

RESEARCH ARTICLE

# Strengthening Invasion Filters to Reassemble Native Plant Communities: Soil Resources and Phenological Overlap

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## Abstract

Preventing invasion by exotic species is one of the key goals of restoration, and community assembly theory provides testable predictions about native community attributes that will best resist invasion. For instance, resource availability and biotic interactions may represent “filters” that limit the success of potential invaders. Communities are predicted to resist invasion when they contain native species that are functionally similar to potential invaders; where phenology may be a key functional trait. Nutrient reduction is another common strategy for reducing invasion following native species restoration, because soil nitrogen (N) enrichment often facilitates invasion. Here, we focus on restoring the herbaceous community associated with coastal sage scrub vegetation in Southern California; these communities are often highly invaded, especially by exotic annual grasses that are notoriously challenging for

restoration. We created experimental plant communities composed of the same 20 native species, but manipulated functional group abundance (according to growth form, phenology, and N-fixation capacity) and soil N availability. We fertilized to increase N, and added carbon to reduce N via microbial N immobilization. We found that N reduction decreased exotic cover, and the most successful seed mix for reducing exotic abundance varied depending on the invader functional type. For instance, exotic annual grasses were least abundant when the native community was dominated by early active forbs, which matched the phenology of the exotic annual grasses. Our findings show that nutrient availability and the timing of biotic interactions are key filters that can be manipulated in restoration to prevent invasion and maximize native species recovery.

**Key words:** carbon addition, community assembly, functional traits, limiting similarity, nitrogen, phenology

## Introduction

Ecologists have long been fascinated by invasions as natural experiments in community assembly (e.g. Elton 1958). The process by which species enter a community from a regional species pool is frequently visualized as a series of “filters” which are determined by environmental variables, properties of the native community, and attributes of the invader (Diaz et al. 1998; Weiher & Keddy 1999). Ecological restoration provides the opportunity to test this framework, whereby the restoration practitioner can manipulate these filters to reassemble the desired native community and prevent invasion by exotic species (Funk et al. 2008).

Here we focus on restoration of the diverse herbaceous community associated with Southern California coastal sage scrub (CSS). This semiarid shrub community, characterized

by drought-deciduous shrubs and diverse herbaceous annuals, has been greatly impacted by habitat loss (Westman 1981), increased fire frequency (Keeley et al. 2005), and nitrogen (N) deposition (Cione et al. 2002). Further, this community is highly invaded by exotic annual grasses of European origin which have been resistant to prior restoration efforts (Cox & Allen 2008). Thus, manipulation of both environmental and biotic filters may be important in designing effective strategies to prevent invasion into restored CSS communities.

Soil N availability may be one of the most critical environmental filters because N enrichment, via disturbance or anthropogenic input, is thought to promote invasion (Davis et al. 2000). Experiments frequently find that N enrichment favors exotic species over native species performance (reviewed in Daehler 2003). Restoration efforts thus frequently aim to reduce N availability and favor native species establishment (James et al. 2010). For instance, carbon (C) amendments such as sucrose or sawdust generally lower soil N availability by promoting immobilization in the microbial biomass (Zink & Allen 1998; Blumenthal et al. 2003; reviewed by Perry et al. 2010). These techniques have mixed success in shifting the competitive balance between native and exotic species (James

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et al. 2010), however, suggesting that additional factors may influence the effectiveness of C amendments in restoration.

The influence of soil N on invasion may vary depending on biotic interactions between invaders and the native community. Experimentally manipulated communities with high species richness are frequently found to more completely utilize resources (e.g. reviewed in Cardinale et al. 2011) and have low rates of invasion (although there are many exceptions, reviewed in Fridley et al. 2007). This can occur because diverse assemblages exhibit complementarity in resource use and are more likely to contain species that draw down resources and prevent invasion (reviewed in Hooper et al. 2005). In particular, the concept of limiting similarity (Abrams 1983) predicts that exotic species will be less likely to establish in communities where ecologically similar native species are already present because of more intense resource competition (Elton 1958). Some experimental tests have found species are less likely to invade when members of the same functional group are present in the native community (Fargione et al. 2003; Pokorny et al. 2005; Hooper & Dukes 2010; Petermann et al. 2010), but this is not always the case (Emery 2007). This variation may be driven by phenological variation within functional groups, that is, the time during the growing season when species are active.

Phenology may play a key role in determining the outcome of biotic interactions between native and exotic species (Marushia et al. 2010; Wolkovich & Cleland 2011). For instance, annual species that germinate from seed each year are more likely to have early phenology than perennial species (Reynolds et al. 2001). Early active species such as annuals may be successful at preempting resources (Verdú & Traveset 2005) and thus benefit from a “seasonal priority effect” (Wainwright et al. 2012). An annual life history is more common among exotic species than in the native flora of many regions (Pyšek & Richardson 2007), which may allow many exotic species to benefit from seasonal priority effects. While established native perennials can resist invasion by exotic annual species (Seabloom et al. 2003), temporal matching of native species with potential invaders could be important for successful restoration of recently disturbed systems where perennials have not yet established (Grman & Suding 2010; James et al. 2010; Marushia et al. 2010; Wainwright et al. 2012). Nutrient availability can alter phenology directly (Cleland et al. 2006), and hence could have indirect influences on the strength of limiting similarity by altering the temporal dynamics of species interactions.

Interestingly, while much research has focused on the separate roles of environmental filters and biotic interactions in preventing invasion by exotic species, few studies have evaluated their joint role. Here we investigated whether the strength of biotic interactions between native and exotic species varies depending on soil N availability or species phenology by testing the following hypotheses: (1) exotic species will be least abundant when soil N availability is low, (2) native species will prevent invasion by functionally similar exotic species, and (3) timing plays a key role in the strength of biotic interactions, such that native species would be most

likely to prevent invasion by exotic species that are active during the same time period, maximizing competition for resources. To test these hypotheses, we created experimentally restored communities varying native species composition and soil nutrient availability along a highly invaded roadside. We monitored species phenology and growth, and measured exotic species abundance as an index of restoration success.

## Methods

### Study Site

This study was conducted on a roadside edge of the Laguna Coast Wilderness Park, in Southern coastal California (33°34'.05°N 117°45'.50°W, at an elevation of 48 m.a.s.l.). The experimental area was initially dominated by non-native species including annual grasses such as *Bromus diandrus* (rip-gut brome) and *Avena fatua* (wild oat), and forbs such as *Raphanus sativus* (wild radish) and *Brassica nigra* (black mustard). The road, CA-Hwy 133, is a busy two-lane road with an Annual Average Daily Traffic of 35,000 vehicles per day in 2010 (<http://traffic-counts.dot.ca.gov>), likely contributing significant N deposition to roadside vegetation.

### Experimental Design

In November 2004, the experimental site was prepared by first removing the existing non-native vegetation. The resident seed bank was reduced by allowing germination to occur, mowing, and finally applying an herbicide 2 weeks before experimental treatments began. In January 2005, we employed a randomized block design to seed 1 × 1.5 m plots with a combination of seed mixtures and N treatments (described in detail below). Eight blocks were arranged in parallel along the road such that block identity statistically accounted for plot distance from the road edge.

Species composition was manipulated by sowing seed mixes with varying proportions of 20 native focal species (Table 1). Six mixes were planted with 10 g seeds/m<sup>2</sup> per plot. The first mix had the highest functional diversity—an equal representation of all 20 species. Five additional mixes had decreasing functional diversity through increasing dominance by species of a particular life form: annual grasses, perennial grasses, early season forbs, late season forbs, and N-fixing annual forbs. These latter five seed mixes contained 75% seed mass of species of the dominant life form, and 25% seed mass from the remaining 16 species. In the first 2 months after seeding, plots were weeded to remove non-target species.

N availability was manipulated by (1) adding N to mimic anthropogenic N deposition (9 g N/m<sup>2</sup> per year as calcium nitrate) and (2) reducing N (428 g C/m<sup>2</sup> per year added as sucrose to induce N immobilization by soil microbes). This level of sucrose addition was chosen because a previous study found that between 333 and 529 g C was sufficient to lower soil nitrate availability (Blumenthal et al. 2003). Amendments were divided into three applications, in February, March, and April of each year. The sugar and N were applied to plots

**Table 1.** Target native species planted in experimental restoration plots, those that were seeded in only 1 year are indicated.

Functional Group	Scientific Name	Common Name
Annual grass	<i>Aristida adscensionis</i>	Six-weeks three-awn
	<i>Hordeum jubatum</i> (2005)	Foxtail barley
	<i>Muhlenbergia microsperma</i>	Littleseeded muhly
	<i>Vulpia microstachys</i>	Small fescue
	<i>Vulpia octaflora</i> (2006)	Six-weeks fescue
Perennial grass	<i>Bromus carinatus</i>	California brome
	<i>Nassella lepida</i>	Foothill needlegrass
	<i>Nassella pulchra</i>	Purple needlegrass
	<i>Poa secunda</i>	Pine bluegrass
Early forb	<i>Clarkia purpurea</i> (2006)	Winecup fairyfan
	<i>californica</i>	California poppy
	<i>Lasthenia californica</i>	Dwarf goldfields
	<i>Phacelia cicutaria</i> (2005)	Caterpillar phacelia
	<i>Sisyrinchium bellum</i> *	Blue-eyed grass
Late forb	<i>Eremocarpus setigerus</i>	Dove weed
	<i>Hemizonia fasciculata</i>	Fascicled tarweed
	<i>Heterotheca grandiflora</i>	Telegraph weed
	<i>Eriophyllum confertiflorum</i> *	Golden yarrow
Leguminous forb	<i>Lotus purshianus</i>	Spanish clover
	<i>Lupinus bicolor</i>	Miniature lupine
	<i>Lupinus succulentus</i>	Arroyo lupine
	<i>Trifolium tridentatum</i>	Tomcat clover

All forbs are annual except for the two perennial species indicated by \*.

immediately prior to rain events so they quickly dissolved and avoided unintended effects such as the attraction of ants.

The 6 seed mixes were planted in 8 replicate blocks, at the 3 levels of N availability, for a total of 144 plots. Two blocks were mistakenly mowed in the second year of the experiment during a fire reduction program, leaving six replicates of each treatment for some measures. In the second year of experimental restoration, the same experimental treatments were applied with two exceptions. Due to poor germination, two native species were replaced (Table 1). Seeds were added again in the second year to maintain the experimental manipulations because it was felt that there was not yet sufficient seed production of the focal native species. In addition, no weeding took place in the second year to allow natural invasion to occur.

#### Soil N Availability

To test if plots closer to the road had higher rates of N deposition from car exhaust, N availability was measured prior to experimental treatments in each plot using a potassium chloride extraction of fresh soil (Bremner 1996). Plant-available N in soil during the growing season was measured using ion exchange resins in each plot (Binkley & Hart 1989), installed in January and removed in April each year. We also measured the pool of N held in the microbial biomass to test our hypothesis that soil C addition would cause soil microbes to take up N, thus lowering N available for plant growth (Blumenthal et al.

2003). Microbial biomass was measured with the chloroform fumigation and extraction procedure (Brookes et al. 1985) at the time of peak early season plant production, only in the even seed mix plots. Organic N was subsequently reduced to inorganic N in both fumigated and unfumigated soil extracts with a persulfate digest, and total N held in the microbial biomass was calculated as the difference between the two extracts.

#### Functional Group Classifications

Native and exotic species were classified into functional groups according to their life form (grass or forb, there was no woody vegetation), life span (annual or perennial, with biennial species classified as perennial), phenology (early or late, see next section), and N-fixation capacity (identified taxonomically, in our case all were members of the Fabaceae). These classifications were based on the Jepson Manual, the standard flora for California (Hickman 1996).

#### Timing of Growth and Development in the Field

In order to determine whether native and exotic species at our site had overlapping seasonality, we surveyed the even seed mix plots on seven dates during 2006 (10 and 23 February, 9 and 23 March, 11 and 25 April, and 25 May), and recorded the mean growth stage of each species (pre-flowering, flowering, fruiting, senesced). These observations were used to confirm our classifications of native forbs as having early or late phenology, and to classify the phenology of exotic species that recruited into the plots.

#### Measuring Restoration Success

In April and June of each year, all biomass in a 0.3 m<sup>2</sup> area was harvested, sorted by origin (native or exotic), and dried to constant weight. In May of the second year each 1 × 1.5 m<sup>2</sup> plot was surveyed for percent cover, and the relative cover by exotic species was used as an integrated measure to evaluate how the treatments influenced exotic species relative to native species.

#### Statistical Analyses

All statistical analyses were performed using SAS v. 9.2 (SAS-Institute 2008). We used regression analysis to examine how pre-treatment soil N availability varied with distance from the road and used AIC scores to determine the best form, that is, linear and quadratic, of the functional relationship. We used a general linear mixed model analysis to test whether native and exotic species differed in their seasonality (survey date of peak flowering) by including species as a random factor nested within origin (a fixed factor with two levels—native or exotic), and also included soil amendment as a fixed factor with three levels (seed mix was not included in this analysis because seasonality was only monitored in the even seed mix plots). The effect of seed mix and soil amendment treatments on soil nutrients and exotic cover were evaluated simultaneously using a two factor mixed effects linear model, with six levels

of seed mix and three levels of soil amendments. Biomass harvests were analyzed in a four factor repeated measures mixed model where seed mix and soil amendment were fixed effects, origin was treated as a split-plot effect, and harvest was a fixed effect repeatedly measured in each plot. For all datasets measured over more than 1 year the analysis was conducted separately for each year. Significant differences of least squared means (DLSMs) were as assessed using post-hoc tests for significant factors with more than two levels, and for significant interactions. We considered statistical significance at the level of  $p < 0.05$ .

## Results

### Roadside Edges are Highly Invaded and N Enriched

Of the 30 exotic species that naturally recruited into our plots (Table S1, Supporting Information), 20 are listed on the California Invasive Plant Council's Invasive Plant Inventory (<http://www.cal-ipc.org/ip/inventory/weedlist.php>), including all of the exotic annual grasses that made up the majority of the exotic biomass at our site.

Pre-experiment measures show that soils 6 m from the road edge had three times higher extractable N concentrations than soils 30 m from the road (Figure S1, Supporting Information). The best model fit involved a quadratic term indicating that these edge effects decline quickly towards the interior of the preserve.

### Soil C Addition Decreases N Availability via Microbial Immobilization

Plant N availability was significantly influenced by the soil amendments in both years (Fig. 1a, 2005:  $p < 0.0001$ ,  $F_{[5,101]} = 17.4$ ; 2006:  $p < 0.0001$ ,  $F_{[2,126]} = 44.5$ ). Examination of the DLSMs showed that N availability was approximately doubled by N addition (2005:  $p = 0.0004$ ,  $t = 3.7$ ; 2006:  $p < 0.0001$ ,  $t = 6.6$ ), and C addition lowered N availability by approximately one-third (2005:  $p = 0.02$ ,  $t = 2.4$ ; 2006:  $p = 0.02$ ,  $t = 2.4$ ). Soil available N did not vary with seed mix (2005:  $p = 0.34$ ,  $F_{[5,101]} = 0.5$ ; 2006:  $p = 0.9$ ,  $F_{[5,126]} = 0.33$ ). Denominator degrees of freedom (df) vary between years because of a number of broken resin bags in the first year.

Soil amendment significantly influenced microbial N pools only in the second year (2005:  $p = 0.32$ ,  $F_{[2,18]} = 1.2$ ; 2006:  $p = 0.04$ ,  $F_{[2,21]} = 3.7$ ). In 2006, C addition increased the N content of microbial biomass as compared to controls (Fig. 1b), indicated by significant DLSMs ( $p = 0.01$ ,  $t = 2.7$ ). Denominator df vary between the 2 years because of three lost soil samples in 2005.

### Native and Exotic Species Have Differing Seasonality

The species present in these roadside communities varied remarkably in their seasonality (Species  $p < 0.0001$ ,  $F_{[31,166]} = 22.6$ , Fig. 2), and exotic species flowered earlier

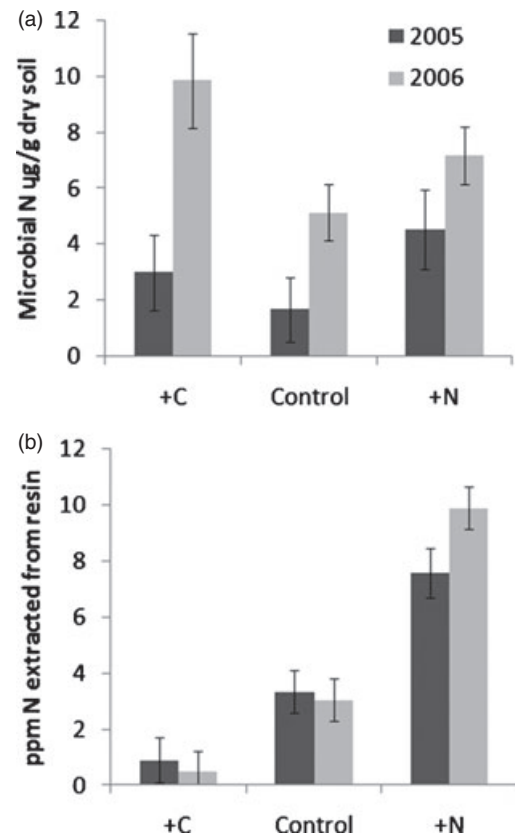


Figure 1. Mean soil microbial N (a) and plant available N (b) across plots with C addition (+C), N addition (+N), or controls. Means are averaged across seed mixes and error bars reflect 1 SEM.

in the growing season than did native species (Origin  $p < 0.0001$ ,  $F_{[1,166]} = 20.6$ ). No exotic species reached an average stage of fruiting or senescence until the final survey of the season, and only two native species (*Aristida adscensionis* and *Escholzia californica*) were found fruiting or senescing before the date of the final survey. The soil amendment treatments had no significant effect on flowering time ( $p = 0.12$ ,  $F_{[2,166]} = 2.1$ ).

### Timing and Growth Responses of Native and Exotic Species

Differences in seasonality between native and exotic species were evident in the patterns of resource capture in aboveground biomass; in both years there was a significant origin  $\times$  harvest interaction (Fig. 3, see Table 2 for  $F$  and  $p$  statistics). In the first year, when most exotic biomass was weeded out of experimental plots, the late harvest had greater biomass driven by the native species seasonality. In the second year when exotic species were allowed to invade there was higher biomass in the early harvest, driven by the early phenology of the exotic species.

Exotic biomass accumulation was also more sensitive to N availability; soil amendments did not have any impact in 2005 when native species dominated the biomass. In 2006, exotic species dominated the biomass and drove the response to soil



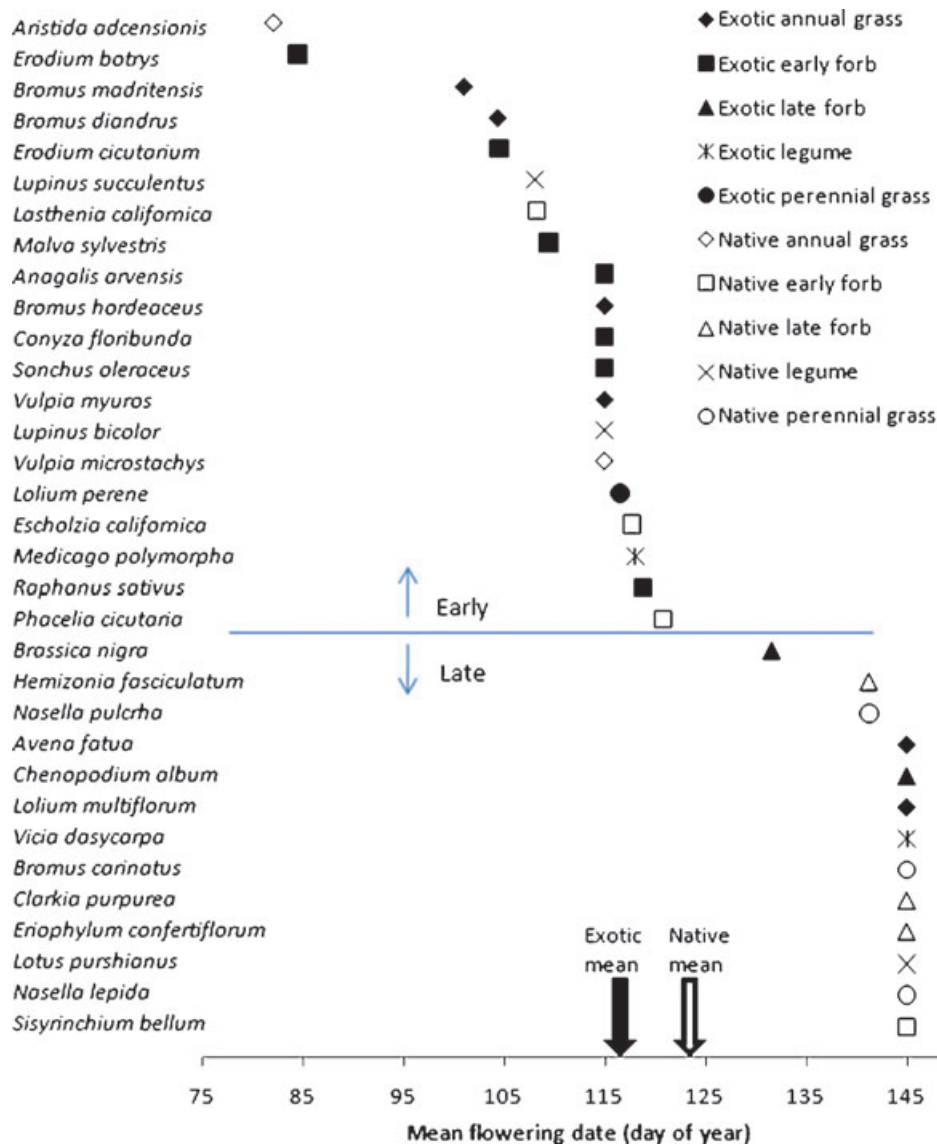


Figure 2. Mean flowering date of native and exotic species in the even seed mix plots, averaged across soil amendment treatments, which did not influence the means. Each data point represents the mean for a species, with the scientific name to the left. The early versus late season designation reflects a visual breakpoint.

amendments (significant soil amendment  $\times$  origin interaction); exotic biomass strongly increased with N addition (DLSM:  $p < 0.0001$ ,  $t = 4.9$ ) and decreased with C addition (DLSM:  $p < 0.0001$ ,  $t = 4.0$ ), compared with controls.

A soil amendment  $\times$  harvest interaction in the second year revealed stronger influences of soil amendment treatments during the early part of the growing season, suggesting that phenology can influence the degree of N limitation and competition for limiting nutrients. Also in the second year there was a significant seed mix  $\times$  origin interaction indicating that seed mixes varied in their resistance to invasion. We chose to explore this interaction in depth with the percent cover dataset (next section) because the results were similar to those

seen with biomass, and percent cover was collected on a larger spatial scale relevant for restoration.

**Measuring Restoration Success: Percent Cover and Richness of Exotic Species**

Cover of exotic species was significantly influenced by the soil amendments (Fig. 4, F and p statistics shown in Table 3). Plots that received C additions had lower cover by exotic species than control plots (DLSM:  $p < 0.0001$ ,  $t = 5.4$ ), and plots that received additional N had significantly greater cover by exotic species ( $p = 0.017$ ,  $t = 2.44$ ). Overall relative exotic cover was also influenced by seed mix, and there was no interaction with soil amendment treatment. Overall the plots

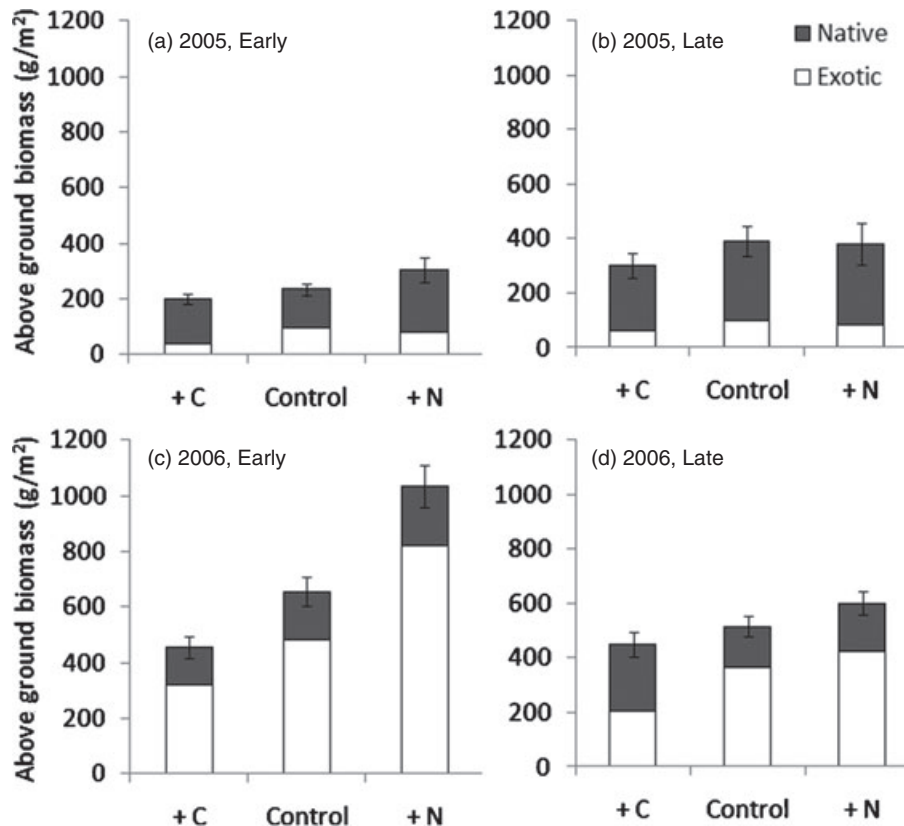


Figure 3. Aboveground biomass harvested over 2 years at two times during the growing season, early (a and b) or late (c and d). Error bars indicate 1 SE of the total mean biomass.

**Table 2.** Analysis of variance table summarizing how biomass in 2005 and 2006 was influenced by soil amendment, seed mix, origin (native or exotic), and harvest date (early or late in the growing season).

	2005	2006
Soil amendment	$F_{[2,126]} = 1.47, p = 0.23$	$F_{[2,126]} = 20.6, p < 0.0001$
Seed mix	$F_{[5,126]} = 0.66, p = 0.65$	$F_{[5,126]} = 1.9, p = 0.10$
Origin	$F_{[1,297]} = 45.2, p < 0.0001$	$F_{[1,292]} = 116.3, p < 0.0001$
Harvest	$F_{[1,297]} = 6.42, p = 0.012$	$F_{[1,292]} = 16.1, p < 0.0001$
Seed mix $\times$ amendment	$F_{[10,126]} = 0.63, p = 0.78$	$F_{[10,126]} = 0.81, p = 0.62$
Origin $\times$ amendment	$F_{[2,297]} = 0.94, p = 0.39$	$F_{[2,292]} = 19.1, p < 0.0001$
Harvest $\times$ amendment	$F_{[2,297]} = 0.30, p = 0.74$	$F_{[2,292]} = 7.0, p = 0.0011$
Origin $\times$ seed mix	$F_{[5,297]} = 0.84, p = 0.52$	$F_{[5,292]} = 4.1, p = 0.0013$
Harvest $\times$ seed mix	$F_{[5,297]} = 0.68, p = 0.64$	$F_{[5,292]} = 2.1, p = 0.072$
Harvest $\times$ origin	$F_{[1,297]} = 4.0, p = 0.047$	$F_{[1,292]} = 22.5, p < 0.0001$
Origin $\times$ seed mix $\times$ amendment	$F_{[10,297]} = 0.34, p = 0.97$	$F_{[10,292]} = 1.7, p = 0.084$
Harvest $\times$ seed mix $\times$ amendment	$F_{[10,297]} = 0.73, p = 0.70$	$F_{[10,292]} = 0.56, p = 0.85$
Harvest $\times$ origin $\times$ amendment	$F_{[2,297]} = 0.36, p = 0.70$	$F_{[2,292]} = 0.36, p = 0.70$
Harvest $\times$ origin $\times$ seed mix	$F_{[5,297]} = 1.8, p = 0.11$	$F_{[5,292]} = 2.7, p = 0.07$
Four-way interaction	$F_{[10,297]} = 0.50, p = 0.89$	$F_{[10,292]} = 0.48, p = 0.90$

Numerator and denominator degrees of freedom for each  $F$ -test are indicated, respectively. Significant effects are highlighted in bold.

receiving the late forb seed mix had the lowest levels of exotic cover, the perennial grass and early forb mixes also had low levels of exotic cover that were not significantly greater than the late forb mix, and all other mixes had significantly greater exotic cover than the late forb mix (Fig. 4). There was significantly higher exotic cover closer to the road and

in the most interior block, where propagule pressure was high from the surrounding invaded area, resulting in a significant block effect (data not shown). Consistent with this, exotic species richness increased slightly in the block closest to the road (Block:  $F_{[5,85]} = 2.6, p = 0.03$ ), but was not otherwise influenced by any factor.

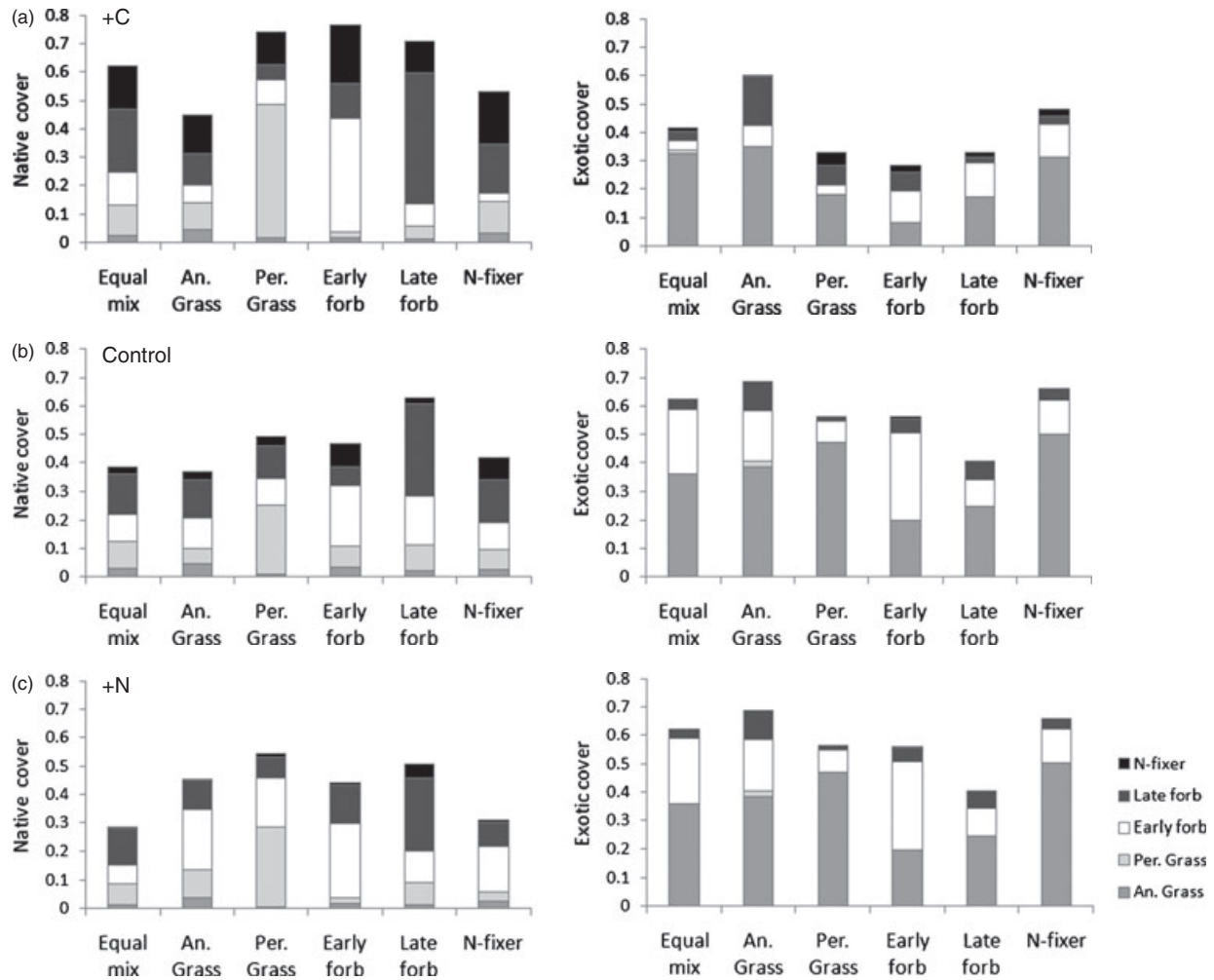


Figure 4. Fractional cover of native and exotic species of differing functional types, arrayed by soil amendment treatment ((a) carbon addition, (b) control, (c) nitrogen addition), the identity of the native seed mix is indicated on the horizontal axis of each inset figure.

The results of the analysis differed somewhat when examining the relative abundance of particular functional groups of exotic species (Fig. 4, Table 3). For instance, exotic early forb cover was not influenced by the identity of the seed mix, and exotic late forb cover was not altered by soil amendment. The identity of the most effective seed mix for lowering exotic cover also differed when the analysis was performed on particular exotic functional groups. Plots receiving the early forb mix best resisted the invasion of exotic annual grasses, all other seed mixes except for the late forb mix had significantly higher cover of exotic annual grasses. The late active exotic forbs had the highest cover in the annual grass and early forb seed mixes, with all other seed mixes having similarly low cover of this functional group.

## Discussion

Our findings demonstrate how soil nutrient availability and biotic interactions can act as environmental filters influencing

the abundance of exotic species. Our results were consistent with past studies showing that nutrient availability exerts an important influence over the abundance of invading species (Daehler 2003). Roadsides are frequently disturbed and may act as conduits for invaders (Gelbard & Belnap 2003), due to a combination of high propagule pressure and N enrichment from car exhaust. C addition was effective at increasing microbial N immobilization and lowering both soil N availability and the abundance of exotic species. Here C was added in the form of sugar which, though effective, is likely to be economically prohibitive in many restoration sites. Easily decomposable C substrates such as rice straw may be a good substitute, although it is not clear they are always as effective (Zink & Allen 1998), and may have additional effects such as allelopathy (Chung et al. 2001), shading and increased soil moisture (Wolkovich et al. 2010).

A signal of biotic interactions was also evident in our results: seed mixes strongly varied in their effectiveness at limiting abundances of different functional types of exotic species. Although increasing evenness among species abundances has

**Table 3.** Analysis of variance table summarizing how block, soil amendment, and seed mix influenced exotic relative cover in the experimental plots in 2006.

	Overall Exotic Cover	Exotic Annual Grasses	Exotic Early Forbs	Exotic Late Forbs
Block	$F_{[5,86]} = 12.1, p < 0.0001$	$F_{[5,86]} = 6.4, p < 0.0001$	$F_{[5,76]} = 2.8, p = 0.02$	$F_{[5,77]} = 3.2, p = 0.01$
Soil amendment	$F_{[2,86]} = 32.2, p < 0.0001$	$F_{[2,86]} = 18.6, p < 0.0001$	$F_{[2,76]} = 6.5, p = 0.002$	$F_{[2,77]} = 2.3, p = 0.10$
Seed mix	$F_{[5,86]} = 5.5, p = 0.0002$	$F_{[5,86]} = 6.2, p < 0.0001$	$F_{[5,76]} = 1.8, p = 0.12$	$F_{[5,77]} = 2.5, p = 0.04$
Mix $\times$ amendment	$F_{[10,86]} = 0.8, p = 0.65$	$F_{[10,86]} = 1.02, p = 0.43$	$F_{[10,76]} = 1.8, p = 0.07$	$F_{[10,77]} = 1.5, p = 0.14$

Separate analyses evaluated exotic cover overall, and cover of three exotic functional groups: annual grasses, early, and late forbs. Numerator and denominator degrees of freedom for each  $F$ -test are indicated, respectively. Significant effects are highlighted in bold.

sometimes decreased invasion (e.g. Smith et al. 2004), we found that there was generally lower exotic abundance in plots dominated by particular native functional groups. Native seed mixes did not differ in productivity or soil nutrient availability, so our results cannot be explained by reduced invasion in more productive mixtures. Nor can the mechanism driving the variation in invasion resistance be attributed to abundance of similar functional types because exotic functional group abundance was never lowest in the seed mix dominated by that same native functional group. However, this may reflect limitations in our functional group categorizations, because the outcome of interactions between native and exotic species was influenced by their temporal patterns of resource-uptake, which could be associated with other unmeasured functional traits (Funk et al. 2008).

Our results suggest that phenology is likely to be a key functional trait predicting the strength of biotic interactions in invasion resistance. We found that exotic species flowered and accumulated biomass earlier in the growing season than native species, suggesting that early active native species may be an important component of successful restoration in Southern California. While annual grasses are problematic invaders in California, they are a rare component of the native flora (D'Antonio et al. 2007), and native and exotic annual grasses differ in a variety of functional traits (Sandel & Dangremond 2011). The lowest abundance of exotic annual grasses in our experiment was found in plots where N availability had been reduced by C addition and the native community was dominated by early active native forbs, the only native functional group that was active during the same time of the season as the exotic annual grasses. These findings are consistent with other studies that have shown phenology to be a key trait predicting competitive exclusion between native and exotic species (Fargione et al. 2003; Hooper & Duker 2010), and suggest that manipulating the native community to match the seasonality of potential invaders could increase invasion resistance of restored communities.

Community assembly theory shows great potential to guide successful restoration (Temperton et al. 2004), especially in developing strategies to favor desirable native species over problematic invaders. Our results show that the common exotic species in this Southern California roadside community were highly sensitive to both nutrient availability and native species community composition, particularly early in the growing season when the exotic species were most active. This combination of nutrient reduction and phenological matching

offers a promising strategy for intensive roadside restoration that could ideally act as a buffer to prevent invasion into the interior of nature reserves at the urban-wildland interface.

### Implications for Practice

- The highest rates of invasion were associated with N enrichment; this association of high N and invasion highlights the need to reduce N inputs at preserve edges from car exhaust, dust, or other sources, in order to prevent further invasion.
- While numerous studies show that seeding with a high diversity native seed mix is desirable, even representation of all species may not achieve the lowest rate of invasion by exotic species. Instead, invasion is likely to be reduced when functionally similar native species are disproportionately introduced in seed mixes. Phenology should be considered when defining species functional classifications.
- Phenology may play important roles in both invasions and in successful restoration. In this system exotic species were active earlier in the growing season than natives. In future efforts, planting or seeding native species to match the seasonality of common exotics may help reduce invasion by exotic species.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Extractable soil N in plots before the start of the experiment, showing higher available N closer to the road.

**Table S1.** List of exotic species that naturally recruited into experimental plots, including their traits, functional group classification used in Figure 4, and their rating according to the California Invasive Plant Council's Invasive Plant Inventory. Note that exotic shrubs were only present as seedlings in our experiment and hence were classified for our analysis as late active forbs, because they did not flower during the period of our observations.