NONINDIGENOUS PLANT SPECIES DISTRIBUTIONS: MODELING THE ROLE OF HUMAN DISTURBANCES AND PREDICTING MANAGEMENT RESPONSES

by

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ABSTRACT

The current paradigm of nonindigenous plant species (NIS) management assumes all NIS populations are invasive and ignores that different populations of the same species have different dynamics and respond differently to perturbations in dissimilar environments. Species distribution models (SDM) can predict spatial patterns of NIS environmental suitability and form a link between management objectives and species distributions. The objectives of this dissertation were to evaluate the utility of SDMs for NIS management. Specifically, the spatial transferability of models, the importance of land uses in explaining NIS distributions, and the relationships between management efficacy and SDM predictions were assessed.

The first objective evaluated the transferability of SDMs for two NIS among neighboring regions representing a three-point gradient of human disturbance intensities. The models did not adequately transfer between the two management units representing the least and greatest intensities of human disturbances. This suggested NIS might be distributed differently in response to human disturbances. The second objective compared the relative roles of environmental, current land use, and historical land use variables on explaining occupancies for six NIS. Historical land use explained greater amounts of the variation in NIS occupancies as compared to only environmental variables or environmental plus current land use variables. Land uses currently or previously irrigated for agriculture increased predicted probabilities of occurrence for multiple NIS, including an introduced perennial forage species. The final objective assessed the applicability of SDMs to prioritize NIS populations for management treatments. Herbicide treatments were applied to populations of two NIS located along a gradient of their respective SDM predictions. The effect of herbicide treatment on NIS densities varied either positively or negatively with predicted environmental suitability depending on the specific species. Thus, NIS population responses may be predictable and treatment prioritized using SDM predictions; however, contrasting responses between the two NIS evaluated suggested management should be adapted for species and site specific conditions. This study showed that human disturbance history can affect how NIS are distributed, and, thus, SDMs should be generated from site specific data. Further, SDMs can guide managers as to which NIS populations should be prioritized for management.

CHAPTER ONE

INTRODUCTION

Prologue

The current paradigm of weed management is primarily species-centric. That is, particular species are detrimental and need to be actively managed to prevent, eradicate, or contain their occurrence. Often we see images on television, in newspapers, on signs in public parks, and even sometimes as professional weed science meetings perpetuating the notion that weeds are *bad*, are the *enemy*. In fact, we often hear terminology such as the "war on weeds" or "weed warriors" to describe weed control practices and the people who administer them. Protecting our field research sites from *vigilante* weed warriors is a running joke among weed scientists. There are several summer days at Burke Park in Bozeman, Montana where I have seen a nicely laid pile of spotted knapweed stems placed by a trail head indicating someone as taken it upon himself to hand pull as much as he could from existing patches in the park. Of course, such individuals do not know that Dr. Maxwell takes his undergraduate weed ecology class there every year to make measurements of patch densities and areas to teach students about the importance of monitoring and illustrate how not all weed patches are invasive (i.e., increasing in density and/or spatial extent over time). It was while I was serving as a teaching assistant for that same class when I learned a graduate student in a social sciences department, on whose committee Dr. Maxwell served, found remarkable similarities between how weeds are

currently depicted in the media and how Native Americans were in the 1800s. Thus, the prevailing public perception is that weeds are bad.

There are examples that certain weedy species are detrimental (Mack 1981; D'Antonio and Vitousek 1992; Mack et al. 2000). However, just as a parasite poses little threat without a host, so may be many species of plants when lying dormant as seeds or growing under less than optimal conditions. Still, there is a perception that weeds are bad regardless of the environmental conditions in which they occur. Some species of weeds growing in certain environments may very well be bad insomuch as they interfere with crop productivity, displace desired vegetation, alter multi-trophic organismal interactions, and potentially alter biotic processes so greatly they affect abiotic processes as well (e.g., increasing wildfire frequency) (Brooks et al. 2004). But, the question remains, are weeds the drivers or the passengers of the vehicle inducing environmental changes? Some hypothesize that human presence on a landscape is the real driver, and humans cause disturbances that favor the occurrence of weeds. Thus, weeds are the consequences or symptoms of the real underlying problem. Surely, the answer lies somewhere between these two extremes. Maybe weeds are "back-seat drivers." At first they are just along for the ride, but over time they become a party to the actual agents of change. Whatever the answer, it seems clear that individual species are not the problem; rather, certain interactions of weed populations with their environments may be problematic (Davis et al. 2000).

The research presented in this dissertation was intended to better understand the processes affecting weed species distributions and how understanding weed distributions

could facilitate more efficient and efficacious weed management. This is particularly necessary in range and wildland areas where knowledge of what weed species occur where and how they interact with their environments could facilitate better management decisions (Rew et al. 2007). More suitable environments may harbor more aggressively growing weed populations. Thus, such populations may have relatively more invasive potential than other populations of the same species growing in less suitable environments (Davis et al. 2000). Likewise, we might expect population responses to management treatments to differ among populations growing in different environmental conditions. Thus, our current species-centric paradigm for weed management does not sufficiently exploit our current ecological understanding of the associations between individual plant growth responses and plant population dynamics with environmental suitability. Some weed scientists recognize that there is a need for a paradigm shift that focuses on populations rather than individual species (Lehnhoff et al. 2006; Rew et al. 2007; Maxwell et al. 2009).

My research addressed two overarching objectives that could be applied to practical weed management decisions. The first objective dealt with characterizing environmental suitability and what factors affect predictions of suitability. Accurate characterization of environmental or habitat suitability is an integral component of metapopulation and source-sink theories, which deal with how species are spatially distributed and how those spatial configurations contribute to dynamics of populations. However, such a characterization is challenging for many species, especially for plants who can occupy areas of unsuitable habitat as dormant seeds, areas of exceptional habitat as thriving

rooted populations, and many environments in between (Eriksson 1996; Freckleton and Watkinson 2002). The first two data chapters in this dissertation pertain to how nonindigenous plant species (NIS) are distributed across heterogeneous landscapes and what factors, particularly anthropogenic activities, contribute to their occupancy of certain environments.

The second objective addressed how using such characterizations of NIS distributions could inform management decisions. Specifically, I was interested in the relationships between NIS population dynamics and population responses to management with predictions of environmental suitability models. If predictable relationships exist between simple models of environmental suitability and responses to management, such models could be used to guide the prioritization of populations targeted for management treatments (Rew et al. 2007). Such a prioritization framework could result in more efficient allocation of limited management resources while reducing the spread or abundance of NIS.

Justification for This Research

Species distribution models (SDM) are hypothesized to be useful for testing theories about ecological niches but are rarely evaluated for such purposes (Guisan and Thuiller 2005). SDMs are typically generated by regressing presence/absence data for a specific species on a set of environmental predictor variables to obtain estimates of the species' probabilities of occurrence (Guisan and Zimmermann 2000). The research presented in this dissertation contributes to our knowledge of niche theory and applying niche models (i.e., SDMs) to management decisions at local spatial scales. I tested the hypothesis that

environmental responses of species (i.e., response curves or niche axis positions) to variables defining their niches are consistent among different geographic regions (Thompson et al. 1993; Hill et al. 2000; Prinzing et al. 2002) by evaluating the transferability (i.e., generalization or extrapolation) of SDMs for NIS among neighboring management units with varying intensities of human disturbance. I further assessed the relative role of current and historical land uses for characterizing patterns of NIS occupancy and, thus, influence on species' niches. It is currently poorly understood how SDMs could be used to integrate ecological principles with weed management. Thus, this research also investigated the relationships between NIS environmental suitability as predicted by SDMs and population responses to herbicide applications.

To address the gaps in our current understanding of the portability of NIS distribution models, the role of current and historical land use on NIS distributions, and potential applications for ecologically based prioritization of NIS management using SDMs, three specific questions were addressed and correspond to a standalone chapter/manuscript in this dissertation.

1. How well do nonindigenous plant species distribution models transfer between three neighboring management units that represent a gradient of human disturbance intensities?
2. How do current and historical uses of land affect predicted probabilities of nonindigenous plant species occupancy?

3. What are the relationships between predicted probabilities of nonindigenous plant species occurrence and the responses of target species populations and off target plant communities to chemical weed management?

Study Areas and Data

Presence and absence data for a defined list of NIS were collected between 2001 and 2010 in three neighboring management units representing a gradient of human activity/influence within the Greater Yellowstone Ecosystem (GYE) (Figure 1.1). NIS data collected in these three systems were used to evaluate research questions 1 and 2 relating to the transferability of SDMs and the relative role of land use history for modeling NIS occupancy. Data from these study areas were used to generate SDMs for the species evaluated to answer research question 3. Table 1.1 details the NIS species evaluated in this thesis.

Tables and Figures

Table 1.1 Nonindigenous plant species (NIS) studied in dissertation chapters

Species	Functional Group	Life Cycle[a,b]	Reproduction[c]	Primary Dispersal	Dissertation Chapter	Sources
Bromus inermis Leyess.	Grass	Perennial[a]	Seed; Veg	Wind	4	Heide (1994)
Bromus tectorum L.	Grass	Annual	Seed	Animal	3, 4, 5	Mack (1981)
Centaurea maculosa (Dorn 1984)	Forb	Perennial[a]	Seed	Wind	4	Jacobs and Sheley (1998); Sheley et al. (1998)
Cirsium arvense L.	Forb	Perennial[a]	Seed; Veg	Wind	3, 4	Donald (1994)
Cynoglossum officinale L.	Forb	Perennial[b]	Seed	Animal	4	Upadhyaya et al. (1988)
Linaria dalmatica (L.) Mill.	Forb	Perennial[a]	Seed; Veg	Wind	5	Vujnovic and Wein (1997)
Verbascum thapsus L.	Forb	Biennial	Seed	Wind	4	Gross and Werner (1982); Donnelly et al. (1998)

[a] iteroperous perennial
[b] semelparous perennial
[c] mode of reproduction either by seed (Seed) and/or vegetative (Veg) reproduction

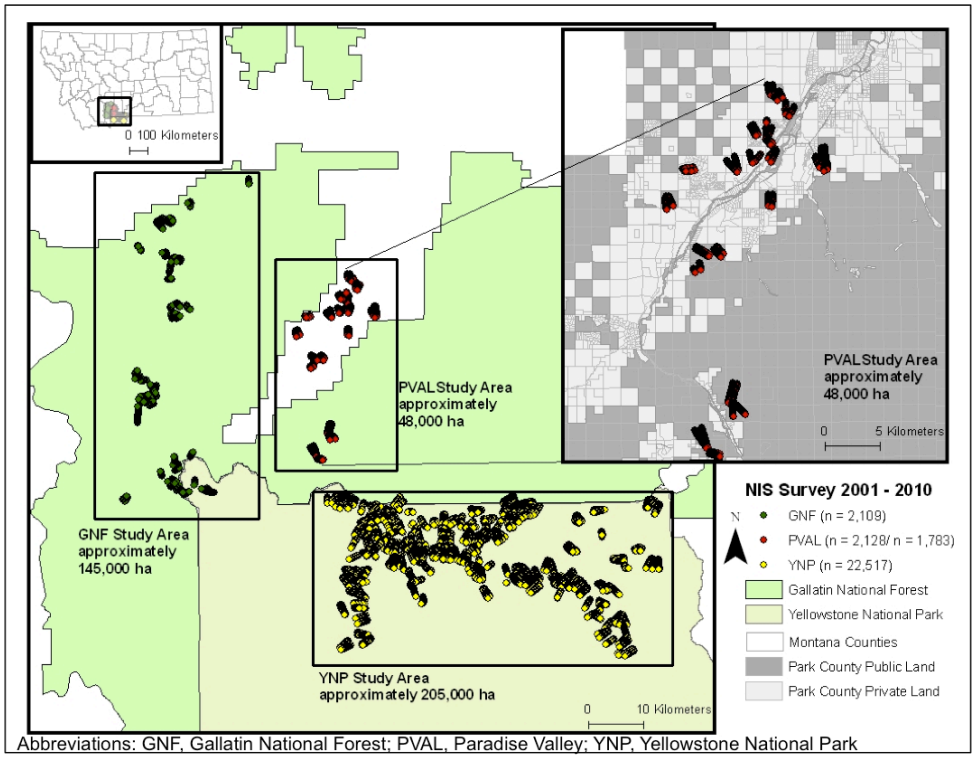


Figure 1.1 Three neighboring management units where presence and absence data for various nonindigenous plant species (NIS) were collected between 2001 and 2010

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CHAPTER TWO

BACKGROUND

Nonindigenous Plant Species Distribution Modeling

Nonindigenous plant Species distribution models (SDM) for nonindigenous plant species (NIS) are presumably useful for land managers and policy makers as they are often applied to guide and prioritize sampling, monitoring, and management decisions (Rew et al. 2007; Fox et al. 2009; Maxwell et al. 2009; Baxter and Possingham 2011; Ervin and Holly 2011; Giljohann et al. 2011). Such models are typically correlative models relating locations of a species' presences and absences to geo-referenced environmental variables (Guisan and Zimmermann 2000). SDMs are commonly used to generate maps characterizing the probability of a species' occurrence. The theoretical foundation for SDMs is based on the concept of a species' ecological or environmental niche (Hutchinson 1957; Guisan and Zimmermann 2000). Hutchinson (1957) defined a species' niche as the multivariate hypervolume of environmental conditions in which a species can complete its life cycle. However, it is currently unresolved as to which niche form SDMs are really modeling (Guisan and Thuiller 2005; Mitchell 2005; Kearney 2006; Soberon 2007). Soberon (2007) provided some clarification suggesting species' niches should be defined relative to the spatial extent being modeled and the scale of environmental variables used to characterize niches. For example, variables important for defining distributions at the individual or population level such as demographic, physiological, or intra- and interspecific competition variables are typically measured at

fine scales (e.g., fine resolutions of up to a few square meters maximum for most plant species), much finer than most geographic information systems (GIS) data. However, Measurement of such fine scale biotic constraints is not practical for most species (Soberon 2007). In contrast, abiotic variables are more important for characterizing the spatial distribution of a species across a region or continent and are typically measured at relatively coarse spatial scales (e.g., from 10 m^2 to $\geq$ 1 km^2 for most plant species).

Models of species' theoretical niches are only approximations of the species' realized distributions that can be sampled under field conditions, and niche models rely on *a priori* knowledge of and access to the environmental variables defining niches (Guisan and Zimmermann 2000). Various studies have addressed uncertainty by evaluating measures of predictive power and model goodness of fit for predicting probabilites of occurrence (occupancy) (Pearce and Ferrier 2000; Allouche et al. 2006; Hirzel et al. 2006). Such studies have compared the predictive performance of various modeling approaches in combination with different spatial scales (Guisan et al. 1999; Manel et al. 1999; Hirzel et al. 2001; Guisan et al. 2002; Anderson et al. 2003; Segurado and Araujo 2004; Elith et al. 2006); however, there remains uncertainty in which methods consistently result in accurate predictions of species occupancy. Adding spatial autocorrelation structures (Gelfand et al. 2006; Latimer et al. 2006; Dormann 2007; Dormann et al. 2007) and/or mechanistic processes (e.g., dispersal kernels) (Rouget and Richardson 2003; Kearney and Porter 2009) to generate better fitting or more realistic models of a species' potential distribution have also been explored. Although some of these additions have resulted in better predictions on a site and species specific basis, it is

unclear whether slight improvements in model validation using common model assessment techniques (Pearce and Ferrier 2000) would be meaningful for NIS management (Lobo et al. 2008). Moreover, survey method and data type (e.g., presence and absence data, presence and pseudo absence data, presence only data) affect model outcomes and validation (Peterson and Cohoon 1999; Manel et al. 2001; Stockwell and Peterson 2002; McPherson et al. 2004; Hernandez et al. 2006; Pearce and Boyce 2006; Rew et al. 2006). There is evidence that, when available, data containing observations of a species' presences and absences are preferable compared to observations of presences only (Brotons et al. 2004) in conjunction with some kind of stratified survey for data collection (Guisan et al. 2006; Rew et al. 2006) for generating SDMs.

Modeling NIS distributions presents a special challenge, particularly if the species is in the early stages of invasion or colonization and does not yet occupy its full potential range in the introduced region. An underlying assumption for a SDM is that the modeled species has dispersed throughout the entire area being modeled and is in equilibrium with its environment (Elith and Leathwick 2009). When a species is recorded as absent from a location at a particular time it may be because the location is environmentally unsuitable, the location is occupied but the species is not detected, or the location is environmentally suitable but the species has not yet dispersed to and established a population. Likewise, anthropogenic alterations across a landscape may rapidly change environmental conditions, disturbance regimes, biotic interactions, and plant community dynamics in ways that provide more or less suitable habitat for an invader (Byers 2002; Moles et al. 2012) complicating the modeling of such a species (Welk 2004). The assumption of a

species in equilibrium with its environment should take into account the spatial resolution and extent over which a species' probabilities of occurrence are being modeled. As the area (i.e., spatial extent) of a modeled system increases and/or the prediction scale decreases (i.e., resolution of survey and environmental predictors), the number of unique environmental conditions and potentially novel environments for the invader to occupy also increases. Inferences and conclusions drawn from models of NIS distributions must take into account the survey methods and the limitations of data used.

Climate matching between a species' native and introduced ranges has been used to predict potential NIS distributions and used as a means of overcoming potential violations of species-environment equilibrium (e.g., Curnutt 2000; Hoffmann 2001; Welk et al. 2002; Mau-Crimmins et al. 2006). Ignoring biotic interactions with the species in its native range or potential adaptations of the species to novel conditions once in the introduced range are among the criticisms of climate matching modeling methods (Davis et al. 1998). Explicitly modeling dispersal processes is another method used to predict a species' potential distribution (e.g., Rouget and Richardson 2003; Kearney and Porter 2009). However, it remains necessary to survey NIS over time to accurately characterize how NIS distributions may be changing and whether these species have reached a stable equilibrium (Welk 2004; Stohlgren and Schnase 2006; Rew et al. 2007; Elith and Leathwick 2009).

SDM Transferability in Space

Transferability of a SDM is parameterizing a model in one region and using that parameterization to predict a species distribution in other regions (Randin et al. 2006;

Elith and Leathwick 2009). The ability to use SDMs to predict NIS occurrence in one region based on its occurrence in another region would be beneficial for land managers given the scarcity appropriate data need to build SDMs. Transferability has been explored for various plant species with limited successes (Randin et al. 2006; Ervin and Holly 2011) despite some evidence of species' niches being consistent between different regions (Thompson et al. 1993; Hill et al. 2000; Prinzing et al. 2002). Randin et al. (2006) evaluated the transferability of SDMs for 54 plant species between regions in Austria or Switzerland. They evaluated two regression methods, generalized linear models with logit link functions (GLM; logistic regression) and general additive models (GAM) at a 25 m^2 prediction resolution. Transferability failed (based on various metrics) for more than 50% of the species tested irrespective of modeling method. Moreover, adequate transferability of a SDM trained in Austria, for example, did not guarantee adequate transferability of a model for the same species trained in Switzerland. The authors called this asymmetrical transferability noting that differences in land use history between the two regions was one of the likely causes. Likewise, differences in current and historical land management was a potential reason for poor transferability of SDMs for cogongrass (*Imperata cylindrica*), an invasive introduced grass species, between regions in Mississippi and Alabama (Ervin and Holly 2011). The Randin et al. (2006) and Ervin and Holly (2011) studies highlighted the potential importance of anthropogenic disturbances such as land use on plant species' distributions.

Nonindigenous Plant Distributions and Anthropogenic Factors

Most biological invasions have been linked to human activity through purposeful or accidental introductions (Vitousek et al. 1996; Vitousek et al. 1997; Mack et al. 2000; Davis 2009), increasing propagule pressure (Mack and Lonsdale 2001; Davis 2009; Taylor et al. submitted Jan. 3, 2012), and altering landscapes creating more suitable habitat (D'Antonio and Vitousek 1992; Grime 1997; Mack et al. 2000; Byers 2002; Moles et al. 2012; Taylor et al. submitted Jan. 3, 2012). Human disturbances can affect natural disturbance regimes (e.g., frequency, duration, and intensity of disturbance) and impact plant community composition, species distributions, and facilitate invasions (Brooks et al. 2004). For example, *Bromus tectorum* L. (cheatgrass) was introduced from Eurasia and its invasion enabled through grazing operations (Mack 1981). Some systems invaded by cheatgrass have been linked to significant changes in natural disturbance regimes such as increasing fire frequency (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998; Brooks et al. 2004; Rew and Johnson 2010).

Deutschewitz et al. (2003) reported that NIS richness was positively associated with moderate levels of both anthropogenic and natural disturbances at regional spatial extents and coarse scales in Germany. A survey of levels of invasion (i.e., proportion of exotic plant species) for various land cover classes across Europe revealed high levels of invasion associated with human land uses such as agriculture, urbanization, and along coastlines where introductions might have occurred (Chytry et al. 2009). More intense historical forest management practices were suggested to the influence population

dynamics, specifically increasing seedling recruitment, of an invasive tree, *Syzygium jambos*, in the Luquillo Mountains of Puerto Rico (Brown et al. 2006).

Protected areas or nature reserves represent some of the remaining land with minimal human influence, and, thus, may be the pristine or "control" environments used to compare human altered environments (D'Antonio and Vitousek 1996). Nature reserves are often part of larger or greater ecosystems that include unprotected areas prone to land use changes, which could result in loses to biodiversity by decreasing the effective size of the reserves (Gude et al. 2006; Hansen and DeFries 2007a; Hansen and DeFries 2007b; Gude et al. 2007). Such unprotected regions surrounding reserves are particularly vulnerable to low density residential or exurban development (Brown et al. 2005; Gude et al. 2006). A potential consequence of exurban development might be an increase in NIS invasions from areas outside to areas inside reserves (DeFries et al. 2007; Hansen and DeFries 2007b; Allen et al. 2009). For example, Alston and Richardson (2006) reported a positive correlation between NIS richness in a protected national forest of South Africa and proximity to suburban land uses.

Applying Nonindigenous Plant Distribution Models to Management

Much of the SDM literature has alluded to their usefulness for land managers and policy makers; however, relatively few studies have experimentally tested the application of such models for decision making. How might modeling NIS distributions be used to make practical management decisions? Fox et al. (2009) evaluated various surveillance strategies of detecting new occurrences of invasive plants within a simulation study. The

authors reported targeted monitoring within suitable habitat was more efficient than other methods investigated in spatially heterogeneous environments regardless of the life history or dispersal abilities of the focal species. Ervin and Holly (2011) tested the use of a distribution model of an invasive grass species, cogongrass, trained in one place and extrapolated to another location as part of an early detection and rapid response (EDRR) monitoring aid. Unfortunately, their modeling approach failed to transfer adequately in terms of model validation metrics to the new location; however, the idea of model transferability and/or methodology similar to what was proposed by Fox et al. (2009) as part of an EDRR program could have tremendous practical applications for land managers.

An understanding of the spatial distribution of NIS populations could be used to prioritize population or patch level management (Rew et al. 2007). Moody and Mack (1988) simulated the tradeoffs associated with containing large or conspicuous weed infestations versus eradication of smaller satellite patches; they concluded detecting and controlling new populations in conjunction with management of the outer edges of the main patch was more important to controlling the overall invasion than concentrating efforts solely on the main or large infestation. Despite the pioneer work of Moody and Mack and other before them (Auld and Coote 1980; Menz et al. 1980), most simulation studies focusing on spatially explicit weed management made simplifying assumptions about the dynamics of target populations and/or assumed management efficacy would be similar across all target populations/patches regardless of environmental suitability. However, metapopulation and population source-sink theories and associated models

(Brown and Kodric-Brown 1977; Pulliam 1988; Hanski 1994a; Hanski 1998; Pulliam 2000) coupled with spatial and temporal fluctuations in resource availability (Davis et al. 2000) predict that not all populations of the same species will have the same demographic vital rates or the same rates of colonization and extinction.

More environmentally suitable areas for nonindigenous plant species may correspond to more invasive populations (Brown et al. 2008), that is, those populations expanding in density and/or area over time. Rew et al. (2007) reported significant positive relationships between predicted probabilities of occurrence and population invasiveness index values, which incorporated changes in population density and spatial extent (Lehnhoff et al. 2006), for populations of two nonindigenous plant species, *Senecio vulgaris* and *Linaria vulgaris*, in western Montana.

Giljohann et al. (2011) combined an SDM for *Salix cinerea*, an invasive plant in the Australian alps, with a decision model for allocating management resources based on cost and budget constraints. Their models recommended allocating moderate control efforts on many locations more likely to be environmentally suitable for *S. cinerea* versus attempting species eradication on fewer areas of high probability of occurrence. How many areas could be treated depended on fiscal considerations. Baxter and Possingham (2011) simulated the potential economic tradeoffs between cursory detection coupled with control management versus collecting more occupancy data needed to make better predictive distribution models. Tradeoffs were based on initial knowledge of the system and the target species' distribution and population dynamics.

Variation in efficacy of nonindigenous plant populations to different management techniques is well documented in the literature (recently reviewed by Kettenring and Adams 2011). Likewise, ecological theory and empirical evidence suggest the response to the same management technique applied to different populations of the same species can be variable (e.g., Cox et al. 2007). Uncertainty to the response of NIS populations to the same or varying management approaches can impact the predictability of management costs, inappropriate allocation of resources, or inadequate control of the target populations (Epanchin-Niell and Hastings 2010). Further, off target effects of management such as declining native species richness (e.g., Matarczyk et al. 2002) or secondary invasion by other undesirable plant species (Kettenring and Adams 2011) can be an unincorporated cost of management efforts (as suggested in Rew et al. 2007).

As all types of weed management practices (i.e., mechanical, cultural, chemical, and biological) have been reported to have some unintended impacts on non-target plant communities (Hobbs and Humphries 1995; Pimentel et al. 2005; Radosevich et al. 2007; Kettenring and Adams 2011), it is important to work toward minimizing negative off target effects and maximizing NIS management efficiency. This may be achievable by prioritizing weed population management along target NIS environmental suitability gradients (Rew et al. 2007; Brown et al. 2008; Fox et al. 2009; Giljohann et al. 2011).

Although some empirical data exist evaluating how spatially explicit weed management scenarios can reduce local site population growth rates (Humston et al. 2005; Emry et al. 2011), field experimentation of patch responses among several sites

(i.e., landscape level) with differing levels of environmental suitability are currently lacking.

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CHAPTER THREE

HUMAN DISTURBANCE REGIMES INFLUENCE THE TRANSFERABILITY OF NONINDIGENOUS PLANT DISTRIBUTION MODELS

Contribution of Authors and Co-Authors

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Contributions: Conceived the study, collected and analyzed output data, and wrote the manuscript.

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Contributions: Assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Abstract

Species distribution models (SDM) have the potential to aid with prioritization of monitoring and management of nonindigenous or invasive plant species. Likewise, the capacity to parameterize models in one region and accurately transfer to another would be beneficial for mangers lacking the resources to adequately survey their management areas. Few studies have addressed SDM transferability for nonindigenous plant species (NIS) in space, especially between local spatial extents. Moreover, various studies have reported positive relationships between anthropogenic disturbances and plant invasions, but very little information exists about how such perturbations may impact the portability of models of NIS distributions. We assessed the transferability of SDMs parameterized for NIS and extrapolated among three neighboring management units representing a gradient of anthropogenic disturbance intensities within the Greater Yellowstone Ecosystem. SDM uncertainty was highest in the system with greatest amounts of human perturbations. Models inadequately transferred when trained and extrapolated between the two management units with the least and greatest intensities of anthropogenic influence, and NIS model transferability among these two units and the intermediately disturbed unit were mixed. Results of this study suggested different processes likely related to varying intensities of human disturbance were acting on NIS distributions across management units, and caution should be taken when parameterizing and extrapolating SDMs between regions with different land use histories.

Keywords: logistic regression, invasion, niche, occupancy, species distribution model, transferability, weed management

Abbreviations: AUC, area under the receiver operating characteristic curve; GNF, Gallatin National Forest; NIS, nonindigenous plant species; PVAL, Paradise Valley, Montana; ROC, receiver operating characteristic curve; SDM, species distribution model; YNP, Yellowstone National Park

Introduction

Connections between human activities and biological invasions are well documented in the literature. Accidental or purposeful species introductions (Vitousek et al. 1996; Vitousek et al. 1997; Mack et al. 2000), increasing propagule pressure (Mack and Lonsdale 2001; Von der Lippe and Kowarik 2007; Taylor et al. submitted Jan. 3, 2012), and the creation of more suitable habitat for invaders resulting from modified land use (D'Antonio and Vitousek 1992; Grime 1997; Mack et al. 2000; Byers 2002) are some of the humans activities that facilitate invasions (Moles et al. 2012). Nonindigenous plant richness has been found to be positively associated with human disturbances (e.g., suburban and road development) (Deutschewitz et al. 2003; Pauchard and Alaback 2004; Alston and Richardson 2006). Thus, nonindigenous plant species (NIS) surveying (Rew et al. 2006) and developing species distribution models (SDM) (Rew et al. 2005) have integrated variables characterizing putative sources of human caused disturbances and propagule dispersal (e.g., proximity to right-of-ways) (Von der Lippe and Kowarik 2007; Taylor et al. submitted Jan. 3, 2012). Abiotic environmental predictors describing terrain

and climatic conditions are commonly used for parameterizing SDMs; however, few studies have explicitly addressed how anthropogenic disturbance could influence the portability of models for NIS distributions, especially among neighboring management areas with similar environmental variation. The utility of SDMs for NIS would be significantly more cost effective if such models could be parameterized in one region and then transferred to another.

The niche positions (i.e., the position of a species along a niche axis such as solar radiation or water availability) between Britain and central Europe remained consistent when comparing Ellenberg's indicator values of plant species common to both regions (Thompson et al. 1993; Hill et al. 2000; Prinzing et al. 2002), which implies models of species' niches (i.e., SDMs) should be transferable in space at certain spatial scales. However, many of the SDM comparison studies concluded that the predictive abilities of different models were often site, species, and modeling algorithm specific (e.g., Brotons et al. 2004; Elith et al. 2006; Peterson et al. 2007) suggesting the generalization of niche models that are applicable for more than one region may have some limitations.

Randin et al. (2006) evaluated the transferability of SDMs for 54 plant species between regions in Austria and Switzerland. The authors reported that transferability failed (based on various metrics) for more than 50% of the species tested irrespective of modeling method (e.g., generalized linear model or general additive model). Furthermore, adequate transferability of a SDM in one direction (e.g., trained in Austria and transferred to Switzerland or vice versa) did not suggest a model trained and transferred from the opposite direction would be equally adequate. The authors noted

that differences in land use history between the two regions, among other factors, was a likely cause for what they termed asymmetrical transferability. Likewise, Ervin and Holly (2011) reported inadequate transferability of fine grain (i.e., 30 m^2) SDMs built with soil variables as predictors for cogongrass (*Imperata cylindrica*), an invasive grass species, between study areas with different land use/cover and management histories in Mississippi and Alabama. The Randin et al. (2006) and Ervin and Holly (2011) studies highlighted the potential importance of human disturbances when parameterizing portable SDMs, especially when training and transferring SDMs at fine spatial resolutions.

Distributions of NIS can respond to both natural and human caused disturbances (Davis et al. 2000; Mack et al. 2000); however, there is evidence that human and natural disturbance regimes do not have the same effect on landscape spatial pattern or ecosystem functioning (DeLong and Tanner 1996). The responses of NIS to similar disturbances are not always consistent. Some NIS have been found to respond negatively to prescribed fires, allowing burning to be used effectively as a weed management tool (DiTomaso et al. 2006); conversely, the same or taxonomically similar species may also respond favorably to wildfires (Rew and Johnson 2010) and, in turn, may alter natural fire regimes (D'Antonio and Vitousek 1992; Brooks et al. 2004). Anthropogenic related disturbances have also been found to significantly alter environments to favor NIS establishment, spread, and competitive interactions (D'Antonio and Vitousek 1992; Grime 1997; Davis et al. 2000; Mack et al. 2000; Mack and Lonsdale 2001; Byers 2002; Pauchard and Alaback 2004; Pauchard et al. 2009). Therefore, some spatially

heterogeneous changes in land uses may actually create more spatially homogeneous conditions with respect to NIS environmental suitability (Grime 1997).

Models/maps describing the distribution of environmentally suitable locations of NIS at scales relevant for local land managers can have tremendous benefits for prioritizing monitoring and management actions (Rew et al. 2007; Fox et al. 2009; Baxter and Possingham 2011; Giljohann et al. 2011). However, such land managers often do not have sufficient resources to allocate toward surveying, monitoring, modeling, and managing all NIS populations legally mandated for management (i.e., noxious weed species in the United States) or those perceived to be ecologically or economically problematic. Therefore, adequate transferability of SDMs trained in one region and used to predict distributions in another region could be a vital tool for land managers lacking the resources to collect the necessary data for generating SDMs and when a NIS has recently been introduced to a region. On the other hand, results from recent literature suggested transferability of SDMs for various plant species among spatially discontinuous regions were complicated by differences in current and historical anthropogenic disturbances (Randin et al. 2006; Ervin and Holly 2011).

We assessed the transferability of SDMs parameterized for NIS and extrapolated those models among three adjacent management units representing an anthropogenic disturbance gradient within the Greater Yellowstone Ecosystem. Specifically, our objectives were to 1) parameterize SDMs for two representative, nonindigenous plant species, *Cirsium arvense* L. and *Bromus tectorum* L., within three neighboring

management units; and 2) assess the predictive performance of those models when transferred among those adjacent management units.

Methods

Representative Nonindigenous Plant Species

Two nonindigenous plant species (NIS) were selected based on being present in the three neighboring management units evaluated and because they served as model species by having contrasting taxonomic groupings, life histories, and growth habit. Further, neither NIS were considered to be dispersal limited within or among the three management units evaluated because both species were naturalized, and the management units were located well within their documented introduced ranges in North America (http://plants.usda.gov, accessed Jan. 16, 2012). *Cirsium arvense* L. is a perennial forb that grows in patchy distributions within the study areas. *C. arvense* is a dioecous, outcrossing species that reproduces by wind dispersed seeds and adventitious roots (Donald 1994). *Bromus tectorum* L. is an annual grass that typically grows in discrete and interconnected patches within the management units. *B. tectorum* is an obligate outcrossing species that reproduces exclusively by seed and is primarily animal-dispersed (Mack 1981). Both species originated from Eurasia and were introduced to North America as contaminants of crop seed (Whitson et al. 2002).

Study Areas and Data Collection

We evaluated three adjacent management units within the Greater Yellowstone Ecosystem, the northern range of Yellowstone National Park (YNP), a portion of the

Gallatin National Forest (GNF), and Paradise Valley, Montana (PVAL) (Figure 3.1), representing a three point gradient of human disturbance intensities to characterize the distributions of our two model species. Intensity of human disturbance was inferred by the amount of land use changes allowed by the government. For example, land protection by the government is greater in National Parks than National Forests, and protection of National Forests is greater than areas where private ownership of land is allowed.

Northern Range of Yellowstone National Park (YNP): The northern range of Yellowstone National Park (YNP) was considered the management unit (i.e., study system) with the least amount and history of anthropogenic activity. YNP was established as a protected reserve and as the United States' first National Park in 1872 (www.nps.gov/yell, accessed Jan. 16, 2012). Presence and absence data of both *B. tectorum* and *C. arvense* were recorded during the growing seasons of 2001 - 2004 at a 10 m^2 resolution along 2 km continuous transects positioned perpendicular from randomly selected start points on roads and trails and end point greater than or equal to 2 km from any other road or trail (Rew et al. 2005; Rew et al. 2006). Additionally, 2 km transects were randomly started along trails in areas greater than 2 km from roads. These data were scaled up to a 30 m^2 resolution. A presence was assigned to a cell when at least one presence was recorded for that cell, and an absence was assigned to a cell if all observations were recorded as absent for that cell. This resolution was selected to match the resolution of environmental predictor variables and to reduce potential autocorrelation in the observations. The resulting data set contained 22,517 observations. Sixty percent

of the observations (n = 13,510) were randomly subset (referred hereafter as YNP) and used to build or train SDMs for each species. The remaining 40% of the observations (n = 9,007) (referred hereafter as YNP.VAL) were used to validate the SDMs generated from the YNP data set (Table 1).

Gallatin National Forest (GNF): The Gallatin National Forest, as with all National Forest lands in the United States, was managed for multiple uses (e.g., timber production and harvest, livestock grazing, wildlife habitat, human recreation) since its establishment in 1899 (www.fs.usda.gov/gallatin, accessed Jan. 16, 2012) and was considered the management unit with an intermediate history and amount of human activity. A portion of the GNF located approximately 25 km northwest of the YNP management unit was surveyed for the presence and absence of *B. tectorum* and *C. arvense* in the same manner as YNP during the growing seasons of 2006 - 2008. Observations from GNF also were scaled up to a 30 m^2 resolution resulting in a total of 2,109 observations (referred hereafter as GNF) (Table 3.1).

Paradise Valley, Montana (PVAL): Paradise Valley, Montana is located in Park County, Montana approximately 20 km north of YNP through which the Yellowstone River flows and contains a spatial mosaic of both public and private land ownership (Figure 3.1). The PVAL management unit has exhibited significant documented changes in land use over the previous half century such as grasslands being converted to irrigated crop and pasture uses as well as increases in rural residential (exurban) development (Parmenter et al. 2003; Gude et al. 2006). Thus, PVAL was considered the management unit with the greatest amount of human disturbance. Presence and absence data for both

B. tectorum and *C. arvense* were collected in PVAL during the growing seasons of 2009 – 2010 using methods similar to those described for YNP and GNF with a few exceptions. Transect lengths varied from 300 m to 1 km. Unlike YNP or GNF, transect end points were not constrained to distances greater than or equal to 2 km from other roads or trails because the greater density of roads made this constraint too difficult. The observations for PVAL were scaled up to 30 m^2 resolution resulting in a total sample of 2,128 observations (referred to hereafter as PVAL) (Table 3.1).

Environmental Variables

All environmental variables used to parameterize models of probabilities of occurrence were derived from GIS data available online or provided by Yellowstone National Park (Table 3.2). Our choice of environmental variables was based on the theoretical foundation for constructing SDMs for NIS (Hutchinson 1957; Austin 2002; Austin 2007; Soberon 2007). Austin (2002, 2007) classified environmental predictor variables used to model plant species distributions into three classes: *Direct*, *Indirect*, and *Resource* variables. Because our interest was in modeling species not native to the management units under study, direct variables were those hypothesized to directly affect NIS plant occupancy (i.e., proximity to putative vectors of propagule dispersal such as distance from roads, streams, and trails and the presence or absence of wildfire. Indirect variables (i.e., elevation, slope) were those thought to be surrogates for climatic or ecophysiological effects, and resource variables (i.e., relative soil moisture characterized as a topographic wetness index and quantity of solar radiation quantified as potential

solar insolation) were those associated with the physiological requirements for plant growth.

All continuous environmental variables were assessed for potential collinearity within each of the management units. No two variables were more than 66% linearly correlated (elevation and slope in PVAL) as measured by Pearson's correlation coefficient. Although elevation was correlated with slope, we hypothesized that each variable was likely related to a different process and the inclusion of both variables were necessary for predicting NIS distributions.

Species Distribution Modeling

Although there is a rich literature pertaining to the comparison of methods for modeling species distributions across varying spatial extents and resolutions (e.g., Guisan et al. 1999; Guisan et al. 2002; Anderson et al. 2003; Elith et al. 2006), there is no consensus as to which methods are most appropriate to use. Therefore, we chose a modeling framework based on parsimony and ease of interpretation by specifying binary logistic regression as the statistical model and evaluating only additive main effects (i.e., no interactions were included in the models). Further, we assumed perfect detection of both species during our field surveys (i.e., probability of detecting a species was equal to 1.0), which, based on field evaluation, was a reasonable assumption (Brummer 2012).

For each management unit, two logistic regression models (i.e., SDMs) were parameterized at a 30 m^2 resolution, one for each NIS. The choice of a 30 m^2 scale for the predictions was based on it being fine enough for easy locating of NIS occurrences for monitoring and management while reducing spatial autocorrelation among

observations along transects. All models were subjected to an internal validation where the predictive ability of each model within each management unit was validated using either an independent data set (YNP model validated with YNP.VAL data set) or using a data set generated by leave-one-out cross-validation. The SDMs for *B. tectorum* and *C. arvense* were transferred (extrapolated) to the other management units and evaluated for predictive ability. Predictive performance was assessed by calculating the mean area under the receiver operating characteristic curve (AUC; ROC) (Pearce and Ferrier 2000) and approximating 95% confidence intervals from a 1000 sample bootstrap distribution of AUC estimates for each model (NCAR 2010). Confidence intervals were approximated based on the 2.5th and 97.5th percentiles of the AUC bootstrap distribution using the reflection method (Kutner et al. 2005). All models were fitted and validated using the base and verification packages in R version 2.13.2 (NCAR 2010; R Development Core Team 2011).

The AUC metric is a measure of a fitted model's ability to discriminate between predicting presences and absences by evaluating accuracy over varying probability decision thresholds (i.e., probability threshold level independent measure of discrimination accuracy) (Pearce and Ferrier 2000). The area under the ROC curve is interpreted as the probability the model will differentiate between presences and absences by predicting higher probabilities of occupancy to locations with observed presences than locations with observed absences, and models with AUC values greater than 0.5 differentiate between presences and absences better than random chance. Although there are disadvantages to using AUC as a metric of predictive performance (Lobo et al. 2008),

it is currently the only measure, to our knowledge, that provides a single, easy to interpret quantity to compare models of the same species within the same spatial extent.

Evaluation of Model Transferability

Adequate SDM transferability was inferred when the AUC resulting from the internal validation was either significantly less or not significantly different ($\alpha = 0.05$) than the AUC resulting from an externally parameterized model (e.g., the AUC from a model built in YNP and transferred to GNF was compared with the AUC from the model built in GNF). Models within management units with non-overlapping 95% confidence intervals for AUC were considered significantly different. A transferred or externally trained SDM could result in inadequate transferability (i.e., significantly different AUC values) but still have sufficient predictive performance (i.e., AUC values significantly greater than 0.5).

Results

Frequency of Nonindigenous Plant Occurrence

The management unit with the highest overall frequency of *B. tectorum* occurrence sampled was PVAL (0.32; Table 3.1); whereas, the frequency of sampled *B. tectorum* occurrence was similar for YNP (0.07) and GNF (0.06). *C. arvense* was slightly more frequent in the sample of YNP (0.04; Table 1) as compared to lower but similar frequencies in GNF (0.02) or PVAL (0.03).

Environmental Variation

Overall, the distribution of environmental covariates sampled within each management unit was similar; however, there were notable differences in the variation of elevation and distance from right-of-ways sampled, especially between the valley site (PVAL) and the other two adjacent mountain sites (Table 3.2). The ranges of elevation and distance from roads sampled were much less in PVAL. Higher densities of roads within PVAL made sampling far from roads virtually impossible and resulted in the lowest median value and the least variability of distance from roads values surveyed among the three management units (Table. 2). Forest road density in GNF resulted in intermediate median distance from roads as compared to PVAL or YNP (Table 3.2).

Internal Validation of Species Distribution Models

Species distribution models parameterized using eight environmental variables for both NIS within each management unit resulted in mean AUC values significantly greater than 0.5 (Figures 3.2 and 3.3), signifying models trained within each of the systems performed better than random chance. However, unexplained variation was greatest for PVAL SDMs as reflected in their low internal validation mean AUC scores (0.71 and 0.63 for *B. tectorum* and *C. arvense*, respectively) relative to those of GNF (0.94, 0.83 for *B. tectorum* and *C. arvense*, respectively) and YNP (0.84 and 0.74 for *B. tectorum* and *C. arvense*, respectively). Models parameterized within GNF resulted in the least uncertainty relative to YNP and PVAL suggesting the set of environmental predictor variables were better at characterizing NIS distributions in GNF as compared to the other two management units.

Transferability of Species Distribution Models

The internal validation for each management unit's SDMs provided the baseline level of model performance to which transferred models (i.e., those SDMs parameterized in other management units) were compared. Overall, SDMs for both NIS trained in YNP resulted in inadequate transferability to PVAL, and vice versa, as suggested by significantly lower mean AUC values ($\alpha = 0.05$) from transferred models (Figures 3.2 and 3.3). One slight exception was that the transferability of the SDM built in YNP for *C. arvense* and extrapolated to PVAL adequately transferred (i.e.., AUC 95% CI for both YNP and PVAL *C. arvense* models overlapped for the PVAL system) but resulted in an insufficient model because the YNP model predicted the probability of *C. arvense* occurrence in PVAL no better than random chance (mean AUC = 0.54; 95% CI = (0.46, 0.62)) (Figure 3.3).

The *B. tectorum* SDM built in YNP adequately transferred to GNF, but the *B. tectorum* SDM trained in GNF fell just short of statistically adequate transferability to YNP at our predefined level of significance ($\alpha = 0.05$) (Figure 3.2) (i.e., example of asymmetrical transferability according to Randin et al. 2006). Nonetheless, we concluded transferability of the *B. tectorum* model built in GNF and transferred to YNP was adequate for purposes of generalizing these results for practical, management relevant interpretations. *B. tectorum* models transferred between GNF and PVAL provided a stronger example of asymmetrical transferability as SDMs trained in GNF did not adequately transfer to PVAL but PVAL models adequately transferred to GNF (Figure 3.2). Inadequate transferability was detected for *C. arvense* SDMs trained and

transferred between YNP and GNF, but transferability was symmetrically adequate and between GNF and PVAL (Figure 3).

Environmental Variables and NIS Distributions

The significance of the eight environmental variables used in the logistic regression models for predicting the occupancy of both *B. tectorum* and *C. arvense* were evaluated (Tables 3.3 and 3.4). *B. tectorum* occupancy increased with distance from streams in both YNP and GNF but decreased with distance from streams in PVAL. Furthermore, *B. tectorum* occupancy decreased with distance from roads in YNP but showed the opposite association in GNF and PVAL, although the relationship was not significant in GNF ($\alpha = 0.05$).

The predicted probability of *C. arvense* occurrence decreased with increasing elevation in GNF and PVAL but increased with increasing elevation in YNP, which was an unexpected relationship (Pauchard et al. 2009) and prompted further investigation. We hypothesized the modeled relationship between elevation and *C. arvense* occurrence in YNP may be due to the greater proportion of areas previously burned at higher elevations coupled with the larger range and variability of elevation values sampled in YNP versus GNF or PVAL (Table. 2). Furthermore, *C. arvense* has a well documented history of being positively associated with the occurrence of wildfire (Rew and Johnson 2010). Therefore, the YNP SDM for *C. arvense* was re-fitted to include an interaction between elevation and the presence/absence of wildfire, and this resulted in a significant positive interaction and a change in the sign of the modeled relationship between the probability of *C. arvense* occupancy and elevation (Table. 2). The interaction between

elevation and wildfire was not significant and the sign of the modeled relationship with elevation did not change for GNF or PVAL when *C. arvense* SDMs were re-parameterized with those respective data sets (Appendix A). Once accounting for that interaction, the *C. arvense* SDM in YNP revealed a negative relationship between distance from roads and *C. arvense* occupancy, which was not detected in modeled relationships in GNF or PVAL irrespective of the presence of the interaction term, rather, predicted *C. arvense* occupancy was found to be positively associated with both wildfire and distance from roads in GNF and PVAL, but the frequency of sample observations in locations previously burned was much greater in YNP (Table 3.2). Because refitted logistic regression models did not result in significantly different metrics for assessing internal validations or transferability (Appendix A), models including an interaction between elevation and wildfire were not further evaluated in this study.

Discussion

Our study compared nonindigenous plant species distributions across three management units within the Greater Yellowstone Ecosystem representing a three point gradient of human perturbations that we hypothesized might influence NIS distributions and, thus, SDM transferability. The general lack of adequate transferability of our target species' models between YNP and PVAL was evidence these species were not similarly distributed in these two management units. Plant SDMs trained in or transferred to the management unit representing an intermediate history of human disturbance (GNF) resulted in a mixture of adequate and inadequate transferability. Thus, our results suggested *B. tectorum* was more similarly distributed in YNP and GNF, and *C. arvense*

was more similarly distributed in GNF and PVAL. The GNF management unit responded like a *transitional* ecosystem between YNP and PVAL in terms of how the two NIS were distributed. Land use changes unique to PVAL such as dry grasslands converted to low density residential and irrigated agricultural uses may represent processes acting on these NIS distributions that were not contributing to distributions in GNF or YNP. Land use and cover variables improved the accuracy of plant species occupancy predictions in Europe (Pearson et al. 2004) and alpine plant species distributions in Austria were better explained when land use was specified in the models (Dirnbock et al. 2003). Additional variables characterizing current or historical land use may help to explain more of the variation in NIS distributions in PVAL as was illustrated in a multiple scale, hierarchical approach to modeling plant distributions in Britain (Pearson et al. 2004).

Asymmetrical transferability as defined by Randin et al. (2006) is when a SDM parameterized in region A adequately transfer to region B, but a SDM parameterized in region B does not adequately transfer to region A. Results of our study indicated asymmetrical transferability for both NIS, especially between GNF and the other two management units, which was similar to the study by Randin et al. (2006) between regions in Austria and Switzerland. They showed that the majority of the 54 plant species they evaluated did not adequately transfer in both directions between their two study regions, which they speculated was, in part, caused by differences in land use history or due to the evolution of different ecotypes within species between the two regions. Likewise, others have reported geographic variability of species' niches resulting in lack of adequate transferability of niche models (Fielding and Haworth 1995;

Glozier et al. 1997; Ervin and Holly 2011). However, as is the case with all observational studies of species occupancy, the specific causes of inadequate and asymmetrical transferability among management units in our study cannot be directly elucidated. Nevertheless, our study was novel because of our choice to model distributions of two NIS, neither of which were considered dispersal limited, within three adjacent management units differing mostly in their histories and amounts of human disturbance. Our results strongly suggested differences in NIS distributions were the result of varying levels of anthropogenic perturbations.

Lack of adequate SDM transferability for plant species in this study and those previously reported (Randin et al. 2006; Ervin and Holly 2011) might have been due to a combination of prediction resolution and the environmental predictors used for parameterizing those models. For example, our evaluation of SDM transferability suggested different processes were acting on NIS distributions among the management units when evaluated at the same spatial scale. Some of the differences in processes were captured in the set of environmental variables used as evidenced by the changes in modeled relationships between NIS occupancy and direct predictor variables among the three management units. However, relatively lower mean AUC and wider confidence intervals for internal validations suggested relatively greater uncertainty remaining in models built in PVAL. Hence, the set of covariates used in our study did not capture the spatial heterogeneity of the target NIS distributions in PVAL as well as they did for YNP and GNF. The choice of what scale NIS distributions are surveyed and modeled informs what set of environmental predictors should be used (Guisan and Thuiller 2005; Austin

and Van Niel 2011), and generalizing SDMs for NIS may require closer consideration of scale. Randin et al. (2006) surmised their 25 m^2 resolution may not have been appropriate for characterizing certain processes governing plant distributions like rockfalls or microtopographic refuges. Likewise, Ervin and Holly (2011) selected most of their predictor covariates to model cogongrass distributions at a 30 m^2 resolution within and between two study areas based on studies of the relationships between soil properties and cogongrass occupancy and growth conducted at finer spatial scales (e.g., Bryson et al. 2010). Likewise, our choice of a 30 m^2 prediction scale in conjunction with our set of environmental predictors may have not captured finer or coarser scale processes associated with anthropogenic disturbances driving NIS distributions.

Despite reports of consistency of niche positions for various plant species among geographically different regions (Thompson et al. 1993; Hill et al. 2000; Prinzing et al. 2002), relationships between probabilities of occurrence and environmental variables for both NIS in this study were inconsistent among the models for the three management units. Other studies have reported similar findings (e.g., Glozier et al. 1997). Relationships between *direct* environmental variables (Austin 2007) linked to human facilitated NIS propagule dispersal and disturbance with NIS occurrence (Gelbard and Belnap 2003; Pauchard and Alaback 2004; Von der Lippe and Kowarik 2007) may differ in their modeled influences on SDM predictions depending on the level of human influence. This was supported with inconsistent relationships between the predicted probability of *B. tectorum* occupancy and distance from roads and streams across the three management units. Again, relationships between occupancy and predictor

covariates exhibited in GNF seemed to represent a transition between the contrasting associations exhibited in YNP and PVAL, especially in terms of significance (i.e., p-values), suggesting the drivers of *B. tectorum's* distribution differed with differing levels of human disturbance.

Conclusions

Many public agencies charged with NIS management at local scales, including the National Park Service, map weed populations in the field and/or employ personnel with expertise in working with geographic information systems software and data. Notwithstanding the growing access to these mapping technologies, land managers often do not possess the resources necessary for conducting comprehensive NIS inventories and surveys within and among growing seasons, thus, reiterating the need for applied scientists to develop and evaluate methods for efficient data collection (Rew et al. 2006) and modeling of NIS distributions on which management can be based (Rew et al. 2007; Fox et al. 2009; Giljohann et al. 2011). However, when spatial data on NIS are scarce, land managers could benefit from knowledge and data obtained in other regions to parameterize SDMs for NIS in their areas of interest (Ervin and Holly 2011). Recent studies, including this one, evaluating the transferability of SDMs for native and non-native plant species at relatively fine spatial resolutions reported inadequate and asymmetrical transferability (Randin et al. 2006; Ervin and Holly 2011). In part, these results could reflect differences in land use and management histories between systems used to train SDMs and those systems to which SDMs were transferred. Based on the results of this study and others (Randin et al. 2006; Ervin and Holly 2011), land managers

should be cautious when extrapolating models of NIS distributions among regions with differing histories and levels of human impact. Likewise, extrapolating SDMs for NIS under future environmental scenarios for regions with high levels and frequencies of human disturbance may be ill advised and result in misleading forecasts of future distributions.

In conclusion, our study of nonindigenous SDM transferability illustrated clear associations between the level of human disturbance and how NIS were distributed, which suggested the spatial distributions of NIS environmental suitability are sensitive to anthropogenic alterations at fine spatial scales across local extents.

Acknowledgements

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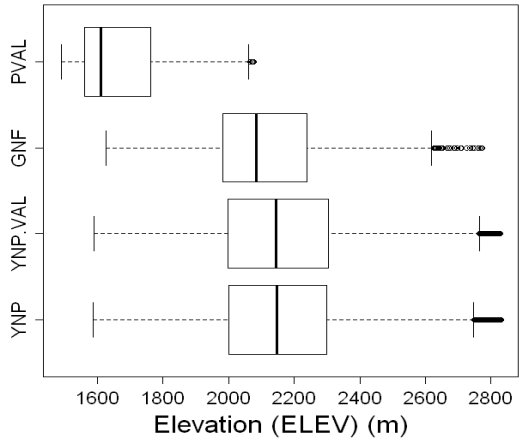
Tables and Figures

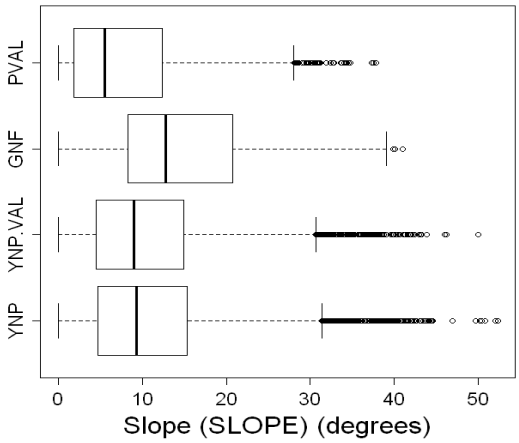
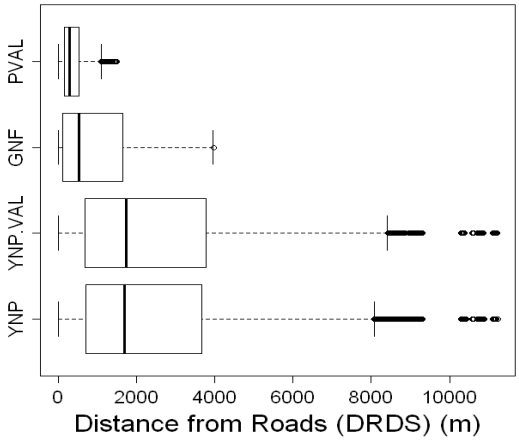
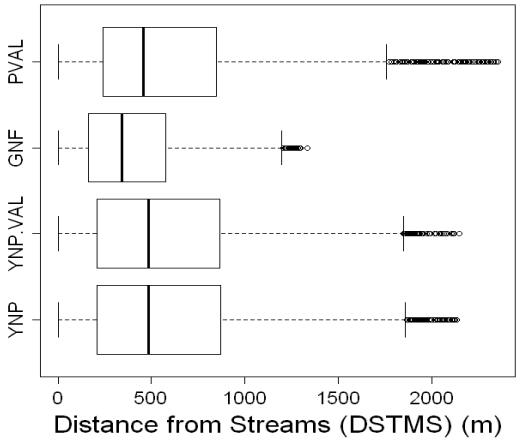
Table 3.1 Number of observations and number of detected presences for Bromus tectorum and Cirsium arvense for each of the neighboring management units

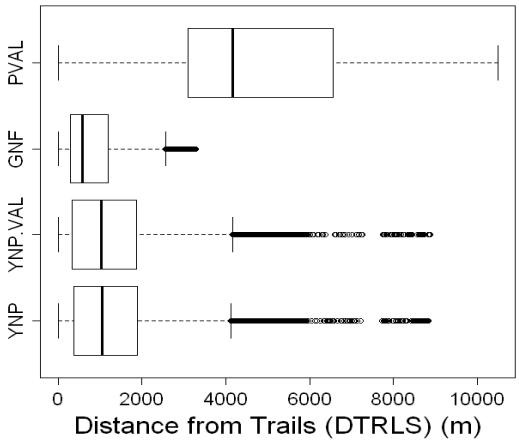
Sample Size	YNP	YNP.VAL[a]	GNF	PVAL
Total (n_t)	13,510	9,007	2,109	2,128
B. tectorum Presences (n_b/frequency)	869 / 0.066	561 / 0.062	32 / 0.015	670 / 0.315
C. arvense Presences (n_c/frequency)	596 / 0.044	455 / 0.051	59 / 0.023	53 / 0.025

[a]YNP.VAL = independent validation data set used for the internal validation of models parameterized in YNP

Table 3.2 Summary statistics depicted as either box and whisker plots and contingency table for the seven continuous and one categorical environmental predictor variables, respectively, used in modeling the probabilities of occurrence for Bromus tectorum and Cirsium arvense

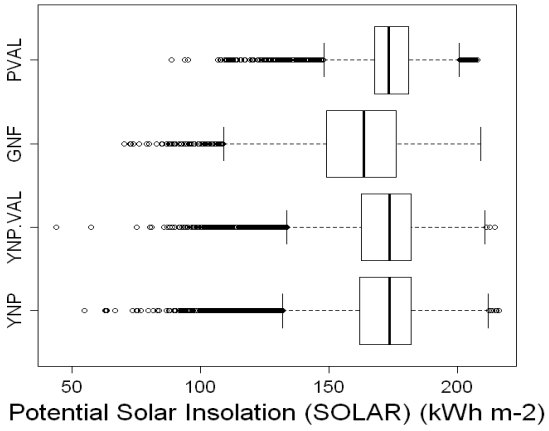
Independent Variable	Figure[a]	Source
Indirect Variables		
Elevation (m) (ELEV)		National Elevation Dataset (courtesy of U.S. Geological Survey via http://seamless.usgs.gov)

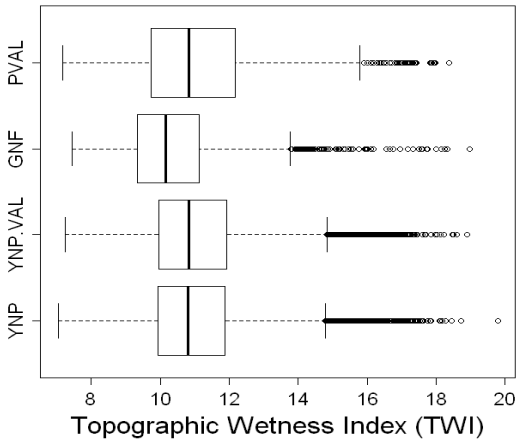
Slope (degrees) (SLOPE)		Derived in Spatial Analyst for ArcGIS 9.3[b]
Direct Variables		
Distance from Roads (m) (DRDS)		MT NRIS/YNP[c] Derived in Spatial Analyst for ArcGIS 9.3 [b]
Distance from Streams (m) (DSTMS)		MT NRIS/YNP[c] Derived in Spatial Analyst for ArcGIS 9.3 [b]

Distance from Trails (m) (DTRLS)		MT NRIS/YNP[c] Derived in Spatial Analyst for ArcGIS 9.3 [b]

Wildfire[d] (WILDFIRE1)	Wildfire	YNP	YNP.VAL	GNF	PVAL	MTNRIS/YNP[c]
	Absent	9140	6094	1913	2051	
	Present	4370	2913	196	77	
	%Present	32.3	32.3	9.3	3.6	

Resource Variables

Potential Direct Incoming Solar Insolation (kWh m^{-2}) (SOLAR)		Derived in SAGA GIS 2.0.7 Module: Terrain Analysis – Lighting, Visibility v.1.0 (SAGA Development Team 2011)

Topographic Wetness Index (TWI)		Derived in SAGA GIS 2.0.7 Module: Terrain Analysis – Hydrology v.1.0 (SAGA Development Team 2011)

[a]Figure = box and whisker plot; "whiskers" extend to 1.5 times the interquartile range; "hinges" equal the first and third quartiles; center line in box equals the median; Contingency table in place of figure for the Wildfire (categorical) variable
[b]ArcGIS (ESRI 1999-2009)
[c]MT NRIS, Montana Natural Resource Information System (nris.mt.gov); YNP, Yellowstone National Park GIS
[d]Wildfire: categorical, binary independent environmental variable describing presence or absence of wildfire within the previous 25 years (since 1985)

Table 3.3 Logistic regression coefficient estimates for models predicting the probability of occurrence of Bromus tectorum for each of the three neighboring management units

Variable[a]	YNP	p-value[b]	GNF	p-value[b]	PVAL	p-value[b]
(Intercept)	4.897E+00	<0.001	8.375E+00	0.067	2.404E+00	0.084
ELEV	-5.434E-03	<0.001	-1.155E-02	<0.001	-6.142E-03	<0.001
SLOPE	8.479E-02	<0.001	1.282E-01	<0.001	4.139E-02	<0.001
DRDS	-1.307E-04	<0.001	4.140E-04	0.288	5.398E-04	0.007
DSTMS	5.833E-04	<0.001	1.412E-03	0.142	-4.957E-04	<0.001
DTRLS	-4.580E-05	0.143	-2.120E-04	0.536	1.329E-04	<0.001
WILDFIRE 1[c]	-4.979E-02	0.667	1.637E+00	0.007	1.646E+00	<0.001
SOLAR	1.075E-02	<0.001	4.585E-02	<0.001	3.808E-02	<0.001
TWI	5.363E-02	0.051	-7.085E-02	0.733	-6.246E-02	0.050

[a]Abbreviations for environmental variables in Table 1
[b]p-values based on the z-approximation to the Chi-Squared distribution
[c]WILDFIRE 1 = categorical variable where 1 = present

Table 3.4 Logistic regression coefficient estimates for models predicting the probability of occurrence of Cirsium arvense for each of the three neighboring management units

Variable[a]	YNP	p-value[b]	GNF	p-value[b]	PVAL	p-value[b]
(Intercept)	-1.398E+01	<0.001	1.609E+00	0.550	7.893E+00	0.137
ELEV	4.565E-04	0.025	-4.811E-03	<0.001	-7.278E-03	0.011
SLOPE	5.295E-02	<0.001	-2.865E-03	0.900	6.487E-03	0.882
DRDS	1.674E-04	<0.001	3.375E-05	0.874	4.674E-05	0.938
DSTMS	6.795E-04	<0.001	-2.625E-03	<0.001	-6.725E-04	0.151
DTRLS	-9.974E-05	0.003	6.862E-04	0.001	1.187E-04	0.117
WILDFIRE 1[c]	5.992E-01	<0.001	1.372E+00	0.002	4.498E+00	<0.001
SOLAR	2.575E-02	<0.001	2.112E-02	0.002	-2.022E-02	0.093
TWI	3.316E-01	<0.001	8.409E-02	0.335	2.449E-01	0.002

[a]Abbreviations for environmental variables in Table 1
[b]p-values based on the z-approximation to the Chi-Squared distribution
[c]WILDFIRE 1 = categorical variable where 1 = present

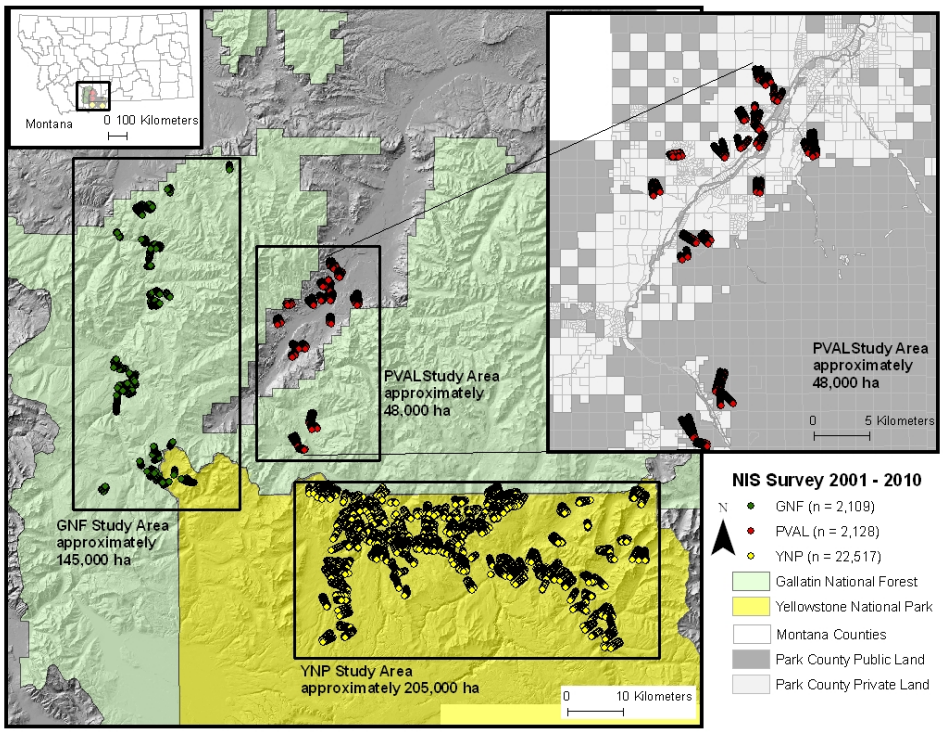


Figure 3.1 Adjacent management units in the Greater Yellowstone Ecosystem

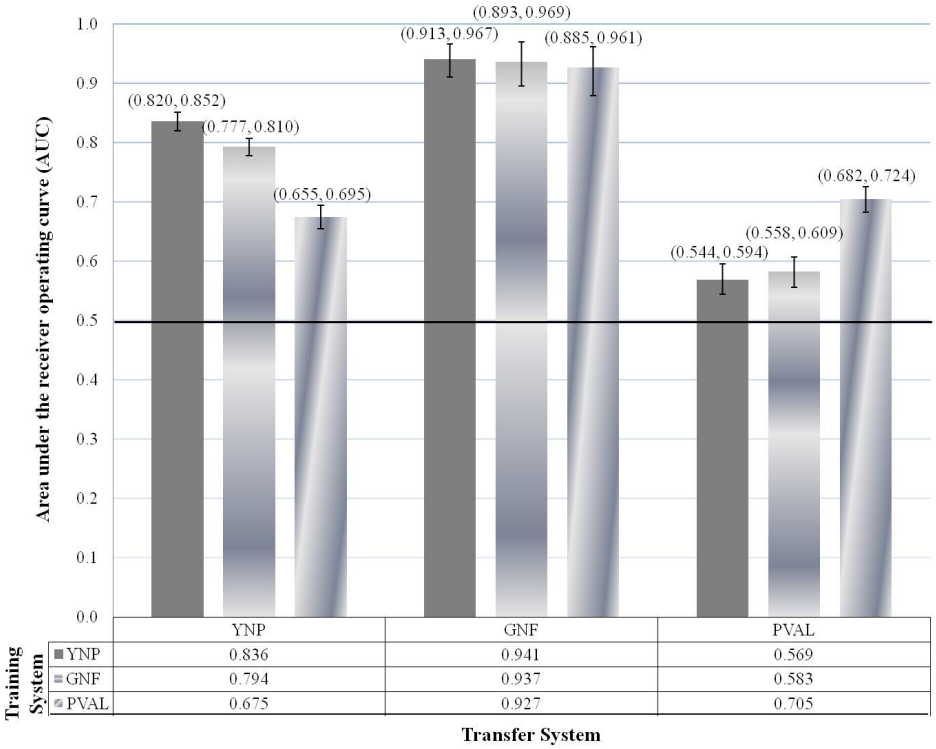
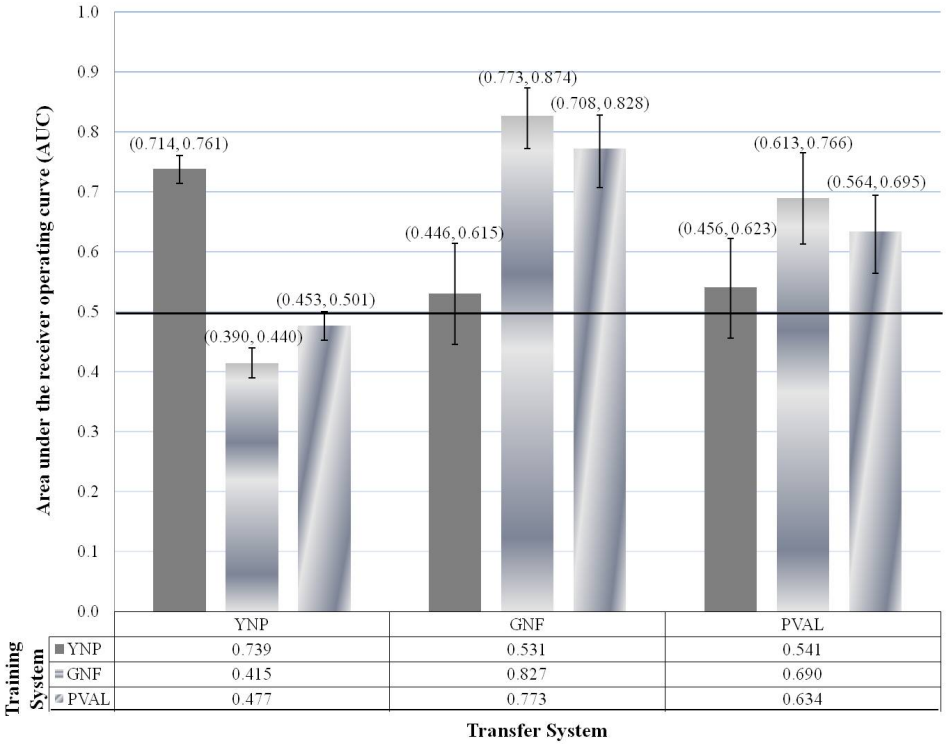


Figure 3.2 Results of predictive performance as measured by the area under the receiver operating curve (AUC) for Bromus tectorum probability of occurrence models parameterized and transferred among neighboring management units. Each bar illustrates the mean AUC calculated for models parameterized in each of the three management units (display pattern of each management unit is shown in the left column of table within the figure labeled *Training System*) and transferred to each of the management units (x-axis; *Transfer System*). Error bars about the mean AUC represent 95% confidence intervals (lower and upper bounds in parentheses above bars) estimated by 1000 bootstrapping iterations of the observations and predicted values followed by calculating the true positive and false positive rates of classification. The AUC calculated for each of the within system/internal validations (i.e., where the *Training System* = *Transfer System*; main diagonal of table in figure) were based on validation data sets for each of the three study systems (YNP had an independent YNP.VAL data set; GNF and PVAL validation data sets based on leave-one-out cross-validations)



Training System	YNP	GNF	PVAL
YNP	0.739	0.531	0.541
GNF	0.415	0.827	0.690
PVAL	0.477	0.773	0.634

Figure 3.3 Results of predictive performance as measured by the area under the receiver operating curve (AUC) for Cirsium arvense probability of occurrence models parameterized and transferred among neighboring management units. Each bar illustrates the mean AUC calculated for models parameterized in each of the three management units (display pattern of each management unit is shown in the left column of table within the figure labeled *Training System*) and transferred to each of the management units (x-axis; *Transfer System*). Error bars about the mean AUC represent 95% confidence intervals estimated by 1000 bootstrapping iterations of the observations and predicted values followed by calculating the true positive and false positive rates of classification. The AUC calculated for each of the within system/internal validations (i.e., where the *Training System* = *Transfer System*; main diagonal of table in figure) were based on validation data sets for each of the three study systems (YNP had an independent YNP.VAL data set; GNF and PVAL validation data sets based on leave-one-out cross-validations)

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CHAPTER FOUR

THE ROLE OF CURRENT AND HISTORIC LAND USES ON THE LOCAL OCCUPANCIES OF NONINDIGENOUS PLANT SPECIES

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Contributions: Conceived the study, collected and analyzed output data, and wrote the manuscript.

Co-Author: Bruce D. Maxwell

Contributions: Assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Contributions: Obtained funding, assisted with study design, discussed the results and implications, and edited the manuscript at all stages.

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Abstract

Human perturbations have been linked to plant invasions through increasing propagule pressure and sufficient alteration of environments that favor nonindigenous plant species (NIS) incursion. One such perturbation is land use/cover change; however, very little information exists on how current and historical uses of land influence models of NIS distributions, especially at local spatial scales. This study assessed the relative role of environmental and current and historical land use/cover variables in characterizing six herbaceous NIS distributions in a region adjacent to Yellowstone National Park within the Greater Yellowstone Ecosystem. We found that including both current and historical land uses into a single land use variable was more important for characterizing NIS occupancy than current land uses only when evaluated at a 30 m^2 spatial scale. Specifically, we found land use histories containing irrigated agriculture or exurban development most influenced NIS distributions, although responses to specific land use histories were variable across NIS. In addition, the inclusion of any land use variables in NIS occupancy models sometimes obscured the importance of environmental variables suggesting interactions between natural environmental conditions and anthropogenic disturbances may be important for predicting NIS distributions. Our results suggested that land use history was more influential than current land use for characterizing NIS distributions at local spatial scales.

Keywords: land use change, nonindigenous species, invasion, species distribution model, nature reserve, greater ecosystem

Abbreviations: NIS, nonindigenous plant species; PVAL, Paradise Valley, Montana

Introduction

Human disturbances have been linked to plant invasions by increasing propagule pressure (Mack and Lonsdale 2001; Davis 2009; Taylor et al. 2011) and altering landscapes creating more suitable habitat for potential invaders (D'Antonio and Vitousek 1992; Grime 1997; Davis et al. 2000; Mack et al. 2000; Byers 2002; Deutschewitz et al. 2003). A survey across Europe revealed high levels of invasion (i.e., proportion of nonindigenous plant species of the total plant species) associated with anthropogenic land uses such as agriculture, urbanization, and along coastlines where introductions might have occurred (Chytry et al. 2009). Alston and Richardson (2006) reported exotic plant species richness within a protected forest preserve was negatively correlated with distance from neighboring, unprotected areas of suburban land use. Comparably, Bridges et al. (2012, in preparation) suggested that nonindigenous plant species (NIS) distributions sufficiently differed between adjacent protected and unprotected regions with differing histories of human perturbations such that models predicting their occurrences could not be generalized between the two regions. Furthermore, several studies have negatively correlated NIS richness and occurrence with distance from roads (Tyser and Worley 1992; Gelbard and Belnap 2003; Seipel et al. 2012). Recent studies quantifying long distance dispersal of plant propagules along roads provide support for vehicles as dispersal agents (Von der Lippe and Kowarik 2007; Taylor et al. submitted Jan. 3, 2012). While the role of vehicles in dispersing propagules and roadsides as suitable habitat for ruderals plant establishment is becoming better understood, the effects

of current and prior land use on plant distributions, particularly in regions containing an exurban/wildland interface (Brown et al. 2005) with heterogeneity of land uses, has not.

Natural disturbances such as wildfire have also been associated with structuring plant communities (Motzkin et al. 1996) and affecting the occurrence of NIS (reviewed in Rew and Johnson (2010). Brooks and Berry (2006) reported the frequency of wildfire as one of the disturbance variables correlated with biomass of *Bromus rubens*, an exotic annual grass. Further, there is growing evidence for interactions between wildfire and the occurrence of non-native, annual grasses leading to altered frequencies of natural fire regimes and, thus, favoring the occurrence of NIS (D'Antonio and Vitousek 1992; Brooks et al. 2004).

Although evidence exists differentiating the effects of anthropogenic and natural disturbance regimes on landscape spatial pattern and ecosystem functioning (DeLong and Tanner 1996), various studies have reported confounding relationships and feedbacks between disturbance types in determining NIS occurrence (Wells et al. 1976; D'Antonio and Vitousek 1992; Brunet 1993; Brooks et al. 2004). Feedbacks and interactions among disturbance variables complicate interpretations of their relative contributions in describing how plant species are distributed (Thuiller et al. 2004). Motzkin et al. (1996) concluded the relative role of wildfire on structuring plant communities in pitch pine—scrub oak forest ecosystems in New England (USA) were interpretable only within the context of prior land use, which suggested both spatial and temporal configurations of human and natural disturbances are important for explaining plant species' distributions. Similarly, variation in documented NIS responses (e.g., establishment/occurrence,

demographic vital rates) to fires characterized as moderate in either intensity or severity suggested the role of wildfire is likely related to other variables important for characterizing NIS distributions such as land use and management history (Rew and Johnson 2010). Furthermore, reclaimed land previously used for agricultural purposes may be vulnerable to NIS invasions because of alternations of disturbance regimes and nutrient availability and cycling as well as impoverished native species diversity (Baer et al. 2009). Thus, considerations of both the spatial and temporal scales of anthropogenic and natural disturbance variables may be crucial for unraveling their relative roles in determining NIS distributions. Nonetheless, processes governing succession after disturbance, particular those associated with human perturbations and NIS occupancy, are poorly understood mainly because many studies have been opportunistic after a disturbance event (e.g., wildfire), lacked information on prior management strategies, or were unable to study such processes over a long period (Wright Jr 1976; Duffy and Meier 1992; Brooks et al. 2004; Rew and Johnson 2010).

Distinguishing the relative role of current and historical land uses from other environmental variables may be important for characterizing patterns of NIS occurrence, particularly near nature reserves where some specific kinds of land uses have been suggested to facilitate the occurrence of NIS (Baer et al. 2009) and, thus, potentially affect biodiversity (Hansen and DeFries 2007b). Managers of protected areas are increasingly concerned with the growing rate of land use changes such exurban development (low density rural residential housing; Brown et al. 2005) and conversion to and from agricultural uses in unprotected areas proximal to reserves (Parmenter et al.

2003; Gude et al. 2006; Gude et al. 2007). Disturbances associated with different land uses and land use changes occurring on the edges of greater ecosystems may reduce the effective size of the reserve (Hansen and DeFries 2007a) and promote increases in NIS richness and occurrence within the reserve (Allen et al. 2009).

A deeper understanding of the relative roles of dynamic natural and anthropogenic disturbances and more static abiotic environmental conditions is vital for characterizing NIS distributions and processes favoring plant invasions at local spatial scales. It is of particular significance to land managers of ecosystems vulnerable to land use changes to assist with their management strategies. Species distribution models (SDM) have generally not included land use history as a potential driving variable of NIS distributions. The objective of this study was to assess the relative roles of current and historic land use/cover variables in addition to typically used environmental variables in characterizing NIS distributions in an unprotected region adjacent to Yellowstone National Park within the Greater Yellowstone Ecosystem.

Methods

Study Region

We surveyed for the presence and absence of various nonindigenous plant species (NIS) (Table 4.1) among sites in Paradise Valley, Montana, U.S.A. (Figure 4.1). The Paradise Valley study area (referred hereafter as PVAL) was approximately 48,000 ha size and located 20 km north of Yellowstone National Park in Park County, Montana. The PVAL study area was located in representative rural area within the Greater

Yellowstone Ecosystem (GYE) characterized by spatially heterogeneous patterns of public and private land ownership. Unprotected areas within the GYE, including PVAL, have exhibited significant documented changes in land use over the previous half century including the conversion of dry grasslands to irrigated cropland and pasture uses and increases in rural residential development (Parmenter et al. 2003; Gude et al. 2006).

Land use and cover within PVAL were digitized in ArcView 3.2 (ESRI 1992-1999) as vector features at a 1:10,000 or finer scale using scanned, ortho-rectified, and geo-referenced aerial imagery corresponding to the years 1948 (courtesy of U.S. Geological Survey), 1979 (courtesy of U.S. Department of Agriculture Farm Services Agency in Park County, Montana), 1991, 1998, and 2003 (Montana Natural Resource Information Service, www.nris.mt.gov). Land use/cover categories were originally classified based on Anderson Level II and III classification schemes and were generalized to approximately match Anderson Level I categories (Anderson et al. 1976).

Categorical, nominal variables for use in species occupancy modeling representing current and historic land uses were derived from the Anderson Level I land use/cover classes and were coded using a similar coding convention (Anderson et al. 1976). Current land uses were recorded in 2003 and field validated (i.e., ground-truthed) while sampling for NIS in 2009 and 2010. Historical land use for each point in space (i.e., grid cell) included unique codes describing the documented land use changes between 1948 and 2010 including current land use. Thus, the historical land use variable represented current land use in the context of prior land use. Both current land use and historical land use variables included rangeland, conifer forest, irrigated agriculture, exurban residential

development, or a combination of land use conversions among these classes in the case of historical land use (Table 4.2). For example, if a grid cell was classified as rangeland (code = 3) in 1948 and 1979, irrigated agriculture (code = 2) in 1991 and 1997, exurban (code = 1) in 2003 and 2010, then the resulting historical land use category would be coded as 321 representing a current exurban land use with a history of rangeland and irrigated agriculture uses. Current and historic land use variables were scaled to a 30 m^2 resolution to match the resolution of other environmental predictors used to characterize NIS occupancy.

Nonindigenous Plant Species (NIS) Data Collection

The presence and absence of six NIS were recorded during the growing seasons of 2009 and 2010 at a 10 m^2 resolution along continuous transects positioned perpendicular from randomly selected start points on roads using methods adapted from Rew et al. (2005; 2006) and described in Bridges et al. (2012, in preparation). Transect lengths were constrained due to the density of roads and depending on where we were granted permission for surveying and varied from 300 m to 1 km but generally provided a representative sample of the range of current land uses.

Binary presence and absence observations for each plant species were scaled up from 10 m^2 to 30 m^2 by creating a ratio of the number of presences to the number of absences sampled at a 10 m^2 resolution within each 30 m^2 grid cell. Current or historical land use classes containing less than 10 observations were omitted resulting in a total sample size of 1,783 collected from 45 transects (Figure 1; Table 2).

Environmental Variables

Environmental predictor variables were selected based on the scale of our study and their ecological applicability to modeling NIS distributions (Austin 2002, 2007). Consequently, we selected one categorical and seven continuous environmental covariates representing processes indirectly (elevation and slope), directly (distance from streams, roads, and trails and presence/absence of wildfire), and resource (solar insolation and topographic wetness index) related to plant growth and occurrence (Table 3) (see Austin 2002, 2007 for more explanation). Two of the continuous environmental variables, namely proximity to roads and trails, could also be considered a description of current land uses and represented variables we considered directly related to the occurrence of NIS (Pauchard and Alaback 2004; Rew et al. 2005; Seipel et al. 2012). However, we considered it most appropriate to consider them as direct variables. The set of environmental variables were derived from geographic information systems data available online.

All continuous environmental variables were assessed for potential collinearity within occupancy regression models using Pearson's r. Pairwise correlations greater than r = +/- 0.48 were detected among only three variables. Slope was positively and negatively correlated with elevation (r = 0.67) and topographic wetness index (r = -0.61), respectively. Despite these correlations, we hypothesized that each of the variables was related to sufficiently different processes and the inclusion of all variables was biologically relevant for predicting NIS distributions.

NIS Occupancy Modeling

Occupancy models of NIS (i.e., NIS distributions) were created and evaluated for six species (Table 4.1). Three probability of occupancy models were fitted with general linear models with logit link functions (i.e., logistic regression) for each species (i.e., 18 total models) (Kutner et al. 2005). Model 1 employed only the eight environmental variables (Table 4.3). Model 2 used the eight environmental variables plus the categorical variable for current land use classes; whereas, Model 3 was parameterized using the environmental variables plus the categorical variable describing historic land uses. All models were assumed to have only additive effects. When overdispersion was detected in models with binomial error structures, it was corrected by using a quasi-binomial error structure (Zuur et al. 2009). Analyses of deviance tables were constructed for each model to assess the relative role of predictor variables and how much additional deviance (i.e., variation) was explained by the inclusion of the land use variables, and box and whisker plots with Tukey's notches were generated to explore differences in distributions of predicted probabilities of occurrence resulting from the inclusion of land use variables. Tukey's notches provide an approximation of the 95% confidence intervals around median values calculated as +/- 1.58 times the quantity of the interquartile range divided by the square root of the observations in a particular category; thus, the significance of the differences between two medians can be assessed (Crawley 2007). Box plots with notches were intended only for assessing trends in the predictions rather than for drawing statistical inferences. All analyses were performed using the base package in R version 2.13.2 (R Development Core Team 2011).

Results

Land Use Variables and Nonindigenous Plant Occupancy

The percent deviance (i.e., variation) in NIS distributions explained by each species' Model 1, which included only environmental predictors (listed in Table 4.3), ranged from 14% for a perennial forb, *Cirsium arvense*, to 29% for *Bromus inermis*, a perennial grass (Table 4.4). The addition of either current or historic land use variables (Models 2 and 3, respectively) explained more deviance for all models of NIS occupancy than environmental variables alone (Model 1). The inclusion of current land use categories in each species' Model 2 resulted in percent deviation explained ranging from 15% for *C. arvense* to 33% for *B. inermis*; whereas, Model 3 improved NIS occupancy estimates to 27% and 44% of deviance explained for the same species, respectively.

The current land use categories exhibiting the greatest changes in predicted probabilities of NIS occurrence were exurban and irrigated agriculture; while, predictions within the rangeland and conifer forest categories showed less fluctuation among species in response to the inclusion of the current land use (Model 2) (Figure 4.2). However, the variation around the median value of predicted probabilities of NIS occurrence within each current land use class was reduced only slightly when the current land use variable was included (Model 2 compared to Model 1) (Figure 4.2), which corresponded to the slight increase in percent deviance explained in each species' Model 2 (Table 4.4).

When historic land uses were included in Model 3, exurban development or irrigated agriculture were among the classes that exhibited the greatest changes in each species'

predicted probabilities of occurrence in Model 3 compared to Model 1 (Figure 4.2). The historical land use variable depicted current land uses further partitioned by previous land uses (i.e., interactions). Comparing Model 3 (historic land use and environmental variables) for each species with environmental only (Model 1) or environmental plus current land use (Model 2) models predicted variable responses within current land use classes, thus, suggesting that interactions between current and prior land uses were influential for characterizing NIS distributions. For example, the inclusion of current land use in Model 2 resulted in decreased mean predictions of the probabilities of *Bromus tectorum* occupancy and increased mean predictions of *B. inermis* probabilities of occupancy within the irrigated agriculture class (Figure 4.2a). Further, *B. tectorum* predictions increased in Model 2 within the exurban class while predictions within the conifer forest and rangeland classes remained similar (Figure 4.2a). However, the inclusion of historical land use in Model 3 resulted in increased predicted probabilities of *B. tectorum* occupancy for current rangeland locations previously used for irrigated agriculture (Codes 23 and 323) and for rangeland converted to irrigated agriculture uses (Code 32) (Figure 4.2a). Predictions increased from Model 3 for *C. arvense* occupancy in locations currently classified as rangeland with a history of irrigation (Code 23) (Figure 4.2b). Conversely, predicted probabilities of *Centaurea maculosa* occurrence decreased in rangeland previously used for irrigated agriculture (Codes 23 and 323) when historical land use was included in Model 3 compared to predictions resulting from Model 1 containing only environmental covariates (Figure 4.2a). The inclusion of current or historical land use variables, however, did not result in significant changes in

predictions among land use classes for either *Cynoglossum officinale* or *Verbascum thapsus* (Figure 4.2b).

Environmental Variables and
Nonindigenous Plant Occupancy

The relative contribution of all the environmental variables for describing NIS distributions changed slightly with the addition of either current or historic land use variables, which suggested the environmental variables were confounded (i.e., interacted) with the land use variables (Table 4.5; Appendix B). However, most changes were relatively minimal suggesting current and historical land use variables contributed unique information not captured in the set of environmental covariates used for describing NIS distributions.

We were interested in parsing the relative roles of disturbance variables (i.e., distance from roads and wildfire) in each of the models to assess their potential for confounding with land use variables. The predicted probabilities of both NIS grass species were significantly positively correlated with the presence of wildfire across all of their occupancy models (Appendix B, Tables B.1 and B.3), but the relative role of wildfire in explaining their distributions changed with the inclusion of land use variables (Table 4.5). Specifically, the presence of wildfire explained more variation in the distribution of the annual grass, *B. tectorum*, with the addition of historic land use in this species' Model 3 than compared with Model 1; whereas, the opposite trend was detected with predicted occupancy of the perennial forage grass, *B. inermis*. Furthermore, a history of wildfire was relatively unimportant at characterizing *C. maculosa* occupancy across all respective

models but was very important for characterizing *V. thapsus* and *C. arvense* distributions (Appendix B, Tables B.6 and B.12). The proportionate contributions of wildfire and historic land use suggested they were important for explaining *C. arvense* occupancy, but the consistent percent contribution of wildfire across all *C. arvense* occupancy models suggested anthropogenic land use changes acted differently on its distribution than did the natural disturbance of wildfire.

Distance from roads decreased in relative importance in predicting occupancies of the NIS grasses with the inclusion of historic land use (Table 4.5). Opposite trends were exhibited, however, with the biennial and perennial forbs where the relative contribution of distance from roads for explaining NIS occupancy increased in their respective Model 3 versus Model 1 (Table 4.5). The increase in the relative contribution of distance from roads in explaining some NIS occupancy suggested historical land use classes were potentially describing anthropogenic related processes associated with NIS distributions not captured in the distance from roads variable.

Discussion

Although more variation in NIS distributions were explained with the inclusion of the current or historical land use variables, the relative role of land use, quantified as percent change in model deviance when land use variables were omitted, were variable across NIS, but historical land use explained more residual deviance for all species. Thus, current patterns of NIS distributions were sensitive to land use history suggesting NIS distributions were sensitive to interactions between current and historic land uses. Moreover, current patterns of NIS distributions were not only affected by spatial but also

temporal heterogeneity. Categories of current land use and cover improved predictions for distributions of native plant species in Britain (Pearson et al. 2004), and prior forest and agricultural land uses were reported to positively influence the occupancy and fecundity of non-native, invasive plants (Brown et al. 2006; Baer et al. 2009).

Human altered landscapes, particularly those in close proximity to nature reserves could impact natural disturbance regimes inside and outside of reserves with subsequent consequences on vegetation patterns (Brooks et al. 2004). One such consequence might be the promotion of NIS invasions from outside to inside the reserve. Travel through Paradise Valley is required to access the North Gate Entrance to Yellowstone National Park, which recorded the entry or exit of nearly 245,000 vehicles between May and September of 2011 (www.nature.nps.gov/stats/, accessed February 28, 2012). We hypothesize human activities occurring outside of Yellowstone Park have the potential to facilitate NIS introduction and establishment inside the Park based on positive correlations reported between non-native plant species richness and the average annual number of visitors in U.S. National Parks (Allen et al. 2009) and based on new insights in vehicle facilitated long-distance plant propagule dispersal (Von der Lippe and Kowarik 2007; Taylor et al. submitted Jan. 3, 2012).

Exurban development is an increasing component of the landscape where this study was conducted and in other rural areas of the western United States. The human population increased 58% and the area of land in exurban land use increased by nearly 350% between 1970 and 1999 within the GYE (Gude et al. 2006). Consequently, researchers and land managers have become increasingly interested in understanding the

human interactions with the environment and potential environmental consequences of exurban development (DeFries et al. 2007; Hansen and DeFries 2007b). We found more variation in NIS distributions was accounted for with inclusion of exurban development as a category in our land use variables suggesting its importance for characterizing NIS occupancy. There was a considerable amount of exurban land use located adjacent to U.S. Forest Land in Paradise Valley, which could facilitate NIS arrival and establishment in these areas similarly to facilitation of introductions in National Parks. A recent study predicted significant increases in exurban development by 2020 within the GYE (Gude et al. 2007), which suggests the immediate importance of understanding how NIS distributions respond to changes in land use from range and forest uses to residential uses. However, our results showed different species responded differently to exurban land use suggesting some but not all NIS are favored with these types of land use changes.

Locations currently or historically used for agriculture have been documented as having modified disturbance and nutrient cycling regimes and can lack sufficient native plant species or their propagules adapted to these altered regimes thereby creating conditions vulnerable to plant invasions (Baer et al. 2009). The results of this study suggested NIS occupancy was related to interactions between spatial and temporal configurations of current and historic irrigation practices, but, again, NIS responded variably to land uses either currently or historically used for irrigated agriculture. For instance, increases in the mean predictions of probabilities of *B. inermis* were increased

in locations previously used for irrigated cropland or pasture. This was not surprising as *B. inermis* was purposefully introduced as a forage crop.

Disentangling the Roles of Natural and Human Disturbance Variables

Land uses and changes within them are typically correlated to naturally occurring environmental conditions. These confounding relationships have complicated other studies interested in the role of land use on patterns of vegetation (Wells et al. 1976; Duffy and Meier 1992; Brunet 1993; Thuiller et al. 2004). Thus, it was expected that current and historical land use variables would be confounded with our set of selected environmental covariates. Disturbance related variables such as wildfire and distance from roads can directly impact some NIS distributions by either facilitating dispersal or generating disturbance regimes favoring weedy species (Von der Lippe and Kowarik 2007; Rew and Johnson 2010; Taylor et al. submitted Jan. 3, 2012). The relative role of wildfire in explaining the occupancy of *B. inermis* decreased with the inclusion of land use variables but increased for *B. tectourm*, which suggested potential interactions between natural and anthropogenic disturbances may be important for characterizing some NIS distributions. Indeed, it is likely that B. inermis had been sown in some areas of Paradise Valley and potentially in other areas surveyed over the previous few decades, which makes B. inermis occurrence positively associated with irrigated and exurban land uses. Motzkin et al. (1996) reported interactions between disturbance types were important for structuring vegetation patterns and suggested land use history influenced the composition of the species pool on which fire acted.

The significance of proximity to right-of-ways such as roads with NIS occurrence and richness were reported in ecosystems with minimal human impact (Pauchard and Alaback 2004; Rew et al. 2005; Seipel et al. 2012; Bridges et al. 2012, in preparation). However, the influence of these relationships in structuring NIS distributions may also interact with other anthropogenic disturbances in systems undergoing land use intensification. Bridges et al. (2012, in preparation) illustrated how the relationship of distance from roads in explaining *B. tectorum* distributions changed from significantly negative to significantly positive as the intensity of human perturbations increased across three adjacent management systems. Comparably, the significance of distance from roads in explaining *B. tectorum* and *B. inermis* occupancy resulting from models containing only environmental predictors was reduced with the inclusion of historic land use. However, proximity to roads did not contribute much in respect to explaining distributions for all NIS evaluated suggesting its significance for explaining NIS occupancy was lessened in more intensely human altered ecosystems. Thus, our study revealed the importance of interactions between current and historical land uses in explaining distributions of nonindigenous plant species at local spatial extents and fine scales.

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Tables and Figures

Table 4.1 Characteristics of nonindigenous plant species (NIS) assessed in this study

Species	Life History[a,b]	Reproduction[c]	Primary Dispersal	Sources
Bromus inermis Leyess.	Perennial[a] Grass	Seed; Veg	Wind	Heide (1994)
Bromus tectorum L.	Annual Grass	Seed	Animal	Mack (1981)
Centaurea maculosa Dorn	Perennial[a] Forb	Seed	Wind	Jacobs and Sheley (1998); Sheley et al. (1998)
Cirsium arvense L.	Perennial[a] Forb	Seed; Veg	Wind	Donald (1994)
Cynoglossum officinale L.	Perennial[b] Forb	Seed	Animal	Upadhyaya et al. (1988)
Verbascum thapsus L.	Biennial Forb	Seed	Wind	Donnelly et al. (1998); Gross and Werner (1982)

[a] iteroparous perennial
[b] semelparous perennial
[c] mode of reproduction either by seed (Seed) and/or vegetative (Veg) reproduction

Table 4.2 Sample sizes by current and historical land use/cover classes. Historical land use/cover classes describe document land use changes and, thus, represent current land uses in the context of prior land use

Code[a]	Current Land Use/Cover	Sample Size
1	Exurban (residential)	124
2	Irrigated Agriculture	110
3	Rangeland	1399
4	Conifer Forest	150
	Historical Land Use/Cover	Sample Size
2	Irrigated Agriculture	73
3	Rangeland/Grassland	1303
4	Conifer Forest	88
23	Irrigated Ag → Exurban	30
31	Rangeland → Exurban	102
32	Rangeland →Irrigated Ag	37
34	Rangeland → Conifer Forest	46
43	Conifer Forest → Rangeland	29
323	Rangeland → Irrigated Ag → Rangeland	15
341	Rangeland → Conifer Forest → Exurban	14
343	Rangeland → Conifer Forest → Rangeland	22

[a]Code refers to the current land use codes based on Anderson land use classifications (Anderson et al. 1976); Code also refers to the land use changes documented between 1948 and 2010 depicted as single digit codes based on Anderson land use classifications

Table 4.3 Environmental predictor variables used for modeling nonindigenous plant occupancy in Paradise Valley (PVAL)

Variable	Abbreviation	Variable Type[a]	Source
Elevation (m)	ELEV	Indirect	National Elevation Dataset (courtesy of U.S. Geological Survey via http://seamless.usgs.gov)
Slope (degrees)	SLOPE	Indirect	Derived in Spatial Analyst for ArcGIS 9.3[c]
Distance from Roads (m)	DRDS	Direct	MTNRIS[d]; Derived in Spatial Analyst for ArcGIS 9.3[c]
Distance from Streams (m)	DSTMS	Direct	MTNRIS[d]; Derived in Spatial Analyst for ArcGIS 9.3[c]
Distance from Trails (m)	DTRLS	Direct	MTNRIS[d]; Derived in Spatial Analyst for ArcGIS 9.3[c]
Wildfire (presence/absence)[b]	WILDFIRE	Direct	MTNRIS[d]
Potential Direct Solar Insolation (kWh m^{-2})	SOLAR	Resource	Derived in SAGA GIS 2.0.7[e] Module for Terrain Analysis-Lighting, Visibility v.1.0
Topographic Wetness Index	TWI	Resource	Derived in SAGA GIS 2.0.7[e] Module for Terrain Analysis-Hydrology v.1.0

[a]Variable type: Austin (2002, 2007) described the use of three types of variables for modeling plant species distributions, indirect, direct, and resource
[b]Wildfire: categorical, binary variable describing the presence or absence of wildfire between 1985 and 2010
[c]ArcGIS 9.3 (ESRI 1999-2009)
[d]MTNRIS: Montana Natural Resource Information System (www.nris.mt.gov)
[e]SAGA GIS 2.0.7 (SAGA Development Team 2011)

Table 4.4 Summary of the analysis of deviance results for occupancy models of nonindigenous plant species (NIS)

Species	Life History	Variation in NIS Distribution Explained (%)[a]			Within Model Variation Explained (%)[b]			
		Model 1[c]	Model 2[c]	Model 3[c]	Current LU[d]	p-value[d]	Historic LU[d]	p-value[d]
Bromus inermis	Perennial Grass	28.46	33.40	44.45	7.42	<0.001	28.79	<0.001
Bromus tectorum	Annual Grass	16.19	16.93	23.50	0.89	0.001	9.56	<0.001
Centaurea maculosa	Perennial Forb	18.64	22.13	24.67	4.48	<0.001	8.03	<0.001
Cirsium arvense	Perennial Forb	13.87	14.86	26.53	1.14	0.223	17.23	<0.001
Cynoglossum officinale	Perennial Forb[e]	22.53	26.50	35.62	5.40	<0.001	20.33	<0.001
Verbascum thapsus	Biennial Forb	28.05	30.85	33.16	4.04	<0.001	7.65	<0.001

[a]Variation in NIS Distribution Explained (%) equal to the percent deviance in NIS occupancy explained by each general linear model
[b]Within Model Variation Explained (%) equal to deviance explained by each land use variable as a percent of total deviance explained in Models 2 and 3, respectively
[c]Model 1, Model 2, Model 3: NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively
[d]LU: land use categorical variable
[e]p-value corresponding to the change in devaince explained within each model when either Current LU or Historic LU were omitted from the fitted models
[e]*C. officinale*: semelparous perennial forb

Table 4.5 Percent deviance (*D*) explained by disturbance related environmental variables within each of the three models built for each nonindigenous plant species (NIS)

	Wildfire			Distance from Roads		
	%*D* explained					
Species	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
Bromus inermis	12.22	7.24	4.12	0.98	0.04	0.05
Bromus tectorum	2.93	2.74	4.19	0.09	0.01	<0.01
Centaurea maculosa	<0.01	0.01	0.03	0.03	0.20	0.45
Cirsium arvense	9.39	8.86	8.24	0.01	0.00	1.25
Cynoglossum officinale	4.48	3.73	2.64	0.01	0.12	0.03
Verbascum thapsus	24.81	27.36	26.91	1.41	2.00	2.81

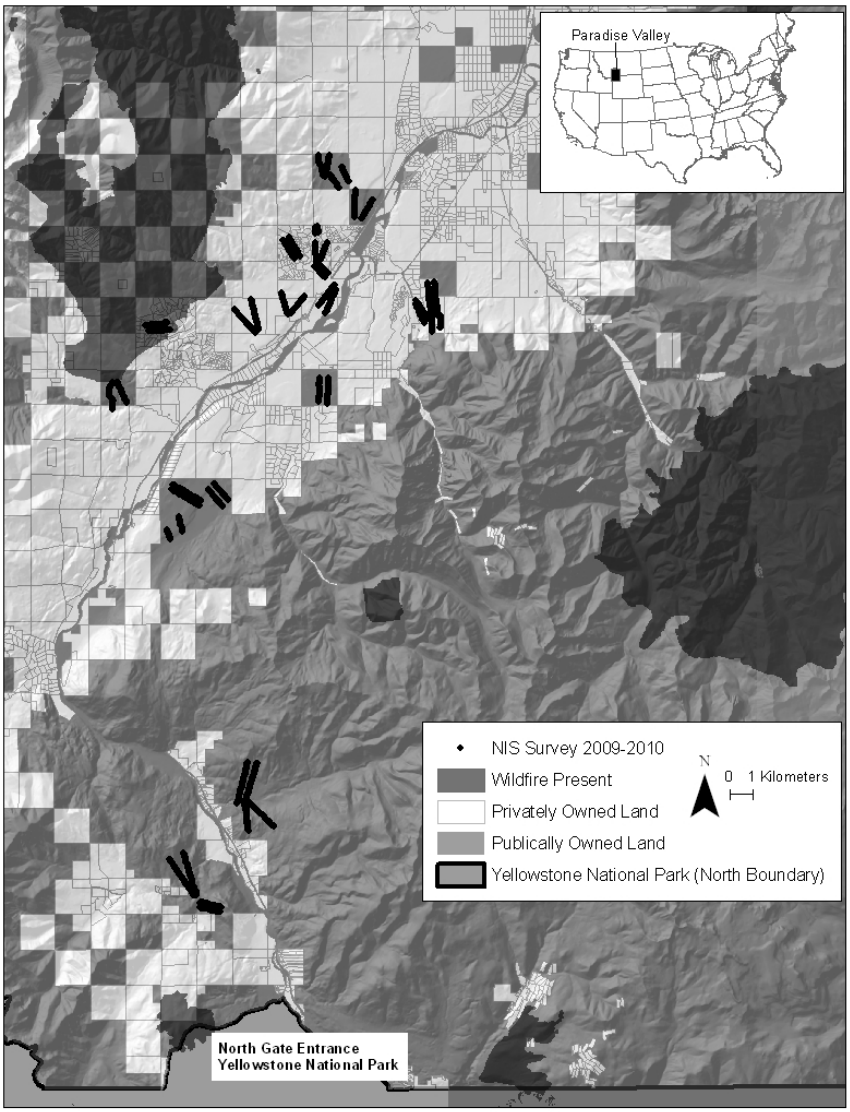
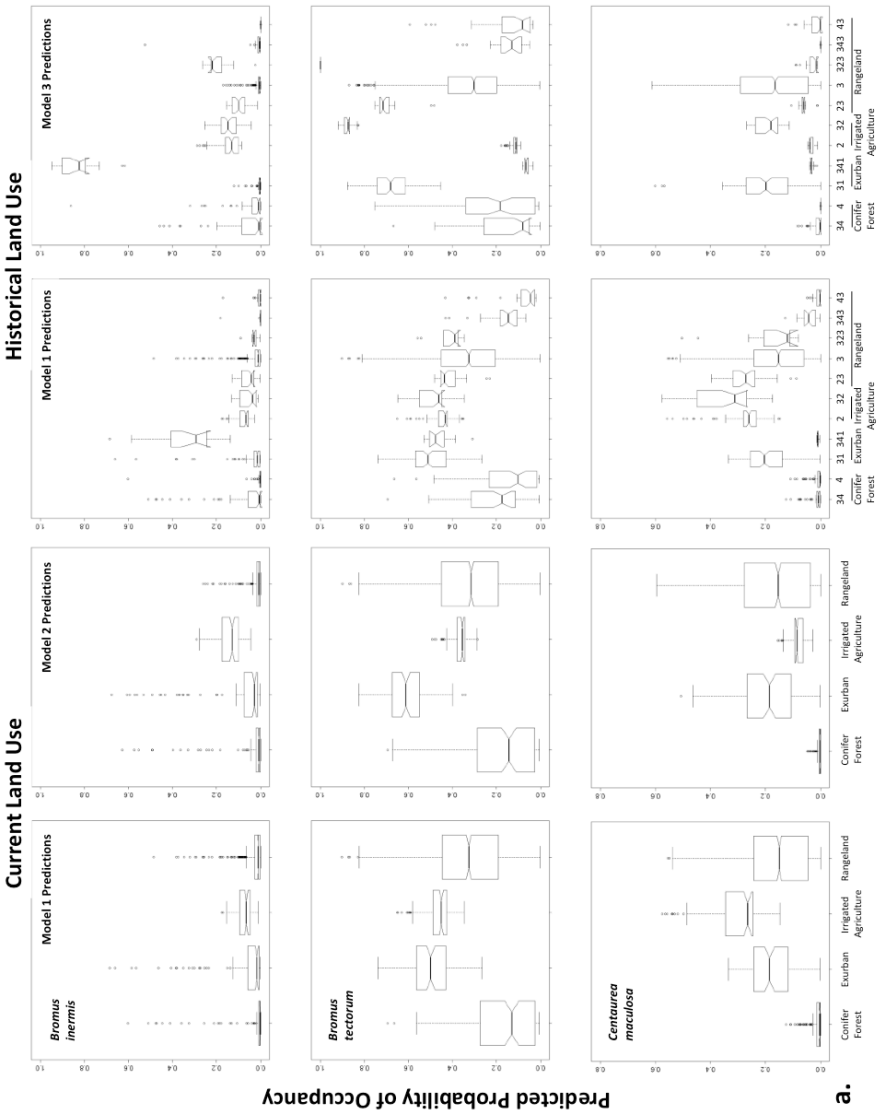


Figure 4.1 Paradise Valley, Montana (USA) study area and nonindigenous plant species survey points collected along transects in 2009 and 2010


Current Land Use
Historical Land Use
Model 1 Predictions
Model 2 Predictions
Model 3 Predictions
Bromus inermis
Bromus tectorum
Centaurea maculosa
Predicted Probability of Occupancy
Conifer Forest
Exurban
Irrigated Agriculture
Rangeland
34
4
31
341
2
32
23
3
323
343
43
a.

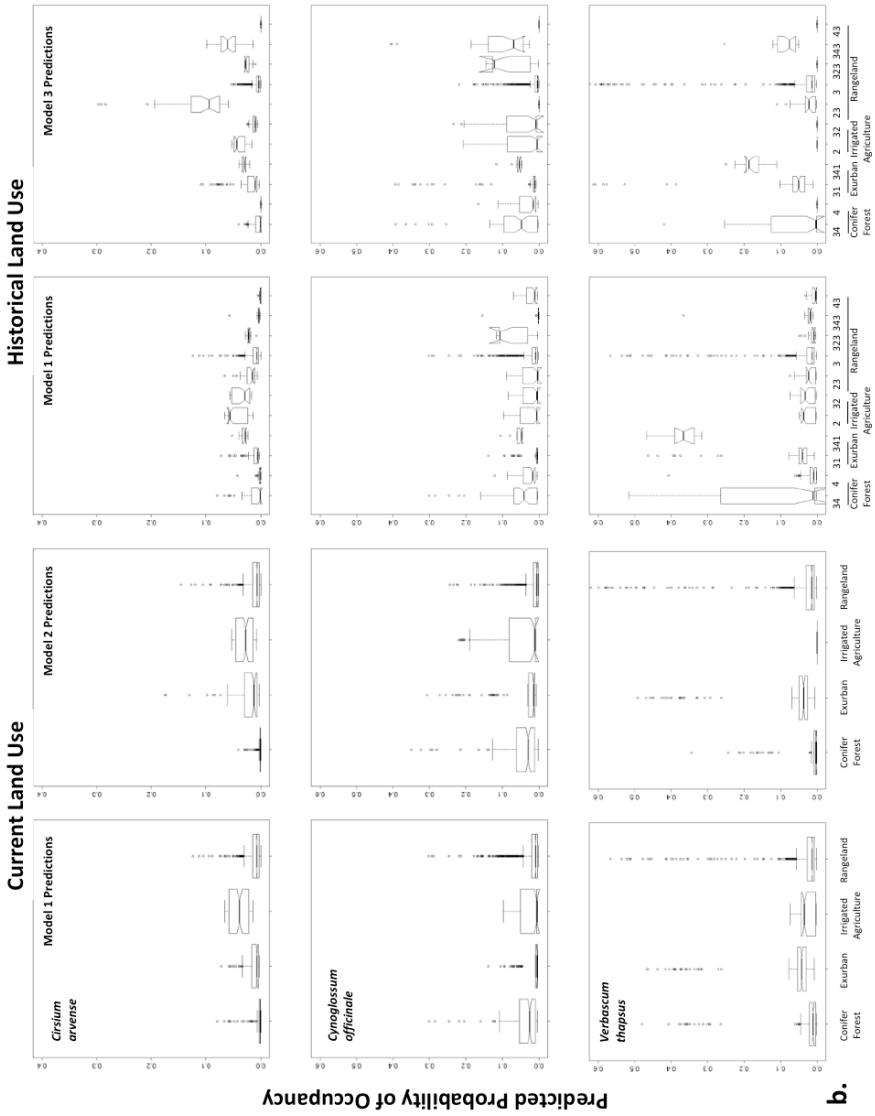


Figure 4.2 Comparison of the predicted probabilities of occupancy for nonindigenous plant species.
Models including only environmental variables (Model 1), models including environmental plus current land use variables (Model 2), and models including environmental plus historical land use (Model 3) plotted against current land use categories. Tukey's notches approximating 95% confidence intervals are displayed as a 'waist' around the median values.

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CHAPTER FIVE

NONINDIGENOUS POPULATION AND OFF TARGET PLANT COMMUNITY RESPONSES TO MANAGEMENT ALONG AN ENVIRONMENTAL SUITABILITY GRADIENT

Contribution of Authors and Co-Authors

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Abstract

1. Concern over the ecological and economic impacts of nonindigenous plant species (NIS) has engendered various pieces of legislation at national and local levels, which mandate the management of several NIS. However, the current NIS management paradigm is based on the assumption that all populations of NIS are invasive and impact ecosystem processes. This view does not account for the effects of spatial and temporal environmental heterogeneity on NIS population dynamics. Models of probabilities of NIS occurrence predict environmental suitability and may be used to prioritize management of NIS populations.
2. We located populations of two NIS, *Bromus tectorum* (L.) and *Linaria dalmatica* (L.) Mill., along their respective gradients of probabilities of occurrence and applied herbicide treatments to those populations. Data on target NIS densities and off target plant communities were recorded prior to and for two seasons after herbicide treatment.
3. *B. tectorum* densities were positively related to predicted environmental suitability; whereas, *L. dalmatica* densities were negatively related to environmental suitability. The effects of herbicide treatment on densities of populations for both target NIS were dependent on environmental suitability but in contrasting ways for each species. Further, *B. tectorum* densities in treated plots began to recover toward pre-treatment levels less than two years after treatment for populations growing in more suitable environments. Responses of

the off target communities were temporarily affected by herbicide treatment for both target NIS.

4. NIS populations responded to herbicide treatment differently depending on how suitable the environmental conditions were suggesting models of probabilities of NIS occurrence could be informative of NIS population responses to management and guide prioritization of management resources.
5. Results of this study suggested that actively managing *B. tectorum* populations in more suitable sites more frequently compared to populations growing in less suitable sites. *L. dalmatica* responses to management were less clear; however, results from both species suggested monitoring populations of the same species growing in a variety of environmental conditions is warranted. We illustrated how an experimental and ecological based approach to NIS management could result in more efficient use of resources.

Keywords: *Bromus tectorum*, invasive species, *Linaria dalmatica*, monitoring, species distribution model, weed management

Introduction

The presence and spread of nonindigenous plant species' (NIS) populations in rangelands or wildlands are associated with both ecological and economic costs (Mack et al. 2000; Pimentel et al. 2005). NIS have been reported to cause a variety of undesired impacts ranging from reducing the values of certain land uses such as rangeland for livestock grazing to altering ecosystem processes by interacting with natural disturbance

regimes (D'Antonio and Vitousek 1992). Such alterations have been reported to impact native or desired species biodiversity at multiple trophic levels (Mack et al. 2000; Brooks et al. 2004). The concern over nonnative species, whether plant or animal, led to the signing of United States (U.S.) Executive Order 13112 in 1999 that mandated the management of such species to prevent their introduction or spread. This Order coupled with local noxious weed laws have emphasized control of a particular set of species. Consequently, control of species, rather than prioritizing monitoring and management of invasive populations, is often part of local managers' land management objectives. This has resulted in millions of dollars in annual NIS control costs within the U.S. (Pimentel et al. 2005) with little documentation of any benefits yielded from management efforts (Maxwell et al. 2009). Despite the legal requirements, land managers often lack the resources to conduct comprehensive inventories or actively manage all populations of NIS within their management areas. Properly implemented efficient NIS surveys (Rew et al. 2006) could be used to develop maps from models of NIS distributions, which characterize their environmental suitability. These predictions of probabilities of NIS occurrences could inform the prioritization of NIS populations to be managed (Rew et al. 2007; Fox et al. 2009; Maxwell et al. 2009; Giljohann et al. 2011).

Exploiting NIS (e.g., weed species) population/patch spatial dynamics to direct where to implement management actions has long been recognized as a valuable tool for spatial prioritization of weed management (Menz et al. 1980; Moody and Mack 1988; Emry et al. 2011). Results of simulation studies suggested management treatments are more efficient and efficacious when satellite patches and/or edges of focal weed patches are

given priority because dynamics of weed patches are more variable at their edges compared to their interiors (Moody and Mack 1988). However, neither local nor regional dynamics of plant populations are well understood. Freckleton and Watkinson (2002) presented several different likely local and regional patterns of growth for plants, but there remains a lack of empirical data that demonstrate how plant population dynamics differ over spatially heterogeneous environments. Pulliam (1988) suggested habitat specific population demography may play a more ecologically meaningful role in population dynamics than mean values of age or stage specific demographic rates. This suggests more environmentally suitable areas for NIS may correspond to more invasive populations, that is, those populations expanding in density and/or area over time (Rew et al. 2007; Brown et al. 2008). Therefore, if population growth rates differ with habitat conditions or environmental suitability, it may not be adequate to assume all populations of the same species will respond to management similarly (Pulliam 1988; Hobbs and Humphries 1995). NIS management should include consideration not just of the target species but also of the environments harboring those species (Hobbs and Humphries 1995; Vila and Weiner 2004). For example, anthropogenic alterations of land use may make habitat more or less suitable for particular populations of NIS (Byers 2002; Baer et al. 2009; Bridges et al. 2012, in preparation) and, thus, the response to weed control practices may too vary with environmental heterogeneity. NIS management based on these ecological principles may reduce costs of control and result in a reduction of NIS invasion (Rew et al. 2007).

Herbicides are the most widely used and possibly most efficacious NIS management tool in range or wildlands over short temporal scales (Kettenring and Adams 2011); however, deleterious off target community effects are generally greatest when using chemical treatments (Hobbs and Humphries 1995; Pimentel et al. 2005). Negative impacts of management may be greater in more suitable environments for NIS as native plant species richness may also be greater in those locations (Stohlgren et al. 1999). However, plant species richness may be less in more suitable areas for NIS, thereby, being more susceptible to NIS invasions (Tilman 1997; Tilman 2002). Thus, it is important to work toward minimizing negative effects to other off target members of the plant community by better understanding the relationships between NIS environmental suitability and plant community responses to management (Rew et al. 2007; Brown et al. 2008; Fox et al. 2009; Giljohann et al. 2011).

Although effective, uniform herbicide application typically does not result in a uniform response from individuals within a weed patch. This is likely due to spatial heterogeneity of intrinsic and extrinsic factors regulating individual plant vigor and population density (as presented in Cousens and Mortimer 1995). Although some empirical data exist evaluating how spatially explicit weed management can reduce local population growth rates (Humston et al. 2005; Emry et al. 2011), field experimentation of population responses at a regional scale with heterogeneous environments are currently lacking.

The goal of this study was to evaluate the utility of species distribution models for landscape level or regional scale NIS population management prioritization. Species

distribution models were created for two NIS using logistic regression, and the resulting probability of occurrence predictions were used to develop environmental suitability indices for each species. Populations for study were selected along each species' environmental suitability gradient. Thus, our specific objectives were to determine 1) if responses of target NIS density and off target plant species richness differed between herbicide treatments along an environmental suitability gradient; and 2) if weed patch spatial dynamics differed with herbicide treatment by evaluating responses on patch edges.

Methods

Target Nonindigenous Plant Species

Bromus tectorum (L.) and *Linaria dalmatica* (L.) Mill. were the two nonindigenous plant species (NIS) selected for evaluation of management efficacy within the study area because of their contrasting taxonomic groupings, life histories, and growth habits. *B. tectorum* is an obligate outcrossing, annual grass (Mack 1981) that typically grows in interconnected patches within the study area. *L. dalmatica* is a perennial forb that grows in patchy distributions within the study area, and this species has both sexual and asexual reproduction (Vujnovic and Wein 1997).

Environmental Suitability Modeling

The probabilities of occurrence were predicted for the target NIS within the northern range area of the Greater Yellowstone Ecosystem (GYE) in Montana (U.S.A) (Figure 5.1) using data collected within Yellowstone National Park (YNP) and Gallatin National

Forest (GNF) (Rew et al. 2005; Bridges et al. 2012, in preparation). Presence and absence data for each species at a 30 m^2 scale were modeled using logistic regression with eight environmental predictor variables (see methods in Bridges et al. 2012, in preparation). Bridges et al. (2012, in preparation) reported *B. tectorum* distributions were similar in sampled areas of YNP and GNF. This suggested extrapolation of logistic regression models built with data collected from both YNP and GNF would be suitable for characterizing *B. tectorum* distributions in the study area for this project. Because few instances of *L. dalmatica* occurrence have been documented in the GNF, predictions of this species' probabilities of occurrence were restricted to areas north and adjacent to the YNP (Figure 5.1).

Species distribution models for both species were validated by estimating the area under the receiver operating characteristic curve (AUC) using independent data sets collected from within YNP and GNF (Pearce and Ferrier 2000). The resulting AUC for *B. tectorum* was 0.84 (lower and upper 95% confidence boundaries equal to 0.82, 0.86, respectively), and the AUC for *L. dalmatica* was 0.86 (lower and upper 95% confidence boundaries equal to 0.84, 0.87, respectively). Thus, models for both species were considered to predict species' occurrences significantly better than random chance (Pearce and Ferrier 2000).

The mapped predicted probabilities of each species' occurrence were assumed to be spatial representations of environmental suitability where locations of higher predicted values corresponded to more suitable environments (Guisan and Zimmermann 2000). Theoretically, predictions could range from 0 to 1.0 where locations predicted as 0 are

completely unsuitable (i.e., no occurrences ever recorded for locations with a particular environmental covariate pattern) and locations predicted as 1.0 would be completely suitable (i.e., occurrences recorded every time for locations with a particular covariate pattern). However, theory also suggests that suitable locations will sometimes be unoccupied (Pulliam 1988) resulting in predictions of maximum probabilities of occurrence being less than 1.0. Thus, predictions of relative environmental suitability for a specific management area require rescaling. The raw predictions for both species were rescaled by dividing each prediction by the range of values predicted from the validation data. This resulted in a relative environmental suitability index where the maximum predicted value became equal to 1.0, and the minimum prediction became equal to 0.

Environmental Suitability Experimental Sites

For each NIS, populations (i.e., sets of patches) were selected at locations with different predicted probabilities of occurrence representing a gradient from relatively low to high environmental suitability. Each site contained a range of suitability values, and the mean value for each site was used as a continuous variable in statistical analyses. Environmental suitability site was equal to five (j =1,..,5) or six (j = 1,…,6) of mean rescaled predicted probabilities of occurrence for *B. tectorum* or *L. dalmatica*, respectively. All sites were located on GNF rangeland (Figure 5.1).

Within Site Experiment

To address treatment effects at each site along the environmental suitability gradient, eight 3 m x 4.5 m management treatment plots were placed along target NIS patch edges and randomly assigned one of two herbicide treatments (i) (n_i = 4), treated or untreated

(Figure 5.2). Because of our specific interest in population responses to environmental suitability and management along patch edges (sensu Moody and Mack 1988), patch edge position (*k*), inner or outer, was represented as a split-plot nested within each *i* treatment plot (Figures 5.2 and 5.3). There were three replications of observations recorded within 0.5 m^2 permanent quadrats within each split-plot ($n_{ijkt} = 3$) for each of three growing seasons of observations (*t*) (Figure 5.3). In season 1 (2009), pre-treatment data were collected including: target NIS stem density, number of off target native and nonindigenous (i.e., exotic) plant species. The same measures within the same quadrats were made at each time *t* in growing season 2 (2010; post treatment year 1) and season 3 (2011; post treatment year 2). Measurements were made in late June through early August for all years *t* of the experiment.

Herbicide Treatments

Imazapic (imidazolinone chemical family) was applied early November 2009 at a rate of approximately 600 ml of product ha^{-1} (8 oz ac^{-1}) using a ~3 m (10 ft) spray boom and CO_2 backpack sprayer to each of the treated *B. tectorum* plots. Likewise, picloram (picolinic acid chemical family) was applied in early June 2010 at a rate of approximately 1.2 L ha-1 (2 pt ac^{-1}) to each of the treated *L. dalmatica* plots. Picloram was applied with 0.25% v/v non-ionic surfactant. Plots were treated with herbicide only once during the experiment.

Statistical Analyses

Generalized linear mixed models were used to assess the response of target and non-target species to herbicide management among sites of different environmental suitability

and to assess the relationship between patch edge dynamics with environmental suitability. We modeled the number of target species stems, number of off target species, and the ratio of the number of off target nonindigenous (exotic) to number of native plant species (EN ratio) as a function of environmental suitability index, herbicide treatment, and patch edge position. To account for nested data, observations (quadrats) within the same treatment plot (3 m x 4.05 m plot) were modeled as a plot specific random effect (Zuur et al. 2009). To indirectly account for measurements made prior to and after herbicide treatment in 2009 and 2010-2011, respectively, herbicide treatment were coded as five categories corresponding to 2009 pretreatment and 2010-2011 untreated and treated ($i = 1,\ldots,5$). The full model for each response included the three-way interaction, all two-way interactions, and main effects (eqn 1).

$$\begin{aligned}\log \text{ or } \operatorname{logit}(R_{ikj}) &= \beta_0 + \beta_1\,(\text{suitability index})_j + \beta_2\,(\text{herbicide treatment})_i \\ &+ \beta_3\,(\text{patch edge position})_k + \beta_4\,(\text{suitability index} * \text{herbicide treatment})_{ij} \\ &+ \beta_5\,(\text{suitability index} * \text{patch edge position})_{jk} \\ &+ \beta_6\,(\text{herbicide treatment} * \text{patch edge position})_{ik} \\ &+ \beta_7\,(\text{suitability index} * \text{herbicide treatment} * \text{patch edge position})_{ijk} \\ &+ \alpha_{jm}\end{aligned}$$

Where $i = 1, \ldots, 5$ herbicide treatments;

$j = 1, .., 5$ or 6 environmental suitability sites;

$k = 1,2$ patch edge positions (inner or outer);

$m = 1, .., 8$ treatment plots;

α_{jm} = the random effect term for nested quadrats within each m plot at each j site;

$\alpha_{jm} \sim N(0, D)$; $R_{ijkt} \sim \text{Poisson}(\mu)$ or $R_{ijkt} \sim \text{Binomial}(\pi, N)$;

$D =$ standard deviation of the random effect.

eqn 1

Response data that were discrete counts (i.e., target NIS density and richness) were analyzed as following a Poisson distribution (log link function in eqn 1), and the EN ratio data were analyzed following a Binomial distribution (logit link function in eqn 1). The EN ratio was modeled as an odds ratio of the number of exotic to native plant species where values close to 1.0 indicated the likelihood of observing an exotic species was equal to that of a native species. Predicted EN ratio values greater than 1.0 indicated a greater likelihood of observing an exotic species compared to observing a native species, and vice versa for predictions less than 1.0. The environmental suitability index values were treated as continuous variables in the models, and the herbicide treatment and patch edge position were categorical variables with 5 levels and 2 levels, respectively. The full model (eqn 1) was considered the final model for target NIS densities; whereas, off target species richness and the EN ratio was modeled with a reduced model containing only the two-way interaction between suitability index and herbicide treatment and main effects. Rather than define *a priori* contrasts or *a posteriori* multiple mean comparisons, we plotted the fixed effects of the interactions and/or main effects of herbicide treatment on the response variables to assess trends across time and environmental suitability indices. Further, this graphical assessment allowed us to interpret the effects of complex interactions remaining in the models. All analyses were performed using the base, stats, lme4, and effects packages in R version 2.13.2 (Fox 2003; Bates et al. 2011; R Development Core Team 2011).

Results

Densities of both target nonindigenous species varied monotonically with their varying levels of environmental suitability in 2009 prior to treatment (Figures 5.4 and 5.5). *B. tectorum* densities increased with increasing environmental suitability (Figure 5.4); whereas, *L. dalmatica* densities decreased with increasing environmental suitability (Figure 5.5).

Bromus tectorum

There were decreases in densities of inner edge untreated plots at higher values of predicted *B. tectorum* environmental suitability in 2010 compared to pre-treatment densities in 2009, although not statistically significant as inferred by overlapping 95% CIs (Figure 5.4a). Densities in untreated outer edges were similar in 2010 to those in 2009. The effect of herbicide treatment on *B. tectorum* approximately eight months after treatment (2010) resulted in similar densities for both inner and outer patch edges irrespective of predicted environmental suitability. Absolute values of densities were most reduced at locations of higher environmental suitability. Although herbicide treatment reduced densities at locations of lower environmental suitability compared to pre-treatment densities, these reductions were not significantly different (Figure 5.4a). Furthermore, the effect of herbicide treatment on densities was similar irrespective of patch edge position (inner or outer) or environmental suitability; however, densities of inner edges were reduced to similar densities as outer edges (Figure 5.4a)

In 2011, approximately 20 months after treatment, *B. tectorum* densities of inner and outer edges of untreated plots were similar to their respective pre-treatment densities

(Figure 5.4b). Densities of treated plots at lower suitability sites remained similar to treated densities in 2010; whereas, the overall trend of densities in treated plots of both edge positions increased at higher environmental suitability sites toward similar densities as in untreated and pre-treated plots (Figure 5.4b).

Linaria dalmatica

L. dalmatica densities increased slightly in the untreated plots in 2010, approximately two months after treatment and retained the same trend of decreased density as predicted environmental suitability increased (Figure 5.5a). The effect of herbicide treatment in the first season on stem densities appeared to be greater in inner patch edges as absolute values of densities decreased more in those treated quadrats relative to outer edges of treated plots. Densities of outer edges of treated plots were not significantly less than densities of outer edges in untreated plots in 2010 or of densities recorded in outer edges prior to treatment in 2009 (Figure 5.5a).

In 2011, there were increases in *L. dalmatica* densities in untreated plots compared to pre-treatment densities in 2009 with the greatest increases recorded for populations at the locations predicted as less suitable (Figure 5.5b). By 2011, approximately 14 months after herbicide application, the effect of herbicide treatment on the reduction of stem densities was more apparent at locations of lower predicted suitability. However, higher densities remained in both the inner and outer edges of treated plots at these locations compared to more suitable *L. dalmatica* sites (Figure 5.5b). Similarly as with *B. tectorum*, the effect of edge position on density did not appear to depend on environmental

suitability or herbicide treatment as trends of density between inner and outer edges were similar (Figure 5.5b).

Off Target Plant Community

Total off target plant species richness declined as *B. tectorum* environmental suitability increased regardless of herbicide treatment or time after treatment (Figure 5.6). Overall, species richness declined across all *B. tectorum* suitability sites with herbicide treatment in the first season (2010) (Figure 5.6a). The greatest reductions of off target richness in treated plots were at locations of lower environmental suitability. By 2011, approximately 20 months after herbicide application, richness had returned to levels similar to richness recorded pre-treatment in 2009 and in the untreated plots in 2011 (Figure 5.6b). The odds of sampling an off target NIS (i.e., exotic plant species) were lower than sampling a native species (EN ratio < 1.0) across all environmental suitability sites regardless of herbicide treatment (Figure 5.7). Thus, greater numbers of native species compared to NIS were present at all *B. tectorum* sites. The EN ratio decreased as environmental suitability increased in response to herbicide treatment in 2010 (Figure 5.7a); however, the ratio recovered in treated plots by 2011 (Figure 5.7b).

Total off target species richness was similar across all *L. dalmatica* environmental suitability sites both prior to herbicide treatment in 2009 and approximately two months after treatment in 2010 (Figure 5.8a). There was a slight increase in the richness of untreated plots across all levels of *L. dalmatica* environmental suitability in 2011, but total richness decreased with increased suitability in the treated plots (Figure 5.8b). The EN ratio decreased from greater than 1.0 to less than 1.0 as *L. dalmatica* suitability

increased irrespective of herbicide treatment or time after treatment (Figure 5.9). Thus, the odds of encountering an off target NIS were greater than encountering a native species at locations with lower predicted *L. dalmatica* suitability. These odds increased in treated plots compared to untreated plots at locations of lower suitability in 2010 (Figure 5.9a), but the odds decreased in treated plots relative to untreated plots at these sites in 2011 (Figure 5.9b).

Discussion

The current NIS management paradigm is based on the assumption that all populations of an NIS are invasive and negatively impact ecosystem processes. However, this view does not account for the effects of spatial and temporal environmental heterogeneity on population dynamics (Pulliam 1988; Davis et al. 2000; Vila and Weiner 2004). Thus, we hypothesized population responses to perturbations, such as the application of management treatments, may also vary with environmental conditions. We found NIS populations had differential responses to herbicide treatment depending on how suitable the environmental conditions were. These were encouraging results as they suggested models of NIS environmental suitability might be more than just useful guides for monitoring or detection of new NIS populations (Baxter and Possingham 2011; Ervin and Holly 2011). We have also illustrated these models may be informative of the dynamics and responses to management of NIS populations inhabiting specific, predictable environmental conditions (Guisan and Thuiller 2005).

B. tectorum populations responded to herbicide treatment and an environmental suitability gradient the way we initially hypothesized. We expected a trend of increasing

densities with increasing environmental suitability as conditions in more suitable areas may harbor populations with more invasive potential (Davis et al. 2000) and competitive advantages (Tilman 2002). Likewise, we hypothesized management may be less efficacious for denser populations growing in more suitable environments. *B. tectorum* populations growing in more suitable environments exhibited these trends; however, it was not measured in and it cannot be inferred from this study if increased *B. tectorum* density occurred in more suitable environments because it was a better competitor. Densities in treated plots of populations located in more suitable environments increased toward pre-treatment levels less than two years after application; whereas, densities of populations in less suitable environments did not increase by 2011.

From a management perspective, it might be wise to target *B. tectorum* populations in higher suitability sites more frequently until sufficient control is achieved; whereas, populations growing in less suitable environments may not need treatment as frequently. Furthermore, off target NIS richness was reduced at sites of higher predicted environmental suitability, and total off target species richness rebounded toward pre-treatment levels by the second season after treatment. These findings suggested there may minimal deleterious impacts to off target plant communities, and the risk of unintended effects on existing plant communities may be low enough to justify a greater intensity of management in more environmentally suitable areas. However, the temporary reduction in off target NIS may be based on the chemical used to treat *B. tectorum* populations. Imazapic is a broad spectrum herbicide that can have phyto-toxic effects on either monocot or dicot species (Shaner et al. 1984), and thus, likely

contributed to the effect of treatment on the reduction of other introduced grass species such as *Poa pratensis*, *Phleum pretense*, and *Bromus inermis*. A different herbicidal compound may have different effects on local plant flora.

L. dalmatica responses to management were less clear compared to *B. tectorum* responses, especially in the first season after treatment. It was not until the second season after herbicide application that the effects of treatment were better detected. Additional temporal data on *L. dalmatica* responses is likely necessary to understand its responses to management, especially for populations at less suitable sites. It was clear, however, that *L. dalmatica* populations growing in more suitable environments were a part of plant communities with higher native species richness. Thus, in addition to lower target NIS densities, the risk of negative off target community effects from herbicide treatment were greater at locations of higher suitability.

The contrasting nature of the *L. dalmatica* responses to its predicted environmental suitability gradient suggested there is great value in monitoring the different populations of the same species located in varyingly suitable environments over time before applying herbicide treatments (Rew et al. 2007). Management decisions based on insufficient monitoring data could result in an inefficient use of resources (Taylor and Hastings 2004) with minimal or no reduction of target NIS local or regional population growth rates. Furthermore, these divergent results between species could be due to their contrasting life histories, or our inference of environmental suitability based on predictions of probabilities of occurrence may be faulty, despite the vast literature relating habitat

quality to predictions of occupancy (Guisan and Zimmermann 2000; Guisan and Thuiller 2005).

The results from the experiment we conducted do not necessarily imply that NIS populations will respond similarly to management in another region as they did in this study. Rather, we illustrated how an experimentally and ecologically based approach to weed management may be very insightful and applicable to the needs of land managers. Such an experiment as the one presented here could easily be implemented in conjunction with existing weed management objectives to guide the prioritization of population level management (Rew et al. 2007).

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Figures

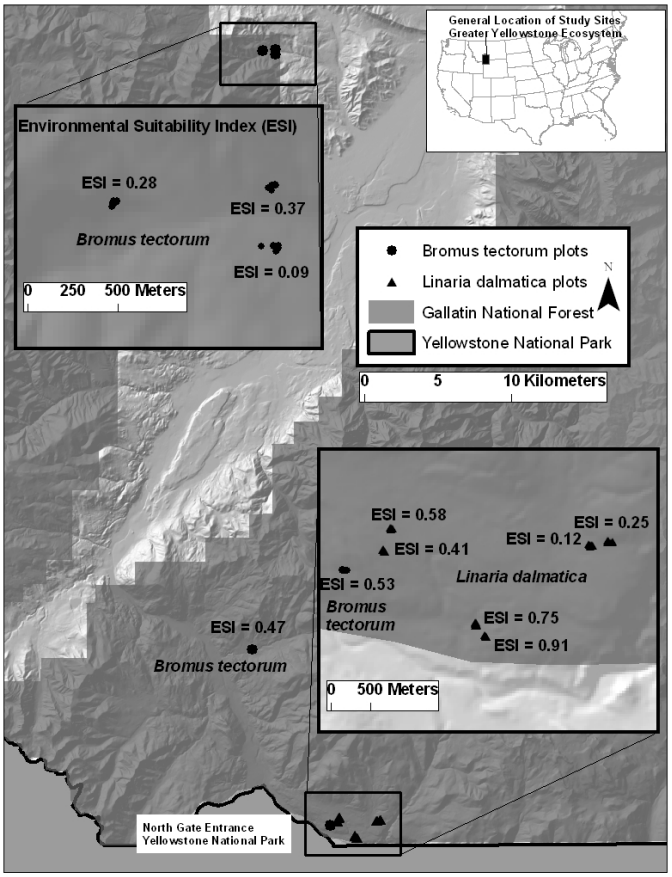


Figure 5.1. Environmental suitability sites with *j* levels representing a gradient of environmental suitability for *Bromus tectorum* and *Linaria dalmatica*.

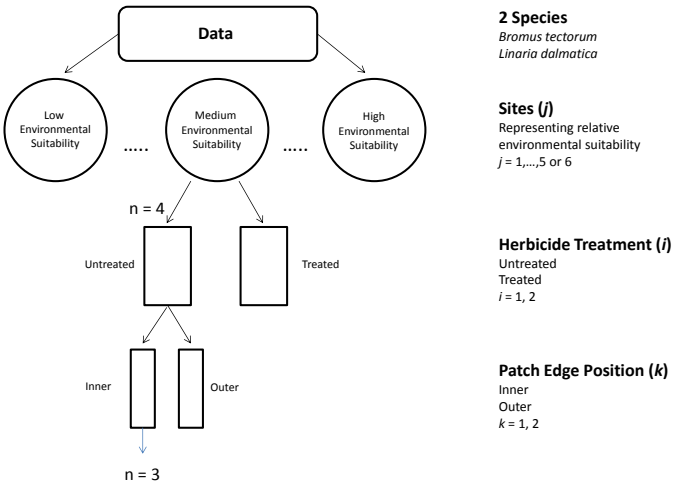


Figure 5.2. Experimental design diagram. Responses of two target nonindigenous plant species, *Bromus tectorum* and *Linaria dalmatica*, and non-target plant species were assessed at *j* levels of environmental suitability predicted by modeled probabilities of NIS occurrence. Within each *j* site, one of two herbicide treatments (*i*) were randomly selected for each of eight treatment plots. Weed patch edge position (*k*) was treated as a nested split-plot within each *i* treatment plot.

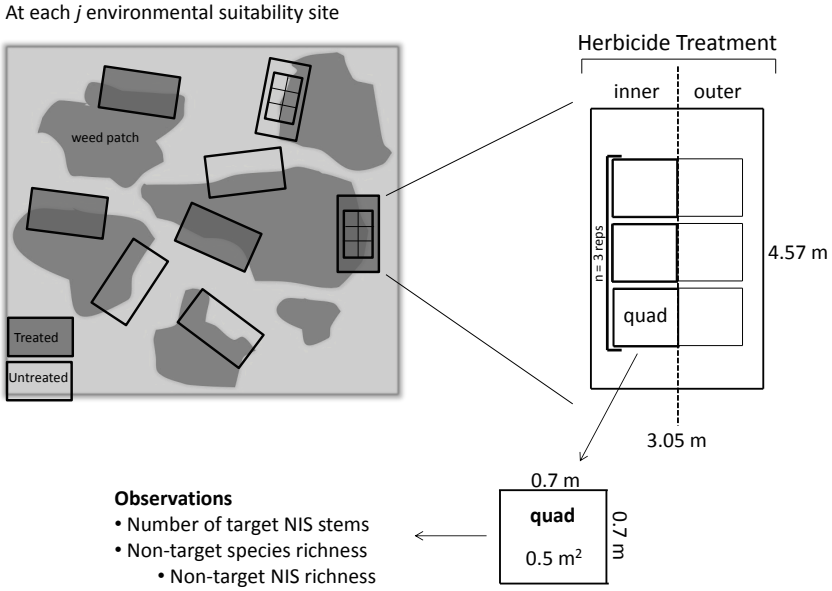


Figure 5.3. Data collection protocol diagram. The figure illustrates a typical environmental suitability site *j* with treatment plots positioned along weed patch edges. Within each weed patch edge position split-plot *k*, data were collected in three 0.5 m^2 permanent replicate quadrats (i.e.quads).

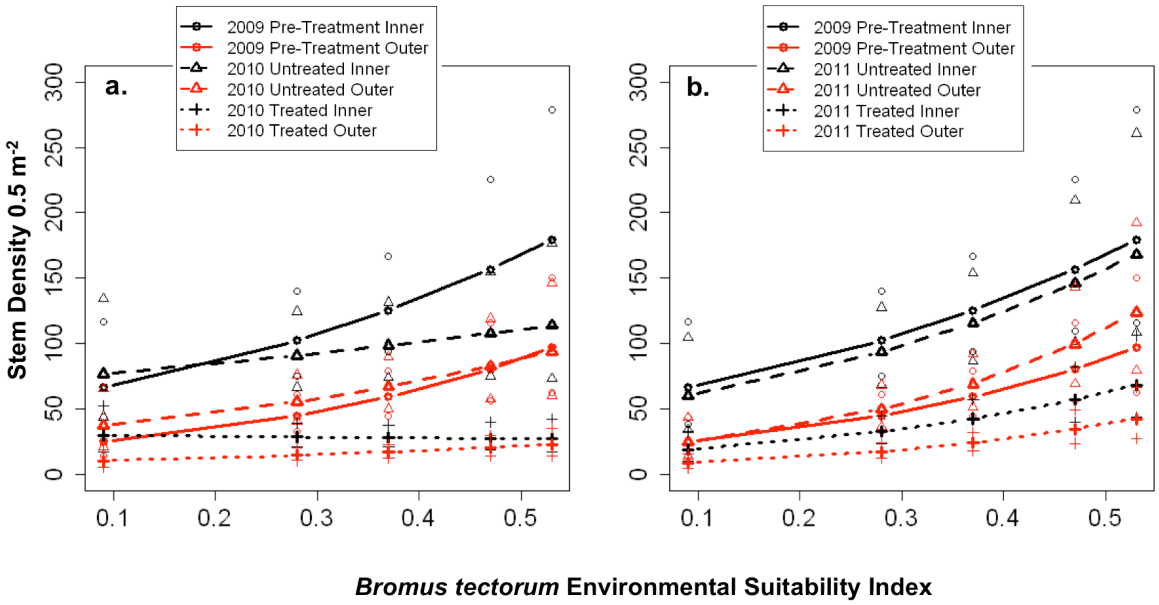


Figure 5.4 Effect of the three-way interaction term among environmental suitability, herbicide treatment, and patch edge position on *Bromus tectorum* density 0.5 m^{-2}. Panel a shows the effect of pre-herbicide (2009) and post 1-herbicide (2010) treatment responses. Panel b shows the effect of pre-herbicide (2009) and post 2-herbicide (2011) treatment responses. Plotted lines represent the mean response and symbols away from lines correspond to approximate upper and lower 95% confidence bounds.

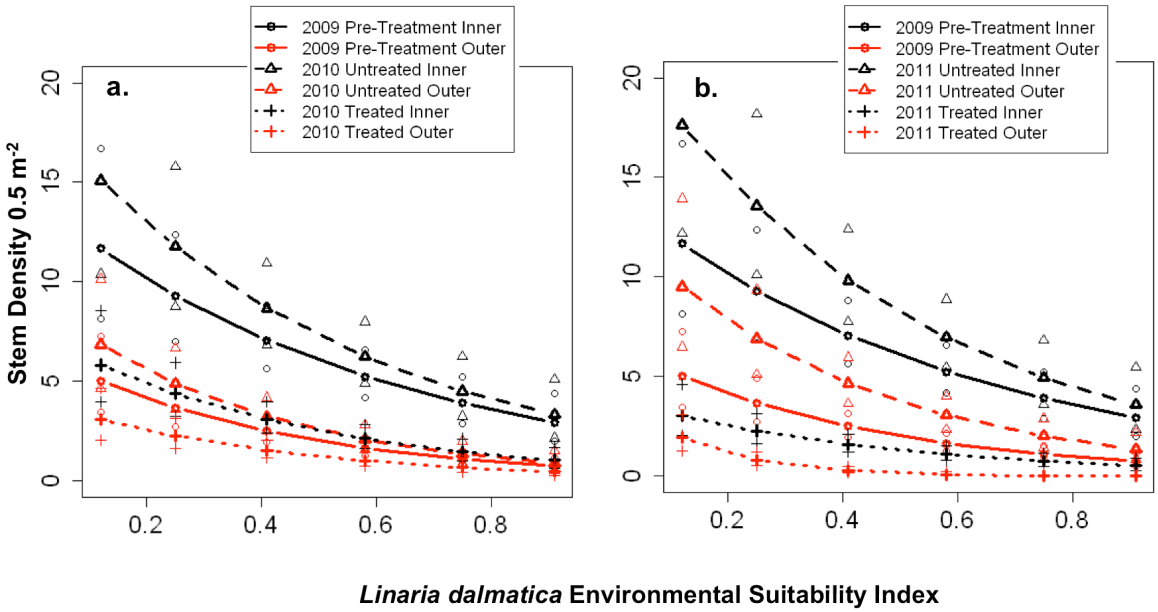


Figure 5.5 Effect of the three-way interaction term among environmental suitability, herbicide treatment, and patch edge position on *Linaria dalmatica* density 0.5 m^{-2}. Panel a shows the effect of pre-herbicide (2009) and post 1-herbicide (2010) treatment responses. Panel b shows the effect of pre-herbicide (2009) and post 2-herbicide (2011) treatment responses. Plotted lines represent the mean response and symbols away from lines correspond to approximate upper and lower 95% confidence bounds.

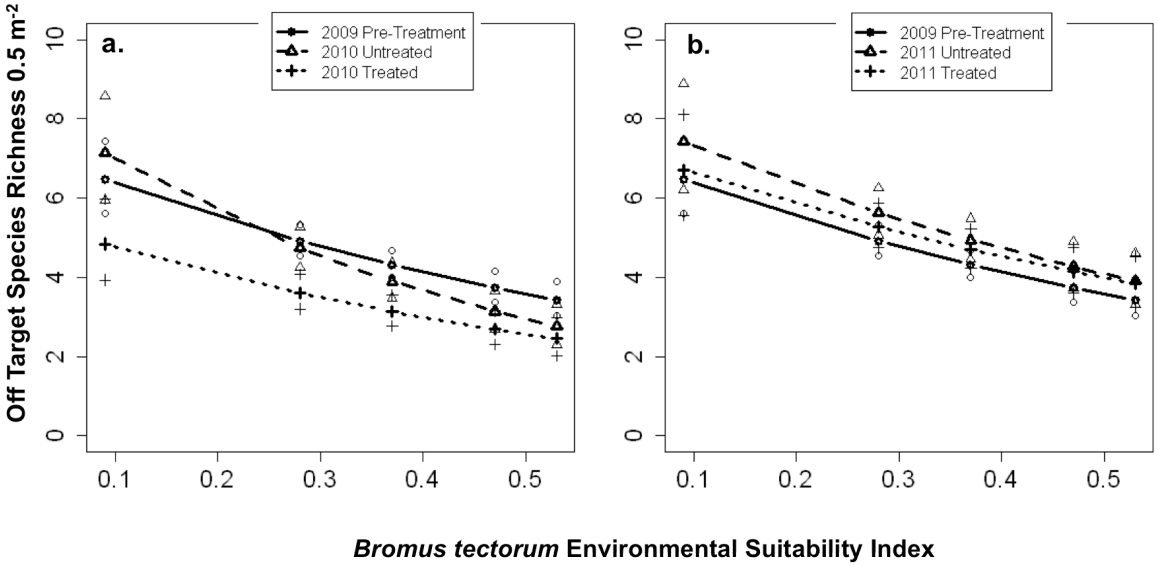


Figure 5.6 Two-way interaction effect between *Bromus tectorum* environmental suitability index and herbicide treatment on off target species richness. Panel a shows the effect of pre-herbicide (2009) and post 1-herbicide (2010) treatment responses. Panel b shows the effect of pre-herbicide (2009) and post 2-herbicide (2011) treatment responses. Plotted lines represent the mean response and symbols away from lines correspond to approximate upper and lower 95% confidence bounds.

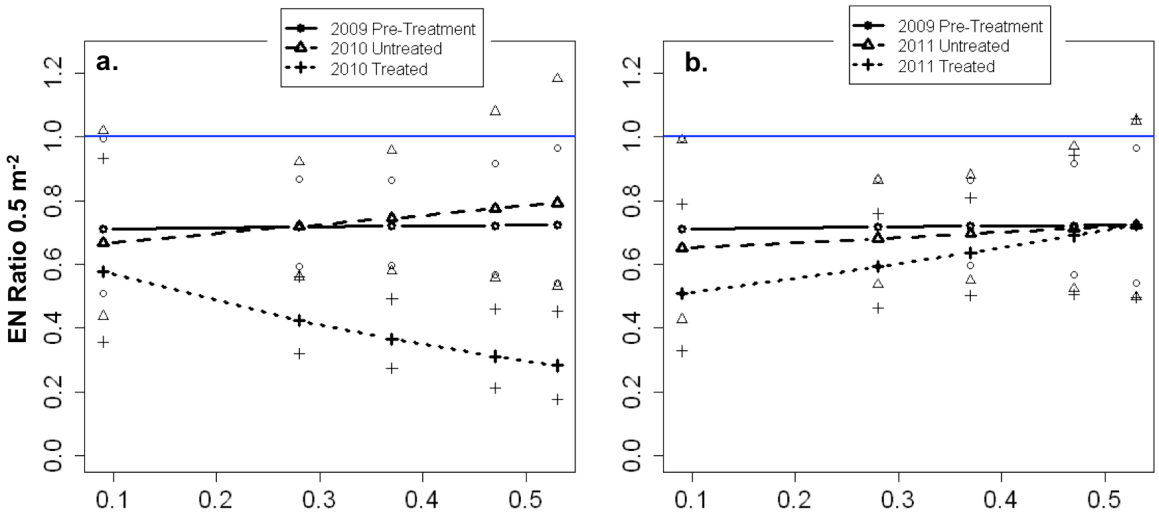


Figure 5.7 Two-way interaction efect between *Bromus tectorum* environmental suitability index and herbicide treatment on the EN ratio (exotic:native ratio). Panel a shows the effect of pre-herbicide (2009) and post 1-herbicide (2010) treatment responses. Panel b shows the effect of pre-herbicide (2009) and post 2-herbicide (2011) treatment responses. Plotted lines represent the mean response and symbols away from lines correspond to approximate upper and lower 95% confidence bounds. The blue line indicates where the EN ratio would be equal to 1.0.

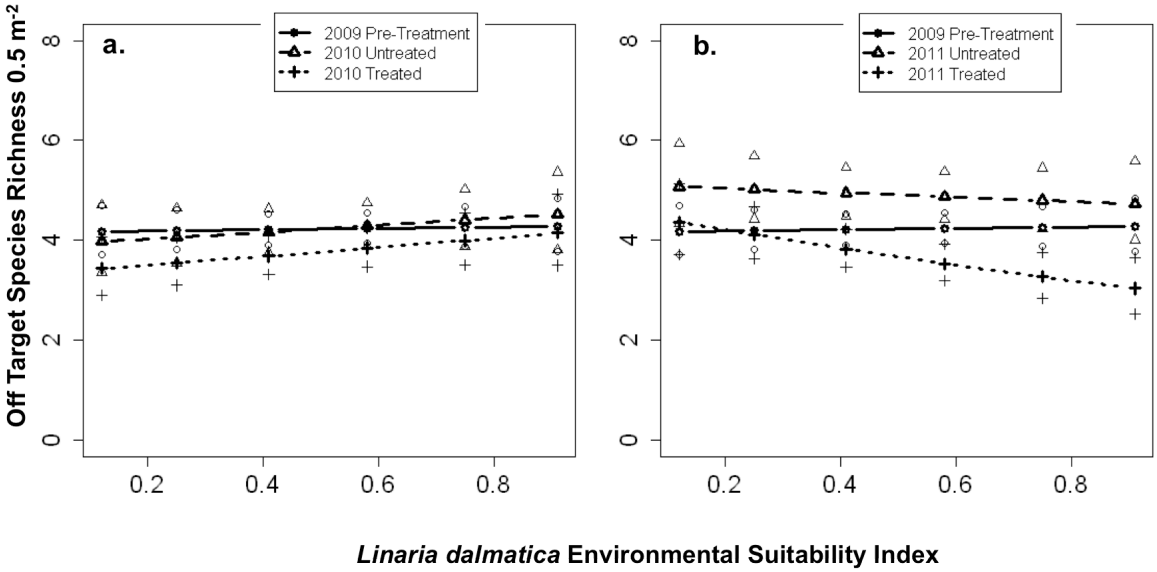


Figure 5.8 Two-way interaction effect between *Linaria dalmatica* environmental suitability index and herbicide treatment on off target species richness. Panel a shows the effect of pre-herbicide (2009) and post 1-herbicide (2010) treatment responses. Panel b shows the effect of pre-herbicide (2009) and post 2-herbicide (2011) treatment responses. Plotted lines represent the mean response and symbols away from lines correspond to approximate upper and lower 95% confidence bounds.

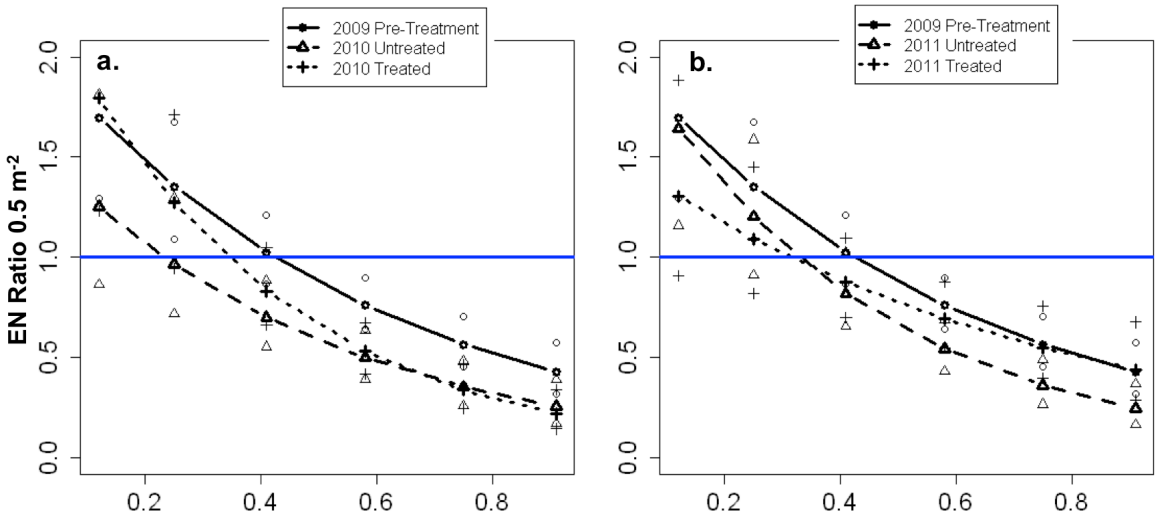


Figure 5.9 Two-way interaction efect between *Linaria dalmatica* environmental suitability index and herbicide treatment on the EN ratio (exotic:native ratio). Panel a shows the effect of pre-herbicide (2009) and post 1-herbicide (2010) treatment responses. Panel b shows the effect of pre-herbicide (2009) and post 2-herbicide (2011) treatment responses. Plotted lines represent the mean response and symbols away from lines correspond to approximate upper and lower 95% confidence bounds. The blue line indicates where the EN ratio would be equal to 1.0.

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CHAPTER SIX

CONCLUSIONS

The research conducted in this dissertation was engendered by a desire to better understand the patterns and possible processes governing nonindigenous plant species (NIS) distributions. Further, the culmination of research presented here was an attempt to apply ecologically based solutions to practical problems in weed management. Land managers charged with weed management across local spatial extents (i.e., management units defined in Chapter 2) are faced with several challenges. First, they are often limited in their resources to manage all NIS populations. Second, they are often data limited insomuch they lack adequate amounts of survey data to accurately characterize the spatial distributions of NIS. Third, managers and scientists alike are constantly torn between competing interests concerning decisions to monitor versus administer management treatments, due to limited funding. Finally, national and local legislation mandating the eradication or control of noxious weeds provides a greater incentive toward a species-centric approach to management, rather than on an ecological or systems approach to reducing the occurrence of undesired NIS.

This dissertation aimed to answer three overarching questions related to characterizing and applying knowledge of NIS distributions to weed management:

1. How well do nonindigenous plant species distribution models transfer between three neighboring management units that represent a gradient of human disturbance intensities?

2. How do current and historical uses of land affect predicted probabilities of nonindigenous plant species occupancy?
3. What are the relationships between predicted probabilities of nonindigenous plant species occurrence and the responses of target species populations and off target plant communities to chemical weed management?

The introductory and background chapters of this dissertation gave a brief review and synthesis of the state of knowledge of species distribution models (SDM) as they pertain to NIS and offered some background on how the accuracy of such models may be affected by insufficient accounting for patterns of human caused disturbances. This chapter further described how SDMs might be applicable within a weed population prioritization management framework.

The first data chapter, Chapter Three, explored whether species ecological niches (Hutchinson 1957) and, thus, their distributions across a landscape remained similar among neighboring management units (Thompson et al. 1993; Hill et al. 2000; Prinzing et al. 2002). The null hypothesis was that NIS would be distributed similarly among management units with similar static abiotic environmental variation (Austin 2007). If the null hypothesis held, data collected in other regions could be used to make predictions in locations where data were scarce. However, results for recent studies evaluating the portability of SDMs for plant species were mixed suggesting there may be complications with generalizing such models between two distinct regions with differences in land use and management histories (Randin et al. 2006; Ervin and Holly 2011). Thus, I evaluated the transferability of SDMs parameterized for two NIS between neighboring management

units within the Greater Yellowstone Ecosystem (GYE) that represented a three point gradient of human perturbation intensities. I concluded that NIS distributions for the two species evaluated were significantly different between the two management units representing the least and greatest intensities of human disturbance, as models built within each of those units did not adequately transfer between them. This result provided empirical evidence signifying that human disturbances may sufficiently alter natural disturbance regimes (Byers 2002; Brooks et al. 2004) such that relatively static environmental predictors thought to affect plant growth (Austin and Van Niel 2011) may not adequately explain NIS distributions.

Based on the results generated by testing the transferability of SDMs for NIS, I looked further into how certain land uses may affect NIS distributions. I evaluated the relative contributions of current and historical land use variables to explaining the probabilities of occurrence for six NIS currently present in many areas within a model study system. Paradise Valley (PVAL) was considered a model system because it has exhibited the characteristics of many rural ecosystems adjacent to National Parks and other protected areas with growing human populations and growing rates of exurban development (Parmenter et al. 2003; Gude et al. 2006). Furthermore, PVAL provided spatially and temporally heterogeneous patterns of agricultural land uses, and as such, I concentrated on land uses currently or previously used for irrigated agriculture, those currently in exurban development, and those classified as dryland rangeland. Interactions among historical and current land uses explained greater amounts of the variation in NIS distributions as compared to only environmental or environmental plus current land use

variables. Moreover, predictions of the probabilities of occurrence for four of the six NIS were significantly changed within rangeland environments previously used for irrigated agriculture. This pattern was somewhat pronounced for *Bromus inermis*, a purposefully introduced perennial forage grass. Current locations of *B. inermis* presence were positively associated with locations currently and previously irrigated for either cropland or pasture. Likewise, increases in the predicted probabilities of *Bromus tectorum* occurrence in locations previously irrigated were very pronounced once historical land use was included in its SDM. Results of this study were suggestive of the temporal impacts of human uses of land on NIS distributions and possibly on facilitating invasion by NIS by altering disturbance regimes (Moles et al. 2012).

Finally, our current paradigm for NIS management does not sufficiently exploit our current ecological understanding of the associations between individual plant growth responses and plant population dynamics with environmental suitability. More suitable environments as predicted by probabilities of NIS occurrence may harbor more rapidly growing populations of target NIS. Thus, such populations may have relatively more invasive potential than other populations of the same species growing in less suitable environments. Likewise, we might expect population responses to management approaches, such as herbicide treatment, to differ among populations growing in different environmental conditions. Further, if predictable relationships exist between environmental suitability quantified by SDMs and management responses, populations of target species may be prioritized for management by exploiting such relationships (Rew et al. 2007). Therefore, I tested the applicability of SDMs to characterize environmental

suitability and inform management decisions by evaluating the responses of two NIS to herbicide treatments along their respective environmental suitability gradients. Results of this study suggested differential responses of populations of the same species to herbicide treatments might vary in a predictable manner with predicted suitability gradients.

B. tectorum populations growing in more suitable environments likely need to be prioritized for management actions more frequently than populations growing in less suitable environments. Conversely, it may be more beneficial to prioritize *Linaria dalmatica* management at populations growing in less suitable environments (as predicted by an SDM) as those populations may contribute more to this species' local and regional growth rates. Although specific trends in the responses with predicted probabilities of occurrence may be species specific within a management unit, an experimental based approach to weed management in range and wildland systems could provide valuable insight for prioritizing populations upon which to expend management resources.

Future Directions

Although insightful, the results of my cumulative research only begin to reveal how NIS environmental suitability models may be implemented to support weed management decisions. Rew et al. (2007) proposed an NIS management framework that emphasized prioritization of the management of NIS populations rather than a focus on the control of individual species. Their prioritization framework highlighted the importance of monitoring NIS populations within a range of environmental conditions to assess their invasive potentials (i.e., their abilities to increase in density and/or spatial extent over

time). The results of the management response study along a gradient of environmental suitability strongly suggested population monitoring could result in more efficient and possibly more efficacious administration of management resources (Maxwell et al. 2009). However, additional temporal data is needed for both species evaluated to draw stronger inferences about the relationships between predicted environmental suitability and population responses.

A fundamental principle of metapopulation dynamics theory, and, thus, its application to modeling such dynamics across a landscape, relies on the accurate characterization of what defines a suitable habitat for the species in question (Pulliam 1988; Hanski 1994b). However, the definition of "suitable" habitat for plant species poses several challenges (Freckleton and Watkinson 2002). Firstly, populations of a species exhibiting a metapopulation structure are those residing within discrete patches of suitable habitat within a matrix of unsuitable habitat (Hanski 1994b). However, plant populations of the same species can inhabit many environments as well as remaining dormant in the seed stage under unsuitable conditions. This suggests there is more likely a gradient of habitat suitability across a landscape, and, thus, defining source-sink dynamics among populations is non-trivial (Eriksson 1996). Nonetheless, an understanding of such dynamics could be fundamental to applying management treatments such that overall metapopulation growth rates decrease over time (Rew et al. 2007).

My research elucidated trends in NIS population responses along probability of occurrence gradients within moderately disturbed rangeland systems of the Gallatin National Forest (GNF). Furthermore, I determined that NIS were distributed differently

based on the level of human disturbance intensities. Thus, continued work evaluating responses to herbicide applications or other management treatments should be explored in environments highly altered by human activities, as these alterations might drive plant invasions (Moles et al. 2012) and the way they are managed.

Epilogue

A natural extension of the research I conducted for my dissertation would be evaluation of the responses of additional NIS populations in other systems to herbicide applications. In fact, I have already started this work. Before starting my Ph.D. research with my advisors at Montana State University, I had started implementing some of their surveying and modeling practices in an area with similar characteristics as Paradise Valley in northern Colorado. Currently, I am working toward analyzing population responses to management along *Cirsium arvense* L. a predicted environmental suitability gradient in northern Colorado and will be comparing those results with results for *C. arvense* in Paradise Valley. There should be great benefit in understanding how consistent or inconsistent relationships are among different regions. Furthermore, I hypothesize this additional study will help to further a shift in the current NIS management paradigm toward more ecological and experimental approaches.

I think the work I have done for my dissertation has contributed to weed science and ecology in furthering our understanding of how we might work with nature rather than against it to solve management problems. It is my sincere hope that I may continue to contribute to this discipline, this discipline that has contributed so much to me. I would like to follow in the footsteps of those weed scientists/ecologists that have inspired me—

Bruce Maxwell, Lisa Rew, to name just a couple. What attracts me to this discipline is its diversity, and I have aimed throughout my academic career to be diverse as well. I have had the opportunity to participate in projects at all levels of biological organization—from molecules to ecosystems—using principles from the most basic to the most applied science. When I first sat down with folks from Colorado State University after the completions of a master's degree to discuss entering a Ph.D. program, I remember explicitly telling them I wanted my experience to cover this range—my exact words were "molecules to ecosystems." In retrospect, I would not suggest to any naïve young scientist (such as I was or may still be) embarking on the start of a Ph.D. to request working on a set of projects that spans such a range, as it may cause undue personal and financial hardships as well as taking much longer to finish! However, I do encourage anyone interested in the weed sciences to get as much exposure as possible to this diversity. The current and future issues in weed science demand it. From problems associated with herbicide resistance to invasion, our discipline will continue to require thinking that integrates principles of physiology, molecular biology, population genetics, ecology, statistics, and quantitative modeling.

I have obtained skills over the last few years upon which to build. These skills include, most importantly, how to think—to question everything in every conceivable way. I want to dedicate my life, both professional and personal, to learning, being a better communicator, and being a better listener. I hope my prior, current, and future experiences afford me the opportunity to be a leader within my discipline and make meaningful contributions.

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APPENDICES

APPENDIX A

CHAPTER THREE SUPPLEMENTARY TABLES

Appendix A is a supplement to Chapter Three of this dissertation. It contains two tables for an extra analysis referenced in the manuscript.

Table A.1 Logistic regression coefficient estimates for models predicting the probability of occurrence of *Cirsium arvense* for each of the three neighboring management units. These models are different from those in the main text as they include an interaction between elevation and wildfire

Variable[a]	YNP	p-value[b]	GNF	p-value[b]	PVAL	p-value[b]
(Intercept)	-1.215E+01	< 0.001	2.071E+00	0.454	7.757E+00	0.143
ELEV	-2.476E-04	0.317	-5.216E-03	< 0.001	-7.174E-03	0.012
SLOPE	4.709E-02	< 0.001	2.416E-03	0.918	6.371E-03	0.884
DRDS	1.800E-04	< 0.001	6.360E-05	0.769	4.710E-05	0.937
DSTMS	7.058E-04	< 0.001	-2.591E-03	0.002	-6.951E-04	0.142
DTRLS	-1.166E-04	< 0.001	6.728E-04	< 0.001	1.174E-04	0.120
WILDFIRE 1[c]	-3.972E+00	< 0.001	-2.719E+00	0.594	2.151E+01	0.561
SOLAR	2.450E-02	< 0.001	2.171E-02	0.002	-2.014E-02	0.093
TWI	3.283E-01	< 0.001	9.692E-02	0.271	2.433E-01	0.002
ELEV*WILDFIRE1[cd]	2.000E-03	< 0.001	1.968E-03	0.419	-9.186E-03	0.646

[a]Abbreviations for environmental variables in Table 1
[b]p-values based on the z-approximation to the Chi-Squared distribution
[c]WILDFIRE 1 = categorical variable where 1 = present
[d]Interaction term

Table A.2 Results of *Cirsium arvense* model transferability to each of the management units for the model built in YNP and summarized in Table A.1

Management Unit	Mean AUC[a]	Lower Bound[b]	Upper Bound[b]
YNP	0.744	0.722	0.768
GNF	0.519	0.440	0.597
PVAL	0.508	0.423	0.598

[a]Mean AUC: mean area under the receiver operating curve; the value for YNP represents an internal validation of the model built in YNP
[b]Lower and Upper bounds for approximate 95% confidence intervals around the mean AUC

APPENDIX B

CHAPTER FOUR SUPPLEMENTARY TABLES AND FIGURES

Summary and analysis of deviance tables for nonindigenous plant species occupancy models and related box and whisker plots

This appendix contains the detailed results for the general linear models with logit link functions used to quantify nonindigenous plant species (NIS) occupancy within our study system, Paradise Valley, Montana, U.S.A. Summary tables for parameter estimates from fitted logistic regression models contain codes and abbreviations for land use and environmental variables described in Table 4.2 and Table 4.3 of the corresponding manuscript. Box and whisker plots were also generated to illustrate the changes in predicted probabilities of NIS occupancy with the inclusion of categorical land use variables. Similar figures were included within the manuscript for which this appendix supplements; however, figures included in Appendix B are presented by species thereby allowing visual comparisons among predictions for occupancy models to be assessed on a per species basis.

Table B.1 Summary table of logistic regression predicting *Bromus tectorum* occupancy (numeric land use history codes in Table 2)

	Model 1[a]		Model 2[a]		Model 3[a]	
Variable	Estimate	p-value[b]	Estimate	p-value[b]	Estimate	p-value[b]
Intercept	7.582E+00	<0.001	7.714E+00	<0.001	4.106E+00	0.001
ELEV	-8.259E-03	<0.001	-8.599E-03	<0.001	-7.997E-03	<0.001
SLOPE	3.361E-02	0.003	3.918E-02	<0.001	2.828E-02	0.023
DRDS	-2.655E-04	0.180	-8.022E-05	0.694	-3.004E-05	0.889
DSTMS	-6.019E-04	<0.001	-5.792E-04	<0.001	-5.127E-04	<0.001
DTRLS	1.221E-04	<0.001	1.419E-04	<0.001	1.390E-04	<0.001
WILDFIRE1	2.221E+00	<0.001	2.195E+00	<0.001	2.851E+00	<0.001
SOLAR	3.275E-02	<0.001	3.271E-02	<0.001	3.569E-02	<0.001
TWI	-9.521E-02	0.002	-5.944E-02	0.071	-6.426E-02	0.075
Exurban			3.502E-01	0.228		
Irrigated Ag.			-8.009E-01	0.016		
Rangeland			-2.337E-01	0.336		
3					1.869E+00	<0.001
4					2.667E+00	<0.001
23					3.090E+00	<0.001
31					2.791E+00	<0.001
32					3.920E+00	<0.001
34					1.326E+00	0.012
43					2.804E+00	<0.001
323					1.845E+01	0.965
341					-1.135E+00	0.317
343					1.791E+00	0.009

[a]Model 1, Model 2, Model 3 refers to NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively

[b]p-values were adjusted for overdispersion and were based on the t-distribution

Table B.2 Analysis of deviance tables describing the percent change in model deviance when each of the variables was omitted for the *Bromus tectorum* occupancy models

	Model 1: 16.19% deviance explained				Model 2: 16.93% deviance explained			
Variable Omitted	Δdf	Deviance (D)	ΔD (%)	p-value[b]	Δdf	Deviance (D)	ΔD (%)	p-value[b]
None		4082.4				4046.2		
ELEV	1	4364.1	6.90	<0.001	1	4319.5	6.75	<0.001
SLOPE	1	4100.1	0.44	0.006	1	4069.1	0.57	0.002
DRDS	1	4086.0	0.09	0.210	1	4046.5	0.01	0.711
DSTMS	1	4135.7	1.31	<0.001	1	4090.5	1.50	<0.001
DTRLS	1	4129.6	1.16	<0.001	1	4106.7	1.10	<0.001
WF	1	4201.8	2.93	<0.001	1	4157.0	2.74	<0.001
SOLAR	1	4220.3	3.38	<0.001	1	4176.3	3.22	<0.001
TWI	1	4102.2	0.49	0.003	1	4052.8	0.16	0.088
LU.C[a]	NA	NA	NA	NA	3	4082.4	0.89	0.001
LU.H[a]	NA	NA	NA	NA	NA	NA	NA	NA

Model 3: 23.50% deviance explained			
Δdf	Deviance (D)	ΔD (%)	p-value[b]
	3726.1		
1	3948.5	5.97	<0.001
1	3736.6	0.28	0.026
1	3726.2	<0.01	0.891
1	3759.1	0.88	<0.001
1	3778.8	1.41	<0.001
1	3882.2	4.19	<0.001
1	3872.1	3.92	<0.001
1	3732.6	0.17	0.081
NA	NA	NA	NA
10	4082.4	9.56	<0.001

a LU.C and LU.H are abbreviations for Current Land Use and Historic Land Use, respectively

b p-values were adjusted for overdispersion and were based on the F-distribution (Zuur et al. 2009)

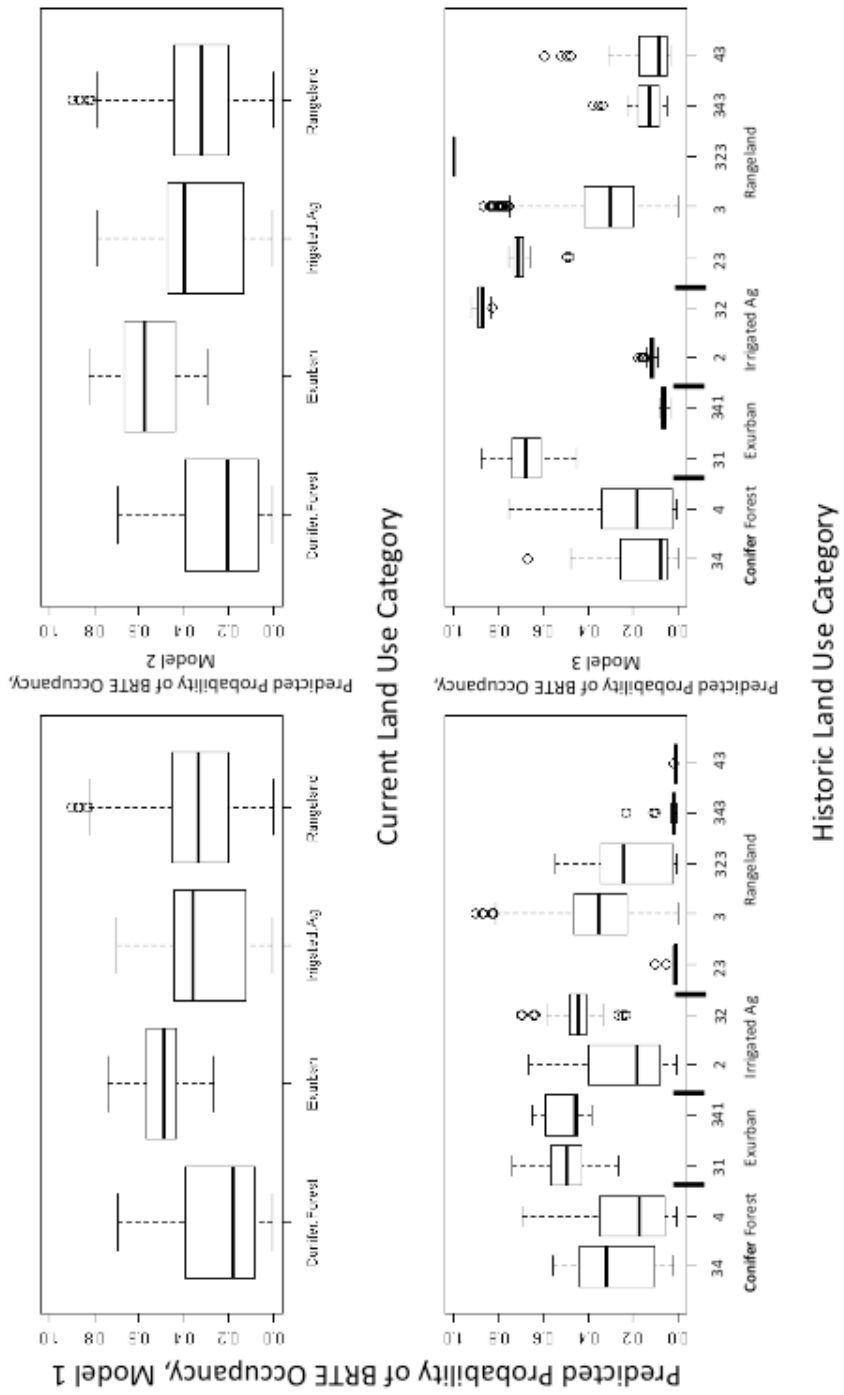


Figure B.1 Predicted probabilities of *Bromus tectorum* (BRTE) occupancy for Models 1 and 2 plotted against current land use categories, and Models 1 and 3 plotted against historic land use
categories

Table B.3 Summary table of logistic regression predicting *Bromus inermis* occupancy (numeric land use history codes in Table 2)

	Model 1[a]		Model 2[a]		Model 3[a]	
Variable	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	2.139E+00	0.536	8.033E-02	0.982	4.248E+00	0.309
ELEV	2.038E-03	0.231	4.036E-03	0.019	3.478E-03	0.089
SLOPE	-2.236E-01	<0.001	-2.124E-01	<0.001	-2.415E-01	<0.001
DRDS	1.164E-03	0.006	2.366E-04	0.634	3.213E-04	0.570
DSTMS	-3.044E-03	<0.001	-2.045E-03	<0.001	-2.481E-03	<0.001
DTRLS	-4.890E-05	0.379	-3.209E-05	0.589	-1.212E-04	0.103
WILDFIRE1	3.826E+00	<0.001	2.881E+00	<0.001	2.703E+00	<0.001
SOLAR	-4.235E-02	<0.001	-4.039E-02	<0.001	-4.407E-02	<0.001
TWI	4.760E-03	0.933	-1.094E-01	0.054	-1.549E-01	0.009
Exurban			1.334E-01	0.722		
Irrigated Ag.			1.270E+00	0.011		
Rangeland			-8.856E-01	0.016		
3					-2.605E+00	<0.001
4					6.796E-02	0.924
23					-3.839E-01	0.401
31					-3.534E+00	<0.001
32					1.423E-01	0.709
34					-1.820E+00	0.006
43					-1.523E+01	0.977
323					8.829E-01	0.118
341					9.782E-01	0.200
343					3.686E-01	0.731

[a]Model 1, Model 2, Model 3 refers to NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively

Table B.4 Analysis of deviance tables describing the percent change in model deviance when each of the variables was omitted for the *Bromus inermis* occupancy models

	Model 1: 28.46% deviance explained				Model 2: 33.40% deviance explained			
Variable Omitted	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value[a]
None		762.7				710.0		
ELEV	1	764.1	0.18	0.241	1	715.2	0.73	0.023
SLOPE	1	813.3	6.63	0.000	1	756.0	6.48	<0.001
DRDS	1	770.2	0.98	0.006	1	710.3	0.04	0.635
DSTMS	1	822.8	7.88	0.000	1	731.0	2.96	<0.001
DTRLS	1	763.5	0.10	0.376	1	710.3	0.04	0.587
WF	1	855.9	12.22	0.000	1	761.4	7.24	<0.001
SOLAR	1	783.8	2.77	0.000	1	727.9	2.52	<0.001
TWI	1	762.7	0.00	0.933	1	713.8	0.54	0.052
LU.C[a]	NA	NA	NA	NA	3	762.7	7.42	<0.001
LU.H[a]	NA	NA	NA	NA	NA	NA	NA	NA

Model 3: 44.45% deviance explained			
Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value
	592.2		
1	595.0	0.47	0.095
1	638.2	7.77	<0.001
1	592.5	0.05	0.570
1	616.0	4.02	<0.001
1	595.0	0.47	0.096
1	616.6	4.12	<0.001
1	606.5	2.41	<0.001
1	599.1	1.17	0.009
NA	NA	NA	NA
10	762.7	28.79	<0.001

a LU.C and LU.H are abbreviations for Current Land Use and Historic Land Use, respectively

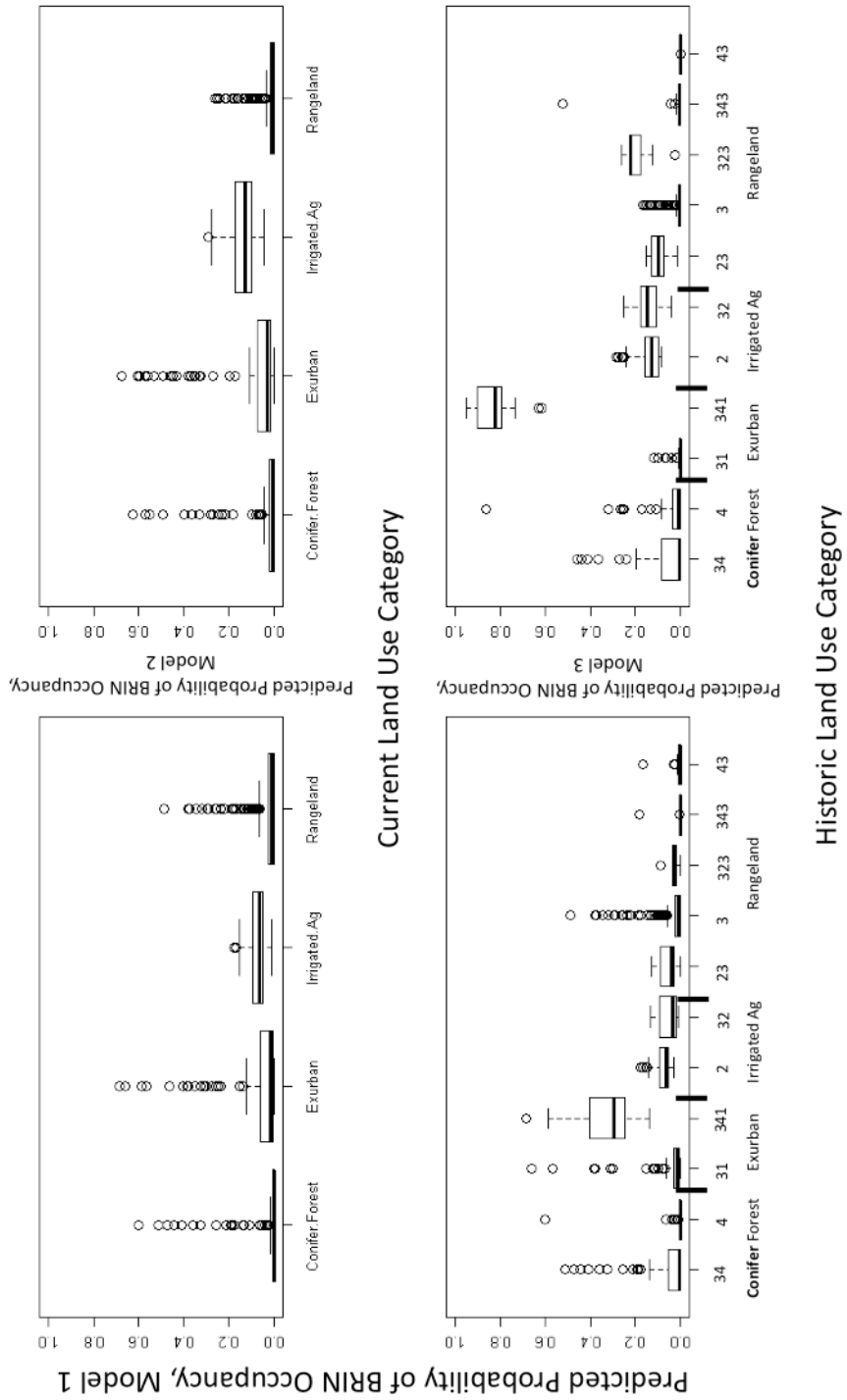


Figure B.2 Predicted probabilities of *Bromus inermis* (BRIN) occupancy for Models 1 and 2 plotted against current land use categories, and Models 1 and 3 plotted against historic land use categories

Table B.5 Summary table of logistic regression predicting *Verbascum thapsus* occupancy (numeric land use history codes in Table 2)

	Model 1[a]		Model 2[a]		Model 3[a]	
Variable	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	6.107E+00	0.032	5.101E+00	0.086	-1.187E+01	0.990
ELEV	-8.146E-03	<0.001	-8.412E-03	<0.001	-7.537E-03	<0.001
SLOPE	5.795E-02	0.001	6.277E-02	0.002	4.638E-02	0.031
DRDS	-1.726E-03	<0.001	-2.073E-03	<0.001	-2.535E-03	<0.001
DSTMS	2.577E-05	0.090	-1.659E-04	0.447	-1.503E-04	0.502
DTRLS	-1.875E-04	0.011	-2.113E-04	0.003	-1.792E-04	0.012
WILDFIRE1	4.779E+00	<0.001	5.109E+00	<0.001	5.289E+00	<0.001
SOLAR	1.491E-02	0.005	1.175E-02	0.028	1.295E-02	0.020
TWI	1.356E-01	0.026	2.266E-01	0.001	2.264E-01	0.001
Exurban			1.061E+00	0.013		
Irrigated Ag.			-1.443E+01	0.975		
Rangeland			1.421E+00	<0.001		
3					1.677E+01	0.986
4					2.113E-01	1.000
23					1.663E+01	0.986
31					1.686E+01	0.986
32					-1.775E-02	1.000
34					1.538E+01	0.987
43					1.606E+00	0.999
323					7.318E-01	1.000
341					1.508E+01	0.987
343					1.876E+01	0.984

[a]Model 1, Model 2, Model 3 refers to NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively

Table B.6 Analysis of deviance tables describing the percent change in model deviance when each of the variables was omitted for the *Verbascum thapsus* occupancy models

	Model 1: 28.05% deviance explained				Model 2: 30.85% deviance explained			
Variable Omitted	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value[a]
None		877.7				843.5		
ELEV	1	913.2	4.06	<0.001	1	878.7	4.17	<0.001
SLOPE	1	887.5	1.07	0.002	1	853.1	1.13	0.002
DRDS	1	890.2	1.41	<0.001	1	860.4	2.00	<0.001
DSTMS	1	877.7	0.00	0.902	1	844.1	0.07	0.441
DTRLS	1	885.1	0.85	0.006	1	853.6	1.19	0.002
WF	1	1097.2	24.81	<0.001	1	1074.3	27.36	<0.001
SOLAR	1	886.0	0.76	0.004	1	848.6	0.60	0.024
TWI	1	882.4	0.54	0.029	1	853.7	1.20	0.001
LU.C[a]	NA	NA	NA	NA	3	877.7	4.04	<0.001
LU.H[a]	NA	NA	NA	NA	NA	NA	NA	NA

Model 3: 33.16% deviance explained			
Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value
	815.3		
1	839.2	2.94	<0.001
1	819.7	0.55	0.035
1	838.2	2.81	<0.001
1	815.7	0.06	0.498
1	822.3	0.86	0.008
1	1034.6	26.91	<0.001
1	821.0	0.70	0.017
1	825.0	1.19	0.002
NA	NA	NA	NA
10	877.7	7.65	<0.001

a LU.C and LU.H are abbreviations for Current Land Use and Historic Land Use, respectively

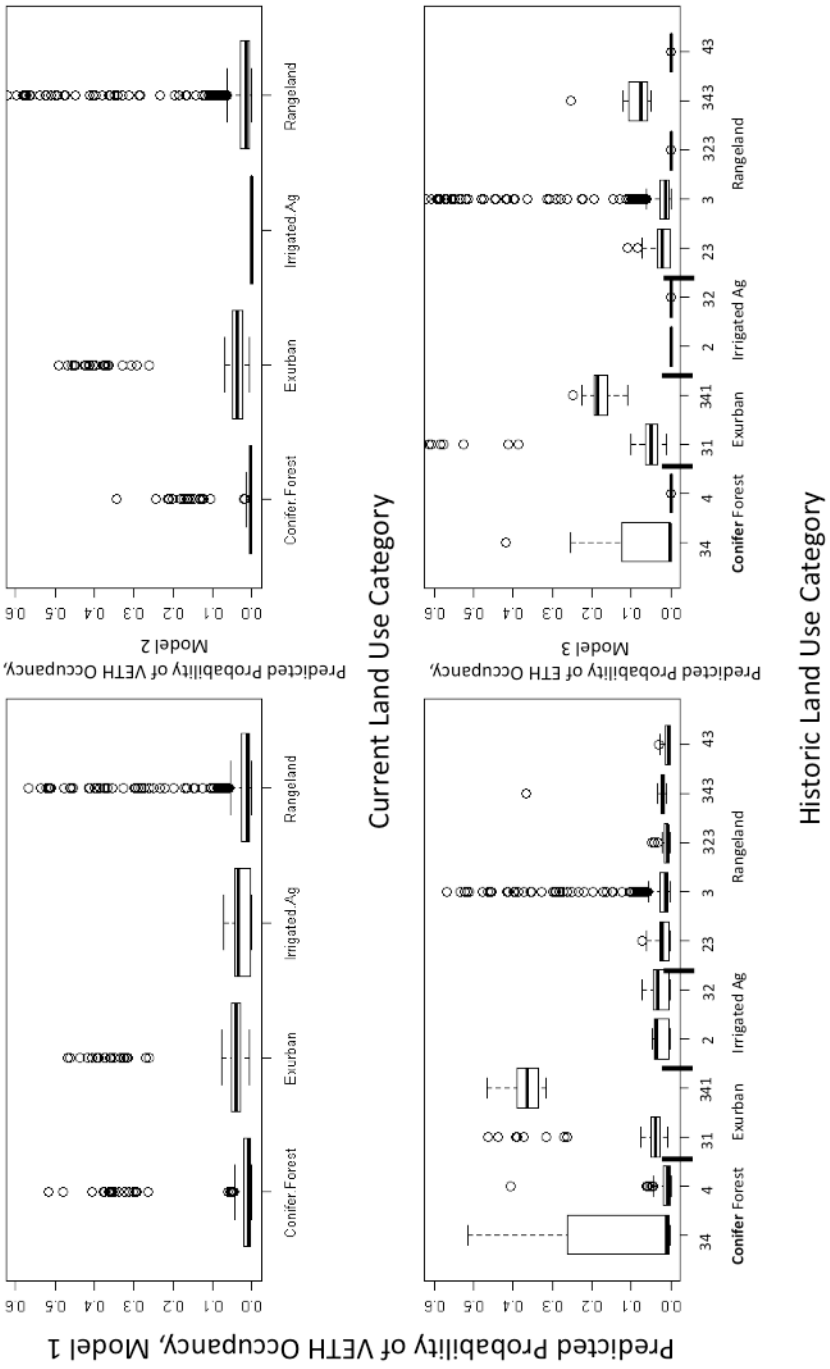


Figure B.3 Predicted probabilities of *Verbascum thapsus* (VETH) occupancy for Models 1 and 2 plotted against current land use categories, and Models 1 and 3 plotted against historic land use categories

Table B.7 Summary table of logistic regression predicting *Cynoglossum officinale* occupancy (numeric land use history codes in Table 2)

	Model 1[a]		Model 2[a]		Model 3[a]	
Variable	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	-1.310E+01	<0.001	-1.252E+01	<0.001	-1.732E+01	<0.001
ELEV	5.565E-03	0.001	5.283E-03	0.002	8.482E-03	<0.001
SLOPE	4.457E-02	0.064	6.045E-02	0.018	4.379E-02	0.124
DRDS	1.097E-04	0.788	-4.179E-04	0.407	-2.099E-04	0.720
DSTMS	-8.339E-04	0.043	-9.444E-05	0.833	-6.040E-04	0.168
DTRLS	4.934E-04	<0.001	5.546E-04	<0.001	6.375E-04	<0.001
WILDFIRE1	2.044E+00	<0.001	1.909E+00	<0.001	1.755E+00	<0.001
SOLAR	-1.921E-02	0.001	-2.002E-02	0.001	-2.119E-02	0.002
TWI	-8.245E-03	0.912	-5.828E-02	0.438	-5.961E-02	0.455
Exurban			1.230E+00	0.010		
Irrigated Ag.			9.975E-01	0.072		
Rangeland			-4.814E-01	0.172		
3					-1.328E+00	0.005
4					-8.410E-01	0.278
23					-1.575E+01	0.985
31					8.627E-01	0.138
32					4.519E-01	0.447
34					-5.914E-01	0.355
43					-1.607E+01	0.987
323					-8.313E-01	0.236
341					-3.891E-01	0.681
343					4.294E+00	<0.001

[a]Model 1, Model 2, Model 3 refers to NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively

Table B.8 Analysis of deviance tables describing the percent change in model deviance when each of the variables was omitted for the *Cynoglossum officinale* occupancy models

	Model 1: 22.53% deviance explained				Model 2: 26.50% deviance explained			
Variable Omitted	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value[a]
None		595.6				565.1		
ELEV	1	606.7	1.87	0.001	1	574.94	1.74	0.002
SLOPE	1	598.9	0.55	0.072	1	570.41	0.94	0.021
DRDS	1	595.7	0.01	0.789	1	565.8	0.12	0.403
DSTMS	1	600.0	0.73	0.037	1	565.14	0.01	0.833
DTRLS	1	676.9	13.64	<0.001	1	659.15	16.64	<0.001
WF	1	622.3	4.48	<0.001	1	586.16	3.73	<0.001
SOLAR	1	606.9	1.89	0.001	1	576.23	1.97	0.001
TWI	1	595.6	0.00	0.912	1	565.71	0.11	0.433
LU.C[a]	NA	NA	NA	NA	3	595.62	5.40	<0.001
LU.H[a]	NA	NA	NA	NA	NA	NA	NA	NA

Model 3: 35.62% devaince explained

Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value
	495.0		
1	513.2	3.67	<0.001
1	497.3	0.46	0.133
1	495.1	0.03	0.719
1	496.9	0.39	0.165
1	596.2	20.45	<0.001
1	508.1	2.64	<0.001
1	505.3	2.08	0.001
1	495.6	0.12	0.450
NA	NA	NA	NA
10	595.6	20.33	<0.001

a LU.C and LU.H are abbreviations for Current Land Use and Historic Land Use, respectively

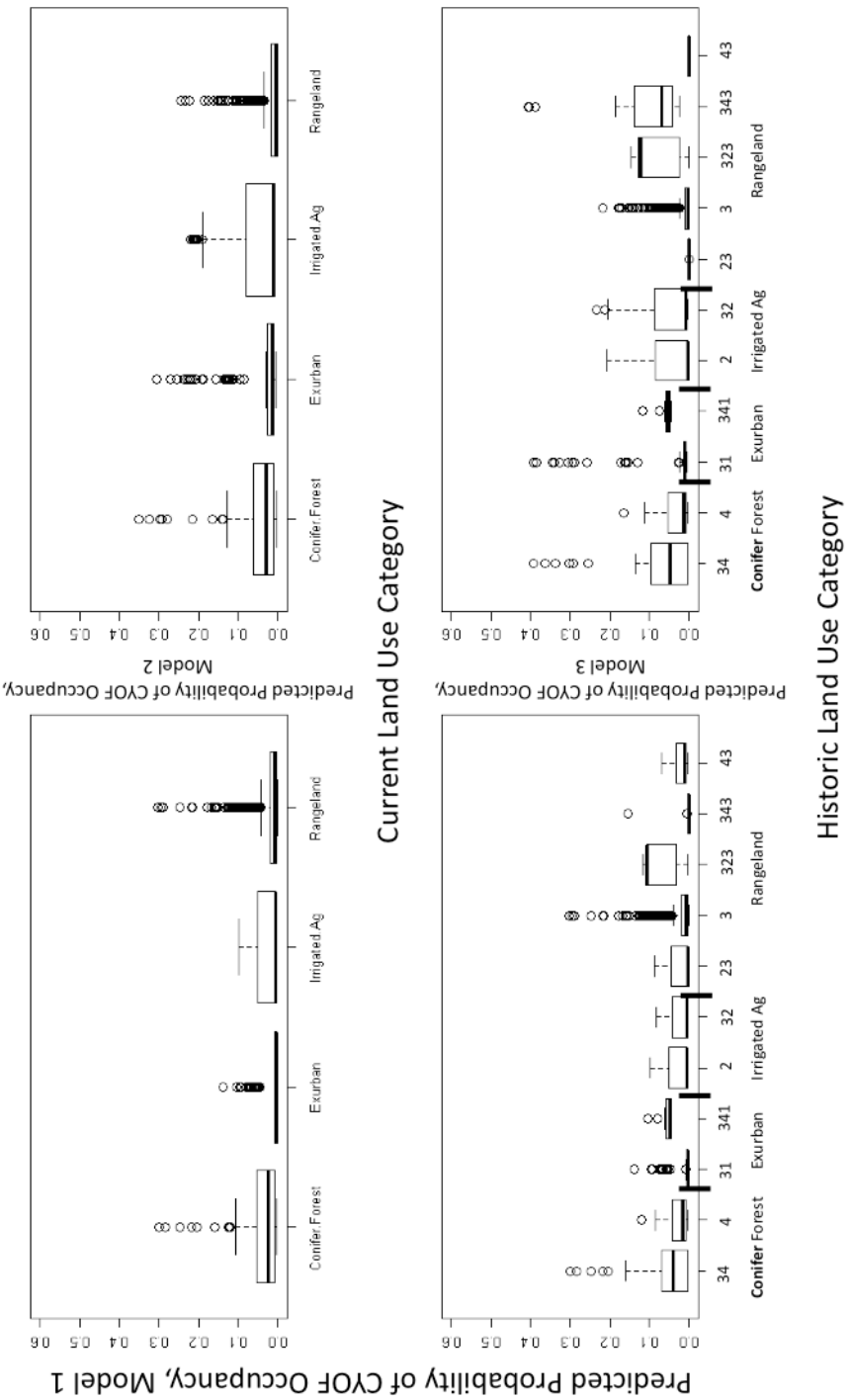


Figure B.4 Predicted probabilities of *Cynoglossum officinale* (CYOF) occupancy for Models 1 and 2 plotted against current land use categories, and Models 1 and 3 plotted against historic land use categories

Table B.9 Summary table of logistic regression predicting *Centaurea maculosa* occupancy (numeric land use history codes in Table 2)

	Model 1[a]		Model 2[a]		Model 3[a]	
Variable	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	1.550E+01	<0.001	1.728E+01	<0.001	1.614E+01	<0.001
ELEV	-1.164E-02	<0.001	-1.416E-02	<0.001	-1.509E-02	<0.001
SLOPE	-1.028E-01	<0.001	-9.250E-02	<0.001	-8.057E-02	<0.001
DRDS	1.498E-04	0.377	4.049E-04	0.021	6.194E-04	0.001
DSTMS	-3.778E-04	0.001	-6.030E-04	<0.001	-7.538E-04	<0.001
DTRLS	8.106E-05	0.001	1.051E-04	<0.001	1.040E-04	<0.001
WILDFIRE1	-1.725E-01	0.869	7.058E-01	0.505	-1.287E+01	0.984
SOLAR	2.363E-02	<0.001	2.523E-02	<0.001	2.168E-02	0.001
TWI	-2.167E-01	<0.001	-1.192E-01	<0.001	-7.444E-02	0.022
Exurban			6.826E-01	0.360		
Irrigated Ag.			-1.463E+00	0.062		
Rangeland			7.623E-01	0.300		
3					3.525E+00	<0.001
4					-1.037E+01	0.981
23					1.072E+00	0.087
31					3.363E+00	0.000
32					1.912E+00	0.000
34					3.606E+00	0.000
43					4.584E+00	0.000
323					1.036E+00	0.351
341					1.853E+01	0.977
343					-1.210E+01	0.991

[a]Model 1, Model 2, Model 3 refers to NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively

Table B.10 Analysis of deviance tables describing the percent change in model deviance when each of the variables was omitted for the *Centaurea maculosa* occupancy models

	Model 1: 18.64% deviance explained				Model 2: 22.13% deviance explained			
Variable Omitted	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value[a]
None		2789.0				2669.3		
ELEV	1	2991.5	7.26	<0.001	1	2912.8	9.12	<0.001
SLOPE	1	2842.9	1.93	<0.001	1	2707.8	1.44	<0.001
DRDS	1	2789.8	0.03	0.378	1	2674.7	0.20	0.021
DSTMS	1	2801.5	0.45	<0.001	1	2696.4	1.02	<0.001
DTRLS	1	2799.7	0.38	0.001	1	2685.3	0.60	<0.001
WF	1	2789.1	<0.01	0.866	1	2669.7	0.01	0.543
SOLAR	1	2804.8	0.56	<0.001	1	2685.7	0.61	<0.001
TWI	1	2852.3	2.27	<0.001	1	2684.0	0.55	<0.001
LU.C[a]	NA	NA	NA	NA	3	2789.0	4.48	<0.001
LU.H[a]	NA	NA	NA	NA	NA	NA	NA	NA

Model 3: 24.67% deviance explained			
Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value
	2581.6		
1	2846.3	10.25	<0.001
1	2609.8	1.09	<0.001
1	2593.3	0.45	<0.001
1	2621.2	1.53	<0.001
1	2596.8	0.59	<0.001
1	2582.3	0.03	0.411
1	2593.8	0.47	<0.001
1	2586.9	0.21	0.021
NA	NA	NA	NA
10	2789.0	8.03	<0.001

a LU.C and LU.H are abbreviations for Current Land Use and Historic Land Use, respectively

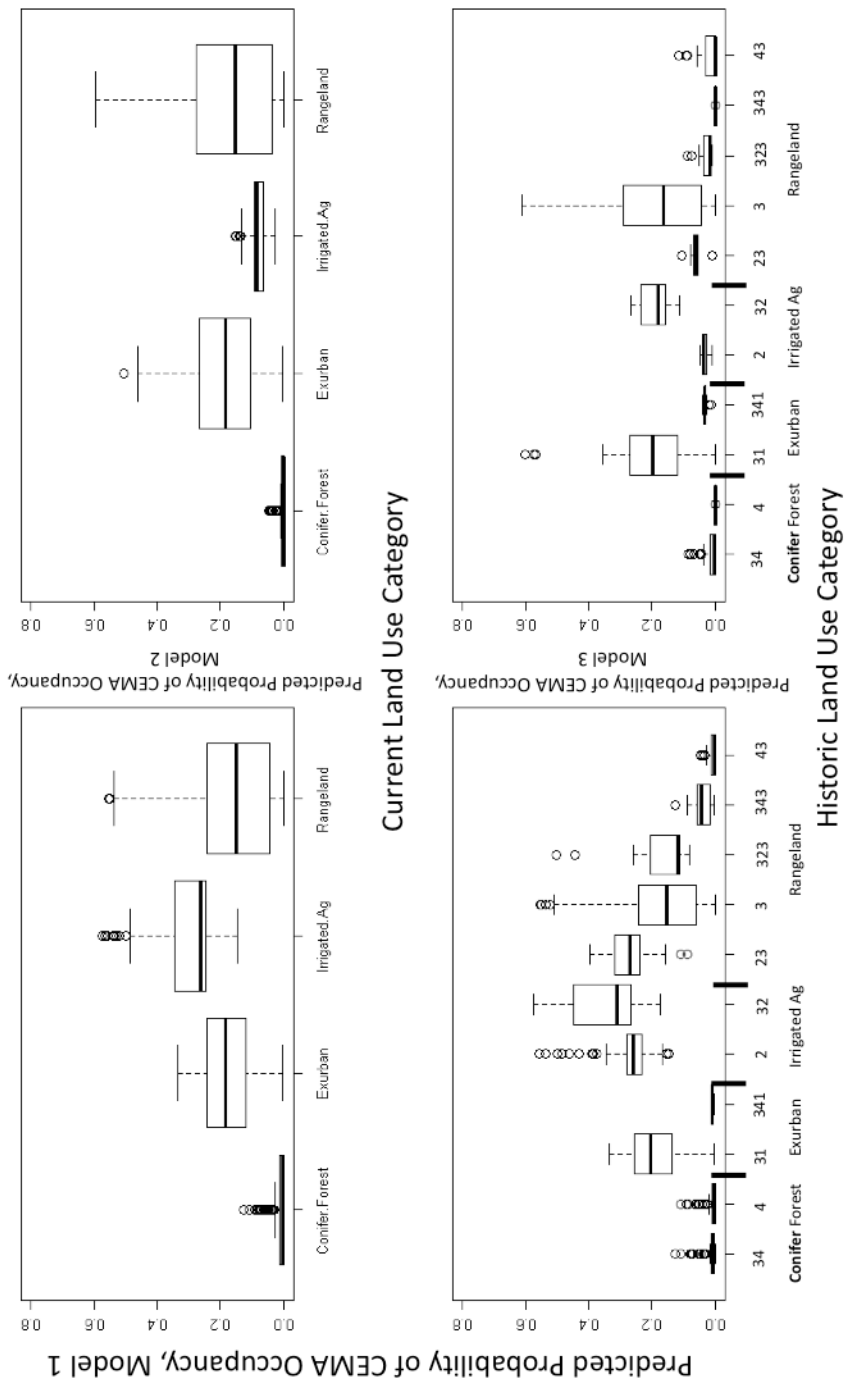


Figure B.5 Predicted probabilities of *Centaurea maculosa* (CEMA) occupancy for Models 1 and 2 plotted against current land use categories, and Models 1 and 3 plotted against historic land use categories

Table B.11 Summary table of logistic regression predicting *Cirsium arvense* occupancy (numeric land use history codes in Table 2)

	Model 1[a]		Model 2[a]		Model 3[a]	
Variable	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	1.165E+01	0.048	1.268E+01	0.055	1.074E+01	0.164
ELEV	-1.112E-02	0.001	-1.249E-02	0.001	-1.108E-02	0.023
SLOPE	3.874E-02	0.350	5.316E-02	0.217	1.403E-02	0.787
DRDS	-1.252E-04	0.822	6.879E-05	0.904	-1.258E-03	0.048
DSTMS	3.339E-05	0.936	-3.053E-06	0.995	3.913E-04	0.433
DTRLS	2.407E-04	0.004	2.599E-04	0.003	3.796E-04	<0.001
WILDFIRE1	5.323E+00	<0.001	5.633E+00	<0.001	6.114E+00	<0.001
SOLAR	-1.462E-02	0.194	-1.685E-02	0.137	-9.100E-03	0.511
TWI	1.843E-01	0.019	2.258E-01	0.009	1.398E-01	0.122
Exurban			1.395E+00	0.211		
Irrigated Ag.			2.153E-01	0.859		
Rangeland			7.872E-01	0.467		
3					-7.584E-01	0.217
4					-1.350E+01	0.986
23					2.079E+00	0.000
31					5.005E-01	0.484
32					-1.122E+00	0.304
34					-1.115E+00	0.392
43					-1.209E+01	0.994
323					-3.747E-01	0.752
341					-6.793E-01	0.610
343					3.520E+00	0.001

[a]Model 1, Model 2, Model 3 refers to NIS occupancy predicted by environmental variables only, by environmental + current land use, and by environmental + historic land use, respectively

Table B.12 Analysis of deviance tables describing the percent change in model deviance when each of the variables was omitted for the *Cirsium arvense* occupancy models

	Model 1: 13.87% deviance explained				Model 2: 14.86% deviance explained			
Variable Omitted	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value	Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value[a]
None		381.8				377.5		
ELEV	1	396.2	3.77	<0.001	1	392.0	3.86	<0.001
SLOPE	1	382.7	0.21	0.365	1	378.9	0.36	0.236
DRDS	1	381.9	0.01	0.821	1	377.5	0.00	0.904
DSTMS	1	381.9	0.00	0.936	1	377.5	0.00	0.995
DTRLS	1	390.6	2.30	0.003	1	387.0	2.53	0.002
WF	1	417.7	9.39	<0.001	1	411.8	8.86	<0.001
SOLAR	1	383.6	0.46	0.187	1	379.8	0.56	0.130
TWI	1	387.2	1.40	0.021	1	384.1	1.76	0.010
LU.C[a]	NA	NA	NA	NA	3	381.8	1.14	0.223
LU.H[a]	NA	NA	NA	NA	NA	NA	NA	NA

Model 3: 26.53% deviance explained			
Δ*df*	Deviance (*D*)	Δ*D* (%)	p-value
	325.7		
1	332.2	1.97	0.011
1	325.8	0.02	0.789
1	329.8	1.25	0.043
1	326.3	0.18	0.438
1	342.1	5.03	<0.001
1	352.6	8.24	<0.001
1	326.2	0.13	0.510
1	328.1	0.73	0.123
NA	NA	NA	NA
10	381.8	17.23	<0.001

a LU.C and LU.H are abbreviations for Current Land Use and Historic Land Use, respectively

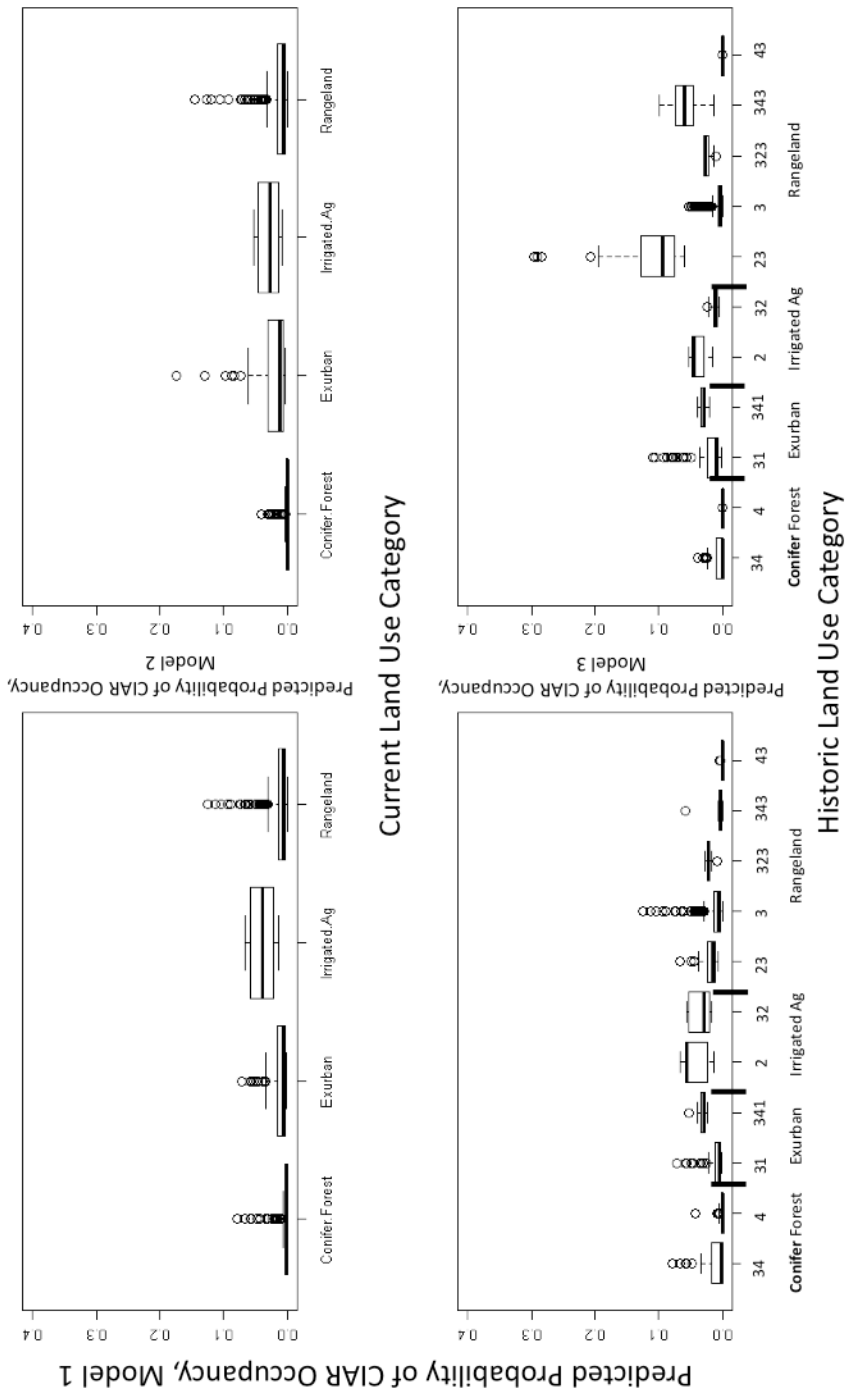


Figure B.6 Predicted probabilities of *Cirsium arvense* (CIAR) occupancy for Models 1 and 2 plotted against current land use categories, and Models 1 and 3 plotted historic land use categories

APPENDIX C

CHAPTER FIVE SUPPLEMENTARY TABLES

Appendix C contains the summary tables for the generalized linear mixed model analyses performed in Chapter Five.

Table C.1 Results of generalized linear mixed models for density of *Bromus tectorum* and *Linaria dalmatica*

	Response: *Bromus tectorum* Density				Response: *Linaria dalmatica* Density			
Model Term	Estimate	Std. Error[a]	z-value	p-value	Estimate	Std. Error[a]	z-value	p-value
Random Intercept[a]	0.835	0.914			0.509	0.714		
Intercept	4.262	0.361	11.795	<0.001	2.944	0.232	12.694	<0.001
Suitability Index	0.894	0.947	0.944	0.345	-1.917	0.423	-4.535	<0.001
Herbicide Treatment[b]								
Untreated 2009	-0.262	0.036	-7.216	<0.001	-0.279	0.099	-2.818	0.005
Untreated 2011	-0.379	0.039	-9.811	<0.001	0.169	0.095	1.783	0.075
Treated 2010	-0.847	0.060	-14.132	<0.001	-0.920	0.144	-6.371	<0.001
Treated 2011	-1.590	0.065	-24.449	<0.001	-1.561	0.171	-9.154	<0.001
Edge (O)[b]	-0.832	0.045	-18.582	<0.001	-0.712	0.129	-5.518	<0.001
Interactions								
Suitability*Pre-Treatment	1.353	0.092	14.760	<0.001	0.178	0.223	0.800	0.423
Suitability*Untreated 2011	1.450	0.097	14.907	<0.001	-0.105	0.217	-0.482	0.630
Suitability*Treated 2010	-1.092	0.158	-6.893	<0.001	-0.273	0.345	-0.790	0.430
Suitability*Treated 2011	2.037	0.156	13.055	<0.001	-0.320	0.417	-0.767	0.443
Suitability*Edge (O)	1.208	0.112	10.753	<0.001	-0.663	0.316	-2.099	0.036
Edge (O)*Untreated 2009	-0.225	0.057	-3.933	<0.001	-0.053	0.160	-0.331	0.741
Edge (O)*Untreated 2011	-0.159	0.067	-2.386	0.017	0.145	0.171	0.850	0.395

Edge (O)*Treated 2010	-0.374	0.093	-4.045	<0.001	0.106	0.207	0.510	0.610
Edge (O)*Treated 2011	0.033	0.098	0.340	0.734	0.825	0.292	2.826	0.005
Suitability*Untreated 2009*Edge (O)	-0.378	0.141	-2.690	0.007	-0.008	0.392	-0.021	0.983
Suitability*Untreated 2011*Edge (O)	0.085	0.162	0.523	0.601	0.224	0.416	0.539	0.590
Suitability*Treated 2010*Edge (O)	0.725	0.236	3.074	0.002	0.444	0.525	0.845	0.398
Suitability*Treated 2011*Edge (O)	-0.589	0.229	-2.568	0.010	-3.979	1.156	-3.443	<0.001

[a]Estimate and standard error (Std.Error) for random intercept equal to the variance and residual standard deviation, respectively
[b]Herbicide Treatment: Untreated 2010 set to zero (baseline); Edge (O): Inner edge set to zero (baseline)

Table C.2 Results of generalized linear mixed models for off target species richness 0.5 m^{-2} at *Bromus tectorum* and *Linaria dalmatica* environmental suitability sites

	Response: Species Richness (*B. tectorum*)				Response: Species Richness (*L. dalmatica*)			
Model Term	Estimate	Std. Error[a]	z-value	p-value	Estimate	Std. Error[a]	z-value	p-value
Random Intercept[a]	0.025	0.158			0.020	0.142		
Intercept	2.159	0.121	17.879	<0.001	1.362	0.104	13.144	<0.001
Suitability Index	-2.160	0.345	-6.253	<0.001	0.162	0.177	0.917	0.359
Herbicide Treatment[b]								
Untreated 2009	-0.164	0.123	-1.334	0.182	0.064	0.112	0.576	0.565
Untreated 2011	-0.024	0.128	-0.187	0.852	0.273	0.117	2.325	0.020
Treated 2010	-0.442	0.172	-2.570	0.010	-0.155	0.144	-1.078	0.281
Treated 2011	-0.140	0.161	-0.871	0.384	0.168	0.140	1.196	0.232
Interactions								
Suitability* Pre-Treatment	0.718	0.359	2.002	0.045	-0.134	0.191	-0.698	0.485
Suitability*Untreated 2011	0.704	0.375	1.878	0.060	-0.250	0.202	-1.237	0.216
Suitability*Treated 2010	0.609	0.491	1.240	0.215	0.075	0.246	0.305	0.760
Suitability*Treated 2011	0.886	0.457	1.940	0.052	-0.622	0.249	-2.503	0.012

[a]Estimate and standard error (Std.Error) for random intercept equal to the variance and residual standard deviation, respectively
[b]Herbicide Treatment: Untreated 2010 set to zero (baseline)

Table C.3 Results of generalized linear mixed models for EN ratio (number of exotic to number of native plant species 0.5 m^{-2}) at *Bromus tectorum* and *Linaria dalmatica* environmental suitability sites

	Response: EN Ratio (*B. tectorum*)				Response: EN Ratio (*L. dalmatica*)			
Model Term	Estimate	Std. Error[a]	z-value	p-value	Estimate	Std. Error[a]	z-value	p-value
Random Intercept[a]	0.176	0.419			0.143	0.378		
Intercept	-0.440	0.276	-1.591	0.112	0.466	0.230	2.028	0.043
Suitability Index	0.392	0.775	0.506	0.613	-2.002	0.410	-4.878	<0.001
Herbicide Treatment[b]								
Untreated 2009	0.096	0.261	0.369	0.712	0.272	0.235	1.157	0.247
Untreated 2011	-0.011	0.270	-0.042	0.966	0.319	0.241	1.323	0.186
Treated 2010	0.037	0.379	0.098	0.922	0.437	0.311	1.406	0.160
Treated 2011	-0.307	0.356	-0.863	0.388	-0.034	0.305	-0.111	0.912
Interactions								
Suitability* Pre-Treatment	-0.354	0.754	-0.470	0.639	0.259	0.423	0.613	0.540
Suitability*Untreated 2011	-0.152	0.782	-0.194	0.846	-0.398	0.444	-0.897	0.370
Suitability*Treated 2010	-2.016	1.095	-1.841	0.066	-0.645	0.564	-1.144	0.253
Suitability*Treated 2011	0.406	1.001	0.406	0.685	0.628	0.562	1.118	0.264

[a]Estimate and standard error (Std.Error) for random intercept equal to the variance and residual standard deviation, respectively

[b]Herbicide Treatment: Untreated 2010 set to zero (baseline)