

The role of plant–soil feedbacks in driving native-species recovery

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Abstract. The impacts of exotic plants on soil nutrient cycling are often hypothesized to reinforce their dominance, but this mechanism is rarely tested, especially in relation to other ecological factors. In this manuscript we evaluate the influence of biogeochemically mediated plant–soil feedbacks on native shrub recovery in an invaded island ecosystem. The introduction of exotic grasses and grazing to Santa Cruz Island, California, USA, converted native shrublands (dominated by *Artemisia californica* and *Eriogonum arborescens*) into exotic-dominated grasslands (dominated by *Avena barbata*) over a century ago, altering nutrient-cycling regimes. To test the hypothesis that exotic grass impacts on soils alter reestablishment of native plants, we implemented a field-based soil transplant experiment in three years that varied widely in rainfall. Our results showed that growth of *Avena* and *Artemisia* seedlings was greater on soils influenced by their heterospecific competitor. Theory suggests that the resulting plant–soil feedback should facilitate the recovery of *Artemisia* in grasslands, although four years of monitoring showed no such recovery, despite ample seed rain. By contrast, we found that species effects on soils lead to weak to negligible feedbacks for *Eriogonum arborescens*, yet this shrub readily colonized the grasslands. Thus, plant–soil feedbacks quantified under natural climate and competitive conditions did not match native-plant recovery patterns. We also found that feedbacks changed with climate and competition regimes, and that these latter factors generally had stronger effects on seedling growth than species effects on soils. We conclude that even when plant–soil feedbacks influence the balance between native and exotic species, their influence may be small relative to other ecological processes.

Key words: California grasslands; climate effects; Coastal Sage Scrub; competition; exotic plants; plant–soil feedbacks; restoration; soil biogeochemistry.

INTRODUCTION

Exotic-plant invasions are well known to alter the cycling of nutrients within ecosystems (Vitousek and Walker 1989, Evans et al. 2001, Levine et al. 2003, Mack and D'Antonio 2003, Yelenik et al. 2007). These impacts arise when exotic and native species differ in their inputs of litter, uptake of nutrients, and influence on microclimate (Wardle et al. 1998, Eviner 2004). Although some of the most impressive examples of exotic-species impacts on ecosystem processes involve the invasion of nitrogen-fixing species, impacts on nutrient cycling have been documented for a wide diversity of exotic plants (Ehrenfeld 2003, Liao et al. 2008). Because nutrient limitation is well known to shape plant community structure (Tilman 1987), many ecologists hypothesize that these exotic-plant effects on nutrient cycles feed back to influence exotic-species dominance. For example, Allison and Vitousek (2004) showed that many exotic plants in Hawaii release nitrogen from their litter more rapidly than native plants, potentially increasing

soil nitrogen availability. The authors then hypothesize that increased soil nitrogen availability should favor the more nitrogen-limited exotic species, contributing to exotic-species success.

Although numerous studies document exotic-plant effects on biogeochemical cycles (Vitousek and Walker 1989, Stock et al. 1995, Ehrenfeld 2003, Mack and D'Antonio 2003), and many go on to hypothesize that effects on nutrient cycling feed back to favor exotic dominance at the expense of native-species recovery (Witkowski 1991, Allison and Vitousek 2004, Suding et al. 2004a, Yelenik et al. 2004, Hawkes et al. 2005, Liao et al. 2008), experimentally testing this hypothesis has proven challenging for several reasons. First, one must separate the effects of exotic plants mediated via soil changes from other forms of impact, such as above-ground competition (Levine et al. 2003, Suding et al. 2004b). Second, quantifying plant–soil feedbacks relevant to the dynamics of invasions in nature requires field experiments incorporating natural climate variation and competitive regimes, both of which strongly influence how plants respond to soil nutrients (Tilman 1987). A minority of plant–soil feedback studies are conducted in field settings (Casper and Castelli 2007, Kulmatiski et al. 2008), and almost none of these explore feedbacks across years differing in climate. Third, one must

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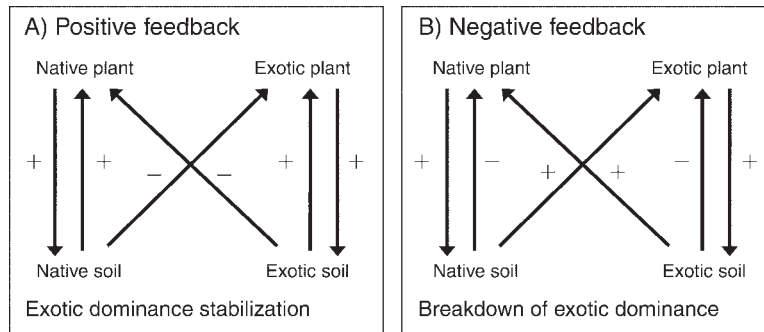


FIG. 1. Schematic diagram of plant–soil feedbacks and plant community dominance (adapted from Bever et al. [1997]). (A) Positive feedbacks can occur when both native and exotic species increase (+) a soil property (e.g., nitrogen or mutualists) that *increases* (+) their own growth rates relative to their competitor (which may be harmed [–] by the soil property). This stabilizes dominance hierarchies in invaded communities, reinforcing dominance of exotic species, and slowing native species recovery. (B) Negative feedbacks can occur when both native and exotic species increase (+) a soil property (e.g., pathogens) that *decreases* (–) their own growth rate relative to their competitor. This causes the breakdown of dominance hierarchies, potentially leading to the recovery of native species in invaded communities. Arrows indicate the direction of causal effects, and “+” and “–” indicate positive and negative effects, respectively. The sign and magnitude of the feedback can be quantified with Eq. 1.

integrate exotic-plant effects on nutrient cycling with the response of both the exotic and its native competitors to changes in soils, creating large factorial experiments (Bever et al. 1997, Bever 2003, Kulmatiski et al. 2008).

An innovative theoretical construct developed for studying feedbacks between plants and soil microbial communities (Bever et al. 1997) can be used to understand feedbacks mediated via soil nutrient cycling (Fig. 1). This theory shows that, depending on the nature of plant–soil interactions, systems can experience positive feedbacks that favor the growth of the more abundant species, or negative feedbacks that favor rarer competitors (Bever et al. 1997, Eppstein and Molofsky 2007). For example, if two species modify soils in ways that favor their own performance over their competitor (Fig. 1A), the resulting positive feedback favors the initially more abundant species. In an exotic-dominated system, such feedbacks impede native-plant recovery. Alternatively, when both species modify soils in ways that favor their competitor over themselves (Fig. 1B), the resulting negative feedback favors the rarer competitor, facilitating native recovery in exotic-dominated systems. In the long run, such negative feedbacks do not drive the once dominant exotic species to exclusion, but instead, favor the coexistence of native and exotic plants (Bever et al. 1997, Chesson 2000, MacDougall et al. 2009).

Somewhat counterintuitively, plant–soil feedbacks can arise when native and exotic plants respond in the same direction to the exotic plant’s effect on soils, as might be expected when exotic species increase resource availability. Here, it is the relative response of the native and exotic competitors to soil changes that determines the strength and direction of feedbacks (Bever et al. 1997, Casper et al. 2008). For example, a nitrogen-fixing exotic plant that elevates soil nitrogen pools only generates a positive plant–soil feedback if the exotic species is more limited by nitrogen than its native competitors. By contrast, if native competitors are the

more nitrogen limited, the plant–soil feedback will favor native recovery in such exotic-dominated systems. Predicting the influence of plant–soil feedbacks on exotic-species dominance therefore requires quantifying how both native and exotic plants respond to changes in soils, but few studies have done so (Kulmatiski et al. 2008).

Also poorly understood is the importance of plant–soil feedbacks relative to other processes in shaping the outcome of interactions between native and exotic species. In addition to the frequency-dependent effect of plant–soil feedbacks (Bever et al. 1997), frequency-independent exotic-plant advantages in competitive ability (MacDougall and Turkington 2005), herbivore tolerance (Maron and Vila 2001), and fecundity (Turnbull et al. 2000, Seabloom et al. 2003) can also determine the outcome of exotic-plant invasions (Bever 2003, Eppstein and Molofsky 2007). Further exploring the importance of soil feedbacks relative to these other ecological factors is critical for understanding their role in driving plant invasions and native species recovery.

In this study, we used the plant–soil feedback framework developed by Bever et al. (1997) to ask whether exotic-species effects on nutrient cycling reinforce their dominance. The exotic annual grasslands on Santa Cruz Island, California, USA, provide a model system for examining this question. Following the cessation of grazing that converted island shrublands to exotic grassland, native shrubs are only slowly recovering (Hobbs 1983, Junak et al. 2000, Yelenik and Levine 2009b). This provides an excellent natural context in which to explore the role of plant–soil feedbacks in driving native recovery rates and the maintenance of exotic-species dominance. Moreover, because these habitats host only two dominant native shrubs, *Artemisia californica* Less. (California sagebrush) and *Eriogonum arborescens* Greene (Santa Cruz Island buckwheat), and one dominant exotic grass,

Avena barbata Pott ex Link (slender oat), we can quantify the small number of pairwise plant–soil feedbacks that drive the majority of habitat change.

Our previous work has shown that the exotic grass alters soil nutrient cycling in the invasion process. *Avena* reduces mineral nitrogen and phosphorus pools and nitrogen mineralization rates relative to soils influenced by the shrub, *Artemisia*. Relative to *Eriogonum*, on the other hand, exotic grasses increase inorganic nitrogen pools and mineralization rates (Yelenik and Levine 2010a). Importantly, the exotic grass is the most nitrogen limited of the three species, responding to a multiyear field fertilization experiment with the greatest proportional increase in biomass (Yelenik and Levine 2010a). Species differences in their effects on soil nutrient cycling, combined with differences in nutrient limitation, set the stage for plant–soil feedbacks that reinforce or breakdown exotic-plant dominance.

Here, we explored the following questions: (1) Do exotic-grass effects on soil nutrient cycling feed back to influence their dominance? (2) How do feedbacks change with variation in climate and competition? And (3) how strong are plant–soil feedbacks relative to the overall effects of climate and competition on native-plant recovery? To address these questions we conducted a field-based soil transplant experiment in which we planted seedlings in soils influenced by exotic grasses or native shrubs, and in the presence and absence of competitors. We replicated this experiment over three years that varied widely in rainfall, and compared the plant–soil feedbacks to observed patterns of native shrub recovery.

MATERIALS AND METHODS

Study system

Santa Cruz Island is 249 km² in size, located 30 km offshore from Southern California (34.02065° N, 119.52146° W), and has a typical Mediterranean climate with cool, wet winters and hot, dry summers. The island was intensely grazed by feral sheep for over a century, which, combined with the introduction of exotic grass seed, converted much of the native shrubland to exotic annual grassland. Native shrubs, primarily *Artemisia* and *Eriogonum*, persisted on steep rocky slopes. Sheep removal in the mid 1980s has led to some shrub recovery in exotic grasslands on south-facing slopes of the island's Central Valley (on lithic to pachic Argixerolls). These colonizing shrubs provided an excellent opportunity to understand species effects on soils, because they have established in otherwise homogeneous grassland (Hobbs 1983). Thus differences in available nutrients beneath shrubs and grasses were due to plant species effects on soils and not preexisting conditions. This assumption was supported by common garden and greenhouse studies that experimentally replicated the species effects on soils (Yelenik and Levine 2010a). Details concerning species effects on soil properties have

been outlined previously (Yelenik and Levine 2010a). Briefly however, the exotic grass *Avena* lowers available soil N and P relative to the native *Artemisia*, although it increases available soil N relative to *Eriogonum*; these differences are largely due to changes in leaf litter quality and quantity (Yelenik and Levine 2010a).

Soil core transplant experiment

In order to quantify plant–soil feedbacks in a field setting with and without competition, we established a soil core transplant experiment in 2004, 2006, and 2007 that switched soils between isolated shrubs and the grass matrix in the zone where native shrubs have begun to recolonize (the “mixed zone”). In 2004, we implemented a fully factorial design with three origin habitats (*Artemisia*, *Eriogonum*, and *Avena*), three destination habitats (*Artemisia*, *Eriogonum*, and *Avena*), three seedling species (*Artemisia*, *Eriogonum*, and *Avena*), and two competition treatments (with and without competition). We established one set of all combinations at each of seven sites (replicate mixed zones), located at least 1 km apart. Previous work has shown that shrub recovery is limited at the seedling establishment stage (Yelenik and Levine 2010b), supporting our focus on this early life stage.

Polyvinyl chloride (PVC) cores with beveled bottom edges (10.2 cm diameter × 15 cm) were used to switch soils between origin and destination habitats in June 2004. Every effort was made to keep the soil within cores completely intact, not changing its aggregate properties or contents, and replacing the original overtopping litter layer after it was placed in its final destination. Once we moved cores, the PVC was left in place to separate origin and destination soil types. We sowed each core with island-collected seed of the assigned seedling species, but due to poor *Artemisia* germination, one-month-old transplants of this species reared on habitat-specific soils were planted into cores in March 2005. In April 2005, all cores were weeded to one seedling. The “without competition” treatment was imposed by cutting away the entire shrub individual in June 2004, or clearing grass from 1 m around cores after winter germination. Destination shrubs were large (50–100 cm in height, with roughly equal width), and the *Avena* matrix was tall by late season (40–80 cm), meaning that competitor removal greatly opened the canopy for the target seedlings (1–15 cm in height). Because PVC remained intact around all seedlings in all treatments, and seedling roots generally did not grow deeper than the 15 cm depth of our cores, our design only allowed us to test the effects of aboveground competition on seedling growth and feedbacks. In June 2005, seedlings were destructively harvested for aboveground biomass. We repeated this experiment in 2004, 2006, and 2007 to evaluate how the strength and direction of plant–soil feedbacks changed across years. These years varied widely around the 50 cm/yr rainfall average (76, 15, and 51 cm, respectively). Experiments and their results are

hereafter referred to by the year the experiment was established (in fall).

In the 2006 and 2007 experiments, modifications were made to the experimental design. The cores were switched just after first rains (in October), when the clay-rich soils went from brittle to pliable, to minimize soil disturbance due to coring (the 2004 experiment involved moving soils in June). We also refined the experimental design from fully factorial to only include origin and destination switches needed for the calculation of *Avena*–*Artemisia* and *Avena*–*Eriogonum* feedbacks (see Eq. 1). Thus, in 2006 and 2007, cores were only switched between *Avena* and *Eriogonum*, and *Avena* and *Artemisia* soil origins and destinations. In addition, we added one replicate, and imposed the without competition treatment only in areas originally dominated by *Avena* (not under removed shrubs). All species were planted in their assigned cores as one or more one-month-old seedlings, previously reared in origin-specific soil, and later weeded to one per core.

The amount of time seedlings grew in treatments necessarily varied between experimental years because core switching and planting was dependant on the timing of natural rainfall. Still, the 4–6 months of growth was representative of natural variability in the length of time seedlings obtain biomass prior to summer drought in mediterranean climates. While we can thus only extrapolate our results to the effects of soils on seedlings, this is the most limiting life stage for shrub reestablishment (Yelenik and Levine 2010b) and stands to be important information for overall community dynamics. However, we note that soils may affect adult shrubs or seed germination differently.

Seedling biomass in the soil core transplant was log-transformed to correct for non-normality. We tested for soil origin, year, and interaction effects with two-way ANOVAs. Because we evaluated soil feedbacks in the presence and absence of competition separately, we conducted separate ANOVAs for each of these treatments. Due to high mortality leading to low sample sizes, destination habitat was not used as a fixed effect, increasing our power to detect soil origin effects. ANOVA analyses were conducted in SAS JMP 7.0 (SAS Institute 2007) with independent variables classified as fixed effects.

Feedback calculations

Following the equation presented in theoretical work by Bever et al. (1997), feedbacks for competitors i and j on respective soils were quantified as

$$\text{feedback}_{ij} = \left[\frac{\text{biomass}_{\text{species } i, \text{soil } i} - \text{biomass}_{\text{species } i, \text{soil } j}}{\text{biomass}_{\text{species } i, \text{soil } i}} \right] + \left[\frac{\text{biomass}_{\text{species } j, \text{soil } j} - \text{biomass}_{\text{species } j, \text{soil } i}}{\text{biomass}_{\text{species } j, \text{soil } j}} \right]. \quad (1)$$

Although previous studies have tended to quantify

feedbacks for individual species (just one of the bracketed terms), Bever et al.'s equation integrates soil effects on both competitors to predict system-level dynamics. Seedling mortality led to uneven sample sizes for the individual biomass terms in Eq. 1, precluding the calculation of a feedback for each replicate site and the resulting mean and variance statistics. Thus, we used nonparametric bootstrapping (coded in R 2.9.1; R Development Core Team 2010) to calculate 95% confidence intervals for each species pair feedback.

Seedling recruitment

To test whether plant–soil feedbacks were predictive of native recovery, we established permanent seedling recruitment plots in areas where shrubs are beginning to recover, spanning the distance between (but not including) pure shrubland and grassland. These “mixed zones” occurred repeatedly across the landscape in lengths ranging from approximately 40–60 m (Yelenik and Levine 2010b). We established six fenced plots that ranged from 48 m² to 130 m² in size. Plots were fenced to exclude rooting activities by feral pigs, which existed on Santa Cruz Island at the beginning of the study. Feral pigs were later eradicated for conservation purposes in 2007; thus, our results are representative of current shrub recruitment dynamics in the absence of disturbance. Plots were located in a subset of the soil core transplant experiment sites, but were established far enough away from cores that they received no disturbance except the yearly census. These data thus represent shrub seedling recruitment in natural competitive regimes. We censused plots for new seedlings every summer from June 2004 to June 2008.

RESULTS

In field cores subjected to competition, *Artemisia* and *Avena* seedlings grew better on soils modified by their competitor than on their own soils (Fig. 2A, B). The dominant exotic grass *Avena*, which depresses available N relative to *Artemisia* shrubs (Yelenik and Levine 2010a), grew somewhat (20%) worse on grass soil as compared to soil modified by *Artemisia* (Fig. 2A, Table 1A), although this difference was not significant. *Artemisia* seedlings, on the other hand, were enhanced by grass modification of soils, growing 200–400% better on *Avena*-modified vs. *Artemisia*-modified soils (Fig. 2B, Table 1A). *Avena*'s response to soils was generally similar in the presence and absence of competition: *Avena* consistently obtained higher biomass on *Artemisia* soils (Fig. 2E, Table 1B). In the absence of competition, however, *Artemisia* seedlings showed no effect of soil origin (Fig. 2F, Table 1B).

Because *Artemisia* and *Avena* seedlings obtained higher biomass in heterospecific soils, plant–soil feedbacks were significantly negative (as evidenced by 95% confidence intervals that do not overlap zero) across years in the presence of competitors (Fig. 3A–D). Theory suggests that negative feedbacks such as these

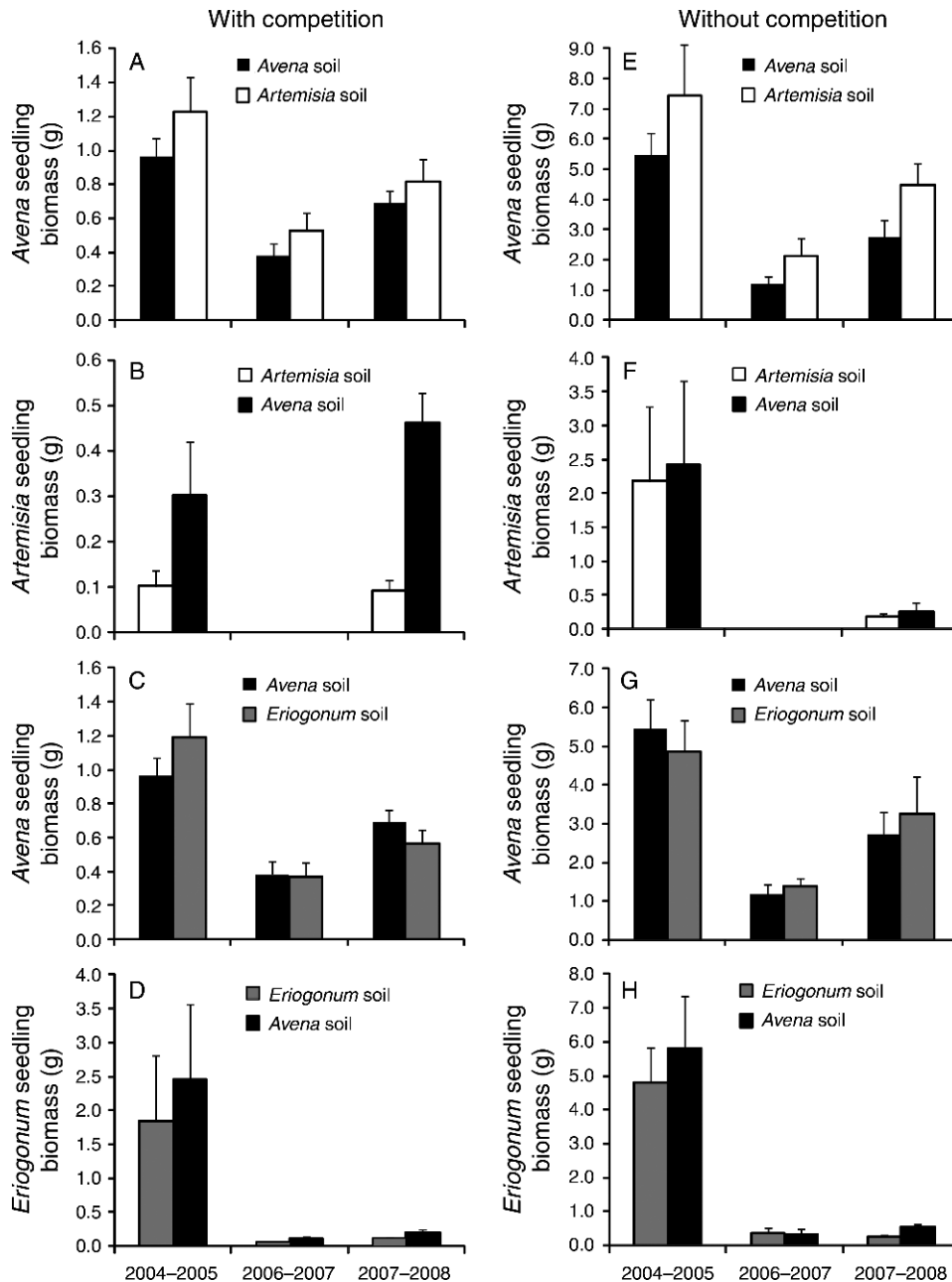


FIG. 2. Plant species response to soils modified by competitors, across years, on Santa Cruz Island, California, USA. In the presence of interspecific competition: biomass of (A) *Avena* and (B) *Artemisia* seedlings in their own and the other's soil; biomass of (C) *Avena* and (D) *Eriogonum* seedlings in their own and the other's soil. In the absence of interspecific competition: biomass of (E) *Avena* and (F) *Artemisia* seedlings in their own and the other's soil; biomass of (G) *Avena* and (H) *Eriogonum* seedlings in their own and the other's soil. *Avena* biomass on *Avena* soil data (panels A and C with competition, panels E and G without competition) are repeated to show the pairwise comparisons used to calculate feedbacks (Fig. 3). The absence of 2006 results for *Artemisia* (B, F) was due to 90% seedling mortality in this severe drought year. See Table 1 for ANOVA statistics. Bars show means + SE.

lead to the breakdown of exotic-species dominance (Fig. 1), and thus a negative *Artemisia*–*Avena* feedback should promote the recovery of the native shrub into the exotic grassland. The strength of the feedback, however, varied with competition. When aboveground competition was removed, the feedbacks remained

negative, but decreased in magnitude and significance (Fig. 3), largely due to the lack of *Artemisia* response to soil origin (Fig. 2F).

Plant–soil feedbacks had a much weaker effect on *Eriogonum* recovery in exotic-grass-modified soils. Previous data showed that *Avena* soil had higher available

TABLE 1. ANOVA table for seedling biomass in soil core transplant experiments (A) with and (B) without interspecific competition on Santa Cruz Island, California, USA.

Variable	<i>Avena</i> – <i>Artemisia</i> feedback				<i>Avena</i> – <i>Eriogonum</i> feedback			
	Target species <i>Avena</i>		Target species <i>Artemisia</i>		Target species <i>Avena</i>		Target species <i>Eriogonum</i>	
	df	<i>P</i>	df	<i>P</i>	df	<i>P</i>	df	<i>P</i>
A) With interspecific competition								
Soil	1, 108	0.326	1, 30	0.020	1, 111	0.894	1, 65	0.002
Year	2, 108	<0.001	1, 30	0.104	2, 111	<0.001	2, 65	<0.001
Soil × year	2, 108	0.773	1, 30	0.120	2, 111	0.732	2, 65	0.906
B) Without interspecific competition								
Soil	1, 66	0.057	1, 16	0.887	1, 74	0.741	1, 69	0.403
Year	2, 66	<0.001	1, 16	0.017	2, 74	<0.001	2, 69	<0.001
Soil × year	2, 66	0.571	1, 16	0.878	2, 74	0.625	2, 69	0.561

Note: Boldface type signifies significant interactions at $P \leq 0.05$.

nitrogen than soils modified by *Eriogonum* (Yelenik and Levine 2010a). In both the presence and absence of competition, *Eriogonum* seedlings grew larger in *Avena*-modified than *Eriogonum*-modified soil (Table 1, Fig. 2D, H), while *Avena* derived little benefit from its soil modification (Table 1, Fig. 2C, G). Such interactions should thus favor *Eriogonum* recovery in *Avena*-dominated grasslands, and indeed, the feedbacks quantified for the *Eriogonum*–*Avena* interaction tended to be negative, but only significantly so in 2007–2008 (Fig. 3).

The magnitude of soil effects on seedlings, however, was smaller and less consistent than that of year or competition effects (Table 1, Fig. 2). Year effects, probably due to differential rainfall, led to larger biomass differences than soil origin. For example, *Eriogonum* seedlings (averaged across competitive treatments) showed a 40% increase in biomass on *Avena* soil, but a 1300% increase in biomass in a high rainfall El Niño year (2004–2005) when compared to an average rainfall year (2007–2008), and a 2600% increase when compared to a drought year (2006–2007). Although *Artemisia* seedlings did not show a year effect in the presence of competition (Fig. 2B), they did when aboveground competitors were removed (Fig. 2F), suggesting that water limitation emerges after light limitation is relieved. It is possible that reduced *Artemisia* seedling growth in the lower rainfall year (without competition) may have resulted from increased evapotranspiration when shading was removed on south-facing slopes.

Aboveground competition also exerted strong effects on seedling biomass. For example, *Avena* grew 45% better in *Artemisia* soil than its own soil (on average across competition treatments), but grew 400% better when aboveground competition was removed (on average across soil treatments: Observe the difference in y-axis scales between competition treatments in Fig. 2). A simple three-factor ANOVA including only main effects of soil origin, year, and competition showed an overwhelmingly strong effect of competition on seedling biomass for both species (for *Eriogonum* seedlings, soil $F_{1,141} = 7.74$, $P = 0.006$; year $F_{2,141} = 74.50$, $P < 0.001$;

competition $F_{1,141} = 30.31$, $P < 0.001$; for *Artemisia* seedlings, soil $F_{1,50} = 1.81$, $P = 0.185$; year $F_{1,50} = 0.56$, $P = 0.456$; competition $F_{1,50} = 13.06$, $P < 0.001$).

The overriding effects of climate and competition may explain why plant–soil feedbacks did not match native-shrub recovery patterns for *Artemisia* (note numbers of recruits below the bars in Fig. 3). In the presence of competition, the *Artemisia*–*Avena* feedback was significantly negative in all years, yet no *Artemisia* seedlings recruited into grassland areas during this time. *Eriogonum*, the native species that successfully recruited into exotic-grassland areas, had its highest recruitment in the wet El Niño year (2004–2005), when *Eriogonum*–*Avena* feedbacks were not significantly different than zero (Fig. 3A).

DISCUSSION

Exotic-plant species are often hypothesized to alter nutrient cycling or soil biota communities in ways that feed back to reinforce their dominance (Klironomos 2002, Van Der Putten 2002, Allison and Vitousek 2004, Callaway et al. 2004, Suding et al. 2004a, Yelenik et al. 2004, Hawkes et al. 2005, Liao et al. 2008). In contrast, results from our multiyear soil core transplant experiment, coupled with a plant–soil feedback framework, predicted that exotic-grass effects on soils enhance the recovery of native shrubs in the Santa Cruz Island ecosystem (Fig. 3). Moreover, the feedbacks were not predictive of which species best recovered in the system, nor the years in which recovery occurred.

Artemisia seedlings in particular benefited greatly from exotic-grass modification of soils (Fig. 2B). All else being equal, plant–soil feedbacks in the system should have enhanced the recovery of *Artemisia* in the exotic grasslands. However, despite ample quantities of germinable *Artemisia* seed falling in grasslands (Yelenik and Levine 2010b), we found no *Artemisia* recovery over four years of monitoring permanent plots. Collectively, these results suggest that factors other than plant–soil feedbacks constrain *Artemisia* return to the island grasslands. Most prominent is competition, which exerted much stronger effects on seedling biomass than

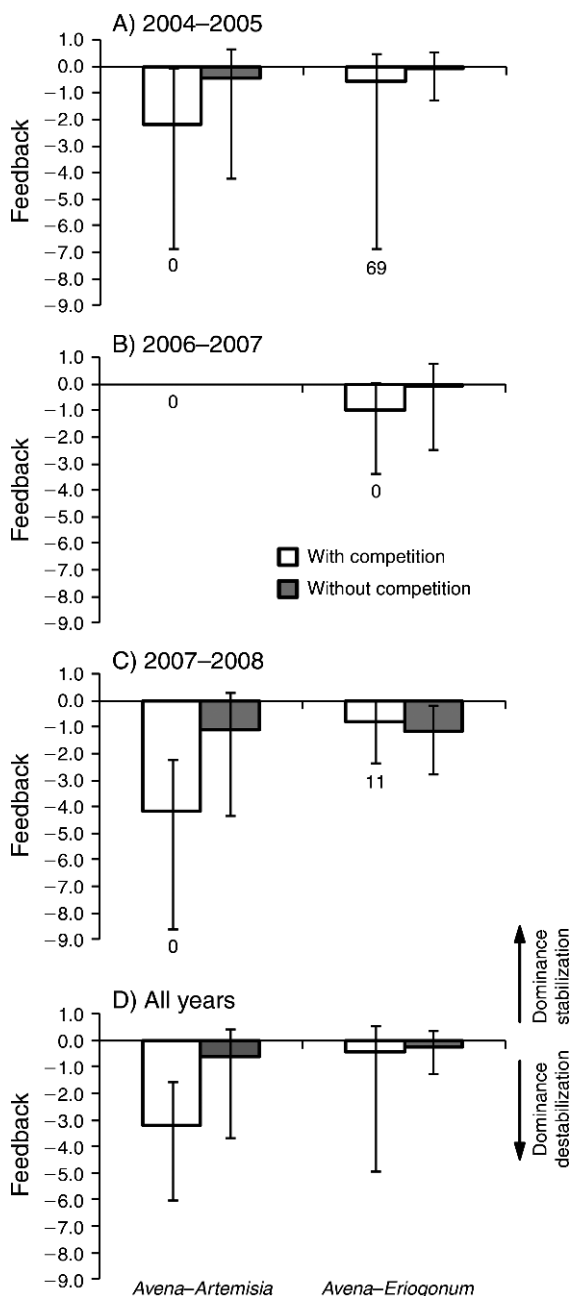


FIG. 3. Plant-soil feedbacks and seedling recruitment for *Artemisia-Avena* and *Eriogonum-Avena* (calculated with data from Fig. 2 using Eq. 1) with and without interspecific competition (A–C) in each experimental year, and (D) averaged over all years. The absence of 2006 results for *Artemisia-Avena* was due to high *Artemisia* seedling mortality in this severe drought year. Bars represent means with bootstrapped 95% confidence intervals. Numbers below the confidence intervals are the number of *Artemisia* and *Eriogonum* seedlings/km² that recruited into *Avena*-dominated grasslands. Seedling recruitment was not quantified without competition.

did soils (Fig. 2). Indeed, previous work in the system showed that competition and interannual variability in rainfall strongly affect seedling recruitment (Yelenik and Levine 2010b).

Although the feedbacks quantified for the *Eriogonum-Avena* interaction were also negative, they were much weaker, and only significantly different from zero in the 2007–2008 growing season (Fig. 3). Still, our finding that exotic grasses modified soils to the benefit of both native shrubs opposes the common hypothesis that plant-soil feedbacks favor exotic plants over their native counterparts.

Even though grass modification of soils was far more beneficial to *Artemisia* than *Eriogonum*, *Eriogonum* was the species showing significantly better recovery over the four years of monitoring. Moreover, the between-year variability in *Eriogonum* seedling recruitment showed no relation to the strength of the negative plant-soil feedback (Fig. 3). These results suggest that even if plant-soil feedbacks influenced native recovery in the island grasslands, they were not a primary determinant of which seedling species recovered, nor the years in which they did so. Other differences between the two shrubs, potentially related to competitive ability with grasses, were likely stronger controls over recovery. In fact, our prior work (Yelenik and Levine 2010b) suggests that the infrequent occurrence of years favorable for shrub recruitment, combined with large effects of grass competition on shrub seedlings largely constrain recovery in the system. More generally, our work provides a counter-example to recent suggestions that plant-soil feedbacks drive exotic-species dominance (Klironomos 2002, Callaway et al. 2004, Yelenik et al. 2004, Hawkes et al. 2005, Wolfe and Klironomos 2005, Bezemer et al. 2006, Kulmatiski et al. 2008, Liao et al. 2008).

Controls over plant-soil feedbacks

We hypothesized that plant-soil feedbacks would arise in the study system because of exotic-grass effects on soil biogeochemical cycles. Indeed, *Avena* lowers soil nitrogen and phosphorus availability relative to the native shrub *Artemisia*, and nitrogen limits both species' growth (Yelenik and Levine 2010a). Therefore, *Avena*'s consistently higher biomass on N and P rich *Artemisia* soils, regardless of rainfall year or competitive regime (Fig. 2A, E), suggests that soil nutrient status is important for plant-soil feedbacks in this system. A similar result was found in a field fertilization experiment, where *Avena* showed nutrient limitation across rainfall years, including a drought year (Yelenik and Levine 2010a).

Why *Artemisia* obtained higher biomass on nutrient-poor exotic-grass soils, and why the soil origin effect disappears when competitors are removed, is less clear (Fig. 2B, F). It should be noted that we did not track nutrient dynamics in the experimental cores through time, which, due to root death and turnover in cores,

may differ from previous results concerning species effects on soils (Yelenik and Levine 2010a). Our results may also relate to species effects on other limiting resources, soil structure, or soil biota (Klironomos 2002, Van Der Putten 2002, Callaway et al. 2004, Wolfe and Klironomos 2005, Casper et al. 2008) and interactions between these mechanisms and competition (Bever 2003, Callaway et al. 2003). It is possible, for example, that the shade provided by the “with competition” treatment lowered soil moisture losses, benefiting *Artemisia* seedlings when competitors were present. With regard to potential microbial effects, however, we note that a soil inoculation experiment following the methodology of Reinhart and Callaway (2006), did not detect an influence of microbially mediated plant–soil feedbacks (Yelenik 2008).

Although we found a limited role for plant–soil feedbacks in our system, our results do suggest that when such feedbacks are thought to be an important, it is crucial to quantify them under natural competitive and climate conditions. This is particularly important given the prevalence of greenhouse experiments in this literature (Casper et al. 2008, Kulmatiski et al. 2008). We found that the *Artemisia*–*Avena* interaction changed from a strong negative feedback to insignificant when aboveground competition was removed (Fig. 3). That aboveground competition was important for biogeochemically mediated feedbacks is not surprising given that plant neighbors can switch the limiting resource from soil nutrients to light (Tilman 1985). Our results have probably underestimated the influence of competition on feedbacks because our intact core approach necessarily excludes belowground competition. While the importance of belowground competition on biogeochemically mediated plant–soil feedbacks remains unknown, understanding the influence of aboveground competition, as done here, is an important first step.

Replication of our experiment across multiple years also allowed us to evaluate how climate variability influenced the strength and direction of feedbacks. Interestingly, although seedling biomass was sensitive to the year of the experiment, species’ response to soils did not differ across years, as indicated by nonsignificant soil by year interactions (Table 1). Although the calculated plant–soil feedbacks did change somewhat in magnitude across years, the feedbacks were always negative (Fig. 3). This result for biogeochemically mediated feedbacks held with our previous finding that California grassland species maintain nutrient limitation even when water is also limiting (Yelenik and Levine 2010a).

Using feedbacks to predict exotic dominance and native recovery

Ecologists studying biological invasions have now accumulated considerable evidence that exotic-plant invasions modify soil nutrient cycling (Ehrendfeld 2003, Levine et al. 2003, Liao et al. 2008). However, whether these modifications reinforce the exotic dominant or

influence rates of native recovery has largely been a matter of speculation (Levine et al. 2006, Eppstein and Molofsky 2007). Our results suggest that the degree to which exotic-species effects on soil nutrient cycling influence their continued dominance depends on the identity of the competing native species; *Artemisia* showed much stronger negative feedbacks with the exotic grass than did *Eriogonum*. This range of feedbacks was consistent with the wide range of effects that exotic plants have on soil nutrient cycling (Ehrendfeld 2003). Despite the between-species variation, however, both shrub species showed soil feedbacks that should favor their recovery in the exotic grasslands of our study system.

The feedbacks we found were not predictive of which species best recovered in the system, nor the years in which recovery occurred. This result was unexpected because prior work showed that plants in the system exerted clear effects on soil nutrient cycling and displayed strong and differential nutrient limitation (Yelenik and Levine 2010a). In combination with a large body of work showing evidence for plant–soil feedbacks in controlled environments, our study points to the importance of understanding an array of ecological factors when seeking the mechanisms that control exotic dominance and native species recovery.

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