversity in an experiment that began in January 2004. The original purpose of the experiment was to examine the effect of manipulated environmental conditions on the growth and survival of planted native species (Thaxton et al. 2011). The experimental design included three factors replicated in three randomized blocks on a treeless, grass-dominated site without native species that was adjacent to an area with native forest canopy (Fig. 1). Non-native species removal was applied as a whole-plot treatment to two 10-m × 15-m plots in each block. Treatment levels were clipping followed by herbicide application to re-sprouting individuals or mechanical removal by scraping the substrate with a bulldozer. All vegetation was removed from the plots, and they were weeded periodically until May 2005. We applied shade (60 % shade or ambient sun) and water (supplemental or ambient) treatments in a factorial design to 3-m × 6-m split-plots within each whole plot. The shade treatment produced shade comparable to a native dry forest tree canopy (~58 %, Cordell et al. 2002). Supplemental water treatments were designed to mimic 15 mm rainfall events occurring once per week, applied by hand directly to each seedling (see Thaxton et al. 2011 for full treatment descriptions).

Fifty seedlings of ten native woody species were planted into a randomized grid in each 3-m × 6-m split-plot in April 2004. The numbers of seedlings per species planted in each split-plot were the following: trees (*Caesalpinia kavaiensis* = 5, *Diospyros sandwicensis* = 6, *Kokia drynarioides* = 3, *Pleomele hawaiiensis* = 6, *Reynoldsia sandwicensis* = 5), shrubs (*Chenopodium oahuense* = 5, *Senna gaudichaudi* = 4, *Sida fallax* = 3), and vines (*Canavalia hawaiiensis* = 4, *Cocculus orbicularis* = 9). The treatments were administered from January 2004 through April 2005. This initial phase concluded in May 2005 when



**Fig. 1** Diagram of experimental design. Clipping and scraping treatments were applied to randomized, 10-m × 15-m whole plots in three blocks. Shade (supplemental shade and ambient sun) and water (supplemental water and ambient water) treatments were applied in a randomized, factorial design to 3-m × 6-m split-plots in each whole plot. Treatments were administered from January 2004 through April 2005. In May 2005, shade and water treatments were discontinued and all native species were removed from a randomly selected half of each split-plot. We report data from the half where native plants remained intact, and refer to these units as plots. The diagram is not drawn to scale

all native plants were removed from a randomly selected 3-m × 3-m half of each split-plot for biomass sampling (Fig. 1). Here, we report data from the remaining 3-m × 3-m half of each split-plot where native species were not removed and refer to the 3-m × 3-m half plots as “plots” for simplicity. Water and shade treatments were concluded at this time, and non-native species were allowed to re-invade plots.

#### Data collection and analysis

We recorded the fate of planted native plants in the plots 6 months (October 7 and 13, November 2 and 9, 2005) and 4 years (April 14 and 15, 2009) after

allowing species to re-invade the experiment. We noted the presence of non-native species in 2005, but they were uncommon and did not contribute significantly to vegetative cover. In 2009, we visually estimated the percent cover of all native and non-native species in all plots using a grid of nine 1-m<sup>2</sup> quadrats. We measured the change in the native plant community from 2005 to 2009 in each plot by calculating the change in native species richness ( $\Delta$  Native Richness), Native Species Loss (# species observed in 2005 and no longer observed in 2009), and Native Species Colonization (# new species observed in 2009). We calculated Native Plant Mortality as # of planted individuals that died between 2005 and 2009. Metrics of invasion magnitude in 2009 were the richness of non-native species and the relative cover of *P. setaceum*. We used the relative cover of *P. setaceum*, not total non-native cover, because *P. setaceum* accounted for over 55 % of the total non-native cover. Furthermore, it has been demonstrated that *P. setaceum* competes with native species for water (Cordell and Sandquist 2008), and it is the species of greatest concern to land managers because of its ability to carry wildfires. We used data transformations when necessary to improve normality: square root for change in native species richness and native species loss, arcsin square root for the cover of *P. setaceum*, and squared for the number of native plants in 2005 when used as a covariate.

We employed general linear models (GLMs) to investigate whether manipulated environmental conditions and initial native species diversity or abundance influenced re-invasion (*Question 1 from Introduction*), using the abundance of *P. setaceum* in 2009 as the dependent variable. We ran two GLMs, one with native plant abundance in 2005 and one with native plant richness in 2005 as the covariate. If native plant richness or abundance made communities more resistant to invasion, we expected the covariates to be significant, and the relationship between *P. setaceum* abundance and the covariates to be negative. The GLMs also included a random block term, a block × non-native species removal interaction term to account for the split-plot design of the experiment, and fixed factors for method of non-native species removal, shade, and water treatments to determine whether there were persistent effects of the previously manipulated environmental conditions. We also tested all two-way interaction terms.

Because we found a positive relationship between native diversity and abundance and invasion magnitude, we used ANOVA to test whether native and invasive plants responded similarly to the previously manipulated environmental conditions. Response variables were cover of *P. setaceum* in 2009, native diversity in 2005 and 2009, and native abundance in 2005 and 2009. The models included a random block term, a block  $\times$  non-native species removal interaction term to account for the split-plot design of the experiment, and fixed factors for method of non-native species removal, shade, and water treatments. We also tested all two-way interaction terms.

We used a GLM to investigate the effect of re-invasion on native species diversity and native plant mortality. We performed three GLMs for the following dependent variables:  $\Delta$  Native Richness, Native Species Loss, and Native Plant Mortality. Since only three plots were colonized by a single native species, statistical tests could not be performed on Native Species Colonization. We tested whether re-invasion was associated with native diversity decline and mortality by using the abundance of *P. setaceum* as a covariate (*Question 2 from Introduction*). We also wanted to account for the possibility that mortality can occur independent of *P. setaceum* or our treatments. In this case, plots with more species in 2005 should show greater native species loss than plots with fewer species by chance, independent of *P. setaceum* abundance or the experimental treatments. Therefore, we also used native species richness in 2005 as a covariate to test whether initial native diversity was associated with  $\Delta$  Native Richness or Native Species Loss, and we used the number of native plants in 2005 as a covariate to test whether initial native abundance was associated with Native Plant Mortality. In all models, we also tested whether there were persistent effects of the previously manipulated treatments by including a random block factor, a block  $\times$  non-native species removal interaction term to account for the split-plot design of the experiment, and fixed factors for method of non-native species removal, shade, and water treatments (*Question 3 from Introduction*). We tested all two-way interaction terms between the fixed factors and between each fixed factor and *P. setaceum* abundance. If the magnitude of invasion accelerated mortality and local extinction rates, we expected the *P. setaceum* abundance covariate to be significant for all models in addition to any other significant effects.

We expected the cover of *P. setaceum* to be negatively correlated with  $\Delta$  Native Richness and positively correlated with Native Plant Mortality and local Native Species Loss. All statistics were run in Minitab 15.

## Results

### Question 1: community invasibility

*Pennisetum setaceum* was the most widespread non-native species, occurring in 23 of 24 plots, and had the greatest abundance of any native or non-native species. Mean  $\pm$  1 SD relative abundance of *P. setaceum* across all plots was  $17 \pm 13$  % and accounted for 55 % of the cover of all non-native species. The mean relative abundance and number of plots occupied by other non-native species was much lower: *Asclepias physocarpa* (0.6 %, 5 plots), *Euphorbia* sp. (0.07 %, 2 plots), *Hypericum perforatum* (3.4 %, 6 plots), *Lantana camara* (4.7 %, 9 plots), *Lactuca serriola* (3.5 %, 11 plots), and *Senecio madagascariensis* (1.9 %, 9 plots). Planted species accounted for 100 % of native plant cover in 2005 and 2009. Mean  $\pm$  1 SD relative abundance of bare ground across all plots was  $62 \pm 19$  %, which is within the normal range of dry forests on young substrates in Hawaii (Kellner et al. 2011).

Results from GLMs showed that the number of native plants in 2005 and native plant richness in 2005 both were associated with *P. setaceum* abundance in 2009 (Table 1;  $F_{\text{Richness}} = 5.64$ ,  $P = 0.042$ ;  $F_{\text{\#Plants}} = 4.91$ ,  $P = 0.054$ ). There were positive, not negative, associations between native plant richness and abundance and level of invasion (Fig. 2).

ANOVA results also showed that the method of non-native species removal had the same effect on the number of native plants in 2005 as on the level of *P. setaceum* invasion in 2009 (Table 2, Fig. 3). Scraped plots had a greater abundance of native plants and *P. setaceum* compared to clipped plots (Fig. 3). There was also an effect of shade on the number of native plants in 2005 (Table 2). Previously shaded plots had greater numbers of native plants than plots with ambient light. There were no treatment effects on native plant abundance in 2009 or native plant richness in 2005 or 2009. These results suggest that non-native species removal treatments had similar effects on the

**Table 1** Native richness and abundance before invasion were positively associated with *P. setaceum* re-invasion

Source	df	Dependent variable: <i>P. setaceum</i> abundance					
		Native richness covariate			Native abundance covariate		
		MS	F	P	MS	F	P
Covariate	1	126.46	5.64	<b>0.042</b>	143.20	4.91	<b>0.054</b>
Block	2	333.08	6.35	0.131	220.49	5.59	0.120
Non-native removal	1	36.42	1.53	0.243	60.44	1.99	0.186
Block × removal	2	53.64	2.39	0.147	41.10	1.41	0.294
Water	1	89.26	3.98	0.077	13.23	0.45	0.518
Shade	1	3.06	0.14	0.720	4.74	0.16	0.696
Removal × water	1	1.27	0.06	0.817	6.58	0.23	0.646
Removal × shade	1	4.00	0.18	0.683	4.20	0.14	0.713
Water × shade	1	1.13	0.05	0.827	17.74	0.61	0.456
Removal × covariate	1	18.92	0.84	0.382	42.95	1.47	0.256
Water × covariate	1	74.57	3.33	0.101	2.17	0.07	0.791
Shade × covariate	1	0.76	0.03	0.858	5.83	0.20	0.665

Results from GLMs with *P. setaceum* abundance as the dependent variable. The covariates for native richness and abundance in 2005 were significant. Model  $r_{\text{ADJ}}^2 = 0.819$  for the GLM with the native richness covariate and  $r_{\text{ADJ}}^2 = 0.764$  for the GLM with the native abundance covariate. Data transformations were used for *P. setaceum* abundance (arcsine-square root) and native abundance ( $\wedge^2$ ). Bold values indicate  $P < 0.06$

abundance of native plants before invasion and the magnitude of re-invasion by *P. setaceum*.

Question 2: re-invasion and native mortality and species loss

*Pennisetum setaceum* abundance explained a significant amount of variation in  $\Delta$  Native Richness, Native Species Loss, and Native Plant Mortality (Table 3, Fig. 4). Across the experiment, approximately one native species went locally extinct from a subplot for every 10 % increase in the cover of *P. setaceum*. There was no effect of native richness in 2005 on  $\Delta$  Native Richness or Native Species Loss; there was no effect of the number of native plants in 2005 on Native Plant Mortality (Table 3).

Question 3: manipulated treatments and native species loss

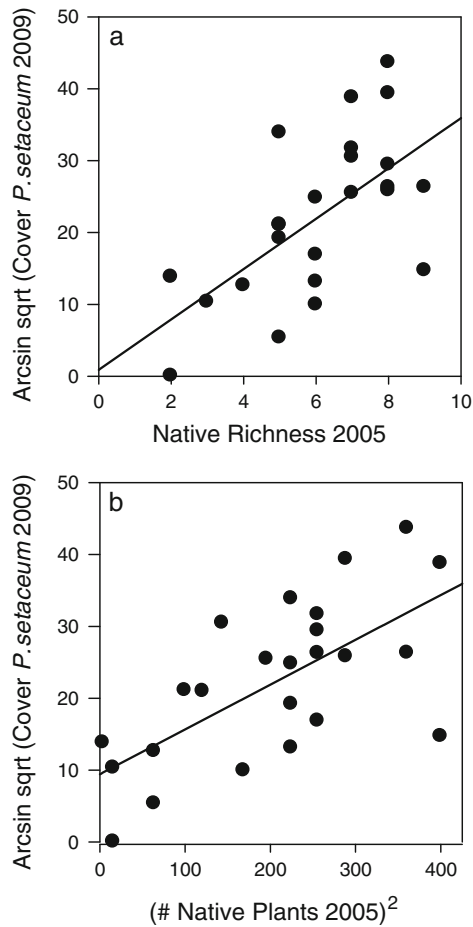
Water treatment, shade treatment, and several interaction terms explained a significant amount of variation in  $\Delta$  Native Richness and Native Species Loss (Table 3). Native Species Loss was higher in previously watered and shaded plots, causing a greater decline in native richness in those plots compared to

plots exposed to ambient conditions. The interaction between *P. setaceum* abundance with water and shade treatments occurred because *P. setaceum* abundance was associated with native species loss in plots exposed to ambient water and sun, but there was no association in plots that previously received supplemental water and shade (Fig. 5). The interaction between *P. setaceum* and non-native removal treatments occurred because *P. setaceum* abundance was associated with native species loss in clipped plots but not scraped plots (Fig. 5). Together, these results suggest that *P. setaceum* and previously manipulated treatments had direct effects on local species loss independent of initial native species diversity. In addition, the relationship between *P. setaceum* and species loss depended on conditions that were manipulated before re-invasion.

## Discussion

### Community invasibility

Restoring native diversity and abundance did not appear to reduce re-invasion in these plant communities. Instead, invasion rates were positively correlated



**Fig. 2** Richness and abundance of native plants at the beginning of the study were positively correlated with the magnitude of invasion. **a** Native richness in 2005 and *P. setaceum* abundance in 2009 ( $r^2 = 0.40$ ,  $P = 0.001$ ); **b** native abundance in 2005 and *P. setaceum* abundance in 2009 ( $r^2 = 0.46$ ,  $P < 0.001$ ). Non-native richness in 2009 was also positively correlated with native richness in 2005 ( $r^2 = 0.31$ ,  $P = 0.005$ , data not shown). Regression lines are included to show the direction of the relationship. Data were transformed for analysis

with native plant diversity (Fig. 2). Although native diversity is often negatively correlated with invasion at experimental scales and positively correlated at larger scales, this pattern has many exceptions (Fridley et al. 2007; Levine and D'Antonio 1999; Souza et al. 2011). Native species in this dry forest ecosystem may not provide resistance to invasion because this ecosystem occurs on young lava flows and is characterized by a high cover of bare ground (Kellner et al. 2011), leaving open room for colonization by invasive

species even when native species are present. In addition, the native flora of this isolated island ecosystem is depauperate compared to mainland ecosystems in terms of taxonomic lineages, functional groups, and environmental adaptations (Caujape-Castells et al. 2010; Denslow 2003). Plant communities may not fully exhaust all available resources, leaving many niches unoccupied and creating colonization opportunities for invasive species. The slow growth of native plants due to water limitation may also delay their ability to fully capture resources and exclude invaders through competition.

Because Hawaiian dry forests have been reduced to less than 10 % of their original range, restoration is an essential tool for maintaining native biodiversity in this ecosystem; however, we found that native woody plant restoration may not be an effective tool to reduce the spread of invasive plants without additional management activities. This finding is similar to studies in wetlands showing that re-invasion into restored communities can be common and problematic (DeMeester and Richter 2010; Matthews and Spyreas 2010) and contrasts with studies showing a positive effect of native restoration on weed control (Abella et al. 2011; Bakker and Wilson 2004; Blumenthal et al. 2003, 2005). Whether native species restoration contributes to weed control appears to depend on qualities of the restored community and also traits of the managed invasive species. Future work is needed to investigate the general principles that can be used to identify which communities can be restored to resist invasion.

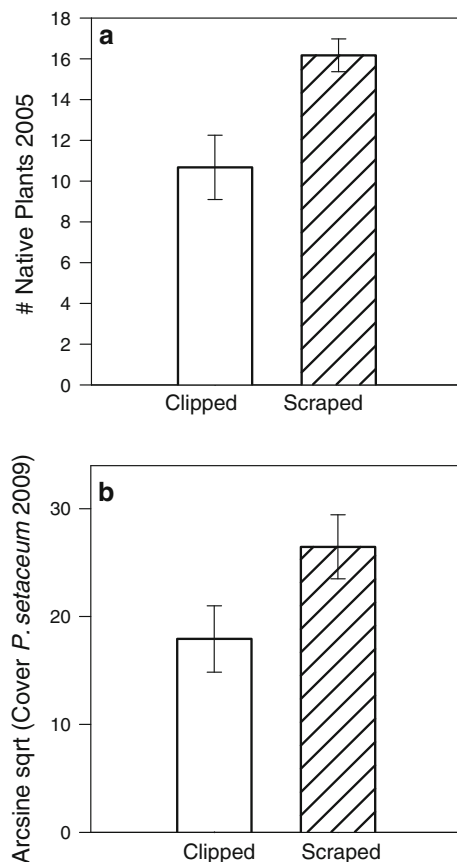
Functional dissimilarity between native and invasive species may also explain the lack of resistance to invasion in these communities. When native species are functionally similar to invaders, they are more likely to use similar resources and exclude invaders through competition (Abrams 1983; Bakker and Wilson 2004; Emery 2007; Fargione et al. 2003; Funk et al. 2008; Hooper and Dukes 2010). *P. setaceum* is a  $C_4$  grass and is functionally different from native communities which are comprised primarily of  $C_3$  woody shrubs, vines, and trees. Its  $C_4$  physiology also allows it to have greater water-use-efficiency and a distinct phenology, where it can grow actively during periods less favorable to native plants, which may also contribute to its ability to invade native communities and compete with native species for water, the limiting resource in this ecosystem (Cordell and Sandquist

**Table 2** Treatment effects were similar on native and *P. setaceum* abundance

Source	df	Dependent variable: native abundance 2005			Dependent variable: <i>P. setaceum</i> abundance 2009		
		MS	F	P	MS	F	P
Block	2	54.29	5.79	0.147	839.48	38.60	<b>0.025</b>
Non-native Removal	1	181.50	19.36	<b>0.048</b>	437.16	20.10	<b>0.046</b>
Block × removal	2	9.38	0.63	0.546	21.75	0.51	0.613
Water	1	10.67	0.72	0.411	8.87	0.21	0.656
Shade	1	66.67	4.51	<b>0.053</b>	28.47	0.67	0.429
Removal × water	1	2.67	0.18	0.678	21.95	0.51	0.487
Removal × shade	1	16.67	1.13	0.308	33.19	0.78	0.394
Water × shade	1	0.17	0.01	0.917	38.11	0.89	0.363

ANOVA results for treatment effects on native abundance in 2005 and *P. setaceum* abundance in 2009. Non-native species removal treatments had similar effects on native and *P. setaceum* abundance. Model  $r_{\text{ADJ}}^2 = 0.654$  for the ANOVA of *P. setaceum* abundance and  $r_{\text{ADJ}}^2 = 0.431$  for the ANOVA of native abundance in 2005. There were no significant treatment or interaction effects for ANOVAs of native abundance in 2009, native richness in 2005, and native richness in 2009. A data transformation was used for *P. setaceum* abundance (arcsine-square root)

Bold values indicate  $P < 0.06$



**Fig. 3** Non-native species removal treatments had similar effects on native plant abundance and *P. setaceum* abundance. Abundance of **a** native plants in 2005 and **b** *P. setaceum* in 2009 was greater in scraped (hatched bars) compared to clipped (open bars) plots. Error bars depict 1 SEM,  $n = 12$

2008; Moser et al. 2011; Thaxton et al. 2011). The presence of disturbance allowed *P. setaceum* to compete with *Heteropogon contortus*, a native grass, but, *H. contortus* tolerated drought better than *P. setaceum*, suggesting that a native grass may outcompete the invasive grass in dry habitats (Goergen and Daehler 2001, 2002). *H. contortus* is typically found in open grassland ecosystems but is not found at our study site. It is not known whether native grasses present in low abundance in forest understories could compete with *P. setaceum*, and this is an important area for future research.

Our study supports the mechanism normally found at regional scales, where a positive relationship between native and invasive abundance and diversity occurs when the resource conditions of habitats vary spatially (Fridley et al. 2007; Souza et al. 2011). Habitats with high resource availability support both native and invasive species, whereas habitats with unfavorable conditions do not support as much plant growth. Specifically, habitats where the substrate was scraped supported both native and invasive species (Fig. 3). Previous results from this experiment demonstrated that scraped habitats had greater soil moisture than clipped plots, which enhanced native plant growth through higher foliar N concentrations, higher photosynthetic rates, and greater water-use-efficiency (Thaxton et al. 2011). Soil moisture provides direct benefits to plant growth and may also contribute to higher soil nutrient turnover and availability. A greenhouse study identified soil moisture as an



**Table 3** *P. setaceum* was associated with native plant mortality and a decline in native species richness following re-invasion

Source	df	Dependent variable: $\Delta$ native richness			Dependent variable: native species loss			Dependent variable: native plant mortality		
		MS	F	P	MS	F	P	MS	F	P
Native richness or abundance 2005 <sup>a</sup>	1	0.00118	0.03	0.861	0.01317	0.29	0.603	2.109	1.52	0.253
<i>P. setaceum</i> abundance	1	0.31645	8.77	<b>0.018</b>	0.31809	7.08	<b>0.029</b>	10.096	7.25	<b>0.027</b>
Block	2	0.46832	6.35	0.111	0.78815	4.90	0.154	8.135	3.22	0.248
Non-native removal	1	0.16015	4.13	0.071	0.09029	1.69	0.223	2.075	1.44	0.260
Block $\times$ removal	2	0.08162	2.26	0.166	0.18489	4.11	0.059	2.461	1.77	0.231
Water	1	0.72911	20.21	<b>0.002</b>	0.75887	16.88	<b>0.003</b>	1.665	1.20	0.306
Shade	1	0.49036	13.59	<b>0.006</b>	0.57011	12.68	<b>0.007</b>	0.696	0.50	0.499
Removal $\times$ water	1	0.17281	4.79	0.060	0.28642	6.37	<b>0.036</b>	27.810	19.98	<b>0.002</b>
Removal $\times$ shade	1	0.01074	0.30	0.600	0.00270	0.06	0.813	5.287	3.80	0.087
Water $\times$ shade	1	0.02139	0.59	0.463	0.02188	0.49	0.505	0.002	0.00	0.972
Removal $\times$ <i>P. setaceum</i> Abundance	1	0.21564	5.98	<b>0.040</b>	0.14299	3.18	0.112	1.748	1.26	0.295
Water $\times$ <i>P. setaceum</i> Abundance	1	0.68509	18.99	<b>0.002</b>	0.74119	16.49	<b>0.004</b>	0.642	0.46	0.516
Shade $\times$ <i>P. setaceum</i> abundance	1	0.47467	13.16	<b>0.007</b>	0.57529	12.80	<b>0.007</b>	0.085	0.060	0.811

Results from GLMs with  $\Delta$  native richness ( $r_{\text{ADJ}}^2 = 0.886$ ), native species loss ( $r_{\text{ADJ}}^2 = 0.854$ ), and native plant mortality ( $r_{\text{ADJ}}^2 = 0.903$ ) as the dependent variables all showed a significant effect of the *P. setaceum* covariate. *P. setaceum* had a greater association with  $\Delta$  native richness and native species loss in ambient water and shade plots, compared to supplemental treatments. *P. setaceum* also had a greater association with  $\Delta$  native richness in the clipped, compared to the scraped non-native species removal treatment. Data transformations were used for *P. setaceum* abundance (arcsine-square root),  $\Delta$  native richness (square root), and native species loss (square root)

<sup>a</sup> Native richness in 2005 was used as a covariate to explain variation in  $\Delta$  native richness and native species loss. Native abundance in 2005 was used as a covariate to explain variation in native plant mortality

Bold values indicate  $P < 0.05$

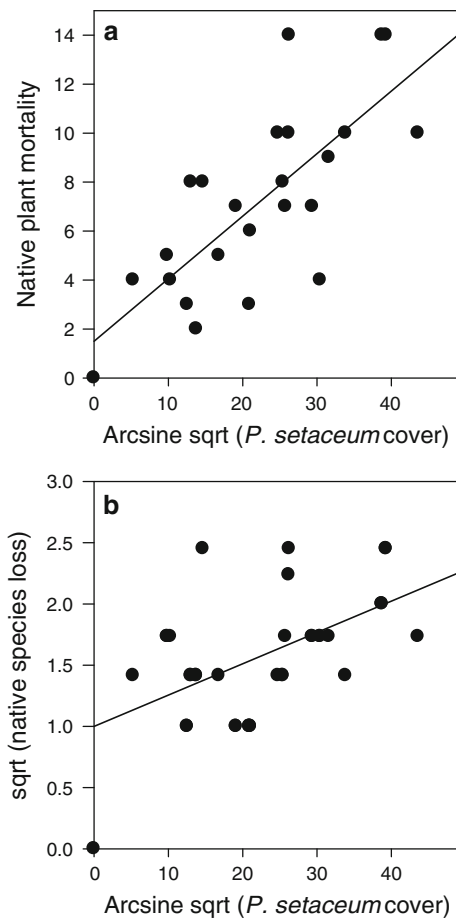
important control of the establishment and growth of *P. setaceum* (Rahlao et al. 2010). Therefore, soil moisture likely contributed to the survival of native plants and the colonization of *P. setaceum* into new habitats during the time of our study because it is tightly linked with plant growth and performance.

### Invasion and native species loss

Several lines of evidence suggested that invasion was related to a reduction in plant diversity, and that environmental conditions were important in regulating this relationship. First, we found that the *P. setaceum* abundance covariate explained a significant amount of variation in both native plant mortality and native species loss. As *P. setaceum* abundance increased native mortality and species loss increased. Second, we found significant treatment  $\times$  *P. setaceum* interaction terms indicating that the relationship between invasion and native species loss differed among the experimental treatments (Table 3). Third,

we found that mean *P. setaceum* abundance was higher in scraped, compared with clipped, plots (Table 2, Fig. 3); but that *P. setaceum* abundance was associated with native species loss in clipped, but not scraped, plots (Fig. 5). Contrasting results like these suggest that *P. setaceum* may have a greater competitive advantage over native species in specific habitat conditions.

Invasive plant species can reduce native plant diversity by several mechanisms, including reducing colonization opportunities and accelerating the mortality of native species. Several studies have found invasive plants to reduce native plant diversity by reducing local colonization rates (Gooden et al. 2009; Yurkonis and Meiners 2004; Yurkonis et al. 2005). Two studies have found associations between *Bromus inermis* invasion and the local extinction of the native plant species *Anemone patens* (Williams and Crone 2006) and *Spartina pectinata* (Dilleuth et al. 2009). We found positive associations between *P. setaceum* abundance and both native mortality and native



**Fig. 4** *P. setaceum* invasion was associated with **a** native plant mortality and **b** native species loss.  $r_{\text{NativeMortality}} = 0.749$ ,  $P < 0.001$ ;  $r_{\text{NativeSpeciesLoss}} = 0.514$ ,  $P = 0.010$

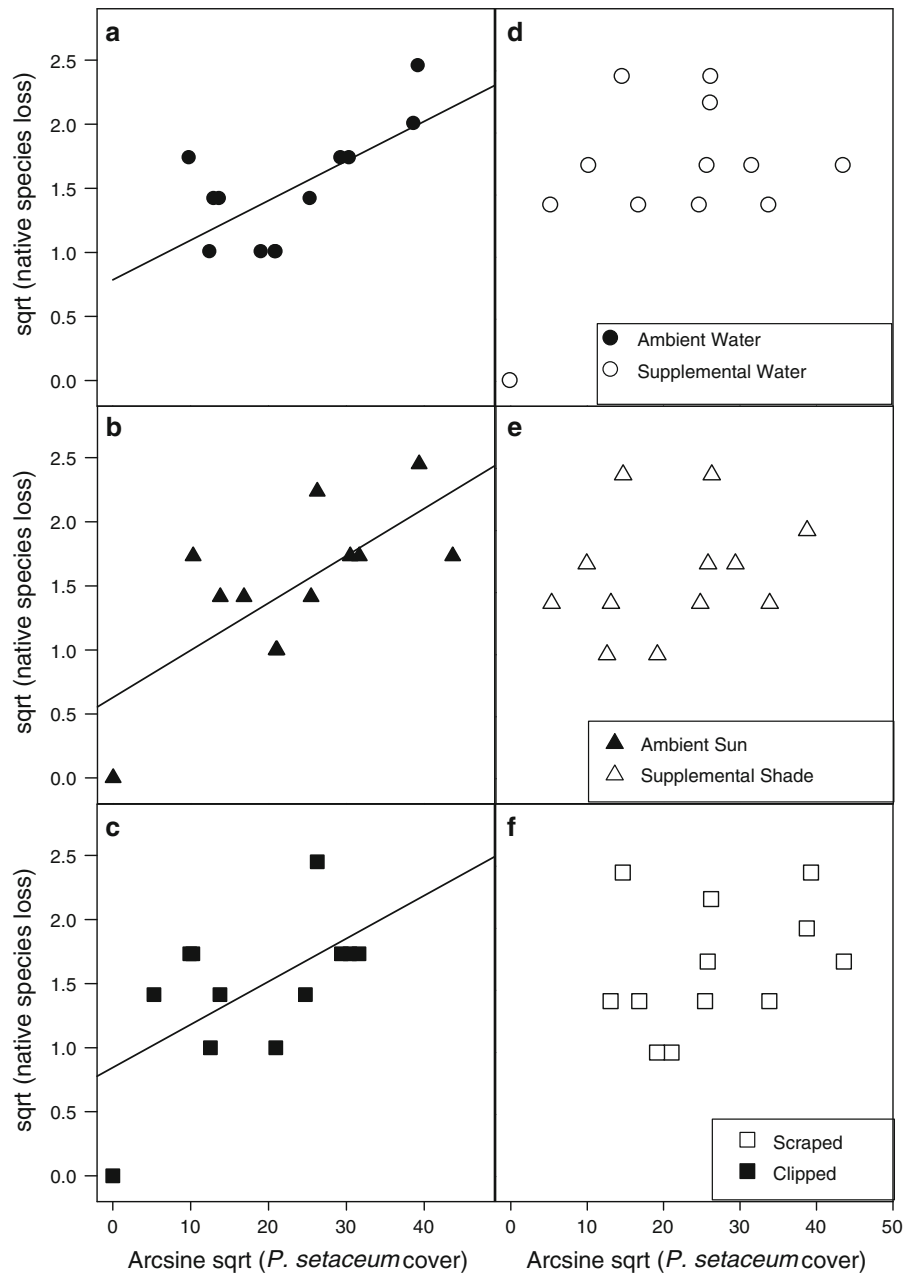
species loss, and no association with colonization; which suggest that invasion may reduce native diversity by accelerating native mortality and local extinction rates in this community.

Invasion was more strongly associated with native species loss in the ambient water, ambient sun, and previously clipped plots. These treatments had lower soil water availability compared to other treatments measured from May to October 2005 (Fig. 3 in Thaxton et al. 2011). In addition, *P. setaceum* reduced soil water availability and plant growth in the initial phase of this experiment (Thaxton et al. 2011) and one other at this site (Cordell and Sandquist 2008). Therefore, it appears that *P. setaceum* may have accelerated native species loss through competition for water, and this effect was strongest in habitats with a history of low water availability. This finding contrasts

those from semi-arid ecosystems in Spain, where there was no interaction between the effect of invasion and drought on native species declines (Matesanz et al. 2008) and a native species was more competitive than a non-native species during water stress (Garcia-Serrano et al. 2007). While some invasive species outperform native species when resources are abundant (Daehler 2003), our results suggest that *P. setaceum* has a higher resource-use-efficiency and is better adapted than native species to low resource conditions (Funk and Vitousek 2007).

Our results further suggest that the impact of an invasive species on native extinction may be regulated by resource supply and environmental conditions, and decoupled from its overall abundance. For example, the abundance of *P. setaceum* was greater in scraped plots compared to clipped plots (Fig. 3); however, the relationship between *P. setaceum* and native extinction was significant only in clipped plots where water availability tends to be lower and competition may be greater (Fig. 5). In addition, total native species loss was greatest in plots that previously received supplemental water and shade, but the association of *P. setaceum* with species loss occurred in the habitats that did not receive supplemental water or shade. These contrasting results suggest that different processes may occur in supplemental and ambient plots. It is possible that when supplemental shade and water treatments ended in 2005, plants in these plots were stressed by the dramatic change in resource supply, causing higher mortality compared to plants that were already acclimated to ambient conditions. Consequently, the effect of invasion on local extinction may have been insignificant where an additional stress also influenced native plant mortality.

Even though the number of invading species appears to be increasing across Hawaiian islands (Sax and Gaines 2008), we found that at local scales in this community an aggressive invasive species may reduce native diversity through the mortality of native individuals. We suggest that the negative effects of the number of invading species on declines in native diversity may be less relevant where “strong” invasive species like *P. setaceum* have disproportionate effects on native plant communities (Ortega and Pearson 2005). Island ecosystems are particularly vulnerable to highly competitive invasive species because of their high levels of invasion and depauperate native floras with poor competitive abilities (Caujape-Castells et al. 2010; Denslow 2003).



**Fig. 5** Manipulated treatments regulated the relationship between invasion and native species loss. *P. setaceum* abundance was associated with native species loss (a–c) and  $\Delta$  native richness (data not shown) in ambient water ( $r_{\text{NativeLoss}} = 0.672$ ,  $P = 0.017$ ;  $r_{\text{NativeRichness}} = -0.803$ ,  $P = 0.002$ ), ambient sun ( $r_{\text{NativeLoss}} = 0.713$ ,  $P = 0.009$ ;  $r_{\text{NativeRichness}} = -0.795$ ,  $P = 0.002$ ), and clipped ( $r_{\text{NativeLoss}} = 0.600$ ,  $P = 0.039$ ;  $r_{\text{NativeRichness}} =$

$-0.701$ ,  $P = 0.011$ ) plots, respectively. There were no significant relationships in plots that received supplemental water (d) and shade (e) or that were scraped (f). Filled symbols and lines show treatments with significant relationships. Regression lines are included to show the direction of the relationship. Open symbols show treatments with non-significant relationships. Data were transformed for analysis

Other studies have shown that depauperate plant communities are more susceptible to the negative effects of invasion (Dukes 2001). Dry forest ecosystems

in Hawaii are species-poor when globally compared to other more diverse communities, which may explain why we found an association between plant invasion

and native species loss here, but this relationship has not been widely reported in other ecosystems (Gurevitch and Padilla 2004). However, within our experiment we did not find evidence that species-poor local communities were more susceptible to invasion-related extinctions. Early in this experiment, treatments had an effect on resource supply and plant performance (Thaxton et al. 2011). During our period of study, previous treatments regulated the relationship between invasion and native species loss (Table 3, significant treatment  $\times$  *P. setaceum* interaction terms) but had no direct effect on native diversity before invasion in 2005 or after invasion in 2009 (Table 2). Thus, a history of low resource supply, and not low diversity, appears to increase the strength of the relationship between invasion and native species loss at local scales. This finding suggests that at local scales within some ecosystems it may be effective to protect sensitive areas with low resource supply from invasion instead of, or in addition to, areas with high biodiversity.

Extensive invasive species management programs are important for preserving rare and endangered species in this community. Because the purpose of these programs is to prevent the extinction of rare species it is impossible to observe the effects of invasive species on natural extinction rates at the population or species level. As a result, we focused on local extinction dynamics as a step toward understanding population-level processes. This approach has the advantage of being highly controlled and tractable, but may not fully represent processes occurring at larger scales. For example, metapopulation dynamics could contribute to population level persistence if local extinctions are balanced with local colonization events elsewhere; however, the almost complete lack of native colonization in our entire experiment suggests that this mechanism is unlikely in this community.

We also note that the five species that reproduced during the experiment could be temporarily locally extinct and could re-colonize a plot from the seedbank, but we think re-colonization is unlikely to alter local extinctions significantly for several reasons. First, our study allowed natural colonization and extinction dynamics to occur over 4 years, and native colonization was extremely low and insignificant. Second, no non-planted native species colonized the experiment at any time even though our plots were adjacent to

native forest canopy, suggesting acute dispersal limitation. Third, *P. setaceum* and other invasive species reduced native colonization and germination ability in two nearby experiments where native seeds were present (Cabin et al. 2000; Thaxton et al. 2010). Thus, we expect our finding of coupled invasion and local extinction rates to be robust to future colonization events.

In addition, five out of ten species in our experiment did not reproduce during the study period. Therefore, our findings are best interpreted as the impacts of invasion on early life stages of these species and may not represent competitive interactions of invasive species with more mature individuals. It is likely that more mature individuals may tolerate competition from invasive species better than early life stages; however, at a population level regeneration is necessary for persistence. It is possible that *P. setaceum* may contribute to population-level extinction of some species by its strong negative effects on early life stages, which could contribute to an “extinction debt”, whereby species extinctions are slow to occur because mature individuals persist with no natural regeneration (Tilman et al. 1994).

## Conclusion

In summary, native restoration did not provide resistance to invasion in this community, and *P. setaceum* invasion was associated with declines in local native species diversity, confirming its status as an important species to control in order to reduce the loss of native biodiversity. Other communities with highly competitive invasive species may also be undergoing a slow process of native extinction as observed here, highlighting the possibility of a large extinction debt of native plant populations due to current plant invasions.

Our work provides a caveat to previous suggestions that invasion impacts will be greatest in the most diverse plant communities (Higgins et al. 1999; Levine 2000). These studies, like ours, found that invasion rates were greatest in favorable habitats that supported the most native species; however, we found that at local scales the actual association of invasion with native species loss occurred in habitats with a history of lower resource supply, independent of native diversity. The decoupling of invasion abundance from its impacts seems counterintuitive, but

lower abundances of invaders with high resource-use-efficiency may have proportionately greater negative impacts in resource-poor environments where competition may be greater. Therefore, invasive plant management plans that focus on sensitive areas with lower resource availability may be necessary to prevent a significant loss of native biodiversity.

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