

Native shrub reestablishment in exotic annual grasslands: Do ecosystem processes recover?

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Abstract. The impacts of exotic plant species on ecosystem processes are well established, motivating numerous efforts to facilitate native-species recovery. Nonetheless, how the return of native species influences ecosystem processes and how these changes feed back to influence the recovery process are poorly understood. We examined these questions in exotic annual grasslands on Santa Cruz Island, California, USA, where the removal of nonnative herbivores has led to the recovery of the native shrubs *Artemisia californica* and *Eriogonum arborescens*. To examine the influence of shrub colonization on nutrient cycling, and the mechanisms by which these changes arise, we measured available nitrogen and phosphorus, and quantified nitrogen mineralization and litterfall rates under shrubs and grasses in the field and in experimental monoculture plots. Both native shrubs altered nitrogen cycling as they colonized the grassland, but they did so in opposite directions. *Eriogonum* depressed nitrogen pools and mineralization rates via large inputs of nitrogen-poor litter. In contrast *Artemisia* increased nitrogen and phosphorus pools and nitrogen mineralization rates. Last, to determine if shrub effects on soils favor shrubs or grasses, we conducted a nitrogen and phosphorus fertilization experiment in the field. Only the exotic grass was significantly limited by nitrogen. Thus the depressed nitrogen availability associated with *Eriogonum* colonization is more harmful to exotic grasses than to the native shrub. By contrast, the elevated nitrogen associated with recovering *Artemisia* favors grasses over the shrub, possibly hindering recovery of the native. Mechanistic studies of the ecosystem impacts of native-plant recovery are useful for managers wishing to predict which native species return ecosystem function, and whether such changes feed back to influence native recovery.

Key words: *Artemisia californica*; California (USA) grasslands; coastal sage scrub; ecosystem restoration; *Eriogonum arborescens*; nitrogen cycling; nutrient limitation; phosphorus; plant effects on soils.

INTRODUCTION

Some of the most dramatic impacts of exotic plant invasions occur via changes in ecosystem processes, such as fire regimes (D'Antonio and Vitousek 1992), hydrology (Wilcox and Thurow 2006), soil erosion (Reed et al. 2005), and nutrient cycles (Vitousek and Walker 1989). Impacts on soil nutrient cycles are some of the best studied (Vitousek and Walker 1989, Ehrenfeld 2003), and occur when native and exotic species differ in input and uptake traits (Hobbie 1992, Eviner 2004). Differences in litter quality can influence nutrient cycling because litter with high carbon-to-nitrogen or lignin-to-nitrogen ratios tends to slow decomposition and nitrogen cycling (Melillo et al. 1982). In addition, differences between native and exotic plants in the timing and quantity of nutrient uptake can drive similar changes (Hooper and Vitousek 1998, Booth et al. 2003a, b, Eviner et al. 2006). Finally, differences in

microclimate under native and exotic species, as well as differences in root exudates, can alter nitrogen transformations in soils (Mack and D'Antonio 2003).

With broadening appreciation for the negative impacts of exotic plant invasions, land managers have curtailed many of the anthropogenic factors that initially favored domination by nonnative plants in the past. These factors include grazing, sowing of exotic seed, and tillage. In addition, there have been large restoration efforts aimed at returning native species to exotic-dominated habitats (Dobson et al. 1997, Young 2000). Although many such efforts have shifted species composition towards native plants (Donlan et al. 2002, Beaver et al. 2008), whether native recovery also returns ecosystem processes remains unclear. One might expect so, because the same mechanisms that shift nutrient cycling during exotic invasion, such as changes in litter inputs and nutrient uptake, are potentially reversed when native species “re-invade” exotic-dominated landscapes. Alternatively, the former dominance of exotic plants may have persistent effects on nutrient cycles, which could feed back to influence native recovery (Suding et al. 2004).

Interest in restoring soil nutrient-cycling regimes to exotic-dominated habitats is pervasive for several

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reasons. First, many ecologists argue that fully restored ecosystems ideally include the return of both structure, as in species composition, and function, as in ecosystem processes, to a given habitat (SER International 2004). Second, exotic plants that increase nitrogen cycling rates can elevate leaching or gaseous losses of nitrogen, which contribute to eutrophication or greenhouse gases (Vitousek et al. 1997). Nitrogen losses are particularly likely when net microbial nitrogen production and exotic-plant uptake are offset in time (Evans et al. 2001, Booth et al. 2003b).

Finally, and most important for the stability of the recovering system, changes in soil nutrients can feed back to alter plant community dynamics, either hindering or reinforcing native recovery (Bever et al. 1997, Casper and Castelli 2007). Indeed, ecologists are increasingly finding that species effects on soils regulate succession, invasions, and dominance patterns in ecological communities (van der Putten et al. 1993, Chapin et al. 1994, Bever et al. 1997, Klironomos 2002, Wardle et al. 2004, Bezemer et al. 2006, Kardol et al. 2006, Casper and Castelli 2007). Exotic plant species, for example, can alter soil mycorrhizal communities in ways that favor their own growth (Klironomos 2002).

Despite recent advances in understanding feedbacks mediated via soil microbial communities (Kulmatiski et al. 2008), as well as considerable evidence that exotic and native species differ in their effects on nutrient cycling (Vitousek and Walker 1989, Evans et al. 2001, Ehrenfeld 2003, Levine et al. 2003, Allison and Vitousek 2004, Yelenik et al. 2007), whether species effects on nutrient cycles feed back to affect community dynamics has proven difficult to evaluate. For such feedbacks to be important, species must change the availability of a nutrient that differentially limits their growth and the growth of their competitors (Casper et al. 2008). For example, a native plant that depresses nitrogen availability can only benefit from such changes if its exotic competitors are more nitrogen limited than it. Progress can thus be made by coupling investigations of species effects on nutrient cycles with fertilization experiments testing for species differences in nutrient limitation.

Here, we ask how recovering native shrubs change nutrient cycles in exotic annual grasslands, and explore the underlying mechanisms. We also ask whether these changes are likely to favor exotic grasses or native shrubs by testing which nutrients are most limiting to each species. We address these questions on Santa Cruz Island, California, USA, where a long history of sheep grazing and exotic-seed introduction converted large areas of the island to exotic annual grasslands dominated by *Avena barbata* (wild oats). Hobbs (1983), Junak et al. (2000), and others have argued that current island grasslands were historically coastal sage scrub communities dominated by species such as *Eriogonum arborescens* (island buckwheat) and *Artemisia californica* (California sagebrush). Since the elimination of sheep from the island in the 1980s, these two shrubs have

slowly begun to recolonize annual grasslands from refugia on steep rocky slopes (Morrison 2007). A mechanistic, trait-based analysis of changes in nutrient cycling with native recovery would be useful to managers wishing to predict the return of ecosystem function.

Given the woody perennial vs. herbaceous growth forms of the native shrubs and exotic grasses on the island, these species likely differ in traits that influence nutrient cycling, such as phenology, effects on microclimate, and litter quality and quantity. In addition, several of the focal species are nutrient limited in other Southern California grasslands (Yoshida and Allen 1988, Harpole et al. 2007), suggesting that shifts in soil nutrients may feed back to influence the pace of native recovery.

We coupled field and laboratory measurements to evaluate how soil nutrient cycling changes as native shrubs recover in exotic grassland, the mechanisms exacting these changes, and whether these shifts alter the availability of nutrients more limiting to native shrubs or exotic grasses. To quantify changes in nitrogen and phosphorus cycling with shrub recovery, we analyzed soils collected from underneath *Avena barbata*, *Artemisia californica*, and *Eriogonum arborescens* in the field and in experimentally established monoculture plots. To explore the influence of litter on changes in nutrient cycles, we quantified litter quality and quantity, and experimentally added litter to monoculture plots. Finally, to assess whether shrub effects on nutrient cycling altered the availability of nutrients more limiting to them or their exotic grass competitors, we conducted a field fertilization experiment.

METHODS

Study system

Santa Cruz Island is 249 km² in size, located 30 km offshore from Southern California (USA) (33°59'49" N, 119°43'34" W), and has a typical Mediterranean climate with cool, wet winters and hot, dry summers. It has two predominating east–west ridge lines that create a 20-km “central valley” that has less coastal influence than the rest of the island (Junak et al. 2000). Average rainfall (as compiled over 1904–1991; Junak et al. 2000) in the central valley of Santa Cruz Island is 50 cm per year. Significant precipitation begins in the fall, which induces germination, and soils dry out after the rains end in late spring (Fig. 1).

All sampling sites were on south-facing slopes of the central valley in “mixed zones” where native shrubs have begun to recolonize exotic annual grassland on lithic to pachic Argixerolls. Here, shrubs and grasses intergrade and individual shrubs of varying sizes can be found surrounded by grassland (see Plate 1). This mixed zone is ideal for studying the effects of native plants on soil nutrient cycling since shrubs have colonized a grassland that is relatively homogeneous with respect to soil depth, particle size, and elevation (Hobbs 1983) and any

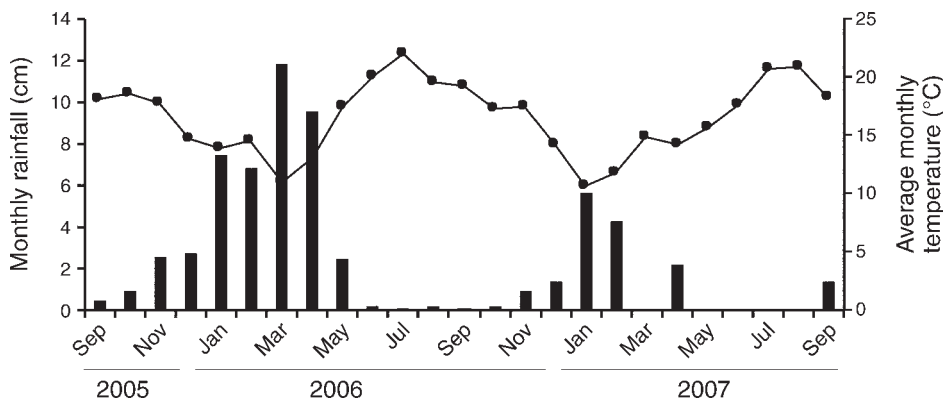


FIG. 1. Total monthly precipitation (bars) and monthly average air temperature (circles and line) for Santa Cruz Island, California, USA, during the period of study, September 2005–September 2007.

differences in soils underneath different species should largely be a function of the colonizing plant.

Our study focused on three mixed-zone sites spaced over 7 km of the central valley of the island. Given the fall to late-spring growing season, our yearly sampling always extended across two calendar years (September to September).

Species effects on nitrogen and phosphorus pools

To investigate the effects of native shrub recovery on soil nutrient cycling, we tracked mineral N and resin-available P pools in field soils from September 2005 to September 2006. We collected soils from underneath six individual shrubs of *Eriogonum* and *Artemisia* at each of the three mixed-zone sites every two months. We chose large individuals to maximize the time the shrubs have had to affect soils; the timing of species effects on nutrient cycling was explored in the monocultures experiment (see *Monoculture plots*, below). *Avena* soil cores were collected 1 m away from sampled shrubs, in areas dominated by the grass.

Beneath the canopy of each shrub and at each grassland location, we extracted a 3-cm-diameter, 10-cm-deep core. Soil was refrigerated until processed through a 4-mm sieve and extracted with 2 mol/L KCl. We measured gravimetric soil moisture by weighing soils before and after oven-drying at 60°C for 48 h. Phosphorus was measured on a subset of the N-sampling dates (September 2005, March 2006, and April 2006) using a resin extraction method (Kuo 1996), as modified by D. Turner (information available online).² We calibrated resin bags with solutions of known concentration to correct sample values.

Soil nitrate, ammonium, and phosphorus in extracts were measured using a Lachat flow-injection auto analyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Soils from the last sampling date were also analyzed for organic-matter content by combustion at

500°C in a muffle furnace. We measured pH in a 2:1 soil:water suspension where soil was allowed to settle prior to measurement.

Species effects on nitrogen mineralization rates

Mineral nitrogen pools are a function of various processes, including plant and microbial uptake, and microbial mineralization. Because high uptake rates in N-limited ecosystems can lead to low pool sizes, even when production rates are high, potential net mineralization rates offer a different measure of plant-available N in soils. Potential net N mineralization provides a measure of the microbial community's potential to produce and consume soil N at optimal conditions given the current organic matter in soils. By contrast, KCl-extracted mineral N offers a snapshot of soil N as affected by microbial production and consumption given current organic matter, as well as plant uptake and abiotic factors. We used laboratory incubations to determine potential net N mineralization rates in fall- and spring-collected soils (the same as those soils collected for analyses of pool sizes). The fall sampling date for mineralization analyses (using the September 2006 soil collections) was selected to capture soil N dynamics at first wet up (i.e., first rainfall after the summer drought period). The spring date (soils collected March 2006) was selected to assess plant-available N when plant growth is maximal and most likely N limited.

We held soils passed through a 4-mm sieve at constant moisture (35% water-holding capacity [WHC]) and temperature (20°C) for one-month incubations. WHC of 35% in these soils corresponds to 12% soil moisture, which is comparable to field values after fall rains (Yelenik 2008). We extracted the t_0 soils 24 h post wet up and the t_1 soils 30 days later. Potential net ammonification rates ($\mu\text{g N} \cdot [\text{g dry soil}]^{-1} \cdot \text{month}^{-1}$) were calculated as $[(\text{NH}_4^+)_{t1} - (\text{NH}_4^+)_{t0}]$ potential net nitrification rates as $[(\text{NO}_3^-)_{t1} - (\text{NO}_3^-)_{t0}]$ and potential net mineralization rates as $[(\text{NH}_4^+ + \text{NO}_3^-)_{t1} - (\text{NH}_4^+ + \text{NO}_3^-)_{t0}]$.

² (<http://www.stanford.edu/group/Vitousek/resinp.htm>)

Litter quality and quantity

To elucidate the mechanisms underlying plant species effects on soil nutrient cycling, we quantified litterfall, standing litter, and litter quality (C:N) for all three study species at all three mixed-zone sites. We collected *Avena* litter by clipping annual grasses within two 0.25×0.25 m quadrats at each site (plus an additional fourth site) in spring 2006 just after grasses had senesced. Samples were dried at 60°C for 48 h and weighed to quantify *Avena* litterfall rates.

We measured shrub litterfall rates by placing one tray ($53 \times 27 \times 10$ cm) underneath nine large-shrub individuals per species at each of the three mixed-zone sites in May 2007. Litter was collected the following August and January, after the shrubs drop the majority of their litter (Gray and Schlesinger 1981). We measured the standing litter of shrubs and grasses by collecting the organic layer from two 2.5-cm-diameter cores taken from underneath all three species (3 individual plants/site) from each of three sites. All litter was dried at 60°C for 48 h, and weighed.

For litter-quality samples we collected shrub leaves that were about to senesce but not yet fallen, by tapping on branches in fall 2005. A well-mixed subsample from each *Avena* litter plot was analyzed for litter quality. We ground all litter with a Wiley mill (Thomas Scientific, Philadelphia, Pennsylvania, USA) followed by a ball mill (Wig-L-Bug amalgamator; Crescent Dental, Lyons Illinois, USA) and used a Carlo Erba NA 1500 CHN analyzer (Fisons Instruments, Beverly, Massachusetts, USA) to measure nitrogen and carbon. For phosphorus analysis, plant litter was sent to the University of California, Davis, Agricultural and Natural Resources Analytical Laboratory.

Monoculture plots

To further distinguish the influence of plant draw-down and litter on soil nutrient cycling, we established monoculture plant and litter plots in December 2003. Plots were located on pachic Argixeroll soils, in an old-field that had been fallow for over 50 years, and was currently dominated by *Avena barbata*. Prior to planting we mowed, removed litter, and then rototilled a 15×24 m area for plots.

We randomly assigned 60 1-m^2 plots with a 1-m buffer to the following treatments: (1) *Artemisia* monoculture, (2) *Eriogonum* monoculture, (3) *Avena* monoculture, (4) *Eriogonum* litter, (5) *Avena* litter, and (6) bare. We did not have an *Artemisia* litter treatment due to low standing litter pools available for collection. To establish the shrub monocultures we sowed island-collected *Eriogonum* and *Artemisia* seed, while *Avena* monocultures grew from the existing seed bank. *Artemisia* establishment was very low, so we planted seedlings in summer 2005. Although these seedlings survived, this treatment had only two years for species effects on soils to develop. At the time we began soil sampling in 2006,

Eriogonum monocultures had a closed shrub canopy and large standing litter pools, while *Artemisia* covered only ~40% of the plot and had almost no standing litter. *Avena* showed 100% cover each year of the experiment. For the litter plots we added sufficient *Avena* litter (from aisles between plots) and field-collected *Eriogonum* litter to match annual litterfall. The bare plot was cleared of all plant biomass and litter in fall 2006.

We weeded plots once every two months between December 2003 and June 2007. We gave the monoculture plots about 10 cm of water in April 2007, a drought year. To measure species and litter effects on nutrient cycling, soils were collected once every two months (September 2006 to September 2007) and analyzed for mineral N as in *Species effects on soil nitrogen and phosphorus pools*, above. Soil nutrients in the monoculture plots were sampled one year later than in field soils, so the monoculture plants would have sufficient time to alter soils. Although this introduces annual rainfall differences into any comparison between monoculture and field soil results, we feel that the relative differences between species should be preserved across years.

Field fertilization experiment

To determine if shrub effects on soil fertility favor shrubs or grasses, we established a nitrogen and phosphorus fertilization experiment in the field in fall 2005. At each of our three focal sites plus an additional fourth site interspersed among the other three, we located eight small *Artemisia* and *Eriogonum* growing within a matrix of exotic annual grasses. We established 1-m^2 plots around shrubs, and randomly assigned two plots at each site to the following treatments: N addition, P addition, N and P addition, or control. We measured the response of *Avena* in 0.25×0.25 m subplots within each shrub plot. The *Avena* subplots were located as far as possible from the shrub, though we noticed no difference in the fertilization response of *Avena* closer to shrubs. We added 5 g N, 5 g P, or both to plots twice per growing season for two years—once before rains began, and once in the middle of the rainy season. We added N as urea and P as KH_2PO_4 , both in solid form. We added nutrients twice per year because these fertilizers release relatively quickly.

In early May 2006 and 2007, after *Avena barbata* seed formation, but prior to seed drop, we clipped production in each grass plot. Although the harvested biomass was not purely *Avena*, this species constitutes over 70% of grass biomass. Shrubs were destructively harvested at the end of two growing seasons, in October 2007. All biomass was dried for 48 h at 40°C and weighed.

Statistical analyses

Species effects on mineral nitrogen and phosphorus were analyzed with repeated-measures ANOVAs. Species effects on soil moisture, organic matter, pH,

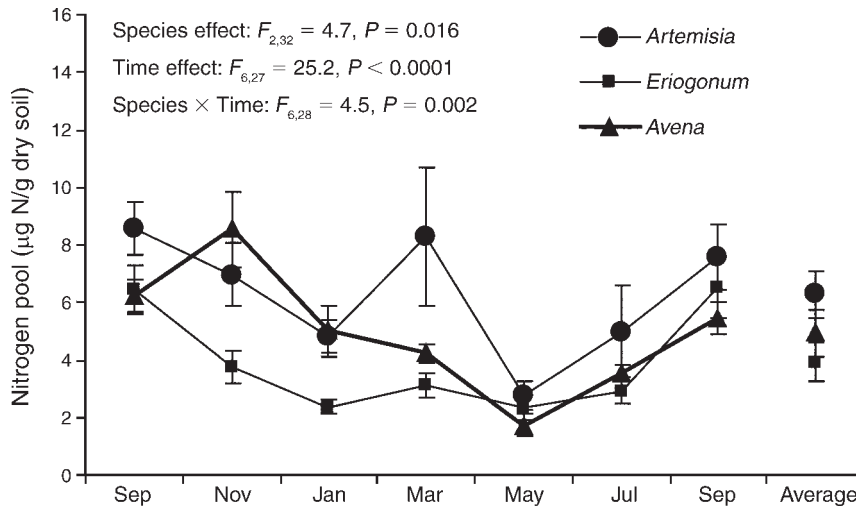


FIG. 2. Total inorganic nitrogen pools ($\text{NH}_4^+ + \text{NO}_3^-$) in soils under *Artemisia*, *Eriogonum*, and *Avena* in field surveys, as well as their average value over all sampling dates. Data are means \pm SE.

nitrogen ammonification, nitrification, and mineralization rates as well as species differences in litter C:N, P content, standing pools, and litterfall rates were tested with two-way ANOVAs with species and site as fixed effects. Whether shrubs differentially colonized sites with specific sand, silt and clay content were tested with one-way ANOVAs because samples were bulked per site.

The effects of fertilization on each species biomass was tested with an ANOVA including the fixed effects of N addition, P addition, their interaction, and site. For *Avena*, whose biomass was measured in each of two years, we ran the model as a repeated-measures ANOVA. All statistics were run with SAS JMP 7.0 (SAS Institute 1989–2007).

RESULTS

Eriogonum influence on soils

As *Eriogonum* recovers in exotic annual grassland, it tended to depress nitrogen availability. Averaging over the year, mineral nitrogen pools were 20% lower in *Eriogonum* than *Avena* soils (Fig. 2). Though a post hoc contrast after the repeated-measures analysis showed that this effect only approached significance ($P = 0.070$), differences between soils under the two species were especially strong in November. In this first month after rainfall, *Eriogonum* soil had 56% lower mineral N than did *Avena* soil ($P = 0.002$ from post hoc contrast after one-way ANOVA, where Species $F_{2,51} = 5.67$ and $P =$

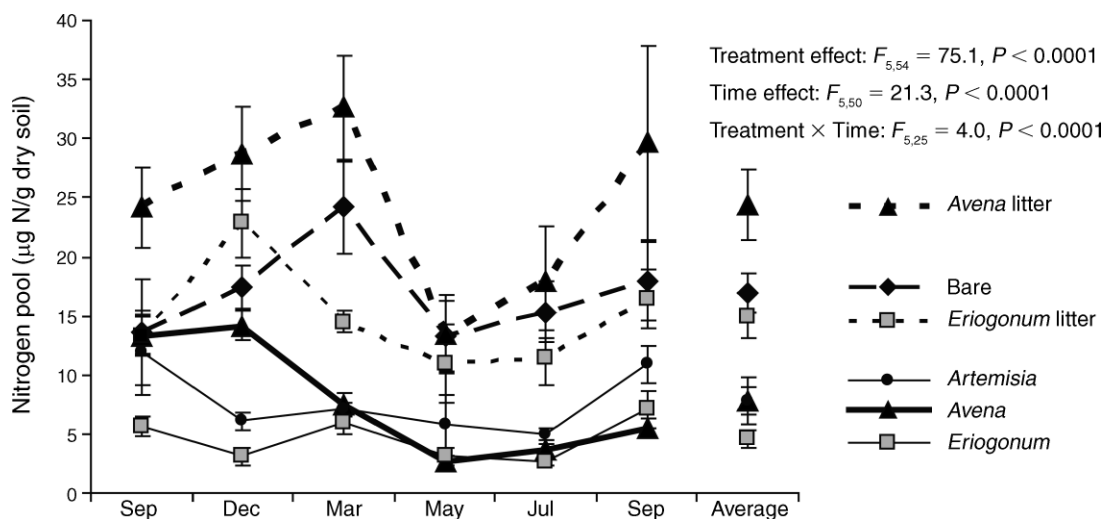


FIG. 3. Inorganic nitrogen pools ($\text{NH}_4^+ + \text{NO}_3^-$) in soils under *Artemisia*, *Eriogonum*, *Avena*, bare monoculture plots, and *Eriogonum* and *Avena* litter plots, as well as the average value over all sampling time points. Plant plots never had litter removed and can be interpreted as exhibiting a mixture of plant drawdown and litter effects. Data are means \pm SE.

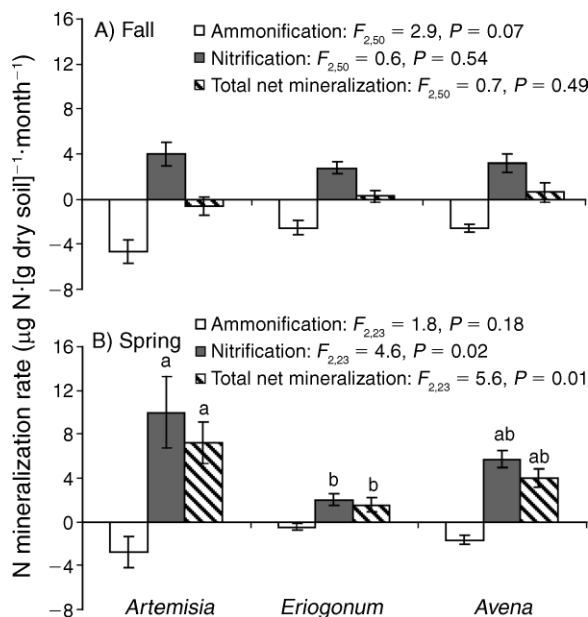


FIG. 4. Potential net nitrogen mineralization rates in laboratory incubations of field-survey soils collected in (A) fall (September) and (B) spring (March). Data are means \pm SE. Different lowercase letters represent significant differences between species for post hoc Tukey tests at a level of $P \leq 0.05$.

0.006). Similar differences were found in the monoculture plots where, on average, *Eriogonum* lowered mineral N 40% relative to annual grass (Fig. 3, $P = 0.050$ from a post hoc contrast after repeated-measures analysis). The largest differences, again, arose just after first rainfall, when *Eriogonum* soil had 78% less mineral N than *Avena* soils ($P = 0.001$ from post hoc contrast after one-way ANOVA, where Treatment $F_{5,54} = 18.54$

and $P < 0.001$). *Eriogonum* N-flux rates were somewhat slower than those in *Avena* soils in spring (Fig. 4B), though the difference was not significant, nor did fall rates differ between the species.

Leaf litter traits likely contribute to the lower N pools and mineralization rates that accompany *Eriogonum* recovery in exotic annual grasslands. We found that *Eriogonum* leaf litter had high C:N ratios relative to exotic grasses (128.7 vs. 50.1; Table 1) and much lower foliar P (0.04% vs. 0.33%; Table 1). *Eriogonum* also had high litterfall rates (Table 1), which coupled with low quality litter, are consistent with this species maintaining almost four times the amount of standing litter as the exotic grass (Table 1). Also consistent is the near-significant increase in soil organic matter under colonizing *Eriogonum* (Table 1). Soil moisture, which can also affect N cycling rates, did not differ between species when averaged through time (Table 1). This general result held when soil moisture was analyzed with a repeated-measures ANOVA (Species effect, $F_{2,51} = 1.71$, $P = 0.190$; Time effect, $F_{5,47} = 427.85$, $P < 0.001$; Species \times Time interaction, $F_{10,94} = 4.74$, $P < 0.001$). Significant species \times time interactions occur because *Eriogonum* tends to have a slightly higher percentage of soil moisture (1–2%) than other species in the summer months, while *Avena* soils hold moisture longer after first rains (2–4%) (data not shown). Soil pH (Table 1) and resin-available phosphorus (Fig. 5) were also unaffected by species.

Results from monoculture plots were consistent with the hypothesis that *Eriogonum* lowers mineral N pools and cycling rates via large inputs of low-quality litter. Driven largely by early season differences, plots with only *Eriogonum* litter had, on average, 40% lower mineral N than *Avena* litter plots (Fig. 3, post hoc

TABLE 1. Means (standard error) and ANOVA statistics for soil and litter properties sampled beneath native shrubs and exotic annual grasses.

Property	<i>Artemisia</i>		<i>Eriogonum</i>		<i>Avena</i>		ANOVA statistics					
							Species effect			Site effect		
	Mean	SE	Mean	SE	Mean	SE	F	df	P	F	df	P
Soil												
Sand (%)	46.0	2.7	48.1	3.4	41.4	(3.4)	1.4	2, 18	0.28	N/A		
Silt (%)	33.5	1.7	31.4	1.6	34.0	(1.8)	0.7	2, 18	0.53	N/A		
Clay (%)	20.5	1.2	20.4	1.3	24.6	(1.9)	2.6	2, 18	0.10	N/A		
Moisture (%)	13.8	0.41	14.5	0.65	14.5	(0.37)	0.8	2, 49	0.47	2.9	2, 49	0.07
pH	6.19	0.05	6.24	0.09	6.3	(0.11)	0.5	2, 49	0.60	7.4	2, 49	0.002
Organic matter (%)	7.45	0.3	8.13	0.3	7.11	(0.3)	2.8	2, 49	0.07	2.4	2, 49	0.10
Litter†												
C:N ratio	39.7 a	2.1	128.7 b	7.2	50.1 a	(12.6)	132.7	2, 45	<0.001	4.0	4, 45	0.007
Phosphorous, P (%)	0.24 a	0.03	0.04 b	0.00	0.33 c	(0.02)	58.8	2, 45	<0.001	3.4	2, 45	0.02
Standing (g/m ²)	1397 a	245	4959 b	551	1294 a	(130)	41.3	2, 22	<0.001	1.7	2, 22	0.20
Litterfall (g/m ²)	84.5 a	7.9	384.2 b	40.8	197.3 c	(26.9)	42.2	2, 56	<0.001	1.7	4, 56	0.17

Notes: Soil moisture was averaged over the year. Soils for sand, silt, and clay soil content were collected underneath all three species at seven mixed-zone sites in February 2004 and analyzed at the University of California–Davis ANR Analytical Laboratory. For sand, silt, and clay, we used one-way ANOVAs for statistical analysis because there was no replication within each of the seven sites. Boldface type indicates $P < 0.05$.

† Within rows, means with different lowercase letters are significantly different between species ($P \leq 0.05$) using one-way ANOVAs with post hoc Tukey tests.

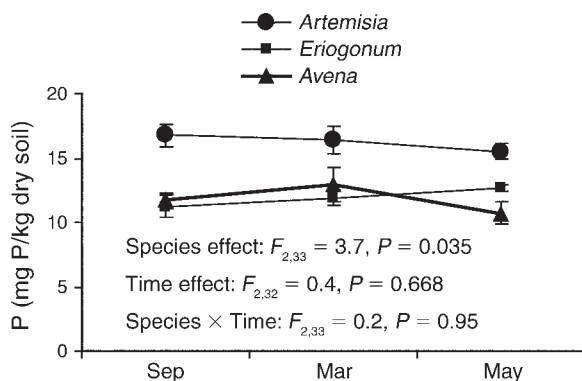


FIG. 5. Resin-available phosphorus in soils under *Artemisia*, *Eriogonum*, and *Avena* in the field surveys. Data are means \pm SE.

contrast of full repeated-measures analysis: $P < 0.001$). *Eriogonum* plots with both plants and litter also showed a 40% reduction in mineral N relative to *Avena* plots with both plants and litter. That the 40% difference held in the presence and absence of plant uptake suggests that litter differences alone might explain why *Eriogonum* and *Avena* differ in their effects on N cycling. Still, the importance of uptake cannot be ignored. For both species, we found lower mineral N pools in plots that contained plants and litter than in plots with only litter or bare plots. Interestingly, *Eriogonum* depressed N cycling in monoculture plots that were previously dominated by *Avena* within four years, showing that the recovery of this shrub can rapidly change ecosystem processes.

Artemisia influence on soils

In contrast to *Eriogonum*, *Artemisia* recovering in exotic grassland increased nutrient availability. In field surveys, mineral N pools were 25% higher in soils underneath *Artemisia* than grasses on average and 100% greater in March (Fig. 2). Although this difference was strongest at the March sampling date ($P = 0.014$ in a post hoc contrast following a one-way ANOVA where Species $F_{2,32} = 4.86$ and $P = 0.014$), repeated-measures analysis also showed a significant difference between *Avena* and *Artemisia* over time (Fig. 2, post hoc contrast $P = 0.025$). Net N mineralization and nitrification rates match mineral N pool data, showing the largest differences between species in March (Fig. 4B). At this sample date, *Artemisia* soils had mineralization rates 75% higher than *Avena* soils, though this difference only approached significance (Fig. 4B, post hoc contrast $P = 0.073$). By contrast there was no difference in net mineralization in the fall sample (Fig. 4A). *Artemisia* also substantially increased available P relative to *Avena* soils across all months (Fig. 5, post hoc contrast $P = 0.017$).

Why *Artemisia* elevates nitrogen cycling relative to exotic grasses is unclear. *Artemisia* drops less litter with similar C:N ratio as *Avena* (Table 1), and the species did

not differ in their influence on soil moisture and pH, two factors that can indirectly influence soil N cycling (Table 1). Although the direction of the *Artemisia* effect on soil mineral N in monoculture plots qualitatively matched that seen in the field surveys, the effect was not significant, and was driven largely by the December sampling date. The weaker *Artemisia* effects in the monoculture experiment might be expected given its <40% coverage in the monoculture plots. Moreover, because we could not establish litter-only *Artemisia* plots in our monoculture experiment, we could not directly test the influence of its litter.

Field fertilization experiment

The two shrubs and exotic grass were differentially limited by N and P, indicating that shrub effects on soils may alter the interactions between the species. *Avena* was the most limited by N in the system, producing 2.5 times as much biomass in N-addition plots as control plots in 2006 and twice as much in 2007 (Fig. 6A). The lower 2007 biomass likely relates to very low rainfall (Fig. 1), but the persistence of a N-addition effect shows that *Avena* is N limited even in dry years. *Eriogonum* also increased with N addition, but this effect was nonsignificant (Fig. 6B). *Artemisia* only responded to N in the presence of P (Fig. 6C).

DISCUSSION

Ecologists require a better understanding of how native-species recovery in exotic-dominated landscapes influences ecosystem processes and how these changes feed back to influence the recovery process. We found that as *Eriogonum* recolonized exotic annual grasslands on Santa Cruz Island (California, USA), it slows nitrogen cycling, reducing the availability of N to both shrubs and grasses. This effect likely arises because *Eriogonum* produces large quantities of low-quality litter. By contrast, as *Artemisia* recovered, it accelerated N cycling, increasing N availability. Shrub effects on N cycling should feed back to influence the interaction between the native and exotic species. We found that the exotic grass was the only species significantly limited by N. Combining plant effects on N with N effects on plants, our work predicts that the depressed N availability associated with *Eriogonum* colonization is more harmful to exotic grasses than to the native shrub, favoring the recovery of the latter. By contrast, the elevated N associated with recovering *Artemisia* favors grasses over the shrub, possibly hindering recovery of this native species.

Species effects on nutrient cycling

We found that the two native shrub species had opposing effects on N dynamics in *Avena*-dominated grasslands; *Eriogonum* tended to lower mineral N pools (especially in certain months) while *Artemisia* increased N and P pools in soils. Species differences in soils from field surveys of the mixed zone could be partially driven

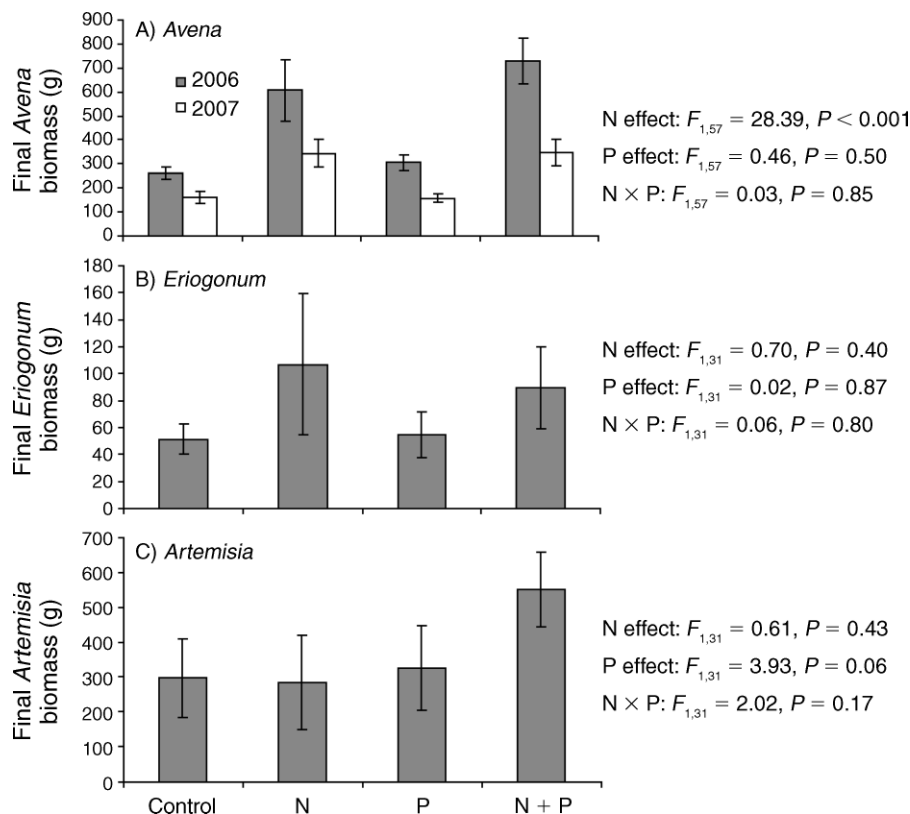


FIG. 6. Field fertilization experiment. Biomass of (A) *Avena* over two years, and biomass of (B) *Eriogonum* and (C) *Artemisia* after two years of fertilization with nitrogen, phosphorus, both, or neither (control). Data are means \pm SE. *Avena* biomass was analyzed as a repeated-measures ANOVA including time, N \times Time, P \times Time, and N \times P \times Time effects (Time and N \times Time effects were also significant at the $P < 0.01$ level).

by preferential colonization of soils with pre-existing differences in N and P. However, we believe this to be highly unlikely because *Eriogonum* effects on soils were reproduced in experimental common gardens, shrubs have colonized soils at random with respect to particle size (Table 1) (Hobbs 1983), and the sampled grassland areas were closely interspersed with shrubs at all sites.

The ability of *Eriogonum* to slow N cycling was likely due to its production of large quantities of low-quality litter. Traits that regulate leaf-litter quality and quantity have long been known to drive species effects on soil N cycling (Melillo et al. 1982, Wedin and Tilman 1990, Hobbie 1996), and appear to be important in our study as well. As compared to grass, *Eriogonum* produces twice the litter, with less than half the amount of N per gram of carbon (Table 1). The low quality of the inputs likely decreases litter decomposition rates, while large inputs of carbon further increase microbial immobilization of N (Hart et al. 1993, Hobbie 1996). These processes are consistent with larger standing pools of litter, lower spring mineralization rates, and lower mineral N pools as *Eriogonum* recolonizes (Table 1, Figs. 2 and 4). Further evidence for the importance of litter in lowering N availability is provided by net immobilization in *Eriogonum* litter-addition plots be-

tween December and March—the same period over which *Avena* litter plots and bare plots were gaining mineral N (Fig. 3). It is also possible that low *Eriogonum* litter quality may have changed insect and microbial decomposer communities thereby exacerbating plant effects on decomposition and N flux rates (Wardle et al. 2004). However, our analyses do not allow us to evaluate this hypothesis.

Why *Artemisia* elevates N availability relative to exotic grasses is less clear. Their C:N ratios are comparable, so differences in foliar litter quality are not likely to be driving *Artemisia* effects on soil N. If *Avena* litter causes net immobilization, then less litter production by *Artemisia* could potentially elevate N. However, litter-addition plots show that *Avena* litter actually increases mineral N pools relative to bare plots (Fig. 3). An alternative mechanism for elevated N in *Artemisia* soils is suggested by the spring pulse in mineralization and mineral N pools underneath the shrub (Figs. 2 and 4). Around this time, when litter traps were not deployed due the near absence of senescing leaves, *Artemisia* drops 18 000 seeds/m², much of which is infertile (Yelenik and Levine 2009). This seed rain has lower C:N ratios (28.22 ± 0.21 [mean \pm SE]; $n = 6$ laboratory replicates) than foliar litter of any species in



PLATE 1. Typical south-facing slope on Santa Cruz Island, California, USA, showing native shrubs that have colonized exotic annual grasslands in the "mixed zone," between stands of pure shrubland (upper left corner of photo) and pure grassland (not shown in photo). Photo credit: S. G. Yelenik.

this study (Table 1), suggesting that this annual input is an important part of the mechanism by which recovering *Artemisia* elevate N availability.

While litter inputs are the most likely explanation for species effects on soil N cycling averaged through the year, plant uptake differences may regulate early season available N pools in the field. We found that the two native shrub species depleted N pools earlier in the growing season than did the annual grass (Figs. 2 and 3). The perennial shrubs can initiate growth and resource drawdown soon after the first rains, while the annual grasses need time for germination and growth. Early grass-seedling mortality can exacerbate these patterns (Eviner and Firestone 2007). The overall importance of plant uptake should be noted as well; monoculture plots that included plants had consistently lower mineral N pools. Low levels of soil N play a large role in plant growth and competition, especially at the height of the growing season (Tilman 1985).

The role of differential plant uptake in explaining these early season differences in N pools is further supported by the fall potential mineralization rates (Fig. 4B). The laboratory incubations remove the direct influence of plant uptake, and as a likely consequence showed no species effects on mineralization. (This may also be due to the overriding effects of soil rewetting on microbial nutrient processing [Schimel et al. 2007].) We

did find stronger species differences in N mineralization rates in spring, and this may reflect the influence of organic matter accumulated over the growing season or longer time scales.

Belowground litter may also contribute to plant effects on nutrient cycling in our system (Silver and Miya 2001, Eviner 2004). Although we did not quantify belowground litterfall, species differences in aboveground biomass and C:N ratios are mirrored in belowground material, as assessed from greenhouse-raised plants (S. Yelenik, *unpublished data*). Thus, although we cannot determine the degree to which aboveground vs. belowground litter drives ecosystem change, we are confident that plant litter differences play a significant role in species effects on nutrient cycling in this system.

Finally, changes in soil microfaunal or microbial communities could contribute to plant species effects on soil nutrients (Belnap and Phillips 2001, Kourtev et al. 2002, Wardle et al. 2004). Although our study did not quantify such changes, other California work has suggested that exotic grasses alter N cycling rates (relative to native perennial grasses) via effects on soil nitrifier communities (Hawkes et al. 2005). In addition, the native shrubs of our system are mycorrhizal (Koske and Halvorson 1989), which can lead to higher N uptake

rates (Ames et al. 1983) and allow shrubs to acquire N earlier in the season than exotic grasses (Figs. 2 and 3).

Artemisia colonization also increased phosphorus availability (Fig. 5). This effect is not likely litter related because *Artemisia* had less litterfall with lower phosphorus content than the exotic grasses (Table 1). While it is possible that *Artemisia* takes up less soil P, this is unlikely because *Artemisia* was the only species to show P limitation (Fig. 6C). In fact, its higher P demand may lead to phosphatase production by roots and microbes, which can elevate available P pools in soils (McGill and Cole 1981).

Our finding that different shrub species can have opposing effects on nutrient cycling in exotic grasslands is consistent with studies of individual shrub species. Many of these studies have focused on N-fixing invasive woody plants and found, not surprisingly, that shrubs increase soil N cycling rates (Vitousek and Walker 1989, Maron and Jefferies 1999, Yelenik et al. 2004). Encroachment by non-N-fixing shrubs, on the other hand, leads to either higher or lower rates of nutrient cycling, depending on the species. For example, soils in remnant stands of *Artemisia tridentata* in the Great Basin (USA) have lower available N and N mineralization rates than soils invaded by cheatgrass, *Bromus tectorum* (Booth et al. 2003a, Saetre and Stark 2005). In contrast, *Artemisia rothrockii* increases net N mineralization rates as it colonizes montane meadows in the Sierra Nevada (Darrouzet-Nardi et al. 2008). The Santa Cruz Island system, then, is a unique example of the possible bi-directional nature of ecosystem change with reestablishing woody species in a single vegetation type.

Feedbacks to recovery

When plant species change soil processes, which in turn influence plant performance, the resulting plant–soil feedbacks can influence community dynamics (Bever et al. 1997, Reynolds et al. 2003, van der Putten 2003, Eppstein and Molofsky 2007). Although numerous studies have documented species effects on nutrient cycling (Hobbie 1996, Wardle et al. 1998, Ehrenfeld 2003, Eviner et al. 2006), whether these changes feed back to influence community dynamics can be more difficult to evaluate. This difficulty arises because one needs to know how all community members respond to the altered soil conditions. Thus, the relatively simple community of three dominant species in the mixed zone on Santa Cruz Island provides an ideal system to explore potential feedbacks.

We found that the shrubs and grass were differentially limited by N and P. Neither shrub was significantly limited by N, while *Avena*, the dominant grass was strongly N limited, more than doubling biomass with N fertilization. Thus, as *Eriogonum* colonization depresses N availability, it disfavors its exotic grass competitor more than itself. Such plant–soil feedbacks should enhance *Eriogonum* recovery by limiting grass competi-

tion, an important constraint on native shrub seedling establishment in this system (Yelenik and Levine 2009).

In contrast to *Eriogonum*, *Artemisia* increases available N, a resource limiting its competitor, *Avena*, more than itself. Thus *Artemisia* effects on N should slow its recovery by favoring the growth of its exotic grass competitor. However, *Artemisia* also increases P availability, and may thereby change the effect of altered N on its recovery. With P addition, *Artemisia* becomes N limited (Fig. 6C), and thus *Artemisia* effects on soil N and P may collectively have little effect on its competitive balance with grasses. In sum, the native-shrub effects on soils may not only influence ecosystem processes, but also regulate their recovery.

One limitation when inferring feedbacks from our fertilization study is that our experimental fertilizer levels were meant to detect N and P limitation, not replicate the changes in soil nutrient pools and fluxes due to species-identity differences. In addition, we acknowledge that other factors, such as competition for light or water, or shifts in soil communities, may also affect the recovery of native shrubs into this exotic grassland (van der Putten et al. 1993, Wardle et al. 2004). Still, our work suggests that the current plant–soil feedback framework (Bever et al. 1997) provides a promising tool for asking how the impacts of invasion on soil nutrients alter the recovery process.

Restoration implications

Although native recovery in our system occurred naturally following the removal of exotic grazers from the island, our results suggest management actions that might accelerate the return of ecosystem processes more generally. Managers seeking to alter nutrient cycling via plant effects could target species that grow quickly, have high litterfall rates, and litter quality that is significantly different from dominant alien species. All of these factors were responsible for our finding that *Eriogonum* could change nutrient cycling over short time scales—within four years. Indeed, to answer the management question posed by our title, shrub reestablishment in this island ecosystem is significantly changing ecosystem processes. However, depending on the shrub species, the changes in nutrient cycling may hinder or aid shrub reestablishment.

Because *Artemisia* and *Eriogonum* are the dominant natives recovering in the annual grasslands of Santa Cruz Island, and each has opposing effects on N availability, native recovery will increase the spatial heterogeneity of resource availability across the landscape. Spatial patterning of soil resources can influence faunal and microbial communities, create litter-decomposition hotspots, and ultimately alter plant composition (Schlesinger et al. 1990, Ettema and Wardle 2002). Indeed, soil heterogeneity at this scale has large implications for plant community dynamics, and may enhance species diversity by increasing niche opportunities (Chesson and Warner 1981, Pacala and Tilman

1994). Our work is also an important reminder to managers that exotic-species effects on soils are best viewed relative to various native species. A pervasive idea in restoration ecology is that exotic plants increase soil N cycling. But our study illustrates that this is not always the case, even within a single ecosystem.

In conclusion, our work shows that understanding the mechanisms underlying ecosystem change is important for predicting the effects of native recovery on ecosystem properties, and potential feedbacks to plant community dynamics. Better understanding these effects is increasingly necessary as we aim to restore both structure and function to landscapes degraded by exotic species.

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