Priority effects, plant-soil feedbacks, and novel climate conditions influence plant community composition in California grasslands

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Abstract

A core challenge in community ecology has been understanding temporal variations in plant communities. This becomes even more challenging with plant communities increasingly exposed to plant invasions and novel environmental conditions. Understanding these changes isn’t only important for conserving and restoring native diversity and controlling noxious invasives but is also important because changes in plant communities can influence multiple ecosystem services. The research presented here focuses on three main grass functional groups of California inland grasslands:

- early-season naturalized exotic annual grasses that dominate most of California’s valley grasslands
- recent noxious invasive annual grasses that are late-season and decrease diversity and rangeland productivity,
- native perennial grasses that are the focus of restoration efforts, and are active throughout the growing season, into the early summer, overlapping with the noxious weeds in late-season phenology.

I assess the roles of plant-soil feedbacks, priority effects, and long-term changes in precipitation in impacting the community dynamics among these three groups using a long-term grassland field experiment in Davis, CA.

In Chapter 1, I investigate the importance of plant-soil feedbacks in California grasslands and whether they mediate interactions between the exotic annual (naturalized and noxious) and native perennial grasses. While short-term greenhouse studies suggest the exotic annual grasses of California grasslands negatively impact native perennial grass growth through PSFs, there is limited knowledge of how these results extend to a more natural setting. I performed a long-term field feedback experiment, assessing multiple soil properties and plant performance variables. I found that both native and exotic grass groups were structured by negative feedbacks, suggesting that soil amelioration may not be necessary for native grassland restoration in California. Feedbacks were only detected by measuring multiple traits (e.g., root biomass, seed production), and was not visible by looking at aboveground biomass alone. While feedbacks were observed in a variable field setting, growing natives in competition with exotics had a far stronger effect on native performance than did the feedback effect.

In Chapter 2, I examined the role of priority effects in determining long-term community composition in a system that experienced high annual variability in weather, including a multi-year drought. The three grass functional groups were planted alone and in mixtures with the other groups, with composition assessed annually over a twelve-year period. I hypothesized that all three groups, when seeded alone and given priority, would have greater cover than when grown in competition, and limit recruitment of another naturally colonizing functional group. I found that priority effects were strong among all three groups in the initial years but were disrupted by the multi-year drought, which reset the communities. Priority effects disappeared between the two exotic annual species groups, but the native perennial grasses were able to continuously exclude the late-season noxious weeds, likely because they share phenology and compete for late-season residual soil moisture.

Finally, in Chapter 3, I investigated how the prevalence of these three grass functional groups differed when exposed to sustained augmented or reduced precipitation, as long-term changes in precipitation can affect interactions between exotic and native species. I found that phenology influenced the exotics’ response to reduced precipitation- the noxious weeds were highly drought sensitive and disappeared while the naturalized exotics increased in abundance.

The impact of drought on natives, however, depended on the initial vegetation community, increasing in noxious weed communities yet decreasing in their own communities. The experiment didn’t successfully achieve an increased rainfall treatment, since the treatment added water to ambient precipitation, and ambient conditions were so dry, that water augmentation still largely led to below-average precipitation. I also assessed the existence of edge effects as potential reservoirs for future invasion by comparing the cover of each grass functional group between the edges and core of plots they were planted in or recruited into. The cover of the natives and the noxious weeds were identical between the core and edges, but the naturalized exotics were generally higher in the plots’ core than edges. This indicates that edges do not serve as a reservoir for future invasion into the plot core.

Introduction

Many ecosystems are facing novel species interactions due to plant invasions and new climatic extremes. Understanding drivers of plant community composition is particularly important when noxious weed control and/or native species restoration are management priorities, and is especially challenging in annual-dominated systems where composition can reset each year (Heady 1958, Hobbs and Mooney 1995). The concepts of functional groups and priority effects may improve our understanding of vegetation change. Priority effects are defined as when the timing and order of species arrival during assembly determines which species can later enter the community, leading to alternative stable states, alternative transient states, or compositional cycles (Fukami 2015). Priority effects can occur through niche modification or pre-emption and play crucial roles in native-exotic plant interactions. In this dissertation, I investigate the role of priority effects and novel climatic conditions in modifying plant composition in California's inland grasslands using a long-term field experiment in Davis, CA.

California's grasslands allow me to examine questions on community assembly while also addressing key management concerns. California's grasslands have been dominated by annual grasses and forbs from Eurasia that arrived over 250 years, which are now so prevalent they are considered naturalized. Native perennial grasses exist in remnant populations, more prominent in coastal grasslands but less so in interior grasslands, and so are the focus of widespread restoration efforts. Even though dominated by exotic species, these grasslands are still considered a global hotspot of diversity and habitat to 90% of the state's threatened and endangered species, as well as provide crucial ecosystem services such as 75% of the state's livestock forage, carbon sequestration, and water filtration (Eviner 2016). A new set of noxious weeds, however, are currently invading California's grasslands. Medusahead (*Elymus caput-*

medusae) and goatgrass (*Aegilops trichiasis*) cause widespread ecological and economical harm by forming monocultures that reduce diversity, degrade wildlife habitat, and are of low forage quality (Davy et al. 2008, Kyser et al. 2014, Eviner 2016). Control of these noxious weeds is thus a high priority in California grassland management.

These three grass groups are the focus of my dissertation. Importantly, their differences in phenology impact their competitive dynamics. The naturalized exotic annuals outcompete native grass and forb seedlings, as they germinate and grow faster, depleting shallow soil moisture and creating light-limitation (Holmes and Rice 1996, Dyer and Rice 1999, Hamilton et al. 1999, Deering and Young 2006, Grman and Suding 2010). While the noxious weeds germinate at the same time as the earlier exotics, their above-ground growth is concentrated above-ground growth after rains have ended and the naturalized grasses have senesced (Peters et al. 1996, Enloe et al. 2004, Stannard et al. 2010). Thus, in dry years there may not be enough residual soil moisture for their growth (Hironaka 1961) but in wet years the noxious weeds will lack competition from the senesced exotics for any late-season residual moisture (Davy et al. 2015). Native perennial grasses, however, are active during the late-season and so share phenology with the noxious weeds and can compete for the residual soil moisture.

Chapters 1 and 2 both explore priority effects among native perennial grasses and the early and late-season exotic annuals in California's grasslands. Chapter 1 specifically focuses on the mechanism of niche modification. I explore the importance of plant soil-feedbacks (PSFs) and whether they mediate interactions between the native perennial and exotic annual grasses. PSFs occur when a plant species changes soil chemical, physical, or biological properties in such a way that impacts either their growth or the growth of other species, thus impacting the trajectory of the community (Ehrenfeld et al. 2005). While short-term greenhouse studies suggest that exotic annual grasses negatively impact native perennial grass growth through changes to the nitrogen cycle and soil microbial community (Grman and Suding 2010, Larios and Suding 2015), it is unclear how these results extend to a more natural setting. I hypothesized that either both species groups perform best on their own soil, indicating that PSFs play a role in maintaining the exotic invasion and preventing native restoration (Ehrenfeld 2003, Suding et al. 2013) or that both will be structured by negative plant-soil feedbacks, which are common in plant communities and help maintain diversity by decreasing dominance (Klironomos 2002, Crawford et al. 2019).

Chapter 2 examines the role of general priority effects in determining long-term community composition under multiple extreme climatic events. Generally, when two species share a resource niche and have similar competitive strength, the earlier arriving species dominates resource use and fills the niche to the exclusion of later arrivals (Fukami 2015, Fukami et al. 2016). In this chapter I compared composition among communities planted in field plots with the native perennial grasses, the early-season naturalized exotic annuals, the late-season noxious weeds, and mixtures of the species groups. I followed the plant communities for 12 years. I hypothesized that all three groups, when seeded alone and given priority, would have greater cover than when grown in competition, and limit recruitment of another naturally colonizing functional group. I predicted that the multi-year drought would weaken priority effects during and beyond the drought in favor of the early-season naturalized exotics, as they have will have first access to soil moisture.

Chapter 3 also focuses on climatic change and investigates how these same functional groups respond to sustained precipitation reduction and augmentation. Novel precipitation regimes can impact the competitiveness of an invader against native species (Carboni et al. 2018) and soil moisture mediates the competitive dynamics of the native perennials and early- and late-season exotics. I hypothesized that the reduction in precipitation would benefit the early-season naturalized exotics over the later-season native perennials and noxious weeds. Additionally, plant communities are often patchy and may be vulnerable to invasion when exotic species are highly prevalent along patch edges. Thus, this chapter also has a spatial component and examines the role of plot edges in serving as a reservoir for future invasion into the more competitive core as well as whether these edge effects are mediated by the sustained precipitation treatments.

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Chapter 1: Plant-soil feedbacks and their role in California grassland restoration: a long-term, field-based study

ABSTRACT

Plant-soil feedbacks (PSFs) occur when a plant changes soil properties that then directly affect plant growth, influencing community assemblage. Often, plant species experience negative feedbacks (perform worse in their own soil) due to pathogen build up, which allows for species diversity. However, invasive plants often produce positive feedbacks that hurt native species. In California grasslands, Eurasian grasses are known to alter nitrogen cycling, deep soil organic matter, and microbial community composition. Short-term greenhouse studies suggest these changes negatively affect native grasses. We investigate the significance of PSFs in California grasslands in a more realistic long-term field setting as well as their relative importance in relation to competition. From a larger grassland experiment in Davis, CA, 90-cm deep soil cores were taken from 16 plots dominated by either exotic or native grasses for 10 years to compare soil properties. Denuded plots were divided into subplots, seeded with either native mix, exotic mix, or native + exotic mix. Plant performance variables encompassing all life stages were measured for two growing seasons. Exotic-conditioned soils had lower net mineralization and nitrification rates in the top 15-cm of soil, as well as distinct bacterial and fungal community composition. Native grasses performed better in exotic-conditioned soil in height, cover, and flowering individual count, but only in the native mix, as natives did not establish well in competition with exotics. These results suggest that native performance is not hurt by exotic changes to the soil, but is instead likely governed by pathogen build up, and more importantly, competition.

INTRODUCTION

Understanding the drivers of plant community composition is increasingly critical as many ecosystems face novel species interactions due to invasion and global change. Plant-soil feedbacks (PSFs) can impact plant neighbor interactions and drive legacy effects of former plant communities on current community composition (Ehrenfeld et al. 2005, Van der Putten et al. 2013). Plants can change soil physical, chemical and/or biological properties, which can impact plant growth or fitness, and thus the trajectory of the community (Ehrenfeld et al. 2005). A large body of scholarship demonstrates the existence of PSFs but there are still key gaps in our understanding of how important they are, relative to other drivers of plant community composition, and thus, many have called for investigating the role of PSFs in long-term field settings that incorporate competition at the community level (Van der Putten et al. 2013).

Recent studies demonstrate that plant-soil feedbacks may be dependent on the length of the experiment, and often differ in field settings compared to greenhouse conditions (Callaway et al. 2004, Heinze et al. 2016, Schittko et al. 2016, Forero et al. 2019, Beals et al. 2020). Short conditioning phases (time given for plants to alter the soil) may over-emphasize the role of microbial communities and nitrogen cycling and miss the impacts of longer-term changes to soil organic matter and water holding capacity (Kardol et al. 2013, van der Putten et al. 2016). Similarly, short feedback phases (assessing how changes to soil influence plant performance) can fail to capture the impact of annual variation in environmental conditions (van der Putten et al. 2016) or how feedbacks can develop over time (Casper and Castelli 2007, Hawkes et al. 2013). Further, in variable field environments, it may be important to not only consider surface soil, but also plant impacts on subsurface soil. Similarly, it may be important to go beyond a focus on aboveground biomass as an indicator of feedback, instead assessing multiple traits across multiple life stages (Dudenhöffer et al. 2017, Miller et al. 2019).

There is particular interest in the scientific and management communities in understanding how plant-soil feedbacks may mediate interactions between invasive and native plant species. PSF studies have shown that native plants tend to have negative feedbacks, often through accumulation of pathogens decreasing native plant performance. This negative feedback likely drives plant co-existence and diversity (Klironomos 2002, Bever 2003, Bonanomi et al. 2005, Kulmatiski et al. 2008, Mangan et al. 2010, Chung and Rudgers 2016, Bennett and Klironomos 2019, Crawford et al. 2019). In contrast, invasive plants can shift microbial community composition and physical and chemical properties to benefit themselves (Ehrenfeld 2003, Callaway et al. 2004, Kulmatiski 2018), sometimes to the detriment of native growth (Suding et al. 2013). This suggests that successful restoration of natives into invaded sites may require an initial step of restoration of soil conditions.

Both inter- and intra- specific plant competition influence the overall importance of PSFs in natural communities. Direct competitive interactions among plants are known to interact with (weaken, strengthen) or be additive to plant-soil feedbacks (Callaway et al. 2004, Casper and Castelli 2007, Yelenik and Levine 2011, Shannon et al. 2012, Hawkes et al. 2013, Lekberg et al. 2018). For example, feedbacks impacting a weaker competitor's performance may be overwhelmed by competition from a stronger neighbor (Larios and Suding 2015, Lekberg et al. 2018) or feedbacks negatively impacting a stronger competitor may allow co-existence of the weaker species (Lekberg et al. 2018). By assessing feedbacks on plants growing in a community instead of neighbor-less plant individuals, we can better evaluate their relevance in a natural setting (Kulmatiski et al. 2008).

We use multiple plant performance variables to assess the importance of PSFs in California grasslands with a long-term field experiment using mixed communities composed of native and/or exotic species. These grasslands are heavily invaded with exotic annual grasses and forbs, with the loss of natives occurring more than 300 years ago (Jackson 1985, Bartolome et al. 2007). Exotic-induced changes to soil have been proposed as a limiting factor in native restoration success, with short-term greenhouse studies demonstrating that native perennial grasses perform worse in soil conditioned by exotic annuals (Grman and Suding 2010, Larios and Suding 2015). Exotic annual grass roots concentrate in the top 30 cm of soil while native perennial roots extend over 1 m (Hull and Muller 1977, Holmes and Rice 1996) and so invasion reduces nutrient cycling, soil organic matter and water holding capacity in deeper soils (Koteen et al. 2011, Waitman 2019). The exotic and native grasses have also been found to cultivate different soil food webs (Baty 2012) and microbial communities (Steenwerth et al. 2003, Hawkes et al. 2006), which may have many direct and indirect effects on plant performance (Van Der Heijden et al. 2008). Further, exotic annual seedlings outcompete native grass seedlings for soil moisture and light (Holmes and Rice 1996, Dyer and Rice 1999) and so exotic vs native competition needs to be included to properly address the importance of PSFs in California grasslands.

In this experiment, mixes of native perennial or exotic annual grasses conditioned soil for 11 years before a 2-year feedback phase where the native and exotic mixes were seeded and measured for multiple traits. The native and exotic mixes were seeded alone to test for general feedbacks, as well as together to address the role of competitor identity in the feedback. Both the conditioning and feedback phases of the experiment experienced extreme variability in precipitation. As with most PSF experiments, our experimental design focuses on the net feedback effect of all plant-induced changes to the soil, and we can only make inferences about which mechanisms may drive these feedbacks.

We hypothesize that 1) the exotic and native grasses differ in their effects on the physical and chemical properties of the soil and cultivate distinct microbial communities. We expect these differences to be particularly strong in the sub-surface soil, where native roots are abundant, and exotic roots are sparse. We also hypothesize that 2) the soil changes will lead to feedbacks in plant performance, and whether the feedback is positive or negative will vary across life stages. 2a) One possible outcome could be that both species groups perform best on their own soil, mediated by changes in carbon and nitrogen cycling, indicating that feedbacks are playing a role in the exotic invasion (Ehrenfeld 2003, Suding et al. 2013). Alternatively: 2b) despite the chemical changes to soil discussed above, plant performance for both native and exotic species will be dominated by negative plant-soil feedbacks due to the build-up of localized pathogens (Klironomos 2002, Crawford et al. 2019). Further, we hypothesize 3) that competition that occurs from growing the natives and exotics together will eclipse the effects of any feedbacks, as exotic annuals generally outcompete native seedlings (Dyer and Rice 1999).

METHODS

Study site

Plots were located in UC Davis Campbell Tract Experimental Site in Davis, California (38.545751, -121.784780). Prior to plot establishment, the land was used for agricultural purposes and then lay fallow for twenty-two years. The site is composed of two soil types, 75% classified as Reiff series soil (fine sandy loam) with the remaining Brentwood soil series (silty clay loam) (https://casoilresource.lawr.ucdavis.edu/gmap/). The site experiences a Mediterranean climate, with hot, dry summers (mean maximum temperature 33℃, 1991-2020) and wet, cold winters (mean maximum temperature 14℃, 1991-2020). Rainfall has high inter- and intra-annual variability, with mean annual precipitation of 445 mm (1991-2020). During Phase 1, the soil conditioning phase (2008-2018), California experienced a historic drought between the 2012-2015 water years, followed by one of the wettest years on record in 2017. Phase 2, the feedback phase, occurred over 2 years of precipitation extremes--the first with 760 mm and the second with only 262 mm (https://cimis.water.ca.gov/) (Figure S1.1).

Phase 1 was set up in fall of 2007. To minimize the seed bank and resident vegetation at the time of treatment seeding, the soil was disked, irrigation was used to germinate the seedbank, and germinating seedlings were sprayed with herbicide (glyphosate). Irrigation and herbicide treatments were performed twice. Eight hundred and forty 1.5 x 1.5 meter plots were seeded at a rate of 139 g live seeds/plot with one of the following vegetation treatments, in a randomized block design (24 replicates): (1) native perennial grasses and annual forbs commonly used in restoration, (2) naturalized exotic annual grasses and forbs that dominate California grasslands, (3) noxious exotic annual grasses that are causing widespread ecological damage, (4) all possible mixes of these three groups, and (5) monocultures of each species used in the experiment (see Table 1.1 for species list).

For this particular study, a subset of plots was chosen that were either dominated by native perennial grasses or exotic (noxious and naturalized) annual grasses for ten years (Figure S1.2). Eleven native-soil conditioned plots were chosen with the following criteria: originally seeded with only native grasses and for each year from 2013-2017 had greater than 50% native grass cover and a native to total exotic grass (noxious + naturalized) cover ratio of greater than three. After the first year of establishment, the native grass plots maintained similar species composition over time, due to the long-lived nature of these species. Eleven exotic-soil conditioned plots were chosen based on the following criteria: originally seeded with noxious exotic grasses and/or naturalized exotic grasses and during 2013-2017 had at least 60% average exotic grass cover and less than 5% average native cover but no more than 12.5% in any given year. The exotic annual grass plots were consistently dominated by annual exotics over the 11 years of Phase 1, but varied year to year in the dominant species, and the relative proportion of noxious and naturalized exotic annual species.

Phase 1: Conditioning

Measures in the conditioning phase address our first hypothesis, that native vs. exotic grassland communities differ in their effects on soil water holding capacity, soil organic matter, total C and N content, soil nitrogen cycling (net mineralization and nitrification), and microbial community composition (bacteria and fungi). Soil cores were collected in August 2018, after 11 growing seasons of soil conditioning. Soil samples (5 cm diameter core) were taken at four depths (0-15, 15-30, 30-60, 60-90 cm) to capture effects due to differences in rooting depths between the exotic annuals and native perennials. Soil was sieved (2mm) within 36 hours and stored at 4°C from the time of collection until analysis. Time sensitive analysis of N cycling extractions and incubations were performed within 48 hours. Subsamples were stored at -20°C for microbial DNA sequencing for 26 months.

Soil chemical and physical properties

Water holding capacity was measured by saturating soil and determining the % soil moisture the soil retained after draining under gravity for 24 hours at 100% humidity (Jarnell et al. 1999, Romano and Santini 2002). Soil organic matter was determined by combustion in a muffle furnace at 550°C for 4 hours (Sollins et al. 1999). Total carbon and nitrogen content of dried, ground soil was analyzed with an elemental analyzer interfaced with a mass spectrophotometer by the UC Davis Stable Isotope Facility. To grind the soil, air-dried samples were placed in a scintillation vial with grinding bars (Grainger catalog # 5WE59) and then set on a roller mill for four days.

To determine net mineralization and nitrification rates, we measured inorganic N (NH_4^+ and NO_3^-) concentrations in 5g (field wet weight) of fresh soil as well as in 5 g of soil that was incubated for a week in the dark at room temperature. These soils were extracted with 25 mL of 2 M KCl (Bundy and Meisinger 1994, Robertson et al. 1999), shaken on a mechanical shaker for an hour, filtered using pre-leached Whatman No. 1 filter paper, and stored at -20℃ until analysis on the spectrophotometer. From these extracts we quantified nitrate and ammonium concentrations following methods developed by Forster (1995). Soil moisture measures were used to calculate extractable N per gram dry weight of soil. To determine gravimetric soil moisture, within 24 hours of soil sampling, soil was dried at 105°C until reaching constant mass.

Microbial DNA extraction, amplification, and sequencing

DNA was extracted from the 88 soil samples (22 plots at 4 depths) using the Power Soil^{TM} kit (MolBio, Carlsbad, CA). The 16S rRNA (bacteria) and ITS2 region (fungi) were amplified in a two-step PCR procedure, with the final pooled library quantified via qPCR and sequenced using 300-bp paired-end method with an Illumina MiSeq instrument (Illumina) in the Genome Center DNA Technologies Core, University of California, Davis. DNA extractions and library preparation were performed by the UC Davis Host Microbe Systems Biology Core Facility. Detailed experimental procedures and primers are found in Supplementary Methods and Tables S1.1 and S1.2.

Bioinformatic analysis

The sequencing data for both bacteria and fungi were analyzed as Amplicon sequence variants (ASVs) using the “dada2” package (v1.18.0; Callahan et al., 2016a) following the dada2 pipeline workflows (Callahan et al. 2016b). The SILVA (Quast et al. 2013) and UNITE (Nilsson et al. 2018) databases were used to taxonomically classify the bacteria and fungi sequences. Data were further processed using the “phyloseq” package (McMurdie and Holmes 2013) for downstream analysis and raw sequence reads were normalized using the “metagenomeSeq” package (Paulson et al. 2013), as rarefying reads has statistical concerns (McMurdie and Holmes 2014). Further ASV processing details are found in Supplementary Methods.

To assess functional differences in the fungal community, functional guilds were assigned to the already taxonomically classified fungal ASV dataset using the FUNGuild database (Nguyen et al. 2016). Only ASVs with guild assignations of ‘probable’ or ‘highly probable’ were used for analysis on functional guilds, representing 43% of the taxonomically classified dataset. We simplified the guilds to the following: arbuscular mycorrhizae, ectomycorrhiza, plant pathogen, endophyte, and saprotroph, as well as plant pathogen – saprotroph, endophyte – saprotroph, and plant pathogen – endophyte – saprotroph which exhibit traits of multiple guilds. We excluded non-plant pathotrophs, orchid and ericoid mycorrhizae, and plant pathogen – endophytes due to low presence.

Phase 2: Feedback

To address our second hypothesis and determine whether exotic and native communities were structured by negative or positive feedbacks, we compared both native and exotic performance on soils that were cultivated by either native or exotic plants. Each group was grown alone and in competition with the other group to determine whether competition influences the strength of the feedback. Seeding treatments were applied to a subset of the Phase 1 plots, resulting in 8 native-soil and 8 exotic-soil plots. Phase 1 plots not used in Phase 2 were excluded due to the 2018 percent cover levels not meeting the original plot selection criteria (which is not surprising, given that it was an extreme dry year that followed an extreme wet year). The 8 exotic-soil plots included 7 of the original 11 Phase 1 plots with another exotic-soil plot that met the selection criteria for Phase 1 but whose soil was not sampled.

To initiate Phase 2, all aboveground vegetation and litter were removed from the plots shortly after the soil sampling of Phase 1. In December of 2018, after rains (> 0.75 inches) induced germination of the seedbank, the seedlings were killed with RoundUp ProMax (glyphosate, 1.5% solution). After waiting 10 days for complete herbicide disintegration in the soil, and directly preceding another germinating rain, the original 1.5-m x1.5-m plot was split into three subplots in a design that gave equal area and perimeter to each subplot. The locations of seedling treatments were fixed (Figure 1.1), and each subplot was seeded with the dominant grasses found in the community treatments used in the conditioning phase: native community, exotic community, and native + exotic mix (see Table 1.2 for species list and seeding info). In the 2nd growing season, two native-conditioned, native community subplots were excluded due to ground squirrel or flooding disturbance.

We assessed a variety of responses encompassing the life span of the plants for two growing seasons (2018-2019 and 2019-2020) to test how soil conditioning influences plant performance. Learning which life stages are most affected by plant-soil feedbacks will help determine the overall strength of the feedback and the ultimate impact on plant fitness (Dudenhöffer et al. 2017). While the entire plot was seeded, only the inner 1.2-m x 1.2-m square was used for measurements, resulting in each subplot having an area of 0.48 m^2.

Germination

To assess potential soil feedbacks on germination, we glued 5 seeds/species/subplot to toothpicks and inserted them at the same time as plot seeding, positioned so the seeds lay flush with the soil surface. Germination was checked every day for a week following the first germinating rain and then every 2-3 days for the following two weeks, with seeds removed upon germination.

Productivity measures

Height, which provides a useful proxy for growth and avoids destructive sampling, was measured throughout both growing seasons to assess how soil conditioning affects timing of growth. In each subplot, eight individuals of each species were haphazardly chosen and measured. Each season, natives were measured at three monthly time points once they could be identified from the exotic seedlings. The exotics were measured only once each season, as they reach full height by the time they are identifiable by seed heads.

Aboveground biomass of the exotic seeded subplots (E, N+E) was taken twice each growing season (earlier for naturalized exotics and later for noxious weeds) because phenology varies, and no one time point can capture peak biomass for all species. The native subplot was assessed only in the late season to minimize destructive sampling of the young perennials. Samples were clipped within a haphazardly tossed 10-cm diameter ring, oven dried at 50℃, and weighed. Belowground biomass was sampled within the aboveground biomass ring, the same day as the second aboveground sampling, with a 5-cm diameter core at 3 depths (0-15 cm, 15-30 cm, 30-60 cm). Roots were washed from the soil, dried, and weighed. We visually measured percent cover of each species with the Daubenmire method at three monthly time points during each growing season, ending once peak flowering of all species was captured.

Reproductive measures

To assess how soil conditions might feedback and affect the community in the next generation, we measured seed production of each species. Seed production of the exotic annuals was measured at the end of the first growing season by counting seeds from ten haphazardly chosen inflorescences/species/subplot. Seed production of the natives was assessed at the end of the second season, as native perennial grasses rarely set seed their first year. The measurements for native seed production differed from exotic grasses because all surviving exotic individuals flower by the end of the season, but substantially fewer native individuals flower. Thus, for natives we measured seed count per individual (8 individuals/species/subplot), which assesses average seed production of the flowering subset of the population only, and we counted the total number of flowering individuals, which assesses overall reproductive capacity of the native population.

Statistical Analyses

Phase 1: Conditioning

To test our first hypothesis and determine whether the exotic and natives differ in their effects on water holding capacity, total %C and %N, C:N, soil organic matter, and net rates of mineralization and nitrification at different depths throughout the soil profile, we fit linear mixed effect models for each soil property (R Development Core Team). No response variable required transformation to meet assumptions of normality. The fixed effects for each model included soil conditioning (native or exotic), depth (0-15, 15-30, 30-60, 60-90 cm), and their interaction, while the random effects were plot (repeated measures for multiple depths) and block (plot placement in the overall experimental site that accounts for differences due to soil, which includes a sand lens that goes through a small area of the experiment). Analyses of variance (ANOVA) were run followed by post-hoc multiple comparison tests. Analyses were performed with the “lme4” (Bates et al. 2015) and “emmeans” (Lenth 2018) R packages.

To further test our first hypothesis and determine whether potential feedbacks may be driven by the microbial community rather than solely soil chemical or physical properties, we looked at the net impact of soil conditioning on fungal and bacterial community composition. Analyses were performed on the entire soil profile as well as each depth separately, as the variation attributed to depth may overshadow differences from soil conditioning, for not only do rooting depths differ but physical soil conditions vary across depths and influence composition independently of plant conditioning (Eilers et al. 2012, Yao et al. 2018, Upton et al. 2019). Community composition was examined with permutational multivariate analysis of variance (PERMANOVA) using the Bray-Curtis dissimilarity matrix on normalized reads, with soil texture and soil conditioning as fixed effects. Soil texture was included additively (Bach et al. 2010), but not in interaction with soil conditioning due to the unbalanced sample sizes. Community dissimilarity was tested for homogeneity of dispersion with the betadisper function from the “vegan” package (Oksanen et al. 2006) and visualized with non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity matrix on 3 dimensions.

Because previous studies in California grasslands found that native and exotic-dominated grasslands differ in fungal guilds and nitrifying bacteria (Hawkes et al. 2005, 2006, Carey et al. 2017), we focused on these key taxa in addition to the overall fungal and bacterial communities. We compared total relative abundance of each fungal guild and nitrifying family (*Nitrospiraceae*, *Nitrosomonadaceae*, *Nitrosococcaceae*, *Nitrososphaeraceae*, *Nitrincolaceae*) with Kruskal-Wallis tests on the normalized reads but assessed composition only for the nitrifying community, as fungal guilds had too few ASVs for adequate analysis.

Phase 2: Feedback

To evaluate whether exotic vs native conditioning of the soil results in a plant-soil feedback (hypothesis 2), and whether the feedback is influenced by the competitive environment (hypothesis 3), we fit models for each performance variable according to the type and distribution of the data. Exotic and native grass groups were analyzed individually, since we were interested in how each group's performance varied with soil conditioning. While other model terms such as year and depth may be significant on their own, we only addressed them further if they significantly interacted with the soil conditioning and community treatments.

The traditional feedback design involves pairing up individual plants in 'home' and 'away' soil and then calculating a feedback effect variable (FEV) for each pair (see Brinkman et al. 2010). However, due to the complexity of our experimental design, which involves multiple time points and depths, and an interaction with the competitive environment, we tested for potential feedback due to soil conditioning by model fitting with the original data (Brinkman et al. 2010, Bates et al. 2020). Model fitting is less sensitive to smaller *n*, allows for unbalanced designs (common in field experiments), and is easier to calculate variances (Bennett and Cahill 2016, Dudenhöffer et al. 2017, Bates et al. 2020). Our experimental design for many performance measures requires subsampling multiple individuals within plots, and model fitting with random effects allowed for the incorporation of the variance among subsamples, which would be lost if we took the average to calculate an FEV.

The performance measures of biomass, cover, and height were log transformed and fit with linear mixed effect models (see Table S1.3 for model details). We performed model selection using backwards stepwise Akaike Information Criterion and the ran ANOVAs followed by post-hoc multiple comparison tests. Percent cover was modeled at a) the community level (which combined cover of all species) to capture net community feedbacks that may be hidden when comparing smaller differences among species and b) the individual species level (species as a term in the model) to see if a particular species was driving the feedback. Biomass was assessed only on the community level. Plant height was modelled individually for each species, as height inherently differs due to natural history, and we are primarily interested in how soil conditioning effects within-species height variation.

Seed production measures were fitted with generalized linear mixed-effects model for the negative binomial family with the “glmmTMB” package (Brooks et al. 2017) (see Table S1.4 for model details). Likelihood ratio tests were used to determine significance of fixed effects. Native flowering individual was modeled on both the individual species level and community level, as done previously for percent cover. Kruskal-Wallis tests were used on *A. triuncialis* and *S. pulchra* seed production, as the data violated model assumptions due to few surviving individuals.

Germination of all seeded species (end of first season: *E. caput-medusae, B. hordeaceus*) was analyzed with a time-to-event model using the “drc” and “drmSeedGerm” packages (Ritz et al. 2013, Onofri et al. 2018). This method models the cumulative germination curve with the interaction of soil conditioning and community treatment, assuming a log-logistic distribution of germination time and accounting for ungerminated seeds. The model parameters that correspond to time to reach 50% germination and maximum germination were compared via the compParm(‘-’) function (Ritz et al. 2013) to evaluate the drivers of differences in germination patterns between conditioning and community treatments.

Correlation of phase responses

Due to our experimental design, we can only attribute our feedback measures to the net effect of the plant-induced changes to the soil, as it is possible we did not capture all soil differences, or the soil variables could be interacting in unknown ways. However, in attempt to shed further light on the importance of each soil variable, we regressed the significant feedback measures against the main soil variables that are known to have the most direct impact on plant growth, such as plant pathogens and arbuscular mycorrhizae.

RESULTS

Phase 1: Conditioning

After 11 years of conditioning, the native and exotic plant communities differed in their effects on nitrogen cycling rates and the microbial community, but did not differ in their impacts on soil organic matter (SOM), water holding capacity (WHC), %C, %N, or C:N at any depth (Table S1.6). In the top 0-15 cm of soil, native-conditioned plots had significantly higher net mineralization and nitrification rates than the exotic soil (Table S1.5, Figure 1.2), and there were no differences between the conditioning treatments in deeper soils.

Fungi

The exotic and native grasses each cultivated a significantly different fungal community across the soil profile and within each depth measured (Table S1.6, Figure 1.3). The native conditioned fungal communities in the 15-30 and 60-90 cm depth zones had greater dispersion than those conditioned by exotic grasses (Table S1.7). Additionally, the relative abundance of certain fungal functional groups differed across native vs. exotic-conditioned soil (Table S1.8, Figure 1.4). When assessed across the whole soil profile, plant pathogen abundance was significantly greater in the native soil than exotic soil ($p=0.007$) (Table S1.8), but when evaluating individual soil depths, there were no significant differences (but there was a strong trend ($p=0.06$) in the 0-15 cm depth) (Figure 1.4). The plant pathogen-saprotroph guild was similarly in greater abundance in native soils (entire soil profile: $p = 0.02$, 30-60 cm: $p = 0.023$, 60-90: $p = 0.051$), as were saprotrophs (entire soil profile: $p < 0.001$, 15-30 cm: $p = 0.017$, 30-60 cm: $p = 0.035$, 60-90 cm: $p = 0.045$) and endophytes (entire soil profile: $p = 0.002$, 0-15 cm: $p = 0.029$). In contrast, arbuscular mycorrhizae (AMF) were more prevalent in the exotic conditioned soil (entire soil profile: $p < 0.001$, 0-15 cm: $p = 0.002$, 15-30 cm: $p < 0.001$). The ectomycorrhiza, endophyte-saprotroph and plant pathogen-endophyte-saprotroph guilds did not show any differences in relative abundance. Interpreting relative abundance of the fungal functional guilds must occur with some caution, for only half of the fungal ITS sequences were taxonomically classified to the phylum level, and of those, only 43% had a functional guild assignation. The high percentage of unassigned ASVs suggests that much is still unknown about the fungal community and its function in our system.

Bacteria

Bacterial community composition differed between native and exotic plants across the entire soil profile, and in the shallow (0-15 cm) and deep (60-90 cm) soils (Table S1.6, Figure 1.5). Additionally, the native shallow (0-15 cm) soil bacterial communities were more dispersed than the exotic soil community (Table S1.7). These differences from soil conditioning occurred despite the two soil textures in our site (defined categorically by location) strongly structuring the bacterial community at all depths (Table S1.6, Figure S1.3).

Analyses on the nitrifiers alone showed the same patterns as the greater bacterial community—with significant differences between native and exotic conditioned soils across all depths, and specifically in the shallow and deep soils (Tables S1.6 & S1.7, Figure 1.6). Of the 5 present nitrifying families in the soil, the two most abundant, *Nitrospiraceae* and *Nitrosomonadaceae,* had higher abundance in exotic vs. native-conditioned soils, at the deeper depths (below 30 cm) (Table S1.8, Figure 1.7). Specifically, *Nitrosomonadaceae* classified ASVs were greater in exotic soil when totaled across the entire soil profile ($p = 0.049$) and in the 30-60 cm zone ($p = 0.028$). while *Nitrospiraceae* relative abundance was higher in the deep soil zones of 30-60 cm ($p = 0.009$) and 60-90 cm ($p = 0.001$).

Phase 2: Feedback

Exotic grasses

When exotic grasses were grown in exotic- vs. native-cultivated soils there was no difference in their total percent cover, aboveground biomass, seed production, or seed viability. However, exotic grasses had greater belowground biomass in native soils across all depths and years (p = 0.009, Table S1.9, Figure 1.8), being particularly strong in the deeper soils. Weak negative feedbacks occurred in height (only for the exotic grass, *Bromus hordeaceus*), and germination (only for the exotic grass, *Avena fatua)* (Figures S1.4 & S1.5). When exotic species were seeded in competition with natives, very few native individuals established. It is thus not surprising that there was no effect of being grown in monotypic vs. mixed stands on any exotic trait, other than germination timing of *Avena fatua*.

Native grasses

Similar to our findings with exotic plants, native grasses experienced negative feedbacks when grown in their own soil, but more traits were affected--with native grasses grown in exotic soil having higher percent cover, height, flowering individual count, and seed head count. No feedbacks were observed in germination, seed production per flowering individual, aboveground biomass ($p > 0.05$, data not shown) nor in belowground biomass (Table S1.9, Figure 1.8). The strongest feedback was seen in percent cover during both years (Table S1.10, Figure 1.9, total native cover was significantly greater in exotic soil–the native subplot showed a 15% increase in absolute cover (a 1.75-fold increase). In contrast, the native and exotic mix subplot only had a 2% increase in absolute cover, but this was a doubling in cover compared to when this mix was grown in native soil. Together, these data indicate that native establishment and success is strongly limited by growing in competition with exotic annual grasses, eclipsing the effects of feedbacks. To assess how different native species contributed to the increase in native cover in exotic soils, the model which separated out native cover by species showed that the all 3 native perennial grasses- *Elymus glaucus, E. triticoides,* and *Stipa pulchra* increased in cover in exotic soil when grown in the native mix community (Table S1.10).

When grown in the native mix community, mid- to late- season native grass height in the 2nd year was higher in exotic than native soils, but it was only statistically significant for *S. pulchra* ($p = 0.014$, Table S1.11, Figure 1.10), which had no feedback in March, but had a 20% increase in height in exotic-conditioned soil in April ($p < 0.05$), and a 39% increase in May ($p < 0.05$). Soil conditioning by native vs. exotic plants did not impact how many seeds a flowering individual produced ($p < 0.05$, data not shown), but native seed production per plot was higher in the exotic soils due to 85% more flowering individuals compared to when grown on native soil (Table S1.12, Figure 1.11). The feedback was observed for each native species, indicating all three contributed to the net community effect.

Correlation of phase responses

While Phase 1 showed that nitrogen cycling rates and AMF and pathogen fungal abundances significantly differed between treatments, and Phase 2 showed that the main feedbacks were observed in native cover and exotic belowground biomass, there was no single soil variable that clearly explained what was causing the feedback in our correlation regressions ($p > 0.05$). This may be due to our small sample size or that plants are responding to a net soil effect that cannot be measured by single variables.

DISCUSSION

This long-term field study demonstrated that native and exotic communities both experienced negative feedbacks-- performing better in the other community's soil. The eleven-year conditioning phase provided a unique opportunity to assess feedbacks in response to soil changes that may take years to develop, such as build-up of soil organic matter. The two-year feedback phase allowed later-developing responses in the perennial species to be observed. Setting both experimental phases in the field was necessary to understand the overall strength and role of feedbacks in structuring plant communities in a more realistic setting, as both phases experienced high environmental variability. Any long-term soil changes due to vegetation composition were strong enough to be detected over the observed variability in soil texture, ground squirrel disturbance, and annual precipitation (i.e. extreme multi-year drought followed by a historic wet year). The two-year feedback phase also experienced strong variation in annual precipitation, as it included an extremely wet year followed by an extremely dry year (760 and 262 mm, respectively). The detection of feedbacks required measuring multiple plant responses, as the natives and the exotics did not exhibit feedbacks within the same trait, nor did either show a feedback in aboveground biomass, the most commonly measured indicator of plant fitness. Overall, our results suggest the need to measure multiple traits and life stages to capture potential responses to soil conditioning (Batten et al. 2008, Hawkes et al. 2013, Bennett and Cahill 2016, Dudenhöffer et al. 2017).

We detected negative feedbacks on both native and exotic grasses, suggesting California grasslands are structured by negative feedbacks, similar to many other systems (Klironomos 2002, Bonanomi et al. 2005, Kulmatiski et al. 2008, Chung and Rudgers 2016, Bennett and Klironomos 2019), and that positive feedbacks are not a main factor in exotic grass dominance (Callaway et al. 2004, Suding et al. 2013). The feedbacks were stronger for the native community, which had improved performance in exotic soil, as measured by cover, height, and reproductive productivity. These results are similar to a number of other studies, indicating that negative plant-soil feedbacks are stronger for native than exotic species (Klironomos 2002, Agrawal et al. 2005). Previous greenhouse studies of California grassland species showed that in the short term (6-8 weeks), native species experienced positive feedbacks and performed worse in exotic conditioned soil, the opposite of our results (Grman and Suding 2010, Larios and Suding 2015). This may be due to different feedback mechanisms at play in a shorter conditioning phase or the difference in life stages tested.

The exotic grass community had greater belowground biomass in native-conditioned soils. Another feedback experiment with similar species linked greater deep-root exotic biomass to the increased soil organic matter and water holding capacity in deep soils cultured for 10 years by the native perennial *Stipa pulchra* (Waitman 2019). Our study did not detect these physical and chemical soil differences but that may be because our site was drier and had higher clay content. It is also possible that these soil changes did occur and were ecologically but not statistically significant in our study. It is also possible that other driving mechanisms increased exotic deep root-growth in native soils at our site, such as potentially enhanced soil aggregation from the deeper perennial roots with more fine root hairs (Hull and Muller 1977, Holmes and Rice 1996, Koteen et al. 2011) which would increase plant suitability due to more pore space and water flow (Angers and Caron 1998).

Vegetation-induced changes to soils, and potential for driving feedbacks

The native vs. exotic communities did not differ in their effects on soil water holding capacity, percent carbon or nitrogen, nor soil organic matter. Differences did arise in their effects on net nitrogen mineralization and nitrification, and fungal and bacterial community composition. The exotic plant communities cultivated significantly different fungal and bacterial community compositions from those cultivated by natives, similar to many other studies (Kourtev et al. 2002, Steenwerth et al. 2003, Mummey et al. 2005, Batten et al. 2006, Hawkes et al. 2006, Hausmann and Hawkes 2009, Bunn et al. 2015, Hilbig and Allen 2015, Checinska Sielaff et al. 2018, Zhang et al. 2019). The fungal communities were distinct across soil conditioning treatments at all soil depths, but the bacterial communities differed by conditioning treatment only in the shallowest and deepest soil zones, supporting our hypothesis that differences in rooting depths are a factor in soil conditioning. Changes in microbial composition may directly impact plant performance (e.g. pathogens or symbionts), or may indirectly alter plant performance by changing resource availability (e.g. nutrient availability, soil water storage).

The native vs exotic communities also differed in effects on the abundances of nitrifying bacteria, AMF, fungal pathogens and saprotrophs, and soil nitrogen cycling, and below we'll discuss how similar changes have been linked to plant performance in other feedback studies. However, determining the causal mechanisms behind the observed feedbacks is beyond the scope of this experiment, as the observed net feedbacks might be due to these differences in soil properties, properties not measured in this study, or from their interactions.

Pathogens

Fungi in the plant pathogen and plant pathogen-saprotrophs guilds were greater in abundance in native-conditioned soil compared to exotic soil. This difference may be due to the life histories of the two grass groups, as the perennial native roots provide a constant food source for pathogens whereas the annual exotic roots die off every spring. Alternatively, fungal pathogenic richness is positively correlated with specific root tip number, which is likely higher in native roots as they are deeper with more fine root hairs (Wang et al. 2019). Greater pathogen abundance in native-conditioned soil plots could also be attributed to being largely dominated by *S. pulchra* in the conditioning phase, and evidence suggests that greater soil pathogen accumulation occurs under monocultures (Maron et al. 2011, Schnitzer et al. 2011, Lekberg et al. 2018).

Negative plant-soil feedbacks are common and thought to maintain plant diversity, and are often attributed to the buildup of localized pathogens (Bever 1994, Klironomos 2002, Bever et al. 2015, Semchenko et al. 2018). Thus, the strong negative feedback observed in the native grass community may be influenced by lower exposure to pathogenic attack in exotic-conditioned soils. In a study with similar species, native grasses also experienced a strong negative feedback, but doubled in growth when native soils were sterilized (Waitman 2019), supporting the suggestion that pathogens are driving the feedback. Further, pathogens accumulate over time, and the longer conditioning phase of our experiment may explain the difference in feedback direction compared to shorter-term studies (Grman and Suding 2010, Larios and Suding 2015). The lower fungal abundance in exotic-cultured soils did not benefit exotic grasses, however, as they performed worse in their own cultivated soils. They may culture their own specific pathogens and also be less susceptible to generalist pathogens than native grasses (Kendig et al. 2021).

Saprotrophs were also greater in native-conditioned soils and could potentially have become parasitic (biotrophic) which can occur when soils are dominated by a single species, and the native soils were largely conditioned by *S. pulchra* (Semchenko et al. 2018). However, while these could potentially contribute to the natives' negative PSF, these effects might be short-lived, as saprotroph composition can change quickly in response to the current plant community (Jongen et al. 2021).

Arbuscular mycorrhizae

Exotic-conditioned soil had more AMF than the native-conditioned soil, with several native-conditioned plots lacking AMF completely. Across ecosystems, exotic plant effects on AMF abundance are highly variable, demonstrating increases, decreases, or no effect on AMF abundance (Niu et al. 2007, Jordan et al. 2012a, Lekberg et al. 2013, Zubek et al. 2016, Zhang et al. 2019). In our experiment, the increased AMF abundance of the exotic-conditioned soils could be independent of native vs exotic plants, and instead associated with the greater plant species richness (Jin et al. 2004, Schmid et al. 2019) and the inclusion of forbs (Mummey et al. 2005, Batten et al. 2006, Lekberg et al. 2013, Bunn et al. 2015) in the exotic plant conditioning community compared to the native plant conditioning community, which was largely dominated by *Stipa pulchra*.

In our study, native grasses performed better in the exotic-conditioned soils, but we cannot say whether differences in AMF abundance and community are playing a role in the observed feedbacks, especially as our sampling method cannot confirm root colonization. Many native plots lacked AMF, which prevented us from determining compositional differences between exotic and native soils. The fact that several native plots had no AMF sequences is perplexing, as another study found that native perennial grasses in California are preferred hosts to AMF and had higher arbuscular colonization than their exotic neighbors (Hausmann and Hawkes 2009). It seems unlikely that exotic soil benefits to native plants was due to AMF, since many studies have shown that exotic plant changes to AMF communities have either no effect or detrimental effects on native plant performance (Niu et al. 2007, Zhang et al. 2010, Jordan et al. 2012b, Lekberg et al. 2013, Zubek et al. 2016). Other studies have found that there is no clear distinction on how exotic vs native plants respond to a conditioning species' cultivated AMF community (Bunn et al. 2015, Majewska et al. 2018).

Nitrogen cycling rates

We did not find any difference in total N between the two conditioned soils, but net mineralization and nitrification rates were lower in soils conditioned by exotic grasses compared to the native perennials. These results are similar to those found by Parker et al. 2012 and Carey et al. 2017. Lower net rates can occur because decomposition and N release are slower (e.g. due to poorer litter quality), and/or when there is higher microbial immobilization, resulting in high competition between plants and microbes for N (Bremer and Kuikman 1997, Schimel and Bennett 2004). If the difference in rates of N cycling influenced native performance, we would expect greater native aboveground biomass on native-conditioned soil, which we did not see. Corbin and D'Antonio (2004) suggest that changes in mineralization and nitrification rates are easily reversed under a new plant community, and so would not lead to feedbacks.

We also detected changes in the nitrifying bacteria; ammonia oxidizing (AOB) and nitrite oxidizing bacteria (NOB) were both greater in the deeper exotic-conditioned soils than the native-conditioned soils. As there are fewer deep roots in exotic plots, bacteria in those soils have greater access to ammonia and nitrite. Similarly, Hawkes et al. (2005) looked at soils under the native *S. pulchra* and exotics *B. hordeaceus* and *A. barbata*, species used in our study, and also found greater AOB abundance in exotic soils.

The role of competition in feedbacks

The presence of a competitor can eclipse, neutralize, or change the strength of a feedback in a species (Callaway et al. 2004, Casper and Castelli 2007, Yelenik and Levine 2011, Shannon et al. 2012). Assessing plants grown in a community with both intra and inter-specific competition can thus help us understand the proportional role of feedbacks in community structure, particularly if we are interested in communities comprised of species commonly found together in nature, such as our native mix and our exotic mix. Our community treatments do not allow us to tease apart individual species' contributions to soil conditioning nor touch on whether the direction and magnitude of a feedback is dependent on the specific identity of the conditioning plant and the feedback plant (Brandt et al. 2009, Majewska et al. 2018), but did show feedbacks were still observed overall in our two communities. In California grasslands, certain groups (e.g. natives vs. exotics) can remain dominant over time, but the stability of the group is due to variations in which species dominate within the groups, as environmental conditions change (Seabloom et al. 2005, Chapter 1). Our results thus are relevant to the diverse and shifting communities found in California grasslands, especially as feedbacks can be non-additive in a community compared to monoculture (Hawkes et al. 2013).

Community type (native-only community or in mixed native-exotic community) played a major role in native grass abundance, and only slightly affected the exotic grasses. Native establishment was so poor in the mixed native and exotic community that we were not able to analyze most performance measures. This is not surprising, as exotic annual grasses in this system both germinate and grow much faster than native perennials, which allows them to outcompete the native seedlings for light and soil moisture (Dyer and Rice 1997, 1999, Hamilton et al. 1999, Humphrey and Schupp 2004, DiVittorio et al. 2007). The few native individuals growing in competition with the exotics, however, still experienced a negative feedback in percent cover. Thus, feedbacks influence natives more subtly in full competition with exotics but can be a stronger control in restoration settings where competition by exotics is actively minimized. As the exotic grasses are the better competitor at the seedling stage, competition with natives did not alter exotic feedback overall. Our results show that competition among native and exotic grasses clearly outweighs the role of plant-soil feedbacks in community structure, with exotic dominance resulting regardless of soil provenance.

Implications

Our results do not support our hypothesis that exotic annual grass invasion negatively impacts native restoration through the soil, suggesting that soil amelioration may not be necessary to improve restoration success. Studies comparing remnant, restored, and invaded grasslands found that soil biotic communities take years to recover (Steenwerth et al. 2003, Potthoff et al. 2006), although another found mycorrhizal communities specific to *S. pulchra* returned quickly after restoration (Nelson and Allen 1993). Fortunately, it appears that exotic soil conditioning at our site does not majorly hinder native establishment and restoration success but rather benefits natives, even though exotic soils still have been found to decrease native performance when compared to sterilized soil (Waitman 2019), highlighting native grass susceptibility to pathogens. When establishing native cover is the main goal of a restoration project, reaching 30% native cover is considered a success. Higher cover is very important for the long-term success of a project, as once established, native perennial grasses become more competitive against future exotic annual seed pressure (Seabloom et al. 2003, Corbin and D’Antonio 2004b, Lulow 2006). Thus, the 15% difference in percent cover observed in our study is substantial. However, competitive suppression of native seedlings by exotics eclipsed the feedback effect, highlighting the need for weed control in the restoration process.

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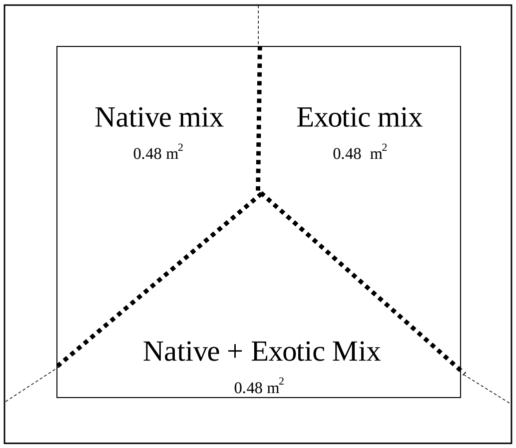


Figure 1.1. Diagram of how each plot was subdivided for the three seeding treatments (0.48m^2 each).

Table 1.1. Species included in seeding treatment of conditioning phase

Seeding treatment	Live seeding rate	Seeded species	Seed source
Native mix	46 g/0.48m^2	*Elymus glaucus*	Hedgerow Farms, Winters, California
		E. triticoides	
		Stipa pulchra	
Exotic mix	46 g/0.48m^2	*Aegilops triuncialis*	Yanci Ranch, Winters, California
		E. caput-medusae	Putah Creek Riparian Preserve, Davis, California
		Avena fatua	Russell Blvd, Davis, California
		Bromus hordeaceus	S&S Seeds, Carpinteria, California
Native and exotic mix	92 g/0.48m^2	All above species	

Table 1.2. Species composition of each seeding treatment in the feedback phase.

Native grasses and forbs	Noxious exotic annual grasses	Naturalized exotic annual grasses and forbs
*Elymus glaucus**	*E. caput-medusae*	*Avena fatua*
*E. triticoides**	*Aegilops triuncialis*	*Bromus hordeaceus*
*Stipa pulchra**		*Festuca perennis*
Bromus carinatus		*Trifolium subterraneum*
Festuca microstachys		*B. diandrus***
Acmipson americanus		*Hordeum murinum***
Lupinus bicolor		

*maintained dominance in native mix plots compared to other native species

**not originally seeded, but now considered a component of the naturalized exotic grasses

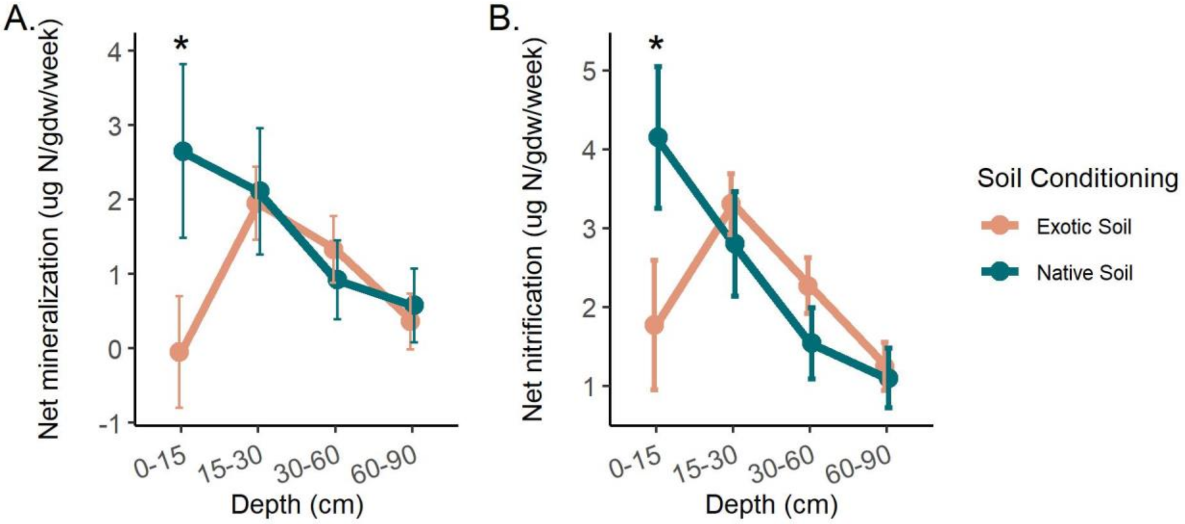


Figure 1.2. Net mineralization (A) and nitrification (B) rates (ug N/gram dry weight of soil/week) across the soil profile. Soil conditioning significantly interacted with depth (ANOVA, *p* < 0.01 for both rates); post-hoc multiple comparisons were made within each depth, with an asterisk indicating a significant difference at the p < 0.05 level between soil conditioning groups. Note the difference in y-axes.

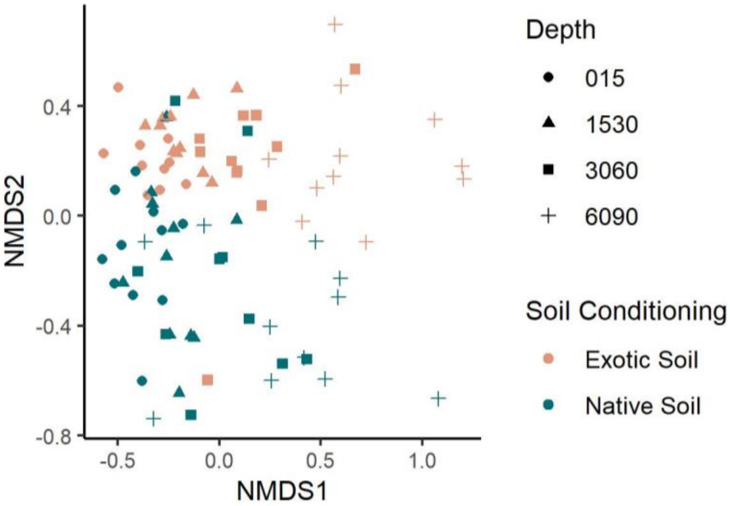


Figure 1.3. Non-metric multidimensional scaling ordination (stress = 0.17) using Bray-Curtis dissimilarity of the fungal (ITS) community composition showing the significant effect of soil conditioning (PERMANOVA, p = 0.001) and depth (PERMANOVA, p = 0.001).

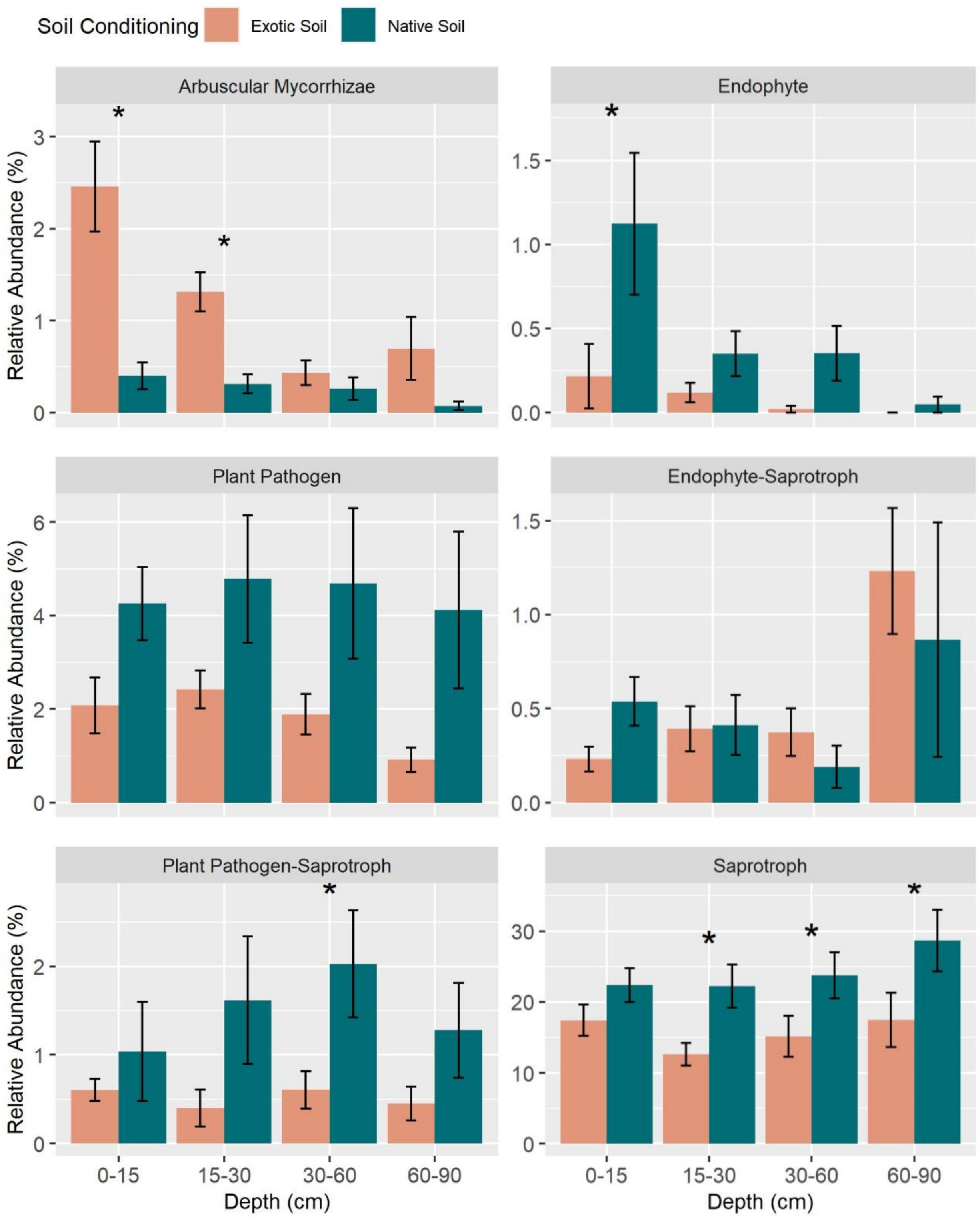
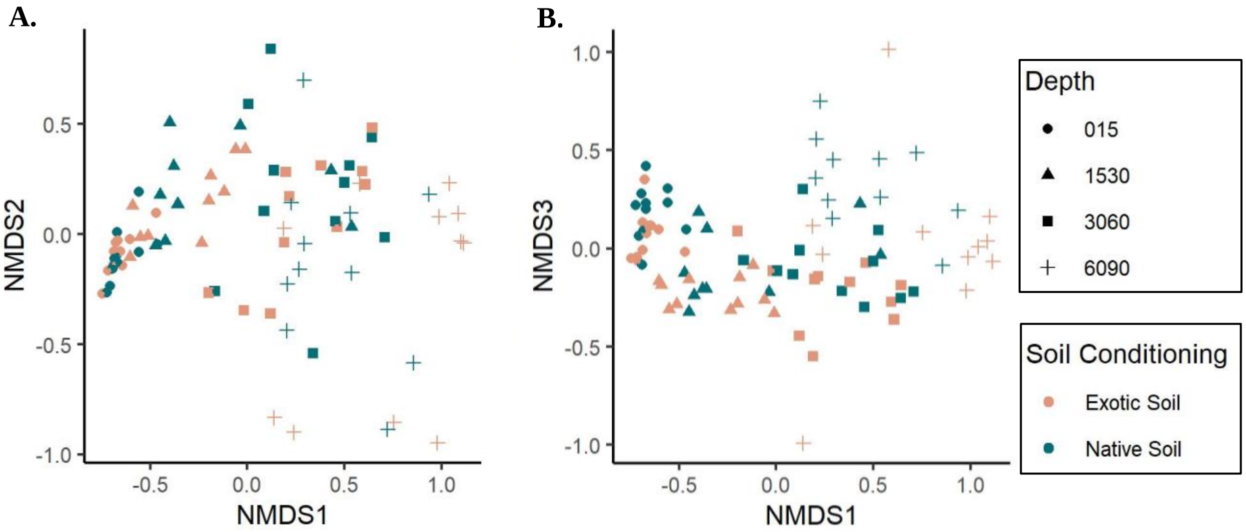


Figure 1.4. Relative abundances of fungal functional guilds to total ASV abundance classified at the phyla level in native and exotic soils. Comparisons were made within depths using Kruskal-Wallis tests, with an asterisk indicating a significant difference at the $p < 0.05$ level between soil conditioning groups. Note the difference in y-axes.



C. **0-15 cm**

D. **60-90 cm**

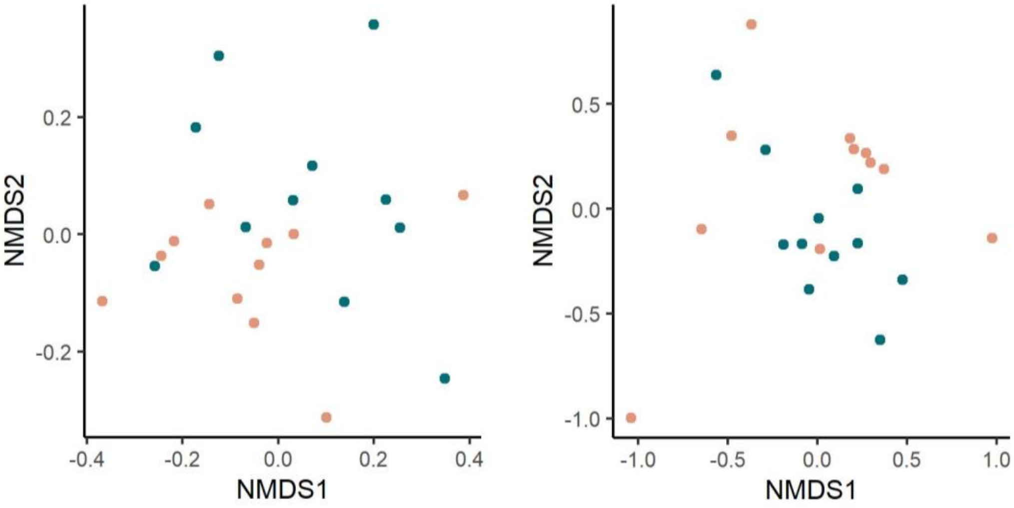
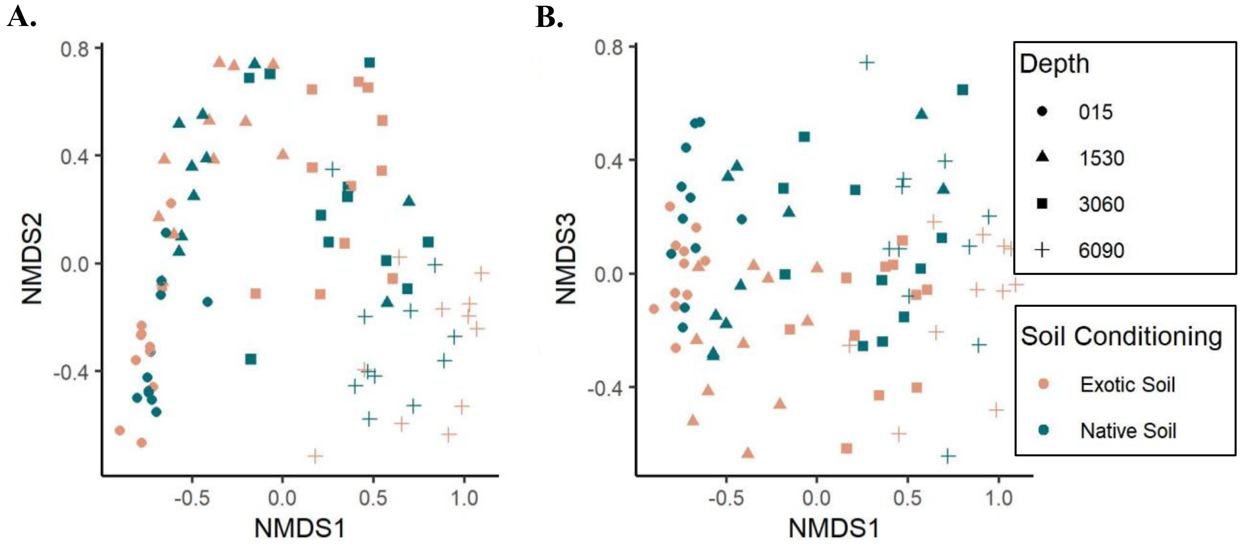


Figure 1.5. Non-metric multidimensional scaling ordinations using Bray-Curtis dissimilarity on the species composition of the bacterial (16s) community, highlighting the (**A**, **B**) effect of soil conditioning and depth along the 2 of the 3 axes of the same ordination (stress = 0.09). When each depth is analyzed separately, soil conditioning only significantly influences bacterial community composition in the (**C**) 0-15 cm (stress = 0.16; PERMANOVA, p = 0.027) and (**D**) 60-90 cm (stress = 0.11; PERMANOVA p = 0.027) depths of the soil profile.



C. 0-15 cm

D. 60-90 cm

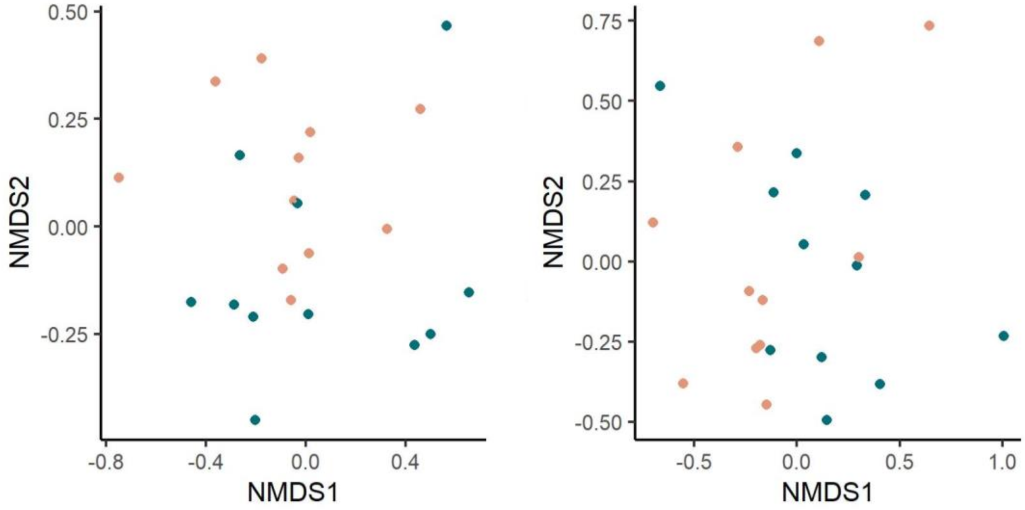


Figure 1.6. Non-metric multidimensional scaling ordination using Bray-Curtis dissimilarity on the beta diversity of the nitrifying bacterial community, highlighting the (**A**, **B**) effect of soil conditioning and depth along the 2 of the 3 axes of the same ordination (stress = 0.11). When each depth is analyzed separately, soil conditioning only1/ significantly influences nitrifying bacterial community composition in the (**C**) 0-15 cm (stress = 0.12; PERMANOVA, p = 0.006) and (**D**) 60-90 cm (stress = 0.13, PERMANOVA, p = 0.003) depths of the soil profile.

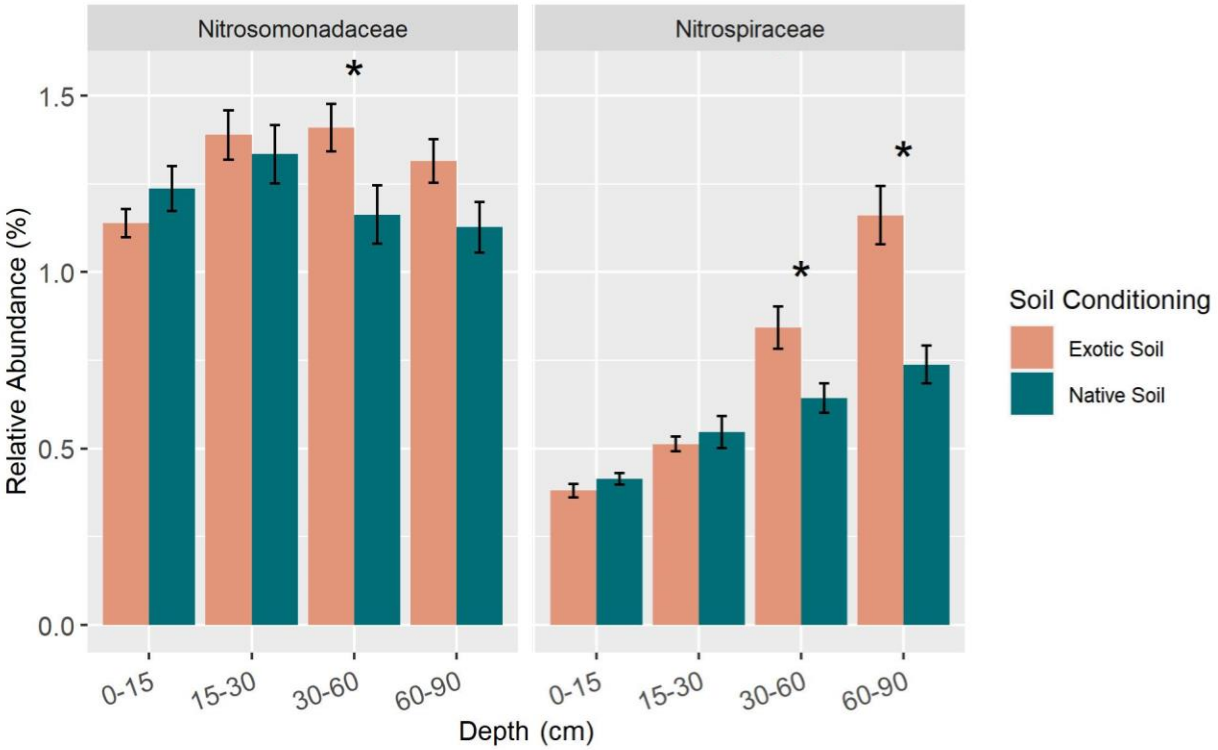


Figure 1.7. Relative abundance (compared to all bacteria) of the nitrifying bacteria families *Nitrosomonadaeceae* and *Nitrospiraceae*. Comparisons were made within depths using Kruskal-Wallis tests, with an asterisk indicating a significant difference at the $p < 0.05$ level between soil conditioning treatments.

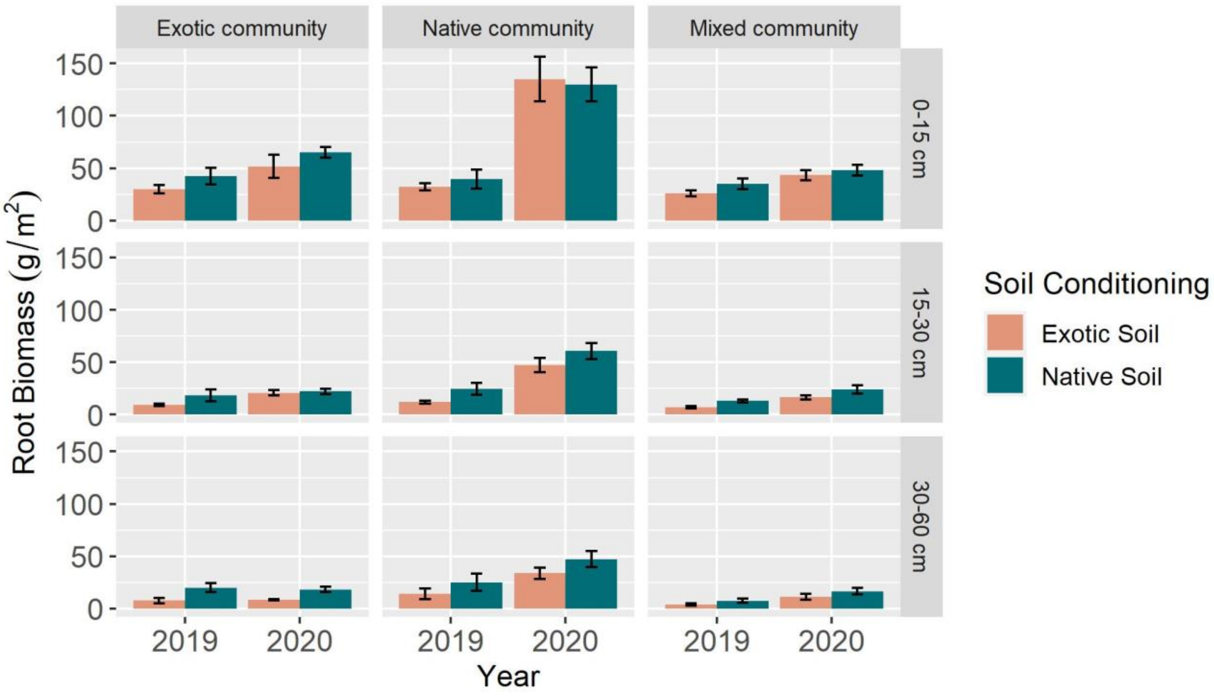


Figure 1.8. Belowground biomass (g/m^2) as seen in each depth, year, and community. Belowground biomass in the exotic (ANOVA, $p = 0.009$) and mixed (ANOVA, $p < 0.001$) communities, but not the native community, was greater in native soil across all depths.

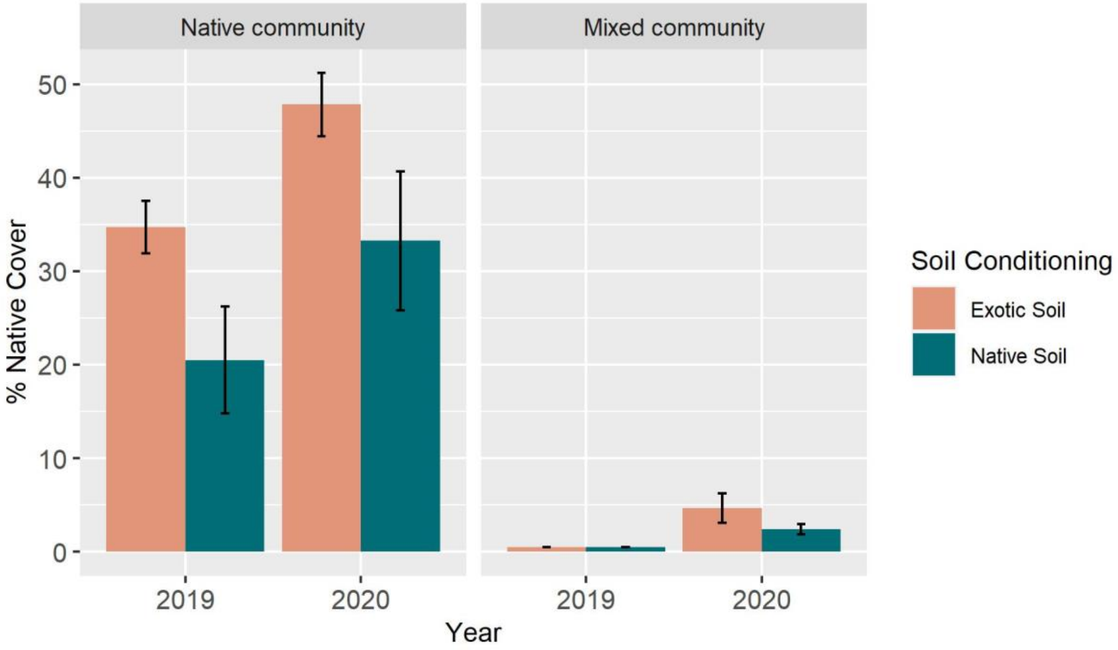


Figure 1.9. Percent cover of native grasses is higher in exotic soil than their 'home' soil across competitive community and year (ANOVA, $p = 0.025$). Being seeded with exotics also significantly reduces native cover across years and soil conditioning groups (ANOVA, $p < 0.001$).

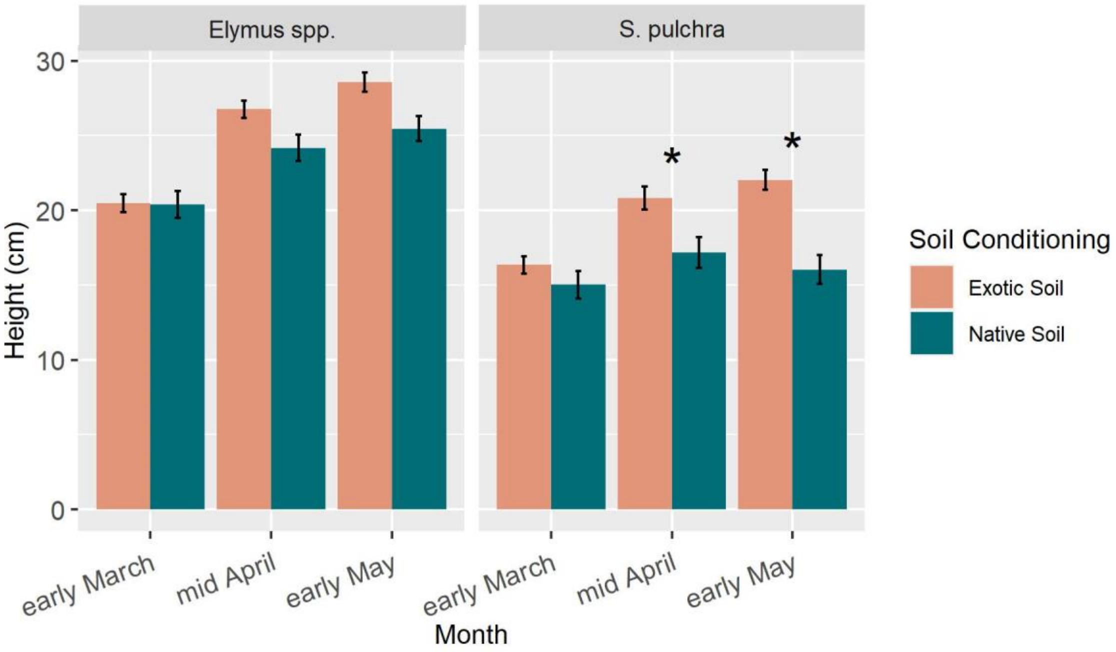


Figure 1.10. Height of native grasses over time in the second growing season showing a significant negative feedback in the later months for *S. pulchra* (ANOVA, soil conditioning x month, p = 0.014) but only trending for *Elymus spp* (p = 0.087). An asterisk indicates significant difference of $p < 0.05$ in a post-hoc comparison of means between soil conditioning groups.

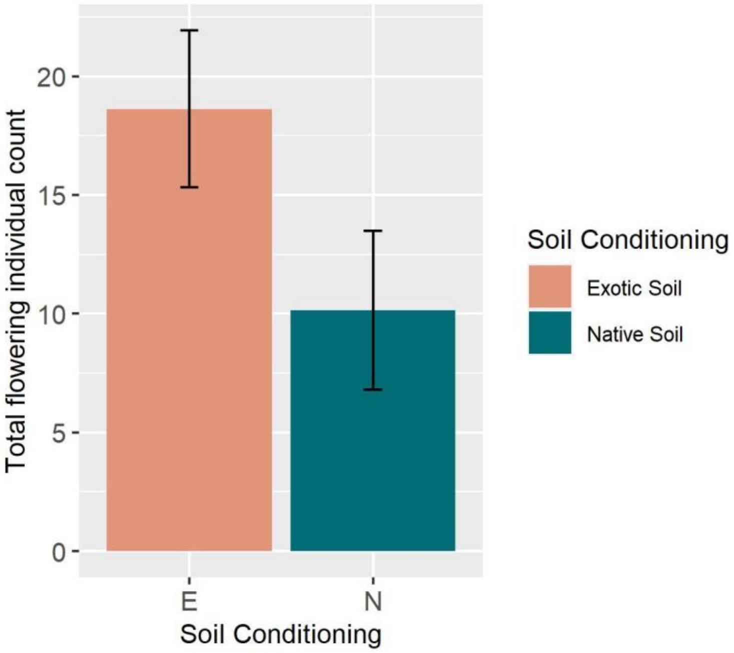


Figure 1.11. Count of flowering individuals in the native community, showing a negative feedback. Native species produced significantly more flowering individuals (ANOVA, p = 0.029) in exotic-conditioned soil plots than their own conditioned soil.

SUPPLEMENTARY METHODS

Sequencing of microbial communities

In a two-step PCR procedure, the V3-V4 domain of the 16S rRNA was amplified using primers 341F and 806R (**Table S1**), while the ITS2 region was amplified with primers ITS3 and ITS4 (**Table S2**). In step one of the PCR procedure, primers included an Illumina tag, spacer, linker, and target sequence and each reaction (25 μl) contained 1 Unit Kapa2G Robust Hot Start Polymerase (Kapa Biosystems), 1.5 mM MgCl2, 0.2 mM final concentration dNTP mix, 0.2 μM final concentration of each primer and 1μl of DNA for each soil sample (95°C for 3 min; 25 (16S) or 35 cycles (ITS) of 95°C for 45 s, 50°C for 30 s, 72°C for 30 s; and 72°C for 3 min). In the second step, a unique barcode combination of forward and reverse primers (Illumina adapter sequence, barcode, partial matching sequence from step one's Illumina tag) was added to each sample for both 16S and ITS amplification (**Table S1 and S2**). Each reaction in step two contained 1 Unit Kapa2G Robust Hot Start Polymerase (Kapa Biosystems), 1.5 mM MgCl2, 0.2 mM final concentration dNTP mix, 0.2 μM final concentration of each uniquely barcoded primer and 1ul of the product from the PCR reaction in step one diluted at a 10:1 ratio in water for each sample (95°C for 3 min; 9 cycles of 95°C for 30 s, 58°C for 30 s, 72°C for 30 s; 72°C for 3 min. The final product was quantified on the Qubit instrument using the Qubit High Sensitivity dsDNA kit (Invitrogen). Individual amplicons were pooled and cleaned using Ampure XP beads (Beckman Coulter), and then checked for quality and proper amplicon size on an Agilent 2100 Bioanalyzer (Agilent Technologies). Finally, the pooled library was quantified via qPCR and sequenced using 300-bp paired-end method with an Illumina MiSeq instrument (Illumina) in the Genome Center DNA Technologies Core, University of California, Davis. DNA extractions and library preparation were performed by the UC Davis Host Microbe Systems Biology Core Facility.

ASV processing steps for bioinformatic analysis

For bacteria data, one sample (native conditioned soil, 15-30cm) was removed as it had no sequences due to an extraction error. We further removed sequences that were classified as chloroplast, mitochondria, or eukaryotic, as well as any sequence that was observed in only one sample or was not classified at the phylum level. Only 0.7% of ASVs (168/22512) were not classified at the phylum level. For fungal data, we removed one sample (native conditioned soil, 30-60 cm) with no sequences due to an extraction error. All sequences were observed in at least two samples. We removed sequences that remained unclassified taxonomically, as they could potentially be artefacts of the sequencing (Lankau and Keymer 2016). However, fifty percent (1387/2778) of the sequences were unclassified taxonomically, which can be common in non-agricultural systems, and so it remains possible that a large portion of the fungal community is not identified and thus playing an unknown role in the community.

Lankau, R. A., and D. P. Keymer. 2016. Ectomycorrhizal fungal richness declines towards the host species' range edge. Molecular Ecology 25:3224–3241.

SUPPLEMENTARY MATERIALS

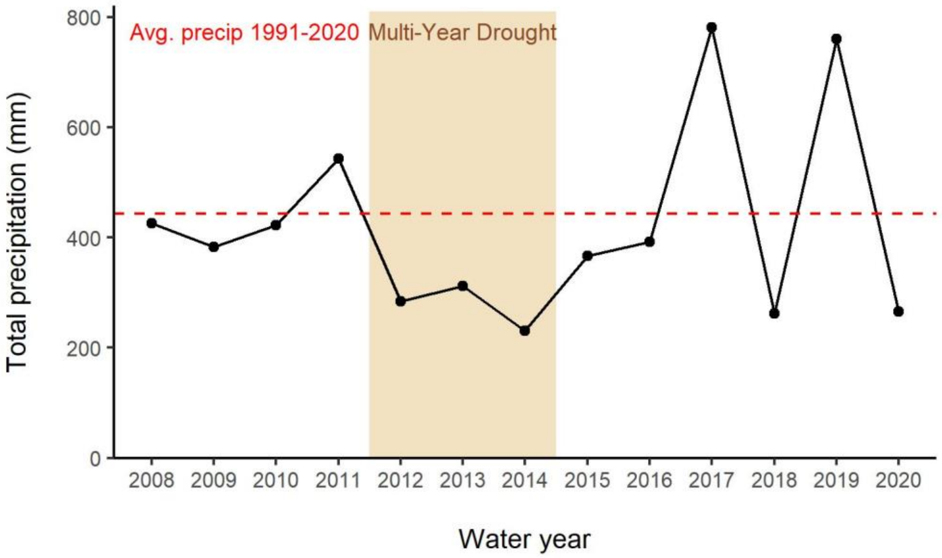


Figure S1.1. Total precipitation (mm) for each water year (Oct 1st of previous year to Sept 30th of reference year) of the experiment. The conditioning phase was 2008-2018 and the feedback phase was 2019-2020. The red dashed line refers to the 30-year average (1991-2020).

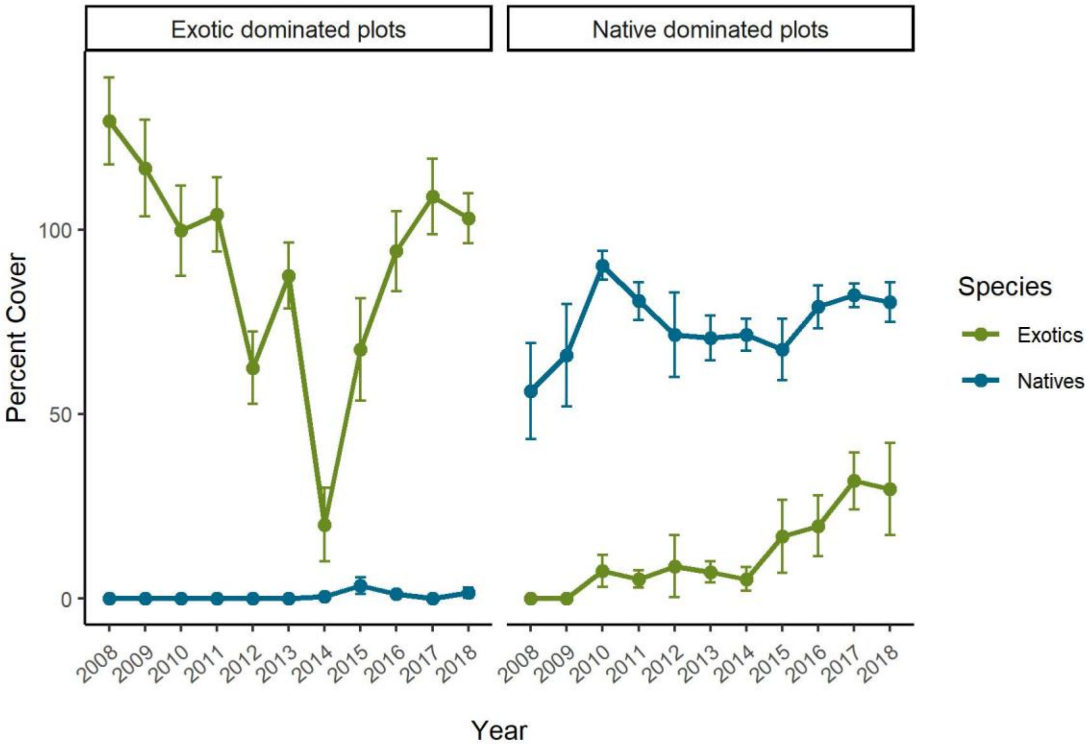


Figure S1.2. Variation in species group composition of the exotic and native dominated plots over the 11-year conditioning phase.

Table S1.1. 16S rRNA amplicon primers. In step one, each primer includes an Illumina tag sequence (bolded) and a variable length spacer (341F: no spacer, A, CA, or GCA; 806R: no spacer, G, TG, ATG), as well as a linker sequence (italicized) and the target 16S sequence (underlined). In step two, forward primers include an Illumina P5 adapter sequence (bold), unique eight nucleotide barcode (N), and a partial matching sequence of the forward tag sequence from step one (underlined). Reverse primers are the same except for an Illumina P7 adapter sequence and a partial matching sequence of the reverse tag.

Step One	**Sequence**	**Identifier**
Illumina 16S rRNA sequencing primer forward	**TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG**(spacer)*TG*CCTACGGGNGGCWGCAG	341F
Illumina 16S rRNA sequencing primer reverse	**GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG** (spacer)*CC*GGACTACNVGGGTWTCTAAT	806R
Step Two	**Sequence**	
Forward primer	**AATGATACGGCGACCACCGAGATCTAAC**NNNNNNNNTCGTCGGCAGCGTC	
Reverse primer	**CAAGCAGAAGACGGCATACGAGAT**NNNNNNNNGTCTCGTGGGCTCGG	

Table S2. ITS amplicon primers. In step one, each primer includes an Illumina tag sequence (bolded) and a variable length spacer (ITS3: no spacer, C, TC, or ATC; ITS4: no spacer, G, TG, ATG), as well as a linker sequence (italicized) and the target ITS2 sequence (underlined). In step two, forward primers include an Illumina P5 adapter sequence (bold), unique eight nucleotide barcode (N), and a partial matching sequence of the forward tag sequence from step one (underlined). Reverse primers are the same except for an Illumina P7 adapter sequence and a partial matching sequence of the reverse tag.

Step One	**Sequence**	**Identifier**
Illumina ITS rRNA sequencing primer forward	**TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG**(spacer)*GT*GCATCGATGA AGAACGCAGC	ITS3
Illumina ITS rRNA sequencing primer reverse	**GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG**(spacer)*CG* TCCTCCGCTTATTGATATGC	ITS4
Step Two	**Sequence**	
Forward primer	**AATGATACGGCGACCACCGAGATCTAAC**NNNNNNNNTCGTCGGCAGCGTC	
Reverse primer	**CAAGCAGAAGACGGCATACGAGAT**NNNNNNNNGTCTCGTGGGCTCGG	

Table S1.3. Details of the linear mixed effect models used to assess log-transformed biomass, cover, and height feedback measures. Species group and community subplot indicate which data subset is used in the analysis. All models include plot as a random effect to account for either subsampling or repeated measures.

Feedback measure (log transformed)	**Species group**	**Community subplots**	**Fixed effects**	**Notes**
Aboveground biomass	Natives	N	Soil conditioning Year	• Natives rarely present in N+E mix subplot, so N mix analyzed only
	Exotics	E, N+E	Soil conditioning Community Year Season	
Belowground biomass	Natives	N	Soil conditioning Depth Year	• Sampling depths = 0-15cm, 15-30 cm, 30-60 cm. To compare across depths, and account for the 30 cm increment of the 30-60 cm depth (compared to the 15 cm increments of the shallower root cores), the biomass for the 30-60 cm depth was halved • Root biomass cannot be separated out by species group in N+E subplot, so the mixed community treatment is analyzed separately
	Exotics	E		
	Mixed	N+E		
Percent cover (species level)	Exotics	E, N+E	Species Soil conditioning Community Year	
	Natives	N, N+E	Species Soil conditioning Community	• Native seedlings were not identifiable to species for first year, only second year modeled
Total percent cover (community level)	Exotics	E, N+E	Soil conditioning Community Year	
	Natives	N, N+E		
Height	Individual exotic species	E, N+E	Soil conditioning Community Year	• *A. triuncialis* did not have enough surviving individuals to run statistical analyses.
	Individual native species	N	Soil conditioning Month	• Each year modeled separately, as seedlings were not identifiable to species for first year. • 2nd year: the two *Elymus* species were grouped at the genus level. • Natives too rarely present in N+E mix subplot, so N mix analyzed only

Table S1.4. Details of the generalized linear mixed effect models (negative binomial family) used to assess seed production measures. Species group and community subplot indicate which data subset is used in the analysis. All models use the random effects of plot except for the total flowering measure which did not require including plot due to data structure.

Feedback measure	**Species group**	**Community subplots**	**Fixed effects**	**Notes**
Seed production per individual	Individual exotic species	E, N+E	Soil conditioning Community Year	• *A. triuncialis* was assessed separately with a Kruskal-Wallis test, as data violated model assumptions due to few surviving individuals
	Elymus glaucus	N	Soil conditioning Year	• Natives too rarely present in N+E mix subplot, so N mix analyzed only • *S. pulchra* was assessed separately with a Kruskal-Wallis test, as data violated model assumptions due to few surviving individuals
Flowering individual (species level)	Natives	N	Species Soil conditioning	• Natives too rarely present in N+E mix subplot, so N mix analyzed only
Total flowering individual (community level)	Natives	N	Soil conditioning	• Natives too rarely present in N+E mix subplot, so N mix analyzed only

Table S1.5. ANOVA results from linear mixed effect models on the effect of soil conditioning (SC) treatment and soil depth (D) on soil properties with plot and block as a random effect. Bold values indicate significance at a $p < 0.05$ level.

		% C		% N		C/N		% SOM	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
SC	1, 16	0.91	0.35	0.69	0.42	1.62	0.22	1.51	0.24
D	3, 60	315.06	**< 0.001**	283.84	**< 0.001**	15.13	**< 0.001**	112.67	**< 0.001**
SC X D	3, 60	0.4	0.75	0.79	0.5	1	0.4	0.52	0.67

		% WHC		Net mineralization (ug N/gdw/week)		Net nitrification (ugN/gdw/week)	
	df	*F*	*p*	*F*	*p*	*F*	*p*
SC	1, 16	0.5	0.49	0.44	0.52	0.14	0.71
D	3, 60	0.68	0.56	4.79	**0.005**	10.54	**< 0.001**
SC X D	3, 60	1.01	0.33	5.72	**0.002**	6.82	**< 0.001**

Table S1.6. Results of PERMANOVA (adonis function, *vegan* package) testing whether fungal bacterial, and nitrifying bacterial communities vary in species composition when (A) the full soil profile is clustered by soil conditioning, texture, or depth and (B) each depth is clustered by soil conditioning or texture, using the Bray-Curtis distance metric and 999 permutations.

A.

		Fungi (ITS)			Bacteria (16s)			Nitrifying bacteria (16s)		
	df	*F*	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*
Soil Texture	1	3.21	0.03	**0.001**	9.05	0.06	**0.001**	6.95	0.04	**0.001**
Depth (D)	3	4.72	0.14	**0.001**	20.10	0.39	**0.001**	26.75	0.46	**0.001**
Soil Conditioning (SC)	1	4.75	0.05	**0.001**	2.67	0.02	**0.001**	3.13	0.02	**0.018**
D X SC	3	1.19	0.03	0.12	1.12	0.02	0.31	0.98	0.02	0.45

B.

		0-15 cm			15-30 cm			30-60 cm			60-90 cm		
	df	*F*	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*	*F*	R^2	*p*
Fungi (ITS)													
Soil Conditioning	1	2.10	0.09	**0.001**	2.65	0.11	**0.001**	1.60	0.08	**0.003**	2.03	0.09	**0.002**
Soil Texture	1	1.86	0.08	**0.002**	1.4	0.06	0.072	1.14	0.06	0.17	1.26	0.06	0.13
Bacteria (16s)													
Soil Conditioning	1	1.62	0.07	**0.027**	1.27	0.06	0.19	1.2	0.05	0.17	1.87	0.07	**0.027**
Soil Texture	1	3.36	0.14	**0.001**	3.31	0.15	**0.001**	4.97	0.2	**0.001**	4.43	0.18	**0.001**
Nitrifying Bacteria (16s)													
Soil Conditioning	1	2.11	0.09	**0.006**	1.37	0.06	0.18	1.54	0.06	0.08	2.88	0.11	**0.003**
Soil Texture	1	2.61	0.11	**0.002**	3.26	0.14	**0.005**	3.55	0.15	**0.001**	3.21	0.13	**0.001**

Table S1.7. Results of permutation test for homogeneity of multivariate dispersions (betadisper function, vegan package) testing whether fungal, bacterial, and nitrifying bacterial communities varied in dispersion when (A) the full soil profile is clustered by soil conditioning, texture, or depth and (B) each depth is clustered by soil conditioning or texture.

A.

		Fungi (ITS)		Bacteria (16s)		Nitrifying bacteria (16s)	
	df	*F*	*p*	*F*	*p*	*F*	*p*
Soil Conditioning	1	6.60	**0.008**	0.19	0.68	0.03	0.84
Soil Texture	1	8.04	**0.004**	0.17	0.73	4.34	0.048
Depth	3	1.24	0.28	15.17	**0.001**	6.73	**0.002**

B.

		0-15 cm		15-30 cm		30-60 cm		60-90 cm	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Fungi (ITS)									
Soil Conditioning	1	1.72	0.21	10	**0.003**	3.53	0.07	24.48	**0.001**
Soil Texture	1	5.17	**0.04**	3	0.11	1.36	0.27	0.67	0.43
Bacteria (16s)									
Soil Conditioning	1	4.89	**0.036**	3.33	0.09	1.31	0.25	0.17	0.72
Soil Texture	1	6.93	**0.015**	5.04	**0.032**	0.31	0.59	0.64	0.44
Nitrifying Bacteria (16s)									
Soil Conditioning	1	0.54	**0.47**	1.86	0.21	2.56	0.12	0.44	0.52
Soil Texture	1	4.72	**0.037**	4.94	**0.038**	1.20	0.29	1.80	0.18

Table S1.8. Results from Kruskal-Wallis tests on the effect of soil conditioning on the relative abundance of fungal functional guilds and nitrifying bacteria families across the full soil profile as well as each individual depth. Only significant ($p < 0.05$) values shown.

		Soil conditioning effect				
		full soil profile	0-15 cm	15- 30 cm	30-60 cm	60-90 cm
Fungal Guild	df	$\chi^2(p)$	$\chi^2(p)$	$\chi^2(p)$	$\chi^2(p)$	$\chi^2(p)$
Arbuscular Mycorrhizae	1	17.61 (<0.001)	10.17 (0.002)	11.89 (<0.001)		
Plant Pathogen	1	7.36 (0.007)				
Saprotroph	1	15.32 (<0.001)		5.74 (0.017)	4.46 (0.035)	4.01 (0.045)
Endophyte	1	8.95 (0.002)	4.72 (0.029)			
Plant Pathogen - Saprotroph	1	5.44 (0.02)			5.11 (0.023)	
Endophyte - Saprotroph	1					
Nitrifying bacteria family						
Nitrospiraceae	1				6.73 (0.009)	10.57 (0.001)
Nitrosomonadaceae	1	3.88 (0.049)			4.8 (0.028)	

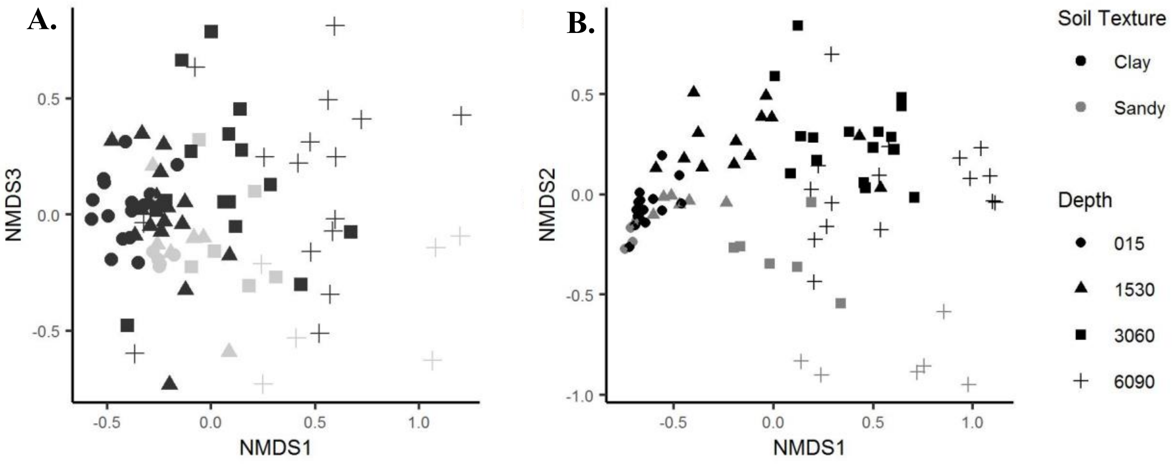


Figure S1.3. Non-metric multidimensional scaling ordination using Bray-Curtis dissimilarity on the species composition of (**A**) fungal (ITS) and (**B**) the bacterial (16s) community showing the effect of soil texture and depth. Communities are significantly structured by soil texture and depth.

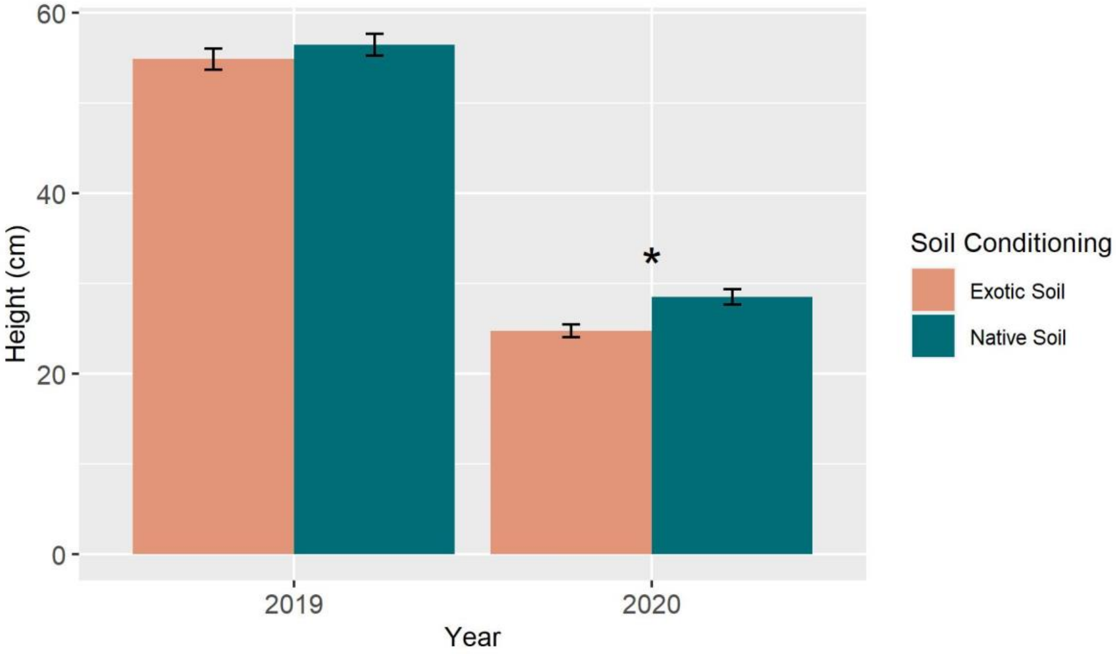


Figure S1.4. *B. hordeaceus* height across years and soil conditioning, averaged across competitive subplot. Height was 3.76 cm taller in native soil, but only during the 2nd growing season (which was much drier than the 1st) (ANOVA, soil conditioning x year, $p = 0.032$), was not influenced by competition with natives. Analyses were performed on the log transformation. Asterisks indicates significant difference of $p < 0.05$ in a post-hoc comparison of means between soil conditioning groups.

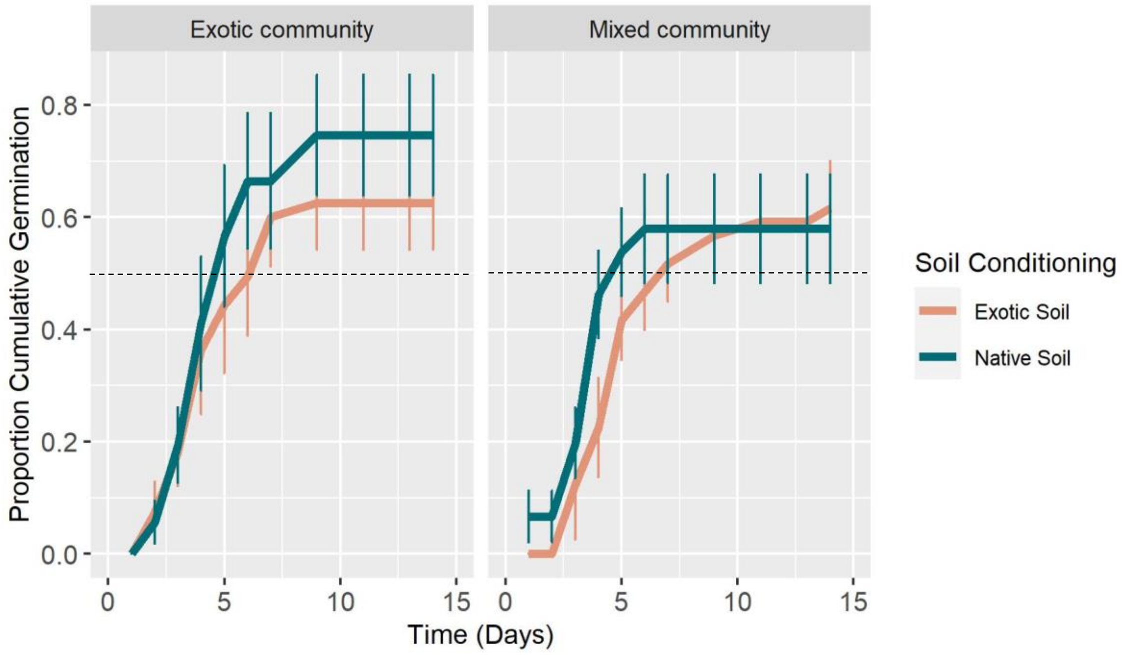


Figure S1.5. Germination curves of *A. fatua* in the exotic community and mixed exotic and native community. *A. fatua* had a negative feedback, reaching 50% germination (dotted line) 1.5 (+/- 0.62) days earlier in native soil but only when grown with native species (not when grown alone in the exotic mix), indicating that the presence of native seeds may have prompted faster germination (t = 2.45, p = 0.014). Total maximum germination did not differ significantly by soil conditioning for either community.

Table S1.9. ANOVA results from linear mixed effect models on the effect of soil conditioning treatment and soil depth on log-transformed belowground biomass with plot as a random effect for each competitive community. Interactions were only tested when included in the model of best fit as determined by stepwise AIC comparison. Bold values indicate significance at a p < 0.05 level.

	Native community			Exotic community			Native + Exotic community		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Soil Conditioning	1, 13	3.63	0.079	1, 14	9.06	**0.009**	1, 12	17.87	**0.001**
Depth	2, 72	38.01	< **0.001**	2, 77	60.66	< **0.001**	2, 77	54.13	< **0.001**
Year	1, 72	127.42	< **0.001**	1, 77	18.99	< **0.001**	1, 77	85.32	< **0.001**

Table S1.10. ANOVA results from linear mixed effect models on the effect of soil conditioning and community treatments on log-transformed percent cover measures with plot as a random effect for native and exotic grasses. Models were run on the species and community (total cover of all species with no species term) levels. Interactions were only tested when included in the model of best fit as determined by stepwise AIC comparison, *community* could not be included in the exotic grass species level model due to singularity of fit. Bold values indicate significance at p < 0.05.

	Native grass cover					
	Species-level			Community-level		
	df	*F*	*p*	df	*F*	*p*
Soil Conditioning	1, 51	4.07	**0.049**	1, 12	6.54	**0.025**
Community	1, 51	140.82	**< 0.001**	1, 39	589.1	**< 0.001**
Year	-	-	-	1, 39	45.32	**< 0.001**
Species	1, 51	77.61	**< 0.001**	-	-	-
Species X Community	1, 51	6.43	**0.014**	-	-	-
Community X Year	-	-	-	1, 39	6.5	**0.015**

	Exotic grass cover					
	Species-level			Community-level		
	df	*F*	*p*	df	*F*	*p*
Soil Conditioning	1, 14	1.31	0.27	1, 14	0.4	0.54
Community	-	-	-	1, 46	0.04	0.84
Year	1, 230	1.1	0.3	1, 46	0.21	0.65
Species	3, 230	62.02	**< 0.001**	-	-	-
Species X Year	3, 230	16.2	**< 0.001**	-	-	-
Species X Soil Conditioning	3, 230	2.95	**0.03**	-	-	-

Table S1.11. ANOVA results from linear mixed effect models on the effect of soil conditioning treatment (SC), community treatment (C), and either year (Y) or month (M) on log-transformed height measurements with plot as a random effect for each species in the experiment. Interactions were only tested when included in the model of best fit as determined by stepwise AIC comparison. Bold values indicate significance at $p < 0.05$.

	B. hordeaceus			*E. caput-medusae*			*A. fatua*		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
SC	1, 7	8.69	**0.022**	1, 7	0.03	0.87	1, 14	0.28	0.61
C	1, 492	0.1	0.75	1, 468	0.04	0.85	1, 494	0.001	0.98
Y	1, 492	977.07	< **0.001**	1, 468	71.57	< **0.001**	1, 494	148.73	< **0.001**
SC X Y	1, 492	4.83	**0.032**	-	-	-	-	-	-
C X Y	1, 492	4.6	**0.028**	-	-	-	-	-	-
	Native seedlings (Native community) 1st season			*S. pulchra* (Native community) 2nd season			*E. glaucus* (Native community) 2nd season		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
SC	1, 7	2.27	0.17	1, 7	7.39	**0.03**	1, 7	1.03	0.34
M	2, 856	828.43	< **0.001**	2, 262	14.31	< **0.001**	2, 584	54.35	< **0.001**
SC X M	2, 556	1.56	0.21	2, 262	4.31	**0.014**	2, 584	2.46	0.087

Table S1.12. Results of likelihood ratio tests for generalized linear mixed effect models with negative binomial distribution and plot as random effect, testing the effects of soil conditioning (SC) and species (S) on the number of native flowering individuals in the native community. Flowering individual count was modeled on both the species level and community level. Bold values indicate significance at the $p < 0.05$ level.

	Flowering individual count (species level)			Total flowering individual count (community level)		
	χ2	df	*p*	*χ2*	df	*p*
SC X S	0.41	2	0.82	-	-	-
SC	4.73	1	**0.03**	4.76	1	**0.029**
S	36.68	1	**<0.001**	-	-	-

Chapter 2: Long-term priority effects in California grasslands and the disruptiveness of drought

ABSTRACT

The high variability of California's stable annual-dominated grasslands defies prediction of community trajectories by traditional frameworks of succession and makes management challenging. Utilizing the concept of priority effects (i.e. when the first species to arrive alters the trajectory of the community) may help us better understand community change, particularly when considering functional groups rather than individual species. California grasslands are composed of three main grass functional groups that differ in phenology: early-season naturalized exotic annuals, late-season noxious weed annuals, and late-season native perennials. To assess the importance of priority effects in determining the long-term trajectory of plant community composition, we investigated whether each functional group, when seeded alone (and thus given temporal priority) will a) have higher cover than when grown in competition, and b) limit recruitment of another naturally colonizing functional group. We measured composition annually for 12 years in experimental grassland plots that were seeded with all combinations of each functional group, and which were allowed to be naturally colonized once established for 1 or 2 years. We found that priority effects among functional groups were initially strong but disappeared or weakened during an extreme multi-year drought. However, priority effects persisted when species groups had similar phenology – the late-season noxious weeds and native perennials limited the growth of the other when grown in competition as well as limited the other's recruitment. The native perennials more strongly limited noxious weed recruitment due to niche-preemption of the long-lived individuals, suggesting that native grassland restoration should be a priority in areas vulnerable to noxious weed invasion.

INTRODUCTION

Understanding long-term plant community dynamics has been a key challenge in ecology (Clements et al. 2013, D'Amen et al. 2017), made even more challenging by the increased frequency of plant invasion and novel environmental conditions. A number of studies have demonstrated that new climatic extremes, such as severe and prolonged drought, may have long-term legacies on plant communities by affecting resource availability and altering dominant species (Weltzin et al. 2003, Jiménez et al. 2011, Smith 2011, Griffin-Nolan et al. 2018). In systems dominated by long-lived perennial plants, novel disturbances can disrupt generally predictable successional change (Young et al. 2001). Understanding the impacts of novel disturbances on vegetation dynamics is even more challenging in annual-dominated plant communities, where composition can reset each year (Heady 1958, Hobbs and Mooney 1995).

Annual systems have high turnover in species composition due to multiple biotic and abiotic drivers with high inter-annual variability (Heady 1958, Hobbs and Mooney 1995). Drivers such as the timing and amount of precipitation and temperature (Becchetti et al. 2016), fungal pathogens (Schafer and Kotanen 2004), and herbivores (Borchert and Jain 1978, Peters 2007) act on seed production, seed survival and germination, seedlings, and mature plants (Heady et al. 1991, Bartolome et al. 2007). In addition, vegetation can be influenced by the quantity of litter from the previous season (Bartolome et al. 2007, Dudney et al. 2017, Grinath et al. 2018, Hallett et al. 2019). Thus, species composition in annual systems is difficult to predict (Jackson and Bartolome 2002, Bartolome et al. 2007) and manage (Bartolome et al. 2007, Malmstrom et al. 2009).

These controlling variables are often strongly impacted by previous species composition, and thus predicting community changes in annual systems may benefit from considering priority effects. Priority effects are when the timing and order of species arrival during assembly determines which species can later establish in the community, leading to alternative stable states, alternative transient states, or compositional cycles (Fukami 2015). Priority effects have been observed to affect composition and diversity in multiple systems (Sarneel et al. 2016, Grainger et al. 2018, Korner et al. 2008). In perennial systems, a long-lived species can physically hold space against competitors over time, occupying this niche to the exclusion of later arrivals (Fukami 2015, Fukami et al. 2016). In fact, planting of perennial grasses is frequently used as a way to suppress annual weeds (Corbin and D'Antonio 2004, Lulow 2006, Blank et al. 2015, Ott et al. 2019). Among annual plants, priority effects may occur through mechanisms such as litter build up, seed production and faster germination, and plant-soil feedbacks related to changes in pathogen and symbiont communities (Uricchio et al. 2019).

Priority effects are stronger among species with high overlap in resource use, resulting in greater niche co-option and exclusion of later arrivals of similar function and phenology (Cleland et al. 2007, Tucker and Fukami 2014, Fukami 2015). Assessing vegetation community dynamics in California's annual grasslands may thus benefit from defining functional groups in terms of phenology (Seabloom et al. 2005, Stevens and Fehmi 2011, Dickson et al. 2012), which dictates when California grasses compete for the limited resource of soil moisture. California's grasslands are dominated by early-season exotic annual species that are now so entrenched in the landscape they are considered naturalized; they generally outcompete native grass and forb seedlings, as they germinate and grow faster, depleting shallow soil moisture and creating light-limitation (Holmes and Rice 1996, Dyer and Rice 1999, Hamilton et al. 1999, Deering and Young 2006, Grman and Suding 2010). Several priority experiments have shown that native perennial grasses in this system benefit from a two-week head start over naturalized exotic species (Wainwright et al. 2012, Vaughn and Young 2015, Young et al. 2017).

A newer set of invading exotic annual species, including the grasses *Elymus caput-medusae* and *Aegilops triuncialis,* are classified as noxious weeds and are of particular concern because they produce thick layers of thatch that is slow to decompose and prevents germination of other species (Davy et al. 2008, Stannard et al. 2010, Kyser et al. 2014). These noxious weeds germinate at the same time as the early-season exotics, but their above-ground growth primarily occurs after rains have ended and the earlier season grasses have senesced (Peters et al. 1996, Enloe et al. 2004, Stannard et al. 2010). In drier years, early-season naturalized exotic growth can limit noxious weeds by utilizing all soil moisture, but cannot prevent noxious weed growth if late-season moisture is present (Hironaka 1961). Native perennial grasses, which are active during the late-season, may compete with noxious weeds for the dwindling late-season soil moisture. However, how long priority effects last on all three functional groups is unknown.

We established field plots consisting of early-phenology naturalized exotic annual species, late-phenology annual noxious weeds, and native species commonly used in restoration mixes (i.e. perennial grasses and annual forbs and grasses). Each group was seeded alone or simultaneously in mixtures with other groups to compare to assess the importance of being seeded without initial competition. All plots were then allowed to be naturally colonized by non-seeded species in the experiment, but with a subset of plots receiving a one-year weeding treatment to provide additional priority. We assessed composition over a twelve-year period that included an extreme multi-year drought followed by a historic wet year, and then another severe drought year. Such extreme weather events in other systems have been shown to disrupt plant community dynamics, reducing cover of resident species and increasing invasion (Jiménez et al.

2011). This experiment is particularly valuable because the majority of priority effect studies take place in the greenhouse and for less than a year in duration, and it is widely recognized that more field and long-term experiments are needed to determine the strength of priority effects in varying conditions (Young et al. 2017, Weidlich et al. 2021). Of the few long-term studies, the current literature has shown both that priority effects either persist or disappear depending on the system and the species involved (Collinge and Ray 2009, Werner et al. 2016, Veen et al. 2018, Stuble and Young 2020).

We hypothesized that all three functional groups of species, when seeded alone, will: (1) have greater cover than when grown in competition, and (2) limit recruitment of another naturally colonizing functional group. An additional year of priority will lead to stronger long-term priority effects. We also predict that the multi-year drought will weaken priority effects during and beyond the drought in favor of the early-season naturalized exotics, as they have will have first access to soil moisture.

METHODS

Site Information & Experimental Set Up

Plots were located in UC Davis Campbell Tract Experimental Site in Davis, CA (38.545751, -121.784780). Prior to plot establishment, the land was used for agricultural purposes and then lay fallow for twenty-two years. The site was primarily on Reiff series soil, with a sandier lens of Brentwood soil series on 25% of the site (https://casoilresource.lawr.ucdavis.edu/gmap/). Under a Mediterranean climate, the site experienced hot, dry summers (mean maximum temperature 33°C) and wet, cold winters (mean maximum temperature 14°C) that correspond with the growing season of cool season grasses.

Rainfall has high inter- and intra-annual variability, with mean annual precipitation of 445 mm (1990-2019). During the experiment, California experienced a historic drought between the 2012-2014 water years (water year: Oct 1st of previous year to Sept 30th of reference year), followed by 2 years with precipitation levels that were substantially closer to the 30-year precipitation average, and then followed by one of the wettest years on record in 2017, then a dry year, followed by another historic wet year (Figure 2.1).

Prior to initial seeding at the start of the experiment in fall 2007, the seed bank and resident vegetation were minimized by disking the soil, irrigating to germinate the seedbank, and spraying germinating seedlings with herbicide (1% glyphosate). Irrigation and herbicide treatments were performed twice before planting. Plots were seeded with one of the following vegetation treatments in a randomized block design (15 replicates): (1) native perennial grasses and annual forbs, (2) exotic annual noxious grasses, (3) naturalized exotic annual grasses and forbs, and (4) all possible combinations of these three groups (see Table 2.1 for species composition), at a rate of 139 g seed/plot. Plots were 1.5 x 1.5 m with a 1m buffer between them (with larger buffers between blocks).

For each single functional group mix, equal proportion of seeds of each species were added. For functional group mixes, an equal proportion of each functional group seed was added, with equal proportion of individual species within each functional group. Given that the common design of seeding equivalent weights across all treatments design results in the multi-group treatments having less seed per species group (Guo 2011), short-term conclusions may be influenced by seed limitation as well as priority effects. However, the effects of seed limitation should be short-lived given the annual species in this experiment are highly prolific and able to rebound from extremely low to high cover from one year to the next, as well as naturally selfthinning (Eviner 2016). While natives are seed limited, low density can still result in high cover (Seabloom 2011), and so changes in native cover can be attributed to changes in individual size as well as population response.

Percent cover of each species present was assessed visually with a modified Daubenmire bin method (<1%, followed by every 10%) of the inner 1m x 1m core. Composition was measured twice each season annually from 2008 to 2019 to capture peak flowering species with different phenologies (early April vs. late May/early June). The highest cover value across the two sample points each year for each species was used for analysis.

Priority Levels

There were multiple levels of priority in this experimental design. For a given functional group, the seeding treatment in which they were seeded alone in monotype is the highest level, as they accessed the space first with no competition from other functional groups. The seeding treatments in which that functional group were seeded simultaneously with another group are a secondary level of priority, as they shared first access to the space. The remaining seeding treatments are those in which the functional group in question was not seeded, thus they had no priority at all. If present later in the experiment, they recruited into the space after initial colonization by the planted functional group, and thus faced high competition for resources from established residents (native perennials) or high propagule pressure (annuals). Given the spatial distribution of the experimental plots, every plot was close to a seed source of another functional group from neighboring plots and the unplanted walkways between plots and blocks became quickly colonized, indicating that the species were dispersing throughout the site quickly.

Superimposed on the above listed priority levels was a weeding treatment to determine the difference between one vs two years of priority. Natural colonization was either allowed immediately (one year of priority for 7 blocks) or postponed an extra year due to hand-weeding after the first year to maintain the initial species compositions of the seeding treatments (two years of priority for 8 blocks). Since then, all plots were occasionally weeded for agricultural weeds that were not part of the study but species that self-recruited and are typical species in California grasslands (e.g., *Bromus diandrus*, *Erodium* species, *Geranium* species, *Galium* species) were not weeded.

Statistical analysis

Hypothesis 1: Giving temporal priority to a functional group will result in greater cover than when grown in competition

To evaluate the role of priority effects in long-term community composition, we assess the difference in cover when a functional group is seeded alone, with full priority, to when seeded with other functional groups, and how these differences change over time. For each functional group, we compared percent cover in the treatment where it was seeded alone in a monotypic stand to the three treatments where it was seeded in combination with the two other functional groups (secondary level of priority) (Table 2.2). We fit linear mixed effect models with percent cover of each functional group as the dependent variable, specifying seeding treatment, priority length (1 or 2 years), year (2008-2019), and their 3-way interaction as fixed effects, and random effects included plot (to account for repeated measures) and block (to account for within site variation). Significance was tested with analysis of variance (ANOVA) followed by post-hoc multiple pairwise comparison tests ($p < 0.05$) using estimated marginal means. We focused on the following three terms of the model, as their ecological meaning was determined *a priori* to be most interpretable and relevant to our question: year, seeding treatment*year, and seeding treatment*year*priority length.

While the year term in the model implicitly accounts for annual precipitation, it also incorporates variation from other factors such as legacy in cover and cannot sufficiently address the potential role of annual precipitation. We more specifically assessed the role of annual precipitation (and the multi-year drought) by conducting simple linear regressions to determine the correlation between each functional groups' cover in their monotypic planted mix and annual precipitation.

Hypothesis 2: Temporal priority will result in resistance to recruitment of other functional groups

Priority effects can be the outcome of the seeded species having both higher propagule pressure and biotically resisting the recruiting species and we are interested in the long-term trajectory of the initially planted communities and the extent to which they are naturally colonized by functional groups that have been planted nearby. To test our hypothesis, we performed two comparisons. First, for each year, we compared cover of the recruiting functional group in its monotypic seeding treatment, which presumably represents the best conditions for performance as it has the highest level of priority, to the three seeding treatments in which the functional group was not planted (**Table 2.3**). If the recruiting functional group cover is higher in its own monotypic treatment, then it would suggest that the functional groups originally planted are providing some level of resistance. Second, we compared the recruiting functional group's cover as it changed over time within each seeding treatment it was not planted into, such as whether recruiting species cover stays consistently low or increases with time. This took into consideration potential annual population fluctuations due to environmental conditions and provides detail on resistance not captured by the first comparison. Both comparisons are necessary to determine whether low presence of a recruiting functional group is due to biotic resistance or poor environmental conditions. We also compared cover between the one- and two-year priority weeding treatments.

Both comparisons were assessed with the same linear mixed effect model but differed in how we performed the post-hoc analysis. First, we fit linear mixed effect models with percent cover of each recruiting functional group as the dependent variable, specifying seeding treatment, priority length (1 or 2 years), year (2008-2019), and their 3-way interaction as fixed effects and plot (repeated measures) and block as random effects. Significance was tested with analysis of variance (ANOVA). Both comparisons were assessed with post-hoc multiple comparison tests using estimated marginal means ($p < 0.05$) on the interaction of seeding treatment and year when significant in the ANOVA (and the potential three-way interaction with priority length) but differed in the order of terms used. The first compared cover across the different seeding treatments within each year while the second compared over across the 12 years within each seeding treatment.

All statistical analyses were conducted in R 4.0.3 (R Development Core Team). Linear mixed effect model fitting was performed using “lme4” (Bates et al. 2015) and “lmerTest” (Kuznetsova et al. 2017). Multiple comparison tests were conducted using “emmeans” (Lenth 2018).

RESULTS

Hypothesis 1: Giving temporal priority to a functional group will result in greater cover when grown in competition

Noxious weeds

We tested our hypothesis by comparing cover in the monotypic seeded plots to the seeding treatments planted with other functional groups. The interaction of seeding treatment and year was significant ($F = 14.91$, $p < 0.001$, Table 2.4), showing that the impact of priority seeding on noxious weed cover depended on year. In the first three years of the experiment, there was strong evidence of priority effects, as noxious weed cover was significantly higher when seeded alone compared to when seeded simultaneously with either the natives, naturalized exotics, or the mix of them all ($p < 0.05$, Figure 2.2A, Table S2.1). After the onset of drought (2012) and until the end of monitoring, noxious weed cover was similar when seeded alone and with the naturalized exotics ($p > 0.05$, Figure 2.2A, Table S2.1). Being seeded with natives resulted in lower noxious weed cover ($p < 0.05$, Figure 2.2A, Table S2.1) on and off until the last 3 years of monitoring, when noxious weed cover was similarly low across all treatments ($p > 0.05$, Figure 2.2A, Table S2.1). Future data will be needed to determine whether suppression of noxious weeds by natives has disappeared or persists.

Naturalized exotic annuals

The impact of priority seeding on naturalized exotic cover also changed over time, with a significant interaction between seeding treatment and year ($F = 4.93$, $p < 0.001$, Table 2.4). In the first year of the experiment, there was no significant evidence for priority effects, as naturalized exotic cover was similarly high in all treatments ($p > 0.05$, Figure 2.2B, Table S2.1). Priority effects did arise the following year, with naturalized exotic cover greatest when planted alone ($p < 0.05$, Figure 2.2B, Table S2.1) for 3 years until the onset of the drought. During and after the drought, naturalized exotic cover was no longer impacted by seeding treatment *(*$p > 0.05$, Figure 2.2B, Table S2.1).

Natives

While the first year of native cover consisted primarily of the seeded annual native forbs and grasses, the later years were dominated by the native perennial grasses. The full interaction of seeding treatment, priority length, and year significantly affected native cover (F = 1.77, $p = 0.006$, Table 2.4). Regardless of the priority length weeding treatment, native cover was highest in its monotypic priority seeding treatment in the early years of the experiment before the drought ($p < 0.05$, Figures 2.2C, 2.2D, Table S2.1), but by the second year of the drought native cover was no longer highest when seeded alone ($p > 0.05$, Figures 2.2C, 2.2D, Table S2.1). The priority length weeding treatment then impacted the seeding treatment and year interaction post-drought, as only in the 2-year priority plots was native cover generally higher in the native and native + naturalized exotic mixes alone than when noxious weeds were also seeded ($p < 0.05$, Figure 2D, Table S2.1). When comparing the impact of the weeding treatment within each seeding treatment each year, only native cover in the monotypic priority significantly differed; being given an extra year of priority resulted in higher native cover post-drought in 2016-2018 than when given only one year of priority ($p < 0.05$, Figure 2.3).

Annual precipitation and composition variation

For all functional groups, year was significant in determining cover ($p < 0.001$, Table 2.4), Prior to 2017, all functional group's cover positively correlated with annual precipitation ($p < 0.001$, native $R^2 = 0.23$, naturalized exotic $R^2 = 0.32$, noxious weed $R^2 = 0.28$, Figure S2.1), as generally occurs in a water-limited system. Including the last three years of the data, however, resulted in no correlation despite the two high rainfall years of 2017 and 2019; this break in general expectation further emphasizes the impact of the multi-year drought had on community composition and priority effects.

Hypothesis 2: Temporal priority will result in resistance to recruitment of other functional groups

Noxious weed recruitment into native and naturalized exotic plots

Noxious weed cover was significantly impacted by the seeding treatment and year interaction (F = 29.57, $p < 0.001$, Table 2.5), indicating the impact of priority effects on recruiting species cover changed with time. In the first three years of the experiment, noxious weed cover was lower in the naturalized exotic plots than in the monotypic noxious weed plots ($p < 0.05$, Figure 2.4A, Table S2.2). After greatly increasing in the 1st year of drought ($p < 0.05$, Table S2.3), however noxious weed cover became equivalent in both treatments throughout the rest of the study ($p > 0.05$, Figure 2.4A, Table S2.2), including the same yearly fluctuations of decreasing with drought and making a modest post drought recovery (Table S2.3), which demonstrates that naturalized exotics lost resistance to noxious weed recruitment. In contrast, there was extremely limited noxious weed establishment in native plots throughout the entire duration of experiment (Figure 2.4A, Table S2.2), which stayed consistently low with no yearly fluctuations ($p > 0.05$, Figure 2.4A, Table S2.3).

Naturalized exotic annual recruitment into native and noxious weed plots

Naturalized exotic cover was also significantly impacted by the interaction of seeding treatment and year (F = 15.87, $p < 0.001$, Table 2.5). Prior to the drought, the native mix, noxious weed mix, and native and noxious weed mix seeding treatments had lower naturalized exotic cover than in the monotypic naturalized exotic plots. (Figure 2.4B, Tables S2.2 & S2.3). Starting in 2013, the second year of the drought, naturalized annual cover no longer differed among treatments ($p > 0.05$, Table S2.2), and showed similar yearly fluctuations across all treatments (Table S2.3), indicating that both natives and noxious weeds lost their initial resistance. While the natives lost resistance to the naturalized exotics, by 2019 naturalized exotic cover was again lower in the native mix plots than the naturalized exotic plots ($p < 0.$ 0.05, Figure 2.4B, Table S2.2).

Native recruitment into naturalized exotic and noxious weed plots

The native cover model showed a significant interaction between seeding treatment and year ($F = 15.42$, $p < 0.001$, Table 2.5). Native recruitment began during the drought and progressively increased afterwards ($p < 0.05$, Figure 2.4C, Table S2.3), but to suppressed levels as native cover was almost always significantly greater in its own monotypic priority plots compared to the treatments seeded without natives ($p < 0.05$, Table S2.2). Notably, as seen in the last three years of the data, native recruitment was at least twice as high in the naturalized exotic mix plots than the noxious weed mix plots.

DISCUSSION

Our study assessed the role of priority effects in determining long-term community composition in a system that experienced high annual variability in weather, including a multi-year drought event followed by one of the wettest years on record, and then another historic dry year, and another historic wet year (Wang et al. 2017, Ullrich et al. 2018). These conditions are representative of extreme climatic events that are predicted to become more common (IPCC 2007) and are expected to have different outcomes on plant community function and productivity than more gradual climatic change (Smith 2011, Dreesen et al. 2012), such as increasing invasion by lowering a community's biotic resistance (Diez et al. 2012). This long-term field experiment provides important insights into the strength and nature of priority effects, showing they can be important even in systems with high annual variability, and can have different roles prior, during, and after the severe drought. Our study aimed to test priority effects in as natural a setting as possible, and so we relied on natural colonization throughout the site (Weslien et al. 2011, Plückers et al. 2013, Roscher et al. 2014) rather than explicitly controlling the order of arrival through seed addition, as is most common (Weidlich et al. 2021); as such we are relying on our knowledge of species movement throughout site but cannot verify similar propagule pressure among plots.

We initially observed strong priority effects between all three functional groups, both in maintaining the highest cover when seeded alone as well as suppressing the establishment of other recruiting species. However, the benefit of being planted alone weakened over the course of the multi-year drought; in most cases, species composition became the same regardless of seeding treatment by the third drought year. Similarly, recruitment of unplanted species began during the drought, also showing a weakening of priority effects, but with the notable exception of native perennial grasses continuing to suppress noxious weeds. The large compositional shift strongly suggests that drought served as a catalyst to reset the communities. Drought often disrupts communities by reducing cover, lowering seed production, increasing thatch, and impacting the microbial community (Davis et al. 2000, Meisner et al. 2013, Felton and Smith 2017), and can make the community more susceptible to invasion if the current resident species cannot recover as quickly as recruiting species can establish (Davis et al. 2000, Jiménez et al. 2011, Dreesen et al. 2015, Manea et al. 2016, Mojzes et al. 2020). Both exotic annuals and native grasses are negatively impacted by drought (Gerakis et al. 1975, Armstrong and Huenneke 1992, Copeland et al. 2016, LaForgia et al. 2018), but in our experiment the annual noxious weeds were most affected.

After the drought, we began to observe differences among each functional group in whether priority effects had truly disappeared or may have only not been observable due to low statistical power during the drought years. Priority effects among the two exotic annual grass groups completely disappeared and they reached co-existence, for each group's cover was the same when planted alone, with each other, and where each recruited into the other's priority plots. The loss of priority effects between the annuals may be attributed to a reduction in seed production (Sherrard and Maherali 2006, Becchetti et al. 2016) during the multi-year drought, as decreased neighborhood propagule pressure can increase susceptibility to invasion (Davis et al. 2016, Ibáñez et al. 2021), and as well as the reduction in decomposition (Coûteaux et al. 1995) since thatch build up can hinder germination (DiTomaso et al. 2007). Both exotic groups, however, were able to suppress recruitment of the native perennials after the drought, as expected with their higher propagule pressure and competitive seedling dynamics, although not as successfully as before the drought.

Priority effects persisted in the system when natives were involved, with the strongest effects observed between the native perennial and noxious annual grasses, which share the later-season-phenological niche. Each group continued to reduce cover of the other when seeded together and limited the other from recruiting into their monotypic seeded priority plots. However, while the role of phenology affected priority for both groups, the additional aspect of niche pre-emption of long-lived individuals resulted in stronger priority effects for the native perennials, which continuously kept noxious weed cover below 5%. The perennial deep-root system of the natives can limit soil moisture availability by using it early in the season and competing for residual moisture into the dry season. These results follow with the idea of limiting similarity, in that a species cannot invade if the niche is already occupied (MacArthur and Levins 1967, Fargione et al. 2003, Funk et al. 2008) and that priority effects are stronger among species of similar functional groups (Cleland et al. 2013, Fukami 2015). These principles are employed in restoration (Hooper and Dukes 2010, Byun et al. 2018, Hess et al. 2019), and perennials are often planted to suppress grassland weeds (Corbin and D'Antonio 2004, Blank et al. 2015, Ott et al. 2019).

The ability of the native perennial grasses to consistently suppress noxious weed recruitment despite the drought was striking when compared to their contrasting lack of resistance to the naturalized exotic annuals. The sharp increase in naturalized exotics after the natives decreased in cover during the drought isn't surprising, since native biomass is an important factor in preventing invasion (Lulow 2006), and niche pre-emption of perennials is dependent on individuals continuing in the same space overtime. Naturalized exotic recruitment in the native monotypic priority plots could have negatively impacted the adult natives (Hamilton et al. 1999), which may explain why by the final year native cover was the same where planted alone and with the naturalized exotics. Regardless, native perennial cover increased to high levels when seeded, indicating that once individuals are established, they can persist among exotics, although they remain strongly seed limited (Dyer and Rice 1999, Lulow 2006, Seabloom 2011).

For natives, the importance of seedlings being given an extra year of priority before potential natural colonization of exotic annuals arose only during post-drought recovery, eight years into the experiment. In native priority plots, giving two years of priority resulted in greater cover than those given one year, as well as resulted in significant observable priority effects over being seeded with the noxious weeds for most of the post-drought recovery. Root establishment the first year is crucial to native seedling survival (Hamilton et al. 1999, Brown and Rice 2000), and an extra year without competition for light and resources may have led to greater and deeper root biomass with greater belowground competitive ability (Cahill and Casper 2000). More root surface area to access available water likely leads to faster recovery post-drought (Fry et al. 2018). A quicker recovery post-disturbance would limit open opportunities for invasion (Hobbs and Huenneke 1992, Davis et al. 2000). From a restoration standpoint, this suggests that an extra year of weed control may have long-lasting benefits to project success and add resiliency to future drought disturbance.

Whether the changes we observed in the community composition would have still occurred without the drought is unknown and we cannot be certain about whether the strong priority effects would have lasted longer in less extreme conditions. Similarly, it is not clear if some of the weaker priority effects in the last couple years of monitoring are due to a weakening of priority effects over time, or variation in the strength of priority effects. Other long-term studies found that priority effects maintained lasting effects on the identity of the species present, but the communities converged in trait and functional diversity (Fukami et al. 2005, Veen et al. 2018). A nine-year experiment on native vernal pool species showed strong initial priority effects between the seeded species, but could not comment on long-term dynamics, as an extreme wet year followed by a drought year led to dominance of a non-seeded exotic species across all plots (Collinge and Ray 2009, Collinge et al. 2011).

Management Implications

Our study has implications for management of annual grasses, which are increasingly common across many systems (e.g. Great Basin in western United States (Knapp 1996), Fynbos in South Africa (Visser et al. 2017). Late-season noxious weeds are invading naturalized exotic-dominated rangelands, forming extensive monocultures of poor forage quality and causing economic and ecological harm (DiTomaso 2000, Eagle et al. 2007). Our study suggests targeting noxious weed management during drought years as well as prioritizing native restoration along the invasion front (Byun et al. 2018, Hess et al. 2019, Brisson et al. 2020, Weidlich et al. 2021). However, our results also confirm the necessity of weed control in the beginning of restoration (Stromberg et al. 2007) as well as the need to manage for naturalize exotics after drought events. Overall, our study adds to the evidence that giving priority to native species can enhance their establishment (Stevens and Fehmi 2011, Martin and Wilsey 2012, Schantz et al. 2015, Young et al. 2017), as well as suppress future invasions, particularly when the natives and invasives share similar functional roles or phenological niches (Hooper and Dukes 2010, Lang et al. 2017, Brisson et al. 2020).

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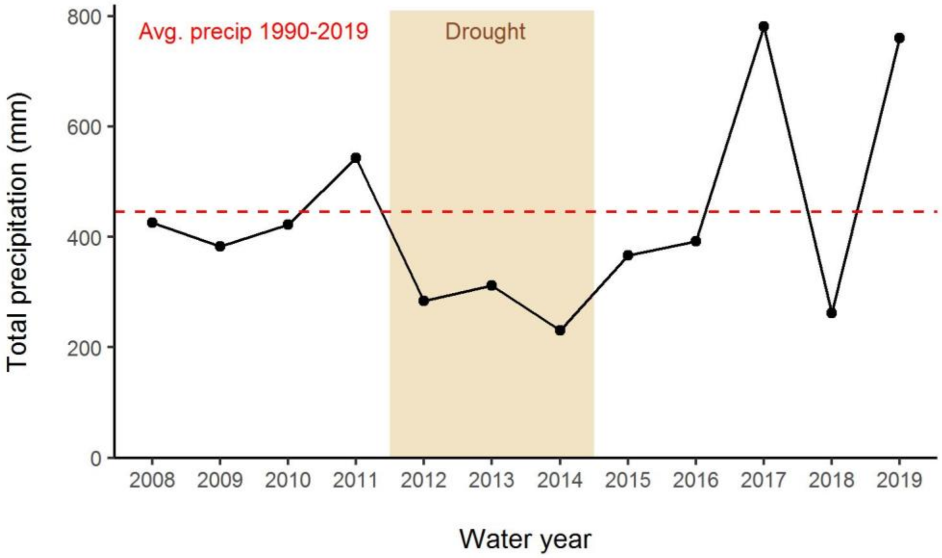

Figure 2.1. Total precipitation (mm) for each water year (Oct 1st of previous year to Sept 30th of reference year) of the experiment. The red dashed line refers to the 30-year average (1990-2019).

Table 2.1. Species composition of each functional group mix.

Natives (N) (grasses and forbs)	**Noxious exotic annual weeds (W)** (grasses)	**Naturalized exotic annuals (A)** (grasses and forbs)
*Elymus glaucus**	*E. caput-medusae*	*Avena fatua*
*E. triticoides**	*Aegilops triuncialis*	*Bromus hordeaceus*
*Stipa pulchra**		*Festuca perennis*
Bromus carinatus		*Trifolium subterraneum*
Festuca microstachys		*B. diandrus***
Acmipson americanus		*Hordeum murinum***
Lupinus bicolor		

*perennial species that maintained dominance in native mix plots compared to the annual species after 1st year
**not originally seeded, but now considered a component of the naturalized exotic annuals

Table 2.2. Seeding treatments compared to assess whether temporal priority provides long-term advantage in abundance for each functional group (Hypothesis 1). Percent cover of each functional group is compared in its monotypic seeding treatment to combination seeding treatments.

Functional group	**Monotypic seeding treatment** (highest priority)	**Combination seeding treatment** (secondary priority)
Natives (N)	N mix	N+W, N+A, N+A+W
Noxious annual exotic weeds (W)	W mix	N+W, W+A, N+A+W
Naturalized exotic annuals (A)	A mix	N+A, W+A, N+A+W

Table 2.3. Seeding treatments compared to assess the ability of a functional group to suppress recruitment of another functional group (Hypothesis 2). Percent cover of the recruiting functional group is compared between its monotypic seeding treatment and the seeding treatments it was not planted into.

Recruiting functional group	**Monotypic seeding treatment** (best conditions for recruiting species group)	**Seeding treatment not planted with recruiting functional group** (priority over recruiting species group)
Natives (N)	N mix	A, W, A+W
Noxious exotic annual weeds (W)	W mix	N, A, N+A
Naturalized exotic annuals (A)	A mix	N, W, N+W

Table 2.4. ANOVA results from linear mixed effects models testing the importance of priority seeding treatment (seeded alone or simultaneously with other functional group), priority length (1 or 2 years), year (2008-2019), and their potential interactions on the percent cover of three functional groups (native, naturalized exotic, and noxious weed) (Hypothesis 1). Only parameters hypothesized to be the most ecologically relevant are included. Post-hoc comparisons of the seeding treatment and year interaction are found in Table S2.1.

	Native Cover			Noxious Weed Cover			Naturalized Exotic Cover		
	df	F	p	df	F	p	df	F	p
Year	11, 569	31.53	< 0.001	11, 566	107.36	< 0.001	11, 569	100.76	**< 0.001**
Seeding treatment* Year	33, 569	12.8	< 0.001	33, 566	14.91	< 0.001	33, 569	4.93	**< 0.001**
Seeding treatment* Year*Priority length	33, 569	1.77	0.006	33, 566	1.2	0.2	33, 569	0.59	0.97

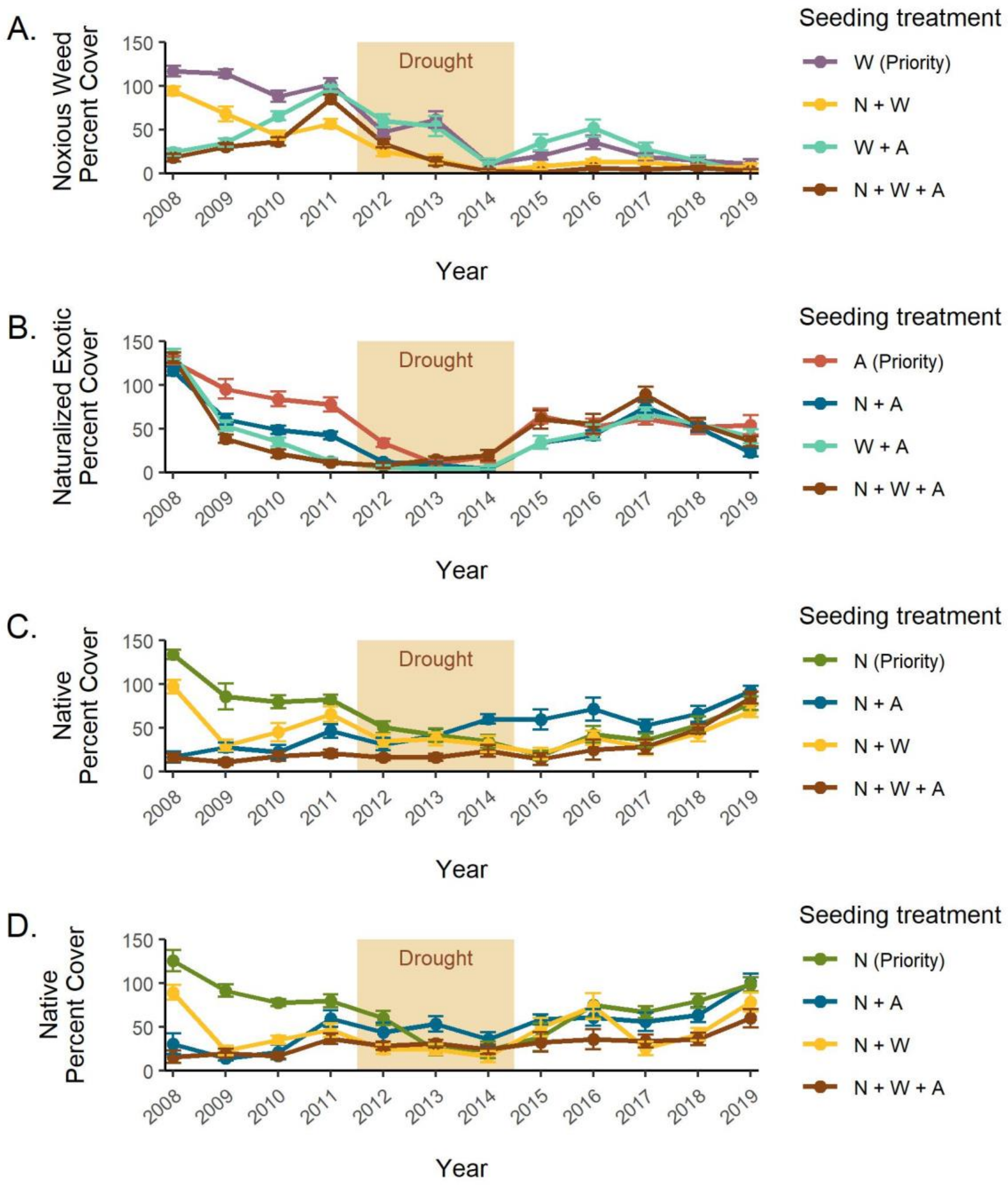

Figure 2.2. Percent cover of each functional group over time in their priority monotypic and combination seeding treatment plots (seeding treatment * year: $p < 0.001$ for all three models). Noxious weed cover (**A**) and naturalized exotic cover (**B**) did not show a difference in seeding treatment groupings by the length of priority treatment, and values shown include both priority length treatments. Native cover was impacted by the interaction of seeding treatment, year, and priority treatment ($p = 0.006$); thus the 1-year priority treatment (**C**) and 2-year priority treatment (**D**) are plotted separately. Asterisks indicate years in which percent cover of the species group in its monotypic seeding treatment differed significantly ($p < 0.05$) from at least one of the combination seeding treatments. See Table S1 for post-hoc analysis results on the seeding treatment and year interaction.

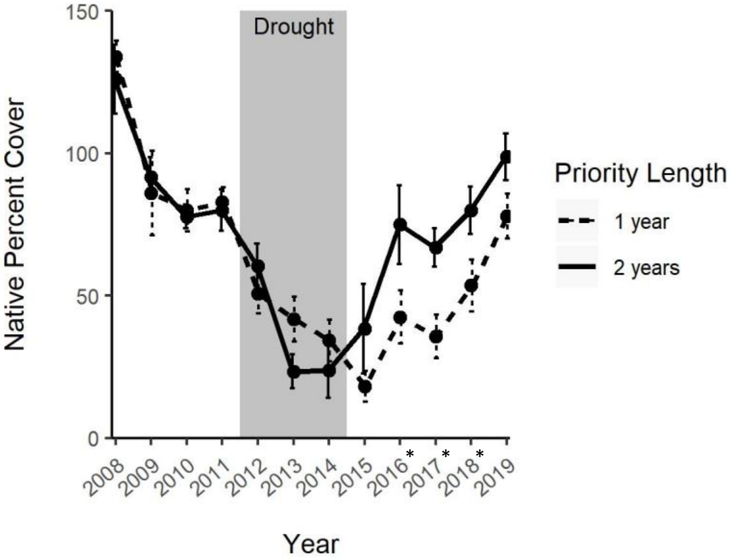

Figure 2.3. Native species percent cover in the native monotypic seeding treatment plots compared across one vs two years of priority. Asterisks indicate years with significant differences between priority length treatments at a $p < 0.05$ level in the post-hoc analysis of the full seeding treatment, priority length, and year interaction ($p = 0.006$).

Table 2.5. ANOVA results from linear mixed effects models testing functional groups' resistance to a recruiting functional group by assessing the effects of seeding treatment, priority length, time, and their potential interactions on the percent cover of three invading functional groups (native, naturalized exotic, and noxious weed) (Hypothesis 2). Only parameters hypothesized to be the most ecologically relevant are included. Post-hoc comparisons of the seeding treatment and year interaction are found in Tables S2.2 & S2.3.

	Native Cover			Noxious Weed Cover			Naturalized Exotic Cover		
	df	F	p	df	F	p	df	F	p
Seeding treatment* Year	33, 565	15.42	< 0.001	33, 567	29.57	< 0.001	33, 568	15.87	< 0.001
Seeding treatment* Year*Priority length	33, 565	0.73	0.87	33, 567	1.16	0.26	33, 568	0.64	0.95

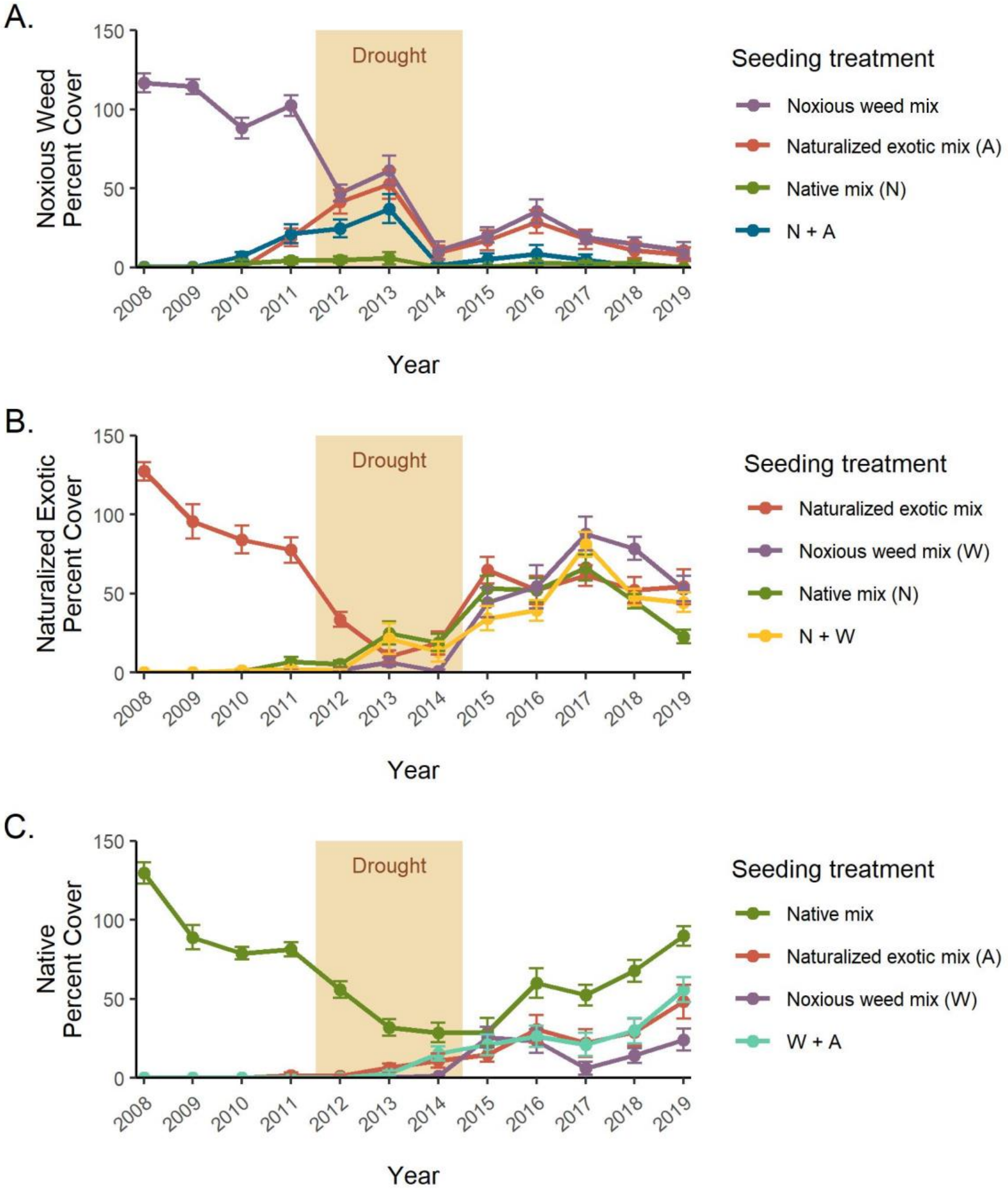

Figure 2.4. Percent cover of each functional group over time in their monotypic seeding treatment plots and the plots in which they were not planted (seeding treatment * year: $p < 0.001$ for all three models). All seeding treatments limited recruitment prior to the drought. Noxious weeds (**A**) recruited into the naturalized exotic mix but not the native mix plots. Naturalized exotic annuals (**B**) recruited into all seeding treatments at high levels, while natives (**C**) recruited into all but at lower levels. See Tables S2.2 & S2.3 for post-hoc analysis results on the seeding treatment and year interaction.

SUPPLEMENTARY MATERIALS

Table S2.1. Results of post-hoc multiple comparisons testing using *emmeans* showing how percent cover of each species group compares across seeding treatments (in which functional group was originally seeded) for each year of the experiment (Hypothesis 1). For the native species group, cover was significantly affected by the full interaction seeding treatment, year, and priority length, and so the post-hoc results are for each set of priority length treatment plots. Different letters indicate significant differences ($p < 0.05$) among seeding treatments within each year for each given response variable (*a* indicates the lowest mean). For brevity, the symbols in the seeding treatment are as follows: N = native mix, W = noxious annual weed mix, A = naturalized exotic annual mix.

Response variable	Seeding treatment	Year											
		2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Noxious weed percent cover	W	c	c	c	c	bc	b	a	bc	b	ab	a	a
	W + A	b	b	b	c	c	b	a	bc	b	b	a	a
	N + W	a	a	a	b	a	a	a	ab	a	ab	a	a
	N + W + A	a	a	a	c	ab	a	a	a	a	a	a	a
Naturalized exotic percent cover	A	a	b	c	c	b	a	a	b	a	a	a	b
	N + A	a	a	b	b	ab	a	a	a	a	ab	a	a
	W + A	a	a	bc	a	a	a	a	a	a	ab	a	ab
	N + W + A	a	a	a	a	a	a	a	b	a	b	a	ab
Native percent cover (1-year priority)	N	c	b	b	c	b	a	ab	a	ab	a	a	a
	N + A	a	a	a	ab	ab	a	b	b	b	a	a	a
	N + W	b	a	a	bc	ab	a	ab	a	a	a	a	a
	N + W + A	a	a	a	a	a	a	a	a	a	a	a	a
Native percent cover (2-year priority)	N	c	b	b	b	b	a	a	a	b	c	b	b
	N + A	a	a	a	ab	ab	b	a	a	ab	bc	ab	b
	N + W	b	a	a	a	a	a	a	a	b	a	a	ab
	N + W + A	a	a	a	a	a	ab	a	a	a	ab	a	a

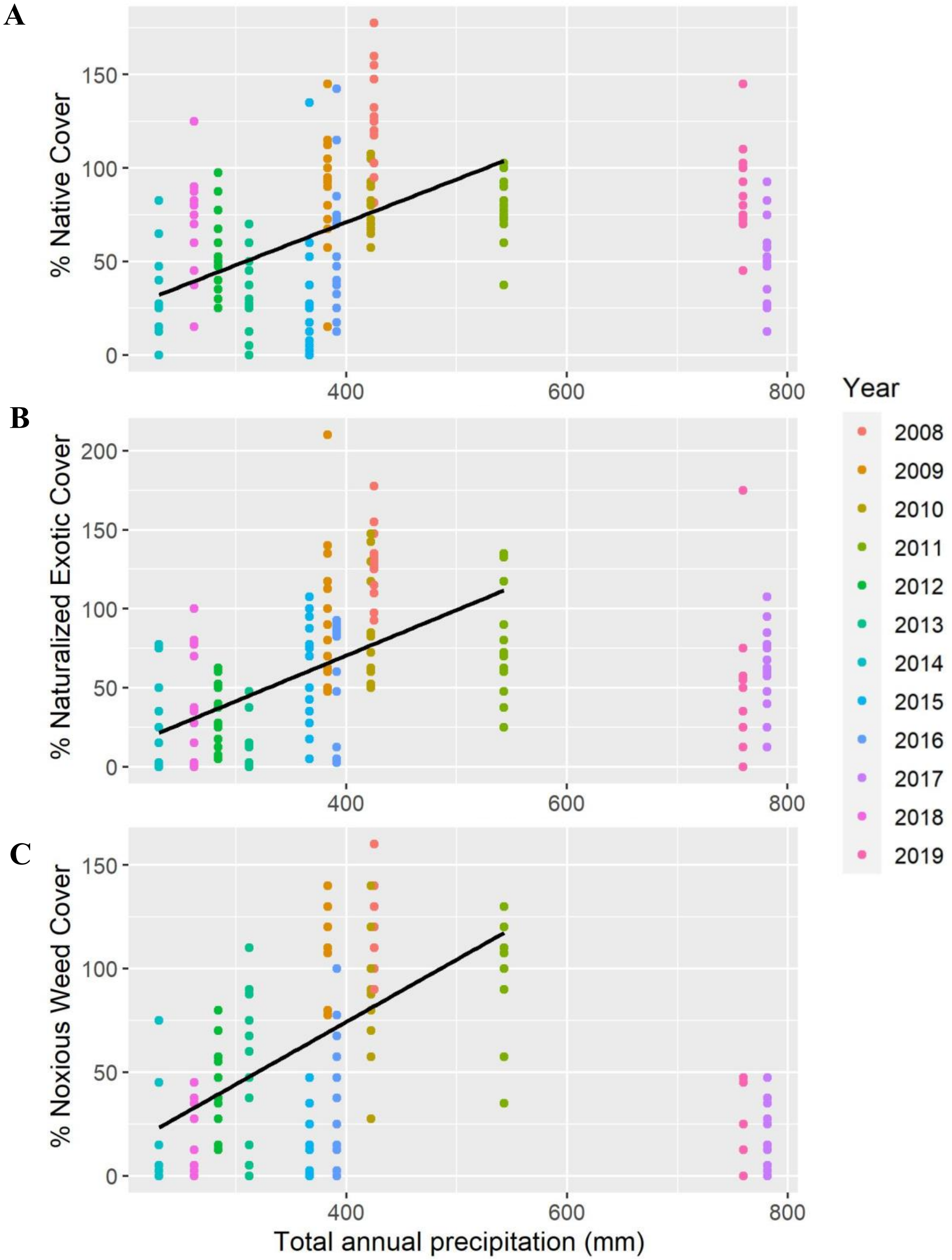

Figure S2.1. Correlation of percent cover of (**A**) natives, (**B**) naturalized exotics and (**C**) noxious weeds and total annual precipitation. Linear regression ($p < 0.05$) shown is on years prior to 2017.

Table S2.2. Results of post-hoc comparisons using *emmeans* showing whether percent cover of a recruiting functional group is greater in its monotypic seeding treatments than in the treatments into which it recruited for each year (Hypothesis 2). Different letters indicate significant differences at a $p < 0.05$ level and are grouped by year (*a* indicates the lowest mean). For brevity, the symbols in the seeding treatment are as follows: N = native mix, W = noxious annual weed mix, A = naturalized exotic annual mix.

Response variable (Recruiting functional group cover)	Seeding treatment	Year											
		2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Noxious weed percent cover	W	b	b	b	b	c	c	a	b	b	b	a	a
	A	a	a	a	a	c	c	a	b	b	ab	a	a
	N	a	a	a	a	a	a	a	a	a	ab	a	a
	N + A	a	a	a	a	b	b	a	ab	a	a	a	a
Naturalized exotic percent cover	A	b	b	b	b	b	a	a	b	a	a	a	b
	N	a	a	a	a	a	a	a	ab	a	ab	a	a
	W	a	a	a	a	a	a	a	ab	a	b	b	b
	N + W	a	a	a	a	a	a	a	a	a	ab	a	ab
Native percent cover	N	b	b	b	b	b	b	b	a	b	b	b	c
	W	a	a	a	a	a	a	a	a	a	a	a	a
	A	a	a	a	a	a	a	ab	a	a	a	a	b
	W + A	a	a	a	a	a	a	ab	a	a	a	a	b

Table S2.3. Results of post-hoc comparisons using *emmeans* showing how percent cover of a recruiting functional group compares across years in each seeding treatment it was not planted into (Hypothesis 2). Different letters indicate significant differences at a $p < 0.05$ level and are grouped by seeding treatment (*a* indicates the lowest mean). For brevity, the symbols in the seeding treatment are as follows: N = native mix, W = noxious annual weed mix, A = naturalized exotic annual mix.

	Invading species group								
	Noxious weed cover			Naturalized exotic cover			Native cover		
Year	N	A	N + A	N	W	N + W	A	W	W + A
2008	a	a	a	a	a	a	a	a	a
2009	a	a	a	a	a	a	a	a	a
2010	a	a	abc	a	a	a	a	a	a
2011	a	ab	bcd	a	a	a	ab	a	a
2012	a	cd	cd	a	a	a	ab	a	a
2013	a	d	d	abc	a	abc	ab	a	a
2014	a	a	ab	abc	a	ab	abc	a	ab
2015	a	ab	abc	cd	b	bc	abc	b	ab
2016	a	bc	abc	cd	bc	bc	cd	b	b
2017	a	ab	abc	d	d	d	bc	ab	ab
2018	a	ab	a	bcd	cd	c	cd	ab	b
2019	a	a	a	ab	bc	c	d	ab	c

Chapter 3: The impact of sustained drought and augmented precipitation on plant community composition and noxious weed performance in plot cores vs edges

ABSTRACT

A changing climate presents new challenges to invasive plant management. Novel climate conditions can impact an invasive species' range as well as its competitive dynamics with native species. California is expected to have extended drought periods as well as increased late-season rains. As California's grasslands are a soil moisture-limited system and the main three grass functional groups differ in phenology (and thus timing in soil water use), the plant communities are expected to vulnerable to the changing climate. We investigate how the prevalence of these three groups differed when exposed to sustained augmented or reduced precipitation. Phenology influenced the exotics' response to reduced precipitation- the noxious weeds were highly drought sensitive and disappeared while the naturalized exotics increased in abundance. The impact of drought on natives depended on the initial vegetation community, increasing in noxious weed communities yet decreasing in their own communities. The experiment saw no impact from augmentation due to dry ambient conditions. We also assessed the existence of edge effects as potential reservoirs for future invasion by comparing the cover of each group between the edges and core of plots they were planted in or recruited into, and whether the spatial pattern was affected by the sustained precipitation treatment. The cover of the natives and the noxious weeds were identical between the core and edges, but the naturalized exotics were generally higher in the plots' core than edges. This indicates that edges do not serve as a reservoir for future invasion into the plot core. The different precipitation treatments had no impact on the spatial patterns.

INTRODUCTION

Controlling invasive plants is a common management priority since plant invasions can reduce native biodiversity, wildlife habitat, and ecosystem services (Vilà and Ibanez 2011). Effective long-term weed management and restoration must consider future environmental conditions, as novel climate conditions may cause a shift in which species are invasive and may also cause invasive species to increase in both range (Hellmann et al. 2008, Pauchard et al. 2009) and competitiveness against native species (Carboni et al. 2018). Ecosystems may be particularly vulnerable to increased invasion under climate change, as increased variation in precipitation and extended droughts can disrupt current plant communities (Questad et al. 2012, Carboni et al. 2018, Hulvey and Teller 2018) and, thus, invasion resistance.

Communities may be particularly susceptible to invasion when there is a prevalence of exotic species along patch edges. Native grassland restoration sites often have a high edge to area ratio, as a common practice is to plant natives in strips or patches with the aim that the gaps will be filled in over time, minimizing cost (Shaw et al. 2020). Compared to patch interiors, edges can have lower density of the planted species and higher susceptibility to propagule pressure from entering species, due to a combination of the differences in vegetation structure, microclimate, and disturbances/dispersal opportunities (Fagan et al. 1999, Theoharides and Dukes 2007, Vilà and Ibanez 2011, Porensky et al. 2012). These edge effects may enhance the potential of encroaching noxious weeds to take over the patch center during disturbances that are either favorable for the weeds or harmful to natives.

In California’s grasslands, soil moisture is a limiting resource that shapes plant communities (Hamilton et al. 1999, Everard et al. 2010), making them vulnerable to changes in response to projected changes in climate, including extended drought periods and increased late-season precipitation from more frequent El Nino events (Cayan et al. 2007, Pathak et al. 2018, Swain et al. 2018, Ying et al. 2022). California grasslands are also composed of various species groups that differ in phenology and thus timing of soil moisture use, which may influence their response to changes in climate and ability to compete with each other. For example, the increased late-season rains promote newer noxious weeds with a later phenology (Davy et al. 2015).

This paper addresses how soil moisture and plant density across a patch influence invasive and native plant communities in California grasslands. We compare plots planted with monotypic groups and combinations of three common California grassland species groups: late-phenology native perennials, early-phenology naturalized exotic annuals, and late-phenology noxious exotic annual grasses. We determine how the prevalence of these grassland groups differs when exposed to ambient rainfall, compared to sustained augmentation, vs. sustained reduction of rainfall, and whether these community responses differ in the core versus edge of planted plots.

Previous work on these experimental plots demonstrated that initial planting of different vegetation communities had long-term effects on vegetation composition, even with large year-to-year variation in ambient precipitation. Native perennial grasses limited recruitment of late-season noxious weeds, in both wet years and dry years. The long-term composition in plantings of the two different exotic annual grass groups converged to a similar composition, with dominant species varying depending on annual precipitation (Chapter 2). Under ambient variation in rainfall, the late-season noxious weeds decreased in cover in drought but recovered post-drought (Chapter 2). This chapter explores how these communities, after 3 and a half years of establishment under ambient rainfall, respond to sustained increases or decreases in precipitation over a 7-year period. Other rainfall manipulation studies show that outcomes depend greatly on the ecosystem, species, and seasonal patterns of precipitation (see Fay et al. 2003, Suttle et al. 2007, Grime et al. 2008, Collins et al. 2012, Baez et al. 2013, Liu et al. 2018)., We first hypothesize that phenology is a main driver behind how the three grass communities respond to different climatic conditions. Under sustained drought, we expect late-season noxious weeds to greatly decrease in cover, but under augmented rainfall, their prevalence will increase only when they are planted with naturalized exotic species, while native species will continue to suppress the cover of the noxious weeds.

Our second hypothesis is in two parts. A) We hypothesize that patch edges are more vulnerable to compositional changes and so predict they will have lower cover of planted species, and higher cover of unplanted colonizing species compared to the core. This is because patch edges receive higher density of seeds from potentially colonizing species, and experience higher fluctuations of light and wind (Báldi 1999, Gols et al. 2021), while the center of patches receive higher seeds of planted species and may experience positive feedbacks (e.g. thatch facilitating seedling establishment, plant-microbial interactions). As our plot edges directly contact walkways of mixed species composition, they also face seed pressure from non-seeded species, creating a seed pressure gradient of colonizing species. We expect these edge effects to be particularly strong when noxious weeds are colonizing native plots (and vice versa), since these species suppress each other in the more competitive core (Chapter 2). Additionally, in relation to our previous hypothesis that phenology will drive the general response of each of the three species groups to the different precipitation treatments, we also expect the spatial pattern of invasion to differ with precipitation. Thus, B) We hypothesize that these spatial patterns will be determined by the interaction between each functional groups' phenology and the different climatic conditions. For example, wetter conditions are expected to enhance the recruitment of late-season noxious weeds in plot edges yet still benefit the planted natives and naturalized exotics in the core, resulting in greater edge vs core differences compared to the ambient and dry conditions. In contrast, drier conditions are expected to increase native and naturalized exotic recruitment in noxious weed-planted plot edges.

METHODS

Site information and experimental set-up

This project took place in experimental plots located at the UC Davis Campbell Tract Experimental Site in Davis, CA (38.545751, -121.784780). Prior to plot establishment, the land was used for agricultural purposes and then lay fallow for twenty-two years. The site was set on two soil types, 75% of the area was classified as Reiff series soil with the remaining as Brentwood soil series (https://casoilresource.lawr.ucdavis.edu/gmap/). Under a Mediterranean climate, the site experienced hot, dry summers (mean maximum temperature 33°C) and wet, cold winters (mean maximum temperature 14°C) that correspond with the growing season of cool season grasses. Rainfall had high inter- and intra-annual variability, with mean annual precipitation of 445 mm (30-year avg, 1989-2018).

Prior to initial seeding at the start of the experiment in fall 2007, the seed bank and resident vegetation were minimized by disking the soil, irrigating to germinate the seedbank, and spraying germinating seedlings with herbicide (glyphosate). Irrigation and herbicide treatments were performed twice before planting.

After clearing the seedbank, in fall 2007, 154 plots were seeded with one of the following vegetation treatments in a randomized block design (14 replicates): (1) native perennial grasses and annual forbs (N mix), (2) noxious exotic annual weeds (W mix), (3) naturalized exotic annual grasses and forbs (A mix), (4) all 2-way combinations of these three groups (A+N, W+N, W+A), and (5) monocultures of the native perennial grasses *Stipa pulchra, Elymus glaucus,* and *E. triticoides,* and the noxious weeds *E. caput-medusae* and *Aegilops triuncialis* (see Table 3.1 for species composition of each mix). All treatments were seeded at a rate of 139 g live seed per 1.5 x 1.5 m plot. For each single functional group mix, equal proportion of seeds of each species were added. For functional group mixes, an equal proportion of each functional group seed was added, with equal proportion of individual species within each functional group. Plots within blocks had a 1m buffer between them (with larger buffers between blocks). The walkways between plots were heavily walked upon by researchers during the growing season, flattening grasses, causing disturbance, and dispersing seed.

After seeding, plots were hand-weeded to maintain the original species composition for one year following planting, and then were allowed to be naturally colonized by other species in the experiment. Species that self-recruited and are common in California grasslands (e.g. *Bromus diandrus, Erodium* species, *Geranium* species, *Galium* species) were not weeded. All but 7 of the 154 plots were directly adjacent to a plot planted with the species group not planted in the target plot (Figure S3.1).

Plots established over three and a half growing seasons under ambient rainfall, and rainfall manipulations started mid-way through the 4th growing season, in February of 2011. These first 4 years of the experiment all experienced roughly average rainfall. The first full growing season of rainfall manipulation (2011-2012) was the first year of an extreme 3-year drought. These 3 drought years were followed by two near-average precipitation years and then a historic wet year and another drought year (Figure S3.2).

Reduced rainfall was achieved by installing open-sided 14.6 m x 18.3 m arched greenhouses (1.8 m tall at the edges, 3.6 m tall under the arch) covered in clear plastic (HiTunnel 24, AgraTech, Pittsburg, CA) over the established vegetation treatment blocks. These contained gutters which emptied into water storage tanks, collecting rainfall so that we could use rainfall to irrigate (thus not altering chemistry of the plots by using ground water for irrigation). A pump was used to irrigate from the water tanks to a sprinkler system designed to evenly distribute water across the block. Three replicate blocks received reduced precipitation (25% decrease in Sept-Feb, 35% decrease in March-April, precipitation excluded all other times). Augmented plots received ambient rainfall and supplemental irrigation from water collected from the rain shelters to achieve 25% increase in Sept-April, 50% May-June, with 3 weeks of rain added at the end of the season. The remaining 8 control blocks received ambient precipitation. Rain gauges were spread across blocks to determine the actual amount of precipitation each treatment received, and to ensure even distribution across each block (Figure S3.2).

Vegetation Composition

In 2018, we assessed vegetation composition in the 7th growing season of precipitation manipulation (the 11th total growing season) in both the core (inner 1m^2) and edge (outer 0.25m edge) of each plot of all eleven vegetation treatments. Percent cover of each species present was determined with the Daubenmire method (using the bin means of <1%, 5%, 25%, 50%, 75%, 95%, 100%). The core measurement focused on the inner 1m^2. The four edges (0.25 cm outer edge for a total edge area of 1.25 m^2) were assessed individually and averaged. Composition was measured twice (early April and late May) to capture peak cover of flowering species with different phenologies. The highest cover value across the two sample points for each species was used for analysis.

Statistical Analysis

To investigate the effects of precipitation, initial vegetative community, and edge effects on cover, we developed mixed effects linear models for each species group. Percent cover was log-transformed to meet assumptions of normality. Plot part (core and edge), seeding treatment, precipitation treatment, and their interactions were specified as fixed effects. Plot was specified as a random effect to account for the relatedness of plot part; we did not include a nested random effect term of plot part within plot because it led to model singularity. Significance was tested with analysis of variance (ANOVA) followed by post-hoc multiple pairwise comparison tests ($p < 0.05$) using estimated marginal means when a term was significant in the ANOVA. All analyses were conducted in R 4.0.3 (R Development Core Team) with the packages “lme4” (Bates et al. 2015) and “emmeans” (Lenth 2018).

RESULTS

Vegetation cover depends on initial planting treatment and precipitation treatment

Our study shows the two exotic annual species groups were significantly impacted by the precipitation treatment (*ANOVA* precipitation: $p < 0.001$, Table 3.2), responding differently to sustained drought conditions. The early-season naturalized exotics increased in abundance (post-hoc comparison of means: $p < 0.05$, Figure 3.1), while the late-season noxious weeds almost disappeared (post-hoc comparison of means: $p < 0.05$, Figure 3.1). The augmented precipitation treatment did not significantly impact naturalized exotic or noxious weed performance in comparison with ambient precipitation (post-hoc comparison of means: $p > 0.05$, Figure 3.1), although noxious weeds tended to be higher with enhanced precipitation. There were no interactions between precipitation treatment and vegetation treatment for either of the exotic grass groups (Table 3.2), indicating that the effects of precipitation did not vary with the initial vegetative community, nor did the effects of vegetation treatment vary due to precipitation. Both exotic groups had similar cover in all seeding treatments except for the two native monocultures of *S. pulchra* and *E. triticoides*, which had significantly lower exotic cover, compared to plots where each exotic group was seeded (post-hoc comparison of means: $p < 0.05$, Figure 3.1, Table S3.1).

In contrast to the exotic plants, the native cover response to precipitation was dependent on the initial seeding treatment (*ANOVA* precipitation x seeding treatment, $p = 0.013$, Table 3.2). In the noxious weed mix plots (W), native cover was significantly higher under reduced precipitation (post-hoc comparison of means: $p < 0.05$, Figure 3.1). In contrast, in the native mix (N) and *S. pulchra* (SP) plots, native cover was significantly lower in the reduced rainfall plots (post-hoc comparison of means: $p < 0.05$, Figure 3.1). The remaining two native *Elymus* monocultures and exotic-seeded plots showed no significant impact of precipitation on native cover ($p > 0.05$, Figure 3.1).

The precipitation treatment also influenced the role of the initial community on long-term native cover. Under ambient precipitation, native cover was significantly higher in treatments where it was seeded compared to where it was not initially seeded (post-hoc comparison of means: $p < 0.05$, Figure 3.1, Table 3.3). This same trend occurred under augmented precipitation, but with more variability, likely due to fewer replicates (post-hoc comparison of means: $p < 0.05$, Figure 3.1, Table 3.3). Under reduced rainfall, differences of native cover could not be detected among the seeding treatments, also likely due to the fewer replicates (post-hoc comparison of means: $p > 0.05$, Figure 3.1, Table 3.3).

Plot core and edge effects on cover

Naturalized exotic cover was significantly impacted by plot part and had 9% greater cover in plot cores compared to edges in all plots (*ANOVA* $p < 0.001$, Figure 3.2, Table 3.2). In contrast, the noxious weeds did not significantly differ between core and edge in any seeding treatment (*ANOVA* $p = 0.29$, Table 3. 2). Natives did not have strong differences between the core and edge; while plot part was significant (*ANOVA* $p = 0.027$, Figure S3.3, Table 3.2), the average difference was only 2.8% higher in the core compared to the edge.

The precipitation treatments did not significantly impact how cover differed among the plot core vs. edge for any of the 3 species groups (for all 3 species groups *ANOVA:* plot part x seeding treatment x precipitation treatment $p > 0.05$, plot part x precipitation treatment $p > 0.05$, Table 3.2).

DISCUSSION

This study was designed to investigate the impact of sustained precipitation treatments on three grass functional groups in the soil moisture-limited grasslands of California, as well as to assess the existence of edge effects as potential reservoirs for future invasion. Long-term changes to precipitation regimes are expected to alter the ranges of invasive species or alter the competitiveness of existing exotic species with natives (Hellmann et al. 2008, Bradley 2009, Hulme 2017), with the impact of wetter vs. drier moisture being dependent on the system and species (Blumenthal et al. 2008, Questad et al. 2012). Seasonality of the species can also mediate their response to precipitation changes; for example, winter rainfall additions can increase winter exotic annuals abundance at the expense of warm season native grasses and forbs, but not affect cool season native perennial grasses (Prevéy and Seastedt 2014). In our study, the exotic species with early-season (naturalized group) vs. late-season (noxious weed group) phenology had opposite responses to sustained drought conditions, while the native perennial grasses' response depended on the initial seeding community. None of the three groups were statistically affected by augmenting precipitation, but the noxious weeds tended to have higher cover in the wetter conditions.

Synthesizing across long-term rainfall manipulations in other grassland studies, results depend greatly on the ecosystem, species, and seasonal patterns of precipitation. Two long-term experiments, both over ten years and comparing grasses to other functional types such as forbs, found that species composition changed annually with variability in precipitation, but largely remained stable in the long-term and between precipitation treatments (Grime et al. 2008) or were more impacted by other drivers such as fire and grazing (Collins et al. 2012). In other studies, both sustained drought (Liu et al. 2018) or rainfall additions (Suttle et al. 2007) have shifted dominance towards grasses away from forbs. Further, studies comparing among grass species show different outcomes depending on the climate - in a mesic C4 grassland, subdominant grasses were more impacted by a reduction in precipitation than the dominant species (Fay et al. 2003), while in desert C4 grassland, the opposite occurred (Baez et al. 2013). Thus, these studies show that when determining the impact of future climatic conditions on invasiveness, it is important to address factors such as phenology specific to the ecosystem. Our study looks among grass groups in a soil moisture-limited system and shows that phenology drives the competitive outcomes under different precipitation levels.

Could not detect an impact of augmented precipitation

Under augmented precipitation with an extended rainy season, we had expected both native perennials and noxious weeds to increase in cover given their later-season phenology.

Native perennials are found in greater abundance and are more competitive against the early-phenology naturalized exotics where soil moisture is more prevalent (Everard et al. 2010, Fitch et al. 2019). Noxious weeds utilize late-season moisture after the naturalized exotics have senesced and increase in years with late-spring rains (Davy et al. 2015). Our experiment likely did not achieve these higher moisture levels. The below-average rainfall experienced in most years of the experiment may not have added sufficient soil water to impact composition (achieving less intense drought, rather than augmented rainfall), and the high rainfall year was so excessive that it’s unlikely additional moisture would have impacted vegetation. Thus, we cannot draw any conclusions about vegetation response to wetter conditions. Additionally, the generally declining noxious weed cover found throughout the site by the time of our sampling (Chapter 2) may have contributed to their muted response, as low cover could have lowered statistical power to find differences.

Reduced rainfall causes compositional shift

All three species groups responded strongly to reduced rainfall, but the most drastic outcome was the virtual disappearance of the noxious weeds, suggesting high drought sensitivity. While the naturalized exotics dominated most of the noxious weed seeded plots in these conditions, the natives were also able to establish in the noxious weed mix plots at higher levels than they could in ambient and augmented precipitation, likely establishing when noxious weeds declined. Our results are supported by a long-term cover analysis of the ambient precipitation plots that showed a sharp decline in noxious weed cover over the course of the multi-year drought (Chapter 2). Other studies support our findings of drought sensitivity; medusahead dropped 60% in cover following two extreme drought years in California (Davy and Dykier 2017) and had a substantially decreased seedbank (Young et al. 1998) and lower relative growth rate relative to natives in dry conditions in the Great Basin (Mangla et al. 2011). High phenotypic plasticity in goatgrass may help avoid drought stress (Dyer et al. 2010, Dyer 2017), but the grass has still performed poorly in drought conditions (Thomason and Rice 2017).

In contrast, naturalized exotic cover was highest in the reduced rainfall plots regardless of initial seeding composition. Though negatively affected by drought (Gerakis et al. 1975, Copeland et al. 2016, Chapter 2), higher naturalized exotic cover in plots where they were planted may be from dominance switching to the more drought-tolerant species of *Avena fatua* and *Bromus diandrus* within the species group, as seen in Batzer 2019. Not surprisingly, the drought conditions increased the magnitude of naturalized establishment, as these early-season species draw down soil moisture, limiting growth of the late-season noxious weeds and natives (Hironaka 1961, Hamilton et al. 1999). In ambient conditions, noxious weeds experienced a sharp decline during the drought, but recovered in wetter seasons (Chapter 2). The noxious weeds had no such recovery in the reduced rainfall plots, likely caused by the naturalized species overwhelming the plots with high propagule pressure with their own greater performance, further decreasing the noxious weeds.

As expected, when comparing reduced rainfall to ambient rainfall treatments, drier conditions increased naturalized exotics into native seeded plots. Other studies have shown that lower soil moisture can stress adult native perennial grasses (Hamilton et al. 1999, Fitch et al. 2019), resulting in weaker competitive ability (Everard et al. 2010). We had previously found that under ambient rainfall conditions, naturalized exotics increased in native plots only after natives decreased during the drought (Chapter 2). Our current study provides mixed support for lower native competitive ability in reduced precipitation, as native cover was only negatively affected in the N mix and native *S. pulchra* treatments; neither the two native *E. triticoides* and

E. glaucus treatments nor the treatments in which natives were seeded in competition with exotics were impacted. Additionally, even in the dry plots the *S. pulchra* and *E. triticoides* seeded monocultures had the lowest naturalized exotic cover of all treatments. These results suggest that already established native perennial individuals (as all plots established 3.5 years before the precipitation treatment) are somewhat resilient to drought conditions and can persist in the community despite several years of severe drought. Of course, they may disappear in the long-term if no active management is taken to reduce the naturalized exotics (Questad et al. 2021).

Overall, our findings suggest California will undergo strong compositional shifts with prolonged drought. However, limitations of the study must be addressed to properly discuss our findings. The precipitation treatment was implemented the year California entered an extreme three-year drought, which was followed by an extremely wet year and another drought year (Wang et al. 2017, Ullrich et al. 2018). As the amount of precipitation added or reduced was in proportion to ambient precipitation, the reduced rainfall plots mostly experienced severely dry conditions and the augmented plots largely experienced below average rainfall. Additionally, we only sampled composition for one year and it is possible we are missing important variations in wetter vs drier years within the precipitation treatments, as California has high inter-annual compositional variation (Heady 1958, Hobbs and Mooney 1995, Chapter 2). Lastly, the small sample size of the precipitation treatments (vs. higher replication of ambient treatments) could have resulted in low statistical power to detect differences in vegetation treatment effects at lower vs. higher rainfall.

Edge Effects

Only naturalized exotic species followed our hypothesized patterns, with lower cover in the edges compared to the core plot. This spatial arrangement was consistent regardless of if the vegetation treatment initially included this group or if the naturalized exotics recruited into plots that didn't initially include them. This indicates that these grasses may be impacted by edge effects, and may be generally negatively affected by an edge microclimate, that can be more variable and have potentially drier and warmer soils (Báldi 1999, Gehlhausen et al. 2000, Gols et al. 2021), or are more impacted by positive feedbacks in the core such as thatch accumulation or microbial feedback. Lower edge cover may provide an open opportunity for invasion (Fagan et al. 1999, Theoharides and Dukes 2007, Vilà and Ibanez 2011), but we did not see greater cover of native and noxious weeds as was expected In fact, no recruiting species group had higher cover in the edge vs core of any plot. We are unable to make conclusions about noxious weed cover spatial variations, since cover was extremely low, likely due to its decline during the multi-year drought (Chapter 2). Additionally, our plots are relatively small (1.5m x 1.5m) and more of the area may be affected by edge effects than we considered in our design. The low presence of noxious weeds may also account for a lack of recruitment ability into the other species groups' patches, if they could not incur sufficient propagule pressure on patch edges.

In terms of native restoration, the lack of edge effects on native patches may be beneficial. Equal native cover across the patch suggests that native individuals are not harmed by edge conditions. Their ability to establish in plots where they weren't initially planted lends support to the approach of using strip seeding as a more cost-effective way to restore natives across broad areas (Shaw et al. 2020). Native patch edges also had low noxious weed invasion, indicating they are not providing spatial refuges for those weeds to invade at a future date.

Further study on larger scales is needed to determine whether California grassland managers need to address invasive species on restoration edges, or whether they can continue to focus weed control on the entire patch, through practices such as burning and grazing (Stromberg et al. 2007).

Conclusion

Our study addressed the impact of different climatic conditions on the compositional outcomes of California grasslands. Our results highlight that the impact of sustained drought on grassland composition and exotic invasion can be dependent on phenology of the exotic species in question. In our soil moisture limited system, the early-season annual naturalized exotics increased while the late-season annual noxious weeds almost disappeared, with the native perennial grasses decreasing in only certain instances. Further work should be performed under above-average precipitation to better conditions predict grassland compositional change under future climate conditions.

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Table 3.1. Composition of each species group used in seeding treatment mixes.

Natives (N mix) (grasses and forbs)	**Noxious exotic annual weeds (W mix)** (grasses)	**Naturalized exotic annuals (A mix)** (grasses and forbs)
*Elymus glaucus**	*E. caput-medusae*	*Avena fatua*
*E. triticoides**	*Aegilops triuncialis*	*Bromus hordeaceus*
*Stipa pulchra**		*Festuca perennis*
Bromus carinatus		*Trifolium subterraneum*
Festuca microstachys		*B. diandrus***
Acmipson americanus		*Hordeum murinum***
Lupinus bicolor		

*perennial species that maintained dominance in native mix plots compared to the annual species after 1st year
**not originally seeded, but now considered a component of the naturalized exotic annuals

Table 3.2. ANOVA results from linear mixed effect models testing the interaction of plot part, seeding treatment, and long-term precipitation on percent cover of each species group. Plot is included as a random effect. Bolded values indicate significance at $p < 0.05$.

	Noxious weed cover			**Naturalized exotic cover**			**Native cover**		
	df	**F**	**p**	**df**	**F**	**p**	**df**	**F**	**p**
Core vs Edge (CE)	1, 119	0.99	0.29	1, 119	25.91	< **0.001**	1, 119	4.36	**0.027**
Seeding treatment (S)	10, 119	4.31	< **0.001**	10, 119	4.38	< **0.001**	10, 119	7.6	< **0.001**
Precipitation treatment (P)	2, 119	21.1	< **0.001**	2, 119	7.53	< **0.001**	2, 119	2.24	0.06
CE x S	10, 119	0.96	0.49	10, 119	1.28	0.25	10, 119	0.93	0.43
S x P	20, 119	1.26	0.22	20, 119	1.29	0.19	20, 119	1.99	**0.013**
CE x P	2, 119	0.35	0.71	2, 119	1.7	0.19	2, 119	1.1	0.11
CE x S x P	20, 119	0.90	0.59	20, 119	1.17	0.29	20, 119	1.02	0.36

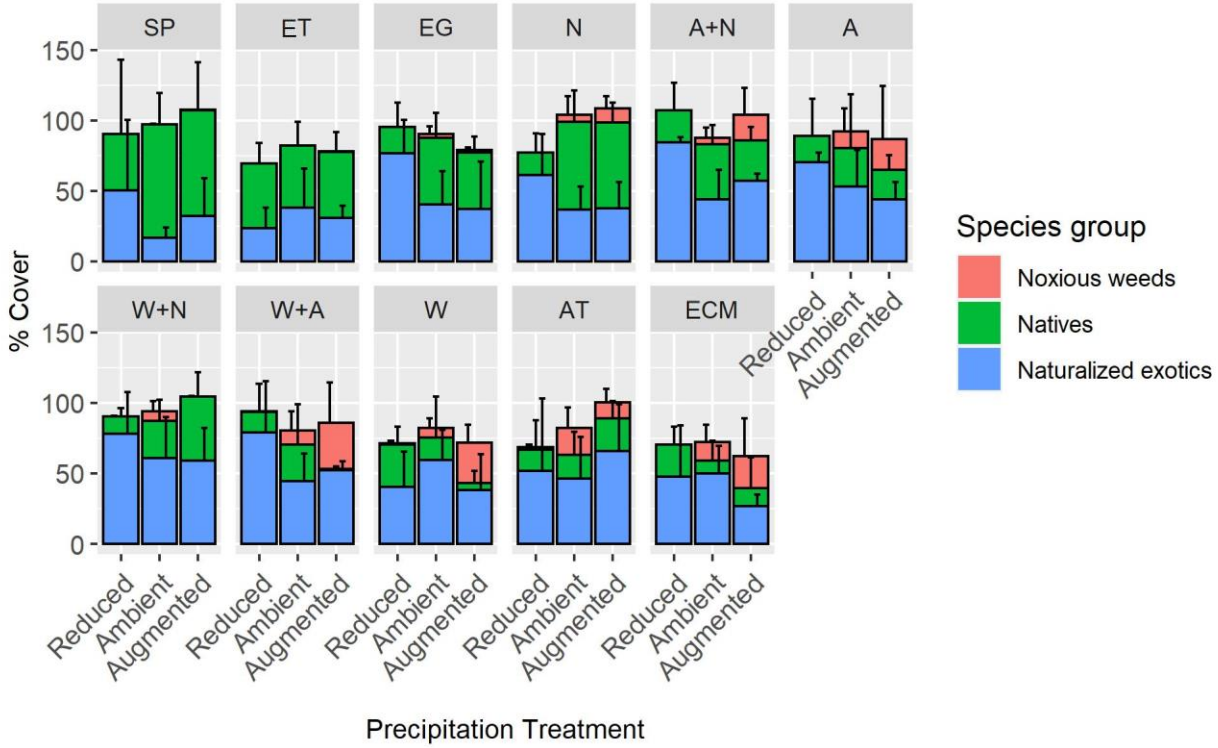

Figure 3.1. A stacked bar graph of percent cover of noxious weeds (red), natives (green), and naturalized exotics (blue) in each seeding treatment (each panel) and precipitation treatment (along x-axis). Height of each colored bar represents the percent cover of that species group; error bars represent standard errors. Noxious weed cover is significantly lower in the reduced precipitation treatment (post-hoc comparison of means: $p < 0.05$) while naturalized exotic cover is significantly greater (post-hoc comparison of means: $p < 0.05$). Native cover's response to precipitation is dependent on the initial seeding treatment (*ANOVA* seeding X precipitation: $p = 0.013$; in the W mix, native cover is higher under reduced precipitation (post-hoc comparison of means: $p < 0.05$) while in the SP and N mix, native cover is lower under reduced precipitation (post-hoc comparison of means: $p < 0.05$). Seeding treatment abbreviations are as follows: SP – *S. pulchra*, ET – *E. triticoides*, EG – *E. glaucus*, N – natives, A – naturalized exotics, W – noxious weeds, AT – *A. triuncialis*, ECM – *E. caput-medusae*.

Table 3.3 Results of post-hoc multiple comparisons analysis using *emmeans* showing how percent native cover compares across seeding treatments for each precipitation treatment in the 2018 sampling year. Different letters indicate significant differences ($p < 0.05$) among seeding treatments within each precipitation treatment. Seeding treatment abbreviations are as follows: SP – *S. pulchra*, ET – *E. triticoides*, EG – *E. glaucus*, N – natives, A – naturalized exotics, W – noxious weeds, AT – *A. triuncialis*, ECM – *E. caput-medusae*.

Precipitation treatment	Seeding Treatment										
	SP	ET	EG	N	A+N	A	W+N	W+A	W	ECM	AT
Ambient	a	abc	abc	ab	abc	cd	bcd	cd	d	d	cd
Reduced	a	a	a	a	a	a	a	a	a	a	a
Augmented	a	abc	abcd	ab	abcd	bcd	abcd	d	d	cd	abcd

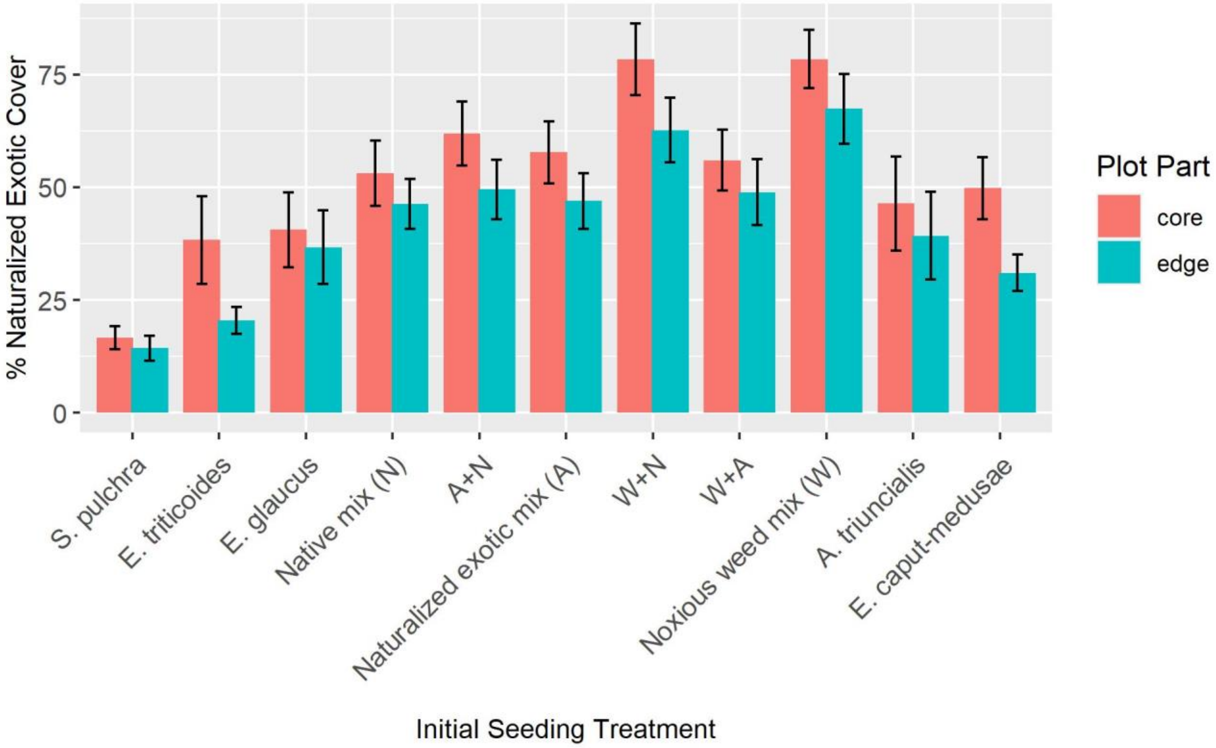

Figure 3.2. Naturalized exotic annual cover in the plot core (red) and edge (blue) of each seeding treatment, showing only the ambient precipitation plots as an example, as it has the most power. Plot part is significant at $p < 0.001$, with 9% higher cover on average in the plot core. Error bars signify standard errors.

SUPPLEMENTARY MATERIALS

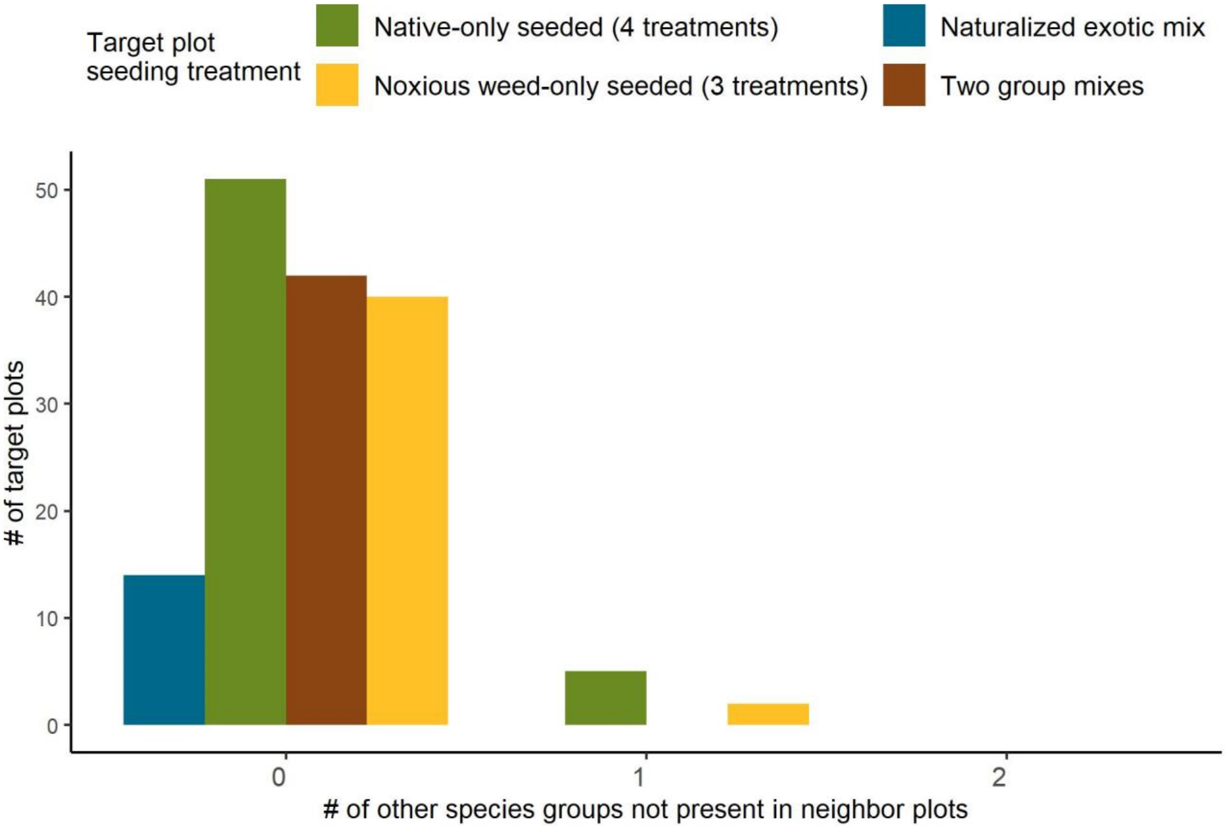

Figure S3.1. The number of non-seeded species groups that are not present in a directly adjacent plot to the target plot. Only 7 of the 154 plots were not located next to a plot seeded with another species group. Native-only seeded plots (green) include the native (N) mix, *S. pulchra, E. triticoides, and E. glaucus* treatments; Noxious weed-only seeded plots (yellow) include the noxious weed (W) mix, *A. triuncialis and E. caput-medusae* treatments; the two group mixes include the W+A, W+N, A+N treatments (A = naturalized exotics).

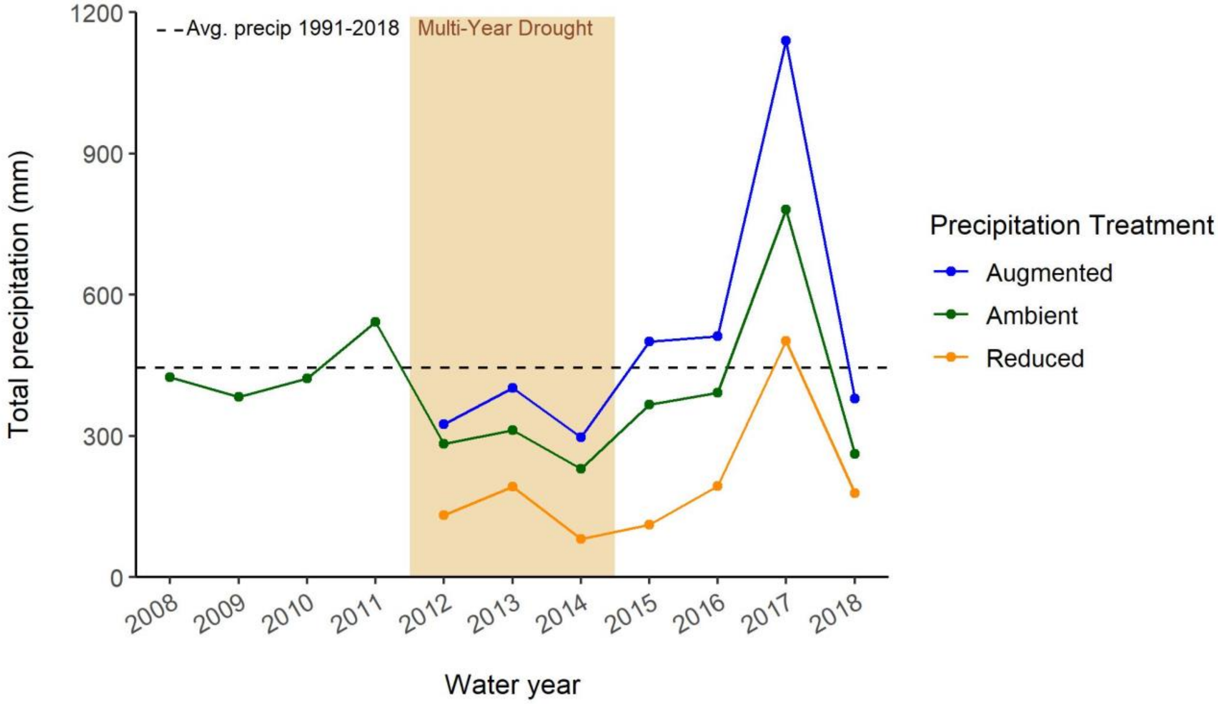

Figure S3.2. Total precipitation (mm) for each water year (Oct 1st of previous year to Sept 30th of reference year) of the experiment. The dashed line refers to the 30-year average (1989-2018); the precipitation treatments began in 2012. Data collection occurred in 2018.

Table S3.1. Results of post-hoc multiple comparisons analysis using *emmeans* showing how percent noxious weed and naturalized exotic cover compares among seeding treatments, across the three precipitation treatments. Different letters indicate significant differences ($p < 0.05$) among seeding treatments. Seeding treatment abbreviations are as follows: SP – *S. pulchra*, ET – *E. triticoides*, EG – *E. glaucus*, N – natives, A – naturalized exotics, W – noxious weeds, AT – *A. triuncialis*, ECM – *E. caput-medusae*.

	Seeding Treatment										
	SP	ET	EG	N	A+N	A	W+N	W+A	W	ECM	AT
Noxious weed cover	a	a	ab	ab	ab	ab	ab	b	b	b	b
Naturalized exotic cover	a	a	ab	ab	b	b	b	b	ab	ab	b

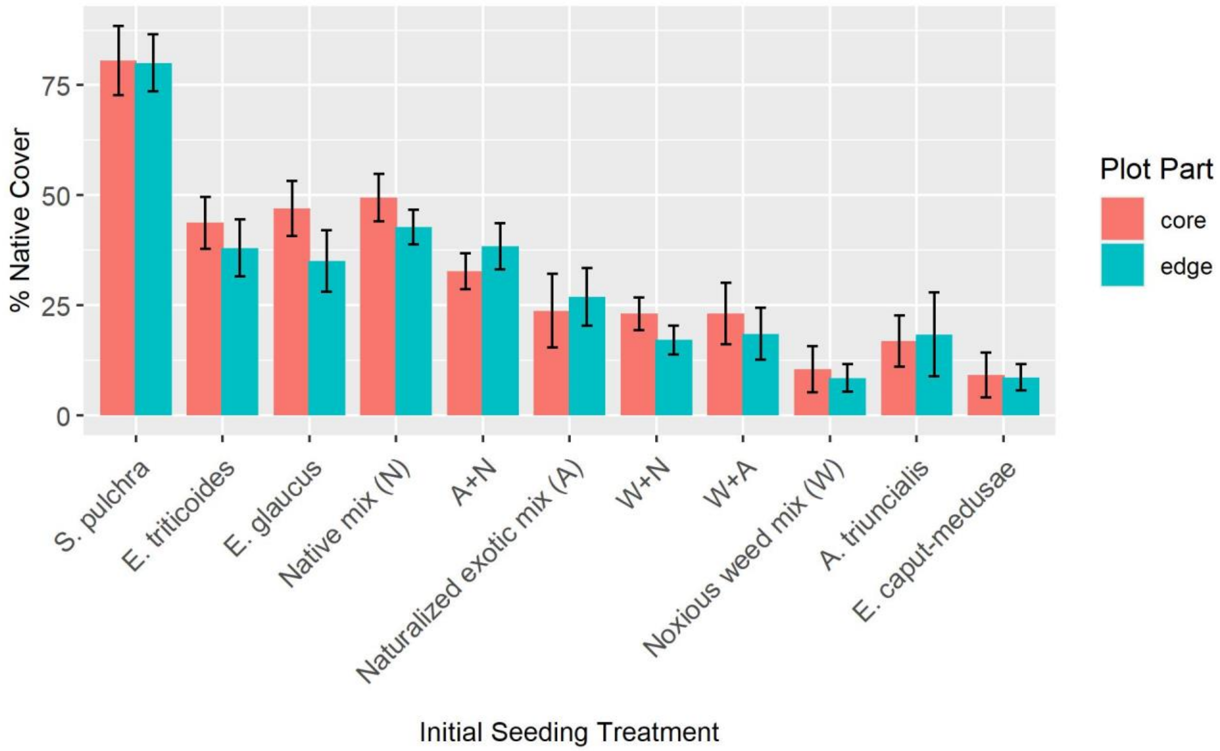

Figure S3.3. Native cover in the plot core (red) and edge (blue) of each seeding treatment, showing only the ambient precipitation plots as an example, as it has the most power. Plot part is significant at p = 0.027, with 2.8% higher cover on average in the plot core. Error bars signify standard errors.