SPECIES DYNAMICS AND RESTORATION IN RARE SERPENTINE GRASSLANDS UNDER GLOBAL CHANGE

by

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THESIS ABSTRACT

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Conserving rare serpentine grasslands is a challenge with ongoing nitrogen deposition. Nutrient-poor patches are fertilized by nitrogen-rich smog and exotic grasses can rapidly spread. Water resources are also being altered in this system via climate change. Using a greenhouse experiment and a long-term survey, I test how rainfall variability interacts with nitrogen deposition to shift native patches to an exotic state. We found that wetter years interact with intermediate nitrogen to drive invasion. Restoring exotic-dominated patches is difficult once an established layer of litter reasserts exotic dominance. Capitalizing on a long-term dataset, I test burning and grazing as restoration tools to promote native forb recovery. I found that a burn and continual grazing is effective in controlling exotic cover and litter levels to restore invaded patches to a native state. As global change continues to reinforce exotic dominance, continual and well-timed management is necessary to maintain native serpentine grasslands.

This thesis includes both previously published/unpublished and co-authored material.

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CHAPTER I

INTRODUCTION

Serpentine systems in California, including remnant and endangered serpentine grasslands in the Bay Area, cover only 1% of the state’s area and contain 10% of California’s endemic plant species (Kruckeberg 1984). Native forbs like *Plantago erecta* and *Layia platyglossa* in serpentine grasslands serve as important habitat for the federally threatened and endemic Bay checkerspot butterfly (*Euphydryas editha bayensis*) (Weiss 1999; USFWS 2009). The number of serpentine patches has markedly decreased due to land-use development. Remaining patches of high native diversity serpentine grasslands now (and will continue to) face global change like nitrogen (N) deposition that is associated with diversity loss, creating a further challenge for the conservation of these high-diversity systems (Weiss 1999).

Serpentine grasslands are particularly vulnerable to N deposition due to serpentine soil’s deficiency in N. Plant species adapted to thrive in these conditions do so by growing to short statures, as well as other resource-conservative traits. Nitrogen deposition from industrial and on-road sources in the Bay Area produces N-rich-smog that fertilize nearby serpentine grasslands (Weiss 1999). As serpentine grasslands experience N-enrichment via N deposition, resource-acquisitive species can capitalize on increasing soil N to grow and reproduce rapidly (Hobbs et al. 1988; Huenneke et al. 1990; Vallano et al. 2012) that otherwise struggle to maintain populations in N-poor serpentine soil but can spike in abundance in wetter years (Hobbs et al. 2007).

One of these resource acquisitive species is *Bromus hordeaceus*, an introduced annual winter grass from Eurasia. *Bromus* invasion in serpentine grasslands has been facilitated by N deposition, however, it has a demonstrated pattern of invading and receding over time. California grasslands are limited both by N and water, and this pattern may be jointly shaped by N deposition and climate variability. A Mediterranean climate ecosystem, serpentine grasslands are characterized by wet and dry years, or high rainfall variability. Thus, rainfall variability is an additionally important component to consider as N deposition acts over time, particularly because rainfall variability is increasing with climate change. The second chapter of my thesis pairs a greenhouse experiment with *Plantago*, *Layia*, and *Bromus* as focal species, and a long-term field survey in a serpentine grassland experiencing N deposition, to test how rainfall variability interacts with chronic N deposition over time to drive invasion.

Restoring serpentine grasslands post-invasion is difficult with ongoing N deposition (Weiss 1999). Cumulative levels of nitrogen continue to favor exotic grass growth and the production of a deep and persistent layer of litter upon senescence further enhances this proliferation (Huenneke et al. 1990; Weiss 1999). Accumulating exotic litter been shown to prevent native recruitment while favoring the exotic’s own germination, feeding back to its dominance (Weiss 1999; LaForgia 2021). This biotic feedback acts to produce a deeper litter layer that does not decompose quickly and requires intervention, such as cattle grazing to remove this biomass to promote native forb recovery (Weiss 1999). Another restoration tool that can remove this litter layer is fire, however, it is not a current practice used to manage exotic litter buildup in serpentine grasslands (Harrison et al. 2003). The third chapter of my thesis capitalizes on a long-term monitoring study to understand the effect of grazing and burning on serpentine grassland communities in both the short and long term and assess how these two restoration techniques can be used most effectively either alone or in combination.

My thesis is a synthesis of 1) understanding the mechanism by which multiple global change drivers interact to shift serpentine grasslands from native-dominated to exotic-dominated ecosystem states, and 2) assessing the effectiveness of two restoration tools to restore exotic-dominated serpentine grasslands to a native-dominated state. In my approach, I partnered with restoration practitioners and scientists, leveraged long-term datasets, and conducted an experiment to robustly test my questions.

CHAPTER II

INCREASING RAINFALL VARIABILITY INTERACTS WITH NITROGEN DEPOSITION TO CONTROL INVASION DYNAMICS IN RARE SERPENTINE GRASSLANDS

Eliza Hernández (EH), Lauren M. Hallett (LMH) conceived and designed the greenhouse study; EH conducted the greenhouse experiment; EH analyzed the data; LMH, Andrew J. Muehleisen (AJM) helped with data analysis; LMH, Richard J. Hobbs (RJH) conducted the long-term field survey; EH wrote the manuscript; LMH, AJM edited the manuscript

1. Background

Global change drivers are altering the availability of multiple limiting resources in ecosystems worldwide (Smith et al. 2009). Understanding the interactive effect of resource alterations from different drivers is a key challenge for predicting and addressing ecosystem responses to global change (Smith et al. 2009). Global change drivers can be chronic and push ecosystems along novel trajectories of change while eroding their capacity to recover to or persist in a desirable state (Folke et al. 2004; Smith et al. 2009). However, past models of chronic drivers assume constant change over time in a constant climate (Smith et al. 2009). In fact, many ecosystems experience naturally high climate variability, and this variability is increasing with climate change – another global change driver (Yoon et al. 2015; Swain et al. 2018). Understanding what environmental conditions maintain system resilience, and when and how systems will change in response to multiple global change drivers, remain critical yet difficult questions to test in ecology (Smith et al. 2009). Further complicating these dynamics is that global change drivers are inherently variable over time, and thus, their interactions may have nonlinear effects that may vary over time (Smith et al. 2009). Plant communities are particularly sensitive to global change drivers and can further mediate non-linear responses, also contributing to changes in ecosystem responses (Smith et al. 2009; Underwood et al. 2018; Komatsu et al. 2019). Therefore, the ultimate trajectory of change will depend on both the interaction of different global change drivers and the plant species available to respond (Smith et al. 2009).

Nutrient enrichment of ecosystems via chronic nitrogen (N) deposition is commonly associated with state shifts in N-limited systems one (Huenneke et al. 1990; Weiss 1999; Fenn et al. 2010; Vallano et al. 2012; Pasari et al. 2014), typically from a native-dominated stable (desirable) state to an exotic-dominated (undesirable), while likely rendering ecosystems susceptible to other global change drivers, such as climate change (Eskelinen & Harrison 2015). In systems co-limited by N and water, increased rainfall variability from climate change can interact with cumulative N deposition to increase system volatility (Smith et al. 2009). California serpentine grasslands are emblematic of this conundrum (Eskelinen & Harrison 2014; Eskelinen & Harrison 2015), and thus, are an important model system to test the interactive effects of these two global change drivers in ecosystems over time. First, N and water are co-limiting resources in this system. Serpentine soil is characteristically deficient in N (Turitzin 1982; Hobbs et al. 1988; Eskelinen & Harrison 2015) and serpentine grasslands are a semi-arid system with pronounced dry and wet seasons (Hobbs & Mooney 1991; Hobbs et al. 2007) and are projected to increase in intensity and frequency with climate change (Yoon et al. 2015). Second, both N deposition and rainfall variability collectively affect the structure of serpentine grassland communities. Nitrogen deposition can increase soil N availability and favor exotic annual grasses whose litter reinforces their dominance (Hobbs et al. 1988; Huenneke et al. 1990, Pasari et al. 2014; LaForgia 2021), whereas wetter and dryer years promote invasive grass and native forb growth, respectively (Hobbs et al. 2007; LaForgia et al. 2020). Lastly, N-poor patches of serpentine grasslands in California have long served as refugia for native annual forbs from competition with invasive annual grasses and have high conservation value as they maintain a significant portion of California's remaining native plant diversity (Murphy & Ehrlich 1989). Given the global change drivers at play in the systems, it is increasingly important to understand and predict shifts in serpentine grasslands from native- to exotic-dominated stable states.

Disturbance-based frameworks like alternative stable states predict a state shift following a disturbance-driven pulse in resources (Holling 1973). Using the alternative stable states framework, we would expect low and high rates of N deposition to maintain native and exotic stable states in N-limited systems like serpentine grasslands, respectively (Stevens 2016). Under these conditions, rainfall variability could favor or disfavor communities between years without necessarily altering the overall ecosystem state (Figure 2.1a; see Appendix A for all figures). In contrast, under intermediate levels of N, dry and wet years (i.e., rainfall variability) could toggle the system between native and exotic-dominated alternative states, respectively (Figure 2.1a). However, predicting the interactive effects of N deposition and increasing rainfall variability over time is difficult (Smith et al. 2009). This is because the former acts slowly yet cumulatively to increase soil N over time and the latter acts like a disturbance-driven pulse or hold in water resources during wetter and dryer years, undermining stability under intermediate levels of N (Smith et al. 2009).

According to the “hierarchical response framework” (Smith et al. 2009), ecosystem responses to chronic global change drivers like N deposition are intrinsically non-linear over time (Figure 2.1b). As N depositions acts over time, accumulating N can slowly promote the growth of resource-acquisitive species, such as exotic annual grasses and native weedy forbs (Weiss 1999; Fenn et al., 2003; Zavaleta 2003; Bobbink et al. 2010; Cleland & Harpole 2010). Favorable (i.e., wetter) years can accelerate this process, but naturally unfavorable years can curtail this growth and bolster resource-conservative native forbs, reordering species’ abundances (species reordering; Figure 2.1b) (Smith et al. 2009). However, as N accumulates to higher levels over time and extreme favorable years via climate change increase exotic propagules (i.e., species immigration; Figure 2.1b), the system can inch toward and convert to an exotic-dominated stable state (Figure 2.1b) (Smith et al. 2009).

To address ecosystem changes (e.g., diversity loss via state shifts) to ongoing and future environmental conditions, it is imperative that we test and find methods that succeed in understanding how populations and plant communities respond to multiple global change drivers over time. A promising approach under the umbrella of Modern Coexistence Theory (Chesson 2000) is invasion analysis, which posits that species can coexist when they are mutually invasible (i.e., when each species has a positive growth rate when rare). By testing this mutual invasion criterion, we can begin to refine the threshold levels of N, rainfall, and their interactions to determine species coexistence (or competitive exclusion) and community trajectories over time. Furthermore, linking empirical tests of Modern Coexistence Theory (Chesson 2000) with long-term observational data can ground truth theoretical insights, offering critical understanding as to how communities may change over time in response to multiple global change drivers.

Here, we focus on the response of three serpentine grassland species to the interactive effects of nitrogen (N) deposition and rainfall variability: *Plantago erecta*, a dominant native forb (hereafter the dominant native), *Layia platyglossa*, a native forb that is a sub-competitor on serpentine (hereafter the subordinate native), and *Bromus hordeaceus*, a non-native annual grass (hereafter the exotic) (Figure 2.2a). We pair a long-term survey of these focal species in serpentine grassland communities with a greenhouse experiment designed to determine the competitive success of each species when rare across factorial combinations of N, water, and seeding manipulations. According to the alternative stable states framework, we hypothesize that 1) serpentine grasslands co-limited by N and water will be the most susceptible to rainfall variability under intermediate levels of N, where dry and wet years will toggle the system between native- and exotic-dominated alternative states, respectively (Figure 2.1a). In line with the “hierarchical response framework” (Smith et al. 2009), we further hypothesize that 2) the interaction of these two global change drivers will be non-linear over time, where species will first reorder in dominance in response to changing water and N conditions. Then, following this period of reordering, increasing exotic propagules (i.e., species immigration) will ratchet communities to an exotic-dominated stable state (Figure 2.1b). To test our questions, we estimated each species’ growth rate when rare to determine pairwise species coexistence across all N-water treatments. We then simulated population abundances over time using starting ecological conditions (1983; Figure 2.2a) and historical climate data (Figure 2.2b) to compare species dynamics to real data (Figure

2.2a). Using this approach, we are able to recreate invasion patterns from the field data by accounting for how N deposition and increasing rainfall variability interact.

2. Methods

2.1 Study Site and Field Survey

Long-term data were collected from 1983 to 2019 at the Jasper Ridge Biological Preserve (hereafter Jasper Ridge) in San Mateo County, California, USA (Hobbs & Mooney 1991; Hobbs et al. 2007). The study site is a serpentine grassland comprised primarily of annual forbs and a few annual grasses that germinate in the autumn, set seed in spring, and senesce over summer (Figure2. 2a). The soil is shallow (<40 cm), low in nutrient concentrations, and high in heavy metals. This site experiences a Mediterranean climate (wet, mild winters and hot, dry summers). Growing season rainfall is highly variable at the site, ranging from 235 to 1250 mm over the course of the study, with an average of 565 mm (Figure 2.2b; PRISM Climate Group, OSU 2019). This variability has increased at Jasper Ridge within the past 12 years, where two prolonged droughts preceded El Niño-Southern Oscillation conditions in 2017 (Figure 2.2b). Consistent with climate model projections, California is expected to experience more frequent and extreme drought and wet periods (Yoon et al. 2015). Nitrogen deposition rates at Jasper Ridge have been estimated to be between 4-6 kg N ha^{-1} yr^{-1} (Weiss 1999), but recent development, N accumulation over time, exotic grass invasion, and projected increased N deposition (Fenn et al. 2010) likely indicates that Jasper Ridge may be experiencing greater N deposition rates.

In 1982, RJH established three replicate control plots containing a grid of 24 continuous 0.5 m^2 quadrats that were arranged in two 1 m x 3 m strips with a 0.25 m central alley between them for sampling (Figure S2.1; see Appendix B for all supplementary figures). Plots were spaced at least 5 m apart in a large area of serpentine on a north-facing slope at Jasper Ridge. Species percent cover in each quadrat was visually estimated annually using the following scale: 1%, 2%, 5%, 10%, and intervals of 10% thereafter. Here, we use a subset of this long-term composition data at Jasper Ridge to show the mean percent cover of the focal dominant native, subordinate native, and exotic species from 1983-2019 (Figure 2.2a).

2.2 Greenhouse Experiment

To test the effect of rainfall availability on species coexistence along a N deposition gradient we conducted a greenhouse experiment in which we manipulated N (low, intermediate, high) and rainfall (wet and dry) in a fully factorial design. Within each treatment we seeded a competition experiment in which our three focal species were grown both in a monoculture and as phytometers (focal individual) within each other's monocultures (hereafter background competitor) at three different densities (alone, low, and high) for a total of 42 unique treatments. Each treatment was replicated across four pots in a random block design for a total of 168 pots.

The experiment was conducted from 14 October 2019 to 29 February 2020 at the University of Oregon Greenhouse Facility (Eugene, OR). Serpentine soil was collected from the McLaughlin Natural Reserve, part of the University of California Natural Reserve System, located in Napa, Lake, and Yolo Counties approximately 120 km northwest of Davis, CA (38°51'17" N, 122°23'54" E). We collected soils from McLaughlin because it supports a similar species composition to Jasper Ridge but experiences very low deposition rates, enabling us to achieve a low N treatment

(Eskelinen & Harrison 2014). Soil was sifted through a 2 mm sieve to remove most rocks and amended with a 2:1 addition of vermiculite to serpentine soil to improve drainage and prevent root rot in greenhouse pots (reference). Approximately ~250 g of amended serpentine soil was added to each 103.2 cm^2 x 8.9 cm tall pot. Pot size reflected the high stem density and low plant stature observed in the system (Hobbs & Mooney 1985).

Our N treatments reflected no N deposition (low – 0 mg N/pot), one year of N deposition typical of south San Jose serpentine grasslands (intermediate – 11 kg N/ha ≈ 11.4 mg N/pot), and five years of accumulated N deposition (high – 55 kg N/pot ≈ 56.8 mg N/pot) (Weiss 1999; Vallano et al. 2012). Nitrogen treatments (NH_4NO_3 ACS grade, Fisher Chemical) were dissolved in 50 mL of water and randomly applied to pots after seeding treatments were sown. Our dry and wet treatments consisted of maintaining pots at least 10% and 30% volumetric water contents (VWC), respectively, consistent with a past serpentine greenhouse study using the same species where VWC = 30% represented saturated soil and VWC = 10% represented dried soil (Funk et al. 2015). Water treatments were applied by measuring the VWC of each pot every other day with a handheld soil moisture reading device (METER Teros 12 Sensor and ProCheck Sensor Read-Out) and adding 150 mL and 250 mL to dry and wet pots, respectively, whenever a pot did not meet its target VWC.

We seeded our background monocultures at both low (5 g seed/m^2 ≈ 51.6 mg seed/pot) and high (20 g seed/m^2 ≈ 206.5 mg seed/pot) densities and included a no-background treatment to assess performance in the absence of competition. Seeding rates which were adapted from similar studies (Kraft et al. 2015; Alexander & Levine 2019) but modified to account for higher stem densities typical of California serpentine grasslands (Hobbs & Mooney 1985); see Table S2.1 for average number of seeds added by treatment and background competitor (and see Appendix B for all supplementary tables). All seed was immersed in water for one day to simulate soaking from winter rains and ensure germination. We added three to four of each non-background focal species and thinned these phytometers to one individual after germination. If no phytometers germinated, phytometers grown in a separate tray with untreated amended serpentine soil were transplanted to establish phytometers within experimental pots weekly for a month. Additionally, phytometers that germinated but did not survive within one month were replaced by transplants (n=13); after this period, phytometers were no longer transplanted.

All pots were initially placed on two separate greenhouse benches for four experimental blocks (two blocks per bench) in a north-facing greenhouse and were subjected to a constant temperature of 75°C throughout the entirety of the experiment, representative of warm conditions in South Bay serpentine grasslands in the spring (Funk et al. 2015). As the day length shortened during winter, pots were moved to an adjacent north-facing greenhouse on 4 December 2019 (~7 weeks after the start of the experiment) with light fixtures that were programmed for a 12-hour day length consistent with spring conditions, potentially accelerating species' phenology (Figure S2.2). Each block was rearranged on four separate greenhouse benches (one block per bench) under one 400 W lightbulb for the remainder of the experiment.

All species germinated within one week of sowing and were maintained for a growing season's length of time. All species are self-pollinating except for the subordinate native, which was hand-pollinated once flowers were mature to simulate insect pollination (Kearns & Inouye 1993). Throughout the experiment, we harvested and collected phytometers when they reached 50% senescence to determine seed production (a good proxy for post-peak production; reference), except for the subordinate native. We collected the seed heads from subordinate native individuals before they could disperse by air circulation but left these individuals intact for potential additional flowering; all other species' seed were securely held by their respective reproductive structures. Remaining phytometers and background competition were harvested regardless of seeding in February 2020, concluding the experiment after a growing season's length of time. All samples were dried in the oven for 48 h at 60°C in the lab to reduce moisture content and prevent mold. We counted seeds and weighed biomass produced by phytometers and background competition for all focal species except for the exotic, which continued to grow without maturing seed. Thus, we estimated exotic seed production allometrically from a subset that did produce mature seed, which was the majority of samples (Table S2.2). We speculate that continual watering up to the end of the experiment in high N pots likely continued to support exotic growth, but not seed maturation (Figure S2.3).

2.3 Models and Parameterization

Using the per capita seed production from each species in each pot, we parameterized annual plant population models to project growth rates across environmental and competitive conditions. Population growth rates were calculated using the Beverton-Holt equation (Levine & HilleRisLambers 2009), a two-species discrete-time competition model that we generalized to more than two species:

Equation 1. $\frac{N_{x,t+1}}{N_{x,t}} = s_x(1 - g_x) + \frac{\lambda_{x,t} g_x}{1 + \alpha_{xx,t} g_x N_{x,t} + \sum_{y=1}^{n} \alpha_{xy,t} g_y N_{y,t}}$, where the population growth rate of species *x* is the number of viable seeds of species *x* at the beginning of the next growing season, $N_{x,t+1}$, over the population size of species *x* in the current growing season, $N_{x,t}$. This is a function of species *x's* seed survival rate, s_x, its germination fraction, g_x, and its intrinsic growth rate weighted by competition. The first term, $s_x(1-g_x)$, is the carryover of seeds from species *x* in the seed bank. The numerator in the second term is the intrinsic growth rate of species *x* in the absence of competition, $\lambda_{x,t}$, which varies given the growing season's environmental conditions. The denominator is the per-capita competition term experienced by species *x* for any number of species, where $\alpha_{x,y,t}$ and $\alpha_{x,y,t}$ are the per-capita intra- and inter-specific competition coefficients experienced by species *x* from itself and species *y* at time *t*, which also vary given the growing season's environmental conditions. Seed germination and survival fractions were derived from the literature and we made the assumption that these fractions did not vary with environmental conditions (Table S2.3).

Intrinsic growth rates and per-capita competition coefficients were parameterized for each focal species in each N-water treatment individually using the Hamiltonian Monte Carlo method with RStan v2.21 (Stan Development Team 2020). Models were fit with three chains until all parameter estimates converged with an $\hat{R} < 1.05$, indicating chains have mixed well and that the between- and within-chain estimates agree. Models were also fit using uninformed priors and constrained for biological feasibility except for one species and treatment combination, *Bromus* in the low-water-high-N treatment, due to a good model fit without constraining priors. To ensure good model fits, we compared competitive coefficients (α) of all interspecific combinations and intrinsic growth rates (λ) (Table S2.4) to per capita seed outputs with and without competition (Figure S2.4) by

N-water treatment.

2.4 Invasion Analysis

To determine pairwise coexistence between focal species we used the mutual invasion criterion (i.e., invasion analysis). In invasion analysis, species coexist when species are mutually invasible, or each have a positive growth rate when rare (GRWR), in a community of the other species. If a species has a negative GRWR, that species will be competitively excluded by the other species with a positive GRWR, and coexistence will not occur. Growth rates are calculated when one species is rare (i.e., the invader) and the other is at its equilibrium population abundance (i.e., the resident community). First, we established resident equilibrium communities by simulating the growth rate of each focal species in each of the six N-water treatments without interspecific competition (Equation 1) until they reached steady-state populations, as determined by a net population growth rate of zero. We then invaded a single seed of each species as an invader into each of the possible resident communities across all treatments and calculated its GRWR; we performed this analysis on all pairwise species and treatment permutation (R Core Team 2018).

2.5 Time Series Simulations

To determine if we could reconstruct the species dynamics observed in the field record at Jasper Ridge from 1983-2019 (Figure 2a), we converted the mean cover for each species in 1983 shown in Figure 2.2a into species abundances via multiplying mean cover by the equilibrium abundance of each species calculated across all N-water treatments and adjusted based on area. Thus, we assumed that equilibrium abundance equated to 100% cover in the field. We simulated abundances for each species every year thereafter (Equation 1) using the starting calculated abundances and estimated intrinsic growth rates and competition coefficients for each N-water treatment (Table S2.4) that corresponded to environmental conditions in that given year (Figure 2.4d). Using the historical rainfall conditions at Jasper Ridge from 1983-2019 (PRISM Climate Group, OSU 2019; Figure 2.2b), we categorized each year as “wet” or “dry” if mean annual precipitation from September to April was greater or less than the 50th percentile for that time span, respectively (Figure 2.4d). We then jointly categorized each year as “low N” from 1983-1994, “intermediate N” from 1995-2006, and “high N” from 2007-2019 (Figure 2.4d) as a rough proxy for accumulating N deposition every ~10 years that is consistent with N projections for the area (Fenn et al. 2010). We simulated the following three scenarios: 1) abundances of the dominant native and the subordinate native over time without exotic propagule pressure, and 2) abundances of all species over time. In scenario 3), we limited exotic seed germination to zero in the seed banking term of Equation 1 until 2008 to represent the lack of a seed bank before greater seed production (i.e., species immigration) with increasingly favorable conditions.

3. Results

3.1 Invasion Analysis

Invasion analysis revealed that under low N, the dominant native had a positive growth rate when rare (GRWR) in both water treatments when invading both resident communities of the subordinate native and the exotic (Figure 2.3a & b). Conversely, the subordinate native had a negative GRWR in both water treatments when invading resident communities of the dominant native, indicating that the dominant native will exclude the subordinate native (Figure 2.3a). The exotic had a negative GRWR in dry conditions, but a positive GRWR in wet conditions when invading resident communities of the dominant native (Figure 2.3b), indicating coexistence between the exotic and the dominant in wet conditions, but that the dominant native will exclude the exotic in dry conditions.

Under high levels of N, the exotic had a positive GRWR in both water treatments when invading both resident communities of the dominant native and the subordinate native (Figure 2.3b & c), and both the dominant native and the subordinate native had a negative GRWR when invading resident communities of the exotic, regardless of water (Figure 2.3b & c). The negative GRWR of the subordinate native was more negative than those of the dominant native in both water conditions (Figure 2.3 b & c), but still indicates that the exotic will exclude both the dominant native and the subordinate native under high N despite water conditions.

Under intermediate levels of N, the success of the subordinate native and the dominant native depended on water conditions when invading resident communities of the dominant native and the exotic, respectively. While the dominant native could invade the subordinate natives' resident communities in both water conditions, the subordinate native only had a positive GRWR in wet conditions when invading resident communities of the dominant native (Figure 2.3a). Similarly, while the exotic could invade the dominant natives' resident communities in both water conditions, the dominant native only had a positive GRWR in dry conditions when invading exotic resident communities (Figure 2.3b). These results point to coexistence between the dominant native and the subordinate native under wet conditions, but the dominant native will exclude the subordinate native under dry conditions. Conversely, coexistence will only occur between the dominant native and the exotic under dry conditions, but the exotic will exclude the dominant native under wet conditions. The subordinate native, however, had a negative GRWR in both water conditions when invading exotic resident communities, indicating the exotic will exclude the subordinate native (Figure 2.3c) – and this is the case in all N-water treatments (Figure 2.3c), suggesting the subordinate native is a poor competitor against the exotic.

3.2 Time Series Simulations

Simulated species abundances from 1983-2019 for two of our three species (the exotic and dominant native) reflected overarching patterns observed at Jasper Ridge, but not for the subordinate native. The exotic increased in abundance over time while the dominant native decreased over time (Figure 2.4a). The subordinate native, which increased over time in the long-term dataset before declining, was consistently low in the simulated data. However, when the exotic's seed bank carryover was limited until 2008 by setting the germination fraction to zero, we observed the pattern for the subordinate native in Figure 2.2a. The subordinate native increased while the dominant native was still abundant but declined in parallel with the dominant native as the exotic started to increase rapidly in the last 5 years of the time series (Figure 2.4b; Figure 2.2a).

4. Discussion

Understanding the interactive effects of multiple drivers is critical to predicting and addressing ecosystem responses to ongoing and future global change (Smith et al. 2009). Here, we showed how increased rainfall variability via climate change interacts with chronic N deposition to affect a serpentine grassland over time. Framing ecosystem shifts (i.e., native to exotic) around alternative stable state theory (Holling 1973), we hypothesized that rainfall variability would be the greatest driver of change under intermediate levels of N to toggle between native and exotic alternative states in dry and wet years (Figure 2.1a). Consistent with our first hypothesis, we found that serpentine grassland communities were the most sensitive to rainfall variability under intermediate levels of N, where wetter years allowed the exotic to outcompete the dominant native and subordinate native, as well as promote the coexistence of the subordinate native with the dominant native.

Our second hypothesis based on the “hierarchical response framework” (Smith et al. 2009; Figure 2.1b), predicted that rainfall variability would interact with increasing N deposition to produce non-linear responses over time, demarcated first by species reordering and then by species immigration. Supporting this hypothesis, we found that species first reshuffle in dominance in response to changing environmental conditions, and then, with increasing rainfall variability and N deposition enhancing exotic seed production (i.e., species immigration; Figure 2.1b), facilitated the conversion to an exotic-dominated stable state. Furthermore, via simulations we were able to recreate a coarse depiction of focal species’ responses in the long-term field record at Jasper Ridge based on rainfall and N conditions (Figure 2.2a).

According to alternative stable state and resilience theory, as a system moves along a novel trajectory of change toward a critical threshold, the resilience of that system is reduced, and a small perturbation can rapidly tip it to an alternative state (Holling 1973). Here, our results parallel and differ from the alternative stable state framework: as soil N increases over time, rainfall variability acts as a perturbation to produce an alternative state, but it does not rapidly shift the system to an exotic stable state. Rainfall variability produced many alternative unstable states under intermediate levels of N, and fluctuations increasingly pushed the system toward state conversion, particularly when wetter years coincided with higher N levels. As Smith et al. (2009) propose in their “hierarchical response framework”, both changing environmental conditions and species availability need to be considered over time, and that traditional frameworks based on disturbance-driven change are limited in this regard. The “hierarchical response framework” was a successful model for predicting responses to chronic N deposition in our system. Accordingly, both alternative stable states and hierarchical response framing proved useful models for disentangling the interactive effects of multiple global change drivers in an ecosystem – one chronic (i.e., N deposition) and the other disturbance-like (i.e., increased rainfall variability via climate change).

Despite these successes, we acknowledge the following limitations in our study. First, we did not account for different N deposition rates from year to year, and different forms of inorganic N from different sources of N deposition have either increased or decreased over time. For example, the reduction of NO_x emissions has been successful, however, the control measures used to reduce NO_x emissions produce NH_3, which is also increasing from on-road sources (Fenn et al. 2018). Thus, while NO_x emissions have decreased, NH_3 emissions are slowly increasing over time (Fenn et al. 2018), making it difficult to determine N deposition rates over time for predictive power. Second, we assumed N accumulation in the soil over time, which has been documented in serpentine grasslands in San Jose, California, but not at Jasper Ridge (Weiss 1999). Third, our study was constrained by three focal species and it may not reflect overall ecosystem dynamics.

For example, another co-dominant native at Jasper Ridge is *Lasthenia californica*, and the addition of this species in our experiment would have been more comprehensive. We speculate that multiple co-dominant natives could be more successful at resisting exotic invasion (Hobbs et al. 2007).

Fourth, we only partially factored in species characteristics by limiting the exotic's ability to develop a seed bank, and we did not account for biotic feedbacks such as exotic litter accumulation. To navigate the high interannual rainfall variability that characterize Mediterranean climate ecosystems, native forbs in serpentine grasslands have adapted to intermittent dry and wet years through facultative multiyear seed dormancy, also known as seed banking (Baskin & Baskin 1998). Introduced species like exotic annual grasses typically cannot develop long-term seed banks that last more than 2 years (LaForgia et al. 2018) as they usually compensate with high fecundity when resources like water are abundant (e.g., wetter years), producing population spikes (Hobbs & Mooney 1991; Hobbs et al. 2007). While we considered this in our simulations, we did not vary seed bank parameters with environmental conditions due to limited information about the germination and survival fractions of our focal species across N and water levels. Additionally, when non-native annual grasses like the exotic in our study reach high enough abundances, they produce a persistent litter layer that can inhibit the recruitment of native forbs (Hobbs et al. 1988; Huenneke et al. 1990; Weiss 1999), and in some cases, enhance the germination of their propagules, positively feeding back to their dominance (Huenneke et al. 1990; LaForgia et al. 2021). Thus, litter build up is another component to consider in predicting state shifts in serpentine grasslands.

Plant diversity loss via ecosystem shifts can have cascading effects on higher-trophic species that depend on native habitat (Weiss 1999). Here, we focused on two native forbs, a primary host (the dominant native) and a nectar source (the subordinate native), that provide habitat for the federally threatened and endemic Bay Checkerspot butterfly (USFWS 2009). However, our simulations showed that as N deposition and rainfall variability act over time, the exotic eventually excludes both of these key native species, and even a few years without these native forbs could greatly affect already-fragile populations of the Bay Checkerspot butterfly (Weiss 1999). In an ideal world without human-driven species introductions (i.e., exotic propagules), N deposition might not result in the dominance of one species. In fact, our simulations showed that N deposition would increase the abundance of the subordinate native, but not at the expense of the dominant native. Furthermore, both stably coexisted without exotic presence, which would hypothetically provide much more habitat for the Bay Checkerspot butterfly (USFWS 2009).

As N deposition like continues to accumulate in serpentine grasslands and many other ecosystems, management is necessary to address exotic invasion and its biotic feedbacks via litter buildup. In N-enriched serpentine grasslands, cattle grazing has been an effective tool in removing exotic biomass to promote native forb recovery (Weiss 1999), and fire can be used with grazing to maintain these outcomes (Harrison et al. 2003). Because our results suggest that exotics will increase in wetter years, the removal of litter in the summer following a wet growing season may be necessary for successful management to prevent a deep layer of exotic litter accumulation. Alternatively, in dry growing seasons, targeted native seeding, while expensive, may be the most effective under these conditions, as the dominant native prefers dryer conditions.

Serpentine systems, including serpentine grasslands, are some of California’s few remaining patches of high native diversity, containing an estimated 10% of California’s endemic species in about 1% of the state’s area (Kruckeberg 1984). As N deposition remains a chronic global change driver into the future and climate change continues to increase rainfall variability, serpentine grasslands, and many other co-limited ecosystems, face significant declines in diversity and eventual shifts to a homogeneous state (Stevens 2016). Promoting native forb recovery via careful management is important to maintaining these rare patches of high diversity (Weiss 1999). Understanding the effects of multiple global change drivers can better inform land management decisions and when to implement different restoration tools to maintain the high diversity integral to ecosystem functioning (Smith et al. 2009). Fire is another potential tool to remove litter buildup in addition to cattle grazing and has yet to be tested as a management practice in serpentine grasslands (Harrison et al. 2003).

CHAPTER III

FIRE VERSUS GRAZING AS TOOLS TO RESTORE SERPENTINE GRASSLANDS UNDER GLOBAL CHANGE

From Hernández E, Shaw EA, Aoyama L, Brambila A, Niederer C, Weiss SB, Hallett, LM (2021) Fire versus grazing as tools to restore serpentine grasslands. Restoration Ecology 29:e13353

1. Background

Global change poses a challenge to ecological restoration: how to “restore” an ecosystem when the world has changed around it? While traditionally restoration has aimed to recover a historic, self-sustaining ecosystem, ongoing external change may render this goal impossible (Hobbs et al. 2006; Hallett et al. 2013). For example, external inputs of both resources (e.g., nitrogen deposition) and new species (e.g., invasive species propagules) may override the effect of one-time restoration efforts. This challenge is amplified in systems characterized by high temporal variability, as management to address novel drivers may affect a system differently across its range of variability (Vaughn & Young 2010). Consequently, grassland restoration may increasingly require ongoing interventions that counteract the local effects of global change (Hobbs et al. 2011). This may involve redirecting communities to novel but desired trajectories, introducing a new element to the system that counteracts proximate effects of global change, or a combination of the two. While interest has grown in shifting from classic restoration ecology to systems-based intervention ecology, long-term studies that develop and test interventions targeting ongoing change are needed.

California serpentine grasslands are emblematic of the challenges facing ecological restoration in a changing world. Serpentine systems have high conservation value, hosting 10% of California's endemic plant species despite only comprising an estimated 1% of the state's landscape (Kruckeberg 1984). Soil derived from California's state rock, serpentine, is generally rocky and shallow, low in nutrients, and high in heavy metals, resulting in vegetation with low resource-use traits and high native species diversity adapted to these conditions (Kruckeberg 1984; Brady et al. 2005; Anacker et al. 2011). Additionally, serpentine grasslands serve as key hosts and habitat for other endemic species, such as the federally threatened Bay checkerspot butterfly (*Euphydryas editha bayensis*) (Murphy & Weiss 1988; USFWS 2009). Unlike grasslands on more nutrient-rich soils in California, serpentine grasslands have largely resisted dominance by non-native annual grasses – likely because low resources are a barrier to entry, where non-native annual grasses cannot overcome serpentine soil's deficiency in nitrogen (N) (Hobbs et al. 1988; Huenneke et al. 1990; Going et al. 2009; Vallano et al. 2012).

Nitrogen deposition, however, is reshaping California serpentine grasslands. Specifically, serpentine grasslands concentrated around the highly urbanized San Francisco Bay Area receive anthropogenic N inputs from vehicles, agriculture, and other sources (Weiss 1999). A global change driver, atmospheric N deposition generally favors plant species with high resource-use traits, such as non-native annual grasses, simplifying grassland communities while simultaneously increasing plant biomass (Zavaleta et al. 2003; Clark & Tilman 2008; Bobbink et al. 2010; Stevens et al. 2010). Similarly, studies using N fertilizer to simulate local N deposition rates in serpentine grasslands have shown that N addition increases non-native annual grass growth and dominance via enhanced resource acquisition, reducing native species abundance (Hobbs et al. 1988; Huenneke et al. 1990; Weiss 1999; Vallano et al. 2012). Furthermore, high interannual rainfall variability may interact with N deposition, where wetter years spike non-native annual grass abundance (Hobbs & Mooney 1991; Hobbs et al. 2007; Eskelinen & Harrison 2015). Once non-native annual grasses senesce in spring, their high biomass production becomes a thick litter layer that can prevent native forb recruitment and provide fuel for fire (Hobbs et al. 1988; Huenneke et al. 1990; D'Antonio & Vitousek 1992). Consequently, attempts to restore invaded serpentine grasslands must address chronic effects of N deposition in the system, such as litter accumulation.

Grazing and burning are interventions that may counteract the proximate effects of N deposition on native serpentine species. Livestock grazing has been an important tool for restoration and management of Californian serpentine grasslands threatened by non-native annual grasses (Weiss 1999; Safford & Harrison 2001; Harrison et al. 2003; Weiss 2007). Most directly, cattle grazing affects the plant community by selectively consuming non-native grasses in preference to native forbs, resulting in greater abundance of native annual forbs in cattle-grazed compared to ungrazed areas (Huenneke et al. 1990). Cattle grazing can also remove dense litter – which excludes native forbs – by trampling and feeding during the dry season (Heady 1956; Bartolome et al. 1980, 2002; Huenneke et al. 1990). To date most grazing studies have been relatively short-term, although the cumulative effect of trophic and non-trophic grazing effects on species composition may be lagged (Dudney et al. 2017), necessitating long-term study. Furthermore, the effect of grazing on composition may depend on site history, particularly if native species' storage of seeds in the soil, typically through multiyear dormancy, or a seed bank, has been reduced by long periods of grazing removal (Menke 1992; Sternberg et al. 2003).

Fire is another potential tool to remove litter buildup, however, this is not as well studied as grazing in serpentine systems. Previous studies show that fire has variable effects on California grasslands, but like grazing, generally increases forb germination, flowering, and biomass (Hervey 1949; Parsons & Stohlgren 1989). By reducing accumulated litter (Heady 1956), increased light and temperature at the soil surface favors forb and bulb germination, while physical scarification from fire favors legumes. While several studies show that fire effectively reduces non-natives and enhances native cover (Menke 1989; Parsons & Stohlgren 1989; Meyer & Schiffman 1999), fire can also promote non-natives (Heady 1972; D'Antonio 2000). Harrison et al. (2003) found that these effects were environment-dependent, where fire increased species richness of natives on serpentine soils, while increasing species richness of non-natives on non-serpentine soils. This relationship is likely due to native forb prevalence on serpentine soils and non-native forb prevalence on non-serpentine soils, resulting in different seed banks available to respond after fire (Harrison et al. 2003). Across ecosystems, seed banks play a key role in ecosystem response to fire, and thus, managers must consider fire history and frequency for plant biodiversity goals (Kiss et al. 2018). Historically, fire was not a common occurrence in low-productivity serpentine grasslands, and its similarities, differences, and synergies with grazing as a management tool have not been tested.

Here we capitalize on a long-term monitoring study (2004-2012) to understand burning and grazing effects on native serpentine grassland communities in both the short and long-term and assess how these two restoration techniques can be used most effectively either alone or in combination. We use this unique dataset to test the following hypotheses: 1) Burning and grazing have similar effects on native species richness, cover, and composition because they both decrease non-native cover and remove accumulated litter biomass. 2) Burning has a greater effect on the composition of ungrazed than grazed communities, because the effects of grazing and burning are redundant (i.e., both reduce non-native cover and litter accumulation). Alternatively, if these communities have already lost a native seed bank, burning will have less of an effect on ungrazed communities. 3) Burning effects are temporary. We expect that burning will initially increase native diversity, but this response will only persist in grazed communities. 4) Grazing reintroduction will have a lagged effect in which communities slowly shift to resemble continually grazed communities, as native seed availability may initially be limiting. This process may be faster in previously burned compared to unburned communities.

2 Methods

2.1 Site Description and History

Our study is situated on Tulare Hill, a ~130 ha area of serpentine grassland in south San Jose, Santa Clara County, California (37° 13' 16.6" N, 121° 45' 17.2" W). Since at least the 1980s, the site has been invaded by non-native annual grasses such as *Festuca perennis* and *Bromus hordeaceus,* likely due to N deposition from nearby highway sources (i.e., vehicle emissions) (Weiss 1999). From the mid-1980s to 2001, the entire site was heavily grazed (0.83 cattle/ha year-round). Starting in 2001, grazing was reduced to more typical levels for California grasslands (0.20 - 0.25 cattle/ha, with grazing primarily in the spring and occasionally over the summer) throughout most of the hill, but the northern 90 ha were fenced off and not grazed. A wildfire occurred in late May 2004, which was characterized by high winds and surface burning, and burned all the grazed area and some of the adjacent ungrazed area. No prescribed burns took place. In summer of 2008, cattle were reintroduced to all ungrazed areas. Spring and occasional summer grazing was maintained in ungrazed areas through 2011.

We sampled species composition in 0.5 m x 0.5 m permanently marked quadrats. Ten independent quadrats were positioned evenly along 50 m transects (10 quadrats/transect; Figure S3.1; see Appendix D for all supplementary figures). These transects were used to aid with positioning and locating quadrats in the field and not for grouping like quadrats (in some cases, quadrats from opposite ends of the same transect are farther apart than quadrats on two different transects; Figure S3.1). Serpentine grasslands are characterized by fine-scale heterogeneity and are dominated by species with high stem densities and small seed dispersal kernels (several thousand stems/m^2 and dispersal kernels < 1 m, Hobbs & Mooney 1985). As quadrats were a minimum of 5 m apart, we considered them to be independent; this distance between independent replicates is typical of previous long-term studies in this ecosystem (e.g., Hobbs and Mooney 1985, 1991; Weiss 1999; Hallett et al. 2018). Also, to ensure treatment effects are not due to site-specific effects, we accounted for site variation in our analyses and show within-transect variation in Figure S3.2.

Percent species cover was visually estimated once annually at peak biomass (March-April) and percent litter cover was recorded from 2006 onward. The initial design aimed to capture thermal effects of slope and aspect on composition; here we focus exclusively on moderate thermal conditions (habitat stratified between 15-16.49 MJ/m^2 insolation; Murphy & Weiss 1988) with shared slope and aspect to facilitate comparison between grazing and burning. Four transects (40 quadrats) were established in 2001-grazed areas; all these quadrats were burned in 2004. Following the fire, two additional pairs of transects on either side of the burn line (within 20 m of each other) were established in the ungrazed area, resulting in 20 burned-ungrazed and 20 unburned-ungrazed as well as the 40 nearby burned-grazed quadrats. Because the fire covered all grazed areas, we could not include a grazed-unburned contrast. As such, the design allows for a crossing of burn legacy and grazing, with three out of four potential treatment interactions. Over the time period following the burn (2005-2012) we evaluated plant community composition, functional group cover, litter dynamics, and species-specific responses to these three treatment combinations. Grazing was introduced to the previously ungrazed plots in 2008. Therefore, we focus on two time periods: 1) how plant communities changed following the 2004 fire, and 2) how grazing reintroduction in 2008 further altered community trajectories.

We include a focus on *Plantago erecta*, the primary host of the federally threatened Bay checkerspot butterfly (Weiss 1999). While we analyze this species within the same time window (2005-2012), we include a longer timeseries (2001-2018) with lower replication in the supplement to explore potential climate-contingent effects.

2.2 Data Analysis

All analyses were performed in the R statistical computing environment (R Core Team, 2018). Prior to analysis, quadrats that comprised > 80% bare rock cover were removed from plant cover data used in all subsequent analyses – a total of 3 out of 80 quadrats were dropped. We calculated species richness within year, plot, and functional group (i.e., native forb, native grass, non-native forb, non-native grass). Due to low cover and richness of native grasses and non-native forbs (Figure S3.3), we focused our analyses on native forbs and non-native grasses. We focused on relative species cover (species cover divided by total plant cover). For the purpose of subsequent analyses, we refer to burned-grazed, burned-ungrazed, unburned-ungrazed quadrats as “treatments” from this point forward. We calculated annual growing season precipitation as all rainfall from October to April (PRISM Climate Group 2019).

2.3 Species Diversity and Cover Over Time

We used a repeated measures approach to test for treatment effects over time on native forb and non-native grass relative cover and richness, and on the absolute cover of litter (visualized in Figure 3.1; see Appendix C for all figures). We divided the data into two time periods: 1) 2005-2008 after the wildfire and prior to grazing reintroduction, and 2) 2009-2012 after grazing reintroduction. To test for effects of burning and grazing during each of these time periods, we built separate linear mixed effect models using the ‘lme’ function in the nlme package where treatment, year, and treatment*year were fixed effects. Quadrat was included as a random effect to control for site-specific effects over time. We followed this with post-hoc pairwise comparisons of treatments by year using least-square means tests in the emmeans package with Tukey adjustments for multiple comparisons. To understand the relationship between native forbs and litter, we also built general linear regressions of species richness and relative cover of native forbs against absolute cover of litter across years irrespective of treatment. For all tests, we accepted significance at P-values less than 0.05.

2.4 Community Composition Over Time

To test if burning and grazing affected community composition over time, we performed non-metric multidimensional scaling (NMDS) analyses using the ‘metaMDS’ function in the ‘vegan’ package (Oksanen et al. 2018). Using relative cover of plant species by plot, we determined the initial position of the community in multidimensional space using the Bray-Curtis distance coefficient. Separate NMDS analyses were run using years 2005-2008 and 2008-2012 to characterize responses to burning and grazing reintroduction with 4 and 5 dimensions, respectively. The number of dimensions were chosen by plotting stress vs. number of dimensions and choosing the point at which stress was not improved by including additional dimensions. NMDS ordinations were run using 1000 permutations and stress values ranged from 6.3% (burn NMDS, Figure 3.2) to 8.3% (graze NMDS, Figure 3.3), where a stress value less than 10% is ideal (Clarke 1993). We followed NMDS ordinations with permutational multivariate analysis of variance (perMANOVA) to test if communities significantly differed by treatment (burned-grazed, burned-ungrazed, and unburned-ungrazed) for each individual year from 2005 to 2012 (Table S3.1; see Appendix D for all supplementary tables). Multiple perMANOVA analyses were run using 1000 permutations on the Bray-Curtis distance matrix using the ‘adonis’ function in the ‘vegan’ package and subsequent pairwise comparisons between groups with corrections for multiple testing were performed using the ‘pairwise.perm.manova’ function in the ‘RVAideMemoire’ package (Hervé 2019). Lastly, to determine species whose occurrences and abundances have significant associations with each treatment and combinations of treatments, we performed indicator species analyses using the ‘multipatt’ function in the ‘indicspecies’ package (De Caceres & Legendre 2009).

3. Results

3.1 Effects of the 2004 Fire

Native forb richness was significantly greater in the burned-grazed than the unburned-ungrazed in all years following the fire prior to cattle reintroduction (2005-2008; Figure 3.1a, Table S3.2). Burning increased native forb richness (Figure 3.1a, Table S3.2), but this effect in ungrazed areas was temporary. Specifically, native forb richness in burned-ungrazed areas increased and was no different from burned-grazed areas in 2005 and 2006 (Figure 3.1a). In the subsequent two years, all the ungrazed areas, regardless of prior burn, had native forb richness that was significantly lower than the burned-grazed (Figure 3.1a, Table S3.2). There was no effect of burning on non-native grass richness (Figure 3.1b).

Paralleling changes in richness, native forb relative cover was significantly greater in burned-grazed compared to unburned-ungrazed treatments from 2005-2008 (Figure 3.1c, Table S3.2). The relative cover of native forbs in burned-ungrazed shifted over time. Specifically, in 2005 the native forb relative cover in the burned-ungrazed and burned-grazed areas did not differ, and both were significantly greater than in unburned-ungrazed (Figure 3.1c). By 2006, native forb relative cover in the burned-ungrazed was comparable to unburned-ungrazed, and significantly lower than in burned-grazed areas (Figure 3.1c, Table S3.2). *Plantago erecta* cover increased in the grazed area prior to fire (2001-2004) but steadily declined after fire (Figure S3.4). Similar to native forb relative cover, *P. erecta* cover remained greater in burned-grazed compared to burned-ungrazed or unburned from 2005-2012 (Figure S3.4).

The non-native grass relative cover exhibited the inverse pattern of native forb relative cover in response to burning and grazing treatments; whenever non-native grass decreased, there was a corresponding increase in native forb cover and vice versa (Figure 3.1c & d). Specifically, non-native grass relative cover was significantly lower in both burned plots compared to unburned in the first year following the fire (Figure 3.1d) but recovered two years post-fire in ungrazed and grazed areas (Figure 3.1d). Litter data for 2004 and 2005 were not available and immediate effects of burning on litter could not be tested. There were no burning effects on litter cover in subsequent years. However, absolute litter cover was significantly greater in ungrazed plots compared to grazed plots between 2007-2008 (Figure 3.1e, Table S3.2). Litter cover in ungrazed treatments peaked in 2007, mirroring peaks of non-native grasses (Figure 3.1d & e). Within two years of cattle reintroduction, litter cover decreased in previously ungrazed plots and became indistinguishable from grazed plots.

Following the 2004 wildfire, both burned-grazed and burned-ungrazed treatments differed from the unburned-ungrazed in their community composition (perMANOVA, p=0.002 and 0.002 for grazed and ungrazed, respectively, Table S3.3). Within burned treatments, the community composition differed by grazing treatment over time (Figure 3.2). Specifically, the effects of the fire lasted two years on the ungrazed treatment, where the burned-ungrazed was most similar to the burned-grazed in 2005 and 2006 (Figure 3.2a, b & c), but shifted and was no different from the unburned-ungrazed community composition by 2007 (Figure 3.2a & d; perMANOVA, p=0.385, Table S3.3) and remained no different in 2008 (Figure 3.2a & e; perMANOVA, p=0.256, Table S3.3). Continually grazed plots remained different from the unburned-ungrazed treatment through 2008 (Figure 3.2a & e; perMANOVA, all p<0.05, Table S3.3).

Indicator species analysis showed that burned plots, regardless of grazing treatment, shared 5 native forb indicator species in the first two years following the fire, including *P. erecta* and *Lasthenia californica* (Table 3.1; see Appendix C for table). Immediately following the fire (2005-2006), the burned-grazed treatment contained an additional 2 native forbs indicators, while an additional native forb, *Castilleja densiflora,* was an indicator for burned-ungrazed (Table 3.1). In the ungrazed plots, regardless of burn treatment, the non-native grass *Festuca perennis* was a significant indicator species in all years (Table 3.1). As communities shifted in 2007, fewer indicator species were shared between both burned treatments, and native forbs were more associated with the burned-grazed, but not burned-ungrazed treatment (Table 3.1). Several species, including *Trifolium depauperatum, Agoseris heterophylla,* and *Microseris douglasii* were only associated with burned-grazed quadrats over time (Table 3.1).

3.2 Effects of Cattle-Grazing Reintroduction in 2008

Grazing reintroduction in previously ungrazed quadrats immediately increased native species richness to the same levels as continually grazed quadrats and had no effect on non-native richness, which remained no different between treatments (Figure 3.1a & b). Three years after grazing reintroduction, there was no difference in the relative cover of forbs and non-native grasses for previously burned-ungrazed and unburned quadrats (Figure 3.1c & d). Prior burning in ungrazed quadrats did not accelerate the recovery of native forb richness or cover relative to unburned-ungrazed quadrats. Litter significantly decreased following grazing reintroduction in ungrazed quadrats until 2010 (Figure 3.1e), when litter increased across all treatments following two wet years in 2010 and 2011 (Figure 3.1e & f). During this time previously ungrazed quadrats maintained 5-10% more litter than continually grazed quadrats. In addition, increased litter resulted in a corresponding decline in forb richness despite continual grazing presence (Figure S3.5). In 2012, the treatment with the greatest litter cover (previously burned-ungrazed), had the lowest native forb cover and highest non-native grass cover (Figure 3.1e, c, & d).

Before grazing reintroduction in summer 2008, burned communities with different grazing histories differed in composition from one another (Figure 3.3a). Burned-grazed also differed from the unburned community (Figure 3.3b; perMANOVA, $p=0.002$, Table S3.3), while the burned-ungrazed group did not (Figure 3.3b; perMANOVA, $p=0.256$, Table S3.3). Following grazing reintroduction, community composition shifted by treatment over time (Figure 3.3), where all communities differed after the first year of grazing (Figure 3.3c; perMANOVA, all $p<0.05$, Table S3.3). While previously ungrazed communities became more similar to the continually grazed community over time (Figure 3.3a), community composition by treatment remained significantly different up to four years post-grazing (Figure 3.3d, e & f; perMANOVA, all $p<0.05$, Table S3.3). Previously burned-ungrazed plots recovered high *P. erecta* abundance six years after cattle reintroduction (Figure S3.4).

Indicator species analysis showed that before the reintroduction of grazing in 2008, burned groups shared four native forb indicator species (*P. erecta, Lepidium nitidum, Calandrinia ciliata*, and *Crassula connata*, Table 3.1). Additionally, both previously ungrazed groups shared a non-native grass indicator, *Festuca perennis*, prior to grazing reintroduction, which they continued to share throughout the remainder of the study (Table 3.1). Following grazing reintroduction in 2009, previously ungrazed communities gained native forb indicators, including *Epilobium* sp., *Chlorogalum pomeridium*, *Hemizonia congesta,* and *Muilla maritima* (Table 3.1). The forb indicator species gained after grazing reintroduction differed from the indicator species present in earlier years following the fire (Table 3.1). In 2011, following two wet years (Figure 3.1f), burned and unburned groups shared less native forb indicator species, but shared more non-native grass indicator species.

4. Discussion

Systems-based interventions are a promising tool for restoration ecology, allowing a proactive approach to counteract ongoing global change effects. While promising, few long-term studies have assessed these interventions in real-world situations. Long-term monitoring of the plant community at our study site provided the unique opportunity to assess immediate and long-term interactive potential of burning and grazing as interventions for serpentine grasslands experiencing N deposition. We found that burning and grazing had similar effects on native diversity, supporting our first hypothesis: both native forb cover and richness underwent the same positive directional change, while non-native grass cover declined following a fire and grazing reintroduction into the system. However, community change trajectories were dependent on previous grazing or burning history, supporting our second hypothesis. Specifically, burning had the greatest effect on previously ungrazed quadrats, which became more similar to the burned-grazed quadrats, while the burned-grazed had a much smaller shift in community composition with fire. Trajectories after grazing reintroduction did not depend on prior burn history, but instead on duration of grazing, where under continuous grazing the relative higher forb cover was maintained compared to reintroduced areas. Finally, the response time and effect duration of fire and grazing differ. While burning resulted in an immediate response in community composition that lasted for two years, consistent with our third hypothesis, there was a lagged response to grazing reintroduction, with communities slowly becoming more similar over time, supporting our fourth hypothesis.

While changes to N availability are likely the ultimate cause for shifting dominance patterns in serpentine systems, non-native annual grasses reinforce their dominance via establishment of a thick litter layer, which promotes their germination, but excludes many natives, especially native forbs (Huenneke et al. 1990; Meyer & Schiffman 1999). Our results demonstrated that native forb richness and cover declined with increasing litter cover. Yet, burning and grazing are both effective strategies to reduce litter cover. Burned quadrats had lower litter cover two years after the fire and continually grazed quadrats had lower litter cover than ungrazed quadrats. Similarly, the reintroduction of grazing onto previously ungrazed quadrats had immediate negative effects on litter cover. However, litter accumulation is also strongly correlated to rainfall, where high precipitation years are related to high grass biomass production, and subsequently litter accumulation (Bartolome et al. 2002; Dudney et al. 2017). We also found that litter cover increased across all quadrats following the two wettest years (2010 and 2011), resulting in a corresponding decline in forb richness despite continual grazing. While litter cover was not significantly correlated with precipitation in our study, we speculate this may be due to precipitation influencing litter depth more than cover. Identifying a limit of this restoration tool, we highlight here that high litter cover overrides grazing's effectiveness for promoting native forb richness and stress the need to account for other drivers of variability (i.e., precipitation patterns).

Both fire and grazing were effective in reducing the litter layer, allowing native forb recruitment. Other studies show greater native forb emergence and diversity in serpentine grasslands after a one-time fire (Harrison et al. 2003) and with cattle grazing, respectively (Safford & Harrison 2001; Harrison et al. 2003); however, on non-serpentine California grasslands, fire increased non-native forb cover (Harrison et al. 2003; Seabloom et al. 2003) and grazing had little effect on native composition (Jackson & Bartolome 2002). Across ecosystems, seed banks are critical in determining restoration trajectories under stresses such as climate change (Kiss et al. 2018), and the differential responses in serpentine and non-serpentine grasslands suggests that the presence of a native seed bank is key to native recovery after litter removal by fire or grazing. Non-serpentine grasslands have likely already lost their native seed bank over a long period of non-native annual grass dominance (Hamilton et al. 1999; Seabloom et al. 2003; Brandt & Seabloom 2012), while serpentine grasslands likely still have a reserve seed bank allowing for recovery (Seabloom et al. 2003). While the seed bank was not measured in this study, we speculate an intact seed bank aided in native forb recovery following burning and grazing.

The effects of fire on serpentine grassland communities were immediate, but transient, disappearing after two years. Other studies have also found that effects often disappear within a few years of a one-time fire (D'Antonio et al. 2002; Harrison et al. 2003). For example, in a meta-analysis, D'Antonio et al. (2002) found that in the first two years after a burn, fire had a positive effect on native plant richness and a negative effect on non-native grass cover in California annual grasslands; however, these effects disappeared two years post-burn. While fire initially clears non-native annual grass litter and improves growing conditions for forbs, a lagged but high resurgence of non-native grasses has been observed by two years post fire (Hervey 1949; Parsons & Stohlgren 1989; Keeley & Keeley 1981; Menke 1989; D'Antonio 2000). We also observed a lagged, but high recovery of non-native grasses by two years post-fire in both grazed and ungrazed quadrats. This lagged response may be attributed to the nutrient input from fire ash (Menke & Rice 1981) which favors fast-growing, resource acquisitive non-natives (Stohlgren et al. 1999). While burned quadrats with continuous grazing also experienced a resurgence of non-native grasses, grazing appears to control non-natives after the initial resurgence while ungrazed quadrats continue to gain non-native grass cover. These responses depend on the timing of fire and are tightly tied to each group's seed bank density. For example, besides litter layer removal, fire can also reduce non-natives if fire occurs early in the growing season prior to non-native seed dispersal (Eller 1994; Pollak & Kan 1998; Meyer & Schiffman 1999). Similarly, summer burn may also be effective by decreasing the seed bank of exotic grasses *Bromus hordeaceus* and *Taeniatherum caput-medusae* (Menke & Rice 1981). Because the fire at our study site occurred in May 2004 after seed dispersal, we expect it was more effective at reducing litter accumulation, with smaller effects on the non-native seed bank.

We found that native forb relative cover increased more slowly after grazing reintroduction compared to fire. This could be due to slow reduction in non-native grass and litter cover following grazing reintroduction, low forage selectivity by grazers, or patchy, localized changes in non-native cover. Similarly, Meyer & Schiffman (1999) found that litter reduction via grazing was not as effective as complete litter removal (e.g., to bare ground via fire) at promoting native forbs because bare ground provides specific environmental cues that improve annual forb species germination and survivorship (Rice 1989). In our study, grazing reduced, but did not completely remove litter cover. On the other hand, forb recovery after grazing may have a slow response time if the native seed bank has been reduced by years of non-native annual grass dominance. We expect this is not the case, as native forb cover recovered immediately after burning in the ungrazed plots, indicating the presence of a native seed bank for ungrazed quadrats. Thus, the effectiveness of grazing is most likely dependent on grazing intensity (Pasari et al. 2014), timing, and frequency, where greater grazing intensity over the summer may have a faster impact on native forb resurgence from litter removal. However, with a more intensive grazing regime, cattle may consume their preferred nitrogen-rich annual grasses and then move on to consuming the less palatable native forbs. Additionally, the presence of grazers introduces localized deposits of nutrients via their feces and urine, which may promote or sustain non-native species. While the effects on soil nutrients vary, grazing in California’s grasslands generally increases soil nitrogen availability while decreasing phosphorus and sulfur (Vaughn et al. 1986; Stromberg & Griffin 1996) and concentrates nutrients in animal-gathering areas (e.g., under shade and near food/water containers; Jackson & Bartolome 2007).

In the serpentine system, both fire and grazing address a proximate driver (e.g., litter accumulation from annual grass invasion) of native species loss, but they also have differences that may shift ecosystem trajectories. These trajectories are important in restoration decisions. For example, while the fire increased native forb populations in the short term, the highly productive grasses also flourished following the fire in the absence of grazing and regained dominance after only two years. This suggests that a one-time fire alone is likely insufficient to control non-native grass populations. Previous studies also show that sustained increases in native forbs require annual burns in ungrazed areas (D'Antonio et al. 2006). While we acknowledge that we could not compare burned-grazed to unburned-grazed quadrats (as the wildfire at the site burned all of the grazed quadrats), the burned and continually grazed quadrats supported the greatest native forb and lowest non-native grass populations. This suggests that a burn paired with continuous grazing is a promising management approach for removing annual grass litter and supporting native forb populations in serpentine grasslands. We also acknowledge that dynamics in this study may differ across the landscape with topographic variability. However, similar dynamics have been qualitatively noted across serpentine grasslands in high N-deposition zones over nearly three decades, first noted in Weiss (1999) – intensified grass invasions, accumulation of litter, loss of forb cover and diversity, followed by more gradual recovery over several years when grazing is reintroduced. The same responses have been observed across different slopes, and grazing has been a required management action on all conserved lands at our study site.

Success in native plant recovery can extend to other restoration goals, such as supporting higher-trophic species. Here, we focused on *P. erecta* recovery, a primary host plant for the federally threatened and endemic Bay checkerspot butterfly. In 1987, the Bay checkerspot butterfly population was estimated in the low hundreds at our study site (Harrison et al. 1988). It disappeared by 1990 following several years of drought. A few butterflies were observed in 1995, and by 2002, the population was estimated in the low thousands. By 2004, the lack of grazing on the northern part of the hill led to habitat deterioration, and only a small Bay checkerspot butterfly population remained on the southern 40 ha, where annual sightings of adult butterflies ranged 1-5 per year. Indirectly, our results support the use of burning and grazing as management tools that can aid the butterfly through bolstering populations of *P. erecta*. We found that the burn increased *P. erecta* abundance immediately, whereas grazing reintroduction appeared to have a lagged effect in which *P. erecta* did not recover for six years. However, *P. erecta* exhibits a cyclical population dynamic with a peak and trough about every 5-10 years (Hallett et al. 2018), and the burn occurred during a peak whereas cattle were reintroduced during a trough in its cycle. This patterning highlights the need for long-term studies that assess intervention success across a range of natural variability. While we did not measure the direct effect of grazing or burning on butterfly populations, in theory, larval populations could be affected positively or negatively depending on when the management tool is implemented. This, along with potentially different effects on plant functional and community composition, is motivation to consider the timing and intensity of the implemented fire and grazing regimes in future studies.

CHAPTER IV

CONCLUSION

Within the context of ongoing global change, active and continual management may be necessary in ecosystems. Serpentine grasslands under global change exemplify this point: as chronic N deposition acts over time with increasing rainfall variability from climate change, exotic grasses will dominate serpentine grasslands and continue to reassert their dominance via the production of a litter layer. The continual removal of this litter layer via burning and grazing is essential to promoting native forb recovery since reducing N deposition is a complex social issue that will require long-term solutions.

Leveraging our improved understanding of how N deposition and climate change interact to favor exotic annual grasses, I recommend that management like burning and grazing should be implemented in the summer following a wetter growing season. I also encourage future studies to test if native seeding in serpentine grasslands during dry winters can be effective in increasing native populations. While it is an expensive restoration tool, if it is effective in bolstering dominant native forbs in dryer-than-average winters, increased native cover and seed production may resist exotic competition in subsequent wetter years. Together, we can proactively ensure that patches of serpentine grasslands retain their biodiversity and continue to be marveled by current and future generations.

APPENDICES

APPENDIX A: CHAPTER II ILLUSTRATIONS

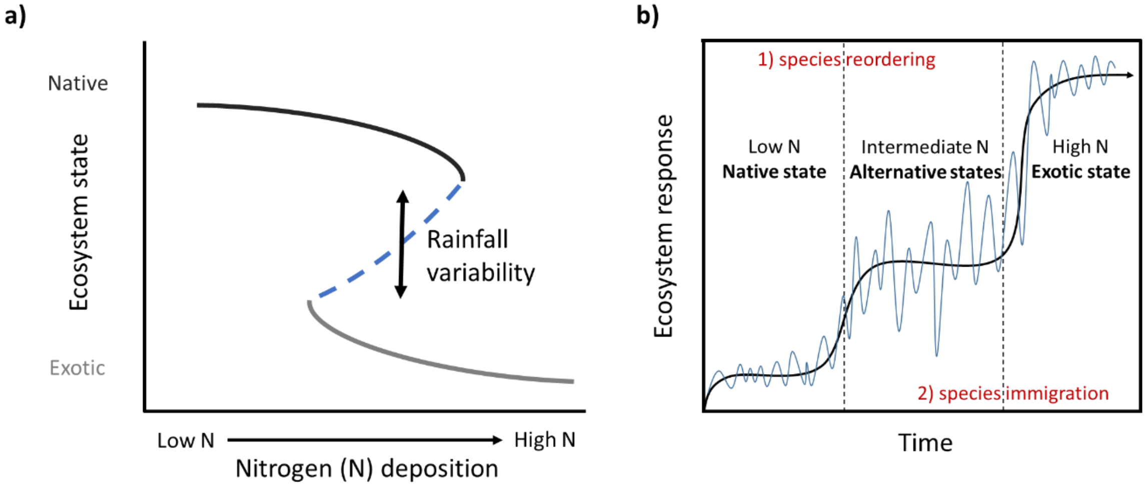


Figure 2.1 Schematic of hypotheses based on alternative stable states theory and the “hierarchical response framework”: a) Under intermediate levels of N, systems co-limited by N and water like California serpentine grasslands will be most susceptible to rainfall variability, toggling the system between native- and exotic-dominated alternative states in dry and wet years, respectively. b) As N deposition slowly and continuously acts with rainfall variability over time, native and exotic species will first reorder in abundance, increasingly fluctuating ecosystem response, and then species immigration, or greater exotic seed production under increasingly favorable N conditions in wet years, will allow for an ultimate conversion to an exotic stable (adapted from Smith et al. 2009).

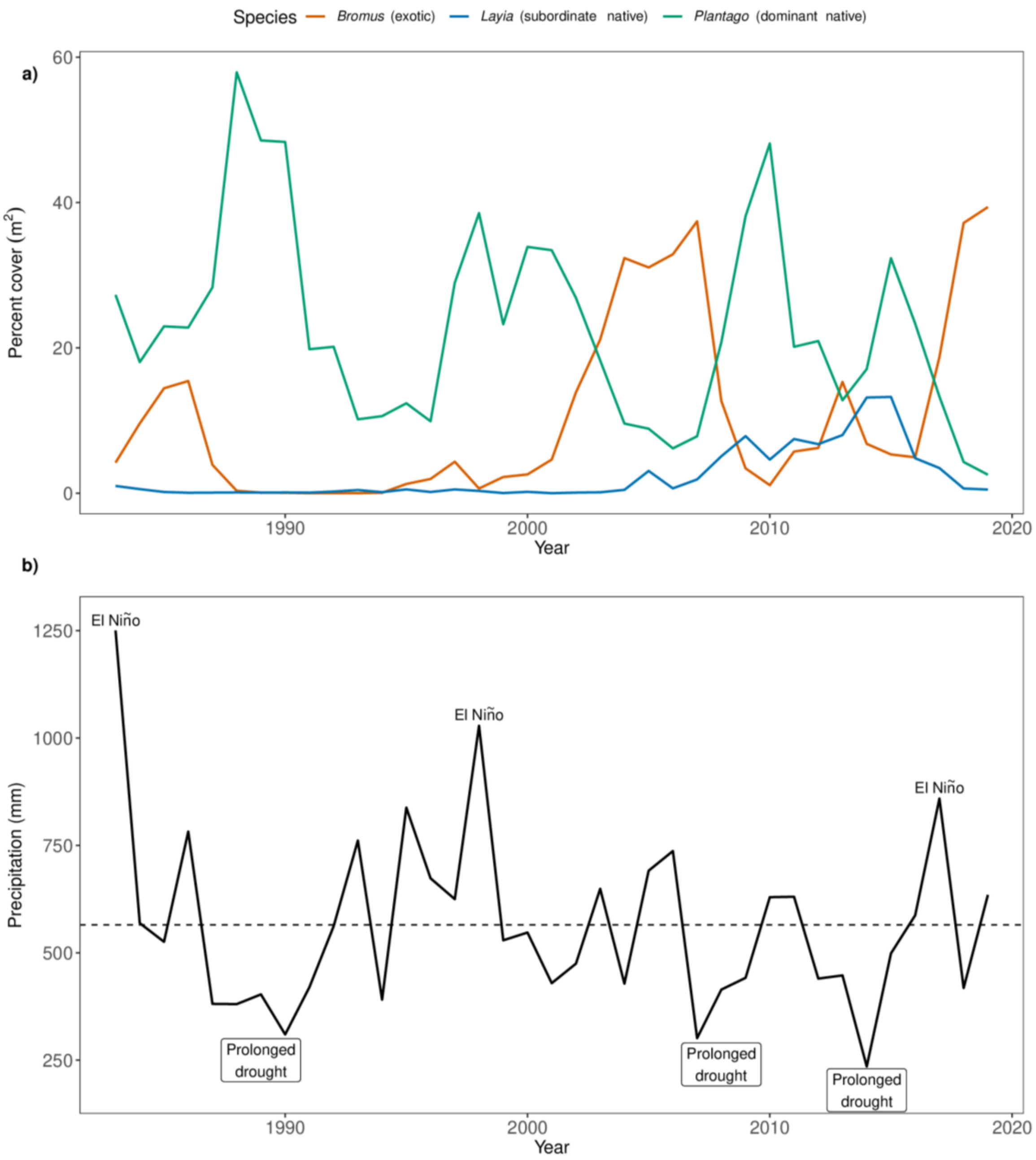


Figure 2.2 Time series from 1983-2019 at Jasper Ridge Biological Preserve in San Mateo County, California, of **a)** mean percent cover (m^2) of the exotic, subordinate native, and dominant native in serpentine grassland plots, and **b)** mean annual growing season precipitation (September-April; mm); dashed line represents the average growing season precipitation (565 mm) during this period and extreme precipitation events are labeled.

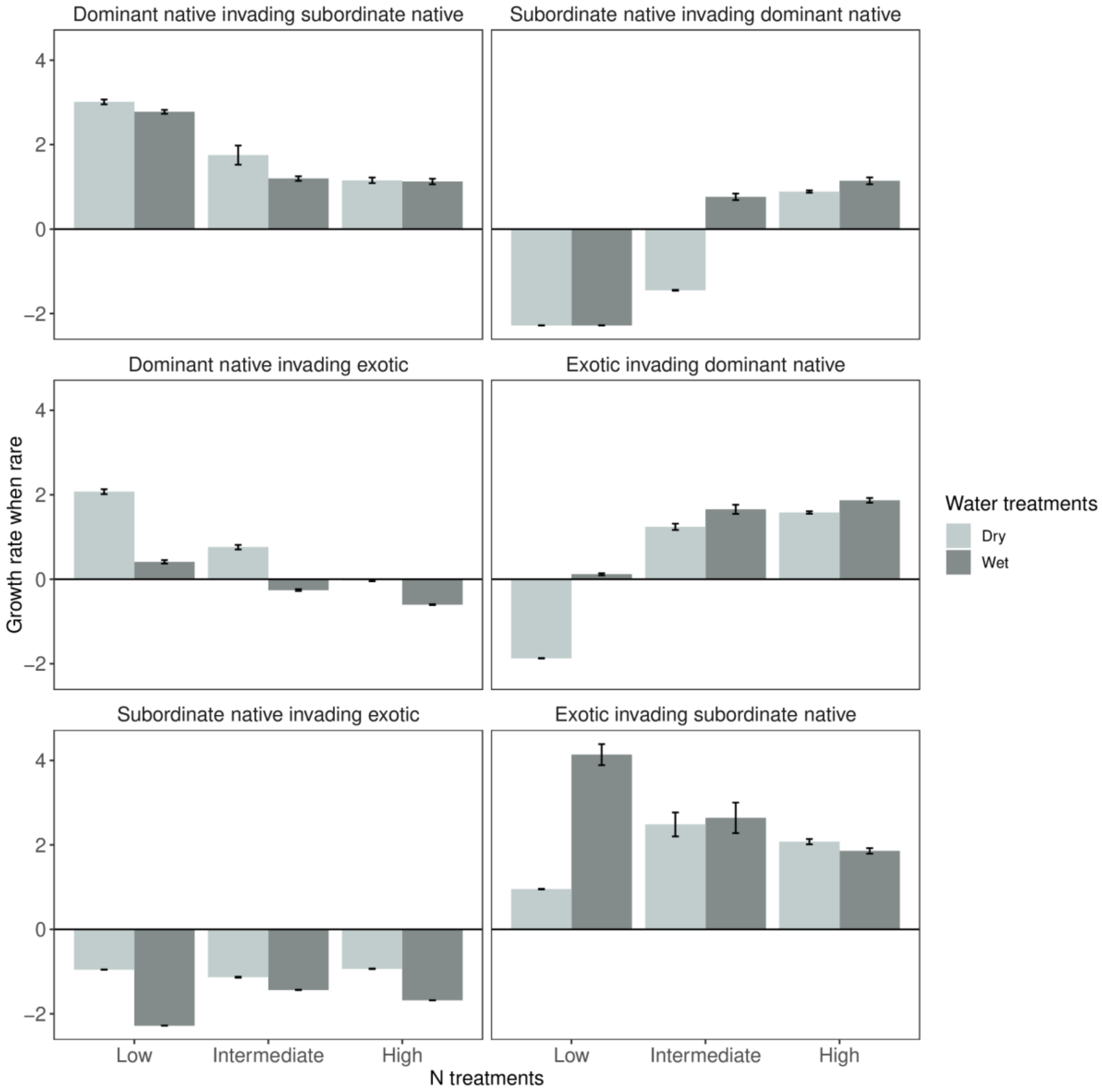


Figure 2.3 Mutual invasion criterion for coexistence for each pairwise species combination across treatments determined by growth rates when rare (GRWR) of each species invading the other's resident community: a) the dominant native and subordinate native, b) the dominant native and exotic, and c) the subordinate and exotic. Error bars indicate ± SE and growth rates are calculated when the focal species is rare and the other is at its equilibrium population abundance (resident community); populations can increase when GRWR is > 0 and coexistence occurs when both species GRWR is > 0.

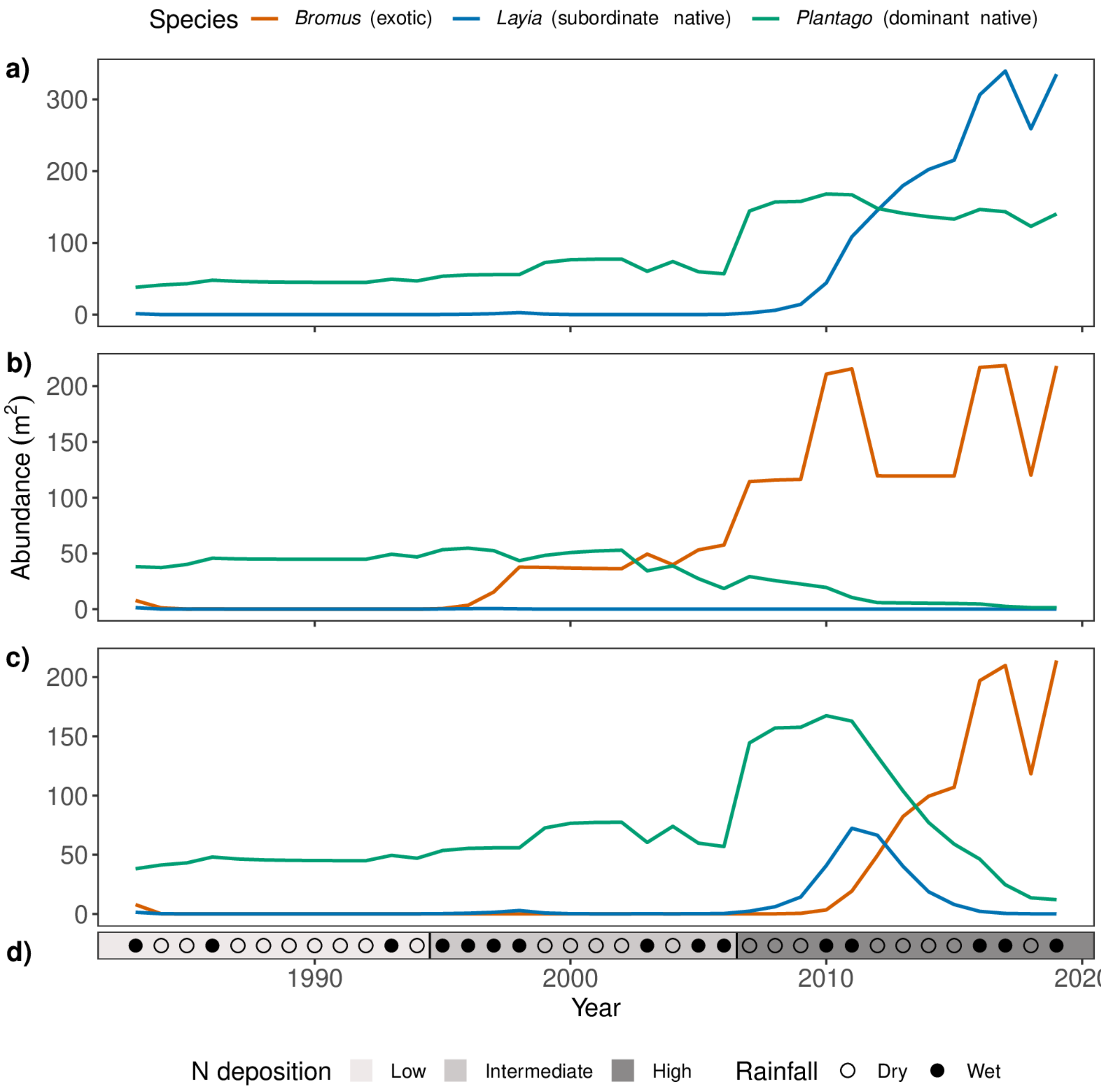


Figure 2.4 Time series simulations (1983-2019) of species abundances (m^2) for a) the subordinate native and dominant native without the exotic, b) the subordinate native and dominant native with the exotic, and c) the subordinate native and dominant native with exotic seed bank limitation and delayed propagule arrival. Species abundances from one time step to the next were calculated (Equation 1) with germination and survival fractions from Table S2.3 and estimated intrinsic growth rates and per-capita competition coefficients for all species by N-water treatments in Table S2.4, which were matched to

d) each year’s environmental conditions by N deposition and rainfall. The first time step in these simulations used starting percent cover conditions in 1983 from Figure 2.2a that were converted into abundances.

APPENDIX B: CHAPTER II SUPPLEMENTARY INFORMATION

Table S2.1. Average number of seeds added to high- and low-density pots by background competitor.

Species	**Low density** (5 $g/m^2 \approx 51.6$ mg seed/pot)	**High density** (20 $g/m^2 \approx 206.5$ mg seed/pot)
Bromus	27	104
Layia	89	361
Plantago	26	104

Table S2.2. Proportion of immature to mature *Bromus* seed collected and counted from the greenhouse experiment.

***Bromus* seed type**	**Immature count**	**Mature count**	**Percent immature**
Background	490	1975	24.8%
Phytometer	28	289	9.7 %

Table S2.3. Germination (*g*) and survival (*s*) fractions for each species from the literature.

Species	***g***	***s***	**Reference**
Bromus	0.98	0.013	*g:* Gulmon 1992 *s:* Muehleisen et al. *in prep*
Layia	0.32	0.15	Rossington 2015
Plantago	0.92	0.75	*g:* Gulmon 1992 *s:* LaForgia et al. 2020

Table S2.4. Estimated intrinsic growth rates (λ) and per-capita competition coefficients (α) for each species in each N-water treatment using the Hamiltonian Monte Carlo method.

Species	**Dry Low N**	**Dry Interm N**	**Dry High N**	**Wet Low N**	**Wet Interm N**	**Wet High N**
Bromus	$\alpha_{b,b} = 0.02$ $\alpha_{b,l} = -0.001$ $\alpha_{b,p} = 0.02$ $\lambda_b = 0.27$	$\alpha_{b,b} = 0.58$ $\alpha_{b,l} = 0.04$ $\alpha_{b,p} = 0.08$ $\lambda_b = 26.0$	$\alpha_{b,b} = 3.1$ $\alpha_{b,l} = 0.4$ $\alpha_{b,p} = 0.50$ $\lambda_b = 376.5$	$\alpha_{b,b} = 0.48$ $\alpha_{b,l} = 0.06$ $\alpha_{b,p} = 0.13$ $\lambda_b = 9.58$	$\alpha_{b,b} = 0.83$ $\alpha_{b,l} = 0.18$ $\alpha_{b,p} = 0.16$ $\lambda_b = 53.1$	$\alpha_{b,b} = 1.1$ $\alpha_{b,l} = 0.24$ $\alpha_{b,p} = 0.22$ $\lambda_b = 241.4$
Layia	$\alpha_{l,l} = 0$ $\alpha_{l,b} = 0$ $\alpha_{l,p} = 0$ $\lambda_l = 0$	$\alpha_{l,l} = 4.8$ $\alpha_{l,b} = 7.6$ $\alpha_{l,p} = 7.6$ $\lambda_l = 224.8$	$\alpha_{l,l} = 0.83$ $\alpha_{l,b} = 2.3$ $\alpha_{l,p} = 0.23$ $\lambda_l = 251.1$	$\alpha_{l,l} = 0$ $\alpha_{l,b} = 0$ $\alpha_{l,p} = 0$ $\lambda_l = 0$	$\alpha_{l,l} = 5.6$ $\alpha_{l,b} = 7.3$ $\alpha_{l,p} = 0.54$ $\lambda_l = 194.3$	$\alpha_{l,l} = 1.4$ $\alpha_{l,b} = 10.4$ $\alpha_{l,p} = 0.39$ $\lambda_l = 590.4$
Plantago	$\alpha_{p,p} = 0.03$ $\alpha_{p,b} = 0.03$ $\alpha_{p,l} = 0.004$ $\lambda_p = 2.2$	$\alpha_{p,p} = 0.10$ $\alpha_{p,b} = 0.06$ $\alpha_{p,l} = 0.02$ $\lambda_p = 8.4$	$\alpha_{p,p} = 0.21$ $\alpha_{p,b} = 0.27$ $\alpha_{p,l} = 0.08$ $\lambda_p = 32.3$	$\alpha_{p,p} = 0.01$ $\alpha_{p,b} = 0.01$ $\alpha_{p,l} = 0.01$ $\lambda_p = 1.7$	$\alpha_{p,p} = 0.08$ $\alpha_{p,b} = 0.09$ $\alpha_{p,l} = 0.03$ $\lambda_p = 5.1$	$\alpha_{p,p} = 0.10$ $\alpha_{p,b} = 0.15$ $\alpha_{p,l} = 0.03$ $\lambda_p = 17.1$

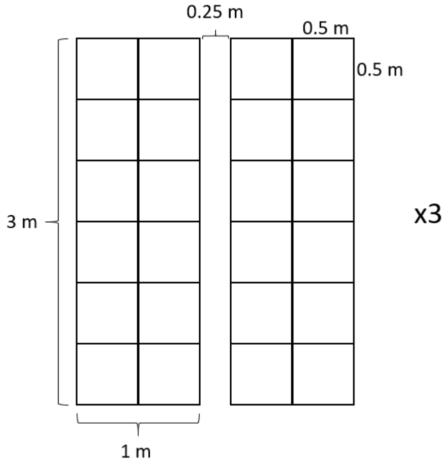


Figure S2.1. Schematic of a survey plot replicated 3 times for sampling at Jasper Ridge, where plots were at least 5 m apart.

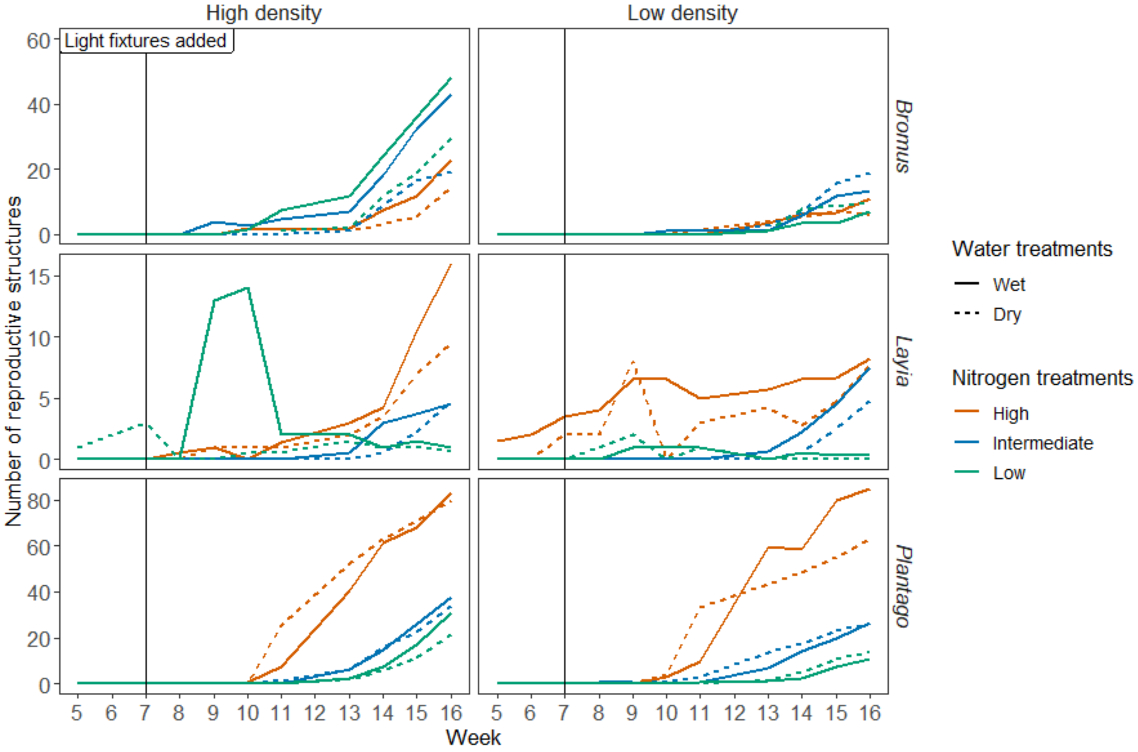
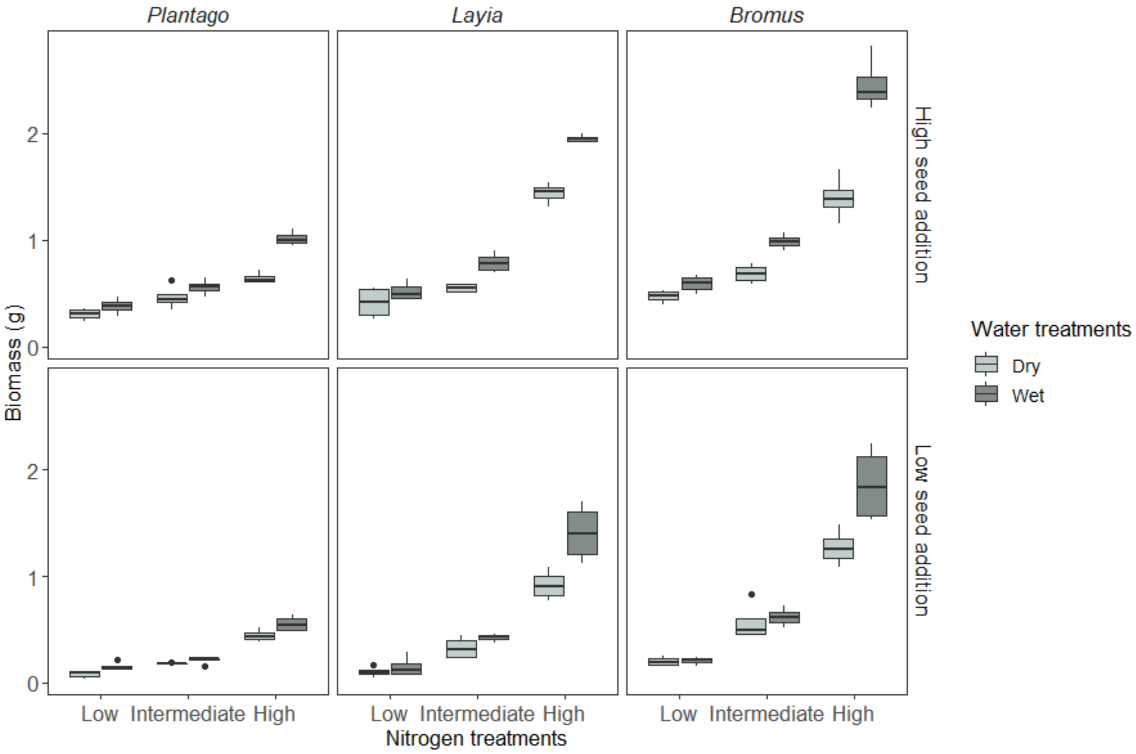


Figure S2.2. Weekly number of flowering culms for *Bromus* and number of stalks with flowers for *Layia* and *Plantago* across N-water treatments from 14 November 2019 to 16 February 2020. Phenology monitoring began 5 weeks after the greenhouse experiment started and continued until 1 week before plants were harvested.

Figure S2.3 (next page). Biomass of each species as the background competitor across N, water, and seeding density treatments.



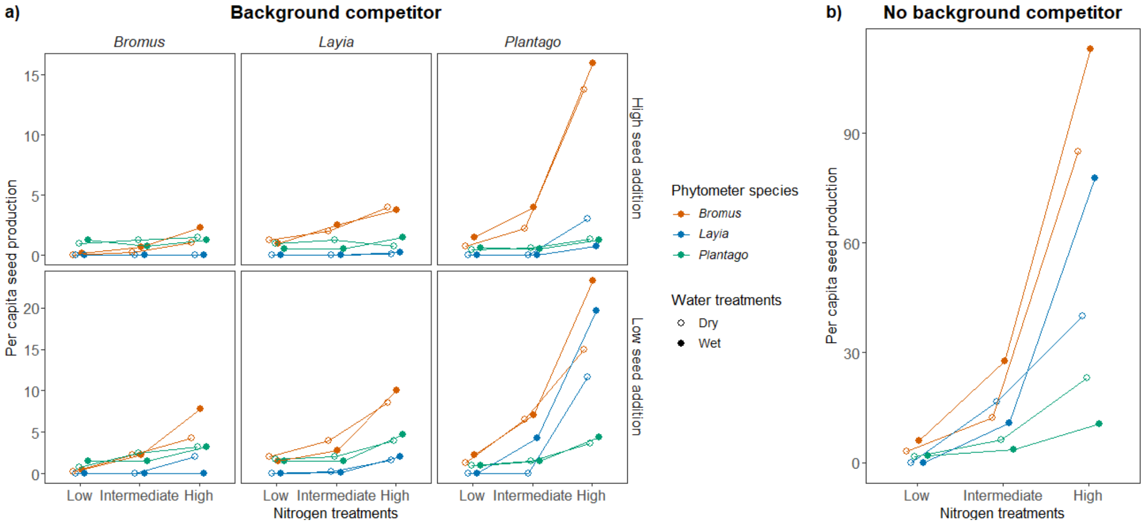


Figure S2.4. Mean per capita seed production of each species as a phytometer in competition with a) each background competitor and b) no background competitor across N, water, and seeding density treatments.

APPENDIX C: CHAPTER III ILLUSTRATIONS

Table 3.1. Multilevel pattern analysis results showing significant indicator species (p<0.05) for a) Native forbs and b) Non-native grasses. Results shown are indicator species in burned-grazed (●), burned-ungrazed (◍), and unburned-ungrazed (○). Only species that were significant indicator species more than one time during the eight years of this study are shown here. For a full list of indicator species, see Table S3.4.

	2005	2006	2007	2008	2009	2010	2011	2012
a) Native forbs								
A. heterophylla			●		●	●		
M. douglasi				●	●			
T. depauperatum	●		●	●		●	●	
P. erecta	●◍	●◍	●	●◍	●			
L. californica		●◍	●	●	●◍	●◍		
L. nitidum	●◍	●◍	●◍	●◍				
A. occidentalis		●◍	●◍			◍○		○
G. tricolor		●◍	●					
C. ciliata				●◍	●◍			●
C. densiflora	◍		●					
C. connata			●	●◍				
Brodiaea sp.		●○	●○	●○	●○			
Epilobium sp.			○	○	◍○	○	○	
C. pomeridianum				○		◍○	◍○	◍○
M. maritima					◍○	○	○	
H. congesta					◍○	◍○		
A. wrangelianus							◍○	●○
b) Non-native grasses								
F. perennis	◍○	◍○	◍○	◍○	◍○	◍○	◍○	◍○
Festuca sp.	●◍						●	
H. murinum					●○		●○	●○
Avena sp.			●		●◍			

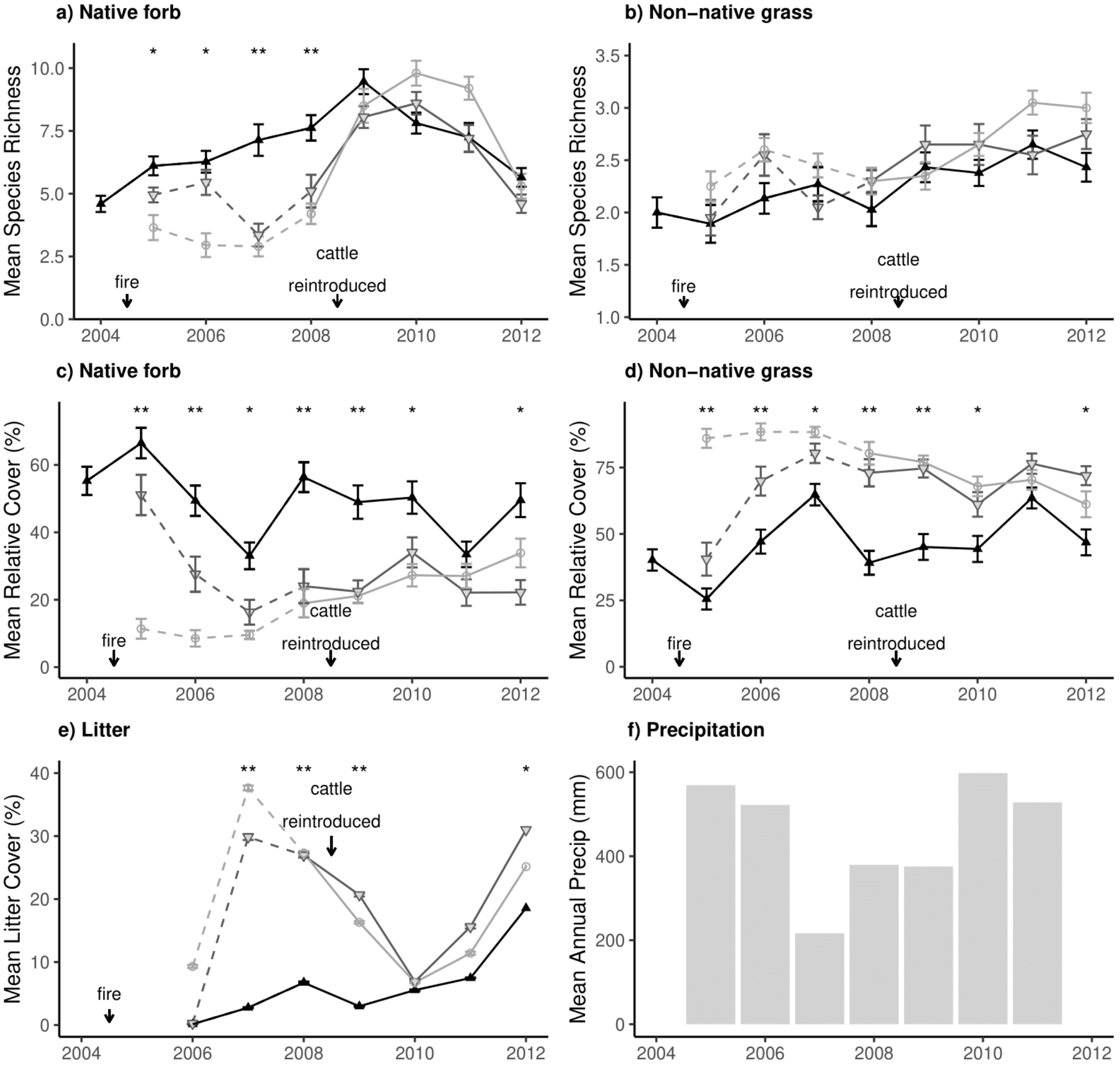


Figure 3.1. Time series of species richness of a) native forb and b) non-native grass, relative cover (%) of c) native forb and d) non-native grass, absolute cover (%) of e) litter, and f) annual precipitation (mm) of the growing season, October to April, from 2004 to 2012. Litter cover data for 2005 and 2006 were not available. Shapes indicate means, error bars represent ±SE, and treatments are differentiated by color and shape: burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). Solid lines indicate periods of grazing and dashed indicates periods in which quadrats were not grazed.

Arrows point to two treatment events: wildfire in May 2004 and grazing reintroduction in previously ungrazed quadrats in summer 2008. In panels a) through e) asterisks are used to represent significant least-square means post-hoc results of yearly treatment effects (Table S3.2). Each asterisk represents a significantly different pair of treatments, ranging from zero (none of the treatments are different), one (two most distant points are different), two (most distant pairs are different), and three (all of the treatments are different).

Figure 3.2 (next page). Non-metric multidimensional scaling ordinations of plant community cover data following a 2004 fire for burned and unburned quadrats by grazing treatment over time. Treatments are differentiated by color and shape: burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). a) Mean community compositional change by treatment over time. Vectors show the compositional shift in ordination space with arrows indicating the direction of change over time, with each point representing a year. The burned-grazed quadrats include 2004 (pre-fire) through 2008 community data. Pre-fire data were not available for ungrazed quadrats and 2005-2008 data are shown. Significant indicator species identified by multilevel pattern analysis (see Table 3.1) are overlaid on the community ordination, non-native grasses are shown in *italic* and native forbs are shown in **bold**. b-e) Community ordinations of all quadrats from 2005 through 2008, respectively. Ellipses show a 95% confidence interval around the mean of each treatment’s cloud of points.

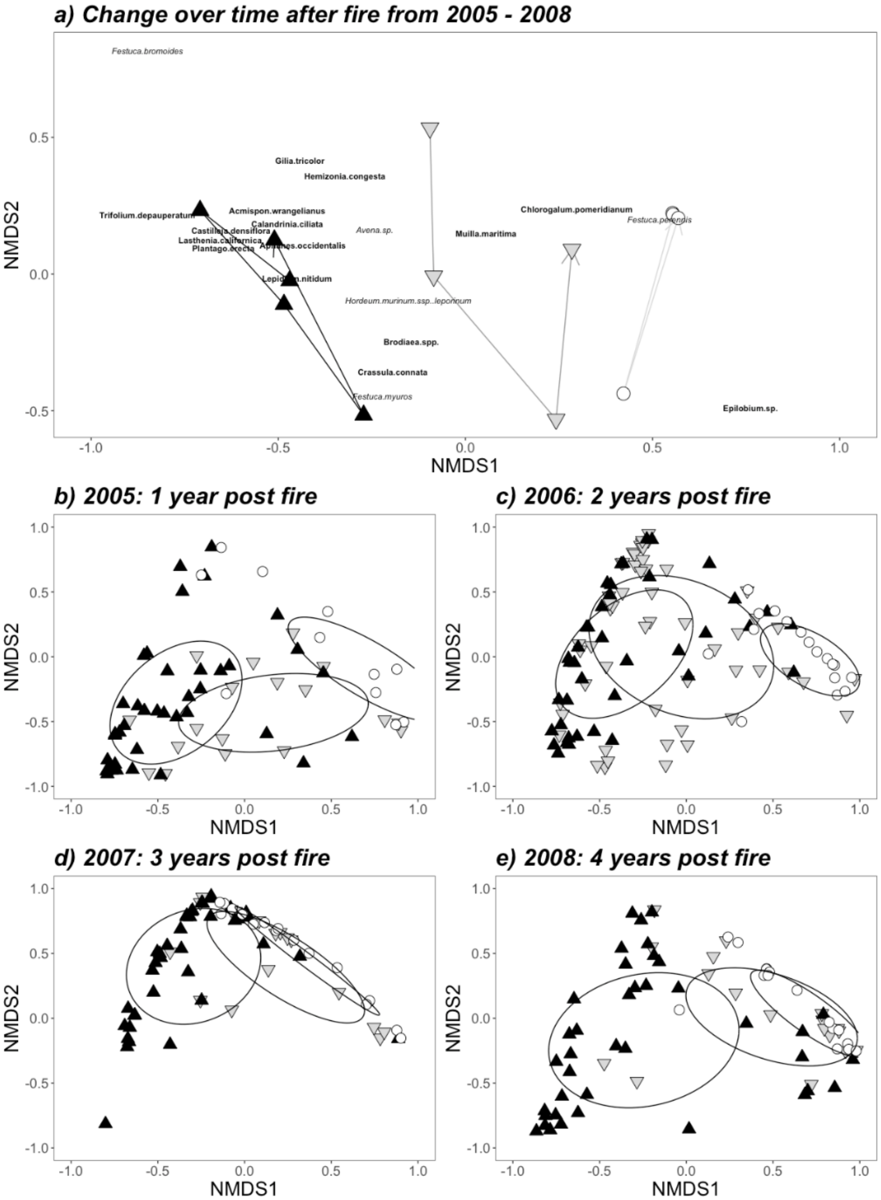
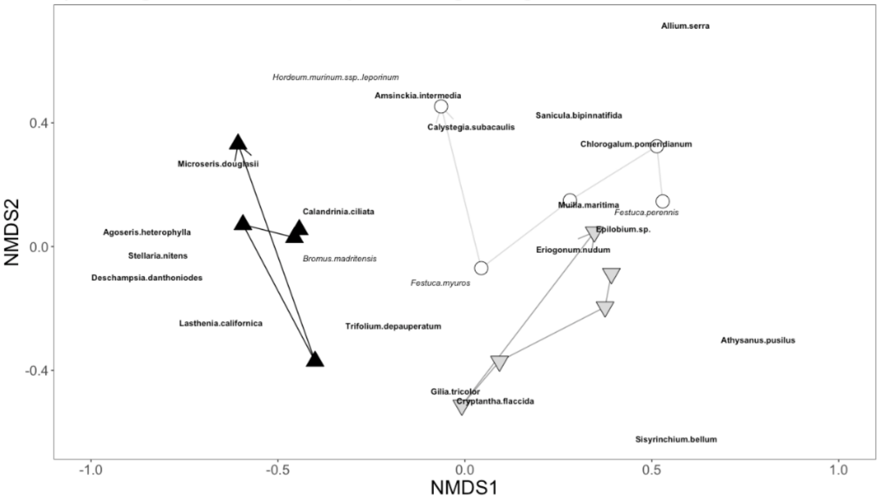
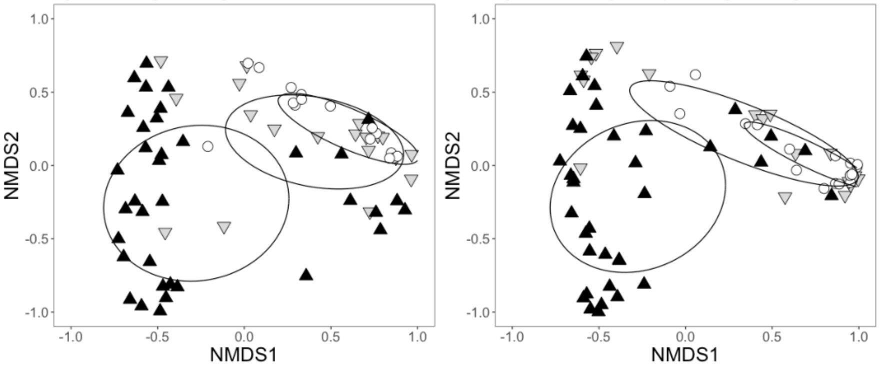


Figure 3.3 (next page). Non-metric multidimensional scaling ordinations of plant community cover data following the reintroduction of grazing for previously burned and unburned quadrats by grazing treatment over time. Grazing was reintroduced in summer 2008. Treatments are differentiated by color and shape: burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). a) Mean community compositional change by treatment over time. Vectors show the compositional shift in ordination space with arrows indicating the direction of change over time, with each point representing a year from 2008-2012. Plant species significantly correlating with treatments (see Table 3.1) are overlaid on the ordination, non-native grasses are shown in *italic* and native forbs are shown in **bold**. b-f) Community ordinations for all quadrats from 2008 through 2012, respectively. Ellipses show a 95% confidence interval around the mean of each treatment's cloud of points.

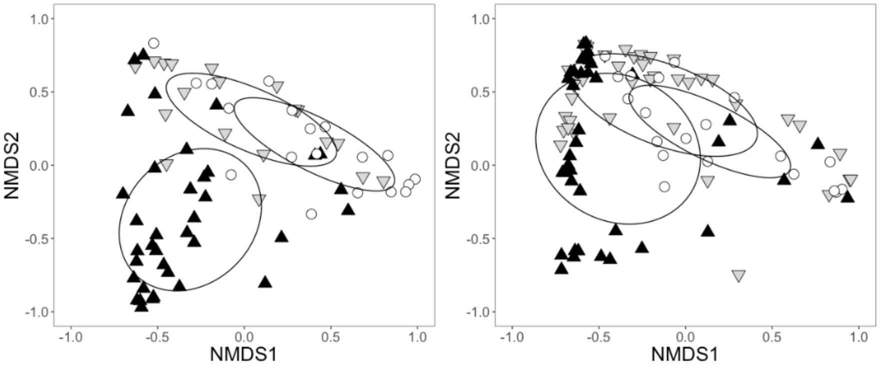


a) Change over time in response to grazing from 2008-2012



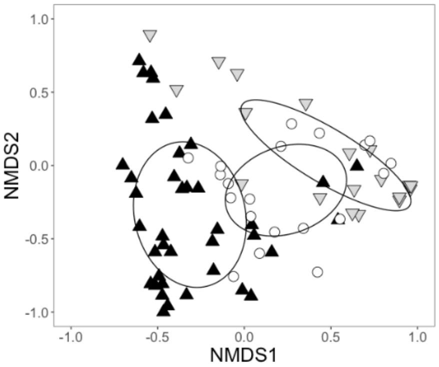
b) 2008: grazing reintroduced

c) 2009: 1 year post-grazing



d) 2010: 2 years post-grazing

e) 2011: 3 years post-grazing



f) 2012: 4 years post-grazing

APPENDIX D: CHAPTER III SUPPLMENTARTY INFORMATION

Table S3.1. Permutational multivariate analysis of variance (perMANOVA) tests (1000 permutations) on the three treatments for each year individually. df= degrees of freedom

	df	Sum of squared means	Mean squares	R2	Pseudo-F	P (perm)
2005						
trt	2	0.12111	0.06056	0.21665	10.23	<0.001
Residuals	76	0.43791	0.00592	0.78335		
Total	78	0.55902				
2006						
trt	2	0.08991	0.04495	0.31798	17.25	<0.001
Residuals	76	0.19283	0.00261	0.68202		
Total	78	0.28274				
2007						
trt	2	0.02288	0.01144	0.2466	12.11	<0.001
Residuals	76	0.06990	0.00094	0.7534		
Total	78	0.09278				
2008						
trt	2	0.01095	0.00548	0.1616	7.13	<0.001
Residuals	74	0.05684	0.00077	0.8384		
Total	76	0.06779				
2009						
trt	2	4.3408	2.17038	0.2185	10.34	<0.001
Residuals	74	15.527	0.20982	0.7815		
Total	76	19.867				
2010						
trt	2	3.8089	1.9045	0.1820	8.23	<0.001
Residuals	74	17.117	0.2313	0.8180		
Total	76	20.925				
2011						
trt	2	2.1061	1.0530	0.1317	5.61	<0.001
Residuals	74	13.881	0.1876	0.8683		
Total	76	15.987				
2012						
trt	2	3.4503	1.7252	0.1614	7.12	<0.001
Residuals	74	17.933	0.2423	0.8386		
Total	76	21.383				

Table S3.2. Pairwise Least-Square Means post-hoc contrasts for linear mixed effects models for species richness, relative cover, and litter absolute cover within each year.

		Least-Square Means Test p-Values								
		Native Forbs			***Non-native Grasses***			***Litter***		
	Year	***Burned Ungrazed - Burned Grazed***	***Unburned Ungrazed - Burned Grazed***	***Unburned Ungrazed - Burned Ungrazed***	***BU - BG***	***UU - BG***	***UU - BU***	***BU - BG***	***UU - BG***	***UU-BU***
Species richness	2005	0.90	*0.04*	0.91	1.00	0.91	0.99	–	–	–
	2006	0.99	*0.00*	0.11	0.80	0.66	1.00	–	–	–
	2007	*0.00*	*<0.0001*	1.00	1.00	1.00	0.92	–	–	–
	2008	*0.03*	*0.00*	0.99	0.99	0.99	1.00	–	–	–
Species richness	2009	0.70	0.97	1.00	1.00	1.00	0.98	–	–	–
	2010	0.91	0.20	0.94	0.98	0.98	1.00	–	–	–
	2011	1.00	0.22	0.37	1.00	0.75	0.63	–	–	–
	2012	0.95	1.00	1.00	0.93	0.24	1.00	–	–	–
Relative cover	2005	0.39	*<0.0001*	*<0.0001*	0.44	*<0.0001*	*<0.0001*	–	–	–
	2006	*0.04*	*<0.0001*	0.33	*0.03*	*<0.0001*	0.32	1.00	0.35	0.54
	2007	0.28	*0.02*	1.00	0.38	*0.02*	0.99	*<0.0001*	*<0.0001*	0.73
	2008	*0.00*	*<0.0001*	1.00	*0.00*	*<0.0001*	1.00	*0.00*	*0.00*	1.00
Relative cover	2009	*0.00*	*0.00*	1.00	*0.00*	*0.00*	1.00	*0.00*	*0.01*	0.99
	2010	0.33	*0.03*	1.00	0.30	*0.02*	1.00	1.00	1.00	1.00
	2011	0.82	1.00	1.00	0.69	1.00	1.00	0.31	0.99	0.99
	2012	*0.00*	0.38	0.90	*0.01*	0.54	0.95	*0.02*	0.71	0.92

Table S3.3. P-values for pairwise comparisons between burned-grazed, unburned-grazed, and burned-ungrazed treatments by year following permutational multivariate analysis of variance (perMANOVA) tests (1000 permutations) on treatments for each year individually.

Year	Burned-Ungrazed + Burned-Grazed	Unburned-Ungrazed + Burned-Grazed	Unburned-Ungrazed + Burned-Ungrazed
2005	**0.001**	**0.001**	**0.001**
2006	**0.002**	**0.002**	**0.027**
2007	**0.002**	**0.002**	0.385
2008	**0.002**	**0.002**	0.256
2009	**0.002**	**0.002**	**0.041**
2010	**0.002**	**0.002**	**0.029**
2011	**0.003**	**0.003**	**0.003**
2012	**0.002**	**0.002**	**0.002**

Table S3.4. Multilevel pattern analysis results listing significant indicator species within group and combination of groups by year. A group or combination of groups with no significant indicator species is shown with an 'NA'.

Year	**Burned-Grazed**	**Burned-Ungrazed**	**Unburned-Ungrazed**	**Burned-Grazed + Burned-Ungrazed**	**Burned-Grazed + Unburned-Ungrazed**	**Burned-Ungrazed + Unburned-Ungrazed**
2005	_Trifolium depauperatum**_ _Koeleria macrantha*_	_Castilleja densiflora**_	_Dichelostemma capitatum*_	_Plantago erecta**_ _Erodium cicutarium*_ _Lepidium nitidum*_ _Festuca sp.*_	NA	_Festuca perennis**_
2006	_Rigiopappus leptoclodus**_	NA	_Sanicula bipinnatifida*_	_Plantago erecta**_ _Lasthenia californica**_ _Aphanes occidentalis**_ _Erodium cicutarium**_ _Gilia tricolor*_ _Lepidium nitidum*_ _Castilleja densiflora*_	_Brodiaea spp.**_	_Festuca perennis**_
2007	_Plantago erecta**_ _Lasthenia californica**_ _Crassula connata**_ _Trifolium depauperatum**_ _Gilia tricolor*_ _Castilleja densiflora*_ _Agoseris heterophylla*_ _Avena sp._	NA	_Epilobium sp.**_	_Lepidium nitidum**_ _Aphanes occidentalis*_	_Brodiaea spp.*_	_Festuca perennis**_
2008	_Lasthenia californica***_ _Trifolium depauperatum**_ _Microseris douglasii*_	_Athysanus pusilus*_	_Epilobium sp.***_ _Chlorogalum pomeridianum**_	_Plantago erecta***_ _Crassula connata***_ _Calandrinia ciliata*_ _Lepidium.nitidum*_	_Brodiaea spp.**_	_Festuca perennis***_
2009	_Plantago erecta**_ _Microseris douglasii*_ _Agoseris heterophylla*_	_Cryptantha flaccida*_	_Chlorogalum pomeridianum**_ _Allium serra*_	_Lasthenia californica**_ _Avena sp.**_ _Calandrinia ciliata*_ _Erodium cicutarium**_	_Brodiaea spp.*_ _Hordeum murinum ssp. leporinum*_	_Festuca perennis***_ _Hemizonia congesta*_ _Muilla maritima*_ _Epilobium sp.**_
2010	_Festuca microstachys*_ _Trifolium depauperatum**_ _Agoseris heterophylla*_ _Streptanthus albidus*_	NA	_Muilla maritima**_ _Epilobium sp.***_	_Lasthenia californica***_	NA	_Festuca perennis***_ _Hemizonia congesta**_ _Aphanes occidentalis*_ _Chlorogalum pomeridianum*_
2011	_Festuca sp*_ _Trifolium depauperatum**_	NA	_Epilobium sp.***_ _Muilla maritima***_	NA	_Hordeum murinum ssp. leporinum*_	_Festuca perennis***_ _Acmispon wrangelianus**_ _Chlorogalum pomeridianum***_ _Trifolium gracilentum**_
2012	_Calandrinia ciliata*_	NA	_Aphanes occidentalis*_	NA	_Hordeum murinum ssp. leporinum*_ _Acmispon wrangelianus*_	_Festuca perennis***_ _Chlorogalum pomeridianum***_

*P < 0.05; **P < 0.01; ***P < 0.001

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure S3.1. Map of experimental transects at our study site, Tulare Hill, California. Lines indicate 50 m transects and treatments are indicated by color: burned-grazed (▬), burned-ungrazed (▬), and unburned-ungrazed (🟩).

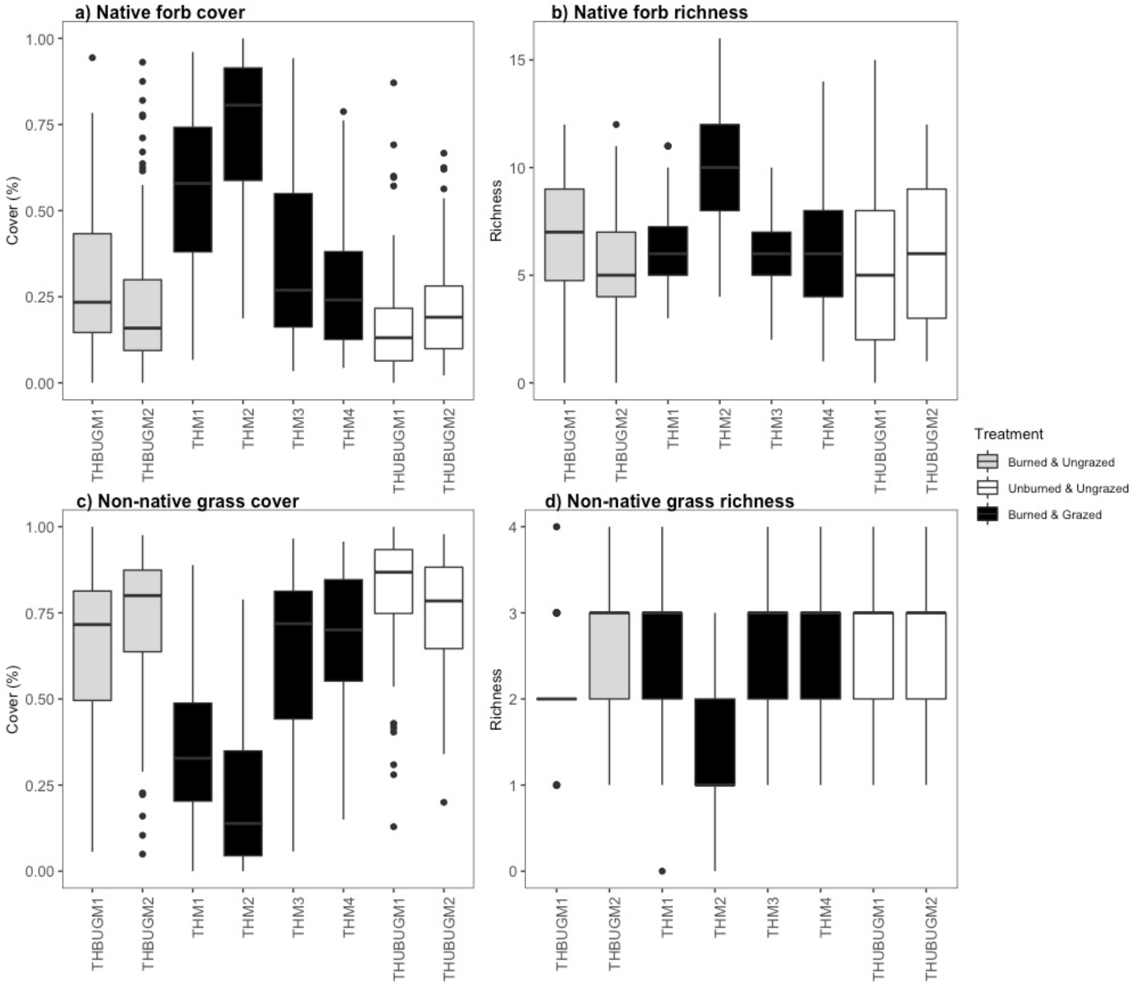


Figure S3.2. Native forb relative percent cover (a), richness (b), and non-native grass relative percent cover (c), and richness (d) by transect from 2005-2012.

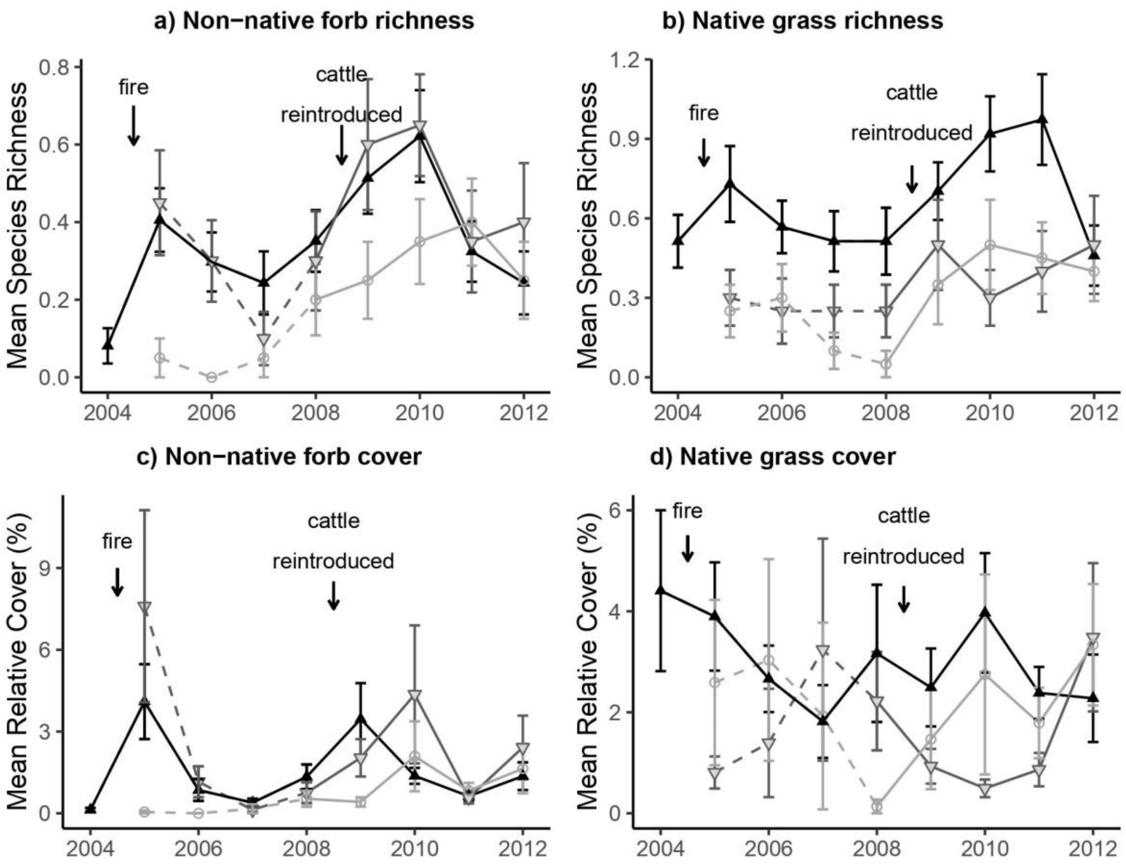


Figure S3.3. Cover and richness response of native grasses and non-native forbs. Shapes indicate means, error bars represent ±SE, and treatments are differentiated by color and shape: burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). Solid lines indicate periods of grazing and dashed indicates periods in which quadrats were not grazed. Arrows point to two treatment events: wildfire in May 2004 and grazing reintroduction in previously ungrazed quadrats in summer 2008.

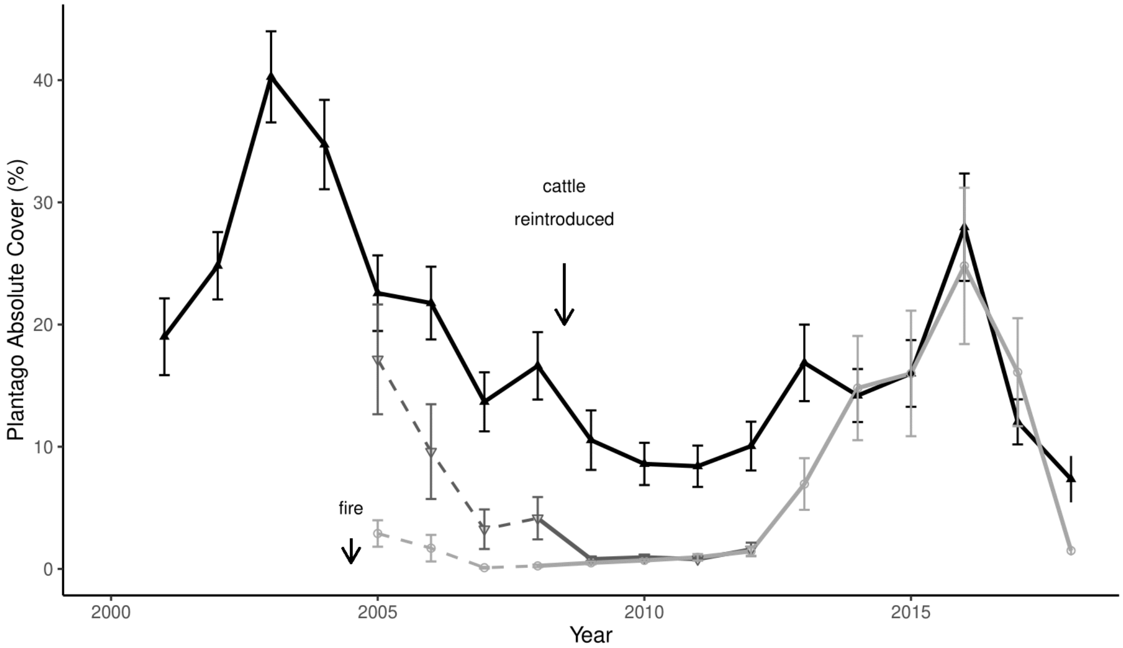


Figure S3.4. Time series of absolute cover (%) of *Plantago erecta* from 2001 to 2018. Shapes indicate means, error bars represent ±SE, and treatments are differentiated by color and shape: burned-grazed (▲), burned-ungrazed (▽), and unburned-ungrazed (○). Solid lines indicate periods of grazing and dashed indicates periods in which quadrats were not grazed. Arrows point to two treatment events: wildfire in May 2004 and grazing reintroduction in previously ungrazed quadrats in summer 2008. Data for unburned, ungrazed treatment from 2013 to 2018 was only available for one transect (10 plots).

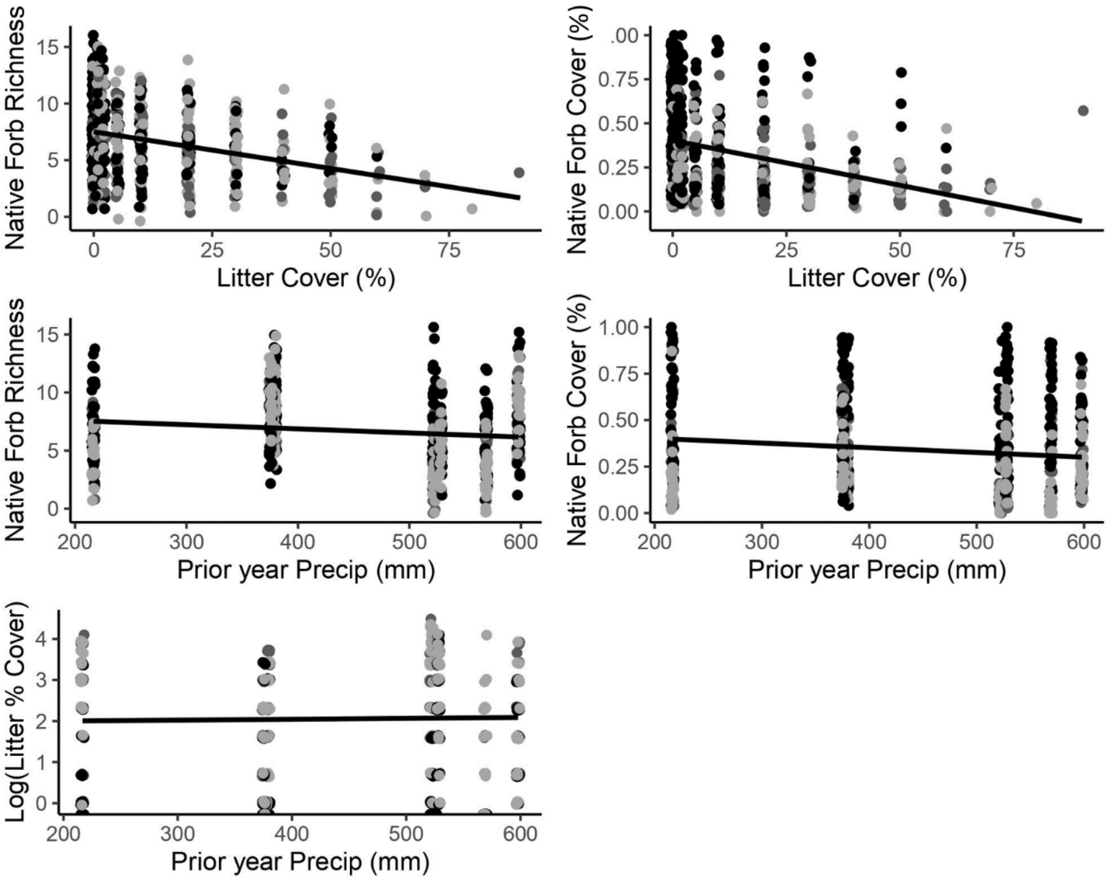


Figure S3.5. Litter and precipitation lag effects on native forb richness and cover + correlation between prior year precipitation and litter cover. Treatments are indicated by color: burned-grazed (●), burned-ungrazed (●), and unburned-ungrazed (●).

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