THESIS

MULLEIN IT OVER: AN EXAMINATION OF THE IMPACTS OF COMMON MULLEIN

(*VERBASCUM THAPSUS*) INVASION AND MANAGEMENT

Submitted by

Peter Leipzig-Scott

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Master's Committee:

    Advisor: Ruth Hufbauer

    Dana Blumenthal
    Matt Wallenstein

ABSTRACT

MULLEIN IT OVER: AN EXAMINATION OF THE IMPACTS OF COMMON MULLEIN

(*VERBASCUM THAPSUS*) INVASION AND MANAGEMENT

Biological invasion is one of the most important problems facing modern ecologists, and while research has shown the detrimental effects caused by many invasive species, the impact of the majority of invaders in largely unknown. I investigated the effects of the ubiquitous exotic plant species common mullein (*Verbascum thapsus*) on plant communities in northern Colorado. Additionally, I studied the impact of a second common invasive species, cheatgrass (*Bromus tectorum*), and examined its interactions with mullein. I conducted a field experiment over two years, manipulating mullein and cheatgrass presence at two sites, either removing the aboveground biomass of one or both of the exotic plants, or leaving them intact. I measured a number of plant community and abiotic characteristics as responses to these treatments.

I found that mullein invasion has few negative impacts, and that the benefits associated with management are lost within a year. Removal of mullein acts as a disturbance, creating physical and ecological openings for cheatgrass and other exotics to occupy. Percent cover of exotic species was highest when mullein was removed and cheatgrass was left intact. Since cheatgrass invasion is associated with undesired changes in the community, I suggest that resources should be used for its management rather than the management of mullein, and that mullein removal in areas with cheatgrass should be accompanied by an aggressive strategy addressing cheatgrass invasion.

ACKNOWLEDGMENTS

DEDICATION

This research is dedicated to my grandfather, Arthur Leipzig, who taught me to take risks and follow my passion. Thank you grandpa.

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CHAPTER 1: MULLEIN IMPACT AT SMALL PLOT AND INDIVIDUAL SCALES

Introduction

Biological invasion is one of the greatest ecological problems facing our planet today. In the United States, invasions are second only to land-use change in threatening rare species to the point of being listed as 'endangered' (Levine et al. 2003). Despite their importance, actually quantifying the total impacts of invaders is difficult. Parker *et al.* (1999) suggested the formula *Impacts = R x A x E*; where *R* represents the size of the invader's range, *A* the average abundance per area unit, and *E* the effect per individual or unit of biomass. While range and abundance are potentially straightforward to measure, determining the effect of each individual is challenging.

Due to the difficulties faced when calculating an invader's effects, there are a number of important gaps in our knowledge regarding the impacts of invasion. One of the largest issues is the inability of ecologists to make broad statements about the impacts of invasive species, even within a taxonomic subset such as invasive plants. Meta-analyses of data on impacts have shown that invasive plants vary in both the direction and magnitude of their impacts (Vilà et al. 2011) and that there is no single measure of impact for plant invasions (Pyšek et al. 2012). This is due to the fact that the effects of plant invasion, as well as invasion by other exotic species, are highly context dependent (Pyšek et al. 2012). For example, the impacts of invasion vary greatly across spatial scales, with effects most visible on a small scale (Powell et al. 2011). Our inability to make broad statements about the effects of invasion, combined with varying interpretations of known impacts of specific invaders, has lead to an ongoing debate over how exotic species affect native ecosystems.

How do introduced species change native ecosystems?

There are two main perspectives regarding how introduced species affect their new ecosystems and, correspondingly, how we should manage them. The first viewpoint is that species invasions are not a significant problem and are given too much attention relative to the threat that they pose (Sagoff 2005, Thomas and Palmer 2015). The opposing perspective is that invasive species are an important and imminent global ecological threat that we need to aggressively address (Simberloff 2005).

A key component of the first is that there is insufficient data documenting invasions as a cause of native species extinction (Gurevitch and Padilla 2004, Sagoff 2005). Where invasions are correlated with extinction, the actual driver of extinction may be some other factor, such as habitat degradation (Gurevitch and Padilla 2004). Additionally, invasive species may be the passengers of ecological changes, rather than the primary cause (Didham et al. 2005). Habitat change could be the true cause of extinction, but also act as a disturbance that increases invasive richness and abundance. A final component of this perspective is that invaders increase total species richness, which benefits the ecosystem (Sagoff 2005). This concept is based on research that has shown a variety of positive effects of increased richness, such as greater net primary productivity and nutrient retention (Hooper and Vitousek 1997), as well as increased ecosystem stability (McCann 2000).

The alternative perspective, that invasive species cause ecological harm and should be controlled, includes the argument that there is a direct connection between invasion and extinction (Clavero and García-Berthou 2005). Extinction is just the last stage of impact from invasion and is less obvious and well-understood than the previous impacts (Clavero and García-Berthou 2005). More common than extinction, the major impacts of invasion may be large

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changes in population size and range (Simberloff 2005). Finally, even if invasion does lead to increased local richness and diversity, it is associated with decreased global diversity (Simberloff 2005). This could lead to the same species in communities around the world, resulting in increased biotic homogeneity.

Known effects of introduced plants

To help address these opposing hypotheses and our gaps in understanding, there is a growing body of research conducted on the impacts of a few invaders, particularly plant species (Hulme et al. 2013). Most studies examine one or a few types of impacts an invasive plant might have (e.g. Bartomeus et al. 2008), while few have looked at a wide array of potential effects stemming from a single invader (Hulme et al. 2013). Together, though, these papers provide a general view of the impacts of invasive plant species.

The most common effects of plant invasions are a reduction in native diversity of the invaded community, linked to increased production of biomass (Vilà et al. 2011). Additionally, the presence of invasive plants is associated with decreased species richness, abundance and local diversity, which in turn leads to increased biotic homogenization (Pyšek et al. 2012). Although there are negative effects of invasion on plant species and communities, there can be positive effects on soil biota richness and abundance, as well as on soil nutrient and water content (Pyšek et al. 2012).

In addition to the community level effects introduced plants can have in their new systems, there are a number of other ways an exotic plant can impact its invaded range. Cheatgrass (*Bromus tectorum*) can alter its soil's biotic and abiotic components (Belnap and Phillips 2001). Cheatgrass invasion is associated with increases in both the amount of ground

litter and the levels of silt, which in turn leads to increased soil fertility as well as a greater capacity to retain water (Belnap and Phillips 2001).

Exotic plants are capable of altering energy and nutrient pools and flows throughout invaded ecosystems (Christian and Wilson 1999). One of the most studied nutrients affected by invasive plants is nitrogen. An invader's specific biology can greatly change how it alters nitrogen levels in the soil, with nitrogen fixing plants having a greater impact on N-cycling (Vilà et al. 2011). While some invasive plants, such as cheatgrass, are associated with increases in nitrogen levels (Evans et al. 2001, Booth et al. 2003), others can decrease soil nitrogen (Hook et al. 2004).

Introduced plants can impact pollinators and their relationships with native plant species. Animal pollinated species, regardless of native status, commonly compete for pollinator services (Robertson 1895). Introduced plants often have longer flowering times (Robertson 1895), making them capable of attracting more diverse pollinators at greater numbers. Showy exotic plants can greatly impact the established relationships between native plants and pollinators (Brown et al. 2002, Muñoz and Cavieres 2008).

The impact of an invasive plant on the native pollination relationship greatly depends on the density of the invader (Muñoz and Cavieres 2008). At high densities, exotic plants can have negative impacts on the native community by decreasing pollinator visitation and native seed output (Muñoz and Cavieres 2008). However, at low densities, the exotic plant may attract and share pollinators that would not have visited the patch of vegetation otherwise (Muñoz and Cavieres 2008).

Outside of the effects that a single invasive species may have, invaders can potentially make the impacts of subsequent invasions, from other exotics, that much greater (Maron and

Marler 2008). This synergistic relationship, that sometimes occurs between multiple invaders in a single range, was described by Simberloff and Von Holle (1999) as an 'invasional meltdown'. This term also describes the ability of invaders to aid in the colonization by other exotics and has been demonstrated in a number of systems (e.g. Meza-Lopez & Siemann 2015; Ness et al. 2013).

Unintended effects of control

In addition to the known effects of plant invasion, a subset of invasive plant research has focused on the impacts of control measures. Invasive plant control covers a wide range of methods, but the most common practices are herbicide application and cutting, followed by burning and hand pulling (Kettenring and Adams 2011). Control programs are usually implemented in an attempt to manage the effects of invasive plants, but these practices can have unintended negative ecosystem impacts (e.g. Ortega & Pearson 2011; Rinella et al. 2009).

Depending on the method of control, management treatments can directly harm non-target native plant species (Ortega and Pearson 2011). Additionally, control practices can lead to decreased competition and increased resource availability (Kettenring and Adams 2011), allowing for the target species to eventually return or for a secondary plant invader to increase its presence (Sheley et al. 2006, Ortega and Pearson 2010). These negative effects of control treatments are often dependent on the density of the target species, with the most deleterious impacts occurring when the species is initially at low densities (Ortega and Pearson 2011). Due to the potentially harmful effects of invasive species management, as well as the high financial costs often associated with its implementation, refraining from control can be seen as a viable alternative (Ewel & Putz 2004).

How can we generalize about the effects of plant invasion and management?

As shown by the breadth of the studies described above, invasive species are as diverse as their native counterparts; therefore it becomes difficult to make broad statements regarding the effects of invasion. A number of papers have broadcasted a call for further research in the area of invasive species impacts, asking for more long-term studies (Blossey 1999, Skurski 2012), as well as the examination of impacts at multiple spatial scales (Parker et al. 1999).

One potential strategy for understanding how invasive plants, as a whole, affect communities is to study many different invaders across a wide range of ecosystems. By investigating a diverse set of invaders and systems, it may be possible to determine general trends in the impacts of plant invaders. The Global Invader Impact Network (GIIN) is using this strategy through collaboration between researchers around the world, measuring a broad array of quantifiable impacts of invaders in different ranges (Barney et al. *In Press*). This coordinated distributed approach to data collection is particularly important, as the effects of invasive species have seldom been examined across a spectrum of physically varying ecosystems (Hook et al. 2004).

Using the framework provided by the GIIN, I sought to answer the following questions regarding plant invasion and its impacts: 1) what effects does invasion have on the plant community? ; 2) does invasive plant management, in the form of mechanical removal, remediate these effects? ; and 3) how do the effects vary between the individual plant and small plot scales? To answer these questions, I studied the impacts of common mullein (*Verbascum thapsus*) in northern Colorado following the GIIN experimental protocol.

Methods

Study System

Common mullein, hereafter referred to as mullein, is an exotic biennial found throughout the United States and much of Canada (USDA 2014). It is a federally listed noxious weed and a Class C noxious weed in Colorado, meaning that management is often considered necessary (USDA 2014). Current control practices involve removing inflorescences and disposing of seeds (Wilbur and Hufbauer 2012). This is a time intensive method, requiring a substantial effort on the part of managers.

Mullein has been the subject of a number of studies but few have examined its impacts. It is known, however, to be one of the most pervasive invaders in Colorado. Alba and Hufbauer (2012) found that mullein densities were much higher for populations within its invaded range (including Colorado) than for those within its native range. After fire, mullein can dominate plant communities, becoming the most widespread exotic plant in burned areas (Fornwalt et al. 2010). This high level of post-fire invasion makes understanding the impacts of mullein invasion and management a clear priority, particularly in states facing recurrent wildfires, which may increase in frequency or severity with global change (Scholze et al. 2006).

In addition to mullein's connection to wildfire disturbances, it is of particular interest due to its biennial lifecycle. The impacts of short-lived invasive plants are generally less well known than their perennial counterparts, but research has lead to several conclusions regarding their success as invaders. For short-lived plants, invasion success is closely related to plant height (Fenesi and Botta-Dukát 2010). Taller plants, such as mullein in its second year stage, are able to better compete for light and attract animal seed dispersers and pollinators (Fenesi and Botta-Dukát 2010). Additionally, short-lived plants are the most successful invasive plants in areas that

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have been anthropogenically disturbed (Fenesi and Botta-Dukát 2010, Golivets 2013). Due to the fact that we are currently living within the Anthropocene, a period defined by the dominant influence of human disturbances on the environment (Crutzen 2002), understanding the impacts of short-lived invaders is crucial.

GIIN Small Plot Study

I conducted a field experiment, over the course of the 2013 (year 1) and 2014 (year 2) summers, based on the framework laid out by the GIIN (Barney et al. *In Press*). I collected data on plant and soil community characteristics, within two populations of mullein in the context of invaded and removal treatments in one by one meter plots (Figure 1). Invaded plots were used to observe how mullein changes its environment and removal plots were meant to demonstrate the impacts of mullein management. Invaded and removal plots were spatially paired and placed within the mullein population. Plot location was selected so that there were approximately equal densities of mullein within the two paired adjacent plots, and treatment was assigned randomly. I recorded the number of mullein individuals in each plot prior to treatment being implemented. I left invaded plots entirely un-manipulated. In removal plots, I removed all mullein individuals by cutting the taproots and removing their aboveground biomass from the plot.

I established the plots in early May 2013 at two sites along Colorado's Front Range, one in the Larimer County Devil's Backbone Open Space (40.47505, -105.1551) and a second in the Nature Conservancy's Phantom Canyon Preserve (40.86145, -105.3168). Treatments were replicated 10 times at each site, totaling 40 plots. In year 2 I observed a >3 fold increase in cheatgrass cover at Devil's Backbone, (growing from 9.6% in year 1 to 34.8% in year 2). These densities seemed likely to mask the effects of the experimental mullein removals. Thus, to examine the effects of cheatgrass invasion, as well as possible interactions with the mullein

manipulation, I used half of the invaded and removal pairs at Devil's Backbone in a second experiment in which I manipulated cheatgrass (see Chapter 2), leaving a total of 10 plots at that site in year 2.

Within each plot, I measured plant species cover, observing what percentage of the plot's canopy was made up of each plant species. I also surveyed native and exotic species richness and percent bare ground and litter cover. In addition to these plant community characteristics, I measured photosynthetically active radiation (PAR) by taking three sets of above- and below-canopy readings at each plot (Model AccuPAR LP-80). This allowed me to calculate the percent transmittance of light passing through the plant cover within plots.

I measured in-situ volumetric water content of the soil, taking three readings at random locations within each plot (Model TRIME-PICO 64). In addition to moisture measurements, I collected soil samples with a 1" diameter soil probe. I gathered five samples from each plot to a depth of 10 centimeters and all samples from a single plot were combined and homogenized. These soil samples were used to determine soil pH, total organic matter, and nutrient levels. The Virginia Tech Soil Laboratory, in accordance with the GIIN protocol, analyzed soil samples. My methods for data collection were the same for both years.

Individual Mullein Removal

In year 2 I further examined the effects of removing mullein, this time at the scale of individual plants. I selected 40 individual first year mullein rosettes at Devil's Backbone, all with a rosette diameter of at least twenty centimeters, and randomly chose half from which I removed the aboveground biomass. At the time of peak-growth (approximately mid-July), I surveyed ground cover at the location of all individuals, including percent-cover for individual species, bare ground, and litter. Where mullein had been removed, I recorded percent cover for an area

with a diameter of twenty centimeters, centered on where the mullein had been cut. Where mullein was left intact, I recorded plant cover below the mullein leaves, within an area with a diameter of twenty centimeters centered on the mullein. I categorized all of the species based on their native status and whether they were grasses or forbs. Unfortunately, by the time of peak-growth, a large number of plant markers were lost or destroyed, leaving a total of ten removed and nineteen intact individuals.

Statistical Analyses

To analyze the data from the small plot study, I ran a mixed model in JMP, using treatment, year, site and initial mullein as fixed effects, as well as an interaction between year and treatment. Initial mullein represented the number of mullein individuals in a plot prior to a treatment being applied. The model also incorporated plot pair and an interaction between plot pair and treatment as random effects. Plot pair was used to account for the spatial pairing of invaded and removal plots. I combined the data from both sites because, although there was a significant effect of site on a number of responses, there were no biologically significant interactions between site and treatment (analysis not shown).

I analyzed the data from the individual mullein removals using a fixed effect model with treatment and original diameter as effects, along with an interaction between the two. Treatment was either 'removed' or 'intact' and original diameter reflected the size of the mullein rosette at the start of the season before treatments were imposed.

For the small plot study, both total and exotic species richness excluded mullein in their counts, allowing me to control for the fact that, by definition, invaded plots had one more exotic species than removal plots. I transformed all percent cover data using an arcsine transformation. I used the raw percent cover data to calculate Shannon-Weiner Diversity scores for all plots using

both exotic and native species, as well as only native species. Diversity scores excluded mullein and were calculated using the formula:

$$H = -Sum[(\text{pi}) \times \ln(\text{pi})]$$

Where pi= percent cover of species i/ total cover

Results

Small plot study

Native and exotic species richness, native plant cover, species diversity, percent bare ground, and soil moisture varied based on year, site, or initial mullein, but were not affected by treatment (Table 1). In contrast, total and exotic plant covers were significantly affected by an interaction between treatment and year (P=0.001 and P=0.0003, respectively, Figure 2). Both responses initially dropped with the removal of mullein in year 1, but by year 2 exotic and total covers in removal plots had returned to invaded plot levels (Table 1). Litter cover was also affected by the interaction between treatment and year (P=0.002), with mullein removal being associated with increased litter in year 1, but equal litter by year 2 (Table 1).

While total species diversity showed no effect of treatment, native species diversity was affected by the interaction between year and treatment (P=0.04, Figure 3). In year 1, native diversity was equal across both treatments, but by year 2 removal plots had lower native diversity, although this intra-annual difference was not statistically significant (Table 1, Figure 3).

Light transmittance was closely connected to plant cover data, with higher year 1 transmittance in removal plots than in invaded plots but no significant effect of treatment in year 2 (P=0.04, Table 1, Figure 4). There was no effect of treatment or the interaction between treatment and year on any of the soil characteristics that I analyzed (analysis not shown).

Individual Removal

Total species richness was higher when mullein individuals were removed than when they were left intact (P=0.01, Table 2). This reflected an increase in exotic richness with removal (P=0.01, Figure 5). Plant cover was unaffected by mullein manipulation or the original diameter of the rosette (Table 2).

Total Shannon-Weiner Diversity scores were higher with mullein removal (P=0.01, Figure 6) and lower with larger rosette diameters (P=0.03), but these trends were primarily driven by differences in exotic species diversity. Although there were no effects of mullein treatment or diameter on native and exotic grasses and forbs, the desirable native grass *Pascopyrum smithii* displayed a borderline significant effect of treatment (P=0.09). There was higher *Pascopyrum* cover when mullein was removed than when it was left intact.

Discussion

Small Plot Study

Removing mullein had immediate positive effects on the plant community at both sites, but many of these were no longer apparent a year later. For example, mullein removal reduced the cover of exotic species and total plant cover, while increasing light transmittance in the first year. By year two, however, transmittance levels and total plant cover were equal across treatments and exotic species cover was actually higher when mullein was removed.

In many cases the community and abiotic responses differed more between years than between treatments. It is likely that annual variation in weather plays a key role in plant community dynamics, as is common in arid environments (Snyder and Tartowski 2006). The fall and spring prior to the second season of data collection was much wetter than the one prior to the first season (NOAA 2015). In addition to annual differences in climate, I may have also been

examining two mullein populations at the tail end of their invasions. There was very little new colonization by mullein in the plots at either site, and even invaded plots lost 90% of their *Verbascum* cover over the course of the experiment (Figure 2).

Individual Removals

The results from my individual plant removal experiment revealed several important negative effects of mullein removal. When mullein was removed, rather than natives responding, exotic plants increased in abundance. This trend was also true when looking at native and exotic species diversity, with exotic diversity increasing with the removal of mullein.

Impact Across Spatial Scales

The overall neutral or positive effects of a plant invasion are not unique to mullein or this study. A review by Rodriguez (2006) found that exotic plant species are capable of facilitating native species in a number of ways. They can create novel habitats for natives, as exemplified by the aquatic plant *Hydrilla ventricillata* in the Chesapeake Bay. The invader increased the survival and growth of native clams by forming greater habitat complexity (Posey et al. 1993).. Invasive plants can also positively impact native species by adding to and diversifying the food source. Invasive plants in the Azores are the largest winter food source for the native bullfinch (Van Riel et al. 2000). Although I did not look at the effects of mullein on animals, these examples demonstrate that mullein is not alone in its potential to benefit native species.

Conclusion and Management Implications

Based on the results of both the small plot study and the individual removal experiment, mullein appears to have few negative impacts on the Colorado Front Range plant community. Management, in the form of removal, yields several short-term positive results, such as increased light transmittance and decreased exotic plant cover, but these potential benefits are quickly lost.

This may be linked to the fact that removal acts as a disturbance event. Removal of mullein creates spatial and ecological openings for colonization by other invaders, which are able to capitalize on the newly available resources more quickly than native species (Davis et al. 2000). By removing mullein, managers run the risk of a more detrimental exotic species, such as *Bromus tectorum*, invading or increasing in density (Figure 9).

Although the primary goal of invasive species management is often to increase the diversity and abundance of native species, removing a dominant invader can have unintended, negative consequences. The removal of a target invasive species leading to the increase in the presence of other exotics has been shown in a number of systems (Hulme and Bremner 2006, Courchamp et al. 2011). This effect of management can occur if the target species suppresses other invaders prior to its removal (Courchamp et al. 2011). Invasive species are often more capable than natives at capitalizing on the disturbance event when a removal takes place (Hulme and Bremner 2006). Through this mechanism, management of one invasive species, such as mullein, may lead to a greater abundance of other non-natives, therefore reducing the efficacy of control treatments.

When weighing the potential benefits of and problems caused by mullein management, it is clear that the resources necessary for removal can be allocated towards fighting an invader with a greater negative impact.

Future Research

As we continue to study the impacts of invasive species, and plants in particular, we need to consider which methodologies will be the most effective at explaining how species affect their new communities and systems. My experiments were replicated over space and one examined the entire life cycle of my study system, yet still, that represents a relatively short-time span (one

and two years). To fully understand the effects of invasion and management we need long-term

monitoring (Blossey 1999). This includes monitoring before and during invasion as well as

before, during and after control or management is implemented (Blossey 1999). Such an

approach would require careful planning on the part of managers and researchers, as well as the

ability to predict where an invasion is headed and begin monitoring early.

The establishment of long-term monitoring would allow researchers to effectively include

a non-invaded control treatment in their experiments. For my study, I originally included plots

that existed outside of and adjacent to the mullein populations, following the GIIN protocol.

These plots were meant to represent the community in a pre-invaded state, acting as a baseline to

which I could compare the other two treatments. Although there were differences between the

non-invaded and the invaded areas, including higher light transmittance, total species richness,

and native plant cover in the non-invaded area (analyses not shown), without previous long-term

monitoring, it was impossible to determine whether mullein was the cause. It was also unclear

why the control plots hadn't been invaded. The protocol assumed that the plots were suitable for

invasion, but that mullein hadn't reached them yet. Although this was possible, there was also

the strong probability that there were other spatial and ecological characteristics preventing or

slowing invasion. The addition of long-term monitoring to impact studies would allow

researchers to more confidently explain the effects of invasion.

In addition to long-term monitoring, removal experiments in natural communities, such

as the one conducted here, will be key in understanding the impacts of invasion and

management. These experiments are more useful than those performed in artificial systems, as

they allow me to examine the interactions between target species and the community (Díaz et al.

2003). Field experiments in which invaders are removed more realistically represent the effects of invasive species management on an actual ecosystem and community.
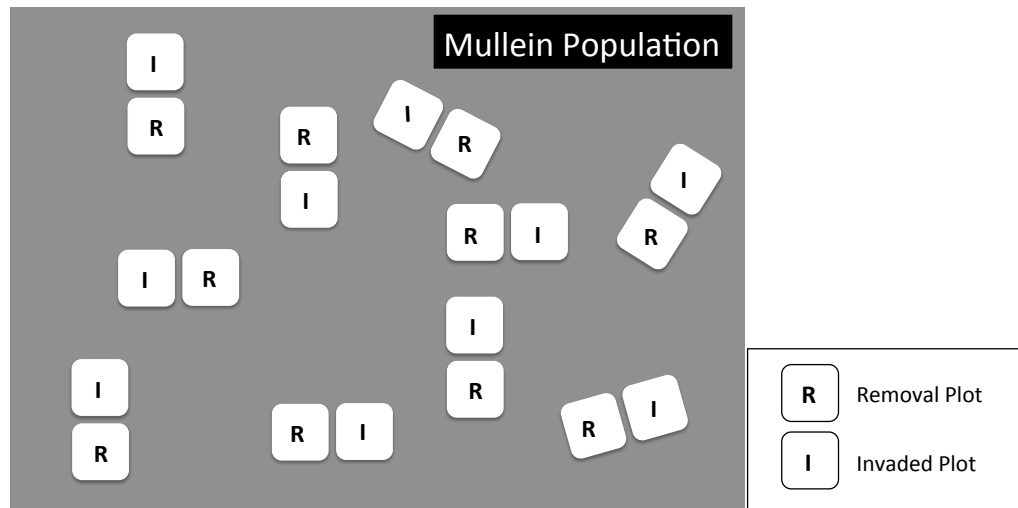
Figures

Figure 1. Schematic of site layout (not to scale). Each square represents a 1x1 meter plot. Invaded and removal plots were paired and randomly placed within a mullein population.
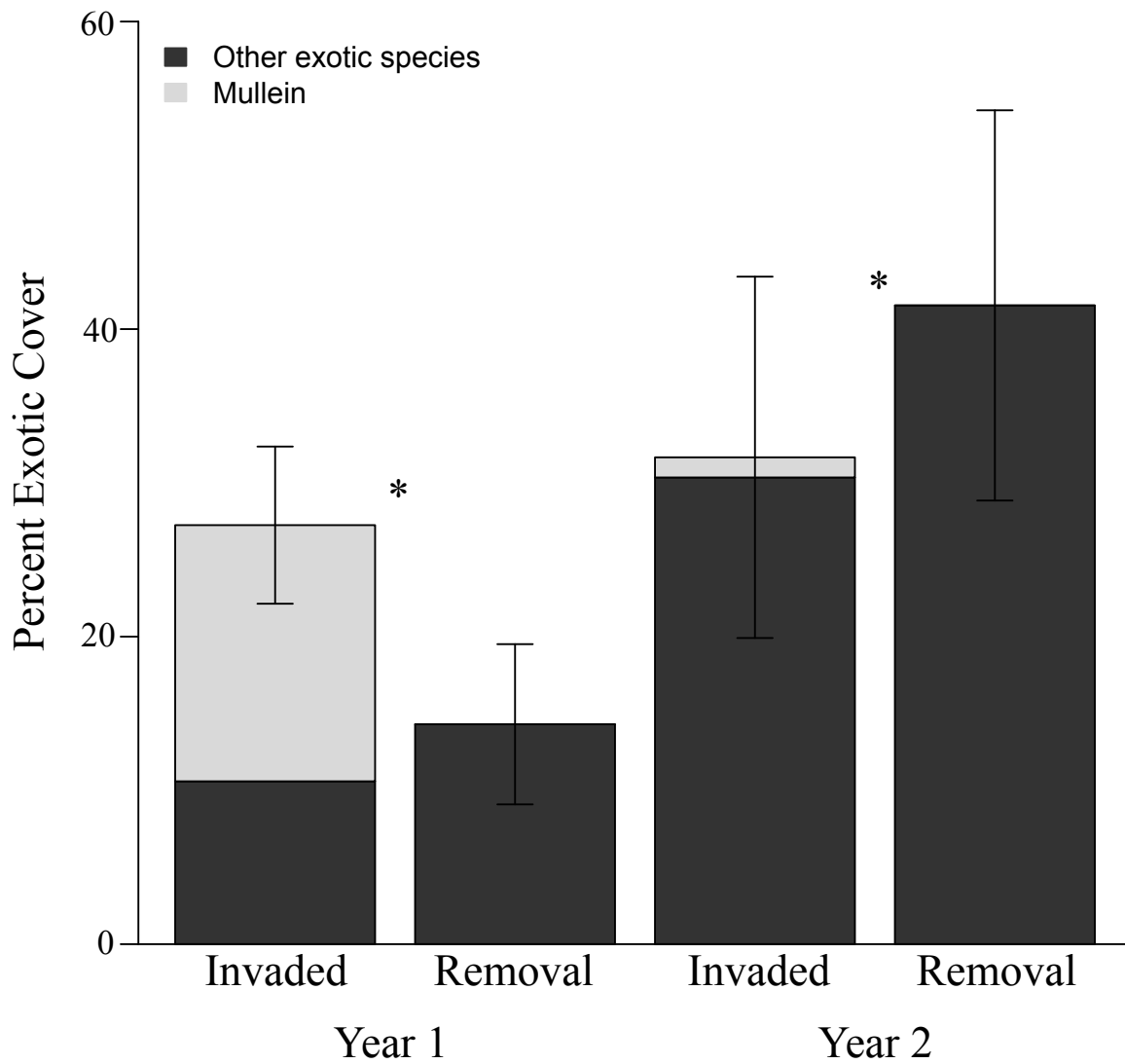
Figure 2. Effect of mullein treatment on percent exotic cover over two years. Values represent least-square means of arcsine-transformed percentages, with contributions from mullein separated from other exotic plant species. Error bars show 95% confidence intervals. Asterisks notate significant (*P*<0.05) differences between treatments in a given year.
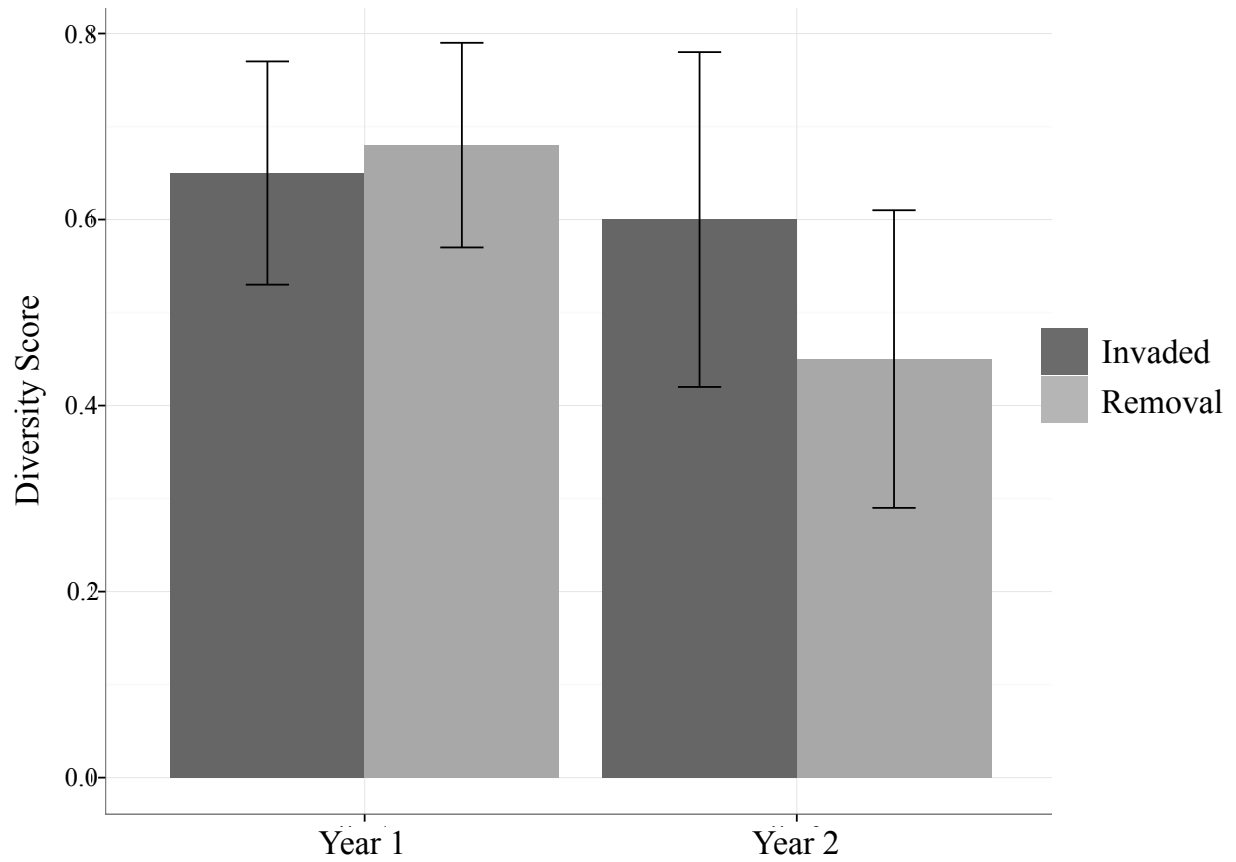
Figure 3. Effect of mullein treatment on native species diversity over two years. Values represent least-square means. Error bars show 95% confidence intervals.
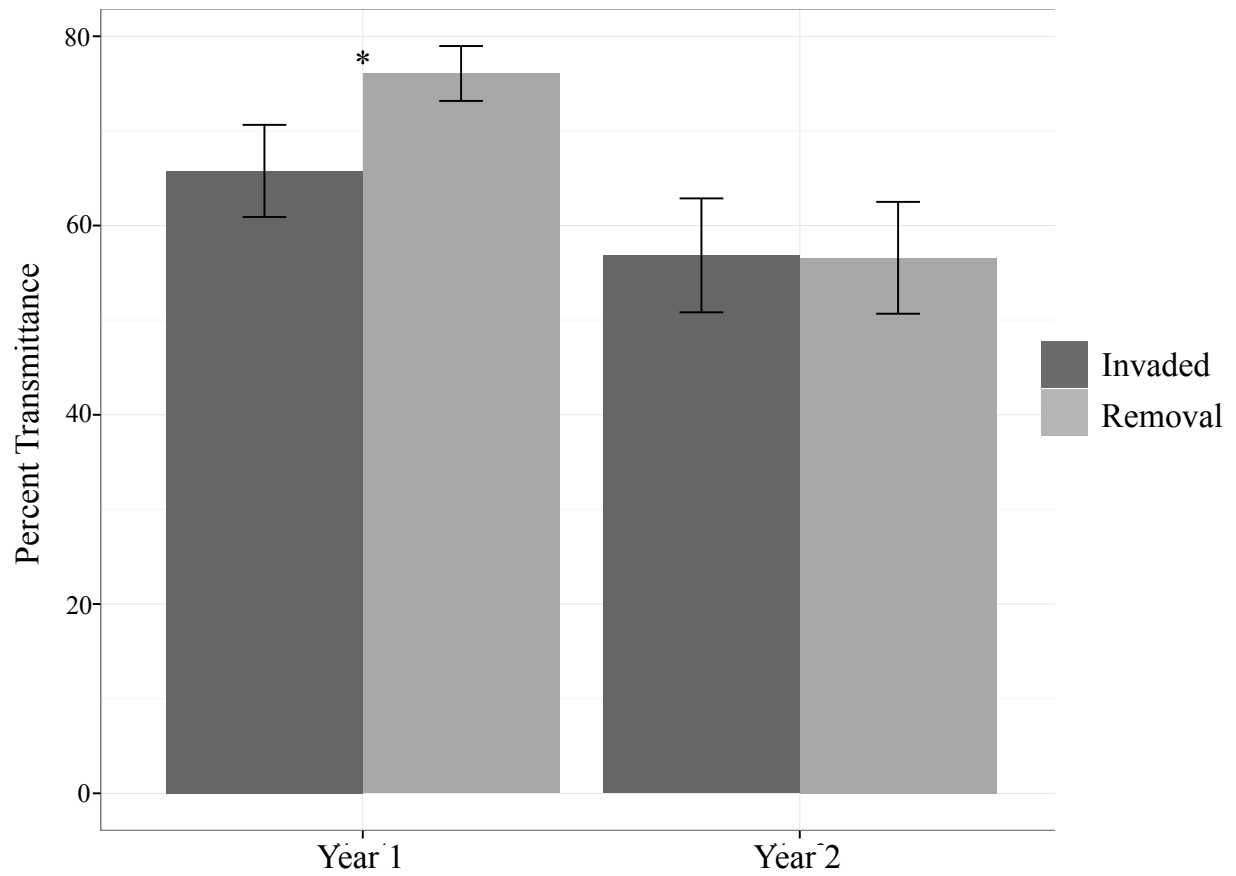
Figure 4. Effect of mullein treatment on light transmittance over two years. Values represent least-square means. Error bars show 95% confidence intervals. Asterisks notate significant (*P*<0.05) differences between treatments in a given year.

Figure 5. Native and exotic species richness directly below intact and removed mullein individuals. Values represent least-square means. Error bars show 95% confidence intervals. Asterisks notate significant ($P<0.05$) differences between treatments.
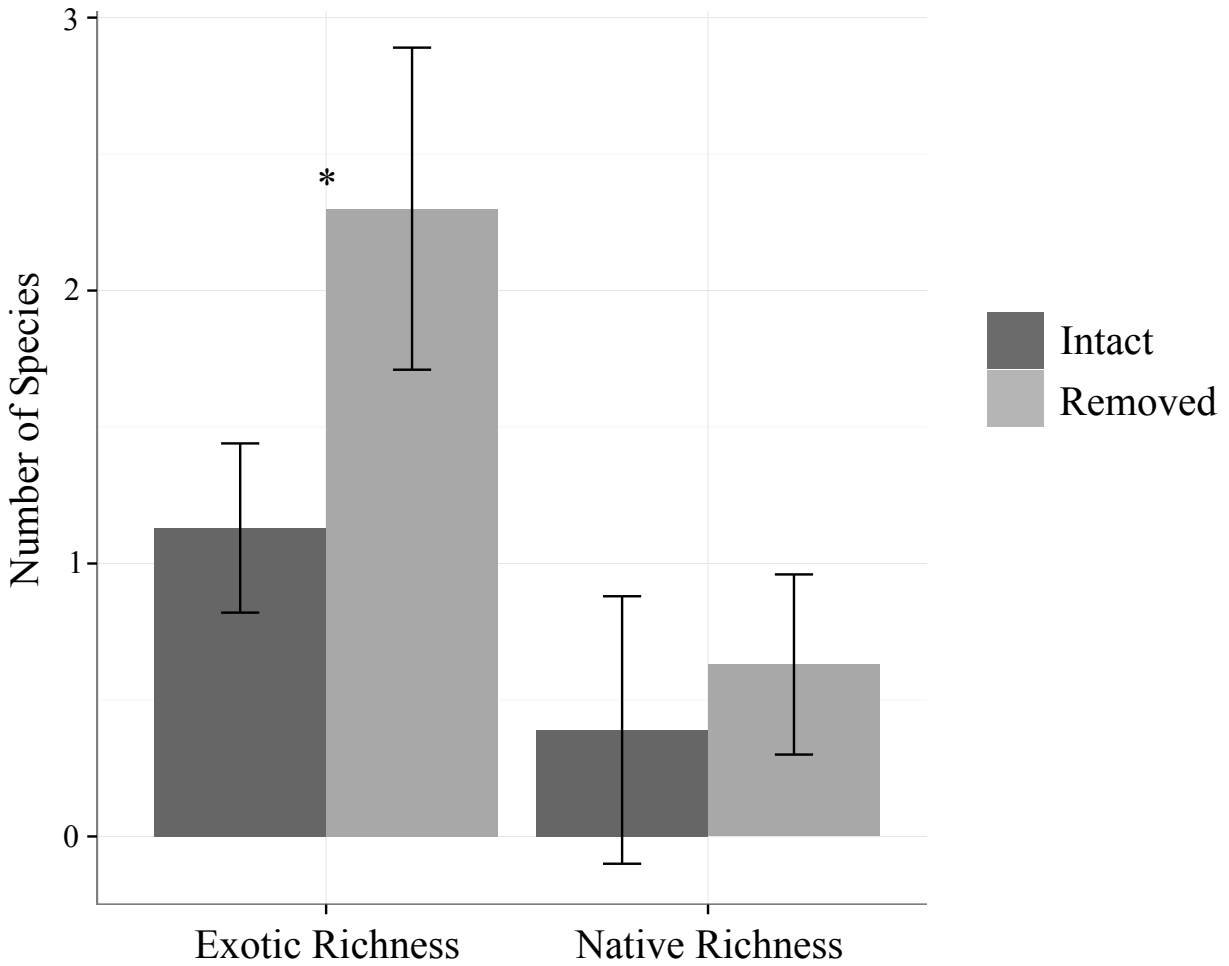
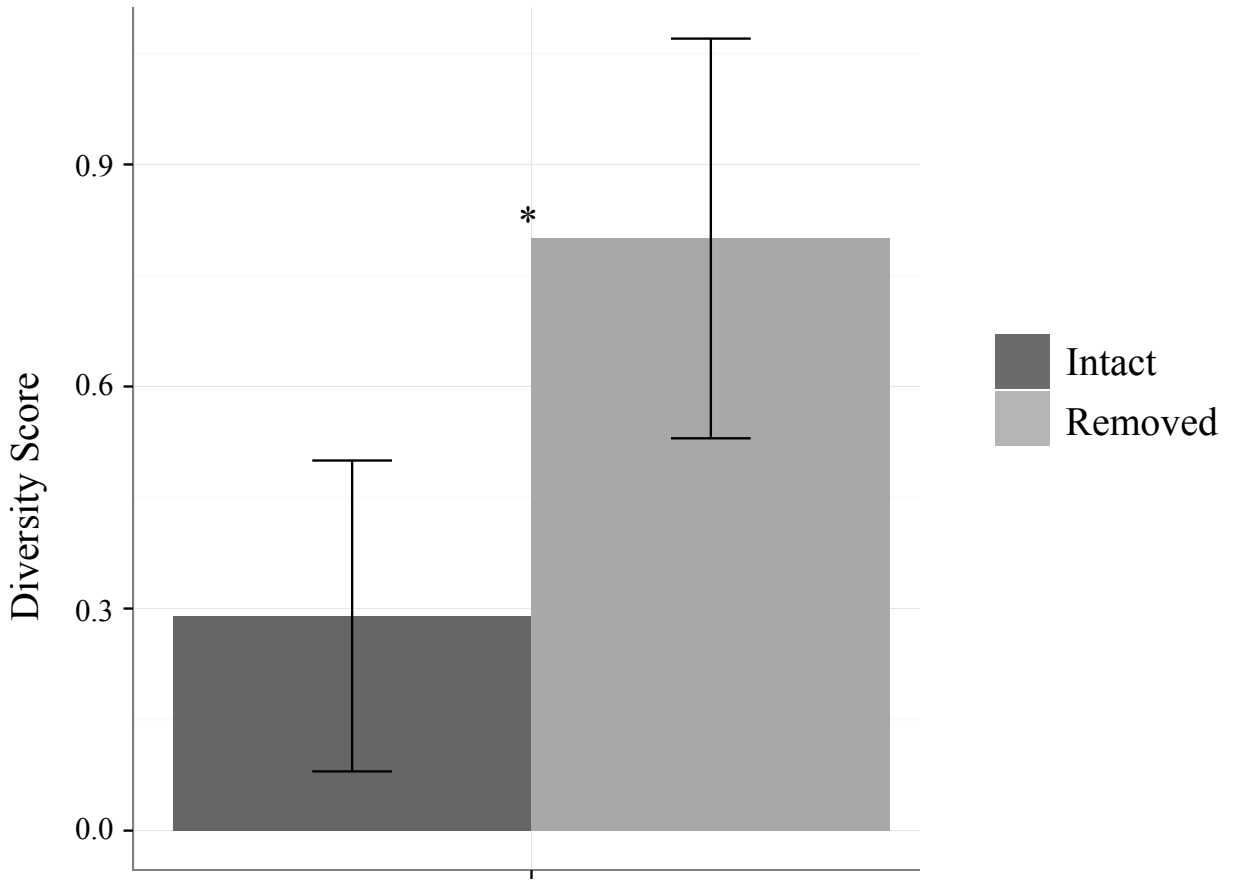Figure 6. Species diversity below intact and removed mullein individuals. Error bars show 95% confidence intervals. Asterisks notate significant (*P*<0.05) differences between treatments.

Tables

Table 1. Community and abiotic responses across both years and treatments. Values show least-square mean (+/- standard error). Bold text indicates significant ($P \leq 0.05$) differences between cheatgrass treatments.

Year	Year 1		Year 2	
Treatment	Invaded	Removal	Invaded	Removal
Species Richness	4.31 (+/-0.26)	4.81 (+/-0.27)	4.43 (+/-0.29)	5.12 (+/-
Native Species Richness	2.73 (+/-0.24)	2.53 (+/-0.25)	2.01 (+/-0.26)	1.83 (+/-
Exotic Species Richness	1.76 (+/-0.20)	1.98 (+/-0.21)	2.72 (+/-0.23)	2.80 (+/-
Total Percent Cover	**48.39 (+/-3.32)**	**36.27 (+/-3.42)**	52.99 (+/-3.74)	64.91 (+/-3.88)
Percent Native Cover	21.14 (+/-3.18)	19.55 (+/-8.3)	22.25 (+/-3.42)	17.98 (+/-3.38)
Percent Exotic Cover	**27.21 (+/-3.06)**	**13.86 (+/-3.18)**	**31.79 (+/-3.44)**	**41.08 (+/-3.44)**
Shannon-Weiner Diversity	1.18 (+/-0.07)	1.24 (+/-0.07)	1.16 (+/-0.08)	1.22 (+/-0.07)
Native Diversity	0.65 (+/-0.06)	0.68 (+/-0.07)	0.60 (+/-0.07)	0.45 (+/-0.07)
Litter Percent Cover	**48.90 (+/-3.12)**	**62.12 (+/-3.30)**	44.73 (+/-3.66)	37.06 (+/-3.66)
Percent Bare Ground	6.36 (+/-1.33)	7.70 (+/-1.38)	4.72 (+/-1.45)	6.40 (+/-1.44)
Percent Soil Moisture	5.15 (+/-0.88)	5.58 (+/-0.88)	12.62 (+/-0.90)	12.50 (+/-0.90)
Percent Light Transmittance	**65.77 (+/-2.29)**	**76.07 (+/-2.41)**	56.85 (+/-2.66)	56.85 (+/-2.68)

Table 2. Effect of mullein individual removal on community composition. Values show least-square mean (+/- standard error). Bold text indicates significant (*P*≤0.05) differences between cheatgrass treatments, italicized text indicates borderline significant (*P*≤0.1).

Mullein Treatment	Intact	Removed
Total Species Richness	**1.52 (+/-0.42)**	**2.93 (+/-0.29)**
Native Richness	0.39 (+/-0.24)	0.63 (+/-0.17)
Exotic Richness	**1.13 (+/-0.33)**	**2.30 (+/-0.23)**
Total Percent Cover	41.66 (+/-10.30)	60.71 (+/-7.15)
Native Percent Cover	10.73 (+/-4.65)	6.39 (+/-3.23)
Exotic Percent Cover	30.68 (+/-5.98)	24.08 (+/-4.15)
Shannon-Weiner Diversity	**0.29 (+/-0.15)**	**0.80 (+/-0.11)**
Native Diversity	0.03 (+/-0.06)	0.6 (+/-0.04)
Native Grass Percent Cover	9.89 (+/-3.8)	3.95 (+/-2.64)
Exotic Grass Percent Cover	25.84 (+/-5.9)	15.65 (+/-4.09)
Native Forb Percent Cover	0.70 (+/-1.5)	22.44 (+/-1.10)
Exotic Forb Percent Cover	4.57 (+/-2.96)	8.21 (+/-2.05)
Western Wheatgrass Percent Cover	*0.20 (+/-1.89)*	*4.05 (+/-1.02)*

CHAPTER 2: INTERACTION BETWEEN CHEATGRASS AND MULLEIN INVASION

Introduction

Cheatgrass (*Bromus tectorum*) is one of the most pervasive and highly managed exotic plants in the Western United States. This Eurasian winter annual is found on every continent except for Antarctica and is a highly successful invader throughout much of its range (Mealor et al. 2013). Cheatgrass has several characteristics that often allow it to dominate its invaded ecosystem. Like many invasive plants, it's capable of quickly colonizing areas where either soil or vegetation has been disturbed (Mealor et al. 2013). Additionally, as a winter annual, cheatgrass has a high growth rate in the winter and early spring, adding biomass before other species are actively growing, allowing it to outcompete many western natives plants for resources (Mealor et al. 2013). After cheatgrass completes its annual growth, its quickly dries out, providing fuel for wildfires (Stewart and Hull 1949). This creates a positive feedback loop, with cheatgrass invasion leading to a greater number of wildfires, which act as major disturbances, allowing the invader to colonize at denser levels.

As a dominant invader, cheatgrass can impact its new system in several key ways. For the reasons described previously, it is capable of outcompeting native plants and can often form monocultures, decreasing native plant cover (Belnap et al. 2005) and diminishing local biodiversity (Young and Allen 1997). By increasing the frequency of wildfires, cheatgrass further decreases native diversity and increases soil erosion (Whisenant 1990). Additionally, cheatgrass invasion has been found to increase nitrogen levels in its invaded range (Evans et al. 2001, Booth et al. 2003).

At the start of my second year studying the impacts of common mullein invasion, it became clear that cheatgrass had greatly increased in density and cover within the invaded area at Devil's Backbone Open Space (40.47505, -105.1551). Average cover had more than tripled, growing from 9.6% in 2013 to 34.8% in 2014. As a dominant invader with the potential for such large ecosystem impacts, there was the possibility of additive or synergistic effects with common mullein. Additionally, there was the strong probability that the impacts of mullein invasion and removal would be masked by the overwhelming presence of cheatgrass. I therefore decided to implement a second field experiment, manipulating cheatgrass within my small study plots at Devil's Backbone. My primary research question was: Is there an interaction between mullein and cheatgrass invasion and management?

Methods

Cheatgrass Manipulation

For my experiment comparing the relative and additive impacts of cheatgrass and common mullein, I used plots that had originally been established at Devil's Backbone as part of my small plot study (see Chapter 1). In 2013 I established 20 1x1 meter plots within a mullein population, imposing two treatments: invaded and removal Invaded plots were un-manipulated, while in removal plots I eliminated all mullein by cutting the taproots of individuals and removing their aboveground biomass from the plot. Invaded and removal plots were spatially paired. Plot location was selected so that initially there were similar densities of mullein within the two paired adjacent plots and treatment was assigned randomly.

In early June 2014, I randomly selected 5 pairs of invaded and removal plots and used scissors to remove all aboveground cheatgrass. These removals created 4 different treatments, crossing plots with and without mullein with those that had or did not have cheatgrass.

In mid-July, 2014 I measured plant species cover, native and exotic species richness, and percent bare ground and litter cover. I also measured photosynthetically active radiation (PAR) by taking three sets of above- and below-canopy readings at each plot. I then calculated the percent transmittance of light passing through plant cover within the plots.

I measured in-situ volumetric water content of the soil, taking three readings within each plot. In addition to moisture measurements, I also collected soil samples with a 1" diameter soil probe. I gathered five samples from each plot to a depth of 10cm and all samples from a single plot were combined and homogenized. These soil samples were used to determine soil pH, conductivity, total organic content, and nutrient levels. Soil samples were analyzed by the Virginia Tech Soil Laboratory, as part of the Global Invaders Impact Network (Barney et al. *In Press*).

Statistical Analyses

I evaluated the effects of invader removal on the plant community, light transmittance, and soil properties using cheatgrass treatment (removed or intact) and mullein treatment (removed or intact) as fixed effects, as well as an interaction between the two. Plot pair, which accounted for a single cheatgrass treatment being applied to each set of paired mullein plots, was treated as a random effect, nested within cheatgrass treatment.

I transformed all percent cover data using an arcsine transformation and used raw percent cover to calculate Shannon-Weiner Diversity scores for plots using both total species and only native species. I used the standard formula described in Chapter 1 to calculate the Shannon-Weiner scores, excluding any diversity contributions from cheatgrass or mullein. All cover data presented below reflects the arcsine transformation. I excluded mullein and cheatgrass when calculating both total and exotic richness in order to control for their removal from plots. Mullein

and cheatgrass contributions were included in the calculations for both total and exotic plant cover.

As a result of my low sample size, I used greater than normal thresholds in assigning significance or borderline significance. For this study I considered $P \leq 0.1$ to be significant and $P \leq 0.2$ to be borderline significant.

Results

I found that mullein treatment had no statistically significant effects on any of the community or abiotic responses that I measured (Table 3). There were however a number of responses that showed an impact of cheatgrass removal that were either significant or borderline significant. Total species richness was lower when cheatgrass was removed (3.9 species versus 4.8, $P=0.1815$). This was mainly driven by a decrease in exotic richness (1.7 versus 2.4, $P=0.1578$), while native richness increased with cheatgrass removal (2.8 species versus 2.05, $P=0.2164$, Figure 7). Total plant cover showed a similar trend, with lower cover when cheatgrass was removed (53% versus 72%, $P=0.1708$). This closely followed the differences in exotic cover (20% versus 51%, $P=0.0064$), while native plant cover increased when cheatgrass was removed (31% versus 17%, $P=0.0581$, Figure 8). Exotic plant cover was the only response that had a significant interaction between mullein and cheatgrass removal ($P=0.0889$, Figure 9). When mullein was left intact, there was comparable exotic cover regardless of the cheatgrass treatment (38% with cheatgrass versus 24% without). When mullein was removed, exotic plant cover was higher with cheatgrass than when cheatgrass was removed (63% versus 17%).

Native diversity scores were higher with cheatgrass removal, although this effect was not statistically significant (0.7 versus 0.5, $P=0.2507$). Light transmittance was strongly affected by cheatgrass management, increasing with removal (66% versus 51%, $P=0.0022$, Figure 10). There

were no biologically significant differences between treatments in any of the soil analyses, although plots where cheatgrass was removed had lower magnesium (128.4 ppm versus 139.2, *P*=0.1457) and higher manganese (9.6 ppm versus 8.7, *P*=0.0863, Table 4).

Discussion

It's clear from the results of this experiment that mullein invasion and management have much lower impacts than cheatgrass invasion and management. The effects of the mullein treatments were lost in the much greater influence of cheatgrass invasion and removal. This was not unexpected, as it has been well documented that cheatgrass has the ability to greatly alter its invaded range in a number of ways. Many of the impacts of cheatgrass that I observed mirrored those described in the literature, such as decreased native biodiversity (Young & Allen 1997) and lower native plant cover. Interestingly, cheatgrass invasion increased total species richness and plant cover, although this was in the form of greater exotic presence. Despite the fact that these results were mainly marginally statistically significant, they show the potential for an invasional meltdown, where cheatgrass invasion facilitates the colonization of other exotics (Simberloff and Von Holle 1999).

The greatest limitation for this study was the small sample size (five plots for each of the four treatments). This was limited by the number of available plots from my small plot study (see Chapter 1), and I was therefore unable to increase replication. Considering this issue, it's not surprising that many of the impacts of cheatgrass shown in my statistical model had p-values greater than the traditional 0.05 cut-off. Examining my results with the small sample size in mind, it's impressive that cheatgrass was able to impact the community and ecosystem so substantially that effects would be this clear. It's also interesting to note that the effects of cheatgrass removal were visible within a single season. In this short time span, native cover

almost doubled when cheatgrass was removed, demonstrating the immediate impact of management (Figure 8).

Another element that's important for the interpretation of my experiment is how cheatgrass was removed. On a small scale, using scissors to remove aboveground biomass was practical and acted to limit disturbances that would have been caused by alternative chemical or mechanical methods of management. On a larger spatial scale, this system would not be feasible and a different method, such as spraying herbicide, would have to be implemented. There are many potential implications for changes in management strategy, including impacts on non-target species (Randall 1996) as well as differences in efficacy. My removal method did not directly harm other plant species, but it also did not yield 100% loss of cheatgrass. At the time of survey, plots where cheatgrass had been removed had an average of 6% cheatgrass cover, compared to 35% in untreated plots. When determining which removal technique to employ, managers will need to weigh the values of each method and consider the necessary resources required.

Management Conclusions

Based on the relative impacts of invasions seen here, management resources, such as time and funding, should be allocated towards cheatgrass control rather than mullein. This is especially true at the current stages of invasion at my study site, where the mullein population is decreasing while cheatgrass is expanding rapidly. Additionally, mullein removal should be viewed as a potential disturbance event on which cheatgrass can capitalize. The danger of managing for mullein and leaving cheatgrass intact was observed here with the increase in exotic cover (Figure 9). If mullein removal is considered necessary in areas with cheatgrass populations, it should be accompanied with an aggressive cheatgrass management strategy.
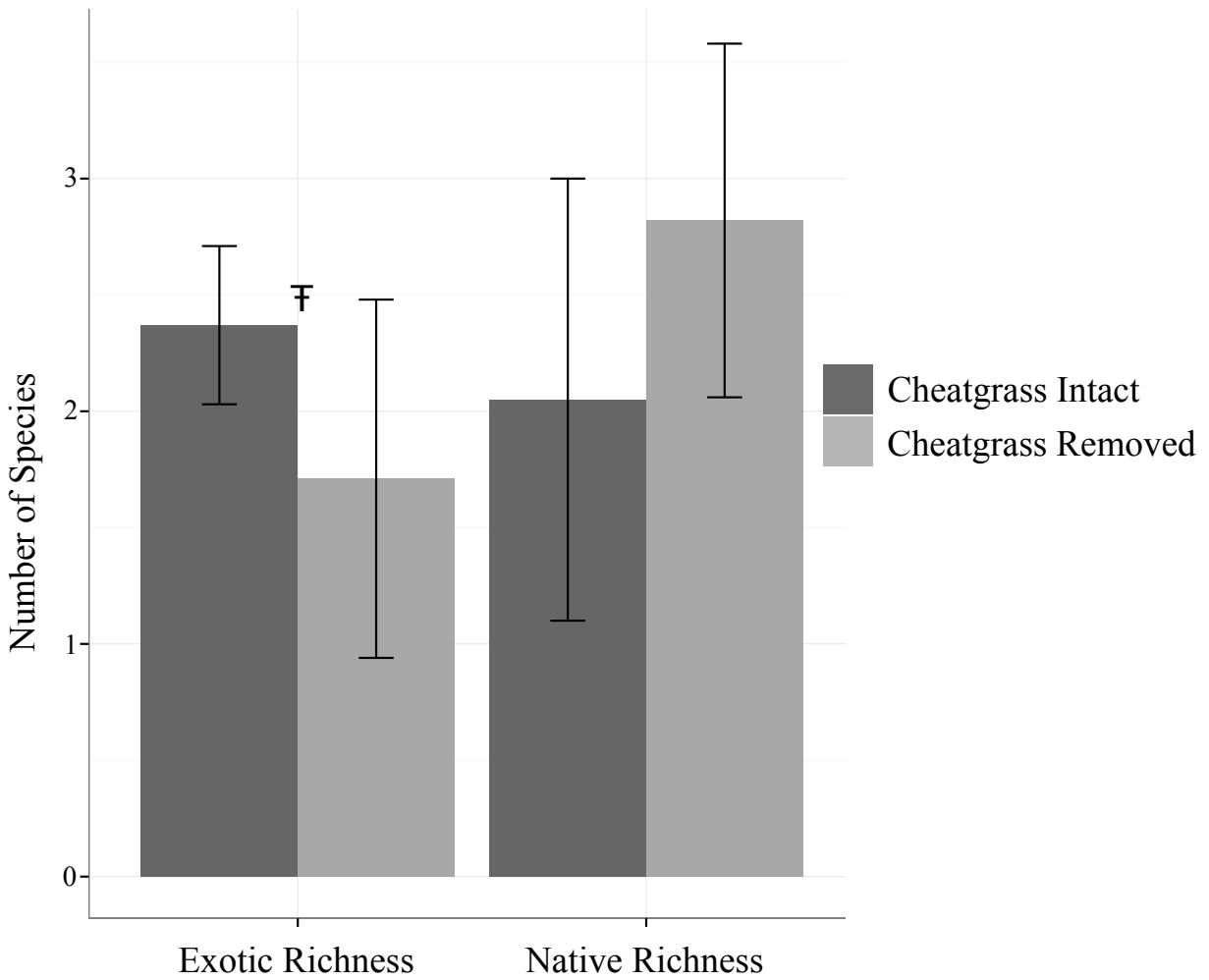
Figure 7. Effect of cheatgrass removal on exotic and native species richness. Exotic richness was calculated excluding mullein and cheatgrass, so as to control for their presence. Error bars represent 95% confidence intervals. Ŧ notates borderline significant differences between treatments (P<0.2).
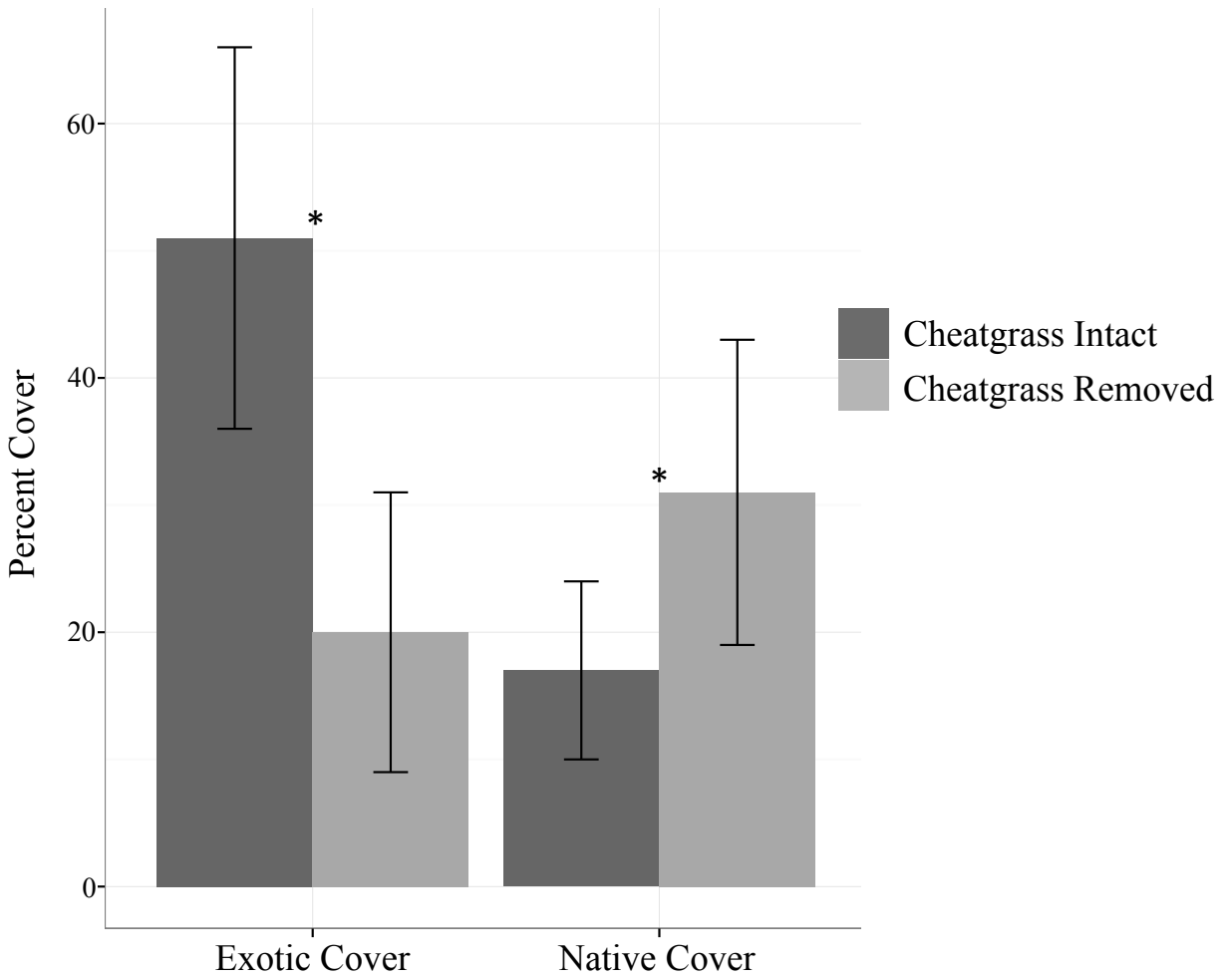
Figure 8. Effect of cheatgrass removal on exotic and native plant cover. Cheatgrass and mullein contributions are included in the exotic cover response. Error bars represent 95% confidence intervals. Asterisks notate significant differences between treatments (*=P<0.1).
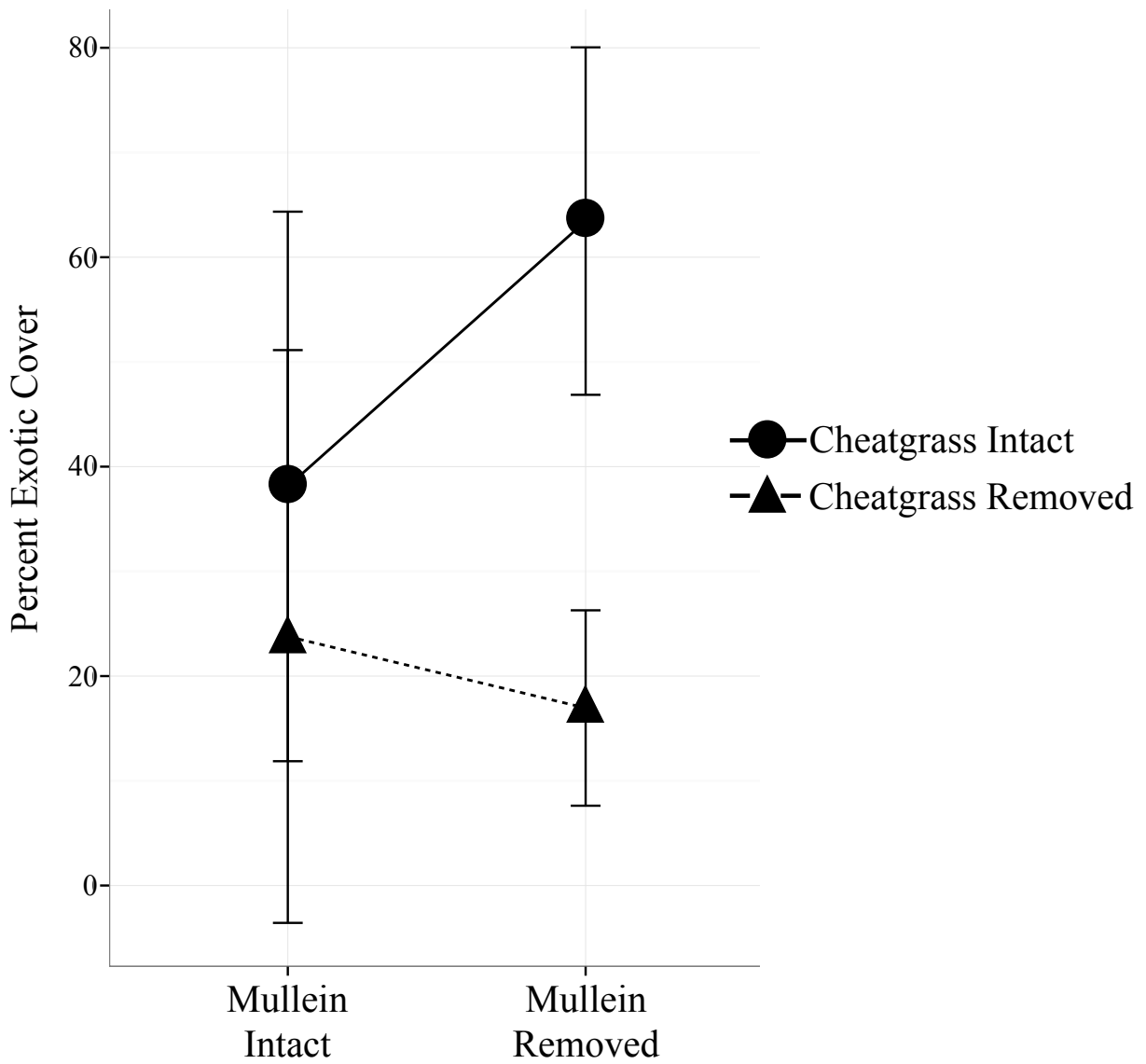
Figure 9. Interaction between mullein and cheatgrass treatments in regards to exotic cover. Error bars represent 95% confidence intervals.
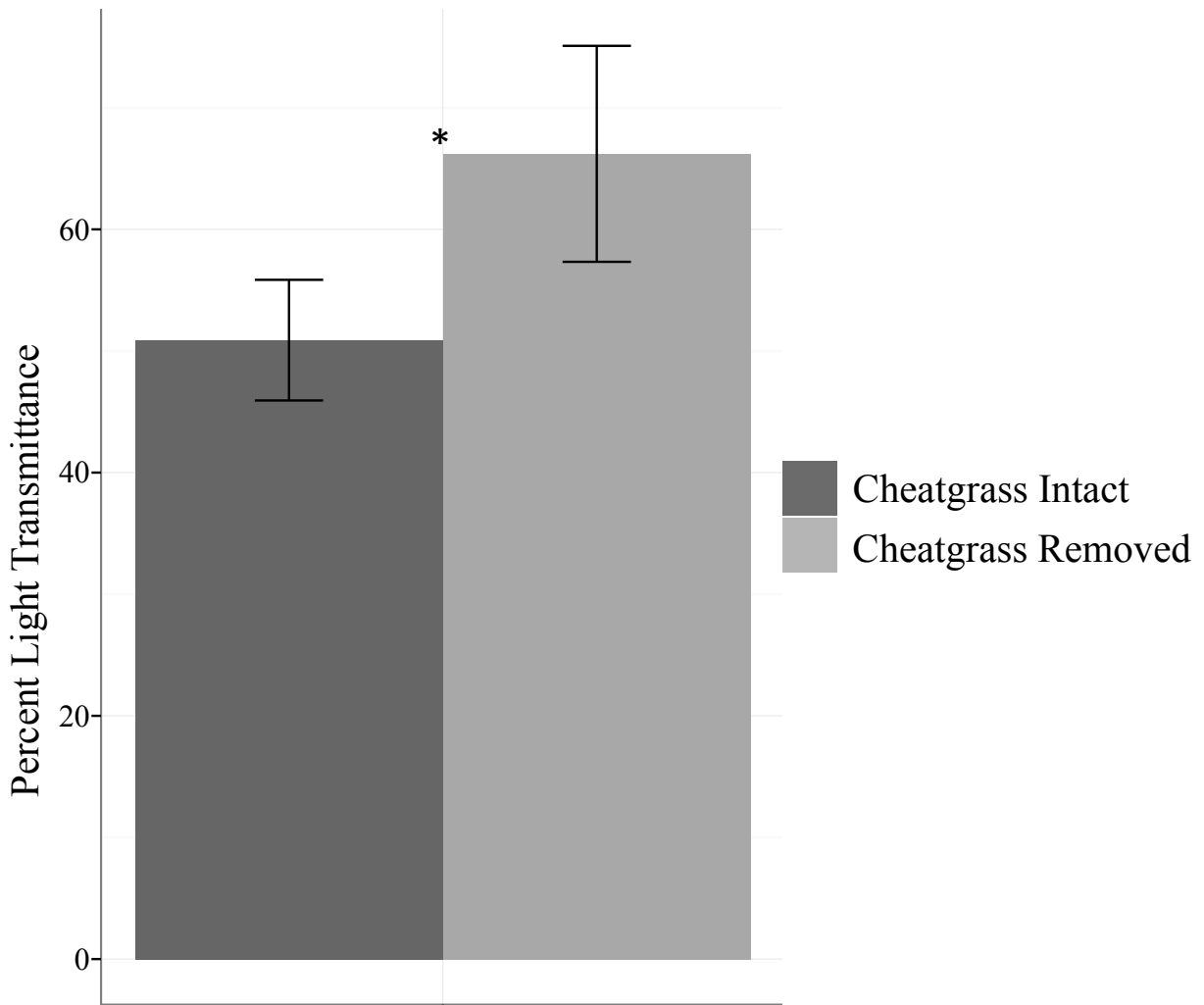
Figure 10. Effect of cheatgrass removal on light transmittance. Error bars represent 95% confidence intervals. Asterisk notates significant difference between treatments (*=P<0.1).

Tables

Table 3. Community and abiotic responses for all four mullein and cheatgrass treatments. Values show least-square mean (+/- standard error). Bold text indicates significant (*P*≤0.1) differences between cheatgrass treatments, italicized text indicates borderline significant (*P*≤0.2).

Mullein Treatment	Removed		Intact	
Cheatgrass Treatment	Removed	Intact	Removed	Intact
Species richness	**3.4 (+/-0.51)**	**4.9 (+/-0.37)**	4.4 (+/-0.75)	4.7 (+/-0.6)
Native Species Richness	2.8 (+/-0.37)	1.9 (+/-0.66)	2.8 (+/-0.58)	2.2 (+/-0.49)
Exotic Species Richness	1.8 (+/-0.58)	2.4 (+/-0.24)	*1.7 (+/-0.4)*	*2.3 (+/-0.24)*
Total Percent Cover	**52.64 (+/-5.92)**	**85.33 (+/-12.43)**	53.07 (+/-8.55)	58.63 (+/-6.93)
Percent Native Cover	**33.67 (+/-6.79)**	**13.77 (+/-4.29)**	28.04 (+/-8.79)	19.29 (+/-4.44)
Percent Exotic Cover	**16.95 (+/-3.28)**	**63.45 (+/-5.95)**	23.78 (+/-9.83)	38.11 (+/-9.46)
Shannon-Weiner Diversity	**1.05 (+/-0.09)**	**1.28 (+/-0.08)**	1.09 (+/-0.16)	1.18 (+/-0.15)
Native Diversity	**0.73 (+/-0.08)**	**0.4 (+/-0.7)**	0.66 (+/-0.19)	0.6 (+/-0.17)
Litter Percent Cover	**47.4 (+/-7.46)**	**26.71 (+/-6.84)**	51.56 (+/-10.17)	45.1 (+/-7.21)
Percent Bare Ground	5.43 (+/-4.26)	1.06 (+/-0.77)	2.11 (+/-1.11)	1.7 (+/-0.75)
Percent Soil Moisture	**5.56 (+/-0.69)**	**6.35 (+/-0.64)**	6.32 (+/-0.62)	5.94 (+/-0.4)
Percent Light Transmittance	68.33 (+/-5.28)	49.45 (+/-2.85)	64.09 (+/-6.45)	52.33 (+/-7.22)

Table 4. Soil characteristics for all four mullein and cheatgrass treatments. Values show least-square mean (+/- standard error). Bold text indicates significant ($P\leq0.1$) differences between cheatgrass treatments, italicized text indicates borderline significant ($P\leq0.2$).

Mullein Treatment	Removed		Intact	
Cheatgrass Treatment	Removed	Intact	Removed	Intact
pH	5.61 (+/-0.15)	5.75 (+/-0.1)	5.71 (+/-0.07)	5.68 (+/-0.12)
Phosphorous (ppm)	36.37 (+/-1.86)	36.62 (+/-2.16)	40.01 (+/-2.27)	37.01 (+/-3.17)
Potassium (ppm)	189.55 (+/-5.5)	205.61 (+/-15.41)	214.2 (+/-10.65)	216.15 (+/-12.8)
Calcium (ppm)	990.54 (+/-17.6)	1039.33 (+/-46.21)	1035.47 (+/-49.67)	1023.49 (+/-46.59)
Magnesium (ppm)	128.59 (+/-3.64)	136.66 (+/-5.74)	*128.12 (+/-2.2)*	*141.75 (+/-8.97)*
Zinc (ppm)	1.45 (+/-0.12)	1.55 (+/-0.11)	*1.64 (+/-0.17)*	*1.33 (+/-0.09)*
Manganese (ppm)	9.29 (+/-0.25)	9.13 (+/-0.3)	**9.86 (+/-10.69)**	**8.28 (+/-0.46)**
Copper (ppm)	0.2 (+/-0.03)	0.2 (+/-0)	0.22 (+/-0.02)	0.2 (+/-0)
Iron (ppm)	6.68 (+/-1.06)	5.45 (+/-0.42)	6.31 (+/-0.8)	5.02 (+/-0.43)
Boron (ppm)	0.32 (+/-0.02)	0.35 (+/-0.02)	0.38 (+/-0.04)	0.36 (+/-0.04)
Percent Organic Matter	3.41 (+/-0.08)	3.5 (+/-0.07)	3.7 (+/-0.2)	3.42 (+/-0.11)

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