THE RELATIONSHIP BETWEEN YELLOW TOADFLAX (*LINARIA VULGARIS*) PRESENCE, TREATMENT HISTORY, AND PLANT SPECIES RICHNESS NEAR WEST YELLOWSTONE, MONTANA

by

Amanda Williams

A professional paper submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Lands Resources and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2020

ACKNOWLEDGEMENTS

I would like to thank Dr. Lisa Rew for her honest guidance on this project and advice throughout this degree program. It was refreshing to have an instructor dedicated to facilitating a meaningful experience for distance learning students. I would also like to acknowledge Teton County Idaho for providing a portion of my funding and thank Vincent Nagashima for help with field data collection and for access to recent Yellowstone National Park noxious weed treatment data.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Table Page

ABSTRACT

Humans have spread plant species to novel ranges throughout history, but the rate of new introductions has drastically increased with globalization. These introduced species are often viewed as a threat to native species richness. *Linaria vulgaris* (yellow toadflax) was introduced to North America in the 1600s as a useful and ornamental plant and has since spread across the continent. It is mandated for control in much of the intermountain west and is thought to form monocultures to the detriment of native species. Despite *L. vulgaris'* long residence time on the continent, causal links to negative effects have not been established. Land managers are typically faced with a long list of species mandated for control and limited resources and thus must prioritize high impact species for control. Herbicide is the management choice for non-native plants in Yellowstone National Park, but it may have negative effects. Therefore, managers need to be sure that treatment is worthwhile, and that the effects of treatment do not exceed the effects of non-native plants.

Consequently, I selected 10 sample sites in the West Yellowstone, Montana area: five with a recent history of herbicide treatment and five without. Data were collected on plant species richness and abundance within and immediately adjacent to *L. vulgaris* patches. Species richness and diversity did not vary between sites based on treatment history. Species diversity did increase where *L. vulgaris* was present, indicating that it may act as a "plus one" in communities and does not dominate where it occurs. Treatment history was not linked to a reduction in *L. vulgaris* abundance, but the abundance of other non-natives was greater in treated sites. These results indicate that land managers should not assume that *L. vulgaris* negatively effects native species richness and diversity in their location and should pair management efforts with rigorous monitoring. In the West Yellowstone area, *L. vulgaris* likely should not be a high priority for herbicide treatments. However, this study is observational and not sufficient to establish causal links.

INTRODUCTION AND LITERATURE REVIEW

The global movement of humans has been accompanied by the global movement of plants and other organisms to non-indigenous ranges. It is the general consensus that humans have accelerated the rate of introductions far beyond non-anthropogenic levels and that this constitutes a threat to ecosystems (Vitousek et al. 1997; Mack et al. 2000; Hulme 2009). In the United States, an estimated 5,000 introduced plant species and 17,000 native plant species exist in natural ecosystems (Pimentel et al. 2005). In 2005, the annual cost to the U.S. economy from introduced plant species in direct damages and control efforts was estimated to be $34.6 billion (Pimentel et al. 2005).

In North America, European contact during the 1500s is generally considered the demarcation between native species and introduced species; i.e., species that existed on the continent before contact are native and species introduced since are non-native (Mack et al. 2000). Many terms are used for introduced species (often imprecisely) both in the literature and in regulatory documents. Among the most common terms are *invasive, alien, exotic, non-native,* and *non-indigenous* (Ricciardi and Cohen 2007). Herein, I will refer to introduced plant species as non-native and the term *invasive* will be used for species that have spread in novel ranges. The term invasive is often used in a way that implies impact, but invasiveness and impact are attributes that may or may not co-occur (Pearson et al. 2016a; Ricciardi and Cohen 2007).

From the earliest waves of European colonization of North America, migrants intentionally and accidentally introduced new plant species. The majority of these are not considered damaging (Mack 2003), though some such as the common dandelion

(*Taraxacum officinale*) are very invasive and have successfully spread across North America. Other non-native species are considered both invasive and damaging. A variety of negative effects have been attributed to non-natives, the most often cited in natural systems is a reduction of native species richness in response to invasion (Vila et al. 2014). Federal and state laws mandating control of certain species have been created to mitigate these perceived impacts; and land managers are tasked with carrying out control efforts. However, the effects of non-native species are not always well documented (Ricciardi and Cohen 2007). Further, effects and their severity are highly "context dependent" and vary based on the species, receiving ecosystem, and scale; and effects fluctuate both temporally and spatially (Vila et al. 2011; Hulme et al. 2013; Lehnhoff 2008). Therefore, finding that a species is impactful in a certain ecosystem or place does not mean that it is also impactful across its geographic range given the diverse ecosystems a species may occupy; and given that effects may change over time.

Yellow toadflax (*Linaria vulgaris*) is a non-native plant species that was intentionally introduced by early European migrants and was regarded as damaging by the mid-1700s (Mack 2003). *Linaria vulgaris* is now established in all 49 continental states and is thought to form "monoculture infestations in the Intermountain West"; its control is legally mandated in most of that area (Sing et al. 2016).

Land managers are typically faced with a long list of non-native plant species mandated for control. For instance, as of early 2020, 35 non-natives are listed as noxious in Montana (MT Dept of Ag.), and 67 non-natives are listed in Idaho (ID Dept of Ag.). Noxious is a legal designation that is usually accompanied by a mandate to control in state statute. The weed control budgets of land management agencies are usually not adequate to address all non-native or even all noxious non-native plant species that occur in their jurisdiction. Thus, land managers must prioritize high impact species and/or high value sites for control. However, the working theory for most managers is that all noxious weed species are negatively impacting ecosystems or plant communities and require control. More information is needed on the local impact of individual non-native species to enable managers to prioritize efforts.

Plant Invasions

Plant invasions are complex, and mechanisms and effects vary across spatial and temporal scales (Kueffer et al. 2013). There is a large body of scientific work dedicated to understanding plant invasions, but for land managers tasked with controlling non-natives, much of this can be boiled down to the critical question of whether non-natives are passengers or drivers of plant community change (MacDougall and Turkington 2005). In the first “driver” school of thought, the theory of “community species richness” is attributed to Elton (1958) wherein a given ecosystem has a finite amount of resources, and therefore a finite number of available niches or space (Mack et al. 2000). Elton (1958) posited that plant communities with more total species richness would better use available resources/niches, and thus be more resistant to invasion (Mack et al. 2000). Plant communities with similar resources that are comparatively depauperate in species would have vacant niches or underused resources and be subject to invasion (Mack et al. 2000). From this follows the ideology that plant communities are determined by interspecific competition and that non-native species that are more competitive can displace native plants by more successfully occupying their niche (Sutton et al. 2007). In this narrative, non-natives are drivers of landscape degradation and a threat to biodiversity (MacDougall and Turkington 2005).

The second "passenger" school of thought contains the theory that ecosystems conducive to high native species richness are also conducive to high introduced species richness. The term "the rich get richer" was used by Stohlgren et al. (2003) to frame the fact that non-native richness is often correlated with native species richness and density. Stohlgren et al. (2006) found that both native and non-native richness was correlated with high resource availability and posit that "inviting habitats" drive total species richness. In this narrative, non-natives are not the primary threat to biodiversity, merely symptoms of environmental change (MacDougall and Turkington 2005).

Meta-analyses have shown that non-natives reduced native plant species abundance and diversity (Vila et al. 2011; Vila et al. 2014), and conversely that non-natives enrich total diversity (Stohlgren et al. 2006). Multiple authors note considerable uncertainty surrounding causal links as much of the work included in the referenced meta-analyses and the scientific literature is observational (Vila et al. 2011; Skurski et al. 2014). Lonsdale (1999) posits that introduced and native plant species richness are correlated without a causal link, and that the correlation is explained by scale. At broader scales, habitat heterogeneity explains higher diversity. The effect of heterogeneity on richness has been found to be "highly scale dependent" (Kumar et al. 2006). Pollnac (2012) concluded that the debate about whether non-native species are damaging to native plant species is not over, but that scale is important.

Why Are Non-Native Plant Species Successful?

Some non-natives have been observed to be more competitive in their introduced ranges than in their indigenous ranges. The “novel weapons” and “enemy release” theories address this phenomenon. Novel weapons is the theory that some non-natives gain a competitive edge from novel allelopathic compounds to which native species have not coevolved and are therefore more susceptible to than species in an non-native’s indigenous range (Callaway and Ridenour 2004). Enemy release (or escape from biotic constraints) is the theory that non-natives in novel ranges are free from the predators and pathogens that suppressed populations in their indigenous range, thus lending them a competitive edge over native species (Elton 1958; Mack et al. 2000; Maron et al. 2014; Lehnhoff 2008).

Another important factor in the success of non-natives is anthropogenic disturbance (Mack et al. 2000). The arrival of European migrants in North America is the demarcation of native vs. introduced plant species. This also heralded a change in the type, magnitude, and frequency of anthropogenic disturbance regimes. European migrants brought with them species coevolved to their disturbance regimes, and these species were able to invade while native species were adapting or evolving (Mack et al. 2000; Lonsdale 1999). Anthropogenic disturbance is ongoing, widespread, and rapidly changing; disturbances such as altered fire cycles, grazing management, and irrigation regimes change plant communities and can favor non-natives over natives (Mack et al. 2000; Lonsdale 1999; Vitousek et al. 1997; Pearson et al. 2016; MacDougall and Turkington 2005).

Finally, propagule pressure is a very important factor in invasion success (Magee et al. 2010; Lonsdale 1999). Lonsdale (1999) found that propagule pressure is a significant explanatory factor for non-native richness, and important for non-native populations to overcome stochastic extinction events. National parks and other protected areas have lower non-native richness and abundance due to fewer introductions (and anthropogenic disturbance) (Vitousek et al. 1997).

Impact of Plant Invasions

Effects of invasive plants may be positive or negative (Vila et al. 2011; Skurski et al. 2014). In a 2007 study, Ricciardi and Cohen performed a meta-analysis and found that a species' invasiveness was not correlated with its impact; and it has been estimated that as few as half of non-native plant species should be considered damaging based on actual effects (Richardson et al. 2000). Most studies on invasion impact last 2-3 years, and thus neglect the temporal scale of invasions (Magee et al. 2010). Due to this lack of understanding of the temporal scale of invasion, and the fact that effects also vary by spatial scale, the effects of non-native plants on natural systems are difficult to parse (Magee et al. 2010; Skurski et al. 2014; Vila et al. 2011). Another compounding factor on evaluating impact is that most invaded ecosystems are subject to multiple non-native species, and synergistic effects are not well documented (Richardson & Pysek 2006). Additionally, the magnitude and direction of impact is context dependent: impact will vary based on the combination of invader and receiving ecosystem (Vila et al. 2011).

Invasive plants are almost universally cited as a threat to biodiversity, but causal effects are not fully established. Meta-analyses found that non-native presence correlated with decreased abundance and diversity of resident species; clonal invaders had a larger impact on richness than non-clonal species (Vila et al. 2011; Vila et al. 2014). Non-native plant species have been found to alter native plant species' relationships with pollinators and mycorrhizal fungi, and to alter microenvironments (Skurski et al. 2014). Impacts may be positive or negative; for instance, pollinator visits to natives may increase or decrease in the presence of non-natives, and native species may be detrimentally shaded by non-natives, or non-natives may improve soil's capacity to retain water (Skurski et al. 2014). Other documented changes include altered fire regimes, nutrient cycling, and animal habitat (Wilke & Irwin 2010; Sing & Peterson 2011). Effects may cascade up trophic levels, though magnitude of impact is thought to be highest within trophic levels (Vila et al. 2011; Skurski et al. 2014). Again, the magnitude and direction of impact depend on the combination of non-native species and receiving ecosystem (Vila et al. 2011; Skurski et al. 2014).

Noxious Weed Legislation

"Noxious" is a legal designation; most states in the U.S. have a state noxious weed statute. Plant species are typically declared noxious if they are perceived to pose a threat to agriculture and/or natural areas. A designation of noxious is usually accompanied by a legal mandate for control. State legislators have the final say in state noxious weed laws and accompanying lists; as such they are political documents. Pearson et al. (2016a) found that in the intermountain west, regulation of a non-native does not necessarily match its impact. So, legislative status should not necessarily be conflated with impact; evaluation of a non-native in local conditions is necessary.

Impacts of Chemical Control

Herbicides were originally developed for the control of weeds in agroecosystems (Wagner et al. 2017). Wildland ecosystems are important for conserving native biodiversity; accordingly, herbicides are now commonly applied in natural (non-crop) settings to control invasive plants. Herbicides applied in natural systems are typically selected to target either forbs or grasses depending on the target non-native. However, limits to selectivity mean that herbicides applied to target non-native forbs will likely impact non-target native forbs (Wagner et al. 2017). Herbicides have been shown to successfully control target populations of invasive plants (Wagner et al. 2017; Kettenring, & Reinhardt Adams 2011; Pearson et al. 2016b). However, several negative, non-target effects have been documented. Negative non-target effects may include: mortality for non-target susceptible species, long term demographic shifts for long-lived resistant species including lack of seed set and seedling recruitment, changes in mycorrhizal fungi communities, shifts in dominance from mixed forbs to grasses, and secondary invasion by other invasive plants (Skurski et al. 2013; Wagner et al. 2017; Maltz et al. 2016; Crone et al. 2009; Pearson et al. 2016b). Herbicide impacts vary based on the combination of chemical, target plant species, application method, and abiotic and biotic factors in the application site (Lindenmayer et al. 2017).

Conclusion

Impacts of non-native plants are context dependent, as are the impacts of chemical control. To make herbicide use worthwhile, it must be effective, and the negative impact of invasive plants must exceed the negative impacts of herbicide use.

Linaria vulgaris is a non-native species targeted for control in and around West Yellowstone, Montana. However, it is unclear that *L. vulgaris* is negatively impactful in this area, that chemical control is effective, and that the impact of *L. vulgaris* exceeds the impact of chemical control. Answering these questions will help managers prioritize control for this species and determine what control methods to use.

Linaria vulgaris (Yellow toadflax)

Species Description

Linaria vulgaris is an upright herbaceous perennial forb in the Plantaginaceae (previously Scrophulariaceae) family (Figure 1). It is usually 0.3-1.0 m tall with multiple ramets sprouting from spreading adventitious root buds (CABI 2020; Sing et al. 2016). Mature plants develop both deep tap roots, 1 m or more long and extensive lateral roots (Sing and Peterson 2011). Leaves are pale green, dense, slightly waxy, linear, and usually alternate. Inflorescences are “snapdragon like”, yellow, and racemose.

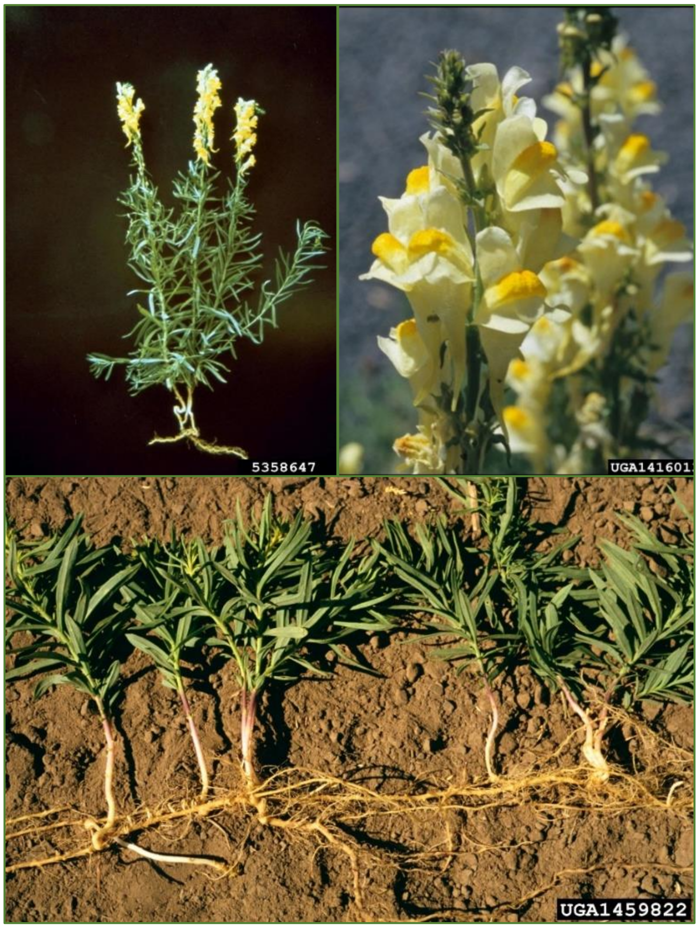


Figure 1: *Linaria vulgaris* plant, flower, and rosettes. Photo Credits: top left L.L. Berry, Bugwood.org; top right Linda Wilson, University of Idaho, Bugwood.org; bottom Steve Dewey, Utah State University, Bugwood.org

Life Cycle and Competitive Ability

Linaria vulgaris reproduces vegetatively via adventitious roots and by seed; it is self-incompatible (Ward et al. 2009). Floral associations with bees, wasps, and syrphid flies have been observed in Poland (Jachula et al. 2018). In North America, native Halictid bees (sweat bees) have been documented as pollinators (Saner et al. 1995; CABI 2020). Mature ramets produce up to 6,000 seeds annually, genets up to 30,000 seeds (Sing et al. 2016; Wilke & Irwin 2009). Seed viability is low; viability has been estimated at less than 25% (CABI 2020) and less than 50% (Sing et al. 2016). Seed dispersal occurs from late summer through winter. Most seeds fall within 2 m of the parent plant, though they may be dispersed over longer distances by humans, wildlife (including ants), wind and water (CABI 2020; Zouhar 2003). Seeds require wet stratification to germinate (CABI 2020). Dormant seeds have been found to remain viable in field conditions for more than 8 years, and in storage at room temperature for 13 years (Sing et al. 2016; CABI 2020).

Seedlings are able to reproduce vegetatively in as little as three weeks; a single seedling (genet) produced 100 shoots (ramets) in its first year in Canada (Zouhar 2003). Root fragments as short as 1 cm can start new plants, and spread is estimated to be faster from new plants established from roots than seedlings (CABI 2020). Patches of *L. vulgaris* can expand vegetatively by at least 1 m annually (CABI 2020). Individual root crowns typically only live about 4 years, but patches can live for more than 13 years (Zouhar 2003).

Linaria vulgaris dies back to ground in the winter. Growth starts in the spring when soil temperatures reach 5-10 °C (CABI 2020). Because of its extensive root system, *L. vulgaris* is able to survive fire, frosts, and other disturbances that kill above ground growth. *Linaria vulgaris* is subject to suppressive soil biota in at least some of its indigenous Eurasian range but seems to be free from these effects in North America (Maron et al. 2014).

Origin and Distribution

Linaria vulgaris is indigenous to temperate areas on the Eurasian continent from the United Kingdom and Spain all the way to China (CABI 2020). Much of its indigenous range is subject to periodic disturbance from grazing, cropping, and silviculture; it is well suited for this regime as it has comfortably accompanied the spread of European migrants and associated disturbance regimes and can now be found worldwide (except arctic regions) (Zouhar 2003; Lehnhoff 2008; CABI 2020).

Linaria vulgaris was deliberately introduced to North America before 1672 by early European migrants as an ornamental and useful plant; it has been historically used medicinally to attempt to treat a wide range of ailments, as a dye, and as an insecticide (CABI 2020, Sing et al. 2016). By 1758, it was considered weedy; a letter from a botanist of the time describes *L. vulgaris* as “never more heartily cursed” and says that "it is the most hurtful plant to our pastures that can grow in our northern climate. Neither the spade, plough, nor hoe, can eradicate it" (Mack 2003). It was reported as “extensively naturalized... on roadsides, commons, wastes, and the borders of fields" by a botanist in 1818 (referring to PA and VA) (Mack 2003). *Linaria vulgaris* was intentionally introduced to homesteads and stage stops in the West Yellowstone, MT area in the 1800s (Lehnhoff 2008). It has since been found in relatively undisturbed backcountry sites in the West Yellowstone area (Pauchard et al. 2003; Sing et al. 2016).

Linaria vulgaris is a temperate species but has a high ecological amplitude. It occupies a variety of habitats across North America (Figure 2). *Linaria vulgaris* grows from sea level to above 2700 m in elevation, and up to 65° of latitude (Saner et al. 1995). It tolerates a wide variety of soil types, moisture regimes, and temperatures. *Linaria vulgaris* is most invasive in sites with an open canopy and is usually found in disturbed habitats such as roadsides, pastures, and cultivated fields (Saner et al. 1995; Sing et al. 2016; CABI 2020).

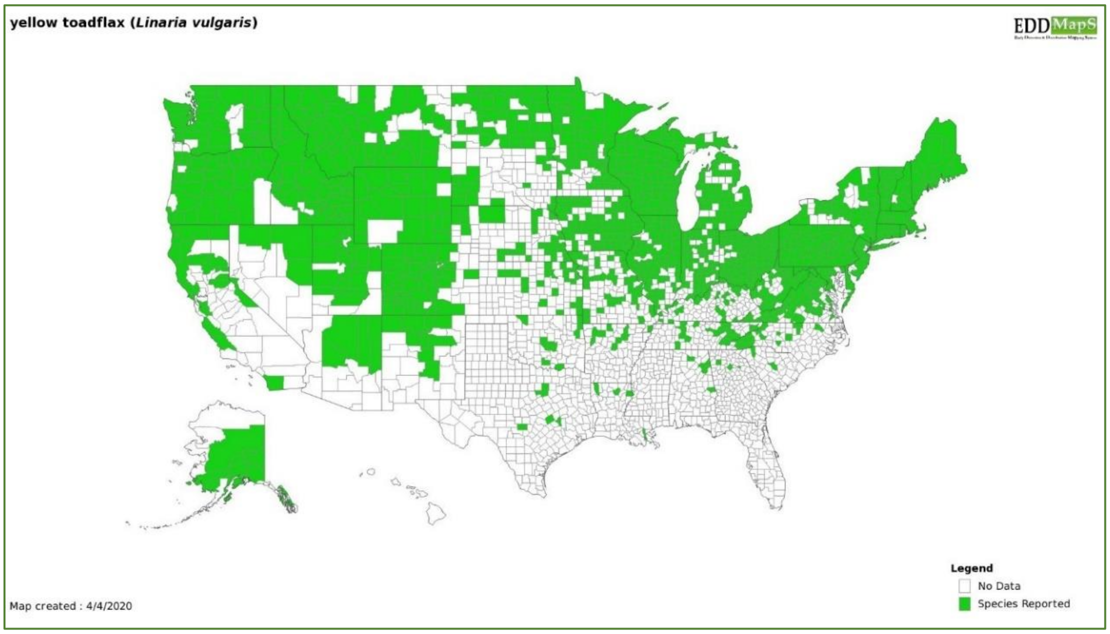


Figure 2: *Linaria vulgaris* distribution in the U.S. (EDDMapS 2020).

Thirteen *Linaria* species are found in North America, but none is indigenous to the continent (Sing et al. 2016). Of the introduced *Linaria* species, *L. vulgaris* and the closely related *L. dalmatica* (Dalmatian toadflax) are regarded as the most problematic. *Linaria vulgaris* and *L. dalmatica* are known to produce fertile hybrids in field settings (McCartney et al. 2019; Sing et al. 2016). *Linaria vulgaris* is designated as noxious in 13 states (Sing et al. 2016).

Impacts of *Linaria vulgaris*

Considering that *L. vulgaris* has been in residence in North America for nearly 400 years and control is mandated in many states, the literature is depauperate on documented impacts of invasion. Sing and Peterson (2011) conducted a risk assessment for *L. vulgaris* and the closely related *L. dalmatica.* They assessed 11 possible effects and found that *L. vulgaris* competitively displaces crop plants in some agricultural systems, that it can host the serious crop pathogen cucumber mosaic virus (as do many other species and transmission has not been documented), and that it is unpalatable but likely not toxic to livestock. The authors note that considerable uncertainty exists, effects are multiplied by exposure to calculate risk (and by extension risk will vary based on exposure or density), and some impacts such as effect on fire cycles or erosion are likely to be site dependent.

In natural systems, competitive displacement of native plants is the most commonly cited impact of *L. vulgaris*, but this is usually not supported by evidence. In Colorado, Sutton et al. (2007) tested whether *L. vulgaris* presence could be predicted by measurable site characteristics. They tested 13 parameters including vegetation type, soil type, and aspect and found that species richness was the best explanatory factor for *L. vulgaris* presence. Their study was observational, but they found that "plots containing yellow toadflax have higher numbers of species than plots that did not contain yellow toadflax" (Sutton et al. 2007).

Pauchard et al. (2003) and Lehnhoff (2008) have both studied *L. vulgaris* in the West Yellowstone, Montana area. Pauchard et al. (2003) conducted an observational study and found that *L. vulgaris* was correlated with a decreased native plant density or abundance, but not decreased richness. They concluded that *L. vulgaris* was a threat to native plant communities but noted that colonization could be the result or disturbance creating bare soils and not real competitive displacement. They also found that increased *L. vulgaris* biomass was not associated with decreased nutrient availability.

Lehnhoff's (2008) study was a combination of experimental and observational work. His main conclusions were that *L. vulgaris* invasiveness varies temporally and spatially, its recruitment is positively correlated with disturbance and propagule pressure, and it is minimally impactful on native vegetation, but its response to disturbance will result in altered plant communities.

Management Efficacy and Impacts

Linaria vulgaris' perennial habit and extensive root system make control by any means difficult, including chemical control. However, DiTomaso et al. (2013) recommends a variety of herbicides for the control of *L. vulgaris* in natural areas. Efficacy and non-target impacts (such as grass and desirable forb damage) vary based on the combination of herbicide and application site. Repeated chemical applications are usually necessary for established patches, and eradication is difficult to achieve. Lehnhoff (2008) found that one treatment with the herbicide picloram resulted in initial suppression of *L. vulgaris* populations (determined by quantifying invasiveness, population growth, and density), but that invasiveness and annual population growth rebounded the year after treatment (Lehnhoff defined invasiveness as "a population increasing in density and/or spatial extent"). In some sites, *L. vulgaris* density increased above pre-herbicide application levels (Lehnhoff 2008). Lehnhoff posits that this phenomenon is the result of herbicide eliminating native forbs from plots, thus freeing *L. vulgaris* from competition.

Linaria vulgaris can re-sprout from root fragments, so pulling and tillage are only effective in very young populations that have not yet developed extensive roots (DiTomaso et al. 2013). Other manual control options like mowing, grazing, and fire are not effective, and may actually increase *L. vulgaris* density by increasing site disturbance and opening the canopy (DiTomaso et al. 2013; Lehnhoff 2008). Grazing and fire are known to promote invasion by other weedy species.

Nine species of insects from *L. vulgaris*' indigenous range have been introduced (usually intentionally, but also accidentally) for the biological control of *L. vulgaris* and the closely related *L. dalmatica* (Sing et al. 2016). In classic biological control or "biocontrol," highly host specific insects from a non-native species' home range are introduced into its novel range in an effort to stress and suppress populations. The impact of biocontrol insects varies; once introduced, biocontrol insects may fail to establish or pick up native parasitoids and/or pathogens. Of the *L. vulgaris* and *L. dalmatica* biocontrol insects, the stem mining *Mecinus* weevils are generally regarded as the most effective; the *L. dalmatica* specific *Mecinus janthiniformis* has been shown to be effective in reducing *L. dalmatica* density (Weed et al. 2017). However, the efficacy of *Mecinus janthinus,* the stem mining weevil specific to *L. vulgaris*, has been less clear.

Negative impacts of biocontrol agents typically consist of non-target damage. For instance, in the early days of intentional biocontrol introductions (the 1960s) a weevil was introduced for the control of the non-native thistle *Carduus nutans* that also targeted native thistles. Now, the screening process is more robust and damage to native plants is no longer acceptable for prospective biocontrol agents. Of the introduced *L. vulgaris* biocontrol agents, the *L. vulgaris* defoliating moth *Calophasia lunula* is known to attack desirable plants like ornamental snapdragons, and *Rhinusa neta*, an accidentally introduced beetle, has not been evaluated (Sing et al. 2016). Negative impacts due to the other *Linaria* biocontrol agents have not been documented.

The working hypothesis of most land managers tasked with invasive plant control is that non-native plants listed as “noxious” are damaging to natural systems and require control (Lehnhoff 2008). Given the difficulty controlling *L. vulgaris*, the limited budgets for non-native control, and the potential negative effects of herbicide use, it is important for managers to understand whether *L. vulgaris* is damaging and whether it is worthwhile to target for control. A serious question for managers is if the cure (herbicide) is worse than the problem (*L. vulgaris*)?

COMPARISON OF PLANT DIVERSITY BETWEEN SITES BASED ON *LINARIA VULGARIS* PRESENCE AND HISTORY OF CHEMICAL CONTROL

Objectives

Control of *L. vulgaris* is mandated in Wyoming, Idaho, Montana, and Yellowstone National Park. *Linaria vulgaris* is common in the West Yellowstone, Montana area (personal observation). Chemical control is the management choice most often used when populations are targeted for control. My project is intended to facilitate future management of *L. vulgaris* by evaluating the relationship between its occurrence and native species richness and diversity between sites with a history of herbicide treatment and untreated sites, and within those sites in *L. vulgaris* patches and adjacent uninvaded area.

The specific objectives of my study are to: (1) compare plant species richness and diversity between sites with a history of herbicide treatment and those without; (2) compare plant species richness and diversity between sites invaded with *L. vulgaris* and adjacent currently uninvaded sites; (3) evaluate the effect of treatment history on bareground cover and abundance of non-natives other than *L. vulgaris*; (4) evaluate the effect of chemical control on *L. vulgaris* abundance, and; (5) investigate relative abundance and species composition differences between comparison groups (treated vs. untreated, and *L. vulgaris* present vs. absent).

Methods

Site Description

I selected 10 sample sites where *L. vulgaris* occurs in the West Yellowstone, Montana area, both inside Yellowstone National Park and on the Custer Gallatin National Forest. I established five sites with a history of herbicide treatments and five untreated sites. The history of herbicide treatment was derived from Yellowstone National Park application records from 2017 and 2018, and my personal experience spraying the treated sample sites from 2011 to 2015. Sites were not a set geographic area, rather they were selected based on *L. vulgaris* presence and my familiarity with their treatment history. At least since 2011, when Yellowstone National Park applies herbicide, it is applied as spot treatments and the herbicides used are Milestone (aminopyralid) tank mixed with Telar (chlorsulfuron) at 7 and 2 oz/acre respectively. The amount of herbicide applied at each location is recorded and annual treatment records are stored in a geodatabase in ArcGIS. The untreated sites have not been sprayed since 2011, but it is possible they were sprayed sometime in the past. Sample locations consisted of seven upland sites and three riparian sites. Elevations ranged from about 2000 m to 2100 m. See Appendix A for more information.

The intent was to find an additional five sites with the biocontrol weevil *Mecinus janthinus,* but this was not possible due to poor establishment at release sites (Kim Ragotzkie, personal communication). However, the biocontrol flower feeder *Brachypterolus pulicarius* was present at all sample sites, as was evidence of damaged flower tips on some ramets; *B. pulicarius* is generally considered to have a low impact on *L. vulgaris* populations (Sing et al. 2016).

The West Yellowstone area is a relatively cold and dry climate with an average maximum annual temperature of 10 °C, and an average annual precipitation of 56 cm, much of which is received as snow (WRCC 2020). The area is typically under snowpack from November to April (WRCC 2020). Soils are typically a mix of sandy alluvium derived from obsidian and rhyolite, and glacial outwash (NRCS 2020).

Sampling

Sampling was conducted on August 18 and 23, 2019; six sites (numbers 1-6) were sampled on the first date, and four sites (numbers 7-10) on the second date. Six plots were sampled at each site: three within the *L. vulgaris* patch and three adjacent to the patch. Plots were 0.5 m^2 frames, and they were placed by tossing: the first three plots were placed by standing outside of the *L. vulgari*s patch and tossing the frames in, then the second three plots were placed by standing within the patch and tossing the frames outside where *L. vulgaris* was not present. For a clonal species like *L. vulgaris*, a patch edge is easy to visually demarcate. This tossing method ensured all plots were fairly close to each other at a given site; well within 100 m of each other though distance was not recorded. In each frame, species present were identified and abundance (as percent cover) was visually estimated and recorded. The percentage cover of bareground and litter for each plot was also recorded.

This sampling method is not random but is appropriate since the main point of interest is how *L. vulgaris* presence relates to species richness and diversity. Looking at richness within a clonal patch, then immediately adjacent to the patch provides a good snapshot of how *L. vulgaris* relates to its neighboring species. This design is observational only; so, a history of herbicide use at a site does not guarantee that my plots were a place where herbicide actually hit the ground. However, this sampling method is appropriate for a preliminary investigation into the relationship between herbicide treatments and species richness and diversity given the many years of herbicide applications at the sites.

Data Analysis

Data analysis was conducted in R version 3.6.3 (2020-02-29) "Holding the Windsock" (C) 2020, including the vegan package. Total species richness is the total number of species present, regardless of the abundance of those species. Total richness was investigated to test the effect of *L. vulgaris* presence, treatment history, and date of sampling on richness using a generalized linear model with Poisson regression. Variables were evaluated with ANOVA and a chi test. Variables for models were first tested for interactions; where there were none, variables were then modeled as additive. If date was non-significant it was removed. The data were subset to include only plots where *L. vulgaris* was present, and the effect of treatment history on richness was again evaluated.

The effect of treatment and sample date on the abundance of *L. vulgaris* and the abundance of other non-native species, and the effect of treatment and *L. vulgaris* presence on the amount of bareground and abundance of other non-native species were evaluated using a linear regression model and ANOVA with a chi test. Before analysis, data were tested for heteroscedasticity and transformed if necessary. Again, variables were tested for interactions; where there were none, variables were modeled as additive and non-significant variables removed.

Alpha diversity indices compare diversity within sites and include both total species richness and the abundance of those species. Simpson's Index "is a weighted arithmetic mean of proportional abundance and measures the probability that two individuals randomly selected from a sample will belong to the same species" (Kiernan 2019). I used Inverse Simpson's (1/D) where possible index values range from one (lowest) to the total number of species (highest); the highest index values would occur if all species were present and perfectly even. The Shannon Index (H) measures the "degree of uncertainty of predicting the species of a random sample" where higher values reflect higher uncertainty and thus that samples are more even (i.e. not dominated by a single species) (Kiernan 2019). Diversity values were calculated for sites with a history of chemical control, and those without, and plots where *L. vulgaris* was present and plots where it was absent. The groups were tested for significant differences using a linear regression model and ANOVA with a chi test.

Beta diversity compares the diversity between ecologically similar sites. Beta diversity was investigated with the Jaccard and Morisita-Horn Indices. The Jaccard index values are the number of species common to each site; i.e. how many species overlap. Morisita-Horn considers abundance, unlike Jaccard, in addition to sample overlap. Index values were calculated for treated and untreated sites, then variance between treatments was calculated using distance matrices (ADONIS). Principal coordinate analysis (PCoA) was used to visualize the beta diversity similarity between sites. The beta-diversity calculations were not appropriate for comparing plots based on *L. vulgaris* presence and absence since plots were paired within sample sites; but were included to account for variance.

Total abundance was calculated by totaling abundance (as percentage cover) for a given species across all plots and then ranking them by order of abundance. Difference in composition between groups was then calculated: total abundance of species in untreated plots was subtracted from total abundance for the same species in treated plots, and abundance where *L. vulgaris* was absent was subtracted from abundance where it was present.

Results

Total Species Richness

A total of 65 different species were found between the 60 sample plots. Total richness ranged from 2 to 10 species within a single plot, with a mean of 6 species per plot. For plots with a history of chemical treatment and those without, the range and mean were the same (2 to 10 species per plot with a mean of 6). A history of chemical treatment was not a significant variable for total species richness ($p = 0.711$; Figure 3). *Linaria vulgaris* presence approached significance as an explanatory factor for total richness ($p = 0.064$; Figure 3), potentially due to its presence. The mean species richness in plots with *L. vulgaris* present was 6, and the mean was 5 where it was absent; the median richness for both *L. vulgaris* present and absent plots was 5. In the subset of data that included only plots where *L. vulgaris* was present, treatment history was not a significant variable for total richness (p = 0.535).

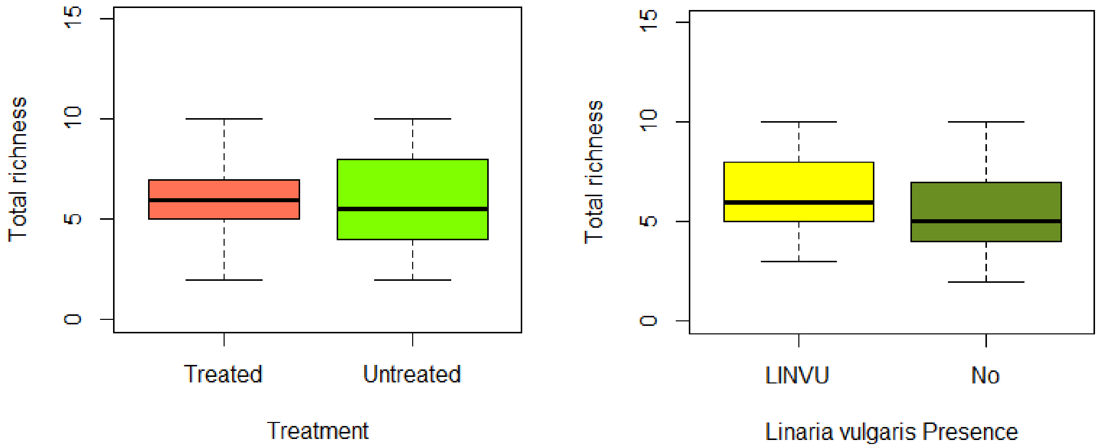


Figure 3: Total species richness between groups based on treatment history (left) and *Linaria vulgaris* presence (right; *L. vulgaris* present (LINVU), or absent (No)).

Treatment History

A history of herbicide treatment did not have a significant effect on *L. vulgaris* abundance within the "*L. vulgaris* present" data subset (p = 0.129; Figure 4). Treatment history did not have a significant effect on amount of bareground (p = 0.284); bareground ranged from 0 to 85% overall with a mean of 41%. In treated sites, bareground also ranged from 0 to 85% with a mean of 41%, and in untreated sites, it ranged from 3 to 85% with the same mean of 41%. Treatment history was, however, a significant explanatory variable for the abundance of non-native species excluding *L. vulgaris* (p < 0.001; Figure 4). The percent cover of non-natives ranged from 0 to 90 overall, with a mean of 12; the range for treated plots was also 0 to 90 but the mean was 22, while the range for untreated plots was 0 to 10 with a mean of 2.

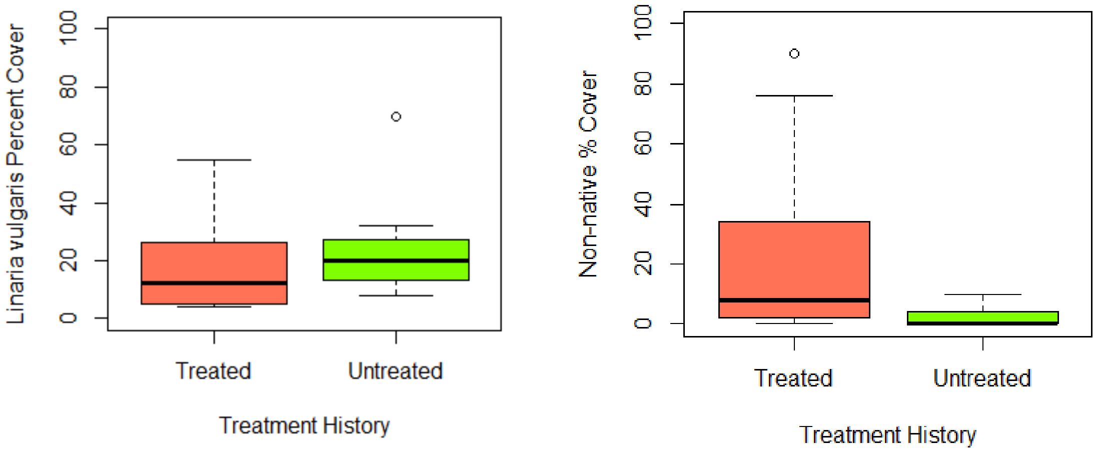


Figure 4: Abundance of *Linaria vulgaris* based on treatment history for the “*L. vulgaris* present” datat subset (left) and non-native species abundance excluding *L. vulgaris* based on treatment history based on full data (right).

Diversity Indices

Alpha diversity values calculated with Inverse Simpson’s Diversity Index (1/D) ranged from 1.23 to 7.57 with a mean of 3.31; diversity values calculated with Shannon’s Diversity Index (H) ranged from 0.36 to 2.05 with a mean of 1.30. Diversity did not vary significantly between sites with a history of chemical control and those without (1/D p = 0.401; H p = 0.605). Similarly, in the subset of data limited to plots where *L. vulgaris* was present, diversity did not significantly vary between sites based on treatment (1/D p = 0.4047; H p = 0.416). Alpha diversity did vary significantly between plots based on *L. vulgaris* presence (1/D p = 0.039; H p = 0.042; Figure 5). Index values were higher where *L. vulgaris* was present, indicating increased diversity- i.e. *L. vulgaris* did not form a monoculture.

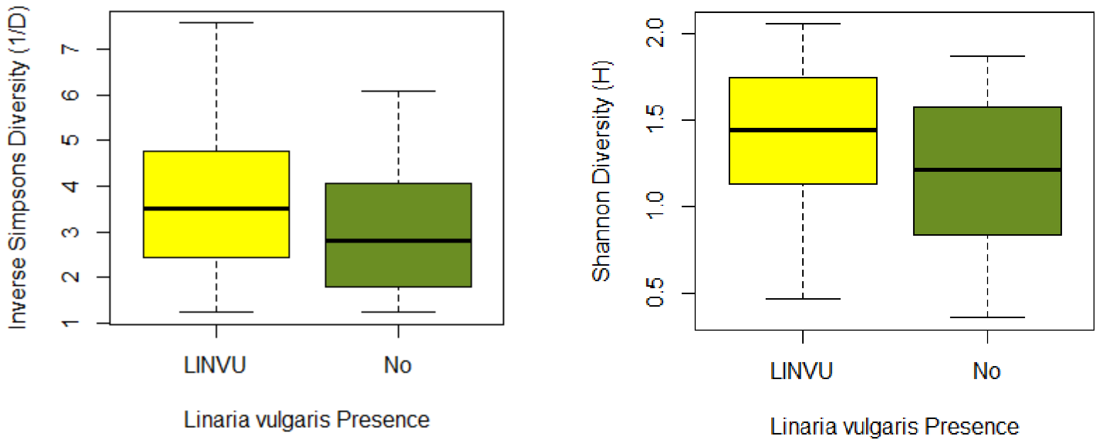


Figure 5: Alpha diversity comparison between plots based on *Linaria vulgaris* presence or absence (*L. vulgaris* present (LINVU), or absent (No)). Inverse Simpson's Diversity Index comparison (left) and Shannon Diveristy Index comparison (right).

Analysis of beta diversity dissimilarity with Jaccard's Index found that overall, treated sites were only 8.3% similar, untreated sites were only 9.7% similar, and untreated sites were only 4.5% similar to treated sites; differences were significant, but treatment only explained 6.02% of the dissimilarity ($p = 0.001$, $R^2= 0.060$). Analysis of abundance based on beta diversity dissimilarity with Morisita-Horn's Index found that overall, treated sites were 18.6% similar, untreated sites were 21.4% similar, and untreated sites were 10.7% similar to treated sites; differences were significant, and treatment explained 10.1% of the dissimilarity ($p = 0.001$, $R^2= 0.101$). This means that, overall sites are ecologically dissimilar and did not share many species though richness is similar. Principal coordinate analysis was used to visually assess the differences (Figure 6).

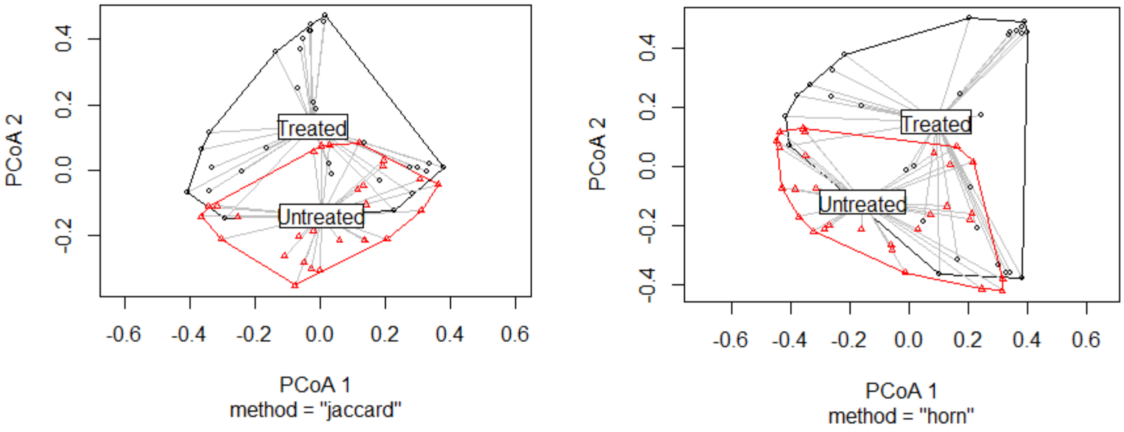


Figure 6: Principal coordinate analysis between treated and untreated sites using beta-diversity index data with the Jaccard Index values (left) and the Morisita-Horn Index values (right).

Relative Species Abundance

Relative species abundance was similar between comparison groups (treated vs. untreated; *L. vulgaris* present vs. absent; Figure 7). However, the composition of those species differs (Table 1). In the treated plots, *Poa pratensis* and *Bromus inermis* were the highest ranked (437 and 132 respectively); neither species was found in untreated plots. In untreated plots, *Eriogonum* spp. (native buckwheat not identified to species level) and *Festuca idahoensis* were the highest ranked (-325 and -153 respectively); these species were not found in treated plots. In plots where *L. vulgaris* was present, it was the most abundant species (597), second was *Eriogonum* spp. (71) followed by *Carex* spp. (55). Where *L. vulgaris* was absent, *Antennaria* spp. (native pussytoes not identified to species level) and *Pascopyrum smithii* were the highest ranked (-130 and -105, respectively).

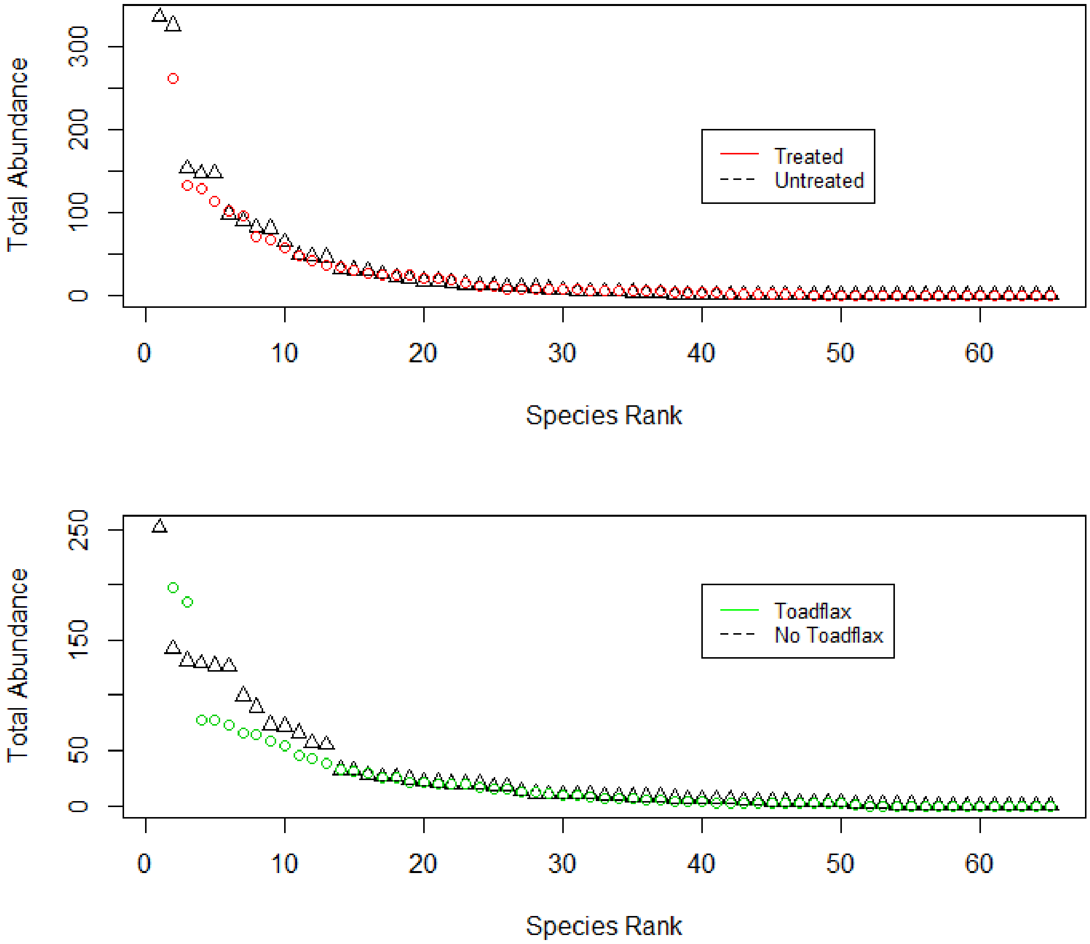


Figure 7: Total species abundance by treated and untreated sites (top) and by *Linaria vulgaris* presence and absence (bottom) with each species ranked by abundance.

Table 1: Ranked species abundance difference between treated/untreated and *Linaria vulgaris* present and absent groups. The values represent differences in composition and are calculated by subtracting totals between groups. Higher numbers indicate greater differences between groups, regardless of positive or negative signs.

Ranked Species Abundance Difference Between Groups

Group	Species	Type	Rank	Group*	Species	Type	Rank
Treated	*Poa pratensis*	*Grass*	437	*L. vulgaris* Present	*Eriogonum* spp.	Forb	71
Treated	*Bromus inermis*	*Grass*	132	*L. vulgaris* Present	*Carex* spp.	Sedge	55
Treated	*Fragaria virginiana*	*Forb*	103	*L. vulgaris* Present	*Solidago missouriensis*	Forb	44
Treated	*Pseudoroegneria spicata*	*Grass*	71	*L. vulgaris* Present	*Mahonia repens*	Sub-Shrub	30
Treated	*Phlox* spp.	*Forb*	70	*L. vulgaris* Present	*Symphoricarpos albus*	Shrub	27
Untreated	*Eriogonum* spp.	*Forb*	-325	*L. vulgaris* Absent	*Antennaria* spp.	Forb	-130
Untreated	*Festuca idahoensis*	*Grass*	-153	*L. vulgaris* Absent	*Pascopyrum smithii*	Grass	-105
Untreated	*Pascopyrum smithii*	*Grass*	-147	*L. vulgaris* Absent	*Poa praetensis*	Grass	-67
Untreated	*Antennaria* spp.	*Grass*	-140	*L. vulgaris* Absent	*Elymus trachycaulus*	Grass	-65
Untreated	*Linaria vulgaris*	*Forb*	-75	*L. vulgaris* Absent	*Eurybia integrifolia*	Forb	-59

*Excluding Linaria vulgaris which had a total 597, making it the top "*L. vulgaris* present" species.

Discussion

Total species richness did not decline, rather it tended to be slightly higher based on *L. vulgaris* presence. The mean richness varied by one, indicating that far from the prevailing narrative that *L. vulgaris* forms a monoculture and displaces native species, it instead acts as a “plus one” in plant communities. My findings are consistent with previous findings that *L. vulgaris* does not seem to adversely affect species richness (Sutton et al. 2007; Pauchard et al. 2003; Lehnhoff 2008). Though *L. vulgaris* does spread clonally and Sing et al. (2016) report that it can form monoculture infestations in the intermountain west, this was not the case for my sample plots. *Linaria vulgaris* tended to occur in an open canopy mixed with other species.

Species richness at sites with a history of herbicide use for the control of *L. vulgaris* did not differ significantly from sites with no known history of herbicide treatments. Potential negative impacts of herbicide use include a decrease in species richness (Pearson et al. 2016b), but this does not appear in the data. Yellowstone National Park typically uses selective herbicides applied as spot treatments (Vincent Nagashima, YNP Resource Management personal communication), which may be a mitigating factor. Although it is good news that chemical control is not associated with decreased total richness, it is less encouraging that *L. vulgaris* abundance was not substantially different in treated and untreated sites. This finding may be a product of the sampling strategy: plots were not randomly spread over a given area, rather they were based on *L. vulgaris* presence. A different sampling method may have produced a different result, but experimental work would still be required to establish causal links. This apparent lack of efficacy means that non-native plant managers should implement rigorous monitoring when they use herbicide or any other management methods to better understand the effects of treatments. For managers, this also warrants investigation into other management options to meet legislative control mandates like the use of biocontrol insects.

The amount of non-native plant cover (excluding *L. vulgaris*) was significantly related to treatment history. The dominant non-native species driving high non-native cover were both invasive, perennial, clonal grasses (*Bromus inermis* and *Poa pratensis*).

One possible explanation is that secondary invasion was possible after suppression of the target non-native forb; i.e., the grasses were released with the application of broadleaf specific herbicide, which would be in accordance with Pearson et al. (2016b) and Wagner et al. (2017). However, another possible explanation is that rather than any effect from herbicide use, the sites where those grasses were present were closer to well-traveled roads, and their presence is simply an artifact of disturbance associated with road construction and/or propagule introductions intentionally for revegetation effort or unintentionally from vehicles.

Alpha diversity values did not vary significantly based on treatment history. This is encouraging, as it indicates that even if herbicide use is promoting secondary invasion (and it's not clear that it is) single species are not dominating plots. The significant difference in alpha-diversity index values based on *L. vulgaris* presence for both Shannon and Inverse Simpson was surprising. If index values were significantly lower where *L. vulgaris* was present, that would fit the narrative that it forms monoculture infestations. However, index values were higher where *L. vulgaris* was present indicating that it did not dominate. So, non-native plant managers should not assume that *L. vulgaris* negatively impacts diversity, but rather evaluate impacts for their sites.

The dissimilarity indices found significant differences between sites, which means that they did not share many of the same species, but also attributed little of the difference to the effect of treatment. This is consistent with sampling- sample sites were chosen from known *L. vulgaris* patches and were widely spaced geographically and differed in proximity to water and roads, and other site characteristics like soil type and fire history. See Appendix A for sample site descriptions and Appendix B for sample site photos.

Relative species abundance was similar between comparison groups (treated vs. untreated; *L. vulgaris* present vs. absent; Figure 7), but the composition of those species differs (Table 1). The differences in rank species abundance based on *L. vulgaris* presence is unexpected since plots were paired at sites within and adjacent to patches. *Antennaria* spp. was the highest difference in the *L. vulgaris* absent plots at rank -130, so *L. vulgaris* may be a direct competitor. However, *Antennaria* also ranks high on the untreated group at -140, so it may be suppressed by chemical control targeting *L. vulgaris.* Another possible explanation is simply *Antennaria's* mat-forming, groundcover type growth habit; in the plots where it did occur, it was very abundant (see Fig. 8). Similarly, *Eriogonum* spp. also has a mat-forming, groundcover type habit. It was the highest rank in untreated sites (-325), so it may be suppressed by chemical treatment, or it may simply be an artifact of its life-form. A better understanding of links between species community shifts and herbicide treatment or *L. vulgaris* presence requires long term monitoring focused on these points.

Figure 8: Photo of site #6 plot #6 where *Antennaria* spp. was present.

Conclusion

As this study is observational, causal links cannot be determined from my data. *Linaria vulgaris* is apparently more likely to be a “plus one” in plant communities (as it is associated with an increase of one species in mean richness) rather than a cause of negative change in species richness or diversity. This does not fit the prevailing narrative and means that non-native plant managers should not assume that control of *L. vulgaris* is warranted at their site. Although a history of herbicide treatment is not associated with negative impacts on species richness or diversity, it is also not significantly associated with a reduction in *L. vulgaris* abundance and may be a factor in secondary invasion. Thus, at least in the short term, *L. vulgaris* should not be a priority for managers to treat with herbicide. Instead, other management options like biocontrol should be explored to meet legislative mandates for control, and more rigorous monitoring programs established to determine the efficacy of treatment when it does occur and to capture plant community shifts over time.

Given the centuries in residence in North America, it is possible that *L. vulgaris* is no longer the “most hurtful plant” (Mack 2003) that it was in the eastern US in the 1700s. It is also possible that even though it is undeniably successful at spreading across the continent, it has never been very “hurtful” in the West Yellowstone area. Another possibility is that the 2019 season captured in my data was an anomalous season for *L. vulgaris;* but my findings are consistent with earlier work showing that *L. vulgaris* did not have a negative impact on native richness (Sutton et al. 2007; Pauchard et al. 2003; Lehnhoff 2008). More complex and long-term experimental work is warranted to establish causal links (or a lack of causal links) between *L. vulgaris* presence and negative effects. However, given the lack of evidence of negative effects after multiple observational studies and nearly 400 years on the continent, it is likely safe to consider *L. vulgaris* a low priority for management. Ultimately, it is important for non-native plant managers to evaluate the impact of non-native species at their sites, and to monitor the efficacy and potential side effects of herbicide use rather than assume that non-native plants are bad and that chemical control is the answer.

REFERENCES CITED

Boutin, C., Strandberg, B., Carpenter, D., Mathiassen, S., & Thomas, P. (2014). Herbicide impact on non-target plant reproduction: What are the toxicological and ecological implications? *Environmental Pollution.* 185: 295-306.

Boswell, A., Sing, S.E., Ward, S.M. (2016) Plastid DNA analysis reveals cryptic hybridization in invasive Dalmatian toadflax (Linaria dalmatica) populations. *Invasive Plant Science and Management*. 9: 112– 120.

CABI. (2020). *Linaria vulgaris*. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc

Callaway, R. M. and Ridenour, W. M. (2004). Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment.* 2(8): 436-443.

Crone, E., Marler, M., & Pearson, D. (2009). Non-target effects of broadleaf herbicide on a native perennial forb: A demographic framework for assessing and minimizing impacts. *Journal of Applied Ecology.* 46(3), 673-682.

DiTomaso, J.M., Kyser, G.B., et al. (2013). Weed Control in Natural Areas of the Western United States. Weed Research and information Center, University of California. 544 pp.

EDDMapS. (2020). Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. Available online at http://www.eddmaps.org/; last accessed April 4, 2020.

Elton, C. S. (1958). The ecology of invasions by animals and plants. Methuen, London, UK.

Grime P.J. (1973). Control of species density in herbaceous vegetation. *J Environ Manage* 1:151–167

Jachuła, J., Konarska, A., & Denisow, B. (2018). Micromorphological and histochemical attributes of flowers and floral reward in *Linaria vulgaris* (Plantaginaceae). *Protoplasma, 255*(6), 1763-1776.

Hulme, P.E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*. 46, 10–18. doi: 10.1111/j.1365-2664.2008.01600.x

Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U. & Vilà, M. (2013). Bias and error in understanding plant invasion impacts. *Trends in Ecology and Evolution*, 28, 212– 218.

James, J., Sheley, R., & Smith, B. (2012). Ecological principles underpinning invasive plant management tools and strategies. *Rangelands, 34*(6), 27-29.

Kettenring, K., & Reinhardt Adams, C. (2011). Lessons learned from invasive plant control experiments: A systematic review and meta-analysis. *Journal of Applied Ecology.* 48(4), 970-979.

Kiernan, D. (2019). 10.1: Introduction, Simpson's Index and Shannon-Weiner Index. LibreTexts. Accessed 4.12.20. <https://stats.libretexts.org/Bookshelves/Applied_Statistics/Book%3A_Natural_Resources_Biometrics_(Kiernan)/10%3A_Quantitative_Measures_of_Diversity%2C_Site_Similarity%2C_and_Habitat_Suitability/10.01%3A_Introduction%2C__Simpson%E2%80%99s_Index_and_Shannon-Weiner_Index>.

Kueffer, C., McDougall, K., Alexander, J., Daehler, C., Edwards, P., Haider, S., Milbau, A., et al. (2013). Plant invasions into mountain protected areas: assessment, prevention and control at multiple spatial scales. *Plant Invasions in Protected Areas*. 89–113.

Kumar, S., Stohlgren, T., & Chong, G. (2006). Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*. 87(12), 3186-3199.

Lehnhoff, E.A. (2008). Invasiveness of Yellow Toadflax *(Linaria vulgaris)* resulting from disturbance and environmental conditions. Doctoral dissertation prepared for Montana State University.

Lehnhoff, E.A., Rew, L.J., Maxwell, B.D., Taper, M.L. (2008). Quantifying invasiveness: A case study of *Linaria vulgaris. Invasive Plant Sci. Manag*. 1:319–325.

Levine JM, Vila` M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc Biol Sci Ser B* 270:775–781

Lindenmayer, D. B., Wood, J., MacGregor, C., Hobbs, R. J., & Catford, J. A. (2017). Non-target impacts of weed control on birds, mammals, and reptiles. *Ecosphere*, 8(5). https://doi.org/10.1002/ecs2.1804

Lonsdale, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80(5), pp. 1522–1536

MacDougall AS, Turkington R (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55

Mack, Richard. (2003). Plant Naturalizations and Invasion in the Eastern United States: 1634-1860. *Annal of the Missouri Botanical Garden.* 90(1): 77-90.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, 10, 689–710.

Magee, T. K., Ringold, P. L., Bollman, M. A., & Ernst, T. L. (2010). Index of Alien Impact: A Method for Evaluating Potential Ecological Impact of Alien Plant Species. *Environmental Management.* 45 (4):759–78.

Maltz, M.R., Bell, C.E., Mitrovich, M.J., Iyer, A.R., Treseder, K. K. (2016). Invasive plant management techniques alter arbuscular mycorrhizal fungi. *Ecological Restoration.* 34(3), 209-215.

Maron JL, Klironomos J, Waller L, Callaway RM, (2014). Invasive plants escape from suppressive soil biota at regional scales. *Journal of Ecology* (Oxford), 102(1):19-27. http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-2745

Maxwell, B., Lehnhoff, E., & Rew, L. (2009). The rationale for monitoring invasive plant populations as a crucial step for management. *Invasive Plant Science and Management.* 2(1), 1-9.

McCartney, K. R., Kumar, S., Sing, S. E., Ward, S. M. (2019). Using invaded-range species distribution modeling to estimate the potential distribution of *Linaria* species and their hybrids in the U.S. northern Rockies. *Invasive Plant Science and Management., 12*(2), 97-111.

McDermott, S., Irwin, R., & Taylor, B. (2013). Using economic instruments to develop effective management of invasive species: Insights from a bioeconomic model. *Ecological Applications*. 23(5), 1086-1100. Retrieved from http://www.jstor.org.proxybz.lib.montana.edu/stable/23441608.

NRCS. Web Soil Survey. U.S. Department of Agriculture Natural Resources Conservation Service. Accessed 3.18.20. <https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm>.

Palmquist, E., Sterner, S., & Ralston, B. (2019). A comparison of riparian vegetation sampling methods along a large, regulated river. *River Research and Applications, 35*(6), 759-767.

Pauchard, A., Alaback, P.B., Edlund, E.G. (2003). Plant invasions in protected areas at multiple scales: *Linaria vulgaris* (Scrophulariaceae) in the West Yellowstone area. *Western North American Naturalist*. 63 (4):416–428.

Pearson, D., Ortega, Y., Eren, Ö, & Hierro, J. (2016a). Quantifying "apparent" impact and distinguishing impact from invasiveness in multispecies plant invasions. *Ecological Applications.* 26(1), 162-173. Retrieved March 9, 2020, from www.jstor.org/stable/24701228

Pearson, D., Ortega, Y., Runyon, J., & Butler, J. (2016b). Secondary invasion: The bane of weed management. *Biological Conservation, 197*(C), 8-17.

Pimentel, D., Zuniga, R., Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economic*s. 52 (3): 273-288.

Pinto, S.M., Ortega, Y.K. (2016). Native species richness buffers invader impact in undisturbed but not disturbed grassland assemblages. *Biol Invasions*. DOI 10.1007/s10530-016-1208-0

Pollnac, F.W. (2012). Non-native plant species in mountainous areas: a case study of *Linaria dalmatica* in the Greater Yellowstone Ecosystem. Doctoral dissertation prepared for Montana State University.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rew, L., Maxwell, B., Dougher, F., & Aspinall, R. (2006). Searching for a needle in a haystack: Evaluating survey methods for non-indigenous plant species. Biological Invasions, 8(3), 523-539.

Ricciardi, A., Cohen, J. (2007). The invasiveness of an introduced species does not predict its impact. *Biological Invasions*. 9 (3):309–315.

Richardson, D.M., Pyšek, P. (2012). Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytologist*, 196, 383– 396.

Richardson, D.M. and Pysek, P. (2006). Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*. 30 (3): 409-431.

Richardson DM, Pysˇek P, Rejma´nek M, Barbour MG, Panetta FD, West CJ. (2000). Naturalization and invasion of alien plants: concepts and definitions. Divers Distributions 6:93–107

Rinella, M., Maxwell, B., Fay, P., Weaver, T., & Sheley, R. (2009). Control effort exacerbates invasive-species problem. *Ecological Applications, 19*(1), 155-162.

Saner, M., Clements, D., Hall, M., Doohan, D., & Crompton, C. (1995). THE BIOLOGY OF CANADIAN WEEDS .105. LINARIA-VULGARIS MILL. *Canadian Journal of Plant Science, 75*(2), 525-537.

Schat, M., Sing, S.E., Peterson, R.K., Menalled, F.D., Weaver, D.K. (2011). Growth inhibition of Dalmatian toadflax, *Linaria dalmatica* (L.) Miller, in response to herbivory by the biological control agent *Mecinus janthinus* Germar. *Journal of Entomological Science*, 46, 232– 246.

Sing, S.E., De Clerck-Floate, R., Hansen, R.W., Pearce, H., Randall, C.B., Toševski, I., and Ward, S.M. (2016). Biology and Biological Control of Dalmatian and Yellow Toadflax. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, West

Virginia. FHTET-2016-01. <https://www.fs.fed.us/rm/pubs_journals/2016/rmrs_2016_sing_s001.pdf>

Sing, S.E. and Peterson, R.K.D. (2011). Assessing environmental risks for established invasivewWeeds: Dalmatian (*Linaria dalmatica*) and Yellow (*L. vulgaris*) Toadflax in North America. *International Journal of Environmental Research and Public Health*. 2011 Jul; 8(7): 2828–2853.

Sing, S.E., Peterson, R.K., Weaver, D.K., Hansen, R.W., Markin, G.P. (2005). A retrospective analysis of known and potential risks associated with exotic toadflax-feeding insects. *Biological Control*, 35, 276– 287.

Skurski, T., Maxwell, B., & Rew, L. (2013). Ecological tradeoffs in non-native plant management. *Biological Conservation*, 159, 292-302.

Skurski, T.C., Rew, L.J., Maxwell, B.D. (2014). Mechanisms underlying nonindigenous plant impacts: a review of recent experimental research. *Invasive Plant Science and Management*. DOI: 10.1614/IPSM-D-13-00099.1

Stohlgren, T., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J., & Master, L. (2006). Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasion*s, 8(3), 427-447.

Sutton, J.R., Stohlgren, T.J. & Beck, K.G. (2007). Predicting yellow toadflax infestation in the Flat Tops Wilderness of Colorado. *Biological Invasions.* 9: 783. https://doi-org.proxybz.lib.montana.edu:3443/10.1007/s10530-006-9075-8

Tosevski, I., Caldara, R., Jovic, J., Hernandez-Vera, G., Baviera, C., Gassmann, A., Emerson, B. (2011). Morphological, molecular and biological evidence reveal two cryptic species in *Mecinus janthinus* Germar (Coleoptera, Curculionidae), a successful biological control agent of Dalmatian toadflax, *Linaria dalmatica* (Lamiales, Plantaginaceae). *Systematic Entomology*. 36 (4): 741-753. 10.1111/j.1365-3113.2011.00593.x

Toševski, I., Sing, S., De Clerck-Floate, R., McClay, A., Weaver, D., Schwarzländer, M., Krstić, O., Jović, J., and Gassmann, A. (2018). Twenty-five years after: post-introduction association of *Mecinus janthinus* s.l. with invasive host toadflaxes *Linaria vulgaris* and *Linaria dalmatica* in North America. *Ann Appl Biol*. 173: 16-34. doi:10.1111/aab.12430

Van Hezewijk, B.H., Bourchier, R.S., De Clerck-Floate, R.A. (2010). Regional-scale impact of the weed biocontrol agent *Mecinus janthinu*s on Dalmatian toadflax (*Linaria dalmatica*). *Biological Control, 55,* 197– 202.

Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Ch Jaros, V., Maron, J.L., Pergi, J., Schaffner, U., Sun, Y., Pysek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*. doi: 10.1111/j.1461-0248.2011.01628.x

Vila, M., Rohr, R.P., Espinar, J.L., Hulme, P.E., Pergl, J., Le Roux, J.J., Schaffner, U., Pysek, P., (2014). Explaining the variation in impacts of non-native plants on local-scale species richness: the role of phylogenetic relatedness. *Global Ecology and Biogeography*. DOI: 10.1111/geb.12249

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek and R. Westbrooks (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21(1): 1-16.

Wagner, V., Antunes, P.M., Irvine, M. and Nelson, C.R. (2017), Herbicide usage for invasive non-native plant management in wildland areas of North America. *Journal of Applied Ecology*, 54: 198-204. doi:10.1111/1365-2664.12711

Ward, S.M., Fleischmann, C.E., Turner, M.F. & Sing, S.E. (2009). Hybridization between invasive populations of Dalmatian toadflax (*Linaria dalmatica*) and yellow toadflax (*Linaria vulgaris*). *Invasive Plant Science and Managemen*t, 2, 369–378.

Weed, A.S., Milan, J., Schwarzlaender, M. (2017). Analyses of nine years of citizen-based biological control monitoring of Dalmatian toadflax, *Linaria dalmatica* (Plantaginaceae) in Idaho, USA. *BioControl*. 58(4). DOI 10.1007/s10526-017-9848-2

Wilke, B.J. & Irwin, R.E. (2010) Variation in the phenology and abundance of flowering by native and exotic plants in subalpine meadows. *Biological Invasions* 12: 2363. https://doi-org.proxybz.lib.montana.edu:3443/10.1007/s10530-009-9649-3

Wolfe, B., Rodgers, V., Stinson, K., & Pringle, A. (2008). The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *Journal of Ecology*, 96(4), 777-783.

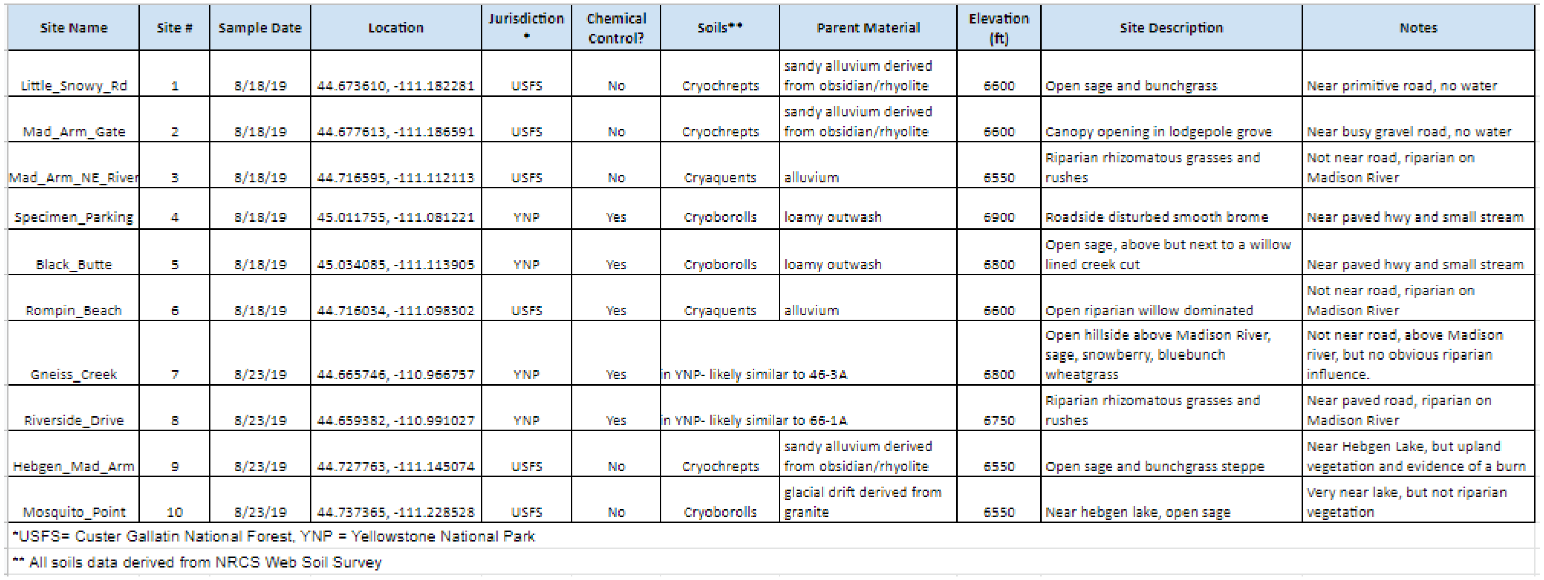
WRCC. West Yellowstone, MT (248857). NOAA Cooperative Stations. Western Regional Climate Center. Accessed 3.18.20. <https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt8857>.

Zoric, A.S., Morina, F., Tosevski, I., Tosti, T., Jovic, J., Krstic, O., Veljovic-Jovanovic, S. (2019). Resource allocation in response to herbivory and gall formation in *Linaria vulgaris*. *Plant Physiology and Biochemistry*. 135: 224-232. https://doi.org/10.1016/j.plaphy.2018.11.032

Zouhar K, 2003. Fire Effects Information System (FEIS)., USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.feis-crs.org/beta/

APPENDICES

APPENDIX A: Sample Site Descriptions

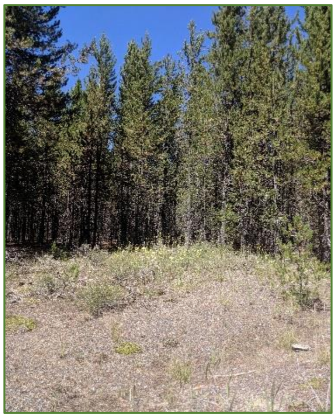


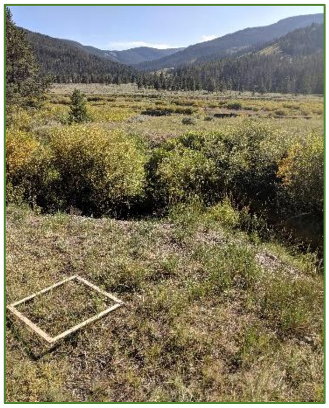
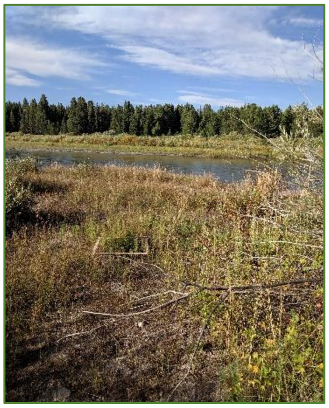
Site Name	Site #	Sample Date	Location	Jurisdiction *	Chemical Control?	Soils**	Parent Material	Elevation (ft)	Site Description	Notes
Little_Snowy_Rd	1	8/18/19	44.673610, -111.182281	USFS	No	Cryochrepts	sandy alluvium derived from obsidian/rhyolite	6600	Open sage and bunchgrass	Near primitive road, no water
Mad_Arm_Gate	2	8/18/19	44.677613, -111.186591	USFS	No	Cryochrepts	sandy alluvium derived from obsidian/rhyolite	6600	Canopy opening in lodgepole grove	Near busy gravel road, no water
Mad_Arm_NE_River	3	8/18/19	44.716595, -111.112113	USFS	No	Cryaquents	alluvium	6550	Riparian rhizomatous grasses and rushes	Not near road, riparian on Madison River
Specimen_Parking	4	8/18/19	45.011755, -111.081221	YNP	Yes	Cryoborolls	loamy outwash	6900	Roadside disturbed smooth brome	Near paved hwy and small stream
Black_Butte	5	8/18/19	45.034085, -111.113905	YNP	Yes	Cryoborolls	loamy outwash	6800	Open sage, above but next to a willow lined creek cut	Near paved hwy and small stream
Rompin_Beach	6	8/18/19	44.716034, -111.098302	USFS	Yes	Cryaquents	alluvium	6600	Open riparian willow dominated	Not near road, riparian on Madison River
Gneiss_Creek	7	8/23/19	44.665746, -110.966757	YNP	Yes	in YNP- likely similar to 46-3A		6800	Open hillside above Madison River, sage, snowberry, bluebunch wheatgrass	Not near road, above Madison river, but no obvious riparian influence.
Riverside_Drive	8	8/23/19	44.659382, -110.991027	YNP	Yes	in YNP- likely similar to 66-1A		6750	Riparian rhizomatous grasses and rushes	Near paved road, riparian on Madison River
Hebgen_Mad_Arm	9	8/23/19	44.727763, -111.145074	USFS	No	Cryochrepts	sandy alluvium derived from obsidian/rhyolite	6550	Open sage and bunchgrass steppe	Near Hebgen Lake, but upland vegetation and evidence of a burn
Mosquito_Point	10	8/23/19	44.737365, -111.228528	USFS	No	Cryoborolls	glacial drift derived from granite	6550	Near hebgen lake, open sage	Very near lake, but not riparian vegetation

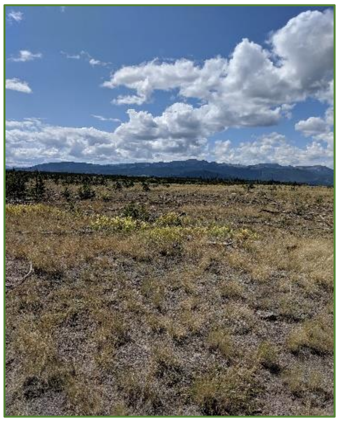
*USFS= Custer Gallatin National Forest, YNP = Yellowstone National Park

** All soils data derived from NRCS Web Soil Survey

APPENDIX B: Sample Site Photos


Sample sites #1-10 from top left to right. Sites 3, 6, and 8 classified as riparian. Site 10, though very close to Hebgen Lake, has no wetland