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Author

Teller, Noah Bigelow

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Understanding and Mitigating Plant Invasions in Natural Areas

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by

Noah B. Teller

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Dissertation Committee:
Dr. Loralee Larios, Chairperson
Dr. Marko Spasojevic
Dr. Janet Franklin
Dr. Darrel Jenerette

The Dissertation of Noah B. Teller is approved:

Committee Chairperson

University of California, Riverside

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ABSTRACT OF THE DISSERTATION

Understanding and Mitigating Plant Invasions in Natural Areas

by

Noah B. Teller

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, September 2023
Dr. Loralee Larios Chairperson

Invasive plants are a major driver of biodiversity loss worldwide. Changes to vegetation cover can alter the frequency and intensity of major ecological disturbances, disrupting native plant communities. Invasive plant control is often disturbance-intensive, which can cause unintended impacts including reinvasion or incomplete recovery of biodiversity. This has led many land management agencies to pursue a strategy of invasive plant mitigation rather than full ecological restoration, leading to a positive feedback loop of disturbance and reinvasion. Fortunately, recent developments in ecological theory regarding the interaction of plant traits, disturbance, and plant community responses may provide new avenues to improve vegetation management outcomes. My dissertation investigates the underlying causes of native plant community responses to plant invasions and disturbance-intensive land management using observational studies and manipulative experiments designed to disentangle these factors. My first chapter assessed the influence of fire roads and bulldozer lines on post-fire plant community recovery, and whether seedling traits could design better seed mixes for postfire restoration. I found that bulldozers increased the spread of invasive grasses from the fire road, but diversity was slightly higher in bulldozer lines than unbulldozed areas. While native species were less abundant in bulldozer lines the first year after fire, they regenerated to similar levels as unbulldozed areas by the second year. Seed treatments were largely ineffective in altering plant community composition in bulldozer lines. These results suggest that although wildland firefighting can increase the spread of invasive grasses, native plant communities can be resilient to multiple disturbances. For my second chapter I conducted an observational study of vegetation cover after an extensive invasion and long-term removal effort. I found that manual removal of the target invader led to near-complete recovery of biodiversity and species richness, with significant but small impacts to plant community composition. My findings indicate that native plant communities can be resilient to extensive invasion, and that disturbance-intensive invasive plant control does not necessarily lead to negative secondary impacts like reinvasion. My dissertation shows how native plant communities can be resilient to disturbance from land management activities, which can help agencies adapt vegetation management to a changing world.

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GENERAL INTRODUCTION

Ecosystems worldwide are experiencing unprecedented losses in biodiversity, species richness, and ecosystem stability, with deleterious consequences for both natural and human communities (Turner 2010; Steffen et al. 2011; Foxcroft et al. 2014; Ceballos et al. 2017). These processes of ecosystem degradation are driven by a multitude of factors, but among them, invasive species stand out as a leading cause of extirpation or extinction across multiple taxa (Claver & Garcia-Berthou 2005). By disrupting the historic conditions that structured native communities, anthropogenic influences including land use change, altered disturbance intervals, and eutrophication are further accelerating the pace of biological invasions and their harmful impacts (DiTomaso 2000; Myers et al. 2000; Cannon & Degraff 2009). Due to the foundational role of plants as primary producers, invasive plants are uniquely positioned to undermine whole ecosystems by suppressing native plant species, disrupting food webs, and altering the frequency and severity of disturbances like wildfire (Walker & Smith 1997; Duncan et al. 2004). For land managers, the high cost of invasive plant control can become a major impediment to achieving multiple goals including biodiversity conservation and fire risk mitigation (De Groot et al. 2013; Lindenmayer et al. 2015). Current trends suggest that species losses and economic impacts will continue to grow (Pimentel 2009). Addressing the growing challenge of invasive plants in the anthropocene will require extensive cooperation between scientists and managers to better understand how to mitigate invasion and restore native habitat.

A common trait among many invasive plants is their propensity to benefit disproportionately from disturbance compared to native plants (Hobbs & Huenneke 1992; Engelberg et al.

2014). Invasive plants tend to be excellent colonizers of disturbed areas where a significant number of plants have recently been removed, burned, or otherwise killed (D’Antonio & Meyerson 2002; Kuebbing & Nuñez 2015; Pearson et al. 2017). Disturbance from management activities like invasive plant removal or fire defense features can further stimulate the establishment and expansion of invasive plants (Buckley et al. 2007; Pearson et al. 2016). While aggressive weed control aimed at locally eradicating invasions is sometimes effective (e.g., Soria et al. 2002), large disturbances associated with eradication attempts can result in reinvasion or secondary invasion (e.g., Shen et al. 2023). Furthermore, vegetation management programs are often not designed to directly monitor outcomes as they relate to goals like biodiversity maintenance, focusing instead on recording the number of invasive plants removed (Downey 2013; Wortley et al. 2013). This type of data collection that monitors the extent of management treatments - but not the ecological impacts of those treatments - does not allow managers to evaluate the success of ecological restoration nor understand the factors that govern variable responses to control efforts (Ruiz-Jaen & Aide 2005). Ecologically sound land management requires monitoring of ecological indicators like biodiversity and species richness, using triage to prioritize invasions, and modifying treatments as appropriate (Downey et al. 2013; Lookingbill 2014). Restoration ecologists therefore have an important role to play in developing tactics and tools to support managers to this end.

The management and expansion of invasive grasses in California exemplifies many of the above challenges. Non-native species introductions have increased with the expansion of the Wildland-Urban Interface (WUI) as construction continues to expand into natural areas (Bar-Massada et al. 2014). In highly populated areas like southern California, nutrient deposition from air pollution has provided an advantage to faster-growing non-native species regionwide (Fenn et al. 2003). While most California native species are slow-growing perennials that retain some moisture year-round, most non-native invasive species are annual grasses that die in the summer months, leaving behind dry and flammable plant matter (Bell & Brooks 2009). The annual proliferation of fine fuels in invaded areas, combined with increased anthropogenic ignitions, has significantly shortened fire return intervals in mid- and low-elevation habitats like Coastal Sage Scrub (CSS) and Chaparral (D'Antonio & Vitousek 1992). This can overwhelm the capacity of native plants to reproduce before another fire, thereby opening space for invasive grasses to establish (Brooks et al. 2004; Davies et al. 2012). Higher frequency of fire in proximity to the expanding WUI has also necessitated increased firefighting effort, which is associated with introductions of invasive species from contaminated equipment (Keeley 2006). As populations and urban areas continue to expand, these combined pressures and their deleterious impacts to natural communities are likely to increase.

In sparsely populated natural areas like national parks and forests, invasive plants have been introduced into even the most remote wilderness areas, where treatment options are limited and expensive (Parks et al. 2005). Invasive plants in natural areas often spread undetected from small source populations along wilderness access features like roads and trails (Mortensen et al. 2009). Due to the large size of many managed natural areas, even the most well-staffed agencies like the National Park Service can be overwhelmed by the volume of work needed to manage invasive plants (Bowcutt 2003). In isolated sites where access is limited, manual removal is one of the only options available to control invasive species (Randall et al. 2000). In some cases, disturbance-intensive manual techniques can be effective at eradicating invaders, but in others manual removal can favor disturbance-adapted invasive species (Prior et al. 2018). This frequently leads to a “conservation treadmill” of constant weed mitigation without progress towards restoration (Stohlgren et al. 2013; Wolsak et al. 2018). The most effective weed management programs are therefore those that can identify and prioritize areas where progress towards restoration can be made with existing resources, and areas where continued attempts at mitigation may not provide significant benefit (Downey et al. 2010). Disentangling the myriad factors influencing which sites are most likely to recover after invasive plant removal is a complex task that will require ongoing research and experimentation.

Even if invasive species can be eradicated, the prior exclusion of native species can result in an incomplete recovery of pre-invasion biodiversity and ecosystem function (Larson et al. 1999; Labat Environmental 2017). With this in mind, land managers sometimes reintroduce native species into disturbed areas like invasive removal sites or burned areas to interrupt the cycle of disturbance and invasion (Byun et al. 2023). Ideally, active revegetation can expedite the re-establishment of a plant community that is resistant to invasion and supports other forms of life like animals and soil microbes (Reynolds et al. 2012; Turnau & Haselwandter 2002). In practice revegetation projects frequently fail, in some cases suppressing the regeneration of existing native species or increasing fuel loads that exacerbate future fires (James & Svejcar 2010; Peppin et al. 2010). These unintended consequences have prompted many land managers to abandon active techniques in favor of passive restoration (reducing invasive propagules only), but this strategy may result in incomplete recovery of biodiversity and other ecosystem indicators if few native species remain to recolonize the site (Schuster et al. 2018). Despite prior failures, understanding the mechanisms governing succession may inform better active restoration techniques to reduce invasion and resist undesirable type conversions (Bakker & Wilson 2004; Laughlin 2014).

Advances in the field of trait-based ecology have improved management outcomes by establishing specific functional criteria for species composition that can predict desirable characteristics like invasion resistance and colonization ability (Laughlin 2014; Staab et al. 2015). These improvements are contingent on correlations between measurable plant traits and resulting plant growth and performance (Funk et al. 2016). For instance, leaf characteristics are often correlated with a plant's growth rate and some types of stress tolerance, while seed traits can predict seedling growth rate and survival (Funk et al. 2016). Furthermore, the diversity of relevant traits in a community (functional diversity) can impact broad-scale ecosystem processes like primary productivity and invasion resistance (Cleland et al. 2013). Continued research in this area has the potential to produce a deeper understanding of how plant traits influence community responses to management treatments (Lienin & Kleyer 2012). This could help managers identify areas where passive restoration after treatment is most likely based on community characteristics and provide an opportunity for to revisit active revegetation as a technique to suppress biological invasions.

Land managers in California face a diverse and growing set of challenges. These may be addressed and mitigated by the growing field of restoration ecology, but a lack of empirical evidence as to which traits and community functional compositions are best suited to achieve specific management goals remains a barrier to translating scientific advances from theory to practice (Spears et al. 2015). In this dissertation I present two case studies of plant community recovery after management actions to control non-native vegetation in natural areas. First, I investigate how the construction of bulldozer lines during wildland firefighting in Chino Hills State Park influenced the spatial pattern of recovery for different plant functional groups. I conducted an observational study comparing plant community recovery after fire between bulldozed and unbulldozed areas adjacent to a fire road. I additionally conducted a plant trait screening experiment to inform the selection of species for active revegetation seed mixes, and tested how mowing interacts with seeding to influence plant community recovery within bulldozer lines. In the second study, I assessed the recovery of native plant biodiversity and community functional composition after an extensive plant invasion and subsequent removal effort in Sequoia National Park. I established vegetation monitoring plots in areas that had been treated for non-native grass invasion and in nearby uninvaded areas to compare the recovery of plant community functional composition. Together, these studies serve as complementary examples of the different conditions, challenges, and strategies that land managers must use to achieve durable solutions to biological invasions. As invasive plants and their deleterious impacts continue to expand regionwide, understanding how different restoration tactics impact the trajectory of recovering plant communities is of paramount importance to determine the necessity of intervention and maximize the effectiveness of land management treatments.

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CHAPTER 1

Plant functional groups show differential responses to disturbance by dozer line construction and post-fire rehabilitation techniques.

Abstract

Understanding the multiple dynamics influencing post-fire recovery of natural areas is of paramount importance to conserve biodiversity and mitigate ecological degradation after severe disturbance. Fire defense features such as roads and bulldozer lines are central to wildland fire defense tactics, but they may also act as vectors for the introduction of non-native invasive species. Individual restoration treatments such as weed control or seed deployment have mixed results for stimulating the successful recovery of native plant species after wildfire. A deeper understanding of the interactions between native and invasive plants via their functional traits provides opportunities to better assess, improve, and integrate postfire ecological restoration. I established a field monitoring site and experiment in multiple bulldozer lines within a burned area in Chino Hills State Park near Corona, CA, USA. I assessed the ecological invasion risk posed by bulldozer lines by observing the spatial spread and abundance of different plant functional groups within and outside the lines. I additionally conducted a plant trait screening experiment to create functionally distinct restoration seed mixes, which I tested in combination with mowing for invasive plant suppression and native plant establishment in the dozer lines. I found that although invasive species were more abundant in bulldozer lines in 2018, this relationship did not persist past the first year. Native species and non-native forb abundance both increased steadily each year, while non-native grass abundance fluctuated. Abundance of all non-native species was spatially influenced by distance from the nearby fire road, but not by bulldozer lines. Mowing increased the abundance of native and non-native forbs and bare ground, while decreasing the abundance of non-native grass. Seed treatments had only marginal impacts on community composition, and none that outperformed the unseeded control treatment. Finally, interactions between different restoration techniques did not influence outcomes of invasive plant suppression or native plant reestablishment. Together these results suggest that invasive species can readily establish into post-fire areas and efforts to reduce invasive propagules should be continued for multiple years.

Introduction

Fire suppression efforts in California and worldwide have dramatically increased over the last 40 years, as have firefighting-associated impacts to landscapes and communities (Dennison et al. 2014). While prescribed fire had been an integral part of Indigenous land management in California for centuries, its prolonged exclusion from public lands has led to higher fuel loads that produce more severe and destructive fires (Mensing 2006). The resulting postfire landscapes can be highly vulnerable to plant invasions, as any incoming non-native plant propagules can perform well due to a combination of low competition from native vegetation and access to plentiful resources (Brooks 2008). In modern firefighting, the extensive use of heavy machinery like bulldozers to construct fire access features like roads and landing zones can serve as vectors for invasive species by introducing seeds and plant fragments from equipment and personnel (Keeley 2006). To disrupt the cycle of disturbance and invasion, it is necessary to suppress postfire plant invasions and establish biotic resistance by reintroducing native propagules rather than waiting for the existing seed bank to re-establish (McIver & Starr 2001). This suggests the need for an integrated approach that considers how firefighting and postfire response techniques can be used to accomplish complementary management goals and compensate for each other's unintended impacts (Prach et al. 2019).

The construction and maintenance of fire defense features such as bulldozer lines may play a role in the decline of native vegetation types and expansion of plant invaders (Brotons et al. 2013). Many prior studies have investigated the impacts of bulldozer fuel breaks on vegetation, but most have focused on preventive fuel breaks that were cleared before fire occurred, or on old fuel breaks surveyed several years after fire (Keeley 2006; Brooks &

Lusk 2009; Shinneman et al. 2019). These studies have demonstrated that plant invasions are often a longer-term outcome of fuel break construction, but they do not directly investigate the factors influencing plant establishment and survival in the months and years immediately following disturbance. Dozer lines create areas of high disturbance, where the top ½ - 1 meter of soil is mechanically scraped to remove all flammable vegetation (Buckley et al. 2007). While native plant seeds, rhizomes, or resprouting roots may remain viable after fire, dozer lines can scrape native propagules out of the bulldozed area (Ozturk & Akgul 2009). Moreover, seeds of non-native plants can stick to bulldozers and other vehicles as they travel from site to site, allowing them to disperse in new areas (Brooks & Lusk 2009). Fire road edges also provide a source for invasive seed introduction, where bulldozers may pick up seed and disperse seeds into the newly scraped area. Dozer-mediated introductions likely do not occur homogenously across a dozer line, but one small introduction is all that is needed for invasive species to disperse broadly across a post-burn landscape (Larios et al. 2013, Schwab et al. 2023). As a result, understanding the spatial spread of invasive species is best accomplished by beginning plant community monitoring within the first year post-fire (Korniss & Caraco 2005).

Suppressing postfire plant invasions while promoting native recovery is a critical component of burned area rehabilitation. Timed weed management like mowing immediately post-fire may mitigate some of the impacts of plant invasions (Reaser et al. 2020). However, focused approaches to invasive plant removal tend to leave behind open and fertile areas of soil, which are prone to reinvasion for similar reasons as recently burned areas (Schuster et al. 2018). Therefore, timing invasive plant removal with native planting is key to minimize secondary invasions. Efforts to constrain biological invasion may benefit from establishing desirable species that are functionally similar to invaders to directly compete with invader (Bakker & Wilson 2004; Foster et al. 2015) or by establishing a group of functionally diverse species that reduce resource availability and limit overall invader establishment (Diaz & Cabido 2001; Funk 2008). Competition between species in general tends to be strongest when they occupy similar niches (MacArthur & Levins 1967). In the case of plants this may include seeking nutrients from the same areas in the soil profile, growing to similar heights, and/or germinating at the same time of year, among other traits (Pokorny et al. 2005; Funk 2008). In a management context this suggests matching the diversity of relevant traits in a community (functional diversity) to the focal invaders may be key to promoting biotic resistance (Diaz & Cabido 2001, Cleland et al. 2013). In this way revegetation may be able to constrain biological invasion by accelerating the establishment of native plants with specific traits (Bakker & Wilson 2004; Foster et al. 2015). However, the success of these efforts may be contingent on the suppression of plant invaders so that native plants may successfully establish immediately post-fire (Flory & Clay 2009). More investigation is needed to facilitate the translation of these advances in ecological theory to practicable methods (Spears et al. 2015; Saatkamp et al. 2019).

These patterns are observable in the degradation of natural plant communities in southern California, where vegetation communities like Coastal Sage Scrub (CSS) are threatened and rapidly disappearing (Minnich & Dezzani 1998). As invasive annual grasses – primarily Mediterranean grasses – have replaced native perennials in the herbaceous understory, the production of fine fuels that die and dry in the summer has contributed to increased fire frequency (Brooks et al. 2004; Paolini et al. 2014). Shorter fire return intervals can at once overwhelm the capacity of slower growing native plants to reproduce before another fire and can open space for invasive grasses to establish, accelerating the grass-fire cycle (D'Antonio & Vitousek 1992; Brooks et al. 2004; Talluto & Suding 2008). This slower native recovery is exacerbated in bulldozed areas, where removal of topsoil by scraping with a bulldozer blade may disrupt or displace important symbionts and compact soil while removing the native seed bank, compromising native regeneration (Brooks 2008). While many California plants possess fire-specific adaptations, they do not readily have the life-history strategies to re-establish in these heavily disturbed areas before reinvasion (Bufford & Daehler 2011).

During the three years immediately following a wildfire, I examined 1) how emergency bulldozer lines ('dozer lines') impact the spatial spread of invasive Mediterranean grasses in burned vs. bulldozed areas, and 2) which management strategies best reduce invader abundance and/or increase native abundance. I hypothesized that dozer lines facilitate the spread of non-native grass. I predicted that non-native grass abundance would be greater than native abundance in dozer lines compared to burned areas. If the fire road serves as a source of invader seed, I predicted that non-native grass abundance would be higher near the road edge and decrease along the dozer line. Second, I hypothesized that integrated management approaches (invader removal and trait-based seeding) would help mitigate invader establishment in dozer lines. I predicted that native plants would be more abundant in plots seeded with a mix of species trait-matched to invasive grasses relative to unseeded plots or those planted with a trait-diverse seed mix. I predicted that combined mowing and seeding would provide the best results pursuant to the management objectives of invasive plant suppression and native plant establishment.

Methods

Study Site. I conducted vegetation monitoring and experimental treatments at Coal Canyon in Chino Hills State Park (33°52’06.5”N 117°41’28.5”W; “CHSP”) near Corona, CA. This site consists of a canyon opening North. The canyon bottom is a seasonal tributary to the Santa Ana River, which runs to the West about 1 km North of the study site. The area is situated in Riversidean CSS, a fragmented and rapidly disappearing vegetation type found in the East-West transitional zone between the Los Angeles Basin and the Mojave & Sonoran deserts (Minnich & Dezzani 1998). Climate is dry Mediterranean. Rainfall was at drought levels in most years except 2019, when rainfall returned to resemble a historical average (254mm 2017; 203mm 2018; 711mm 2019; 152mm 2020; 355mm 100-year average). Mean annual rainfall was 234mm (30% less than historical average). For the duration of the project 2017-2020, summer highs occurred in August at a study period mean of 43.3°C, lows occurred in June at a mean of 15.2°C. Winter highs occurred in January at a study period mean of 26.7°C, lows occurred in December at 6.11°C (NOAA 2021). My 2018 survey of the project site and nearby unburned areas at Coal Canyon found dominant native species to be *Encelia californica (Asteraceae)*, *Artemisia californica* and *Phacelia ramosissima* (*Hydrophyllaceae);* dominant invasives included *Avena barbata (Poaceae), Bromus diandrus (Poaceae), Bromus madritensis (Poaceae)* and *Erodium cicutarium (Geraniaceae).* Species names and classification of origin follow the Jepson Flora (Jepson Flora Project, 2022).

The study site contains a curving fire road that provides access to the Cleveland National Forest in the Santa Ana Mountains and had a fire frequency of 3-4 fires overlapping at different points within the study area between 1914-2011 (Schlotterbeck et al. 2012). On October 9th, 2017, the Canyon 2 Fire was ignited by embers from the Canyon Fire 1 near Coal Canyon. The fire initially burned in a slow-moving wind-driven pattern that moved downslope, causing near complete consumption of aboveground vegetation, and would go on to burn over 8 days and 37 km^2. Several dozer lines were quickly constructed starting from the fire road and proceeding uphill in an attempt to prevent the fire from spreading, though they were ultimately ineffective.

<u>Dozer line vegetation recovery</u>. I selected five 11 m-wide, 60 m-long sections of linear dozer lines with similar aspect (East-facing, +/- 30 degrees), elevation (180-250 m) and slope (+/- 15 degrees), made by bulldozers in the burned area in December 2017. All dozer lines started on the uphill side of a fire road and were on the same hillside. I established a pair of 60m line transects to characterize each of the five dozer lines, one down the center of the bulldozer's path ("B" transects), and another parallel transect 10m down the road, outside the bulldozer line in burned vegetation ("P" transects; Fig 1).

To characterize the impact of dozer lines on vegetation composition during postfire recovery, I recorded relative abundance of vascular plant species in each transect (bulldozed and un-bulldozed) by point-intercept using a 1x1m quadrat, at ten 6m intervals of increasing distance uphill from the road (Fig 1. gridded squares). I counted each plant intersecting a vertical line below each grid intersection (not just the top hit). I sampled at peak biomass in April 2018, 2019, and 2020. In 2018 the quadrat had 400 grid intersections, while in 2019 and 2020 I reduced the number to 81 points per quadrat and re-scaled 2018 data by 81/400 to match the other two years.

Dozer line rehabilitation. To evaluate mowing and seeding management efforts, I overlaid a factorial experiment in which I manipulated seed treatments and mowing in the same dozer lines. I first used plant trait analysis to create two seed mixes, one matched to invader traits (Mix M) and one encompassing the greatest diversity of trait values (Mix D). Within each dozer line I established two parallel sets of nine 5x5 m plots (18 per dozer line) in the spaces between the monitoring plots described in the first experiment (Fig 1). Within each bulldozer line I grouped the 18 plots into three zones of distance from the road edge (near, 0-18 m; medium, 19-36 m; and far, 37-54 m), each with six plots. Within each zone of 6 plots, I seeded two pairs of plots – one pair for each seed mix – and left a third pair unseeded. Across the entire set of 5 dozer lines, each treatment (Mix M, Mix D, No Seed) was applied to thirty plots (n=90). To evaluate the potential of combined invasive plant control and seeding, I used a split-plot design to implement a mowing treatment overlaid on the seeding experiment described above (Fig 1). I randomly assigned the left or right half of all experimental seed plots (n=45) to receive a single mowing treatment in May 2018 using a handheld weed whip, cutting all vegetation that grew 1” or more above the soil surface.

Out of the native species identified at the study site, I selected 17 for trait screening to be potentially included in one of the two experimental seed mixes, M or D (Supplementary Table 1). I additionally selected the 3 most locally abundant invasive grasses, *Avena barbata, Bromus diandrus, and Bromus madritensis,* for comparison.

For the trait screening, I measured three functional traits – specific leaf area (leaf surface area per dry mass, SLA), specific root length (root length per dry mass, SRL), and seed mass. Traits were measured according to procedures described in Pérez-Harguindeguy et al. 2013. High SLA may predict a faster turnover of photosynthate to plant matter, increasing relative growth rate (Wright et al. 2004). SRL can elucidate how a plant invests in its roots to seek water, whether with fast-growing thin fibrous roots at the soil surface or a slower-growing taproot that can reach deeper resources (Kramer-Walter et al. 2016; Fort et al. 2017). High seed mass is predictive of spatial pre-emption of competitors, while smaller-seeded species often build more robust seed banks over time (Turnbull et al. 1999). Trait combinations of high SLA/SRL/SM predict strong colonization and recruitment ability and are often associated with invasive plant species (Van Kleunen et al. 2010).

To estimate seed mass, I weighed 10 replicates of 10 seeds for each study species. To estimate SLA and SRL, I grew 24 individuals of each species for a total of 480 pots. I planted seeds in May 2018, and destructively sampled 8 individuals of each species once per month, for 3 months. Two leaves per individual, for a total of 16 leaves per species, were harvested and scanned at 1200 dpi at each sampling period. Leaf Area was calculated using ImageJ software. Roots of each individual were scanned in a water suspension using WinRHIZO (Regent Instruments 2019). Leaves and roots were dried and weighed to the nearest 1/1000th of a gram. Leaf area and root length were then divided by leaf mass and root mass to calculate SLA and SRL, respectively. I averaged trait values across all 3 sampling periods to calculate mean trait values for each species.

I ran a principal components analysis (PCA) with centered and scaled trait data to visualize differences in trait values among species (Supplementary Fig 1). Based on the relative positions of species in this plot I created two groups, each with six native species. Mix M was designed for low functional diversity but high trait matching to invasive grasses. It included species most similar in trait values to the three invasive grasses, minimizing the distance between species in the PCA (i.e., minimizing distance from invasive species in trait space). Mix D was designed for high functional diversity. For this mix I selected a group of species to maximize total trait space. Native seeds for trait analysis were regionally sourced from S&S Seed Co., but I collected native seeds for field seeding from unburned patches near the study site to minimize potential genetic contamination of local ecotypes. As such, seed availability was limited to 11 total native species, one of which (*Phacelia ramosissima*) was included in both mixes M and D (Supplementary Table 2).

In November 2018 I cast seed by hand into the experimental plots at a rate of 16 lb/acre, which equated to 2.7 kg of seed total, with 45 g of seed per plot, and 7.5 g of seed per species therein (excluding *Marah macrocarpus*). I used my prior seed mass measurements to estimate the number of propagules of each species deployed (Supplementary Table 2).

I sampled plant community cover in these plots using the same methods as the bulldozer line/parallel plots: I placed a 1x1m quadrat with 81 grid intersections in the center of each experimental plot at 1m height and recorded all unique species that intersected a vertical line beneath each grid intersection extending to the ground (Fig 1, blue gridded squares).

<u>Statistical Methods.</u> To evaluate my first hypothesis regarding the effects of dozer lines on plant invasion, I used linear mixed-effects models to analyze differences in community

characteristics (species richness, Shannon-Wiener diversity), and vegetation cover (non-native grasses, non-native forbs, total non-native cover, total native cover). I included the factors of transect type (Bulldozed, Parallel), distance from the fire road (0-60 m), year (2018-2020), and their interactions in a fully factorial model structure. I grouped each dozer line and paired transect and included this grouping as a random factor. I included an autoregressive correlation structure to account for repeated measures. Some response variables were transformed to meet assumptions of normality (Supplementary Table 4). I conducted Tukey's HSD tests for post-hoc comparisons to determine significant pairwise differences between any interactive effects as appropriate. Non-native grass abundance and Shannon diversity were not normally distributed, so I used a Scheirer-Ray-Hare test, a nonparametric test compatible with a two-way ANOVA, to examine one- and two-way interactions between experimental treatments (Schierer-Ray-Hare test, Sokal & Rohlf 1995). In order to incorporate all 3 variables into this test, I subsetted data by year and conducted an independent test for each (2018, 2019, 2020).

To evaluate my second hypothesis regarding the effectiveness of seeding & mowing to influence plant community recovery within dozer lines, I subsetted data to include only the experimental plots within the dozer lines to compare community responses to the various treatments (see Fig. 1). I treated each seed/mow subplot as an independent plot, as each subplot received its own individual pre-mixed seed bag. I analyzed vegetation abundance by grouping species-level survey data by life form (grass, forb, shrub) and origin (non-native, native). I then calculated species richness and Shannon diversity of all species in each plot.

To further explore the effects of mowing and seeding on community composition, I conducted a permutational analysis of variance (PERMANOVA) using life form & origin groupings (non-native grass, non-native forb, bare, native shrub, native forb) of the species cover data. I included the fixed effects of mowing treatment, seed mix, year, and their interactions. I visualized the responses with non-metric multidimensional scaling.

All analyses were done in R version 4.1.2. Multivariate analyses were done with the "vegan" package (Oksanen et al. 2022), mixed effects models were done with the "nlme" package (Pinheiro, DebRoy, & Sarkar 2021), non-parametric tests were done with the "rcompanion" package (Mangiafico 2022), and post-hoc comparisons were done with the "emmeans" package. Figures were produced using the "ggplot2" package (Wickham 2016).

Results

Dozer line Recovery. Species richness was impacted by transect type (p<0.001), distance from road (p=0.029) and year (p<0.001; Figure 2; Table 1). Species richness of all plants was higher overall in bulldozer ("B") lines than parallel ("P") un-bulldozed transects (B 8.13±0.24, P 6.053±0.25; p<0.001). Mean richness of all plots significantly changed year to year, being highest in 2019, while species richness was not significantly different between 2018 and 2020 (2018 & 2020 8.55±0.29, p=0.9944; 2019 6.27±0.21, p<0.001; year, p<0.001). The interaction of transect type and distance from the fire road was significant, as richness increased with distance from the fire road in dozer lines but decreased with distance from the fire road in parallel transects (transect x distance, p=0.021). Transect type, distance from the road, and year interacted to significantly impact species richness (transect, distance, year, p=0.006). In 2018 bulldozed transects had higher species richness with increasing distance from the road, while parallel transects exhibited the opposite relationship (B2018-P2018, p<0.001). In 2019 bulldozed transects had a significantly weaker but still positive relationship between species richness and distance (B2018-B2019, p=0.004). In a complete inversion from 2018, parallel transects in 2019 had a strongly positive correlation between distance and richness (P2018-P2019, p<0.001), though still significantly different from B transects (B2019-P2019, p=0.001). In 2020, both transect types had a similarly non-significant relationship between species richness and distance (B2020-P2020, p=0.454).

Shannon diversity was higher in bulldozed than parallel transects only in 2018, though not by a large amount (transect, 2018 p=0.043, 2019 p=0.244, 2020 p=0.111; Figure 3; Table 2, Supplementary Table 3). Shannon diversity differed with distance from road in 2019 only (2018 p=0.677; 2019 p=0.031; 2020 p=0.503). Finally, the interaction of distance from road and transect type did not significantly impact diversity in any of the three years (distance x transect, 2018 p=0.132; 2019 p=0.461; 2020 p=0.842).

Non-native grass varied by transect only in 2018, where it was significantly more abundant in bulldozed than parallel transects (B2018=34.714±2.266, P2018=29.458±2.202; 2018 p=0.005; 2019 p=0.505; 2020 p=1.000; Table 3; Figure 4). Distance from the fire road did not impact non-native grass abundance in any year (distance, 2018 p=0.414; 2019 p=0.393; 2020 p =0.906). Non-native forb abundance was generally higher at greater distances from the fire road (distance, p=0.008; Table 4, Figure 5), regardless of transect type (p=0.370). Non-native forb abundance did differ by year (p<0.001) and this was dependent on transect type (transect x year p=0.015), where only 2020 bulldozer lines had higher non-native forb abundance than parallel transects. Total non-native cover varied by distance from the fire road, but this relationship changed each year (distance p=0.603; distance x year, p=0.042; Table 4; Figure 6), falling with increasing distance from the fire road in 2018, rising with distance in 2019, and flattening out in 2020 (2018 p<0.001, 2019 p<0.001, 2020 p<0.001). Total non-native abundance was marginally different between transects, being slightly higher in dozer lines than parallel transects (B 55.197±2.836, P 48.579±3.015, p=0.062; Table 4). Native plant abundance overall increased significantly year over year (2018 6.235±1.108, 2019 13.01±1.665, 2020 34.562±3.623; year, p<0.001). Native abundance was significantly lower in bulldozed than parallel transects in 2018 but equalized between transect types in 2019 and 2020 (B2018 2.264±0.503, P2018 10.206±2.015, p=0.033; B-P2019 p=0.505, B-P2020 p=1.000, Table 4; Figure 7). Native plant abundance was positively related to distance from the fire road, but this relationship did not differ from year to year or between transect types (distance, p<0.001).

Rehabilitation of dozer lines. Seed mixes had minimal recruitment in the years following seed deployment. Over the course of the study, I observed 7 of the 10 seeded species in one or more plots, but only 48 plots of 160 (30%) showed recruitment of any seeded species at all. Of these 48, at most 2 seeded species successfully established in any individual plot (10 plots), while only 1 species established in the remaining plots (38 plots). Of the few plots that showed any recruitment of seeded species, 6 received Seed Mix D, 25 received Seed Mix M, and 17 did not receive a seed treatment at all. I found no significant effects of seeding treatment on either species richness or Shannon diversity (Table 5).

Mowing was the only factor that influenced species richness (p=0.023; Table 5; Figure 8), with mowed plots generally having lower species richness than unmowed plots

(M=7.275±0.293, U=7.875±0.304; p=0.023). Shannon diversity was higher overall in 2019 than 2020, though this result was marginally significant (2019=1.404±0.037, 2020=1.232±0.062; Year, p=0.062). The interaction of mowing and year was significant (p=0.007), where unmowed plots in 2020 had similar Shannon diversity to mowed plots in 2019 (p=0.019).

When comparing species composition across treatments, we found that composition significantly differed between mow treatment (p=0.040) and year (p=0.001), only marginally differed among seed mixes (p=0.06), but did not differ by any two- or three-way interaction (Table 6). Specifically, mowed plots tended to contain more bare ground, non-native forbs, and native shrubs, and less non-native grass compared to unmowed plots (Figure 9). Composition in 2019 was strongly structured by non-native grasses while 2020 composition consisted of more native shrubs and non-native forbs (Figure 9).

Discussion

Managing the negative impacts of non-native plant invasions on dozer lines post-fire requires a broader understanding of the potential for invasion as well as an improved understanding of integrated management techniques. Here, I present results from paired observational and experimental studies documenting recovery in dozer lines. In support of my first hypothesis, I found that bulldozer lines facilitate non-native grass establishment in the first-year post fire (2018) but differences in non-native grass cover between transect types disappeared in subsequent years. Total non-native cover in the first-year post fire decreased with distance from the fire road, supporting the prediction that the fire road provided a source of non-native propagules; however, this pattern was seen in both bulldozed and unbulldozed transects.

Unexpectedly, I found that non-native forbs strongly mediated post-fire recovery, such that by 2020 non-native cover was greater in bulldozed transects compared to unbulldozed transects. Contrary to my second hypothesis, I found limited effects of mowing and no effects of seeding on reducing non-native cover or promoting native recovery. I did observe that mowing resulted in some plots with either greater bare ground or native shrub cover, but this result was not consistent across the experimental plots. Together I demonstrated that dozer lines may promote non-native plant abundance and that rehabilitation of these dozer lines may require more intensive management actions. Below I expand on these dynamics.

Many prior studies have found significant correlations between firefighting disturbances and non-native grass invasion, but most were conducted on larger preventive dozer lines that were maintained over the long term (Benson & Kurth 1995; Merriam, Keeley, & Beyers 2006; Brooks 2008). I observed that non-native grasses and forbs can readily establish post-fire in the dozer line and this initial establishment may be promoted by the fire road. Once established, I found that non-native cover equalized along the dozer line with minimal differences in non-native cover between bulldozed and parallel transects, indicating that the fire road and dozer line provided a propagule source into the surrounding area. This is consistent with other studies that have found roads to be a common starting point for biological invasions, as seeds frequently travel on vehicles and footwear and are deposited on the roadside (Mortensen et al. 2009). Unpublished data from one area of the field site showed non-native seeds outnumbered all native seeds combined by a factor of 37:1 in one year alone (Du and Larios unpublished data 2018). Such intense seed rain can overwhelm biotic resistance (Larios et al. 2013), even in unstressed ecosystems (St. Clair & Bishop 2019). For this reason, even supposedly healthy ecosystems may be at risk of invasion when roads create large source populations that can then spread into surrounding vegetation.

In post-firefighting scenarios like this one, the spread of non-native species within fire roads and dozer lines has been known to exacerbate already significant challenges on the path to native plant recovery (as observed in Gressard 2012; Engelberg et al. 2014). I implemented a mowing treatment to reduce propagule pressure and release native plants from competition, but I found very nuanced impacts from mowing, where mowing plots had slightly fewer species on average and different species composition (i.e., less non-native grass and more bare ground). The bare ground may have created a more stressful environment for plant establishment that favored ruderal plants with taproots (Jiang et al. 2021), like the non-native forbs I observed at the site. Integrated management options that reduce invader propagules while creating more favorable microclimates for establishment may improve overall native plant recovery (Herron et al. 2013, Souza-Alonso et al. 2022) and facilitate the rehabilitation of dozer lines like these.

Seeding efforts often have mixed success in restoration projects (e.g., Hunter et al. 2006, Shackleford et al. 2021) due to a variety of factors that may create constraints to establishment (Brudvig et al 2017). My seeding trial resulted in very low establishment, despite using local seed at rates comparable to other local restoration projects. Local seed is advocated to help ensure that individuals are prepared to deal with local stressors (Hufford and Mazer 2003), but historic drought conditions in the region (Mann & Gleick 2015) may have impacted plant performance and ultimately the quality and quantity of the native seed (Cox & Allen 2008; Kimball et al. 2014). My seeds were collected within 2 square miles of the study site and thus were subject to the same drought conditions as the local community, which could have negatively impacted seed quality and germination. Moreover, site conditions can be so stressful that it overrides any benefits from local seed sources, further supporting the need to prioritize measures that also ameliorate site conditions (Robinson et al. 2023).

While the seeding treatment did not provide clear evidence towards one trait combination or another, the ability to restore ecosystems using native plant seed remains a significant need for land managers (James & Svejcar 2010; Shackelford et al. 2021). The high costs and rates of failure for restoration seeding projects have attracted considerable attention in recent years in the form of research targeted to improve efficiency and outcomes. Researchers have addressed individual barriers to restoration success using various seed enhancement technologies targeted to overcome specific challenges to survival for seeded species at a given life-stage (Madsen et al. 2016). These included using surfactant seed coatings to overcome hydrophobic soils and highly targeted use of pre-emergent herbicide to protect desirable plants from competition (Madsen et al. 2016).

Several other studies have found the depth of topsoil or seed addition to be a key factor for determining native seed-based recruitment in restoration contexts (Dixon 2018, Schmidt et al. 2020), and that hand seeding at precise depths is particularly effective at increasing native establishment relative to drill or broadcast seeding (James & Svejcar 2010, Kimball et al. 2015). Future studies should explore how additional seed treatments may better enhance establishment and rehabilitation of dozer lines.

Postfire restoration often includes multiple management goals that may be better accomplished through integrated methods (e.g., Souza-Alonso et al. 2022), but the combination of methods we applied in this case did not improve outcomes and resulted in effects that did not persist year to year. Notably, year was a strong factor influencing species abundance and composition. I observed large fluctuations in the abundance of both native and non-native species from year to year, generally of a greater magnitude than differences in abundance between treatments within a single year. These dynamics are likely driven by rainfall and differing life-history strategies. California was in the depths of an unprecedented drought in 2018, but 2019 was the first year following the drought that rainfall resembled a 100-year historical average (CA Dept. Water Resources 2023).

Mean annual precipitation for the area was highest in 2019, which allowed non-native annual species to take advantage of shallow water resources (Holmes & Rice 1996) and readily increase in abundance (Dudney et al. 2017). Rain returned to drought conditions in 2020, and I observed the population of non-native grass growing or shrinking with the rainfall. Native species also experienced their largest increase in mean abundance in 2019 but unlike non-native grasses continued to increase in abundance in the next year, likely reflecting the stress-tolerant strategy of some native perennial species. This outcome of native shrub establishment in highly disturbed areas has been found in other California shrubland management scenarios, where early successional shrub species such as *Acmispon glaber* (deer weed) were able to establish, resulting in native cover even if it was slightly different from the mature intact vegetation (D'Antonio and Howald 1990). This pattern demonstrates that despite widespread invasion by non-native annual species, some passive recovery of native species (mostly perennial) is still viable but may not be noticeable in the first-year post fire.

Recent studies have found seeding depth and topsoil composition to be key factors in the success of Coastal Sage Scrub restoration, as interactions between bacteria, fungi, insects, and abiotic nutrient conditions can have large impacts on germination (Dixon 2018, Schmidt et al. 2020). This may explain why, while broadcast seeding on the soil surface largely failed to influence community composition by most measures, many native plants from the existing seed bank persisted even surrounded by dense populations of non-native invasive species. The project site prior to the Canyon fires had years to build up its seed bank since the last major known disturbance; these seeds would have been stored lower in the soil profile and would have had more time for their seed coats to interact with surrounding symbionts or abiotic germination triggers (Keeley 1987; Schmidt et al. 2020). Seeds in the soil seed bank were also present during the heat of the fire and subsequently exposed to charred wood – a known germination cue for some Coastal Sage Scrub species (Keeley 1987). For these reasons, broadcast seeding likely only created a marginal difference in effective propagule pressure, if any, compared to the existing seed bank. Future restoration projects using seeding as a primary revegetation technique may benefit from paying close attention to germination requirements and designing seed deployment techniques to maximize germination.

This study underscores the pressing need for research into scalable techniques and technologies that can mitigate the impacts of firefighting features on vegetation cover change and improve the outcomes of seed-based restoration. Given the fast pace of degradation and labor-intensiveness of known effective techniques like topsoil replacement and burying seed to the correct depth by hand (Kimball et al. 2015), improved topsoil amendments and mechanized seeding techniques appear as high priorities for ongoing research. Future studies that seek to expand on how plant functional traits influence seedling survival and community recovery should pay close attention to site preparation and seeding techniques to ensure a robust population of testable plants (see James & Svejcar 2010; Dixon 2018; Schmidt et al. 2020). Slowing or escaping the positive feedback loop of invasive plant expansion, wildfire, and firefighting in Mediterranean climates will require the ongoing commitment of the scientific community, as well as the integration of short- and long-term objectives (i.e., rapid fire suppression vs. re-establishing natural fire regimes) into management strategies that can support follow-up recovery and restoration efforts.

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TABLES AND FIGURES – CHAPTER 1

Figure 1. Layout of experimental treatments and survey plots. Distance was analyzed as a numeric variable in the bulldozer vs parallel experiment, but 3 distance blocks were established as factors for analysis of the seed/mow plots.

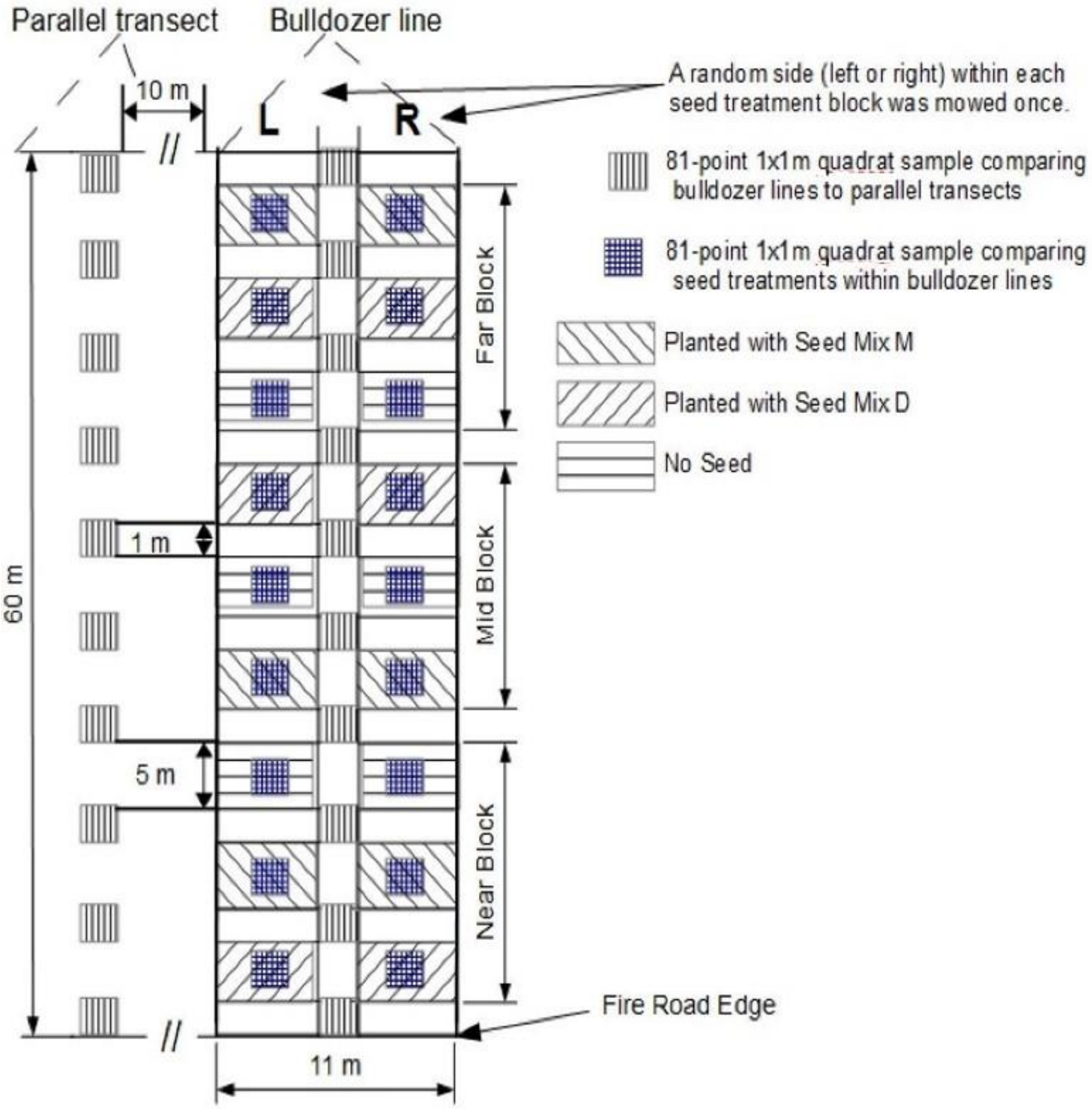

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Figure 2. Species richness of Bulldozed (B) vs. Parallel (P) transects with respect to distance from the fire road edge over time. Species richness was higher in B transects across all years, and its relationship with distance from the fire road was positive in 2018 and 2019. Species richness in P transects had a significantly negative relationship with distance from the fire road in 2018 that switched to positive in 2019. The relationship between species richness and distance became insignificant in 2020.

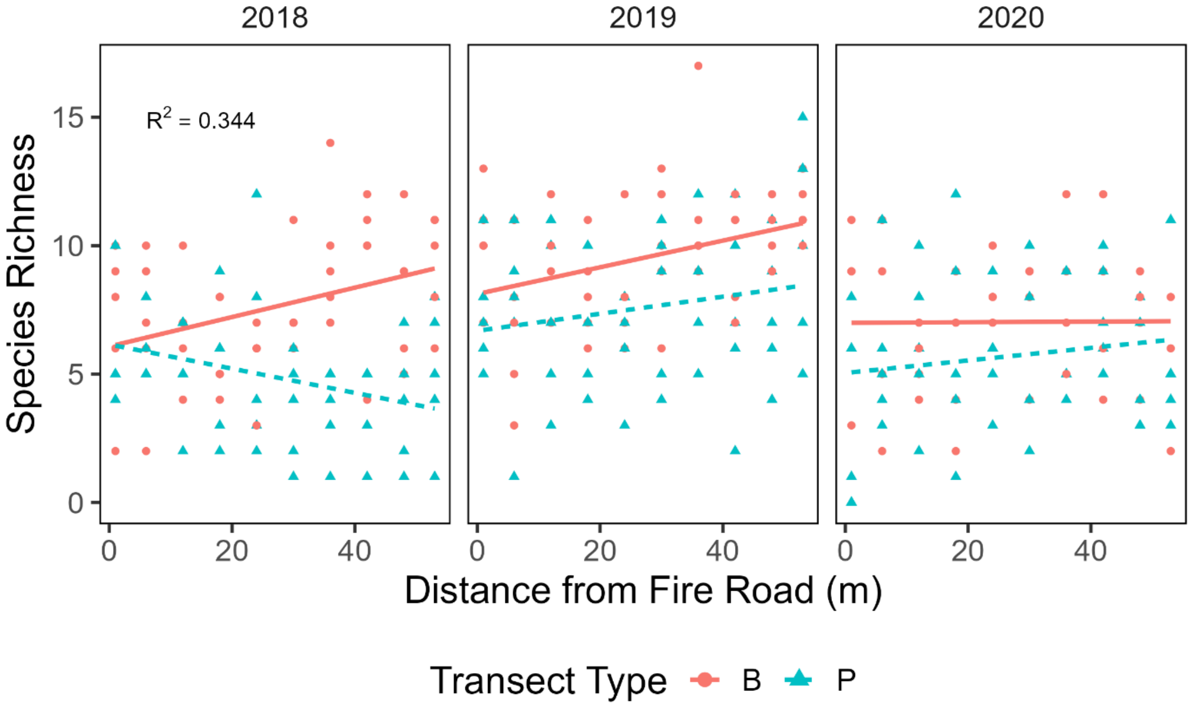


Figure 3. Shannon diversity (H) of Bulldozed (B) vs. Parallel (P) transects over time. Diversity was generally higher in B transects across all years.

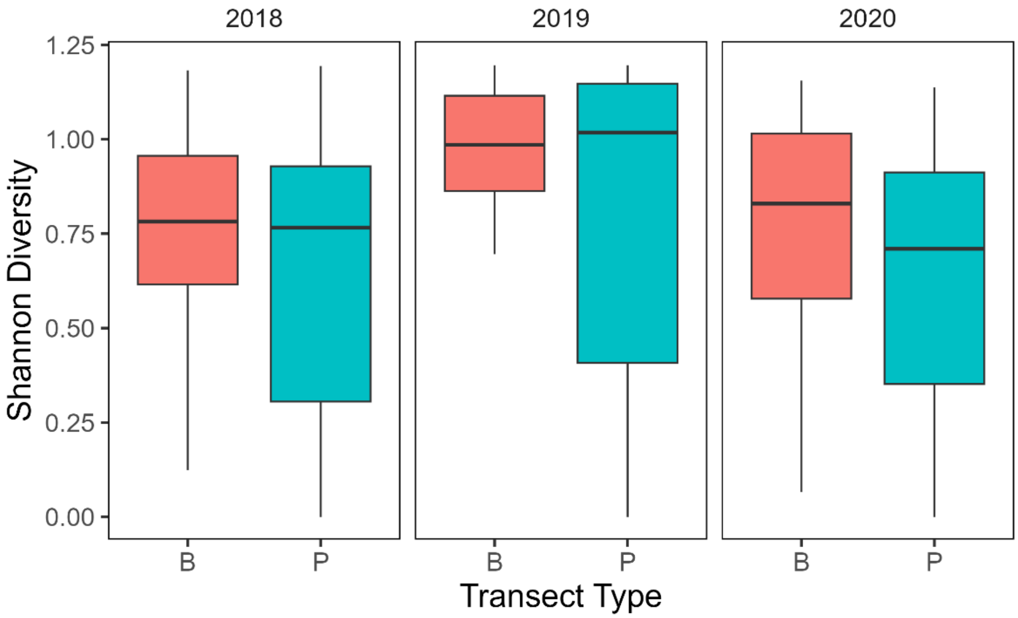


Figure 4. Abundance of non-native grass. Abundance was highest in 2019 but equal between 2018 and 2020. Non-native grass abundance was significantly different between transect types in 2018, but not 2019 or 2020.

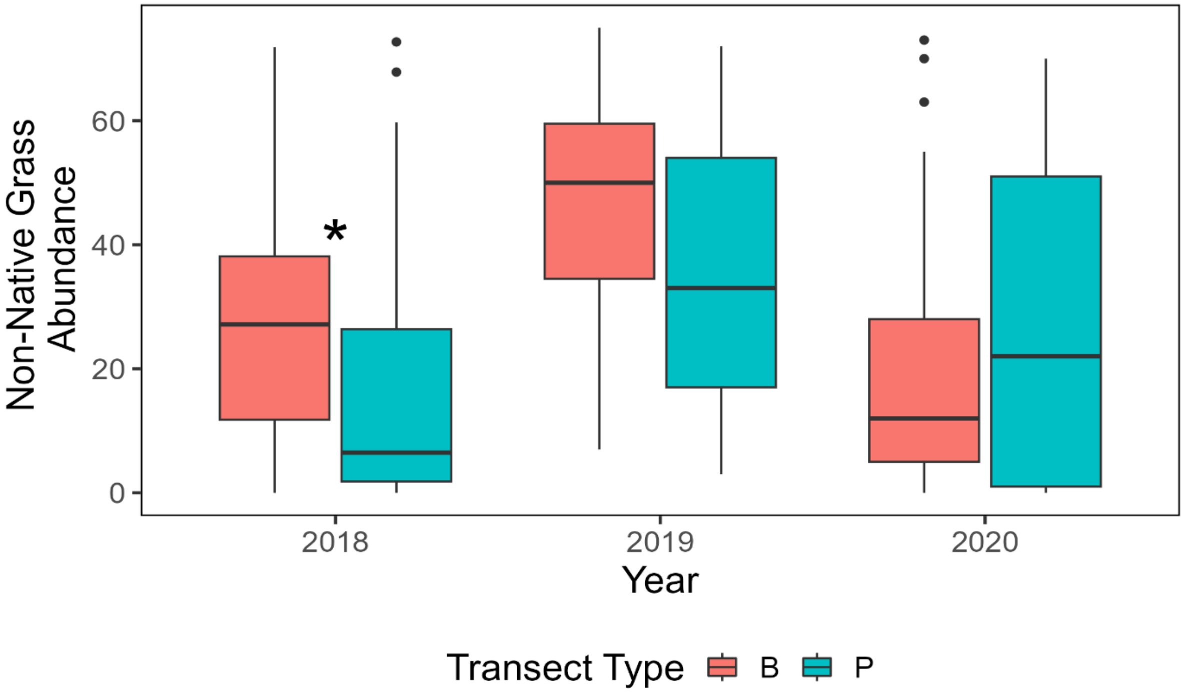


Figure 5. Abundance of non-native forbs. Native forb abundance changed year to year, but differences in abundance between B/P transects for were only significant in 2020.

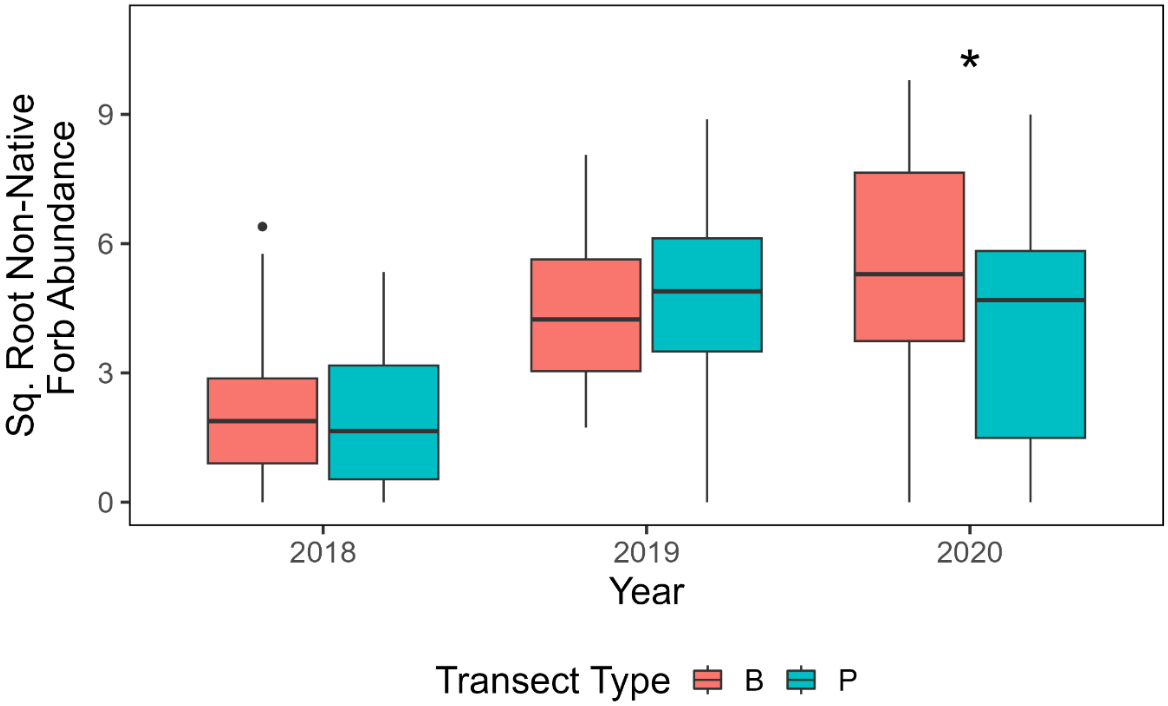


Figure 6. Abundance of all non-native species. Abundance did not differ between transect types but did change significantly from year to year. The relationship between non-native abundance and distance from the fire road changed year to year, inverting 2018-2019 and flattening in 2020.

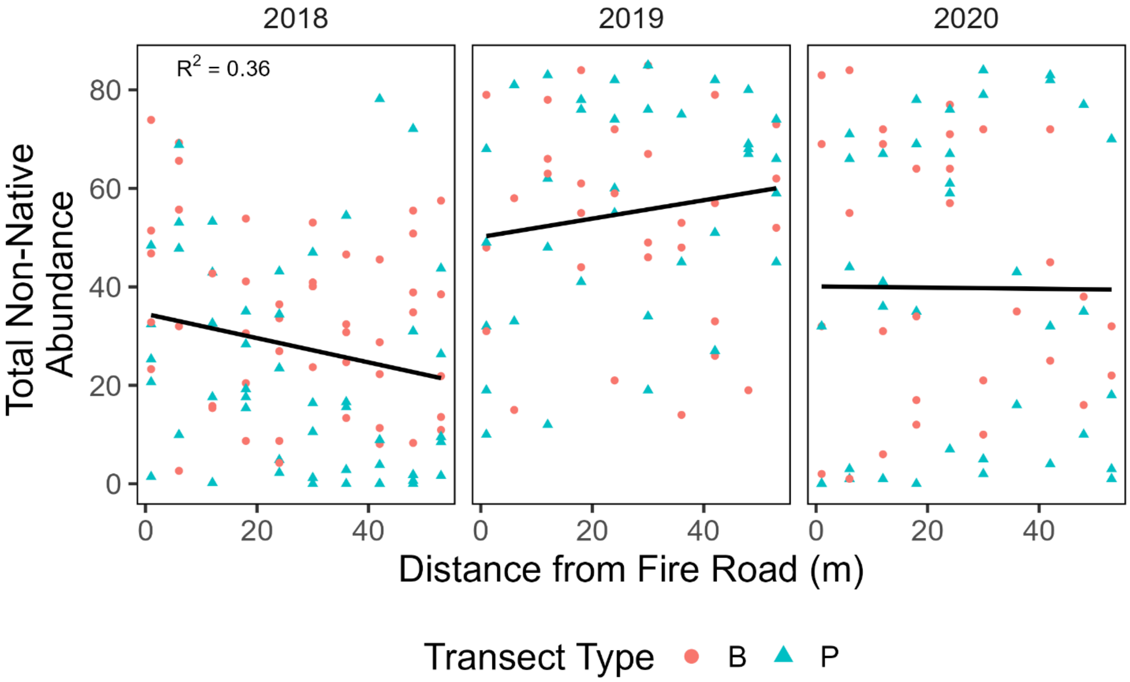


Figure 7. Abundance of all native species. Native abundance increased significantly each year. Differences in abundance between transect types were only significant in 2018.

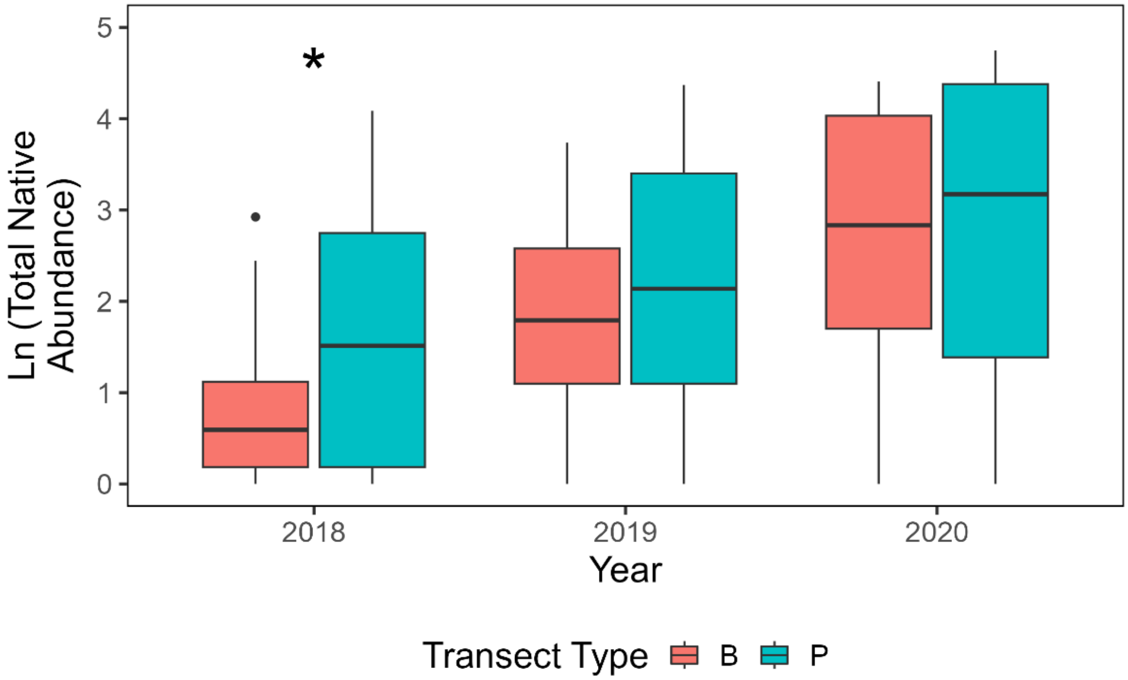


Figure 8. Species richness (A.) and Shannon diversity (B.) of plots included in the seeding/mowing experiment. Mowing reduced species richness but did not interact with year. Mowing produced a significant effect on diversity only in 2020, where mowed plots were lower than all plots in 2019, and unmowed plots in 2020 were equal to all plots in 2019. Richness and diversity did not vary between any seed treatments.

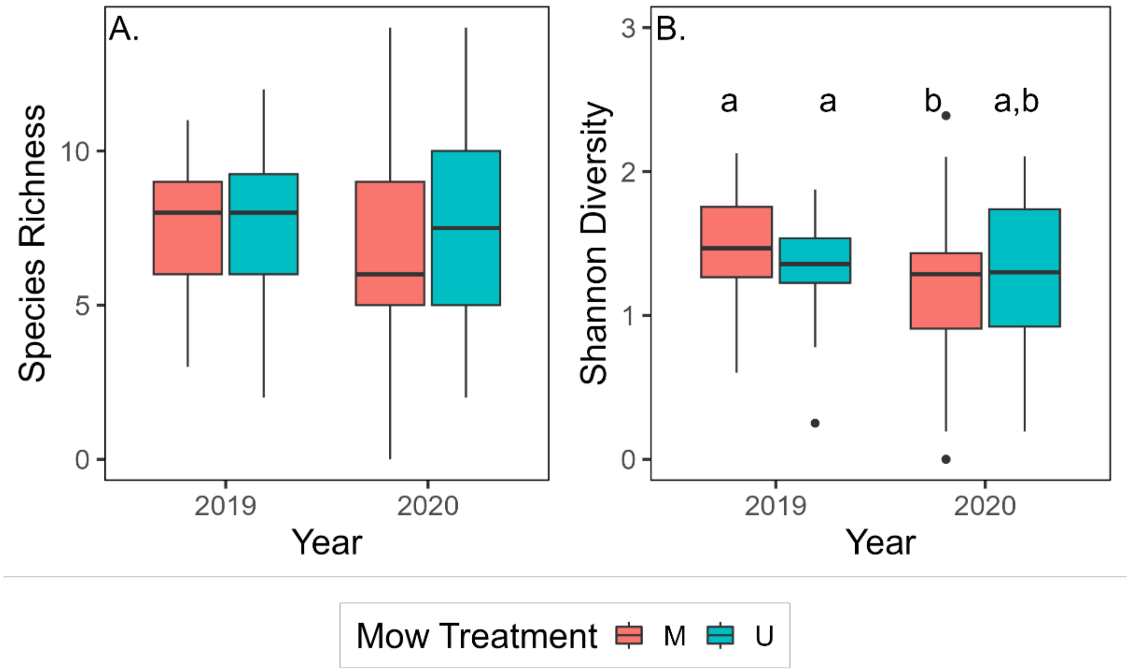


Figure 9. NMDS of all plots included in the seeding/mowing experiment. Year (Panel A; left) had a strong impact on composition, shifting heavily towards native shrubs and away from bare ground. Differences in community composition with respect to mowing (Panel B; right) were driven by more bare ground and non-native forbs in mowed plots.

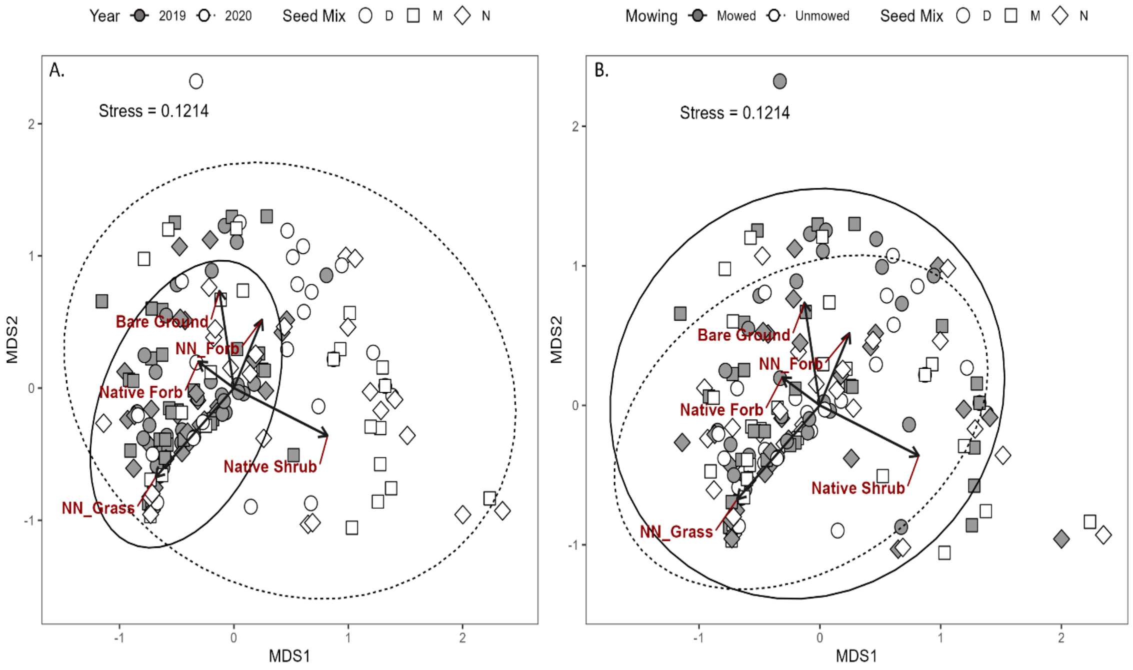


Table 1. Summary statistics of linear mixed effects model evaluating the response of Species Richness to distance from road, transect type, year, and their interactive effects. The model included transect group as a random factor			
Species Richness			
Factors	*DF*	*F*	*p*
Distance	*1*	*4.801*	***0.029***
Transect	*2*	*50.012*	***<0.001***
Year	*2*	*22.392*	***<0.001***
Distance x Transect	*2*	*5.360*	***0.021***
Transect x Year	*2*	*1.337*	*0.264*
Distance x Year	*2*	*3.246*	***0.041***
Distance x Transect x Year	*2*	*5.179*	***0.006***

Table 2. Summary statistics of Scheirer-Ray-Hare models evaluating the response of Shannon diversity by year to distance from road, transect type, and their interactive effects.

Shannon Diversity							
	Year	*2018*		*2019*		*2020*	
Factors	*DF*	*H*	*p*	*H*	*p*	*H*	*p*
Distance	*1*	*6.620*	*0.677*	*18.376*	***0.031***	*8.317*	*0.503*
Transect	*2*	*4.108*	***0.043***	*1.357*	*0.244*	*2.534*	*0.111*
Distance x Transect	*2*	*13.726*	*0.132*	*8.746*	*0.461*	*9.348*	*0.842*

Table 3. Summary statistics of Scheirer-Ray-Hare models evaluating the response of non-native grass abundance by year to distance from road, transect type, and their interactive effects. Data were subsetted by year, as Scheirer-Ray-Hare models cannot account for more than two-way interactions.

Non-Native Grass							
Year		*2018*		*2019*		*2020*	
Factors	*DF*	*H*	*p*	*H*	*p*	*H*	*p*
Distance	*1*	*9.255*	*0.414*	*9.492*	*0.393*	*4.075*	*0.906*
Transect	*2*	*11.214*	***0.001***	*1.390*	*0.238*	*0.108*	*0.742*
Dist. x Trans.	*2*	*1.730*	*0.995*	*7.000*	*0.637*	*4.909*	*0.842*

Table 4. Summary statistics of Linear Mixed Effects (LME) models evaluating the responses of vegetation functional groups to distance from road, transect type, year, and their interactive effects. "All Natives" was log-transformed to meet assumptions of normality. Transect group was included as a random factor.

Vegetation Functional Group		*Non-Native Forbs*		*All Non-Native*		*All Natives*	
Factors	*DF*	*F*	*P*	*F*	*p*	*F*	*p*
Distance	*1*	*7.252*	***0.008***	*0.271*	*0.603*	*18.654*	***<0.001***
Transect	*1*	*0.805*	*0.370*	*3.518*	***0.062***	*11.861*	***<0.001***
Year	*1*	*49.276*	***<0.001***	*50.123*	***<0.001***	*34.734*	***<0.001***
Distance x Transect	*2*	*1.3710*	*0.243*	*0.519*	*0.472*	*0.506*	*0.477*
Transect x Year	*2*	*4.256*	***0.015***	*0.987*	*0.374*	*3.446*	***0.033***
Distance x Year	*2*	*2.274*	*0.105*	*3.207*	***0.042***	*0.191*	*0.826*
Dist. x Trans. x Year	*2*	*1.801*	*0.167*	*0.240*	*0.787*	*0.099*	*0.906*

Table 5. Summary statistics of Linear Mixed Effects (LME) models evaluating the response of species richness and Shannon diversity to seeding and mowing treatments over time.

Community Measure		*Species Richness*		*Shannon Diversity*	
Factors	*DF*	*F*	*p*	*F*	*p*
Mow	*1*	*5.382*	***0.023***	*0.004*	*0.950*
Seed	*2*	*0.903*	*0.408*	*0.544*	*0.582*
Year	*1*	*2.434*	*0.121*	*3.555*	***0.062***
Mow x Seed	*2*	*0.296*	*0.744*	*0.069*	*0.933*
Mow x Year	*1*	*1.955*	*0.164*	*7.459*	***0.007***
Seed x Year	*2*	*1.121*	*0.329*	*1.961*	*0.145*
Mow x Seed x Year	*2*	*0.059*	*0.943*	*0.260*	*0.771*

Table 6. Summary statistics of PERMANOVA for evaluating differences in species composition among seeding and mowing treatments over time. Analysis was conducted on Bray-Curtis dissimilarity.

Factors	*DF*	R^2	*F*	*p*
Mow	*1*	*0.012*	*2.257*	***0.040***
Seed	*2*	*0.026*	*1.402*	***0.060***
Year	*2*	*0.157*	*29.873*	***0.001***
Mow x Seed	*2*	*0.007*	*0.669*	*0.557*
Mow x Year	*2*	*0.008*	*1.545*	*0.142*
Seed x Year	*2*	*0.008*	*0.727*	*0.549*
Seed x Mow x Year	*2*	*0.006*	*0.525*	*0.760*

Supplementary Tables & Figures

Supplementary Table 1: Species selected for train screening & their origin.

Species Name	***Origin***	***Species Name***	***Origin***
Artemisia californica	Native	*Phacelia ramosissima*	Native
Ambrosia acanthicarpa	Native	*Encelia californica*	Native
Baccharis sarothroides	Native	*Stipa pulchra*	Native
Bromus carinatus	Native	*Stipa coronata*	Native
Cirsium occidentale	Native	*Eriogonum fasciculatum*	Native
Isocoma menziesii	Native	*Datura wrightii*	Native
Malacothamnus fasciculatus	Native	*Salvia mellifera*	Native
Phacelia minor	Native	*Heterotheca grandflora*	Native
Marah macrocarpus	Native	*Avena barbata*	Exotic
Bromus diandrus	Exotic	*Avena fatua*	Exotic

Supplementary Table 2: Seeded species, average seed mass, and estimated number of propagules per species in one plot. An equal mass of each species' seed was included in each seed mix, except for Marah macrocarpus, which has very large seeds (orders of magnitude larger than other species here). To compensate for this, I added an equal number (7) of M. macrocarpus seeds to each D-mix plot indicated in the protocol.

Species	**Seed Mass (mg)**	**Est. # Propagules**	**Life Form**	**Seed Mix**
Encelia californica	1.53±0.82	4,901	Shrub	M
Datura wrightii	1.19±0.32	6,302	Forb	M
Stipa pulchra	5.59±0.11	1,341	Grass	M
Bromus carinatus	9.58±0.44	783	Grass	M
Eriogonum fasciculatum	1.13± 0.03	6,637	Shrub	M
Phacelia ramosissima	1.08±0.05	6,944	Forb	M & D
Marah macrocarpus	14929±515	7	Forb	D
Cirsium occidentale	5.92±0.40	1,266	Forb	D
Salvia mellifera	0.69±0.15	10,869	Shrub	D
Heterotheca grandiflora	0.84±.05	8,928	Forb	D
Baccharis sarothroides	0.91±0.07	8,241	Shrub	D

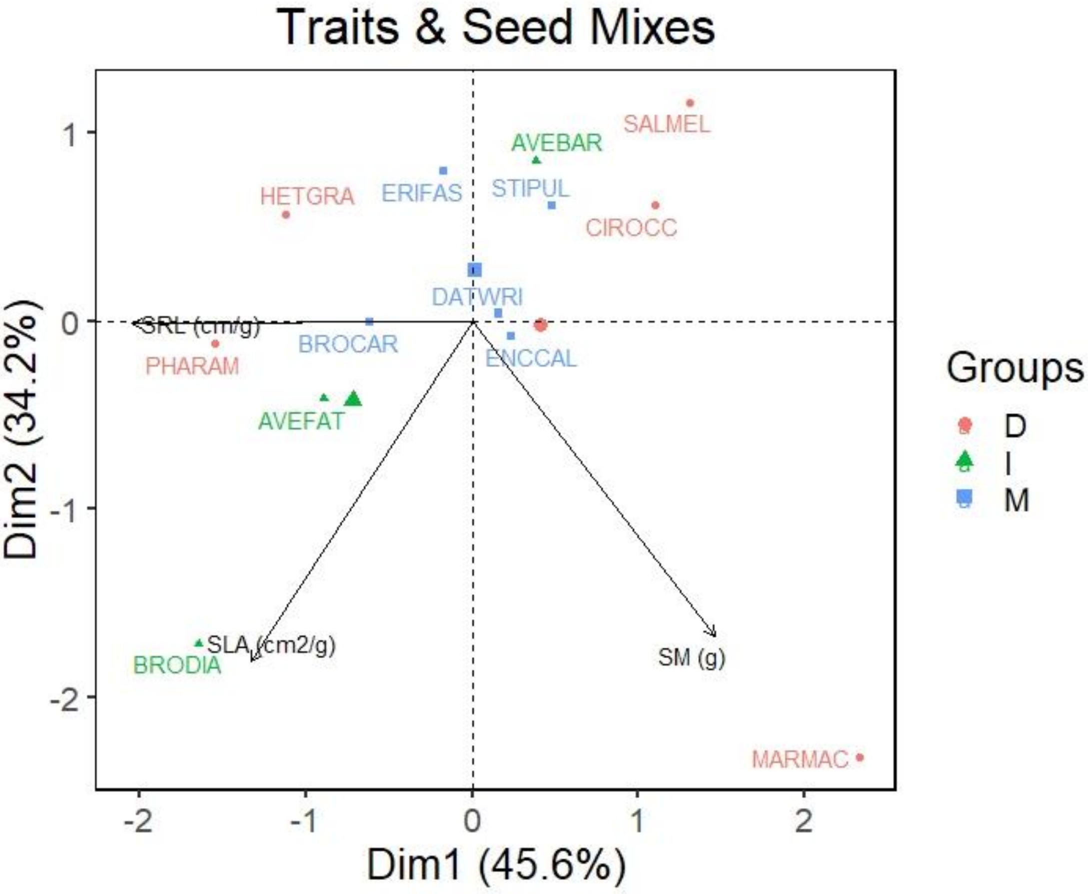
Supplementary Table 3: Mean values & standard errors of species richness and Shannon diversity in Bulldozer (B) and Parallel (P) transects by year.

Year	**2018**		**2019**		**2020**	
	Richness	*Diversity*	*Richness*	*Diversity*	*Richness*	*Diversity*
B	7.620 ±0.376	1.046 ±0.061	9.520 ±0.354	1.491 ±0.055	7.026 ±0.437	1.211 ±0.072
P	4.880 ±0.355	0.852 ±0.070	7.580 ±0.419	1.339 ±0.069	5.700 ±0.418	1.020 ±0.079

Supplementary Table 4: Data transformations to normalize data for Linear Mixed Effects models

Variable	**Transformation**
Non-native forb abundance	*Square root*
All native plant abundance	*Natural log (ln)*

Supplementary Figure 1. Principal Components Analysis (PCA) of species screened for seed mixes. I selected 6 species for Mix M (blue) to include the smallest possible amount of trait variation and highest functional similarity to invasive grasses (green). I selected 6 species for Mix D (red) to include the farthest-outlying trait combinations with respect to Specific Leaf Area (SLA), Specific Root Length (SRL), and Seed mass (SM).



CHAPTER 2

Disturbance-intensive manual removal of *Holcus lanatus* in subalpine wet meadows restores biodiversity and native plant cover in post-invasion plant communities.

Abstract

Managing biological invasions is one of the most pressing and costly challenges facing land managers today. Due to the high cost and variable outcomes of invasive plant removal at scale, vegetation managers must allocate and deploy scarce resources to maximize their effectiveness and minimize secondary impacts. Vegetation managers at Sequoia National Park prioritize invasive plant eradication at higher elevations, where native species generally outnumber non-natives and thus are more likely to colonize sites where invasive species have been removed. The most significant example of this strategy is 15-year effort to eradicate *Holcus lanatus* (Poaceae; "Velvetgrass") from subalpine wet meadows and riparian areas in the Kern Canyon using manual removal. I established vegetation monitoring plots in multiple Velvetgrass removal sites and paired uninvaded sites within the project area. I assessed the recovery of the native plant community by comparing species richness, Simpson diversity, and cover of non-native species. between treated and control sites, as well as between levels of treatment intensity within Velvetgrass removal sites. I found that the removal of Velvetgrass led to the near-complete recovery of the native plant community in treated meadows, except for some minor compositional shifts. Velvetgrass populations declined quickly since the management project reached peak effort in 2012 and have not been replaced by other non-native species. Species richness and biodiversity are largely indistinguishable

between post-invasion and uninvaded areas. These results suggest that, given sufficient native species richness and cover, native plant communities can be highly resilient to plant invasions and to the disturbances associated with eradicating those invasions.

Introduction

Protected natural areas are important reserves of biodiversity and cultural resources during the modern extinction crisis (Olmos-Martinez et al. 2022). Over the last century most ecosystems have experienced significant changes to their structure and function in response to anthropogenic influences, from minor compositional shifts to major habitat loss and extinction (Lewis & Maslin 2015). Despite the best efforts of many land management agencies, the combined threats of land development, climate change, and invasive species are driving rapid ecological changes even in protected natural areas, putting some of the most valuable reserves of biodiversity on earth at risk (Mainka & Howard 2010; Aycrigg et al. 2022). Of these, plant invasions require significant investment to mitigate their impacts and restore invaded areas over the long term (Duncan et al. 2004; Kettenring & Adams 2011).

Due to practical and financial considerations, invasive plant managers often remove invasive species and allow the ecosystem to recover on its own ("passive" restoration) rather than assisting native plant recovery by reintroducing plants or seeds ("active" restoration; Olmos-Martinez et al. 2022). While passive techniques are less cost-intensive in the short run, their long-term success is contingent on the ability of the focal ecosystem to recover from disturbance and provide the necessary propagules to recover biodiversity and species richness (Poorter et al. 2016; Atkinson & Bonser 2020). In some cases, passive restoration can lead to the recovery of biodiversity and habitat quality as invaded areas are recolonized by remnant native plants or the native seed bank (Piaia et al. 2020). However, intense disturbance can act as an environmental filter, selecting for disturbance-adapted invaders and stimulating reinvasion (Fattorini & Halle 2004; Meyer et al. 2021). Furthermore, long-term invasions can locally extirpate native species that would otherwise recolonize the site after weed removal, thwarting successful passive restoration (Gioria and Pysek 2016, Mollot et al. 2017). A better understanding of the local factors influencing the success or failure of passive restoration could yield significant improvements to the efficiency and efficacy of invasive plant management at large.

High-elevation wilderness areas are some of the most valuable and stable reserves of biodiversity on earth, making them ideal targets for conservation and restoration (Di Marco et al. 2019). Ecological **s**tewardship of wilderness areas is an important function of land management agencies in the United States, but the defining legal characteristics of federal wilderness designation presents unique challenges and constraints. Specifically, wilderness managers are required to use the minimum technology possible – not necessarily the minimum disturbance technique – to accomplish management goals: no motorized, mechanized, or battery-powered equipment is to be used unless necessary for safety (Wilderness Act 1964; Lieberman et al. 2018). As a result, invasive plant management is typically done with simple tools (e.g., hand picks, shovels, pruning shears), requiring large crews to access restoration sites by foot and occurring over long periods of time. The large crews can produce significant soil and trampling disturbance, and intense management-associated disturbance can compromise the efficacy of invasive plant removal as a restoration technique if disturbance-adapted invasive species colonize removal sites (Pearson et al. 2016). The repeat visits to sites for invader removal can result in a prolonged disturbance that also increases the probability of the introduction of invader propagules, as shoes can be a source of invasive seeds (Woitke & Diez 2002; Milne & White 2022). Moreover, the extent, timing, and probability of reinvasion or secondary invasion can differ based on the method and intensity of disturbance associated with initial control efforts (González et al. 2017). In one example, the initial method of invasive plant removal determined differential vegetation responses to multi-year weed treatment after the fact, including complete secondary invasion despite repeated attempts at manual removal and herbicide application (González et al. 2017). To achieve wilderness management goals among so many contingencies, managers must carefully consider local site conditions and limited available treatment methods while continually evaluating treatment efficacy through a scientific management process.

The National Park Service oversees invasive plant removal in several wilderness areas. In Sequoia National Park (California, USA), vegetation managers practice a long-term strategy of "top-down" weed management, from high elevation to low elevation, as a means to maximize the potential for passive restoration on a multi-year parkwide scale (A. Demetry & R. Thiel, pers. comm. 2015). Areas below 1,500 meters elevation tend to be dominated by invasive plants in the herbaceous layer, but above 2,000 meters native plants are far more abundant than invasive plants (A. Demetry & R. Thiel, pers. comm. 2015). By targeting areas at higher elevations for intensive weed removal first, managers hope to maximize the chance that native plants, rather than invasive plants, will recolonize disturbed areas where populations of invasive species have been intensively removed. This strategy gave rise to an extensive long-term removal effort of *Holcus lanatus* (common name Velvetgrass) from high elevation meadows in the Kern Canyon. Initial control efforts began in 2007. While demonstrably effective at reducing invasive plant populations over time in many systems

(Cutway 2017), manual removal requires large crews and entails significant disturbances to treated sites, including trampling and soil tillage from vegetation removal. These disturbances may facilitate colonization by other invasive species that are adapted to disturbance, compromising the recovery of native species (Pearson et al. 2016).

In the summer of 2019, 15 years after the start of Velvetgrass control in the Kern Canyon, I established vegetation monitoring plots within the project area to assess the potential for passive restoration. I asked two questions: (1) Is Velvetgrass removal alone sufficient to restore native plant communities in invaded areas? (2) Does plant community recovery depend on the intensity of treatment? First, I hypothesized that manual Velvetgrass removal will effectively restore invaded areas to resemble uninvaded areas (H1). I predicted that Velvetgrass populations would be significantly lower than their peak years in Velvetgrass removal sites. Additionally, I predicted that species richness, Simpson diversity, and plant community functional composition would not differ between Treated and Control sites. Second, I hypothesized that the disturbance caused by manual Velvetgrass removal acts as an environmental filter, leading to functional shifts in plant community composition according to treatment intensity (H2). I predicted that Velvetgrass removal sites would have lower levels of species richness and Simpson diversity at higher levels of treatment intensity, and that shifts plant community functional composition would be significantly different depending on treatment intensity as well.

Methods

Site Description

This study was conducted along a 25 km length of the Kern River, on the canyon floor between 1,900-1,981 m elevation, in the vicinity of the Kern Ranger Station (36°20'43.6"N, 118°24'24.5"W). The Kern River runs due south from its headwaters in northern SNP and has carved out a deep canyon that bears the same name. Evidence of human habitation or through-travel dates at least as early as 100 C.E. by the Tübatulabal, Palagewan, Yawelmani peoples. Significant changes occurred in the last 150 years due to intentional ecosystem modification by colonists and prospectors including the creation of meadows to support sheep and cattle grazing, followed by the forcible removal of all inhabitants within the boundaries of the national park. Today this section of canyon floor in SNP is a mix of pine woodland, grass/sedge wet meadows, and riparian shrub & forb communities. Dominant canopy species include *Abies concolor* (Pinaceae; White Fir), *Calocedrus decurrens* (Cupressaceae; Incense Cedar), and *Salix lasiolepis* (Salicaceae; Arroyo willow). In remnant meadow communities where Velvetgrass commonly invades, community cover is primarily made up of graminoids and forbs including *Carex nebraskensis* (Cyperaceae; Nebraska Sedge), *Festuca rubra* (Poaceae; Red Fescue), *Deschampsia caespitosa* (Poaceae; Tufted Hairgrass), *Carex lenticularis* (Cyperaceae; Lakeshore Sedge), *Equisetum arvense* (Equisitaceae; Horsetail), and *Solidago spectabilis* (Asteraceae; Goldenrod).

Velvetgrass was first discovered in the Kern Canyon by wilderness ranger Laura Pilewski. Since then, the SNP Vegetation Management division has tracked and removed Velvetgrass populations in this area for over 17 years. Treatment efforts were initially limited to small crews of 4-6 people in the first 3 years of the project, which were unable to keep up with the rapid expansion of Velvetgrass populations. SNP contracted an Americorps crew each summer starting in 2010 to provide additional labor, up to a maximum of 17 total people working on Velvetgrass removal for 2-3 months each summer. Managers set up over 80 treatment sites of varying size and tracked removal efforts by counting the number of stems removed within each treatment event (National Park Service internal data 2019). Full-capacity crews were able to remove nearly every known individual of Velvetgrass each year. Control techniques consisted primarily of manual removal of entire plants by the root using a hand pick, which left deep divots of wet soil after treatment. Plants were left to dry and die on exposed rocks and logs to prevent re-rooting. Access to sites was frequently off-trail, and often resulted in large, trampled paths. All workers used boot brushes to clean mud and seeds from boots before leaving any treatment site to reduce the risk of unintentionally spreading more seeds. Apart from this, workers did not do any post-treatment mitigation of soil divots or trampled areas. Treatment generally proceeded from South to North, from lower elevations to higher elevations, to follow phenology and pre-empt seed set.

Sampling Design

I conducted vegetation surveys in 2019 in a paired-plot design (Fig. 1). From the 80 established Velvetgrass removal polygons I identified sites of at least 1000 m^2 that had been treated for at least 10 consecutive years as of my 2019 survey. From this subset I selected 5 sites across a range of treatment intensities that were spaced North to South encompassing most of the project area (approx. 8 km). For each of the 5 Velvetgrass removal sites I established a paired uninvaded Control site in the nearest meadow of comparable size and distance from water. Within each of the 10 sites I established a Modified Whittaker plot, which measures species richness using nested subplots over an increasing survey area for the purpose of creating a species-area curve (Stohlgren et al. 1995; Fig. 2). However, only the relative cover and species richness within the smallest subplots (2 x ½ m; 1 m^2) are considered in this analysis (n=10 at each site; Fig. 2).

Within each of the 100 subplots across the 10 sites, I surveyed species richness and areal cover by species. For species richness, I recorded all vascular plant species encountered within a given subplot even if they were not detected in my cover sampling. For cover, I overlaid a 50-point grid at 1m height above each subplot and recorded the top hit beneath each grid intersection. Because some species in the richness survey do not appear in the cover dataset due to the differing survey methods, the species richness and areal cover were organized in separate datasets. All surveys were conducted before any disturbance by Velvetgrass removal crews occurred in 2019. All species detected had been previously observed within Sequoia National Park and could be found in park records with voucher specimens. Species nomenclature follows *The Jepson Manual of Vascular Plants of California* (Baldwin et al. 2022). I disregarded 12 outlier subplots with >75% cover of rock, algae, standing water, or in one case a monoculture of *Cardamine breweri* (Brassicaceae) that was growing in a flooded plot. I reasoned that because flooded areas with algae, water, or aquatic plants did not support any non-aquatic plant, the effect of extreme outliers in local moisture conditions would only obscure the actual impacts of Velvetgrass removal. For a similar reason, I discarded subplots with large amounts of rock as no plants in the study area are able to grow on bare rock, and the absence of vegetation in these subplots could confound the impact of Velvetgrass removal with local anomalies in resource availability. No more than 3 subplots were discarded from any individual site.

I aggregated the total number of stems removed from Velvetgrass removal plots ("treated" plots) from 2009-2019 and assigned each plot to a category of treatment intensity based on the order of magnitude of stems removed (Low <1000, n=1; Moderate <100,000, n=2; High <1,000,000, n=2). I used stems removed as a proxy for treatment intensity because it interacts with multiple elements of disturbance impacts such as crew size, the extent of direct ground disturbance, and the number of visits a given site received. In aggregate, this is broadly representative of the intensity of both trampling and soil tillage within that site.

The National Park Service provided data on Velvetgrass control efforts over the last 15 years, including total stems removed from each plot per year. In early years, these numbers do not accurately represent the extent of invasion, because crews were smaller and generally unable to remove all Velvetgrass from every plot, so efforts were more focused on mitigation than eradication. Once crew sizes grew to the point where 100% Velvetgrass removal was possible in most sites within a year (2010-2012), I used these peak numbers to approximate the total extent of invasion within a given plot. To evaluate the efficacy of Velvetgrass removal at reducing Velvetgrass populations, I calculated a response ratio between the greatest number of stems removed from each treated plot within a single year ("peak") and the number of stems observed in each plot in my 2019 survey. Using these ratios, I conducted a one-sample t-test to assess whether treatment responses were different from a null response (ratio of 1).

To assess how treated plots responded to Velvetgrass removal I conducted two complementary analyses. First, I compared observed species richness, Simpson diversity, and non-native cover across all 1 m^2 subplots between treated and control plots (Fig. 1). For species richness I ran a linear mixed effects model with species richness as the response variable and treatment as the fixed effect with pair as a random factor. Simpson diversity and non-native cover data did not meet assumptions of normality for a linear model; therefore, I used a Kruskal-Wallis test (nonparametric equivalent to one-way ANOVA) (Kruskal & Wallis 1952). Second, I conducted a multivariate analysis to assess shifts in composition, in which I combined vegetation cover into plant functional groups based on their life form (forb, grass, sedge, rush, shrub, tree). I split each functional category by origin (native, non-native) to differentiate desirable native plants from undesirable non-native plants from the same functional group. To understand whether and how community functional composition changed in response to Velvetgrass treatment, I conducted a PERMANOVA via the ‘adonis2()’ function to compare functional composition between treated and untreated sites (Oksanen et al. 2022). I visualized results using nonmetric multidimensional scaling (NMDS) via the metaMDS() function and ggplot2 (Oksanen et al. 2022, Wickham 2016).

To evaluate how treatment intensity impacted community recovery, I calculated response ratios for species richness, Simpson diversity, and non-native cover. I divided the observed level of species richness, diversity, or non-native cover in each treated subplot by the respective variable’s mean level across all subplots in the corresponding (paired) control plot. A response ratio <1 indicates that treated plots had a lower response compared to control plots, and vice versa. None of the three response variables were normally distributed, so to determine significance I used a Kruskal-Wallis test (nonparametric equivalent to one-way

ANOVA), followed by a Dunn's test with Bonferroni correction to show pairwise comparisons (Kruskal & Wallis 1952, Dunn 1964), with treatment intensity as a fixed factor. Additionally, to evaluate whether treatment intensity impact community composition, I conducted a PERMANOVA analysis as described on only the treated sites above with treatment intensity as the fixed factor.

All statistical analysis and data visualization was performed in R 4.1.2 (R Core Team 2023), using the R packages "vegan" (Oksanen et al. 2022), "tidyverse" (Wickham et al. 2019), "dplyr" (Wickham et al. 2022), "ade4" (Dray & Dufmy2007), "nlme" (Pinheiro et al. 2021), "reshape2" (Wickham 2007), and "ggplot2 (Wickham 2016)."

Results

My surveys recorded 88 unique plant species over the course of the study, covering 10,000m^2, over 14 days of sampling. I encountered 80 native and only 8 non-native species, congruent with anecdotal evidence from park managers that native species are far more abundant than non-natives at high elevations. Native forbs contributed an outsized proportion of species richness, making up 45 of the 80 native species encountered. Of the non-native plants, 4 were grasses and 4 were forbs (Table S1). Within individual subplots, species richness ranged from 2-15 with a mean of 6.56±0.25. Simpson diversity ranged from 0-0.87 with a mean of 0.58±0.20 (Table S2).

Velvetgrass stem counts were significantly lower in every site compared to pre-treatment, with stem counts in 2019 being on average less than 0.01% of peak stem counts for a given site (0.005±0.003, p<0.001; Table 1). In my 2019 survey I detected Velvetgrass in only 2 subplots, which were both within the same treated site. Neither species richness nor Simpson diversity differed significantly between treated and control sites (p=0.225, p=0.437, respectively; Table 2, Figure 3).

Plant community life form composition was significantly different between treated and control sites (p=0.001; Table 3, Figure 4). Treated plots had a high cover of native sedges, while control plots had more varied composition where some plots were more associated with bare ground, native shrubs, native ferns, and other non-native and native grass. Native rushes also drove some variation, appearing most commonly in wet seeps and riparian areas of Velvetgrass removal plots. Native forbs were the most similar group between treated and control sites. Sedges like *Carex nebraskensis* and *Carex lenticularis* formed a dominant cover layer in many treated sites, while longer-lived and taller-stature shrubs like *Salix exigua* and *Lupinus albicaulus* were more common in untreated sites. Importantly, non-native plant cover did not differ between site types (p=0.222; Table 2).

Species richness did not differ among treatment intensities, as treatment intensities had similar response ratios (p=0.118, Table 4). However, Simpson diversity differed significantly between treatment intensities, where plots with low treatment intensity had a larger response ratio of Simpson diversity than plots with high or moderate treatment intensity (p=0.005, p=0.018; Figure 5, Table 4). The response ratio of non-native cover was significantly different between treatment intensities (p=0.020; Table 5), where plots with moderate treatment intensity had a significantly higher response ratio than plots with high or low treatment intensity (Low=0.545±0.545, Moderate=1.983±0.702, High=1.449±1.33; H-L p=1.000, H-M p=0.046, L-M p=0.063). This relationship is tenuous as the generally low abundance of non-native species across the entire study site created significant left-skew (a high number of zeroes), contributing to very high standard error relative to the mean. Only 21 plots out of 91 used in the analysis had any non-native cover at all, and of these only 9 had more than 10% non-native cover. Community functional composition was not significantly different between treatment intensity levels (p=1.000; Figure 6, Table 6).

Discussion

Treatment of non-native plant invasions in remote natural areas presents unique challenges that require deeper consideration of the interaction between management-associated disturbance and ecosystem recovery. Here I present results from an extensive vegetation survey documenting trends in post-invasion recovery of wet meadows after manual removal of Velvetgrass in a remote wilderness area. In support of my first hypothesis, Velvetgrass populations have declined precipitously in every treated site. Biodiversity and species richness were not significantly different between treated and control sites, providing further evidence that Velvetgrass removal has resulted in successfully restored meadows that are comparable to uninvaded areas. Velvetgrass removal areas do have differences in plant community functional (life form) composition compared to untreated areas, but no differences in non-native cover, species richness, or Simpson diversity. This indicates that while treated plots did not exactly resemble uninvaded areas, there is no evidence of reinvasion or secondary invasion. For my second hypothesis, relationships between treatment intensity and community responses were varied. The response ratios of Simpson diversity and non-native cover differed significantly between plots of different treatment intensity, but community functional composition remained unchanged. In summary, I demonstrated that non-native plant removal in natural areas can successfully suppress invasion and allow ecosystem recovery, but that the lasting influence of disturbance may have some ongoing impacts to plant community composition. I will further interpret these relationships below.

The suppression of invasive species is the first step in a complex process to fully recover from biological invasion (Buckley et al. 2007). Despite stem counts once numbering in the hundreds of thousands in some sites, I found that the Velvetgrass population in the Kern Canyon has consistently fallen since the onset of weed control efforts, with some subpopulations disappearing entirely. Furthermore, non-native cover was not different between treated and control sites, suggesting that the disturbance caused by Velvetgrass removal did not stimulate secondary invasion in this context. Initial removal of invasive species is frequently followed by reinvasion of the same species or secondary invasion of another non-native species (Pearson et al 2016); in this system the overall low numbers of non-native species likely resulted in few potential propagules that would promote a secondary invasion. This potential for passive recovery of biodiversity and ecosystem function has been documented in other areas with low anthropogenic disturbance and few other invasive species (Prior et al. 2018). This provides some validation for Sequoia National Park’s vegetation management strategy to focus on invasive plant eradication in high-elevation areas where native plants dominate the herbaceous layer and human travel is restricted by permit.

Even when management actions successfully eradicate local populations of invasive species, legacy effects on species distributions, soil structure, and/or nutrient webs may persist, hindering the recovery of biodiversity and/or ecosystem function after invaders are removed (Cuddington 2011). Although I expected some residual impacts, particularly in the most heavily invaded areas, I found no differences in species richness or Simpson biodiversity between treated and untreated areas. On the other hand, I did observe that Velvetgrass removal sites had more herbaceous and annual species than uninvaded control sites, while the latter had significantly more woody perennial species like *Salix* and *Lupinus* spp. Many of the meadows I studied in this project were initially cleared of woody vegetation by shepherds in the early 20th century to open grazing space and maintained by seasonal trampling and grazing by herd animals. Similar intentional meadows were created in many different mountainous areas of the American west, and prior studies have found shrub and tree expansion to be broadly associated with the cessation of sheep grazing in the 1940s (Miller & Halpern 1998). Velvetgrass is a deeply rooted perennial grass that has been shown to outcompete other perennial species (Bennett et al. 2011) and may have been preventing the establishment of shrubs in these meadows. Removing Velvetgrass is also a disturbance-intensive process that could disrupt the lateral roots of expanding shrubs, further selecting for annual species. Continued vegetation monitoring of these treated areas could provide insight as to whether these potential invader impacts created longer term legacies that might prevent or slow the natural succession of shrubs within these meadows in the future.

Even relatively recently established patterns of disturbance like the Kern Velvetgrass removal project can have strong and lasting impacts on the makeup of plant communities (e.g., Minnich & Dezzani 1998, Milchunas et al. 2000). In particular, disturbances that increase in frequency or severity – like a focused weed removal project – can cause a compositional shift towards annual species, which are usually better at rapidly converting resources to biomass and have a shorter time from germination to reproductive maturity than perennial species (e.g., D'Antonio & Vitousek 1992, Brooks 2008). While the response ratio of species richness did not differ significantly across levels of treatment intensity, the response ratio of Simpson diversity was significantly higher in Velvetgrass removal plots with the lowest treatment intensity. Here, the repetitive low-level physical disturbance of Velvetgrass removal may have created favorable microhabitat that allowed for shifts in species abundance without overall changes in species richness resulting in increases in diversity relative to control areas. Despite differences in biodiversity, any shifts in species abundance did not translate to differences in plant community functional composition between different levels of treatment intensity. I did find a significant relationship between the response ratio of non-native plant cover and treatment intensity, but as stated above, issues with data skew compromise the validity of this relationship – the sum (or difference) of the mean and standard error in some groups crosses the neutral threshold of 1, reversing the direction of the relationship within a single factor. All told, the intensive removal of Velvetgrass allowed for the passive ecological recovery of diverse and robust native vegetation across these sites.

The success of Velvetgrass removal in the Kern Canyon is likely related to a confluence of multiple factors that makes this project area particularly conducive to passive recovery after treatment. First, my study area was quite species-rich, with 88 species observed across 10,000m^2 surveyed. Each functional group I encountered was represented by two or more distinct species, producing a significant degree of redundancy across all functional groups. Functionally redundant ecosystems are generally more stable and resilient than their more species-poor counterparts (Biggs et al. 2020), largely because the loss or removal of any individual species is less consequential when another functionally similar species is locally available to replace it (Rosenfeld et al. 2002). Furthermore, high species pool diversity could buffer the homogenizing effects of disturbance (Catano et al. 2017), allowing areas such as high resource wet meadows to be very resilient to trampling. In some cases, wet meadows may show no lasting impacts to multiple measures of vegetation condition despite intense and chronic disturbance (Stanley et al. 2005). In these ways the high levels of species richness and of functional redundancy may have contributed to the rapid recolonization of Velvetgrass removal areas.

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FIGURES AND TABLES – CHAPTER 2

Figure 1. Project location relative to the state of California (black box), Sequoia & Kings Canyon National Parks (orange box), and the Kern canyon (blue box). Site map includes a 3D rendering of terrain using horizontal lines, with elevation denoted in feet.

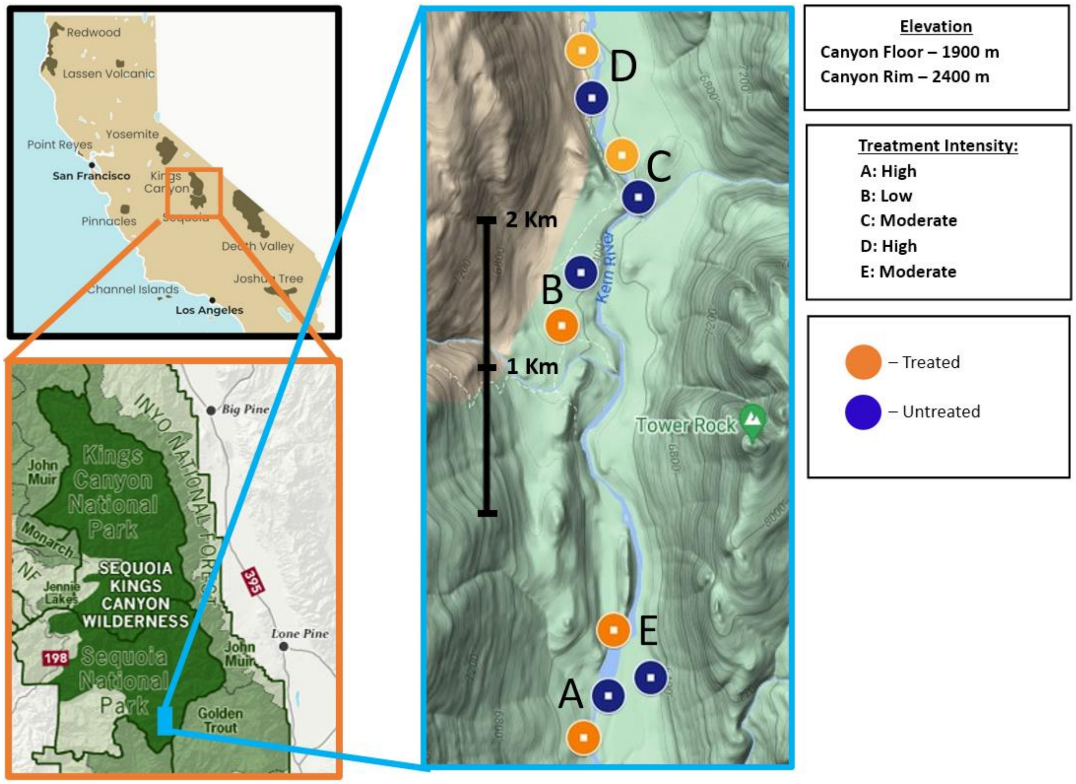

Figure 2. Vegetation sampling scheme using a Modified Whitaker plot (as described in Campbell et al. 2002). Subplots of different sampling sizes were set up within the total 20m x 50m sampling plots. In this paper I present richness & cover data only from the "A" subplots; I did not analyze B, C, and D subplots. To measure aerial cover, I overlaid a 50-point grid on "A" subplots.

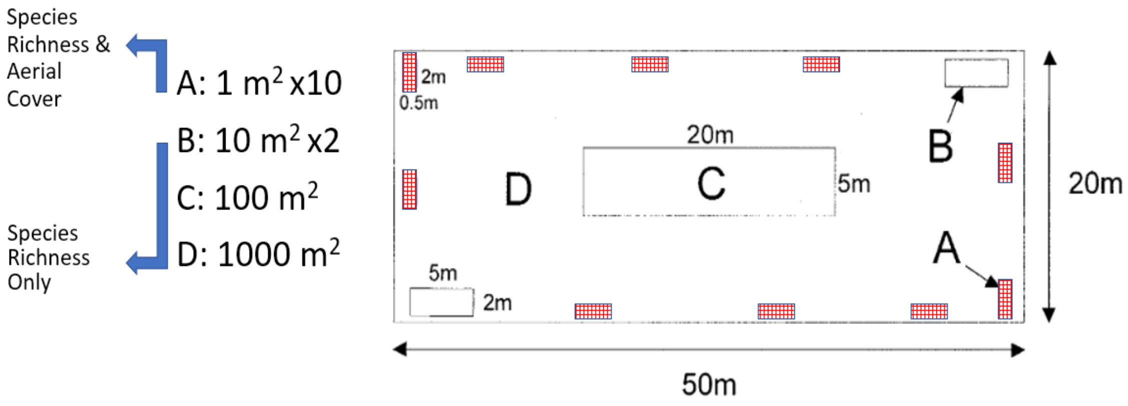

Figure 3. Boxplot comparison of raw species richness (left) and Simpson diversity (right) by treated vs. control plots. Neither comparison was significant.

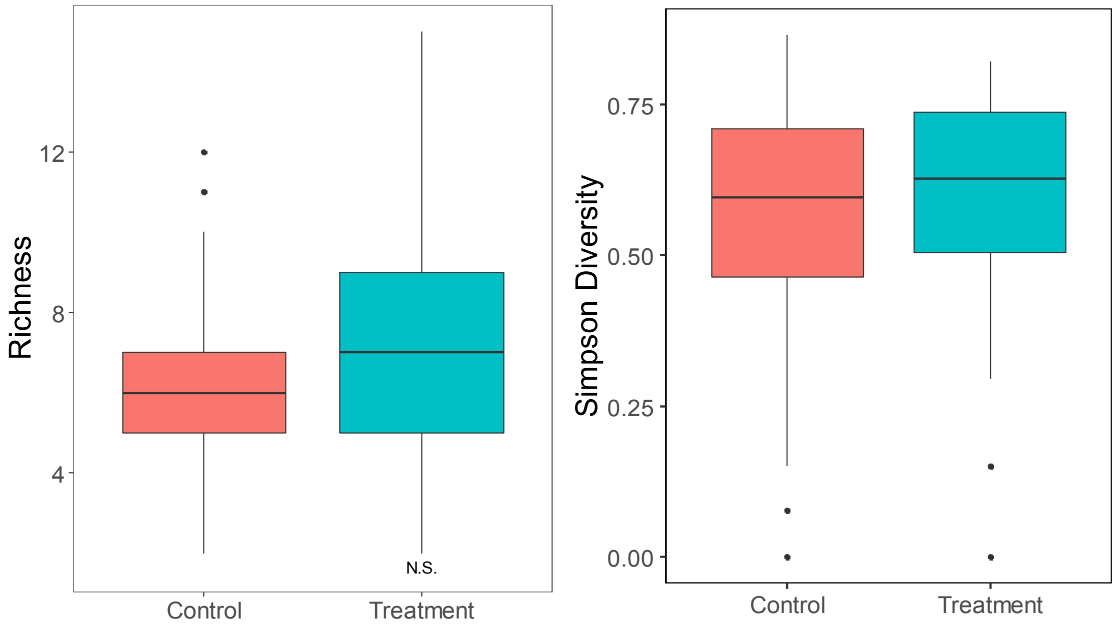

Figure 4. NMDS of functional composition in treated vs. control plots. Treated plots had significantly more native sedges than control plots, while control plots had significantly more native forbs, ferns, and shrubs.

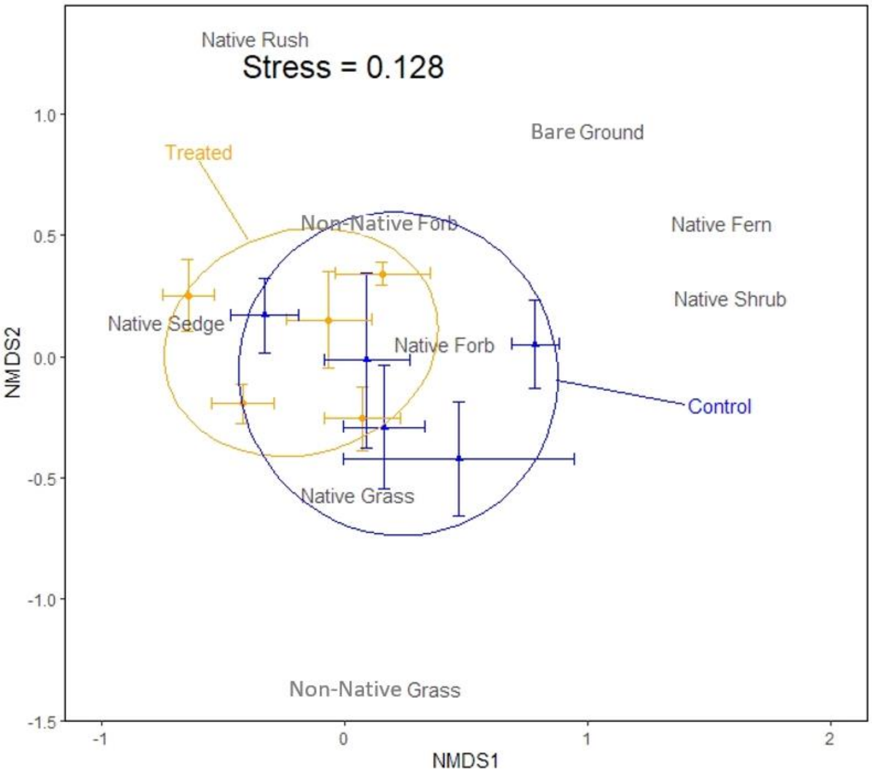

Figure 5. Boxplot comparison of response ratios of species richness and Simpson diversity by treatment intensity. The response ratio of Simpson diversity in Low plots (group A) was greater than in Moderate or High plots (group B); no other comparison of richness or diversity was significant.

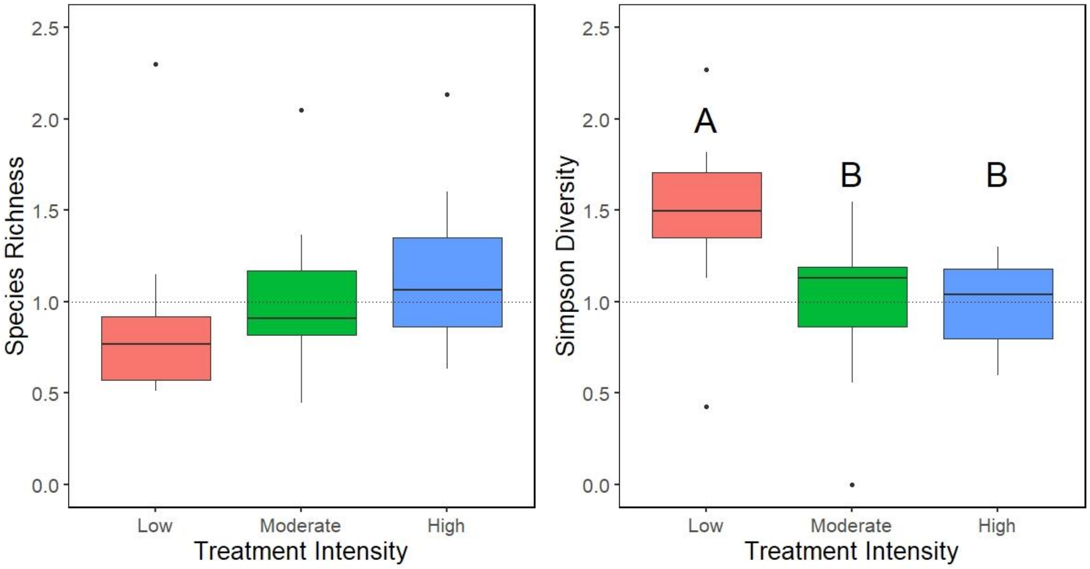

Figure 6. NMDS of functional composition by treatment intensity. There was no significant relationship between varying levels of treatment intensity and functional composition.

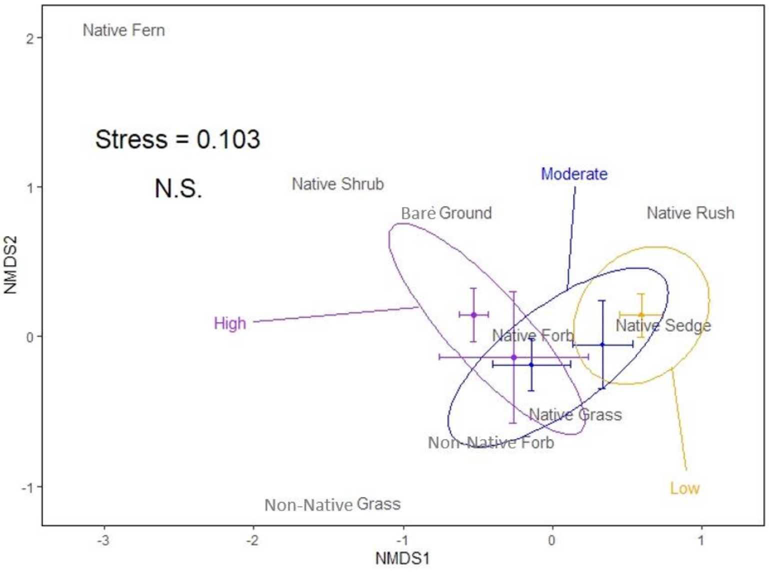

Table 1. One-sample t-test of Velvetgrass stem count responses.

Response Ratio	***t***	***DF***	***p***
Velvetgrass Population	*4.276*	*4*	***<0.001***

Table 2. Models of raw species richness, Simpson diversity, and non-native cover by treatment/control.

Linear Mixed Effects	***DF***	***F***	***p***
Species Richness	*1*	*1.493*	*0.225*
Kruskal-Wallis Test	***DF***	χ^2	***p***
Simpson Diversity	*1*	*0.605*	*0.437*
Non-native cover	*1*	*1.491*	*0.222*

Table 3. Summary of PERMANOVA of plant community functional composition by treatment/control.

Comparison	***DF***	R^2	***F***	***p***
Treated/Control	*1*	*0.047*	*4.372*	***0.001***

Table 4. Kruskal-Wallis Test of response ratios of species richness, Simpson diversity, and non-native plant cover by treatment intensity.

Kruskal-Wallis Test	***DF***	χ^2	***p***
Species Richness	*2*	*4.276*	*0.118*
Simpson Diversity	*2*	*11.003*	***0.004***
Non-native cover	*2*	*7.820*	***0.020***

Table 5. Dunn's (post-hoc) tests of response ratios of Simpson diversity and non-native cover by treatment intensity.

	Simpson Diversity		***Non-native Cover***	
Dunn's Test	***Z***	***p***	***Z***	***p***
High - Low	*-3.149*	***0.005***	*0.144*	*1.000*
High-Moderate	*-0.502*	*1.000*	*-2.422*	***0.046***
Low-Moderate	*0.006*	***0.018***	*-2.306*	***0.063***

Table 6. Summary statistics of PERMANOVA of plant community functional composition by treatment intensity category.

Comparison	*DF*	R^2	*F*	*p*
Treatment Intensity	*2*	*0.189*	*4.392*	*1*

Supplementary Tables

S1. Species List

Species	Life Form	Origin	Duration
Chenopodium album	Forb	Non-native	Annual
Marchantia polymorpha	Forb	Non-native	Annual
Potentilla norvegica ssp. monspeliensis	Forb	Non-native	Perennial
Taraxacum officinale	Forb	Non-native	Perennial
Agrostis capillaris	Grass	Non-native	Perennial
Bromus inermis	Grass	Non-native	Perennial
Elymus repens	Grass	Non-native	Perennial
Holcus lanatus	Grass	Non-native	Perennial
Athyrium filixfemina	Fern	Native	Perennial
Pteridium aquilinum	Fern	Native	Perennial
Achillea millefolium	Forb	Native	Perennial
Acmispon strigosus	Forb	Native	Annual
Agoseris glauca	Forb	Native	Perennial
Allium validum	Forb	Native	Perennial
Angelica lineariloba	Forb	Native	Perennial
Artemisia douglasiana	Forb	Native	Perennial
Barbarea orthoceras	Forb	Native	Perennial
Cardamine breweri	Forb	Native	Perennial
Cirsium scariosum	Forb	Native	Perennial
Clarkia biloba	Forb	Native	Annual
ClaytoniaPalustris	Forb	Native	Perennial
Diplacus brevipes	Forb	Native	Annual
Equisetum laevigatum	Forb	Native	Annual
Equisitum arvense	Forb	Native	Perennial
Erigeron breweri	Forb	Native	Perennial
Erigeron coulteri	Forb	Native	Perennial

Erigeron eatonii	Forb	Native	Perennial
Fragaria vesca	Forb	Native	Perennial
Galium trifidum	Forb	Native	Perennial
Gayophytum diffusum	Forb	Native	Annual
Geranium californicum	Forb	Native	Perennial
Geranium carolinianum	Forb	Native	Annual
Gnaphalium palustre	Forb	Native	Annual
Helenium bigelovii	Forb	Native	Perennial
Hosackia crassifolia	Forb	Native	Perennial
Hosackia nevadensis	Forb	Native	Perennial
Hosackia oblongifolia	Forb	Native	Perennial
Hypericum anagalloides	Forb	Native	Perennial
Iris missouriensis	Forb	Native	Perennial
Lepidium nitidum	Forb	Native	Annual
Lilium pardalinum	Forb	Native	Perennial
Lupinus albicaulus	Forb	Native	Perennial
Lupinus bicolor	Forb	Native	Perennial
Maianthemum stellatum	Forb	Native	Perennial
Mentha arvense	Forb	Native	Perennial
Montia fontana	Forb	Native	Annual
Oxypolis occidentalis	Forb	Native	Perennial
Packera pauciflora	Forb	Native	Perennial
Platanthera leucostachys	Forb	Native	Perennial
Prunella vulgaris	Forb	Native	Perennial
Senecio serra	Forb	Native	Perennial
Sisyrinchium bellum	Forb	Native	Perennial
Solidago spectabilis	Forb	Native	Perennial
Stachys albens	Forb	Native	Annual
Stellaria longipes	Forb	Native	Perennial

Symphotrichum spathulatum var. yosemiteanum	Forb	Native	Perennial
Trifolium longipes	Forb	Native	Perennial
Trifolium macrocephalum	Forb	Native	Annual
Trifolium variegatum	Forb	Native	Annual
Urtica dioica	Forb	Native	Perennial
Vicia americana	Forb	Native	Perennial
Vicia americana	Forb	Native	Perennial
Alopecurus aequalis	Grass	Native	Perennial
Bromus ciliatus	Grass	Native	Perennial
Deschampsia caespitosa	Grass	Native	Perennial
Elumus glaucus	Grass	Native	Perennial
Elymus sierrae	Grass	Native	Perennial
Elymus trachycaulus	Grass	Native	Perennial
Festuca rubra	Grass	Native	Perennial
Koeleria macrantha	Grass	Native	Perennial
Torreyochloa erecta	Grass	Native	Perennial
Juncus bufonius	Rush	Native	Annual
Juncus mertensianus	Rush	Native	Perennial
Juncus nevadensis	Rush	Native	Perennial
Scirpus congdonii	Rush	Native	Perennial
Carex capitata	Sedge	Native	Perennial
Carex lenticularis	Sedge	Native	Perennial
Carex nebraskensis	Sedge	Native	Perennial
Cornus nuttallii	Shrub	Native	Perennial
Linanthus pungens	Shrub	Native	Annual
Manzanita nevadensis	Shrub	Native	Perennial
Pinus jeffreyi	Shrub	Native	Perennial
Rosa woodsii	Shrub	Native	Perennial
Salix exigua	Shrub	Native	Perennial

Salix laevigata	Shrub	Native	Perennial
Abies concolor	Tree	Native	Perennial
Calocedrus decurrens	Tree	Native	Perennial
Pinus contorta	Tree	Native	Perennial
Populus trichocarpa	Tree	Native	Perennial

S2. Mean species richness and Simpson diversity raw values by treatment/control

	Species Richness	***Simpson Diversity***
Treated	*6.854±0.417*	*0.596±0.028*
Control	*6.320±0.303*	*0.558±0.029*

S3. Mean species richness and Simpson diversity response ratios by treatment intensity category

	Species Richness	***Simpson Diversity***
Low	*0.900±0.169*	*1.471±0.153*
Moderate	*1.139±0.175*	*1.017±0.090*
High	*1.166±0.104*	*1.003±0.058*

Afterword

Tens of billions of dollars in direct expenditures and other losses can be attributed to invasive plant species annually in the United States alone, not to mention the incalculable and permanent losses due to the extinction of native species. As global change factors like warming, eutrophication, land use change, and migrations accelerate, so too are plant invasions likely to expand and present new challenges. To face these challenges effectively, developing effective management techniques and strategies is of paramount importance. Well-intentioned efforts to conserve biodiversity and protect ecosystem services have produced costly unintended impacts in the past, but the legacy of these failures calls for increased research and cooperation between scientists and managers to test and develop new techniques. My research investigated contemporary issues of vegetation management that can help managers better tailor their monitoring and weed management strategies to achieve desired outcomes. These findings provide insights into how disturbance and invasion may interact to influence plant community composition, as well as how management responses may influence the trajectory of recovery. As the science of ecology continues to develop, translating theoretical advances to more effective conservation strategies is critical to conserve biodiversity in a rapidly changing world. Ecological theory has propelled us towards an ever-deeper understanding of the natural world; our task now is to protect it.

It is my pleasure to submit this dissertation in partial fulfillment of the requirements for the Doctorate of Philosophy in Plant Biology.