QUANTIFYING NON-NATIVE PLANT IMPACTS: *CENTAUREA STOEBE* L. (SPOTTED KNAPWEED) AND *BROMUS TECTORUM* L. (DOWNY BROME) IN SAGEBRUSH-GRASSLANDS OF THE GREATER YELLOWSTONE ECOSYSTEM

by

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ABSTRACT

Non-native plant species (NIS) are considered a significant threat to individual species, communities, and ecosystems; thus, NIS management is mandated in most natural areas (i.e. non-crop). Controlling NIS in natural areas should, ideally, not only reduce target NIS abundance, but also benefit broader management objectives such as conserving native species and improving wildlife habitat. In this context, the benefits of NIS control must be weighed against the impacts of NIS themselves. This dissertation examines ecological impacts of NIS through a synthesis of previous experimental research and field-based manipulative experiments.

In a review and synthesis of experimental research, we found that NIS caused significant impacts in approximately half of all experiments. Negative impacts were most frequent on community structure, followed in descending order by individual species, ecosystem properties, and ecosystem processes. Contrary to common assumptions, NIS typically caused impacts by modifying the abiotic environment rather than outcompeting native species for resources.

NIS impacts were also examined through experiments conducted in sagebrush-grasslands of the GYE. The first study compared plant community impacts of *Centaurea stoebe* L. and common herbicide treatment for *C. stoebe*. The broadleaf herbicide, picloram, was highly effective at reducing *C. stoebe*, but also significantly reduced native forb cover and significantly increased non-native grass cover. Native forb cover increased with manual removal of *C. stoebe*, suggesting *C. stoebe* had been suppressing native forbs. However, there was an equivalent increase with no treatment. In these communities, *C. stoebe* appears to have a negligible effect on native forb and grass cover and richness.

The final study examined plant community impacts of the non-native annual grass, *Bromus tectorum* L, and relationships between impacts and NIS abundance. In a four-year field experiment, we did not detect significant impacts of *B. tectorum* on native plant cover and richness. Environmental factors, particularly climate variability, are likely more important determinants of current vegetation patterns in these communities rather than the presence of *B. tectorum*. Overall, the research shows NIS often do not have significant detectable impacts on native species and communities, and that the negative non-target effects of herbicide treatments may outweigh the benefits of NIS control.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

It is generally recognized that non-native plant species are a significant threat to the integrity of ecosystems and maintenance of biological diversity. Proposed impacts include diminished native plant diversity (Yurkonis et al. 2005), alteration of community structure and composition (Warner et al. 2003), threats to rare and endangered species (Lesica and Shelly 1996), reduction in wildlife habitat and forage (Thompson 1996; Sheley et al. 1998), alteration of fire regimes (D'Antonio and Vitousek 1992; Brooks et al. 2004), changes in nutrient cycling and energy flows (DiTomaso 2000; Ehrenfeld 2003), and changes in the composition and functioning of belowground communities (Pritekel et al. 2006). Non-native plants can affect multiple levels of ecological organization: individual species, populations, communities, and ecosystems (Table 1.1). However, these categories are not exclusive; interactions and feedbacks can cause population-level impacts to generate ecosystem-level consequences. For example, a non-native plant may out-compete a native forb species resulting in its exclusion--a population effect. But the elimination of this species may alter the microclimate and overall structure of the community from one dominated by forbs to one dominated by grasses, thereby altering the fire regime (D'Antonio and Vitousek 1992). Conversely, altered fire regimes resulting from introduced annual grasses can change the availability of resources and, therefore, the competitive dynamics of organisms within the community.

Historically, assessments of non-native plant impacts have been based on observational, site-comparison studies or anecdotal information. Although the body of research is growing, quantitative data on the impacts of non-native plants on biodiversity and ecosystem function remains limited (Adair and Groves 1998; Levine et al. 2003). More common are assessments of environmental conditions that may predispose ecosystems to invasion (Levine and D'Antonio 1999; Davis et al. 2000), as well as traits that contribute to a species' invasiveness (Rejmánek 1996; Rejmánek and Richardson 1996). It is not uncommon for non-native plant distribution to be equated with impact. However, impacts are a function not merely of the presence of non-native plants, but also a species' biological attributes and population dynamics, site-specific environmental conditions, accompanying symbionts, and the structure and composition of invaded communities (Vilà and Weiner 2004; Rejmánek et al. 2005).

My dissertation examined ecological impacts of non-native plants using two general approaches: (1) a review and synthesis of experimental research (Chapters Two and Three) and (2) field-based manipulative experiments in plant communities of the Greater Yellowstone Ecosystem (GYE) (Chapters Four and Five). The major motivation for this research was recognition that not all non-native plants have significant impacts (Simberloff 1981; Williamson and Fitter 1996) and that current non-native plant management programs are hindered by a lack of quantitative impact data. Maintaining ecosystem integrity and restoring degraded lands are top priorities for land managers; non-native plant species are major obstacles to meeting these objectives. Non-native plant management involves assessing the potential for impacts over large spatial and temporal scales. Limited time, money, and personnel make management of all non-native plant populations untenable. Thus, management must be prioritized to focus on areas of highest ecological or production value where the risk of negative impacts is greatest (Rew et al. 2007). Quantifying non-native plant impacts is a critical step in this prioritization process. The limited availability of impact data, as well as the variability of impacts across different conditions, warrants more regional and site-specific impact assessments. This is particularly true for areas with numerous and extensive non-native plant infestations, such as the GYE. The results of this research will add to the body of knowledge concerning the consequences of non-native plant species and their management and, hopefully, contribute to the on-going evolution of ecologically-based plant management practices.

Overview of Dissertation

A comprehensive synthesis of non-native plant impacts is presented in chapter two. To date there has been no appraisal of the state of the science of non-native plant impact assessment. Previous reviews have advanced our understanding of specific aspects of impacts, such as potential underlying mechanisms (Levine et al. 2003) and effects on soil nutrient cycling (Ehrenfeld 2003); however, there has been no comprehensive synthesis of impact findings. To address these needs, we reviewed all non-native plant experimental impacts research published in English from 2001 through April, 2011. The resulting manuscript is an examination of both research methodologies and overall impact findings across a broad range of studies. The results highlight significant advances and remaining challenges in methods, and identify common impacts and potential sources of variability. This review is unique in that: (1) whereas previous reviews have been largely based on observational research, we focused solely on experimental studies and, thus, provide a synthesis of empirical impact findings; (2) we synthesized experiments from around the English-speaking world that examined a broad range of non-native plant species and growth forms, experimental methods, impact metrics, study locations and habitats; (3) we examined impact assessment methodologies in light of previous research shortcomings and management needs and assessed the degree to which current impacts research relates to natural areas management.

In addition to quantifying impacts, determining the underlying processes is also recognized as essential to understanding and managing the consequences of non-native plant establishment, restoring invaded ecosystems and predicting future invasions. Examining the mechanisms of non-native plant impacts provides insight into many ecological interactions, both among species and between species and their environment, as well as the resilience of these relationships to altered biotic and abiotic conditions. Pragmatically, this issue matters for conservation managers by focusing attention on the ultimate processes driving ecological change rather than perceived limiting factors. The review of mechanisms underlying non-native plant impacts by Levine et al. (2003) generated tremendous interest, particularly by highlighting the lack of experimental research explicitly testing mechanisms; thus, revealing the uncertainty regarding the causes of non-native plant impacts. Levine et al. (2003) stimulated a new generation of experimental research quantifying non-native plant impacts and testing underlying mechanisms. However, there has been no comprehensive synthesis of this recent experimental work.

The manuscript in Chapter Three is a detailed examination of mechanisms underlying non-native plant impacts based on the empirical research reviewed in Chapter Two. This synthesis focused on the experimental studies from 2001 through April, 2011 that explicitly tested potential impact mechanisms. We detailed the methods and findings from 58 mechanistic impact studies and explored potential implications. Examining these causal processes can inform our understanding of species interactions and enable a more targeted approach to non-native plant management.

In Chapter Four, I conducted a manipulative field experiment to quantify the impacts of *Centaurea stoebe* L. (spotted knapweed), and the target and non-target effects of herbicide treatment of *C. stoebe*, on sagebrush-grassland plant communities of the GYE. *C. stoebe* is widespread in western North America and is thought to cause long term damage to plant communities, reduce biological diversity, and degrade natural resource values; thus management is mandated. Controlling non-native plants in natural areas should, ideally, not only reduce target species' abundance, but also benefit broader management objectives such as conserving native species, improving wildlife habitat, and providing ecosystem services. In this context, the effectiveness and non-target impacts of control strategies, such as broadleaf herbicides, must be weighed against the impacts of non-native plants themselves. Despite the long history of establishment in western N. America, and Montana in particular, there are very few experimental field studies quantifying the impacts of *C. stoebe* on plant communities relative to those of common herbicide treatments. We undertook this assessment with a three-year experiment in sagebrush-grassland communities of southwest Montana. Four treatments (manual removal of *C. stoebe*, ground disturbance to mimic that created in removal plots, herbicide treatment, and untreated controls) were implemented across nine *C. stoebe* populations. We quantified the response of native and non-native plant species cover and richness, litter cover, bare ground, and the biomass of two important native forage grasses, over time in response to treatments. We also compared the values of these plant community metrics with those in adjacent uninvaded areas to determine whether invaded and uninvaded areas differed and, if so, whether areas treated for *C. stoebe* became more similar to nearby uninvaded areas three yeas after treatment.

The motivation for this research was twofold. First was the increasing recognition that non-native plant control strategies, particularly in natural areas and wildland ecosystems, often do not result in desirable long-term outcomes (D'Antonio et al. 2004; Reid et al. 2009). A lack of native species recovery and secondary invasion are common hindrances (e.g. Mason and French 2007; Turner et al. 2008; Rinella et al. 2009; Larson and Larson 2010; Kettenring and Adams 2011). Second was the fact that the detrimental effects of *C. stoebe* on natural plant communities have largely been based on observational comparisons of invaded and uninvaded areas. This approach carries the risk of confounding the effects of a non-native plant species with the effects of varied biotic and abiotic conditions across different sites (Adair and Groves 1998). While effectiveness and plant community impacts of herbicide treatment for *C. stoebe* have been assessed, field-based experiments quantifying community-level impacts of *C. stoebe* are rare. Thus, quantitative impact assessments are necessary to weigh the impacts of *C. stoebe* against the impacts of control strategies in relation to overall land management goals. Sound management decisions will consider these tradeoffs in relation to the quantified impacts of non-native plants themselves.

As mentioned, not all non-native plants have significant impacts, and impacts vary considerably depending on the environmental context. One of the important factors in whether and to what degree non-native plant populations will have a significant impact is their abundance. If non-native plant abundance thresholds exist below which impacts are minimal, control efforts could target high-value areas where abundance exceeds this threshold. A threshold of non-native plant impacts might be indicated by a non-linear relationship between non-native plant abundance and plant community metrics (i.e. species richness), exhibiting a sharp decline in the community response variable at a certain level of non-native plant abundance (Panetta and James 1999; Thiele et al. 2010). Quantitative impact data are necessary to identify thresholds and incorporate threshold concepts into integrated weed management programs. However, there is scarce research examining thresholds in natural ecosystems in terms of potential abundance-impact relationships.

In Chapter Five, I examined impacts, and potential impact thresholds, of the non-native annual grass, *Bromus tectorum* L. (cheatgrass, downy brome) on native and non-native plant species cover and richness in sagebrush-grassland communities of the GYE. *B. tectorum* has played a major role in converting sagebrush-grasslands in western N. America from systems dominated by perennial bunchgrasses and shrubs to annual grasslands that experience wildfires at significantly higher frequency and intensity (Whisenant 1990; D'Antonio and Vitousek 1992; Brooks et al. 2004). Although it is speculated that *B. tectorum* displaces native grassland and sagebrush-steppe plant species and reduces species richness and diversity (Knapp 1996; Anderson and Inouye 2001), there is very little quantitative data from field-based experiments. I conducted a manipulative field experiment to: (1) quantify plant community impacts of *B. tectorum*; (2) assess whether there is a relationship between *B. tectorum* abundance (percent cover) and plant community impacts; and (3) if there was a relationship, establish the nature of the relationship (i.e. linear or non-linear), and thus whether an impact threshold was evident. I implemented three treatments (*B. tectorum* removal, small-scale disturbance, and untreated control) across a gradient of *B. tectorum* cover (2 to 82%) and quantified the response of native and non-native plant species cover and richness over three years. I hypothesized a negative relationship between *B. tectorum* cover and native species cover and richness, and a positive relationship between initial *B. tectorum* cover and the increase in these variables in response to removals.

Finally, in Chapter Six, I provided a summary of major results from each chapter and discussed how these results may influence future management of non-native plants, particularly *C. stoebe* and *B. tectorum* in the GYE.

Table 1.1. Potential non-native plant impacts and possible underlying mechanisms

Potential non-native plant impacts	Proposed mechanisms and representative studies
Ecosystem processes & properties	
Alter disturbance regimes (e.g., fire behavior, frequency, intensity; erosion; flooding, grazing) and/or community response to disturbance (e.g., succession)	Differ in size, spatial distribution, phenology, morphology which may: (1) transform fuel properties (e.g., amount & flammability of biomass/ litter, timing of senesce, higher surface area: volume ratio), (2) alter plant community architecture & spatial distribution, (3) alter substrate stability (Caldwell et al. 1981; Busch and Smith 1995; Rossiter et al. 2003; Reed et al. 2005; Cullis et al. 2007)
Alter soil physical properties (e.g., morphology, soil water, organic matter) and/or microclimate	Differ in quantity, quality, timing of soil inputs; access previously unused water (via deeper roots), degree and timing of water use; differ in leaf area index & transpiration rates, canopy architecture, root morphology (Melgoza et al. 1990; D'Antonio and Mahall 1991; Enloe et al. 2004; Boxell and Drohan 2009)
Alter nutrient pool sizes, distribution, & fluxes; alter nutrient availability	Differ in size, physiology, phenology, life-history (e.g., N-fixation, N-mineralization, nitrification & decomposition rates, degree & timing of resource acquisition), differ in quantity, quality & timing of soil inputs, alter abundance/ composition of soil organisms involved in nutrient cycling (Vitousek and Walker 1989; Ehrenfeld et al. 2001; Mack and D'Antoino 2003; Hawkes et al. 2005)
Alter aboveground food-webs, mutualisms, plant-pollinator networks, wildlife habitat	Quantitatively or qualitatively alter food resources and/or habitat (Trammell and Butler 1995; Zedler and Kercher 2004; Levin et al. 2006); siphon pollinators, attract different pollinators (Ghazoul 2004; Bartomeus et al. 2008)
Alter soil food-webs, habitat, and/or symbiotic relationships	Alter quantity, quality, timing of soil inputs; host different and/or inhibit previous mycorrhizae, microorganism, or microbe composition, abundance, diversity, distribution (Duda et al. 2003; Kourtev et al. 2003)

Table 1.1 Continued.

Community characteristics	
Alter plant richness, diversity, abundance, and/or composition	Displace native species, inhibit colonization/ establishment, facilitate other non-native species (Holmes and Cowling 1997; Meiners et al. 2001; Yurkonis et al. 2005)
Alter animal richness, diversity, abundance, and/or composition	Different physiology, morphology, abundance, distribution which alter habitat, food resources, range connectivity (Braithwaite et al. 1989)
Alter soil biota (e.g. bacteria, fungi, arthropods, nematodes) richness, diversity, composition, and/or function	Different vegetative/ root morphology, physiology; different quantity/quality of soil inputs; root exudates (Ehrenfeld and Scott 2001; Belnap et al. 2005; Wolfe and Klironomos 2005)
Individual species and/ or populations	
Alter growth, fecundity, and/ or survival of individual species	Compete for resources, interfere physically (e.g. shading, occupy ground space, smothering), promote apparent competition (attract predators, usurp pollinators, increase heterospecific pollen), hybridize, release phytotoxins (Brooks 2000; Brown and Mitchell 2001; Reinhart et al. 2006)

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CHAPTER TWO

LITERATURE REVIEW

QUANTIFYING NON-NATIVE PLANT IMPACTS FOR NATURAL AREAS MANAGEMENT: A REVIEW OF EXPERIMENTAL RESEARCH

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

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Abstract

Non-native plants are considered a threat to individual species, community structure, and ecosystem properties and processes. However, there is concern that this generality has been largely based on observational studies and limited experimental data. Research that incorporates variability and context-dependency of impacts is necessary for management prioritization in natural areas. We reviewed all non-native plant impacts research from 2001 through March 2011 to assess the state of the science and synthesize impact findings. We focused our synthesis solely on experimental research, but note that 70% of all non-native plant impacts research from the past decade was observational. Impacts on individual species were the most commonly studied (52%), followed by community structure (35%). Quantification of impacts on ecosystem properties and processes was relatively rare, 10% and 3%, respectively. Non-native plants caused a significant impact, under at least some conditions, in approximately half of all experiments. At least 18% of the significant impacts were beneficial. Community structure variables, particularly plant and arthropod abundance and composition, were often negatively impacted, whereas ecosystem processes were rarely affected. Impacts were context-specific, varying across non-native and native species, densities, sites, and abiotic conditions. Much of the research was focused on short-term individual-level responses, leaving significant uncertainty regarding the long-term community- and ecosystem-level impacts.

Synthesis and applications: In this review of non-native plant impacts research, we show that negative impacts are not as ubiquitous as generally assumed, and that impacts vary among species and conditions. Methods used to quantify impacts are improving, but experiments conducted across multiple sites, integration of impacts across multiple ecological levels, and incorporation of disturbance as a covarying factor are still rare. Given the variability of impacts and the undesirable outcomes of many non-native plant control programs, we emphasize the importance of clear objectives, context-specific impact data and relative risk assessments for natural areas management.

Key words: invasive plants, exotic plants, weeds, impacts, variability, context-dependent, weed management, exotic plant management

Introduction

Impact assessment is a crucial yet often overlooked component of a comprehensive non-native plant management program. Rather than being explicitly measured, impacts are often derived from the presence, abundance, distribution, and spread of non-native plants. Although these are informative for many analyses, they do not equate with impact (Rejmánek, Richardson and Pyšek 2005; Ricciardi and Cohen 2007). Relative performance and trait comparisons are also unreliable predictors of impact (Thompson & Davis 2011). Non-native plants establish across a wide variety of communities that are shaped by many physical, environmental, and biological factors, including long histories of natural and anthropogenic disturbance (Ricklefs 1987; Eschtruth and Battles 2009). Impacts caused by non-native plants vary as a function of abiotic conditions (e.g. temperature, water, nutrients, light) (Melbourne et al. 2007) and land-use histories (Byers 2002), and may be exacerbated or ameliorated under certain conditions (e.g. elevated atmospheric CO_2, nitrogen availability). The effects of non-native plants depend on the biological attributes and abundance not only of the non-native species, but also of the extant plant community (Vilà and Weiner 2004). Traditional assessment methods, particularly observational and correlative studies, may not adequately reflect impacts (Hulme 2003; Gurevitch and Padilla 2004), or have the power to distinguish the effects of non-native plants from the effects of other drivers of ecological change (Didham et al. 2005). Integrating multiple research approaches has been recommended as one way to incorporate the variability in impacts across different spatial and temporal scales (Didham et al. 2005; Sagarin and Pauchard 2010).

Variability in non-native species response and interactions between factors complicate experimental design, statistical analysis, and attempts at generalization. However, researchers can capitalize on these aspects of non-native plant impacts to inform management, particularly if they evaluate response at the population level (Rew et al. 2007). The increasing strain on budgets means that not all non-native plant populations can be managed. Identifying high- versus low-impact species, and determining whether impacts vary among different native species, trophic levels, and habitats can facilitate management prioritization (Byers et al. 2002). Furthermore, before initiating costly management programs, the ecological significance of impacts relative to land management objectives should be determined. Determining whether impacts on ecosystem processes are detrimental for individuals, populations and communities requires studies that span multiple levels of ecological organization (Vitousek 1990; Parker et al. 1999). Progress in this type of research has been limited to date (Levine et al. 2003).

A number of specific aspects of non-native plant impacts have recently been reviewed, such as resource pools and cycling (Ehrenfeld 2003; Ehrenfeld 2010), plant-pollinator interactions (Traveset and Richardson 2006; Bjerknes et al. 2007; Morales and Traveset 2009), and effects on native plant richness by graminoid and woody species (Mason et al. 2009), or in Mediterranean-type ecosystems (Gaertner et al. 2009). However, there has yet to be a synthesis of impacts across the broad range of non-native plant species and growth forms, experimental methods, impact metrics, study locations and habitats. Nor has there been an assessment of the degree to which current impacts research relates to natural areas management. Thus, we conducted a comprehensive review of recent experimental impacts research in order to: (1) synthesize the methods and findings of non-native plant impacts research; (2) assess the variability of impacts among multiple non-native species, response variables and environments, as well as interactions with covarying factors; (3) examine potential relationships among impacts at different ecological levels; and (4) assess the applicability of impacts research to natural areas management. We synthesized the findings from a large and diverse pool of experiments, significantly advancing our understanding of the consequences of non-native plant establishment. We discuss a number of ways that current and future non-native plant impacts research can assist managers faced with numerous non-native plant populations, multiple management objectives and limited budgets.

Methods

Literature Search

We conducted database searches in ISI Web of Knowledge, EBSCO Academic Search Premier, CSA Illumina, and Elsevier ScienceDirect using the keywords: (alien or exotic or introduced or invas* or non-indigenous or non-native) AND (alter or effect or impact or influence) AND (forb or grass or plant* or shrub or tree) for studies published in English between 2001 and April, 2011. We also examined references within the publications located through the electronic searches. The initial search generated approximately 2,000 publications, of which approximately 500 explicitly considered impacts caused by non-native plants. Approximately 70% of these were observational studies, a percentage that has been relatively unchanged for at least the past decade (Ehrenfeld 2003; Levine et al. 2003).

Inclusion Criteria

Our focus was non-native plant impacts pertaining to natural communities (non-agricultural) that were quantified using experimental approaches. We put no restrictions on non-native plant species or growth forms, impact metrics, impact targets, study locations or systems, or experimental methods. We included studies that examined impacts of multiple non-native species, as well as those that assessed impacts on multiple response variables, including multiple target species. We included allelopathic studies if impacts of the whole plant could be discerned; thus, we did not include experiments that used manual application of root extracts or synthetically derived phytotoxins. We did not include observational (e.g. site-comparisons), anecdotal, theoretical, or purely modeling-based studies, nor did we include other reviews. However, we did include three non-manipulative studies (Meiners et al., 2001; Jäger et al. 2009; Mills et al., 2009) that quantified changes over time accompanying non-native establishment. In the case of studies that combined experimental and observational approaches, we reviewed the methods and results from the experimental portions, but noted the use of a dual approach. We identified 119 studies that fit these criteria (Appendix A).

Analysis

Most studies involved multiple experiments that we defined as unique non-native species, target species, experimental methods, and/or response variable combinations. We evaluated all combinations; thus, the 119 impact studies comprised 696 distinct experiments. Experiments were categorized by the ecological level of hypothesized impact: (1) individual species (e.g. survival, growth, productivity, reproduction), (2) community structure (e.g. species richness, diversity, abundance), (3) ecosystem properties (e.g. soil moisture, temperature, light, nutrients) or (4) ecosystem processes (e.g. N-mineralization, nitrification or decomposition). We recorded the year of publication, geographic location, habitat or experimental system, temporal and spatial scale, non-native species and associated attributes, impact metric(s), experimental methods, and results. We also quantified a number of methodological attributes of the reviewed impact studies (Appendix B).

We report impact results as an increase, decrease, or no effect in the response variable at the $P < 0.05$ significance level. These results are, in all cases, the impact of the non-native plant, regardless of the experimental methods employed. We separated the results into single factor and multifactor experiments because we were interested in potential interactions between impacts and covarying factors. We report only the final results from multi-year experiments; however, if the experiment was replicated over time, we also report significant impact by time interactions. Finally, we assessed whether impacts resulted disproportionately from certain non-native growth forms, habitats, experimental methods, or study lengths.

Results

Non-Native Species and Growth-forms

All possible non-native growth forms, plant longevities, and photosynthetic pathways were examined in the reviewed studies (Table 2.1). Impacts on individual species, community structure, and ecosystem properties were generally quantified in relation to non-native forbs and C_3 grasses, whereas ecosystem process experiments more often focused on non-native C_4 grasses.

A total of 103 non-native species were examined, 70% of which were in only one study (Appendix C). Twenty-four species were in multiple studies: *Acer platanoides*, *Centaurea solstitialis*, *Dactylis glomerata*, *Lantana camara*, *Lonicera japonica*, *Medicago polymorpha*, *Mimulus guttatus*, *Rhamnus frangula*, and *Typha glauca* (*n* = 2), *Bromus hordeaceus, B. inermis, Euphorbia esula*, and *Poa pratensis* (*n* = 3), *B. diandrus*, *B. madritensis*, and *Carpobrotus* spp. (*n* = 4), *Avena barbata, Centaurea maculosa*, *Lonicera maackii*, and *Taraxacum officinale* (*n* = 5), *Impatiens glandulifera* and *Lythrum salicaria* (*n* = 6), *Alliaria petiolata* (*n* = 7), and *Microstegium vimineum* (*n* = 9).

Impacts of non-native plants were compared to impacts of a co-occurring native in 24% of all studies. Impacts of multiple non-native plant species were compared in 9% of all studies. Of the studies that examined impacts on individual species (*n* = 106), 41% compared the response among multiple target species.

Locations and Experimental Environments

Non-native plant impacts were studied in 23 countries, but predominantly in the USA (65% of studies, Figure 2.1a). Research was conducted in 25 USA states, although 20% of all USA studies took place in California (Figure 2.1b).

Constructed communities were the predominant experimental environment (41% of all experiments, Table 2.2). Grasslands were the most common natural environment for impact studies. These experiments typically involved non-native C_3 grasses and annual and perennial forbs and were mainly conducted in the western USA. Impacts research in hardwood forests was concentrated in the Midwestern and eastern USA and was largely focused on *L. maackii*, *A. petiolata*, and *M. vimineum*. Impacts were quantified across multiple sites in 20% of non-greenhouse studies (*n* = 96).

Experimental Methods, Length, and Scale

Competition experiments were the most common research method, primarily used to quantify impacts on individual species. Non-native removals were more often used to examine impacts on ecosystem processes (57%), ecosystem properties (51%), and community structure (47%). Seven other methods comprised the remaining experiments (Table 2.3).

The spatial scale of experiments, regardless of impact category, was generally small (<1 m^2 or 1-10 m^2). The spatial extent of study areas was not typically reported. In addition to manipulative experiments, 33% of studies also included observational assessments, typically at larger spatial scales. Nearly 70% of experiments lasted for three years or less (Table 2.4).

Impact Levels and Response Variables

Focus was largely on impacts on individual species (52% of all experiments), and community structure (35% of experiments). Despite widespread concern over impacts on ecosystem properties and processes, quantification of these impacts was relatively rare, 10% and 3% of experiments, respectively.

There was broad diversity of specific impact response variables (Supplementary Material). Plant growth (forb, grass, and tree), reproduction, establishment, and survival were the most common individual species impact metrics, together comprising 77% of experiments in this category. Grass and forb abundance, richness, and diversity were the predominant metrics of impact on community structure, together comprising 58% of experiments at this level. Impacts on arthropod abundance, richness, and diversity were also frequently examined (22%). Soil water, nitrogen (N) mineralization, soil N, NH_4^+, and NO_3^-, were the most common ecosystem process and property impact metrics; however, many of the ecosystem response variables were examined in only a few experiments.

Most studies (81%) quantified impacts on multiple response variables; but only 21% integrated impacts across multiple ecological levels. The interaction between non-native plant impacts and additional factor(s) (e.g. site, soil water, non-native density, size/maturity of target species) was examined in 48% of studies. Despite the broad recognition of anthropogenic disturbance as a significant factor in non-native plant establishment, its influence on, or interaction with, impacts was explicitly examined in only 5% of the reviewed studies (mostly logging or land-clearing).

Impact Findings by Ecological Level

Non-native plants caused significant impacts in 51% of all experiments, under at least some conditions (details on multifactor experiments below). Ten percent of significant outcomes were beneficial effects, such as increased native plant diversity or decreased non-native plant abundance (other than the focal species).

Community structure (e.g. richness, diversity, composition) was the only ecological level in which significant impacts resulted for more than half of the experiments; 40% of the experiments in this category led to decreases, and 15% increases, in the response variable. Non-native plants had no significant effect on individual species, ecosystem properties, and ecosystem processes in over half of the experiments in each of these categories. When significantly impacted, ecosystem properties and processes tended to increase (e.g. NH_4^+, nitrification); however, whether these represent improvements in ecosystem function is context-specific.

When all experiments were considered together, impacts were not caused disproportionately by certain non-native growth forms with the exception of perennial forbs, which represented slightly more, and C_3 annual grasses slightly fewer, of the increases than expected based on their overall representation. Relative to the other non-native growth forms, deciduous trees caused the most impacts (68% of experiments involving this growth form had significant outcomes). It should be noted, however, that this growth form was represented by relatively few experiments (Table 2.1). C_3 annual grasses led to the fewest impacts, with only 36% of experiments involving this growth form resulting in significant effects.

Interestingly, there was no relationship between the length of experiment and outcome; shorter experiments did not lead to disproportionately more or fewer significant impacts than longer experiments. Experiments in riparian areas accounted for slightly more of the significant increases than expected, but in general there was not an apparent relationship between impacts and experimental environment. Impacts often varied, particularly as a function of site, soil water, non-native plant density, and target plant size, maturity and spatial aggregation.

Individual Species. Non-native plants had a significant impact in 49% of the experiments that examined individual species response variables. The majority (83%) of these impacts were decreases in the response variable, all of which were undesirable effects, such as reduced native plant growth, with the exception of two cases in which a focal non-native tree suppressed the growth of another non-native tree species. Most of the increases in response variables caused by non-native plants ($n = 30$) were beneficial (e.g. increased native plant growth), although there were several cases of facilitation of other non-native species. Grass reproduction and tree survival were most often negatively impacted, whereas grass and forb establishment and survival were generally unaffected.

Nearly half (47%) of all individual species experiments assessed the interaction between non-native plant impacts and an additional factor (Table 2.5). Of these, 22% resulted in non-native plant impacts that varied depending on the level of covarying factors, specifically: non-native plant density, proximity to non-native plants, density, size/developmental stage and spatial aggregation of native plants, nitrogen level, site, disturbance, timing of non-native plant establishment, soil water and depth and herbivory.

Evaluating the data by species growth form, non-native annual forbs were more injurious than other non-native growth forms, mainly impacting native plant germination, productivity, and reproduction, as well as reducing mycorrhizal colonization of native hardwood trees. Non-native shrubs caused a disproportionate number of the significant increases, benefitting arthropods and native forb and grass growth and reproduction. C_3 annual grasses rarely impacted individual species; 75% of experiments involving this growth form resulted in no significant effect.

Community Structure. Non-native plants had a significant impact in 55% of the community structure experiments--the most of the four impact categories. Most community structure impacts were reductions in native plant abundance and/or diversity. However, there were eight cases of “beneficial” reductions, such as reduced non-native plant cover. Most of the increases in this category would be considered beneficial (e.g. increased native plant abundance), with three exceptions: arthropod extinction rate, quantity of non-native pollen on native flower, and non-native plant evenness.

Shrub and tree abundance were the most consistently negatively impacted; however, these variables were measured in only six experiments. Grass and forb richness and abundance were significantly reduced in approximately 30% of cases that examined these responses (n = 107).

The interaction between non-native plants and additional factors were examined in 55% of community structure experiments (Table 2.6). Of these multifactor experiments, 25% resulted in non-native plant impacts that varied as a function of covarying factors, particularly non-native plant density, site, and grazing.

Among growth forms, non-native C_4 annual grasses and non-native vines caused the most negative impacts on community structure. Shrubs and perennial forbs were more benign, with 58% of experiments involving these growth forms resulting in no significant impact.

Ecosystem Processes and Properties. Non-native plants had a significant impact in 38% of ecosystem process experiments (n = 21) and 49% of ecosystem property experiments (n = 72). Abiotic conditions, particularly air and soil temperature and light, were often significantly reduced, whereas soil resources (i.e. N, P, C, soil water, and organic matter) and process rates (i.e. mineralization and nitrification) were often unaffected. When impacted, soil nutrients and processes tended to increase, which is consistent with previously observed patterns (Ehrenfeld 2003).

Interactions were examined in 40% of ecosystem process and property experiments (Table 2.7). Impacts varied 30% of the time as a function of season, site, water availability, and non-native plant density.

Non-native perennial grasses (both C_3 and C_4) and non-native trees (both deciduous and evergreen) caused the majority of significant impacts on ecosystem properties and/or processes, whereas non-native shrubs and perennial forbs were relatively innocuous in these impact categories.

Impacts in Multiple Studies

Although 25 non-native species were examined in multiple studies, response variables overlapped for only 11 species (Table 2.8). Only one consistent impact was found for the overlapping response variables, which was the reduction in forb growth by *A. petiolata* found in two studies.

Discussion

Many compelling questions can be addressed through the study of ecological invasions; however, there is an urgent need for research that informs management. To be applicable, non-native plant impact studies need to address scales, conditions, and response variables that are relevant to land management objectives. Assessments of variability of impacts within a species and among different non-native species, response variables, habitats, and biotic and abiotic conditions can facilitate management prioritization.

In our review of 119 experimental studies, a wide diversity of non-native species, impact metrics, habitats, and environmental conditions were examined, suggesting that research is largely motivated by the need for context-specific impact assessments. We found that non-native plants caused significant impacts in approximately half of all experiments, and outcomes varied as a function of both dependent and independent variables.

Applicability of Research to Management

Multiple non-native plant species often co-occur in a particular environment and may vary in their effect on individuals, communities and ecosystems. Identifying differences in impacts among multiple non-native species, as well as variability in susceptibility among different target species can help prioritize management and guide future research (Byers et al. 2002). Eleven studies in this review compared the impacts of multiple non-native plant species, and all found significant differences among them. There was also substantial evidence that impacts vary depending on the target species. Impacts were quantified on multiple target species in 41 studies. Of these, 37 found significant impacts and, of these, 33 resulted in impacts that varied depending on the target species. For example, the presence of the non-native tree *Ailanthus altissima* led to a positive growth response for some native tree seedlings and a negative response for others (Gomez-Aparicio and Canham 2008).

Although 25 non-native species were examined in more than one study, there was minimal overlap in response variables. Thus, there is not abundant evidence for any one particular non-native species exerting a certain type of impact, but rather one or two cases each for a variety of impacts. Of the species' impacts that were examined in multiple studies, there was strikingly little consistency in outcomes, further highlighting that not all non-native plants exert negative impacts in all environments.

Multifactor experiments can be more complicated in design, implementation and analysis. However, some of the most important ecological questions can only be addressed by examining interactions among multiple factors (Goldberg et al. 1999; Vilà and Weiner 2004). Interactions between non-native plant impacts and additional factors were examined in approximately half of the reviewed studies and were often found to be significant. The specific biotic and abiotic conditions of a site are one potential determinant in whether and to what degree non-native plants will affect their new environments. Impacts were quantified across multiple sites in 19 studies, and in over half of these experiments impacts varied as a function of site.

The density and maturity of both native and non-native plants can also influence the degree of impact. Eleven studies examined density-dependence of impacts, and this was a significant factor in 80% of the cases (e.g. Hawkes et al. 2005; Stinson et al. 2007; Flanagan et al. 2010). In other studies, impacts only occurred in low native densities or on small/immature native target plants (Badgery et al. 2005; Barrat-Segretain 2005; Morghan and Rice 2006).

Although disturbance has long been recognized as an influential factor in non-native plant establishment and impact (Hobbs and Huenneke 1992; Davis et al. 2000; Byers 2002), it was examined in only six impact studies. The available evidence indicates that impacts tend to either be restricted to, or are of greater magnitude in, areas subject to anthropogenic disturbances, such as logging and livestock grazing (e.g. Hager 2004; Miller and Gorchov 2004; Raffaele 2004; Thomson 2005; Truscott et al. 2008). Non-native plants were better than native plants at establishing in cleared or disturbed areas and often had a suppressive effect on natives once established. However, non-native plants were generally unable to establish in undisturbed areas and in established vegetation (Hager 2004; Raffaele 2004; Truscott et al. 2008). Furthermore, a number of studies found native plants to be sufficiently competitive against non-natives (e.g. Corbin and D'Antonio 2004; Thomson 2005; Corbin and D'Antonio 2010). These findings support the growing body of evidence that some undesirable ecological changes, such as the large-scale transformation of native California grasslands to systems dominated by non-native annual grasses, are often initiated and maintained by disturbance rather than competitive exclusion by non-native plants (Seabloom et al. 2003; Gonzales and Arcese 2008; Yelenik and Levine 2010).

Ecological Significance of Impacts

Managers are typically responsible for maintaining or increasing populations and/or community properties (e.g. species richness, diversity). Thus, it is of interest to know whether impacts on ecosystem properties and/or processes have consequences at these ecological levels. Of the 15 studies that examined impacts on ecosystem properties and/or processes in conjunction with impacts on individual species and/or community properties, 10 found at least some impacts at both levels. For example, in a field competition experiment, Davis et al. (2005) found that non-native perennial grasses caused an increase in light, NH4, and NO3, and a corresponding decrease in survival and biomass of native tree seedlings. Typically, within one study some ecosystem property and/or process variables, as well as some individual species and/or community property variables, were significantly impacted, and others were not. In a 7-year time-series experiment, the non-native perennial tree *Cinchona pubescens* significantly reduced air and soil temperature, light, and relative humidity and also reduced native plant cover. Native species richness, however, was unaffected (Jäger et al. 2009). Similarly, Stinson et al. (2007) found that the decreased light intensity and increased soil temperature caused by *A. petiolata* led to lower abundances of some resident plant species, decreased overall plant diversity, but had no effect on richness. Thus, the available evidence indicates that impacts on ecosystem properties and/or processes often, but not always, translate to a biotic impact. The small number of studies that integrated impacts across levels leaves considerable uncertainty regarding the ultimate consequences of proximate impacts.

Realism of Experiments

Realism of experiments is the degree to which findings can be extrapolated to natural communities (Diamond 1986). Forty-one percent of impact experiments took place in constructed communities, the majority of which were greenhouse competition experiments. While essential for establishing first principles and isolating specific processes, these experiments are unlikely to reflect the effects of non-native plants in real communities because they do not involve the interactions and spatial and temporal variability that drive community dynamics (Diamond 1986; Chesson 2000). Only three studies involved long-term successional experiments in which changes in non-native abundance and community response variables were measured over time. While potentially more logistically challenging than short-term controlled experiments, these types of studies have a high-degree of realism and ideally should comprise a greater proportion of future impacts research.

The predominance of individual plant fitness response variables and the rarity of ecosystem process variables reflect the small spatial scale (< $10m^2$) and short timeframe (< 3 years) of most experiments. Impacts on landscape-scale processes such as fire frequency and hydrology are not likely to be as amenable to experimental approaches as impacts operating at more local scales.

Impacts of Non-Native Plant Removal

Secondary invasion by other non-native plants was common in removal experiments, providing further evidence that controlling non-native plants often results in undesirable outcomes or does not achieve the desired results, and may undermine overall land management goals (Rinella et al. 2009; Kettenring and Adams 2011). Taken together, these findings highlight the need for careful consideration of management objectives and corresponding assessments of non-native plant impacts relative to potential management outcomes. An explicit comparison of the impacts of a non-native plant and the impacts of control of the non-native plant was made in only one study in our review.

Management Implications

Impacts were often found to only be significant at high non-native plant densities (approximately 45% of the experiments that considered density). This suggests that, contrary to the common management strategy of targeting low-density infestations, in many systems the top priority should be to reduce the number of non-native individuals to below threshold densities and address more sparse infestations as limited management resources permit.

Furthermore, native plants were often sufficiently competitive against non-native plants, and the impacts of non-native plants were diminished with greater native densities and/or larger or more mature native target species. Given this, in combination with the fact that non-native plant removal is often counterproductive in terms of land management goals, we suggest that attempting to eradicate non-native plants will often not be the best course of action. Our synthesis concurs with Daehler (2003) and Hulme (2006) that, whenever possible, natives should be encouraged, perhaps even instead of non-native removal. It is also clear from this synthesis that not all non-native plants have negative impacts in all situations. Thus, focusing on populations rather than species and incorporating long-term, multi-site monitoring will result in more effective and efficient management (Smith et al. 2006; Rew et al. 2007).

Conclusion

Our synthesis of experimental studies supports the assertion that non-native plants often have limited significant influence on individuals, communities and ecosystems. The identity, density, and maturity of non-native and native species, as well as numerous abiotic factors, play a role in whether and to what extent non-native plants have an impact. As management budgets become increasingly strained, research that captures this variability and provides relative assessments, particularly comparing the impacts of non-natives with the impacts of management, becomes more crucial to help prioritize management. Despite a large body of research, our understanding of the variability of a species' impact at the landscape-scale and long-term implications of non-native plant establishment remains limited. A growing body of evidence implicates disturbance as a major driver of many ecological changes typically attributed to non-native plants. Deciphering the impacts of non-native plants from other environmental stressors can help avert misguided management and restoration efforts. While disturbance may be difficult to include in replicated experiments, particularly at relevant spatial scales, it is a significant factor that requires greater attention in future impacts studies, possibly through a combination of approaches. Continued research across a broad range of non-native plant species and their populations, native target species, and recipient habitats and environments will help inform current management prioritization, as well as long-term adaptive management strategies.

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List of Appendices and Supplemental Material

The following appendices are located at the end of this dissertation:

Appendix A. References for Reviewed Impact Studies

Appendix B. Methodological Attributes of Impact Studies

Appendix C. Non-native Plant Species, Attributes, and Number of Studies

Table 2.1. Non-native plant growth forms and longevities and representation in impact experiments by ecological level and combined. Values are percent of *n*. (* indicates number of N-fixing species)

Growth form & longevity	Individual species (*n* = 362)	Community structure (*n* = 241)	Ecosystem properties (*n* = 72)	Ecosystem processes (*n* = 21)	All experiments (*n* = 696)
Forbs	44	39	36	19	41
Annual (9 spp.) (2*)	15	14	14	5	14
Biennial (4 spp.)	6	3	4	5	5
Perennial (23 spp.) (3*)	23	22	18	9	22
Grasses	37	27	26	57	32
C_3 annual (11 spp.)	21	9	8	9	16
C_3 perennial (17 spp.)	12	7	5	0	8
C_4 annual (1 spp.)	2	11	6	29	6
C_4 perennial (6 spp.)	2	0	7	19	2
Shrub (15 spp.) (1*)	10	18	19	14	15
Trees	8	13	19	10	11
Evergreen (10 spp.) (1*)	4	11	7	5	7
Deciduous (4 spp.) (1*)	4	2	11	5	4
Vine (3 spp.)	1	3	0	0	1

Table 2.2. Experimental environment of impact studies by ecological impact level and combined. Values are percent of *n*.

Habitat/System	Individual species (*n* = 362)	Community structure (*n* = 241)	Ecosystem properties (*n* = 72)	Ecosystem processes (*n* = 21)	All experiments (*n* = 696)
CC*- greenhouse	42	3	22	24	25
CC*- field	19	16	13	9	16
Grassland/ Prairie	10	15	3	5	11
Forest- hardwood	12	10	4	-	10
Riparian/ Floodplain	1	17	19	-	9
Wetland	2	7	8	28	5
Desert	4	5	-	-	4
Forest- *Nothofagus*	2	4	-	-	3
Forest- tropical dry	-	4	7	19	3
Coastal scrub	1	3	-	-	2
Forest- tropical wet	1	<1	10	5	2
Old agricultural field	-	5	-	-	2
Savanna	-	3	2	5	1
Beach/ Dune	2	-	-	-	1
Forest- conifer	1	1	-	-	1
Forest- sclerophyll	-	2	-	-	1
Fynbos	-	1	6	5	1
Sedge highland		2	6	-	1
Urban field	1	1	-	-	1
Alpine	1	-	-	-	<1
Heathland	1	-	-	-	<1
Rock outcrop	<1	-	-	-	<1

* Constructed community, includes mesocosms and pot experiments

Table 2.3. Experimental methods used to quantify non-native plant impacts by ecological impact level and combined. Values are percent of *n*.

Experimental method	Individual species (*n* = 362)	Community structure (*n* = 241)	Ecosystem properties (*n* = 72)	Ecosystem processes (*n* = 21)	All experiments (*n* = 696)
Competition	44	17	19	9	31
Non-native removal	11	47	51	57	29
Non-native addition	6	14	7	5	9
Native addition	11	6	-	-	8
Soil conditioning*	10	1	14	24	7
Litter manipulation	7	6	3	5	6
Non-native removal plus native addition	8	-	-	-	4
Time series†	-	9	6	-	4
Hand-pollination	3	-	-	-	2

* non-natives, and in some cases natives, were grown in sterilized soil for a set time, removed, and soil was subsequently with natives; growth was compared to natives grown in unconditioned soil and/or soil conditioned by conspecific natives

† response variables monitored as non-native species abundance increased over time

Table 2.4. Experimental length and units of impact experiments by ecological impact level and combined. Values are percent of *n*.

Experiment duration	Individual species (*n* = 362)	Community structure (*n* = 241)	Ecosystem properties (*n* = 72)	Ecosystem processes (*n* = 21)	All experiments (*n* = 696)
< 1 year	57	15	22	24	38
1-3 years	25	40	32	43	31
3-5 years	15	23	40	33	21
> 5 years	3	22	6	-	10
Experimental units					
< $1m^2$	63	33	30	52	49
1- $10m^2$	36	62	57	29	47
10- $100m^2$	1	5	13	19	4

Table 2.5. Impacts of non-native plants on individual species variables. Cell values are percent of experiments within each response variable (% of row total). Impacts are designated as ↓ (decrease), ↑ (increase), and Ø (no effect) at the $P < 0.05$ significance level. Columns with multiple symbols were multifactor experiments in which the impact of the non-native plant varied, either in direction or magnitude, as a function of an additional factor (exps = experiments, germ = germination, # = number).

Response variable	Impacts with no interactions			Impacts with significant interactions					Total # of exps (# of multifactor exps)
	↓	Ø	↑	↓ Ø	↓↓	↑ Ø	↑↑	↑↓	
Forb growth	35	45	10	9	-	1	-	-	80 (42)
Forb reproduction	33	47	4	14	-	-	-	2	55 (29)
Grass growth	28	60	8	4	-	-	-	-	50 (16)
Tree growth	44	32	10	7	5	-	2	-	41 (11)
Forb survival	22	74	-	-	-	4	-	-	27 (22)
Forb germ/establishment	32	60	-	8	-	-	-	-	25 (14)
Grass survival	26	69	-	5	-	-	-	-	19 (7)
Pollinator visits	33	40	16	7	-	7	-	-	15 (9)
Grass reproduction	67	17	8	8	-	-	-	-	12 (3)
Tree survival	50	42	-	8	-	-	-	-	12 (4)
Shrub growth/reproduction	33	33	17	17	-	-	-	-	6 (4)
Arthropod fitness	40	20	40	-	-	-	-	-	5 (0)
Grass germ/establishment	-	80	-	-	20	-	-	-	5 (1)
Mycorrhizal associations	60	20	-	20	-	-	-	-	5 (2)
Shrub germ/establishment	-	75	25	-	-	-	-	-	4 (4)
Consumer activity	-	-	-	-	-	-	100	-	1 (1)
Total # of experiments									362 (169)

Response totals	$n = 325$			$n = 37$				
	↓	Ø	↑	↓ Ø	↓↓	↑ Ø	↑↑	↑↓
Percent of *n*	36	56	8	76	8	8	5	3

Table 2.6. Impacts of non-native plants on community structure variables. Cell values are percent of experiments within the response variable (% of row total). Impacts are designated as ↓ (decrease), ↑ (increase), and Ø (no effect) at the $P < 0.05$ significance level. Columns with multiple symbols were multifactor experiments in which the impact of the non-native plant varied, either in direction or magnitude, as a function of an additional factor. Impacts on species composition are separate because this variable cannot increase or decrease, but only be significantly different from a reference community (exps = experiments, # = number).

Response variable	Impacts with no interactions			Impacts with significant interactions				Total # of exps (# of multifactor exps)
	↓	Ø	↑	↓Ø	↓↓	↑Ø	↑↑	
Grass/forb abundance	31	40	10	4	9	3	3	58 (42)
Grass/forb richness	33	51	4	8	2	-	2	49 (37)
Arthropod abundance	22	44	19	15	-	-	-	41 (17)
Grass/forb diversity	33	48	6	10	-	-	3	33 (20)
Arthropod richness	14	43	43	-	-	-	-	7 (1)
Animal abundance	14	57	29	-	-	-	-	7 (0)
Shrub/tree abundance	50	33	-	-	-	-	17	6 (2)
Arthropod diversity	33	50	17	-	-	-	-	6 (0)
Microbe abundance	-	20	20	20	-	40	-	5 (3)
Microbe richness	-	67	33	-	-	-	-	3 (1)
Mycorrhizal abundance	-	100	-	-	-	-	-	3 (1)
Shrub/tree richness	-	100	-	-	-	-	-	2 (1)
Species composition	sig diff		Ø	sig diff/ Ø				
Plant	60		40	-				10 (2)
Arthropod	50		38	12				8 (1)
Microbe	100		-	-				3 (1)
Total # of experiments								241 (129)
Response totals	n = 209			n = 32				
	↓	Ø	↑	↓Ø	↓↓	↑Ø	↑↑	
Percent of n	29	49	13	50	19	13	16	
Composition	sig diff		Ø	sig diff/ Ø (varied)				
Percent of n	6		3	2				

Table 2.7. Impacts of non-native plants on ecosystem properties and processes. Cell values are percent of experiments within the response variable (% of row total). Impacts are designated as ↓ (decrease), ↑ (increase), and Ø (no effect) at the $P < 0.05$ significance level. Columns with multiple symbols were experiments in which the impact of the non-native plant varied, either in direction or magnitude, as a function of an additional factor (exps = experiments, # = number).

Response variable	Impacts with no interactions			Impacts with significant interactions		Total # of exps (# of multifactor exps)
	↓	Ø	↑	↓Ø	↑ Ø	
Soil H_2O	9	46	18	9	18	11 (10)
N mineralization	-	82	9	9	-	11 (4)
Soil N	-	70	10	20	-	10 (5)
NO_3^-	11	67	22	-	-	9 (2)
NH_4^+	-	75	25	-	-	8 (2)
Soil temperature	40	20	20	20	-	5 (3)
N nitrification	-	60	20	-	20	5 (2)
Soil C	-	60	20	-	20	5 (2)
Soil organic matter	20	60	20	-	-	5 (0)
Light	75	-	25	-	-	4 (4)
Litter	-	25	25	25	25	4 (2)
Soil P	-	100	-	-	-	4 (0)
Decomposition	-	33	67	-	-	3 (0)
Soil pH	-	33	67	-	-	3 (0)
Air temperature	100	-	-	-	-	2 (1)
Relative humidity	-	-	100	-	-	1 (0)
C flux	-	-	100	-	-	1 (0)
N uptake	100	-	-	-	-	1 (0)
Leaf area index (LAI)	-	-	100	-	-	1 (0)
Total # of experiments						93 (37)
Response totals	*n* = 82			*n* = 11		
	↓	Ø	↑	↓Ø	↑ Ø	
Percent of *n*	13	61	26	55	45	

Table 2.8. Impact findings for response variables examined in multiple studies. (-) = significant decrease, (+) = significant increase, ne = no effect, followed by the number of studies that found this result.

Species	Response variables and impact findings
A. platanoides	Tree growth: (-) 2, ne 2
A. petiolata	Forb growth: (-) 2; Forb survival: (-) 1, ne 1; Mycorrhizae: (-) 1, ne 1; Tree growth: (-) 2, ne 2
Carpobrotus spp.	Forb reproduction: (-) 1, ne 1
C. maculosa	Grass growth: (-) 1, (+) 1, ne 1
E. esula	Grass growth: (-) 1, ne 1
I. glandulifera	Pollinator visits to native: (-) 1, ne 1; Plant diversity: (-) 1, ne 1; Plant richness: (-) 1, ne 1
L. camara	Plant richness: (-) 1, ne 1; Tree abundance: (-) 2, (+) 1, ne 2
L. maackii	Forb growth: (-) 1, ne 1; Forb reproduction: (-) 3, (+) 1, ne 2; Forb survival: (-) 1, (+) 1, ne 1
L. salicaria	Forb growth: (-) 1, ne 1
M. vimineum	Nutrient cycling: (-) 1, (+) 1, ne 2 ; Soil nutrients: (+) 1, ne 1; Plant diversity: (-) 3, ne 2; Plant richness: (-) 3, ne 1
Rhamnus frangula	Plant abundance: (-) 1, ne 2; Plant richness: ne 2
Taraxacum officinale	Pollinator visits: (-) 1, ne 1; Forb reproductions: (-) 3, (+) 1, ne 1

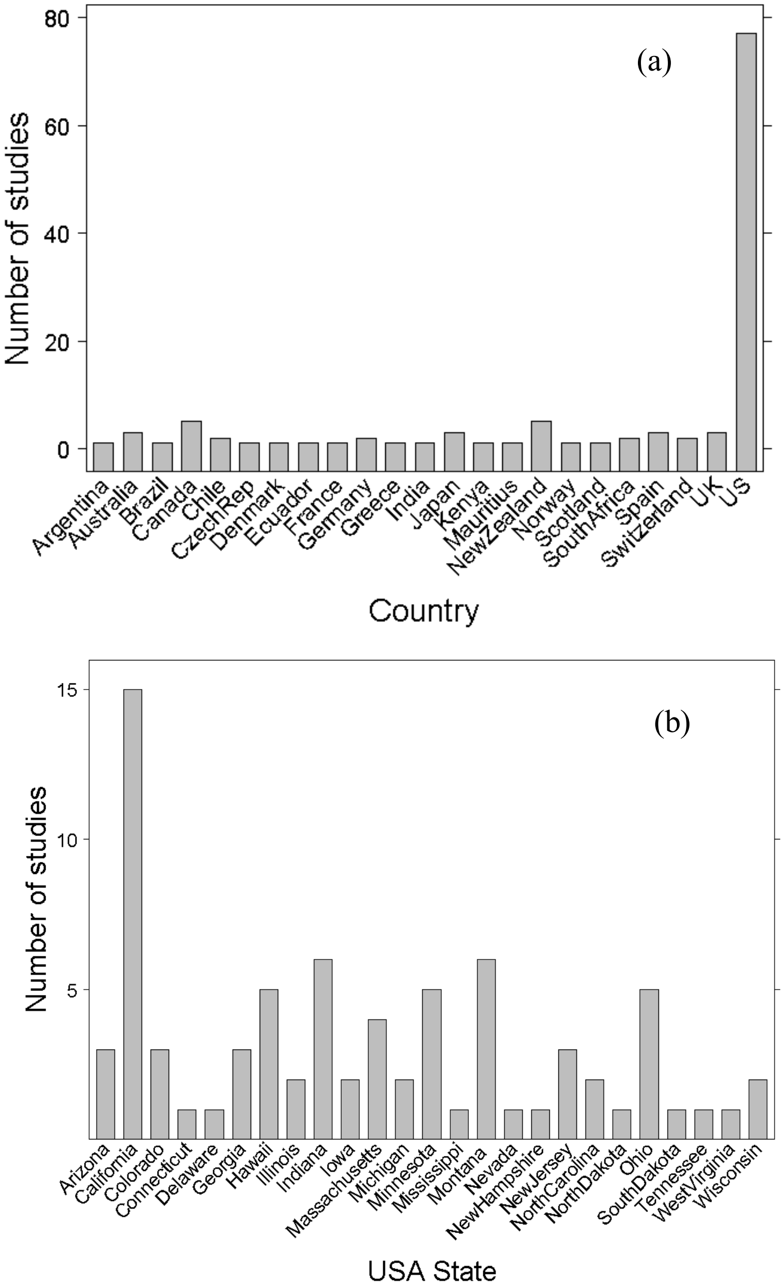

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Figure 2.1. Impact studies by (a) country (*n* = 119) and (b) USA state (*n* = 77).

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CHAPTER THREE

MECHANISMS UNDERLYING NON-NATIVE PLANT IMPACTS: A REVIEW OF RECENT EXPERIMENTAL RESEARCH

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

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Abstract

Non-native plants affect individual species, communities and ecosystems through direct and indirect mechanisms. Examining these causal processes informs our understanding of species interactions and enables a more targeted approach to non-native plant management. We synthesized the significant advances that have been made in understanding the mechanisms underlying non-native plant impacts based on a review of recent experimental research. Approximately half of experimental non-native plant impact studies conducted during the past decade included explicit tests of potential mechanisms. Contrary to common assumptions, non-native plants typically caused impacts by modifying the environment, such as light, temperature and the quantity and quality of litter, rather than by competing for resources. The integration of non-native plants into native plant-pollinator networks was frequently examined, but outcomes varied among studies. Although manual application of non-native pollen to native flowers typically reduced native plant reproduction, this amount of non-native pollen was rarely found under field conditions. Alteration of belowground communities by non-native plants was a driver of impacts on soil properties, native plant growth and invertebrate populations. Experimental results provided some support for allelopathy and apparent competition, but also indicated that other suppressive mechanisms may be operating simultaneously. The consequences of altered ecosystem processes for individuals and communities were rarely examined despite widespread recognition of this research need. Experimental mechanisms research improves the ability to predict and respond effectively to non-native plant establishment, and disturbance more generally. The

increasing trend of this type of research is a hopeful sign that these advances will continue.

Keywords: Non-native plants; invasive plant species; ecological impacts; mechanisms of impact; competition; synthesis; experimental research

Introduction

Non-native plant establishment has led to undesirable ecological changes worldwide, impacting the growth and fitness of native species, the abundance and diversity of plant and animal communities, and the structure and function of ecosystems (Simberloff 2011; Vilà et al. 2011). Responding to non-native plant establishment is generally motivated by the desire to restore and maintain viable native populations, quality habitat and functional ecosystems. Critical to these efforts, as well as to predicting the response of communities to future invasions, is an understanding of the mechanisms underlying non-native plant impacts (Levine et al. 2003; Seabloom et al. 2003). Examining the processes by which non-native plants exert impacts informs our understanding of species interactions and the linkages between species and the environment. This process of examination can reveal thresholds of population viability and ecosystem function. Thus, there is much to be gained by focusing attention on the means by which non-native plants affect individual species, community structure and ecosystem properties and processes.

The utility of understanding the mechanisms of non-native plant impacts has motivated many hypotheses and conceptual frameworks. The most familiar mechanism of non-native plant impacts is direct competition for resources such as water, nutrients, space and pollinators (e.g. Dyer and Rice 1999; Vilà and Weiner 2004; Traveset and Richardson 2006). However, many indirect pathways have been proposed as well. Impacts may arise via allelopathy, whereby non-native plants release secondary chemical compounds that are detrimental to neighboring plants and soil microbial communities (Wardle et al. 1998; Hierro and Callaway 2003). Non-native plants can affect the individual fitness and population dynamics of other organisms by increasing the occurrence of predation, herbivory or disease (‘apparent competition’) (White et al. 2006) and by modifying the physical environment (e.g. moisture, temperature, light, space) (D'Antonio et al. 1998; Crooks 2002). Furthermore, impacts may derive from altered soil communities that can result from non-native plant establishment. The composition and abundance of soil organisms is, in part, determined by the quantity, quality and timing of plant inputs to the soil (e.g., litter, root exudates), which vary as a function of plant physiology, morphology and phenology (Wardle et al. 2004; van der Putten et al. 2007). Soil organisms have a widespread influence on ecosystems--mineralizing nutrients, decomposing organic matter, fixing nitrogen (N), aerating and aggregating soils and forming symbiotic relationships with plant roots (Wolfe and Klironomos 2005). Because of the many linkages and feedbacks between above- and belowground biota (Wardle et al. 2004), the effects of non-native plants on belowground communities may underlie impacts on the fitness and abundance of individual organisms, diversity and composition of communities and fundamental ecosystem processes (Bever et al. 1997; Balser et al. 2002; Callaway et al. 2003; Ehrenfeld 2003; Wolfe and Klironomos 2005).

Non-native plant impacts, and the potential mechanisms underlying these impacts, have been the focus of a substantial body of research. However, previous reviews have found mechanisms were largely predicated on observational studies, leaving causal links between plant invasion and ecological impacts equivocal (Levine et al. 2003; Didham et al. 2005). Additionally, general perceptions of how non-native plants exert impacts have, in part, been shaped by a small number of unique examples, such as ecosystem processes being altered by introduced N-fixing species in areas with low natural nutrient-levels and a lack of N-fixers, (e.g. *Myrica* in Hawaii (Vitousek et al. 1987)) or low nutrients and infrequent N-fixers (e.g. *Acacia* in South African Cape fynbos (Witkowski 1991)). Mechanistic pathways are relatively clear in these contexts. However, this is not the norm for most non-native plant species (Levine et al. 2003), making these cases inapplicable to most management scenarios. Therefore, a better understanding of underlying mechanisms can help address practical, as well as conceptual, problems related to the establishment and impacts of non-native plants.

Experimental research examining mechanisms has increased rapidly over the past decade (Figure 3.1) and significant progress has been made since the review by Levine et al. (2003). Our objectives in this review were to describe recent research that has explicitly tested potential mechanisms of non-native plant impacts and synthesize the current state of knowledge as evidenced by experimental results. This assessment highlights biotic and abiotic relationships influenced by non-native plants and reveals sensitivities and tolerances of these relationships that may apply to natural and anthropogenic disturbances more generally.

Literature Search

We searched for non-native plant impacts literature published in English between 2001 and April 2011 using ISI Web of Knowledge, EBSCO Academic Search Premier, CSA Illumina, and Elsevier ScienceDirect literature databases and the following search term combinations: (alien OR exotic OR introduced or invas* OR non-indigenous OR non-native) AND (alter OR effect OR impact OR influence) AND (forb OR grass OR plant* OR shrub OR tree). To establish a more comprehensive search, we also examined references within the publications located through the electronic searches. We examined studies published from 2001 onwards in order to focus on progress made since the review by Levine et al. (2003), which examined studies up to 2001. Our initial search generated approximately 500 publications concerning the impacts of non-native plants.

Each publication resulting from the literature search was examined for potential inclusion in this review, dependent upon the use of an experimental approach to explicitly test a potential mechanism(s) underlying non-native plant impacts. A prerequisite to this requirement was that the study quantified some type of non-native plant impact(s). We put no restrictions on non-native plant species or growth forms, impact metrics, study locations or systems, or experimental methods. We included studies that examined impacts of multiple non-native species, as well as those that assessed impacts on multiple response variables, including multiple target species. We included allelopathic studies if impacts of the whole plant could be discerned; thus, we did not include experiments that used manual application of root extracts or synthetically derived phytotoxins. In order to synthesize empirical evidence of mechanisms underlying non-native plant impacts, we did not include observational (e.g. site-comparisons), anecdotal, theoretical, or purely modeling-based studies, nor did we include other reviews. However, we did include non-manipulative repeated-measures studies that quantified how community properties changed over time as a non-native plant increased in abundance.

Experimental Studies of Mechanisms Underlying Non-Native Plant Impacts

We identified 58 studies published between 2001 and April 2011 that experimentally tested mechanisms of non-native plant impacts. This was 49% of the total pool of experimental impact studies from this time span that fit our criteria (*n* = 119). The majority of studies examined mechanisms of impact on individual species (43 studies) with most focused on impacts on plants, but several studies focused on impacts on pollinator species and soil organisms. Impacts on community structure were examined in 15 studies: experiments were divided nearly evenly between those that quantified impacts on the abundance, richness, diversity and composition of plant communities and those that measured the same variables but for arthropod communities. Potential mechanisms underlying impacts on ecosystem properties and processes (e.g. nutrient concentrations, N mineralization) were examined in five studies. Additionally, five studies quantified impacts on multiple ecological levels, typically a combination of individual species and community property response variables.

Most studies involved multiple experiments (e.g. the impact of different non-native plant species, and/or impact on different response variables). We evaluated all unique non-native species, target species and response variable combinations; thus, the

58 studies comprised 273 distinct experiments. Some evidence of impacts was found in 85% of the reviewed mechanism studies, meaning that at least one experiment in these studies had a significant outcome ($p < 0.05$). In terms of individual experiments, 56% had significant outcomes, with the majority (80%) of results being reductions in the response variable (or a significant difference, in the case of species composition).

Non-native plant additions and removals, competition experiments (mesocosms, constructed communities) and hand-pollination were the most common experimental methods used to test potential mechanisms of impact. A total of 49 non-native plant species were examined, 11 of which were in multiple studies (Table 3.1). Only four N-fixing non-native species were studied and only three in relation to impacts on soil nutrient cycling and availability. Thus, recent research was not disproportionately focused on N-fixing non-native species, as was the case in earlier mechanisms research (Levine et al. 2003).

Mechanisms of Impact

We identified 14 mechanisms of impact examined among the 58 reviewed studies (Table 3.1). Many studies examined multiple potential mechanisms, none of which are mutually exclusive. One category (competition for soil resources versus non-trophic interactions) overlaps with several other categories; but identifies studies that attempted to distinguish impacts caused by resource competition from those caused by non-trophic interactions (e.g. habitat modification). Thus, the six studies in this category are all in at least one additional category (details below).

Altered Plant-Pollinator Interactions

Alteration of native plant-pollinator interactions was the most frequently investigated mechanism of non-native plant impacts, examined in 20 studies. There are two general ways in which native plant fitness and reproduction can be affected through this mechanism. First, the number of pollinator visits to native plants may be reduced if non-native plants are more attractive or rewarding than native plants (pollinator siphoning) (Rathcke 1983). Second, successful pollination of native flowers may be reduced if the presence of non-native plants leads to the transfer of less conspecific pollen and/or more heterospecific pollen to native plant stigmas (Waser and Fugate 1986). Reduced native plant seed set, reduced native plant population growth, and changes in native plant genetic structure are potential outcomes of these altered plant-pollinator relationships (Traveset and Richardson 2006; Bjerknes et al. 2007).

Results from the plant-pollinator interaction experiments reflect the variability, both in magnitude and direction, characteristic of invasive plant impacts more generally (Vilà et al. 2011). Four studies found no effect on pollinator visits or native seed set (Aigner 2004, Cariveau and Norton 2009, Kaiser-Bunbury and Müller 2009, Bartomeus et al. 2010), one study each found: increased visits and decreased seed set (Flanagan et al. 2010), increased visits and no effect on seed set (Nielsen et al. 2008), decreased visits and no effect on seed set (Totland et al. 2006), and decreased seed set, but no report on pollinator visits (Takakura et al. 2009). Five studies found decreased visits and decreased seed set (Chittka and Schurkens 2001, Brown et al. 2002, Muñoz and Cavieres 2008, Kandori et al. 2009, McKinney and Goodell 2010). Of those that found both decreased visits and reduced native plant reproduction, one found this effect only at high non-native plant densities (Muñoz and Cavieres 2008), and another only with whole non-native plant removal but not flower-only removal, indicating an underlying mechanism other than reproductive interference (McKinney and Goodell 2010). Lopezaraiza-Mikel et al. (2007) found that non-native plants led to greater pollinator abundance, richness and visits to native plants, but effects on native plant fecundity were not reported. Another seven studies (one of which is also mentioned above) were hand-pollination experiments in which non-native plant pollen, or mixtures of non-native and native plant pollen, was manually applied to native flowers (Moragues and Traveset 2005, Jakobsson et al. 2008, Nielsen et al. 2008, Montgomery 2009, Tscheulin et al. 2009, Matsumoto et al. 2010, Da Silva and Sargent 2011). Of these, six resulted in significantly reduced native seed set. However, five concluded, through other experiments or observations, that native plant reproduction was not significantly threatened because the quantity of non-native pollen required for interference was not found on native flowers under normal field conditions, or because the native plants were not pollen-limited in the field (Moragues and Traveset 2005, Jakobsson et al. 2008, Nielsen et al. 2008, Montgomery 2009, Da Silva and Sargent 2011). Details of plant-pollinator impact studies are provided in Appendix D.

Even within one species, mechanistic links between non-native plants and impacts on plant-pollinator interactions were quite variable. For example, the non-native annual forb *Impatiens glandulifera* did not affect pollinator visits to or reproduction of a co-occurring native forb in one case (Bartomeus et al. 2010), yet those same variables were significantly reduced by the presence of *I. glandulifera* for a different co-occurring native forb (Chittka and Schurkens 2001), whereas in a third case, pollinator abundance, richness and visits to co-occurring natives all increased in the presence of *I. glandulifera* (Lopezaraiza-Mikel et al. 2007). However, some consistent patterns were also observed, as in the case of the non-native perennial forb *Taraxacum officinale*. As an introduced species in Japan, it is considered detrimental to the native co-occurring congener *T. japonicum*. Reproductive interference by *T. officinale* was identified as the mechanism underlying the reduced seed set of *T. japonicum* in three separate studies: a field potted-plant assemblage experiment (Kandori et al. 2009), a *T. officinale* flower-removal experiment (Takakura et al. 2009) and a hand-pollination experiment (Matsumoto et al. 2010). In a very different habitat (Chilean alpine) where *T. officinale* is also an introduced species, pollinator visits to and reproduction of two co-occurring forbs were reduced, although only at high *T. officinale* density (Muñoz and Cavieres 2008).

The effect of non-native plants on plant-pollinator networks can also underlie increases in pollinator and native plant populations. For example, by enhancing resource availability (e.g. food, habitat), the presence of non-native plants can help sustain larger pollinator populations, which can, in turn, increase native plant reproduction and population growth (Bjerknes et al. 2007, and references therein). More directly, non-native plants can act as “magnet” species, attracting more pollinators to an area, which can increase pollinator visits to native plants, and potentially increase native plant reproduction (Thomson 1978; Bjerknes et al. 2007). As previously mentioned, Lopezaraiza-Mikel et al. (2007) found this effect with *I. glandulifera*, the presence of which led to significant increases in pollinator richness and abundance, as well as significant increases in the number of pollinator visits to native plants. The plant-pollinator network in areas with *I. glandulifera* was dominated by non-native pollen, which may negate the potential positive effect of increased pollinator visits if non-native pollen interferes with successful pollination of native flowers. However, field observations revealed inconsequential amounts of non-native pollen on native plant stigmas (Lopezaraiza-Mikel et al. 2007). Nielsen et al. (2008) also identified a magnet effect, finding significantly more pollinator visits to *Mimulus guttatus* (a naturalized species in Europe) when planted in stands of the invasive, non-native perennial forb *Heracleum mantegazzianum*. Although manual application of non-native pollen decreased seed set of *M. guttatus*, this effect was not measurable under field conditions; thus, they concluded there was little evidence that *H. mantegazzianum* threatened co-occurring plant species through reproductive interference. Furthermore, based on the increased pollinator abundance, Nielsen et al. (2008) suggest that the presence of *H. mantegazzianum* may counteract the general decline of pollinator populations, particularly in abandoned grasslands. Thus, *H. mantegazzianum* removal could have negative ecological consequences. Nevertheless, magnet effects are not always beneficial. Flanagan et al. (2010) found that the non-native forb *Lythrum salicaria* increased pollinator visits to the co-flowering native *Mimulus ringens*. However, *M. ringens* seed set was significantly reduced, indicating that the mechanism of impact was decreased quality of pollinator services via increased heterospecific and/or decreased conspecific pollen deposition on native flowers.

The variable effects of non-native plants on native plant-pollinator interactions are, in part, a function of the degree of similarity between native and non-native plant species. Pollinator siphoning and reproductive interference are more likely when flower morphology and phenology of non-native plants are similar to those of native plants. Non-overlapping flowering times preclude competition for pollinators and dissimilar flower structures may inhibit deposition of non-native pollen on native plant stigmas (Bjerknes et al. 2007). The abundance and spatial distribution of native and non-native plants are also important determinants of whether non-native plants will negatively affect native plant-pollinator interactions (Muñoz and Cavieres 2008, Flanagan et al. 2010).

Taken together, these studies show that while non-native plants often become well-integrated into plant-pollinator networks, altered native plant-pollinator interactions are not a consistent mechanism of impact. Of the 13 studies that examined the effect of non-native plants on pollinator behavior, visits to native plants decreased in five, increased in three, and had no effect in the remaining five. Similar inconsistencies were found with reproductive interference: native plant reproduction was reduced in approximately 56% of cases, but unaffected in the other 43%. Additionally, half of the cases of reduced reproduction were the result of hand-pollination experiments, which typically did not reflect pollen load under natural field conditions. The significance of this mechanism is context-specific, varying as a function of the traits, abundance and distribution of plants and pollinators. Experimental results indicate that many native plant populations are robust to reproductive interference. Several studies highlighted the need for additional research on how plant density (native and non-native) and spatial and temporal scale influence the effect of altered plant-pollinator interactions on native plant fitness. Like most species interactions, the outcome of non-native plants embedding in native plant-pollinator networks is a function of the intensity and duration of interactions. Thus, long-term studies may be necessary to reveal the ultimate consequences for native populations and communities.

Altered Abiotic Environment

Alteration of the abiotic environment is a primary indirect means by which non-native plants can exert biotic and abiotic impacts (Crooks 2002). The morphology, productivity, architecture and spatial distribution of non-native plants, particularly non-native plant litter, can affect microclimate conditions, such as understory light availability, soil moisture and soil temperature. These changes in abiotic conditions can affect individual species survival and fitness, as well as community structure and ecosystem processes (e.g. nutrient cycling, decomposition). For example, non-native plants often produce greater quantities of and different quality (e.g. C:N ratio, tissue lignin concentration) litter relative to native plants. The introduced litter can inhibit germination and establishment of native plants, promote fungal pathogens or alter soil chemistry to the detriment of native species (Belnap and Phillips 2001; Evans et al. 2001; Mack and D'Antonio 2003).

The results of recent experimental research substantiated altered environmental conditions as an important mechanism underlying non-native plant impacts (Table 3.1). For example, Jäger et al. (2009) determined that the non-native tree *Cinchona pubescens* substantially altered conditions in the formerly treeless fern-sedge highlands of the

Galápagos Islands to the detriment of native plant species. Over the course of a seven year experiment, Jäger et al. (2009) found that *C. pubescens* increased precipitation (through increased fog interception) and reduced air and soil temperature, light and relative humidity, and these changes led to significant reductions in native plant cover and diversity. The non-native grass *Phragmites australis* also altered the physical environment to the detriment of native plants (Minchinton et al. 2006). The results of a 3-year manipulation experiment in a coastal marsh in southern New England, USA indicated that native forb establishment and survival were significantly reduced due to light limitation and physical obstruction by *P. australis* litter and shoots. Notably, the native forbs that did survive in *P. australis* stands grew larger and produced more seeds than those growing in adjacent native-dominated stands.

Changes in the abiotic environment have also been found to underlie non-native plant impacts on other trophic levels. Pawson et al. (2010) found that establishment of the non-native conifer *Pinus nigra* in disturbed grasslands of New Zealand significantly altered light availability to the detriment of many arthropod species. Impacts were strongly density-dependent, but mid- to high-densities of *P. nigra* led to significant reductions in the abundance of 6 of 15 arthropod classes and a substantially different composition of arthropod species. Although the establishment of *P. nigra* was associated with reduced soil moisture, the primary mechanism of *P. nigra* impact on invertebrate assemblages was more likely the lower light intensity caused by increased canopy cover (Pawson et al. 2010).

The effect of altered abiotic conditions on invertebrate communities was also considered for the non-native grass *Microstegium vimineum*. Simao et al. (2010) tested light availability, biomass quantity, vegetation height and native plant richness as potential mechanisms of *M. vimineum* impact in a 3-year constructed community experiment in southern Indiana, USA. The abundance of two out of four arthropod groups, as well as overall arthropod richness, were significantly reduced and species composition was significantly altered (increased ratio of herbivores to carnivores). Results indicated that the reduced native plant richness accompanying *M. vimineum* establishment was the underlying driver of these impacts. Relative to native plants in this community, *M. vimineum* provides less variety and complexity of plant structures, which translates to fewer arthropod food sources and habitat and, therefore, reduced arthropod abundance and richness (Simao et al. 2010).

In some cases, the effect of non-native plants on the abiotic environment can lead to an increase in native species and community properties. In the xeric coastal-scrub ecosystems of southern California, Wolkovich (2010) found, through litter addition and removal experiments, that litter of the non-native C_3 annual grasses *Avena barbata*, *Brachypodium distachyon* and *Bromus madritensis* spp. *rubens* increased soil moisture. This abiotic change increased native shrub growth (*Artemisia californica*), leading to an increase in overall arthropod richness and grazing arthropod abundance, as well as a significant shift in arthropod composition. Non-native litter affected the quantity of native shrub biomass, but did not affect the quality of native plant material (i.e. percentage N of leaf tissue), which was also a hypothesized mechanism of non-native annual grass impact on arthropod abundance (Wolkovich 2010).

In addition to the pollinator siphoning effect discussed earlier, pollinator behavior can also be modified as a result of the abiotic conditions created by non-native plants. McKinney and Goodell (2010) investigated this alternative mechanism of impact for the non-native shrub *Lonicera maackii*. By using an experimental design that eliminated the possibility of soil resource competition and isolated pollinator- and shade-mediated effects, McKinney and Goodell (2010) determined that native forbs experienced reduced pollinator visits and seed set in the presence of *L. maackii*, but not due to pollinator siphoning. Rather, overstory shading from *L. maackii* altered pollinator behavior, which subsequently reduced native plant reproduction.

In addition to numerous biotic impacts, alteration of the abiotic environment by non-native plants can also lead to impacts on ecosystem processes and nutrient availability. Mack and D’Antonio (2003) considered this mechanism in systems invaded by the non-native perennial C_4 grasses *Schizachyrium condensatum*, *Melinis minutiflora*, and *Andropogon virginicus*. In seasonal submontane woodlands of Hawai’i where grasses were historically rare, they quantified changes in soil moisture, temperature, N, carbon (C) and the C:N ratio of soil organic matter (SOM). The results of a four-year removal experiment showed that N mineralization rates were significantly reduced by non-native grasses and that this impact was driven by altered microclimate conditions (i.e. higher soil moisture and lower soil temperature) and increased C:N ratio of SOM. The soil property changes varied depending on the season (wet versus dry) and plant community composition. Farrer and Goldberg (2009) also identified altered abiotic conditions as the mechanism underlying impacts on ecosystem properties and processes by the non-native perennial forb *Typha* X *glauca*. NH_4^+ and N-mineralization rates were significantly increased in a Great Lakes coastal marsh in northern Michigan, USA due to the quantity and quality of *T.* X *glauca* litter.

The synthesis of these studies substantiates alteration of abiotic conditions as an important process driving non-native plants impacts, supported in 16 of the 19 studies that examined this mechanism. Non-native plant litter was a significant driver of impacts, supported in all eight studies in which it was examined. Whether due to litter dynamics or other factors, altered temperature and light availability were consequential effects of non-native plants, supported in 100% and 83%, respectively, of experiments that examined these mechanisms. Altered soil water was much less influential, supported in only 36% of the experiments that tested this mechanism of impact.

Resource Competition versus Non-Trophic Interactions

A number of recent studies attempted to distinguish impacts caused by resource competition between native and non-native plants from those caused by non-trophic interactions. This distinction derives from the recognition of two general models of plant community interactions. The first is a highly interactive community in which a dominant species has superior access to limiting resources and actively suppresses or excludes subordinate species by drawing down resources to levels injurious or intolerable to co-occurring species (Tilman 1990; MacDougall and Turkington 2005). In the alternative, weakly interactive community, impacts arise because non-native plants modify the environment in ways that are detrimental to native organisms or simply because the non-native plants are less affected by disturbances and thus gain dominance by default, not superior competitive ability (Grime 2001; Seabloom et al. 2003; MacDougall and Turkington 2005).

There was minimal evidence of direct competition for nutrients or water between native and non-native plants in recent experimental research. For example, MacDougall and Turkington (2005) examined impacts, as well as potential mechanisms underlying impacts, of the non-native perennial grasses *Poa pratensis* and *Dactylis glomerata* on native plant growth. By comparing the response of native forbs to the removal of both above- and belowground non-native plant biomass with the response to removal of only aboveground non-native plant biomass, they determined that negative impacts on native plant species were the result of reduced access to light rather than competition for soil resources. They concluded this based on equivalent growth responses to the two removal treatments, reasoning that competition for light as well as soil resources would have resulted in a greater (additive) native growth response to the removal of all biomass (above- and belowground) relative to removal of aboveground only. It is worth noting that impacts were species-specific: 45 plant species increased in cover in response to non-native plant removals; however, another 36 species showed no change or decreased significantly in cover in the absence of non-native grass biomass (MacDougall and Turkington 2005).

Coleman and Levine (2007) also examined trophic versus non-trophic interactions, here with respect to impacts of the non-native annual grasses *Bromus* *hordeaceus*, *B. diandrus*, *B. madritensis*, and *Avena barbata* on native forbs in coastal-scrub habitats of southern California, USA. Factorial removals of live non-native grass biomass and non-native grass litter were crossed with water addition treatments. Both live plant removal and litter removal treatments resulted in significant increases in native forb cover; however, the responses did not change with the addition of water, indicating that non-native plants were not competing with natives for water. Rather, shading by live non-native grasses and interference by non-native grass litter caused the reduction in native plant growth (Coleman and Levine 2007).

The experiments of Davis et al. (2005) also did not support direct competition as a mechanism of non-native plant impacts. The results of an old-field competition experiment in Minnesota showed that the non-native perennial grasses *Bromus inermis*, *P. pratensis* and *Phleum pratense* reduced native tree seedling growth and survival, but that these impacts were not driven by competition for light, soil water, NH_3, or NH_4. Rather, Davis et al. (2005) concluded that the impacts derived from some other modification to the soil environment.

Non-trophic, rather than competitive, interactions were also the mechanism underlying impacts of *T.* X *glauca* in wetlands (Farrer and Goldberg 2009). Native plant density and diversity were reduced, and composition altered, with the addition of *T.* X *glauca* litter, whereas the addition of live *T.* X *glauca* plants had no effect. Moreover, live *T.* X *glauca* plants did not alter the availability of soil nutrients or light, further indicating a lack of resource competition. In this system, negative plant community impacts arose either through light reduction or physical obstruction by *T.* X *glauca* litter.

As noted in the previous section, *T.* X *glauca* litter also increased soil N mineralization rates and NH_4^+, which could have implications for native plant growth. Also in a wetland environment, Hager (2004) found that native forb seedling growth was suppressed by *L. salicaria* due to reduced light penetration to the soil surface rather than altered nutrient availability. Light availability is likely reduced because of the greater aboveground biomass and broader horizontal canopy structure of *L. salicaria* relative to native vegetation (Hager 2004).

Additional support for non-trophic mechanisms comes from the multi-trophic impacts of the non-native conifers *Pseudotsuga menziesii* and *Pinus contorta* in *Nothofagus* forests of New Zealand. In a seedling transplant experiment, Dehlin et al. (2008) found that *P. menziesii* significantly reduced native tree seedling survival, and both *P. menziesii* and *P. contorta* had significant negative effects on nematode abundance and diversity. Using root trenching and fine mesh growth tubes, they determined that impacts on native tree seedlings were driven by differences in light, SOM and soil moisture in the non-native tree stands, rather than belowground competition for nutrients or suppression of mycorrhizal facilitation. Dehlin et al. (2008) further concluded that impacts on nematode communities were a consequence of lower microbial biomass, a food source for nematodes, as well as lower soil C in non-native tree stands. Through their feeding activities, soil organisms such as nematodes enhance plant-available nutrients in the soil; thus, negative impacts on tree seedlings may have resulted from lower nutrient availability due to reduced decomposer biota (Dehlin et al. 2008).

In their review of earlier non-native plant impact mechanism studies, Levine et al. (2003) reported that competition was frequently hypothesized to underlie impacts on plant community structure, but rarely was there experimental work to support or refute this assertion. As we show here, substantial efforts have been made over the last decade to rigorously test the assumption of competition. The results of recent field-based community experiments indicate that direct competition for soil resources was rarely a mechanism driving non-native plant impacts. Of the six studies that distinguished resource competition from non-trophic interactions, only one found evidence of direct resource competition (Lenz et al. 2003), whereas all six found support for non-trophic interactions. These results emphasize the overall finding from the previous section that impacts on native species and community structure typically (approximately 85% of cases) resulted from the indirect effects of altered abiotic conditions and microenvironments.

Altered Belowground Communities

The effect of non-native plants on other organisms can be a mechanism underlying impacts on ecosystem processes and properties, such as the influence of soil microorganisms on nutrient dynamics. Non-native plants can promote soil microbes, such as bacteria and fungi, as well as larger soil fauna, such as nematodes, arthropods, that are structurally and functionally dissimilar from those supported by native plants. This shift in composition may, in turn, lead to altered nutrient cycling and availability and/or reduced fitness of native species (Wolfe and Klironomos 2005; van der Putten et al. 2007). Six studies in this review examined altered belowground communities as a potential mechanism of non-native plant impacts (Kourtev et al. 2003, Hawkes et al. 2005, Stinson et al. 2006, Dehlin et al. 2008, Jordan et al. 2008, Bauer and Flory 2011), five of which found experimental support for this mechanism (Table 3.1).

Hawkes et al. (2005) examined whether the non-native annual C_3 grasses *A. barbata* and *B. hordeaceus* supported soil microbial communities that could alter nutrient cycling. A mechanistic link between belowground communities and impacts on ecosystem processes was demonstrated in a four-year constructed community experiment. Nitrification rates doubled in monocultures of non-native grasses, in part due to increased abundance and altered composition of ammonia-oxidizing bacteria. Hawkes et al. (2005) noted that these impacts could affect N budgets in grassland ecosystems because higher nitrification rates increased the potential for N loss through leaching and denitrification. However, nitrification was only affected in non-native monocultures, not in mixtures, suggesting that changes in nutrient cycling rates might not be observed in mixed species grasslands at the community level (Hawkes et al. 2005).

Kourtev et al. (2003) also examined altered soil microbial communities as a mechanism of non-native plant impacts on ecosystem properties and processes. In a soil conditioning experiment, they found that the non-native perennial shrub *Berberis thunbergii* and the non-native C_4 annual grass *M. vimineum* promoted soil microbial communities that were significantly different in structure and function than those supported by a co-occurring native species. *M. vimineum* soils exhibited increased soil pH, organic matter, and nitrification rates relative to native-conditioned soil, which, the authors suggest, may have resulted from altered microbial activity. In a different study, altered soil microbial communities did not play a role in the negative impacts of *M. vimineum* on the abundance, size and reproduction of a native woodland forb (Bauer and Flory 2011), indicating that additional mechanisms also contribute to the impacts of *M. vimineum*.

Although a number of substantial changes in nutrient cycling and soil conditions resulted from non-native plant impacts on soil communities (Hawkes et al. 2005, Kourtev et al. 2003), many soil properties were unaffected: *A. barbata* and *B. hordeaceus* did not affect soil nitrate, ammonium, moisture, pH or N mineralization (Hawkes et al. 2005), *B. thunbergii* and *M. vimineum* did not affect soil nitrate and N mineralization (Kourtev et al. 2003), and *B. thunbergii* did not affect soil pH or organic matter (Kourtev et al. 2003). These outcomes indicate a degree of resilience in some ecosystem properties and processes to changes in belowground communities. Nevertheless, studies such as these that examine impacts across multiple ecological levels are infrequent; thus, the general significance of altered plant-soil feedbacks as a driver of non-native plant impacts on ecosystem properties and processes remains uncertain. Our understanding of ecological thresholds would be well-served by future examinations of the consequences of non-native plant impacts on linkages between different ecological levels.

In addition to the potential abiotic effects, the disruption of belowground communities by non-native plants can also affect the fitness of other organisms. For example, many tree species form mutualistic associations with arbuscular mycorrhizal fungi (AMF), which promote tree growth by facilitating nutrient acquisition. Stinson et al. (2006) found that growth of three native North American hardwood tree species (*Acer* *saccharum*, *A. rubrum*, and *Fraxinus americana*) was significantly reduced when the tree seedlings were grown in soil conditioned by *Alliaria petiolata*, a non-native forb that has become widespread in hardwood forests of Midwestern and eastern USA. Experimental results demonstrated that the negative impact of *A. petiolata* on native tree seedlings resulted from a significant reduction in AMF colonization of tree roots. As described in the previous section, Dehlin et al. (2008) also demonstrated biotic impacts deriving from non-native plants affect on belowground communities. Reduced soil microbial biomass in non-native conifer stands was the mechanism underlying significant reductions in nematode abundance and diversity.

Although based on a relatively small sample size, the recent experimental evidence suggests that altered soil microbial communities may be an important mechanism by which non-native plants affect individual species, as well as ecosystem properties and processes. The findings highlight the likely importance of plant- and animal-microbial interactions and the need for further non-native plant impacts research spanning multiple trophic levels.

Allelopathy

In considering plant-plant interactions, allelopathy is one of the most common alternative hypotheses to direct competition for resources as a mechanism of non-native plant impacts. The theory holds that secondary compounds produced by non-native plants can be injurious to neighboring plants and/or the soil community either through direct toxicity or indirectly by altering the chemical environment of the soil (Wardle et al. 1998, Hierro and Callaway 2003). Allelopathy research has been criticized in the past for experimental designs that are not representative of natural conditions (Inderjit and del Moral 1997; Inderjit and Callaway 2003). To avoid this bias to the extent possible, we only reviewed studies that tested allelopathic effects of intact non-native plants; thus, excluding those that manually applied root exudates or synthetically derived phytotoxins.

Allelopathic effects were typically quantified based on the response to activated carbon (AC) additions. Because of its high affinity for organic compounds, AC is added to experimental soils to reduce potential allelopathic effects by adsorbing inhibitory compounds (Callaway and Aschehoug 2000). If allelopathy is a significant mechanism of impact, native plant growth and/or fitness should improve in AC treatments. An improvement in native plant growth in AC treatments less than that seen when native plants are grown alone indicates that non-native plants are exerting inhibitory effect other than, or in addition to, allelopathy (Mahall and Callaway 1992).

Of the seven studies that experimentally tested allelopathy as a mechanism of non-native plant impacts, five found at least some support (Table 3.1) (Ridenour and Callaway 2001, Cipollini and McClain 2008, Gomez-Aparicio and Canham 2008, Lankau 2010, Murrell et al. 2011). As with many impacts, the occurrence and strength of allelopathic effects were variable and context-specific. For example, Cipollini and McClain (2008) identified negative allelopathic effects of the non-native forb *A. petiolata* on survival and reproduction of the native forb *Impatiens capensis*. Allelopathic inhibition by *A. petiolata* also affected native tree seedlings (Lankau 2010). However, these effects only occurred in sterilized soils, suggesting that soil microbial communities may play a role in mediating impacts, and that certain microbes may inhibit the effects of allelopathic compounds. In another case, no allelopathic effects of *A. petiolata* were detected in the growth and survival of *Panax quinquefolius*, a sensitive native forb in deciduous forests of eastern USA (Wixted and McGraw 2010).

Response to allelopathy also varied among different target species. Gomez-Aparicio and Canham (2008) examined the potential allelopathic effects of the non-native deciduous tree *Ailanthus altissima* on three native deciduous tree species (*Acer rubrum*, *A. saccharum* and *Quercus rubra*) in temperate forests of northeastern USA. In a seed-sowing and seedling transplant experiment, they found that addition of AC shifted the impact of *A. altissima* on seedling growth from neutral or slightly positive to very positive for *A. rubrum*, from negative to positive for *A. saccharum*, but had no effect on the consistently negative interaction between *A. altissima* and *Q. rubra*. These results highlight the differences in susceptibility of native species to allelopathic effects. As seen with effects on plant-pollinator interactions, the strength of allelopathic effects is also a function of the density and spatial distribution of non-native plants. The allelopathic effects of *A. altissima* were proportional to *A. altissima* density and showed a sharp decrease with distance, tending to zero within 5 m from source plants (Gomez-Aparicio and Canham 2008).

Differences in susceptibility to allelopathy were also demonstrated among plant functional groups. In a greenhouse experiment, Murrell et al. (2011) found that growth of four native European forbs was significantly reduced by the allelopathic effects of the non-native hybrid perennial forb, *Fallopia* x *bohemica*. Growth of native grasses, however, was unaffected.

Direct competition and allelopathic inhibition are not mutually exclusive interactions and may operate simultaneously in some cases (Inderjit and del Moral 1997). Results from the reviewed allelopathy studies support this hypothesis. Six studies tested for, and attempted to distinguish between, allelopathic and non-allelopathic effects of non-native plants (Ridenour and Callaway 2001, Cipollini and McClain 2008, Gomez-Aparicio and Canham 2008, Lankau 2010, Wixted and McGraw 2010, Murrell et al. 2011). Five of these studies found evidence of both mechanisms operating concurrently to affect native plant growth (Table 3.1). For example, in addition to the allelopathic affects previously mentioned, Murrell et al. (2011) also tested for non-allelopathic suppressive effects of *F.* x *bohemica* on six native European plants. Factorial combinations of AC addition and *F.* x *bohemica* removal in experimental plant communities indicated that *F.* x *bohemica* reduced native forb growth through allelopathic inhibition, as well as some other type of suppressive influence. A similar experimental design implicated both allelopathic and non-allelopathic mechanisms in the negative impacts of *A. petiolata* on *I. capensis* survival and reproduction (Cipollini and McClain 2008). Although these results demonstrate non-allelopathic mechanisms of impact, the specific processes (e.g. competition for nutrients, physical interference) were not identified.

Concerns have been raised that the addition of AC can alter soil nutrient availability, thereby confounding interpretations of allelopathic effects (Inderjit and Callaway 2003; Lau et al. 2008). The results of several of the reviewed studies substantiated this concern, showing that native plant growth was affected by AC regardless of the presence of a non-native plant competitor (Cipollini et al. 2008, Wixted and McGraw 2010). In another study, a direct effect of AC could not be ruled out (Murrell et al. 2011), which may also be the case in other studies but was not measured. Clearly more research is needed on the effects of AC on soil conditions and plant growth and to what degree these effects bias interpretations of chemical inhibition by non-native plants. Furthermore, only two of the seven allelopathy studies were conducted under natural field conditions. The others were experiments in constructed communities, mostly in greenhouses, leaving uncertainty as to whether allelopathy produces biologically significant effects *in situ*.

In summary, the studies reviewed here provide some experimental support for allelopathy as a mechanism underlying non-native plant impacts on the growth and fitness of other individual plants. However, the research findings underscore that allelopathic effects, like non-native plant impacts in general, vary among different target species and growing conditions. Furthermore, other inter- and intraspecies interactions may be operating simultaneously, making it difficult to tease apart allelopathy from other suppressive effects. Experimental results confirm the potentially confounding effect of AC addition on the interpretation of allelopathy studies and highlight the need for more examinations of this mechanism under natural field conditions.

Apparent Competition

In addition to allelopathy, another indirect mechanism by which non-native plants can affect native plants is through shared predators or herbivores. Consumers may be drawn to areas where non-native plants have established because the plants offer an additional food source, habitat or refuge. The elevated consumer abundance may increase consumer pressure on native plants, driving down individual fitness and/or population growth rates, an effect known as apparent competition (Connell 1990; White et al. 2006).

Four studies investigated non-native plant impacts via apparent competition and all found at least some support for this mechanism (Lau and Strauss 2005, Meiners 2007, Orrock et al. 2008, Da Silva and Sargent 2011) (Table 3.1). In general, non-native plants increased the availability of habitat for native consumers, leading to significant increases in seed predation of native plant species. For example, in a California grassland, Lau and Strauss (2005) tested whether the non-native forb *Medicago polymorpha* affected the fitness of the native forb *Lotus wrangelianus* directly through competition and/or indirectly by increasing herbivory by several insects known to feed on both plant species. The results from two-by-two factorial removals of non-native plants and insects indicated that the presence of *M. polymorpha* reduced *L. wrangelianus* reproduction through both increased herbivory and some other type of competition. Impacts varied between years depending on herbivore abundance, highlighting temporal variability of non-native plant impacts, particularly those involving other organisms with fluctuating population dynamics.

Also in California grasslands, Orrock et al. (2008) combined small-mammal exclosures with seed additions of the native bunchgrass *Nassella pulchra* and determined that increased small-mammal activity in the presence of *Brassica nigra* led to significant reductions in establishment of the native bunchgrass. They concluded that *B. nigra* did not provide an additional food source because the seeds and foliage of the non-native plant contain deterring chemicals. Rather, *B. nigra* plants appear to provide a physical refuge for small-mammals (e.g. mice, voles, squirrels, rabbits). These findings provide one explanation for the prevalence of recruitment limitation of native plants in California grasslands and why, despite being good competitors, native plants often fail to re-establish after non-native plant control (Seabloom et al. 2003; Orrock and Witter 2010).

Increased consumer pressure was also a mechanism underlying impacts of *L. maackii* (Meiners 2007). Non-native plant removal experiments in a mesic hardwood forest of the Midwestern USA demonstrated that predation of native tree seeds by mice and chipmunks was significantly increased in the presence of *L. maackii* (Meiners 2007).

Apparent competition may be particularly detrimental for rare plant species, as was exemplified with the endangered, coastal dune forb *Lupinus tidestromii* (Dangremond et al. 2010). When grown in close proximity to the non-native perennial grass *Ammophila arenaria*, *L. tidestromii* experienced high levels of seed consumption by native rodents, which led to a significantly reduced *L. tidestromii* population growth rate. Projection models indicated that the reduced growth rate was likely to cause some populations to decline toward extinction under the non-native plant-mediated consumption levels. Altered consumption patterns and increased pressure on native plant populations have the potential to alter the landscape-scale distribution and abundance of species, which may lead to more homogeneous communities (Dangremond et al. 2010).

As with allelopathy, in natural systems apparent competition may be operating simultaneously with other types of interactions between native and non-native plants. Only one of the four apparent competition studies investigated this possibility and, as mentioned above, there was evidence of some other type of suppressive mechanism in addition to apparent competition (Lau and Strauss 2005). Overall, the available findings support apparent competition as an important mechanism of non-native plant impacts. However, additional research with other species and environments will help determine the prevalence of this mechanism and will be particularly insightful if designed to test for, and distinguish between, apparent competition and other types of suppressive interactions.

Altered Soil Nutrient Dynamics

It is well-established that some non-native plants can alter ecosystem-level properties and processes, particularly soil nutrient cycling and availability (Vitousek et al. 1987; Mack et al. 2001; Ehrenfeld 2003; Ehrenfeld 2010). Given the ubiquity of plant-soil feedbacks and multi-trophic food web interactions, altered soil nutrient dynamics have the potential to generate widespread effects for individual species, communities and ecosystems (Mack et al. 2000; Wolfe and Klironomos 2005). Nevertheless, only a few of the reviewed studies examined altered nutrient dynamics (other than the nutrient competition discussed above) as a mechanism of impact and, overall, there was limited experimental support.

As previously noted, N-fixing non-native species were examined in only three recent studies of non-native plant impacts on nutrient cycling and availability. In the naturally low-nutrient fynbos soils of South Africa, the non-native N-fixing shrub *Acacia saligna* increased soil N due to large amounts of litter with higher N concentrations than that of native plant species (Yelenik et al. 2004). This input of high-N litter resulted in more N returned to the soil and, therefore, an increase in inorganic N availability. Higher N availability was correlated with higher growth rates of the non-native grass *Ehrharta calycina*. Thus, the effect of *A. saligna* on soil nutrient dynamics was, at least in part, responsible for promoting secondary invasion by another non-native plant species. In contrast, experimental results indicated reduced light and soil moisture, rather than altered N levels, were mechanisms underlying the negative impacts of the non-native N-fixing annual forb, *Melilotus officinalis* on native grass richness, diversity, and productivity (Dickson et al. 2010). Finally, the non-native N-fixing leguminous shrub, *Cytisus scoparius*, did not affect grass growth, NH_4^+ or NO_3^- but led to increased grass reproduction in a year-long pair-wise competition experiment (Shaben and Myers 2010). Thus, only one of three studies demonstrated altered nutrient dynamics as a mechanism underlying impacts of N-fixing non-native plant species. These findings agree with a recent meta-analysis that found that N-fixing non-native plants do not exert greater impacts on community structure or ecosystem processes relative to non- N-fixing non-native species, as has often been hypothesized (Vilà et al. 2011).

Several non-N-fixing species were examined in relation to altered nutrient dynamics as a mechanism of impact; however, support was limited for these non-native species as well. In a wetland mesocosm experiment in Switzerland, Scharfy et al. (2010) found that communities that included the non-native perennial forb *Solidago gigantea* exhibited a significant decrease in soil bacterial biomass and a significant increase in soil fungal biomass. Plant-soil feedback measurements indicated that these impacts were, in part, driven by *S. gigantea* increasing soil C concentrations, which stimulated fungal growth at the expense of bacteria (Scharfy et al. 2010). However, altered nutrient dynamics were not supported as a mechanism underlying impacts of *M. vimineum* on native plant growth. In a microcosm field experiment in a Midwestern USA hardwood forest, the addition of *M. vimineum* significantly reduced the abundance, growth and reproduction of a native forest forb (Bauer and Flory 2011). However, in a subsequent greenhouse experiment, Bauer and Flory (2011) determined that these impacts did not derive from changes in soil nutrient conditions despite previous findings that *M. vimineum* can significantly alter soil N dynamics (Ehrenfeld et al. 2001).

Several other studies clearly showed that non-native plants altered nutrient dynamics, such as non-native perennial grasses in Hawaiian woodlands (Mack and D'Antonio 2003), *M. vimineum* in southeastern USA riparian wetlands (DeMeester and Richter 2010) and *T.* X *glauca* in Midwestern USA marsh wetlands (Farrer and Goldberg 2009). However, it is unknown whether these proximate changes in ecosystem processes ultimately affected other organisms or community properties. Thus, progress towards understanding the consequences of altered nutrient cycling and availability for individuals and communities has been limited despite past recognition of this knowledge gap (Levine et al. 2003). Mechanistic links between altered nutrient dynamics and impacts on individual species and community structure will be depend on species tolerances and thresholds of change in ecosystem processes (Ehrenfeld 2003), underscoring the on-going need for empirical studies that span multiple ecological levels.

Post-Disturbance Establishment

There is increasing recognition that non-native plants may be associated with changes in native plant populations and communities not because of non-native plants' ability to competitively suppress or exclude native plants, but rather by being more resilient to change and more opportunistic than native species in their response to disturbance (Seabloom et al. 2003; Young et al. 2005; Yelenik and Levine 2010). Non-native species may be better able to colonize disturbed areas due to rapid growth and high fecundity and, thus, can achieve densities much greater than those of native vegetation. In addition, native plant populations are often recruitment limited because of low fecundity, limited seed dispersal, or seed predation (Turnbull et al. 2000). As described above, non-native plant-mediated seed consumption was found to reduce the seed supply of the native bunchgrass, *N. pulcra*. Thus, despite being a strong competitor, native bunchgrass re-establishment within its habitat is limited by poor recruitment (Orrock et al. 2008). In a restoration context, MacDougall and Turkington (2005) found limited re-establishment of some native species following non-native grass removal, indicating that many native species were limited by low seed production and dispersal, rather than competitive exclusion by non-native grasses. While more field-based experiments are needed, these examples support the argument that undesirable changes to populations and communities may be the result of multiple interacting factors, not solely the establishment of non-native plants (Didham et al. 2007). Understanding and effectively responding to impacts associated with non-native plants will likely require accounting for the effects of other historical and ongoing environmental stressors.

Conclusions and Future Directions

Managing non-native plants has become a major component of biological conservation and ecosystem restoration programs. Effective and efficient non-native plant control strategies and restoration efforts require understanding the processes driving non-native plant impacts. Our review shows that attention to these processes has steadily increased during the past decade. Approximately half of experimental impacts research included explicit examinations of potential mechanisms underlying non-native plant impacts. This body of research considerably advances our understanding of how non-native plants affect individual organisms, communities and ecosystems. Additionally, these experimental mechanistic studies reveal sensitivities and tolerances of a number of ecological interactions.

Although resource competition was frequently assessed in recent non-native plant impact studies, many indirect mechanisms were examined as well, including altered plant-pollinator interactions, changes to the physical environment, allelopathic interactions and apparent competition. The relative importance of interspecific competition in the realm of non-native plant impacts has been met with uncertainty in recent years (Davis 2003; Levine et al. 2003). Thus, the widening breadth of mechanisms being explored marks an important step towards elucidating the processes underlying non-native plant impacts. Also noteworthy was the development of experimental methods that enable a distinction between impacts caused by direct competition and those resulting from non-trophic interactions.

Experimental outcomes were variable and context-specific, but most results indicated that non-native plants rarely impact individual native plants or native plant communities through competition for soil resources, such as water and nutrients. Support was much more substantial for non-trophic interactions, such as shading, altered soil moisture and physical interference, as the underlying mechanism of negative impacts. Changes in the abiotic environment often arose from non-native plant litter rather than live plants.

There was considerable support for disruption of mutualisms (plant-pollinator, plant-microbe, plant-mycorrhizal fungi) as a means by which non-native plants exert biotic impacts. The findings demonstrate the importance of multi-trophic interactions in ecological systems and indicate that relationships between plants and soil organisms may be particularly sensitive to changes brought about by non-native plants. Nevertheless, it was not uncommon for non-native plants to become integrated into native plant-pollinator networks with no significant consequences for native plant reproduction. Care must be taken in extrapolating the results of hand-pollination studies since experimental conditions were often not reflective of field conditions.

Recent experimental research indicated that allelopathy and apparent competition may be important indirect means by which non-native plants affect individuals and populations. The majority of studies that examined these mechanisms found at least some supportive evidence. However, there were also indications that other types of suppressive interactions were operating simultaneously with allelopathy and apparent competition. Results of allelopathy studies varied among target species and some results were equivocal due to the potentially confounding effects of AC and uncertainty regarding the transferability of results to natural field conditions. Studies should continue to be designed to identify, and distinguish between, allelopathic/apparent competition and other types of competitive interactions. This will help establish the relative importance of different mechanisms of impact and inform future management strategies.

We are beginning to see an increase in research that spans multiple ecological levels, which will be necessary to determine the ecosystem consequences of non-native plant establishment. The reviewed studies showed that relationships between plants and belowground organisms can be affected by non-native plants and that these altered relationships can underlie impacts on plant and invertebrate fitness, abundance and diversity. Although ecological theory supports the prediction that altered soil microbial structure and function may also underlie non-native plant impacts on ecosystem properties and processes, to date there is limited research exploring this connection. Furthermore, despite previous recognition of the research need, there were surprisingly few examinations of whether non-native plant impacts on ecosystem processes, such as nitrogen cycling, lead to impacts on individual species and communities. Experimental evidence did not support competition for soil resources as a common mechanism of impact, suggesting that non-native plant establishment does not substantially alter resource availability and/or native communities are robust to changes that do occur. Nevertheless, there remains much to be learned about the tolerances of biotic and abiotic relationships in highly interconnected natural systems.

The fact that many non-native plant impacts resulted from changes to the physical environment helps explain the variability of impacts, both in magnitude and direction, that is increasingly recognized (Vilà et al. 2011) and why some communities and ecosystems experience significant impacts and others do not. The manifestation of impacts and the relative importance of different mechanisms underlying impacts depend on a constellation of factors including characteristics of the invaded community. Thus, as noted in a number of studies, further research across a range of environments incorporating temporal variability in disturbance regimes will help determine the population- and landscape-scale effects and identify factors contributing to impact variability.

Addressing the undesirable ecological changes associated with non-native plant establishment requires integrating explicit examinations of underlying mechanisms into the quantification of non-native plant impacts. Clearly there are other possible mechanisms of non-native plant impacts that were not examined, particularly those that operate on larger spatial scales and may not be amenable to experimental methods, such as altered fire regimes. Nevertheless, this review details the current trends in mechanistic research and provides a synthesis of the most prevalent mechanisms of non-native plant impacts. Continued attention to the mechanisms of non-native plant impacts will not only benefit the implementation of natural resource management, but will also help address the broader questions of which environmental stressors are driving undesired ecological changes and what are the thresholds of functional ecological relationships and systems.

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List of Appendices

The following appendix is located at the end of this dissertation:

Appendix D. Experimental studies examining non-native plant impacts on native plant-pollinator interactions, 2001- April 2011.

Table 3.1. Mechanisms examined in experimental non-native plant impact studies (n = 58). The mechanisms as listed are not mutually exclusive; many studies examined multiple potential mechanisms. Studies are listed as having found evidence of impact (final column) if results of impact experiments were significant at $p < 0.05$. (See reference section for full citation represented by the number provided). (+) = increased, (-) = decreased, ne = no effect, ss = seed set, N = nitrogen-fixing species, hand-pollination = tested the effect of direct application of non-native plant pollen to native flowers; underlined numbers identify composite study of multiple non-native species.

Potential mechanism of non-native plant impact	Non-native species and reference number () of studies that examined this mechanism/species		Percent of studies () that found evidence of impact mechanism and references numbers
Altered plant-pollinator interactions			
Pollinator visits to native flowers (can be increases and decreases in same study, varying with density or species)	*Carpobrotus* spp. (1) *Cakile maritime* (1) *Carduus nutans* (6) *Heracleum mantegazzianum* (43) *Impatiens glandulifera* (2, 7, 31)	*Lonicera maackii* (35) *Lythrum salicaria* (5, 18) *Phacelia tanacetifolia* (54) *Psidium cattleianum* (25) *Taraxacum officinale* (26, 40)	Overall (69%) Decreased visits (46%) 5, 7, 26, 35, 40, 54 Increased visits (31%) 18, 31, 40, 43
Reproductive interference (reduced native plant reproduction due to (+) heterospecific pollen and/or (-) conspecific pollen)	Field experiments *C. maritime* (1) *C. nutans* (6) *Carpobrotus* spp. (1) *H. mantegazzianum* (43) *I. glandulifera* (2, 7) *L. maackii* (35) *L. salicaria* (5, 18) *P. tanacetifolia* (54) *P. cattleianum* (25) *T. officinale* (26, 34, 40, 53)	Hand-pollination experiments *Carpobrotus* spp. (23, 39) *Euphorbia esula* (38) *H. mantegazzianum* (43) *L. salicaria* (10) *Solanum elaeagnifolium* (55) *T. officinale* (34)	Overall (68%) Field (50%) 5, 7, 18, 26, 35, 40, 53 Hand-pollination (86%) 10, 23, 34, 38, 43, 55

Table 3.1 Continued.

Altered abiotic environment

Light availability	*Alliaria petiolata* (51) *Bromus inermis* (12) *Cinchona pubescens* (22) *Dactylis glomerata* (32) *L. maackii* (35) *L. salicaria* (20) *Melilotus officinalis*^{N} (16) *Microstegium vimineum* (49)	*Phleum pratense* (12) *Phragmites australis* (37) *Pinus contorta* (14) *Pinus nigra* (45) *Poa pratensis* (12, 32) *Pseudotsuga menziesii* (14) *Typha glauca* (17)	(83%) 14, 16, 17, 20, 22, 32, 35, 37, 45, 51
Soil water availability	*A. saligna*^{N} (58) *A. petiolata* (51) *Andropogon virginicus* (33) *Avena barbata* (9, 57) *Brachypodium distachyon* (57) *Bromus diandrus* (9) *Bromus hordeaceus* (9) *B. inermis* (12) *Bromus madritensis* (9, 13, 57)	*I. hildebrandtii* (42) *M. officinalis*^{N} (16) *Melinis minutiflora* (33) *P. contorta* (14) *P. nigra* (45) *P. pratense* (12) *P. pratensis* (12) *P. menziesii* (14) *Schizachyrium condensatum* (33)	(36%) 14, 16, 33, 57
Litter quantity/ quality or soil organic matter (SOM)	*A. saligna*^{N} (58) *A. virginicus* (33) *A. barbata* (9, 30, 57) *B. distachyon* (57) *B. diandrus* (9, 30) *B. hordeaceus* (9, 30) *B. madritensis* (9, 57)	*M. minutiflora* (33) *P. australis* (37) *P. contorta* (14) *P. menziesii* (14) *S. condensatum* (33) *T. glauca* (17)	(100%) 9, 14, 17, 30, 33, 37, 57, 58
Abiotic conditions (air or soil temperature, relative humidity)	*A. saligna*^{N} (58) *A. petiolata* (51) *A. virginicus* (33)	*C. pubescens* (22) *M. minutiflora* (33) *S. condensatum* (33)	(100%) 22, 33, 51, 58
Plant richness/ biomass	*M. vimineum* (49)		(100%) 49

Table 3.1 Continued.

Resource competition versus non-trophic interactions (i.e. altered abiotic conditions)			
Competition for soil resources vs. non-trophic interactions[a] (not mutually exclusive)	*A. barbata* (9, 30) *B. diandrus* (9, 30) *B. hordeaceus* (9, 30) *B. madritensis* (9) *D. glomerata* (32) *P. australis* (37)	*P. contorta* (14) *P. pratensis* (32) *P. menziesii* (14) *T. glauca* (17)	Overall (100%) Competition: (17%) 30 Non-trophic (100%) 9, 14, 17, 30, 32, 37
Altered belowground communities			
Soil microbe and/or mycorrhizal fungi communities	*Agropyron cristatum* (24) *A. petiolata* (50) *A. barbata* (21) *B. hordeaceus* (21) *B. inermis* (24)	*Berberis thunbergii* (27) *E. esula* (24) *M. vimineum* (3, 27) *P. contorta* (14) *P. menziesii* (14)	(83%) 14, 21, 24, 27, 50
Allelopathy			
Allelopathy[b]	*Ailanthus altissima* (19) *A. petiolata* (8, 28, 56) *Centaurea maculosa* (46) *Fallopia* x *bohemica* (41)	*Hedera helix* (4) *L. maackii* (8)	(86%) 8, 19, 28, 41, 46, 56
Competition other than, or in addition to, allelopathy	*A. altissima* (19) *A. petiolata* (8, 28, 56) *C. maculosa* (46) *F.* x *bohemica* (41)	*L. maackii* (8)	(83%) 8, 19, 28, 41, 46
Apparent competition[c]			
Apparent competition	*Ammophila arenaria* (11) *Brassica nigra* (44)	*L. maackii* (36) *Medicago polymorpha*^{N} (29)	(100%) 11, 29, 36, 44
Competition other than, or in addition to, apparent competition	*M. polymorpha*^{N} (29)		(100%) 29

Table 3.1 Continued.

Altered soil nutrient dynamics

Soil nutrients (generally interpreted as resource competition)	*Acacia saligna*^{N} (58) *B. inermis* (12) *Centaurea diffusa* (52) *Cytisus scoparius*^{N} (48) *D. glomerata* (32) *Ipomoea hildebrandtii* (42) *M. officinalis*^{N} (16)	*M. vimineum* (3) *P. contorta* (14) *P. pratense* (12) *P. pratensis* (12, 32) *P. menziesii* (14) *Solidago gigantea*	(18%) 47, 58
Nutrient cycling	*I. hildebrandtii* (42) *M. vimineum* (15)		(50%) 15

a- Attempting to distinguish between direct competition for resources between native and non-native plants and non-interactive effects in which non-native plants alter the environment to the detriment of natives (e.g. physical interference from litter, shading, altered soil temperature). These studies are listed under another mechanism as well, but they explicitly juxtaposed these two general pathways of impact.

b- Native plant fitness negatively affected by secondary compounds released by non-native plant (only experiments that used whole plant treatments were reviewed, not those that used root extracts or isolated compounds).

c- Presence of non-native plant increases the abundance of a native plant consumer, which may negatively affect native plant individual and/or population fitness.

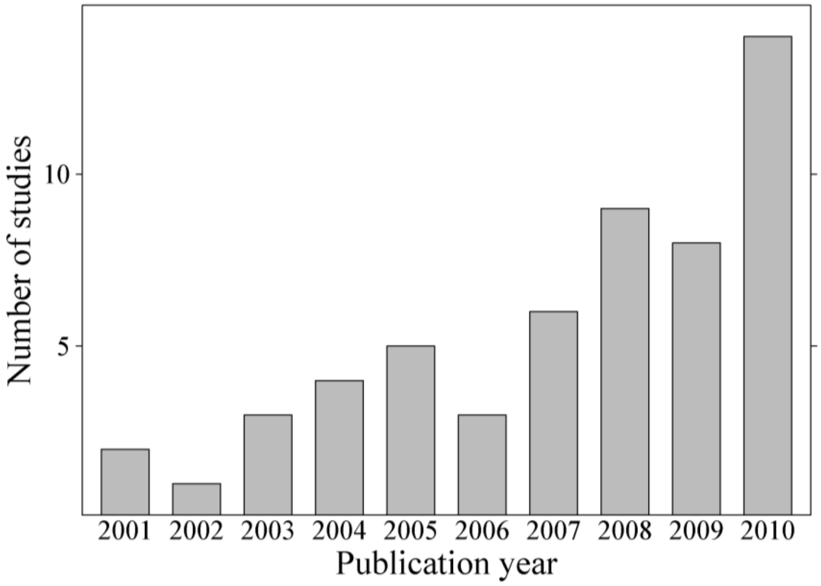

Figure 3.1. Number of studies that experimentally tested potential mechanisms underlying non-native plant impacts from 2001 to 2010 (see text for details on literature search and selection criteria).

Reviewed Studies with Numbers Referenced in Table 3.1

(* indicates study that examined the composite impact of multiple non-native plant species)

1- *Aigner PA (2004) Ecological and genetic effects on demographic processes: pollination, clonality and seed production in *Dithyrea maritima*. Biological Conservation 116: 27-34

2- Bartomeus I, Vilà M, Steffan-Dewenter I (2010) Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. Journal of Ecology 98: 440-450

3- Bauer JT, Flory SL (2011) Suppression of the woodland herb *Senna hebecarpa* by the invasive grass *Microstegium vimineum*. American Midland Naturalist 165: 105-115

4- Biggerstaff MS, Beck CW (2007) Effects of English ivy (*Hedera helix*) on seed bank formation and germination. American Midland Naturalist 157: 250-257

5- Brown BJ, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83: 2328-2336

6- Cariveau DP, Norton AP (2009) Spatially contingent interactions between an exotic and native plant mediated through flower visitors. Oikos 118: 107-114

7- Chittka L, Schurkens S (2001) Successful invasion of a floral market - an exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. Nature 411: 653-653

8- Cipollini KA, McClain GY, Cipollini D (2008) Separating above- and belowground effects of *Alliaria petiolata* and *Lonicera maackii* on the performance of *Impatiens capensis*. American Midland Naturalist 160: 117-128

9- *Coleman HM, Levine JM (2007) Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. Biological Invasions 9: 65-71

10- Da Silva EM, Sargent RD (2011) The effect of invasive *Lythrum salicaria* pollen deposition on seed set in the native species *Decodon verticillatus*. Botany-Botanique 89: 141-146

11- Dangremond EM, Pardini EA, Knight TM (2010) Apparent competition with an invasive plant hastens the extinction of an endangered lupine. Ecology 91: 2261-2271

12- *Davis MA, Bier L, Bushelle E, Diegel C, Johnson A, Kujala B (2005) Non-indigenous grasses impede woody succession. Plant Ecology 178: 249-264

13- DeFalco LA, Fernandez GJ, Nowak RS (2007) Variation in the establishment of a non-native annual grass influences competitive interactions with Mojave Desert perennials. Biological Invasions 9: 293-307

14- Dehlin H, Peltzer DA, Allison VJ, Yeates GW, Nilsson MC, Wardle DA (2008) Tree seedling performance and below-ground properties in stands of invasive and native tree species. New Zealand Journal of Ecology 32: 67-79

15- DeMeester JE, Richter DB (2010) Differences in wetland nitrogen cycling between the invasive grass *Microstegium vimineum* and a diverse plant community. Ecological Applications 20: 609-619

16- Dickson TL, Wilsey BJ, Busby RR, Gebhart DL (2010) *Melilotus officinalis* (yellow sweetclover) causes large changes in community and ecosystem processes in both the presence and absence of a cover crop. Biological Invasions 12: 65-76

17- Farrer EC, Goldberg DE (2009) Litter drives ecosystem and plant community changes in cattail invasion. Ecological Applications 19: 398-412

18- Flanagan RJ, Mitchell RJ, Karron JD (2010) Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. Oecologia 164: 445-454

19- Gomez-Aparicio L, Canham CD (2008) Neighbourhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. Journal of Ecology 96: 447-458

20- Hager HA (2004) Competitive effect versus competitive response of invasive and native wetland plant species. Oecologia 139: 140-149

21- *Hawkes CV, Wren IF, Herman DJ, Firestone MK (2005) Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. Ecology Letters 8: 976-985

22- Jäger H, Kowarik I, Tye A (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galapagos highland vegetation. Journal of Ecology 97: 1252-1263

23- Jakobsson A, Padrón B, Traveset A (2008) Pollen transfer from invasive *Carpobrotus* spp. to natives - a study of pollinator behaviour and reproduction success. Biological Conservation 141: 136-145

24- Jordan NR, Larson DL, Huerd SC (2008) Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. Biological Invasions 10: 177-190

25- Kaiser-Bunbury C, Müller C (2009) Indirect interactions between invasive and native plants via pollinators. Naturwissenschaften 96: 339-346

26- Kandori I, Hirao T, Matsunaga S, Kurosaki T (2009) An invasive dandelion unilaterally reduces the reproduction of a native congener through competition for pollination. Oecologia 159: 559-569

27- Kourtev PS, Ehrenfeld JG, Häggblom M (2003) Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. Soil Biology and Biochemistry 35: 895-905

28- Lankau R (2010) Soil microbial communities alter allelopathic competition between *Alliaria petiolata* and a native species. Biological Invasions 12: 2059-2068

29- Lau JA, Strauss SY (2005) Insect herbivores drive important indirect effects of exotic plants on native communities. Ecology 86: 2990-2997

30- *Lenz TI, Moyle-Croft JL, Facelli JM (2003) Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. Austral Ecology 28: 23-32

31- Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmott J (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. Ecology Letters 10: 539-550

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

33- *Mack MC, D'Antonio CM (2003) Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. Ecological Applications 13: 154-166

34- Matsumoto T, Takakura KI, Nishida T (2010) Alien pollen grains interfere with the reproductive success of native congener. Biological Invasions 12: 1617-1626

35- McKinney AM, Goodell K (2010) Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biological Invasions 12: 2751-2763

36- Meiners SJ (2007) Apparent competition: an impact of exotic shrub invasion on tree regeneration. Biological Invasions 9: 849-855

37- Minchinton TE, Simpson JC, Bertness MD (2006) Mechanisms of exclusion of native coastal marsh plants by an invasive grass. Journal of Ecology 94: 342-354

38- Montgomery BR (2009) Effect of introduced *Euphorbia esula* on the pollination of *Viola pedatifida*. Botany-Botanique 87: 283-292

39- Moragues E, Traveset A (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation 122: 611-619

40- Muñoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. Journal of Ecology 96: 459-467

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CHAPTER FOUR

ECOLOGICAL TRADEOFFS IN NON-NATIVE PLANT MANAGEMENT

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Abstract

Controlling non-native plants in natural areas should, ideally, not only reduce target species' abundance, but also benefit broader management objectives such as conserving native species, improving wildlife habitat, and providing ecosystem services. In this context, the effectiveness and non-target impacts of control strategies, such as broadleaf herbicides, must be weighed against the impacts of non-native plants themselves. We undertook this relative assessment for *Centaurea stoebe*, one of the most widespread and heavily managed non-native plant species in the Intermountain West, USA. While effectiveness and plant community impacts of herbicide treatment for *C. stoebe* have been assessed, field-based experiments quantifying community-level impacts of *C. stoebe* are rare. In a three-year experiment in sagebrush-grassland communities of southwest Montana, USA, we found that the broadleaf herbicide, picloram, was highly effective at reducing *C. stoebe*, but also resulted in a significant loss of native forb cover and a significant increase in non-native grass cover, primarily *Bromus tectorum*. There was a significant increase in native forb cover in response to manual removal of *C. stoebe*, which would seem to indicate *C. stoebe* had been suppressing native forbs. However, there was an equivalent increase in native forb cover with no treatment. In some communities, *C. stoebe* appears to have a negligible effect on native forb and grass cover and richness. Depending on management objectives, the loss of native forb cover and potential secondary invasion may outweigh the benefits of reduced target non-native plant abundance; thus, highlighting an ecological tradeoff of non-native plant management in natural areas.

Keywords: Invasive plant; weed impacts; removal experiment; management effects; native species; natural areas

Introduction

Non-native plants pose a significant threat to biodiversity and ecosystem structure and function (Vitousek et al. 1997; Mack et al. 2000; Simberloff 2011; Vilà et al. 2011), which has led to the implementation of aggressive and sustained control programs throughout the world. The invasion of non-native plants into natural areas and protected lands is particularly troublesome given the importance of these areas for conserving biological diversity and providing ecosystem services. Consequently, controlling non-native plants is either strongly advised or mandated for most natural areas and public lands. However, controlling non-native plants is only one of many land management objectives in natural areas, and whether common non-native plant control strategies are congruent with these other objectives is unclear.

The Intermountain West of North America ('the west' hereafter) exemplifies many of the challenges of managing natural areas for multiple natural resource objectives because it is a region of high conservation and human use value. Numerous non-native plants species have established and spread throughout the region, and one of the species of greatest concern is *Centaurea stoebe* L. (spotted knapweed). *C. stoebe* is a short-lived perennial native to Europe and northern and central Asia that was accidentally introduced to North America in contaminated alfalfa (*Medicago sativa* L.) seed in the 1890s (Roché and Talbott 1986). *C. stoebe* is now one of the most widespread non-native plants and is a designated "noxious weed" in the 11 contiguous western states (NRCS 2012), meaning state and federal land management agencies are mandated to control *C. stoebe* and minimize the economic, ecological, and human health impacts that it causes (Executive Order 13112 of 1999).

The major impacts associated with *C. stoebe* in natural areas of the west (i.e. grasslands, shrublands, sagebrush steppe) are displaced native plant species, reduced forage quality and quantity, and negatively altered wildlife habitat (Hirsch and Leitch 1996; DiTomaso 2000; Duncan and Clark 2005). A number of traits have been indentified that make *C. stoebe* highly competitive against native North American plant species, including extensive mycorrhizal colonization (Marler et al. 1999; Callaway et al. 2004a; Harner et al. 2009), production of allelopathic compounds (Ridenour and Callaway 2001; Bais et al. 2003; Thorpe et al. 2009), greater nutrient-use efficiency relative to native species (Blicker et al. 2002; Zabinski et al. 2002; Thorpe et al. 2006), greater compensatory growth after herbivory relative to native species (Walling and Zabinski 2006), and cultivation of soil biota in the invaded range that increase *C. steobe*'s growth (Callaway et al. 2004b). When seeded into experimental monocultures, *C. stoebe* significantly reduced the biomass of several native western USA forb and grass species (Maron and Marler 2008b). It is generally assumed that *C. stoebe* displaces native plant species in natural plant communities because the presence and abundance of *C. stoebe* is often negatively correlated with native plant species cover, richness and diversity (Tyser and Key 1988; Kedzie-Webb et al. 2001; Ortega and Pearson 2005; May and Baldwin 2011). The only experimental study of *C. stoebe* impacts under natural conditions that we are aware of was that of Lesica and Shelly (1996). They found that removing *C. stoebe* in two western Montana bunchgrass communities led to significantly higher seedling recruitment of a rare native Brassicaceae, Mt. Sapphire rockcress (A*rabis fecunda* Rollins); thus, demonstrating a species-specific competitive effect of *C. stoebe*. Collectively, these studies and others have greatly advanced our understanding of the biology, ecology, and potential impacts of *C. stoebe*. Nevertheless, quantitative field-based evidence linking *C. stoebe* to plant community-level impacts remains scarce.

C. stoebe is the most heavily managed non-native plant on public lands in the west (based on quantity of herbicide used, number of hectares treated, and hours of labor (USFS et al. 2010)). Management objectives in natural areas typically include maintaining native plant diversity and wildlife habitat, increasing forage production, sustaining ecosystem services, and conserving species of concern. It is generally assumed that reducing non-native plants in natural areas will benefit these objectives (Pearson and Ortega 2009). However, the legal mandate to control noxious weeds may compel action before there is sufficient knowledge of how other land management objectives will be affected. Assessing the impacts of non-native plant species, as well as the impacts of the strategies used to control them, are crucial steps in managing natural areas for multiple conservation objectives (Buckley 2008; Pearson and Ortega 2009; Downey et al. 2010).

While there have been numerous studies of the effectiveness (i.e. reduction of *C. stoebe* abundance) and plant community impacts of herbicide treatments for *C. stoebe* (e.g. Rice and Toney 1998; Sheley et al. 2000; Crone et al. 2009; Ortega and Pearson 2010), there have not been similar experimental studies of the community-level impacts of *C. stoebe*. Thus, it is unclear how the benefits of *C. stoebe* management compare with the impacts of *C. stoebe* itself.

We conducted replicated removal experiments to quantify the relative impacts of *C. stoebe* and herbicide treatment of *C. stoebe* on sagebrush-grassland plant communities in southwest Montana. Removal experiments, along with experimental additions, provide the strongest evidence for assessing non-native plant impacts and avoid the confounding effects of environmental variation that arise in multi-site comparison studies (Adair and Groves 1998). The objective of removal experiments is to approximate how a plant community would be structured in the absence of the non-native plant species. Non-native plants are removed with as little disturbance as possible and after a recovery period, impacts are quantified as the change in plant community metrics from before removal. A concern regarding removal experiments is that observed changes may be in response to the disturbance created by the removal process rather than to the absence of the non-native plant. We addressed this concern by including a treatment that mimicked the disturbance created by *C. stoebe* removal, but with no plant material removed. Thus, if *C. stoebe* was having an impact, the effect of manual removal of *C. stoebe* on response variables would be greater than the effects of disturbance and no treatment.

The objectives of this study were to: (1) quantify impacts of *C. stoebe* on sagebrush-grassland plant communities in southwestern Montana; (2) compare the impacts of *C. stoebe* with those of herbicide control of *C. stoebe*, small-scale disturbance, and no treatment; and (3) determine whether invaded plant communities differed from nearby uninvaded plant communities and, if so, whether plant communities treated for *C.*

stoebe became more similar to nearby uninvaded plant communities three yeas after treatment. The response variables measured for all three objectives were the percent cover and species richness and composition of native and non-native forbs and grasses, as well as the aboveground biomass of two native forage grasses. We focused on growth form (i.e. forbs and grasses) and origin groups (i.e. native and non-native) because these are common land management metrics and may be better indicators of a range of ecosystem processes, such as nutrient cycling, decomposition, and water retention, than individual species identity alone (Diaz and Cabido 2001; Cadotte et al. 2011).

Methods

Study Area

The study was conducted in the sagebrush-grassland habitat type of southwest Montana. These communities occupy the transition zone between valley bottoms and Douglas fir-dominated forest (*Pseudotsuga menziesii* (Mirb.) Franco). Perennial grasses feature prominently, ranging between 40 to 60 percent canopy cover (Mueggler and Stewart 1980). The dominant species are bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve), western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), and Idaho fescue (*Festuca idahoensis* Elmer), and frequent species include green needlegrass (*Nassella viridula* (Trin.) Barkworth), slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.), squirreltail (*Elymus elymoides* (Raf.) Swezey), and Sandberg bluegrass (*Poa secunda* J. Presl). Forb canopy cover ranges from 20 to 30 percent and typically includes: arrowleaf balsamroot

(*Balsamorhiza sagittata* (Pursh) Nutt.), buckwheat (*Eriogonum* species), rosy pussytoes (*Antennaria rosea* Greene), hairy false goldenaster (*Heterotheca villosa* (Pursh) Shinners var. *villosa*), prairie sagewort (*Artemisia frigida* Willd.), silvery lupine (*Lupinus argenteus* Pursh), Indian paintbrush (*Castilleja* species), fleabane (*Erigeron* species), phlox (*Phlox* species), scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb.), and milkvetch (*Astragalus* L. species). Shrub canopy cover averages 5 to 10 percent, comprised mainly of big sagebrush (*Artemisia tridentata* Nutt.) and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle). Average litter cover in these communities is 40 to 60 percent and bare ground 5 to 10 percent. Average temperatures in the study area are 19 °C in the summer and -4 °C in the winter. The average annual precipitation is 480 mm, with most falling in April, May, and June.

High forage production and diverse plant communities make sagebrush-grasslands in this region important habitat for numerous large mammals (e.g. elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*) and black bear (*Ursus americanus*)); small mammals (e.g. deer mouse (*Peromyscus maniculatus*), Uinta ground squirrel (*Urocitellus armatus*), bushy-tailed woodrat (*Neotoma cinerea*)); songbirds (e.g. Brewer’s sparrow (*Spizella breweri*), Vesper sparrow (*Pooecetes gramineus*), western meadowlark (*Sturnella neglecta*)); upland game birds (e.g. greater sage-grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Tympanuchus phasianellus*)); and raptors (e.g. golden eagle (*Aquila chrysaetos*), ferruginous hawk (*Buteo regalis*)). Many taxa that are at-risk due to declining population trends and habitat loss ("species of concern") inhabit sagebrush-grasslands in this region for at least part of the year (MNHP 2011).

There is a long history of human activity in the region, including mining, logging, farming, and ranching. In addition, due to moderate topography, open landscapes and proximity to wildlands, the last quarter century has seen rapid growth in recreational use and exurban development in lowland habitats such as sagebrush-grasslands (Gude et al. 2006). All of these activities and their associated transportation networks have likely contributed to the introduction and spread of non-native plant species (Olliff et al. 2001; Parks et al. 2005; Mortensen et al. 2009).

Experimental Design

Nine *C. stoebe* populations were randomly selected across the study area and were located between 45°31' N, 111°15' W; 45°17' N, 110°49' W; and 45°10' N, 110°51' W at elevations between 1515 m and 1790 m. The only selection criteria for the study populations were: that they were in natural areas (i.e. non-crop) and that they were located in areas that retained some native vegetation. This latter criterion was easily met since most *C. stoebe* populations in natural areas of this region exist within a matrix of native plant communities (although other non-native plant species are common as well). The study populations were on south-southeast aspects, 2 to 25% (1 to 14°) slope and were 60 m to 600 m away from roads. Populations ranged from 150 to 650 m^2 in spatial extent and were between 0.1 and 50 km apart. Initial *C. stoebe* cover was 5 to 25%. All of these characteristics are typical of *C. stoebe* populations found in sagebrush-grasslands in this region.

Within each of the nine *C. stoebe* population, two 0.25 m^2 plots were established for each of four treatments: (1) no treatment, (2) manual removal of *C. stoebe*, (3) ground disturbance (with small hand tools) similar to that created in the manual removal treatment but with no plant material removed, and (4) herbicide application (4 treatments × 9 populations × 2 replicate plots per population = 72 plots). As mentioned, the purpose of the disturbance treatment is to control for potential effects of the small-scale ground disturbance caused by removing *C. stoebe* plants in the manual removal treatment. We consider 'no treatment' a treatment in the sense that it is one potential non-native plant management option. Within populations, plots were established to maximize the similarity among treatments in terms of canopy cover, percent bare ground, ratio of forbs to grasses, percent cover of *C. stoebe*, and species richness. Plots were separated by at least 1 m within populations. To examine differences between invaded and uninvaded areas, and whether this changed over time, we established two additional plots approximately 10 m outside of each *C. stoebe* population. Comparisons were made with uninvaded areas close to *C. stoebe* populations to minimize differences in habitat conditions and disturbance characteristics.

Treatments were applied in late June 2007 after pre-treatment data had been collected, which coincides with the middle of the spray season for most local land management agencies. Herbicide plots were broadcast sprayed with the broadleaf herbicide, picloram (Tordon™ 22K), which is the most common herbicide used for *C. stoebe*, at the recommended rate (1.17 liters ha^{-1} = 0.28 kg ae ha^{-1}, Dow AgroSciences 2001). Herbicide was applied using a CO_2 pressure regulated backpack sprayer, which is a typical application method in natural areas of this region. In manual removal plots, *C. stoebe* plants were carefully hand-pulled when soils were wet to minimize disturbance and facilitate removal of entire plants. In disturbance plots, hand tools were used to disturb the same area of soil as in the paired manual removal plots, but with no plant material removed.

Vegetation Sampling

We quantified the percent canopy cover (estimated to the nearest 1%) for each plant species, as well as the percent cover of bare ground, bryophytes, and litter in each plot. Because plant canopies often overlap, the total percent cover per plot could exceed 100%. Measurements were taken annually in June and July 2007 through 2010. Plant taxonomy was based on Cronquist et al. (1977), Dorn (1984), and Lavin and Seibert (2009). We also counted the number of *C. stoebe* stems per plot.

Biomass Estimation

We examined potential effects of *C. stoebe* and herbicide treatment of *C. stoebe* on forage production in natural areas by quantifying the change in the aboveground biomass of *P. spicata* (bluebunch wheatgrass) and *N. viridula* (green needlegrass). These native perennial bunchgrasses were chosen because they are important forage species for domestic livestock and wildlife and because they were present in most of the *C. stoebe* study populations. During peak productivity (mid- July) in 2008 and 2009, we harvested 227 *P. spicata* and 71 *N. viridula* individuals representing a range of sizes (quantified by basal diameter and height) in off-plot areas. Grasses were clipped at the soil surface, bagged, and dried at 60° C for 6 days before being weighed to the nearest 0.001 g. Linear regression was used to calculate the relationship between *P. spicata* and *N. viridula* basal diameter, height and aboveground biomass for each species. The r^2 for the regression models were 0.842 and 0.903 for *P. spicata* and *N. viridula*, respectively (Appendix E).

Data Analysis

Vegetation Metrics

The total percent cover and plant species richness were calculated per plot, as well as cover and richness values within growth form and origin groups: forbs and grasses, native and non-native. *C. stoebe* percent cover and density were analyzed as separate response variables and *C. stoebe* was excluded from all other response variable calculations. Cover values were square root transformed to meet parametric assumptions of normality and homogeneity of variance. There was a total of 22 response variables (Table 4.1).

Treatment Effects

We tested for treatment effects on the absolute value of response variables over time using a mixed effects model. *Plot* was the independent sampling unit. *Treatment* was a fixed effect, *plot* was a repeated measure nested within the continuous random effect, *year*. This model structure accounts for the non-independence of repeated measures on individual plots through time. *Population* was included as a random blocking effect to account for potential unmeasured within-population similarities.

Proportional Change

In addition to examining treatment effects on the absolute value of response variables over time, we also assessed the proportional change for each response variable by treatment. Proportional change takes into account the initial value of response variables and was calculated as: (3 years post-treatment value – pre-treatment value) ⁄ pre-treatment value for each response variable. One-way analysis of variance (ANOVA) was used to examine differences in the proportional change in response variables among treatments. *Population* was again included as a random blocking effect. The two approaches, mixed effects over time and proportional change, allowed a comparison of transitory versus longer-term treatment effects.

Effect Size Estimation

The ANOVA results were a useful indication of which response variables seemed most affected by treatments. However, ultimately we were interested in effect sizes, which provide more biologically meaningful information than the binary significance/non-significance outcome of ANOVA (Rinella and James 2010). Therefore, we estimated the mean effect size of treatments for response variables identified as significant in the initial mixed model and ANOVA analysis using parametric bootstrapping. The 2007 to 2010 proportional changes for each response variable were randomly resampled within treatment group, creating a new data set from which the mean was calculated. This procedure was repeated 1000 times to generate an estimated distribution of the mean effect size of each treatment per response variable.

Comparison with Uninvaded Areas

We tested for differences between treatment plots inside *C. stoebe* invaded plant communities and uninvaded plant communities both before, and three years after, treatment for all response variables using one-way ANOVA. We also quantified the proportion of the total per-plot cover represented by each of the growth form and origin groups (i.e. the proportion of total per-plot vegetation cover that was native forbs, native grasses, etc.) for inside and outside plots. We examined whether these proportional representations differed between inside and outside plots, and if so, whether these differences changed over time. Post hoc contrasts were conducted with Tukey's multiple comparison test ($p < 0.05$).

Species Composition

We tested for differences in species composition among treatments and between invaded and uninvaded areas both before, and three years after, treatment, using permutation-based multivariate ANOVA based on Bray-Curtis dissimilarity matrices. This is a robust alternative to ordination methods for examining whether, and to what degree, variation in a multivariate response (i.e. species composition) can be explained by a linear predictor variable (i.e. treatments) (Oksanen et al. 2011). Test significance was based on 1000 permutations of the abundance-based dissimilarity matrices per-treatment (or uninvaded status) per-year.

Data were analyzed and plotted using R, version 2.14.1 (R Development Core Team, 2011) including packages *ggplot2* (Wickham 2009), *nlme* (Pinheiro et al. 2012) and *vegan* (Oksanen et al. 2011).

Results

Pre-Treatment Conditions

The pre-treatment (2007) levels of response variables were not significantly different among the four treatment groups (no treatment, disturbance, manual removal, and herbicide) at the plot-level, as indicated by non-significant one-way ANOVAs ($\alpha = 0.05$) for native and non-native forb and grass richness and cover, *C. stoebe* cover and density, *P. spicata* and *N. viridula* biomass, and percent bare ground and litter (Appendix F). Species composition was also not significantly different as indicated by non-significant multivariate ANOVA based on 1000 permutation of Bray-Curtis dissimilarity matrices (Appendix F).

Transient versus Long-Term Impacts

Percent cover of native and non-native forbs and grasses, litter, and bare ground; forb richness; and *P. spicata* biomass all changed significantly over time in response to treatments (Figure 4.1 and Appendix G). However, many of these changes were transient and only significant in the mixed model analysis of treatment effect by year. When assessed as a proportional change from pre-treatment levels to three years post-treatment, effects were significantly different among treatments ($p < 0.05$) only for *C. stoebe* cover, total non-native cover (excluding *C. stoebe*), native forb cover, native grass cover, and *B. tectorum* cover (Table 4.1 and detailed below).

C. stoebe Cover

Herbicide treatment was highly effective at reducing *C. stoebe* cover (Figure 4.1). Before treatment *C. stoebe* cover across all plots was 8.7% ± 0.6 (mean ± 1 SE). Three years after treatment, mean *C. stoebe* cover in herbicide plots was 0.8% ± 0.5, whereas untreated and disturbed plots averaged 12.5% ± 2.2 and 13.5% ± 3.2 *C. stoebe* cover, respectively. The proportional change in *C. stoebe* cover from pre-treatment to three years post treatment was significantly different among treatments ($F_{3,60} = 7.98$, $p < 0.001$). Overall, *C. stoebe* cover increased by an estimated 118% ± 2.0 and 145% ± 1.7 with disturbance and no treatment, respectively, and decreased by an estimated 79% ± 4.7 with herbicide treatment. The proportional change in *C. stoebe* cover was not significantly different between manual removal and herbicide treatments (Figure 4.2).

Native Forb, Native Grass and Total Non-Native Cover

The change in total plant cover (not including *C. stoebe*) was not significantly different among treatments; however, the proportional representation of forbs and grasses and native and non-native species shifted, with the largest effects resulting from herbicide treatments (Figure 4.2).

The proportional change in native forb cover was significantly different among treatments ($F_{3,60} = 3.143$, $p < 0.0317$). Three years after treatment, native forb cover had increased by 107% ± 1.6 and 98% ± 1.3 in response to manual removal and no treatment, respectively. A significantly smaller increase in native forb cover resulted from disturbance (36% ± 0.6), whereas native forb cover decreased by an estimated 22% ± 0.4 in response to herbicide treatment (Figure 4.2 and Appendix H).

Native grass cover increased over time with no treatment, manual removal, and herbicide treatment; however, the increase was significantly greater in response to herbicide ($F_{3,60} = 3.01$, $p < 0.0427$) (Figure 4.1). Three years after treatment, the estimated effects on native grass cover were increases of 41% ± 0.3 in response to herbicide, 18.5% ± 0.4 with no treatment, and 14% ± 0.5 in response to manual removal. Disturbance tended to have a slight negative effect on native grass cover (estimated mean decrease of 4.4% ± 0.3).

Total non-native cover (other than *C. stoebe*) increased across all treatments; however, there was a significantly greater proportional increase in response to herbicide relative to the other treatments ($F_{3,60} = 4.041$, $p < 0.011$) (Figure 4.2). Three years after treatment, total non-native cover had increased by an estimated 248% ± 2.9 with herbicide, 62% ± 1.4 with no treatment, 19.4% ± 0.6 with disturbance, and 16.7% ± 0.4 with manual removal. Thus, there was a substantial natural increase in non-native cover over time, but this increase was greatly exacerbated by herbicide treatment. There were marked differences among the treatments in the type of non-native plants that increased. With herbicide and no treatment nearly all of the increase was in non-native grasses and the majority of this was *B. tectorum* (Figure 4.2 and Appendix H). Herbicide treatment led to an estimated mean increase in *B. tectorum* cover of 200% ± 2.9 beyond the 60% ± 2.0 increase that occurred in untreated plots. Surprisingly, *B. tectorum* decreased with disturbance and manual removal of *C. stoebe*, 15% ± 0.5 and 1.9% ± 1.4, respectively. These treatments elicited a greater response from non-native forbs, primarily the annual/biennial Brassicaceae species, *Alyssum desertorum* Stapf and *Berteroa incana* (L.) DC.

It should be noted that there were no response variables for which the effect of manual removal of *C. stoebe* was greater than the effect of no treatment, other than *C. stoebe* cover.

Biomass and Species Composition

Neither the change in biomass of *P. spicata* and *N. viridula* over time in response to treatments, nor the proportional change in biomass from pre-treatment to three years post-treatment, was significantly different among treatments (*P. spicata*: $F_{3,60} = 0.518$, $p = 0.671$; *N. viridula*: $F_{3,60} = 0.632$, $p = 0.597$). Species composition was also not significantly different among treatments before, or three years after, treatment (2007: $F_{3,60} = 0.436$, $p = 0.986$; 2010: $F_{3,60} = 0.851$, $p = 0.642$, based on 1000 permutations of dissimilarity matrices for each year).

Recovery Toward Uninvaded Conditions

The total percent vegetation cover did not differ inside versus outside *C. stoebe* populations before or three years after treatment. However, there were significant differences in the proportional representation of forbs, grasses and native/non-native species (Table 4.2). In 2007, the vegetation cover in uninvaded plant communities was evenly split between forbs and grasses, whereas forb cover was significantly lower and grass cover significantly higher inside *C. stoebe* invaded communities (Table 4.3). During the three years following treatment, forb cover increased and grass cover decreased inside *C. stoebe* invaded communities except in the areas treated with herbicide. In these plots, forb cover remained significantly lower and grass cover significantly higher, than in uninvaded communities (Table 4.3). The proportion of the total vegetation cover comprised of native forbs increased over time in all treatments except herbicide plots. Before treatment, native forbs comprised approximately 18.1 % ± 5.7 of the total vegetation cover in herbicide plots, whereas three years after treatment they comprised only 7.6% ± 3.7, which was a significant reduction ($F_{1,16} = 6.95$, $p = 0.030$). Nevertheless, the proportion of total vegetation cover represented by native forbs was significantly higher in uninvaded communities both at the beginning and the end of the experiment (Table 4.3). Uninvaded communities had significantly less native grass cover in 2007 relative to *C. stoebe* invaded communities, but this difference had dissipated by 2010 due to a significant increase in native grass cover in uninvaded communities. The proportion of non-native grass was also lower in uninvaded communities; however, due to high levels of variability, this difference was not significantly different from inside *C. stoebe* invaded communities (Table 4.3).

The percent bare ground and litter cover did not differ between treated and uninvaded plant communities before, or three years after, treatment (bare ground 2007: $F_{4,77} = 1.648$, $p = 0.186$; 2010: $F_{4,77} = 1.452$, $p = 0.24$; litter 2007: $F_{4,77} = 1.968$, $p = 0.123$; 2010: $F_{4,77} = 2.089$, $p = 0.105$). Species composition was also not significantly different between treatment plots and uninvaded communities before or three years after treatment (2007: $F_{4,77} = 0.568$, $p = 0.967$; 2010: $F_{4,77} = 0.760$, $p = 0.818$).

Of the 22 response variables, native grass cover, *C. stoebe* cover and *C. stoebe* density were the only parameters that changed significantly ($p < 0.05$) in uninvaded plant communities from 2007 to 2010 (Table 4.3). Native grass cover increased from 11% ± 2.2 in 2007 to 17% ± 3.0 in 2010. The cover and density of *C. stoebe* in initially uninvaded communities remained low three years after the start of the experiment: *C. stoebe* cover in 2010 averaged 2% ± 1.2 and *C. stoebe* density, 6 individuals ± 3 per 0.25 m^2. In our study area, *C. stoebe* generally exhibits a patchy distribution, which was reflected at the local-scale by the variability in cover and density in initially uninvaded communities. At the end of the experiment, one-third of the initially uninvaded communities still contained no *C. stoebe*. The majority of plots that became invaded had 1 to 2% *C. stoebe* cover (3 to 4 individuals per 0.25 m^2) by 2010; although one plot had 5% *C. stoebe* cover (12 individuals) and another 12% *C. stoebe* cover (27 individuals) by the end of the experiment.

Discussion

Our results highlight several ecological tradeoffs to consider when managing *C. stoebe* in sagebrush-grassland natural areas. Picloram, the common herbicide used for *C. stoebe,* was highly effective at reducing the cover of *C. stoebe* and had a positive effect on native grass cover three years after treatment, which has also been shown in other systems (Rice et al. 1997; Rice and Toney 1998; Sheley et al. 2000; Ortega and Pearson 2010, 2011). However, we also found that herbicide treatment caused a steady and significant increase in non-native grass cover in the three years following treatment, primarily *B. tectorum*--another major non-native species of concern in conservation and management in natural areas of the Intermountain West. The tradeoff on one non-native plant species for another is an observed side effect of picloram that has become increasingly common (Ortega and Pearson 2010, 2011). Another potentially undesirable consequence of herbicide treatment was a significant reduction in native forb cover. Unlike the findings of Rice et al. (1997) and Rice and Toney (1998), native forb cover in our herbicide treatment plots had not returned to pre-treatment levels by three years post-treatment. Furthermore, our herbicide plots did not become more similar to uninvaded plots over time in terms of native forb cover. Our findings are, however, consistent with several recent studies documenting detrimental effects of picloram on native grassland forbs, particularly arrowleaf balsamroot (Sheley and Denny 2006; Crone et al. 2009; Rinella et al. 2009; Ortega and Pearson 2010, 2011).

What was not previously known was the impact of *C. stoebe* itself on sagebrush-grassland plant communities and how these impacts compare with those of herbicide treatment. The use of field-based removal experiments enabled us to quantify causal relationships. If *C. stoebe* was having a significant impact, we would expect to see a proportional change in the response variable in the manual removal plots greater than that seen with the disturbance treatment or no treatment. We found a significant increase in native forb cover in response to manual removal, which would seem to indicate that *C. stoebe* had been suppressing native forbs. However, there was an equivalent increase in native forbs with no treatment and, to a lesser extent, with disturbance. There were no response variables, other than *C. stoebe* cover, for which the effect of manual removal was greater than the response to either disturbance or no treatment. These results indicate that *C. stoebe* is not exerting significant negative impacts on the cover, richness, or biomass of native forbs or grasses in our study system. *C. stoebe* shows no indication of displacing native species in these sagebrush-grasslands because its presence has not lead to significant shifts in the existing plant community or changes in the proportion of bare ground. Furthermore, the coincident increase in cover of *C. stoebe*, native grasses, and native forbs in plots that received no treatment suggests that, in some communities, coexistence of native flora with *C. stoebe* is possible and that an increase in *C. stoebe* abundance does not necessarily lead to competitive exclusion.

As noted in the introduction, there are very few field-based experimental studies with which to compare our *C. stoebe* impact results. Lesica and Shelly (1996) clearly showed detrimental impacts of *C. stoebe* in a field-based removal experiment; however, the target of impact was a rare native plant species, making community-level comparisons difficult. In a microcosm setting, Maron and Marler (2008a, b) demonstrated that seeding *C. stoebe* into native monocultures and mixtures led to a significant reduction in the biomass of several native forb and grass species. The discrepancy between these results and our findings in natural grassland communities may be related to differences in climate, soil resources, and/or the density and propagule supply of *C. stoebe* and native species. We have not observed, in our region, high density *C. stoebe* infestations (i.e. 60-100% cover) that have been reported in other regions (Tyser and Worley 1992; Ridenour and Callaway 2001).

The uninvaded areas that we examined had significantly higher forb cover, particularly native forb cover, and lower grass cover relative to inside *C. stoebe* populations at the beginning of the experiment. All of the treatments (including no treatment) became more similar to uninvaded areas in terms of total forb cover, native forb cover, and total grass cover, except for the herbicide treatment. These latter (herbicide) plots became less similar to uninvaded areas over time, increasing in grass cover, particularly non-native grass cover, and decreasing in forb cover and richness, particularly native forb cover and richness

The amount of bare ground was not significantly different inside versus outside *C. stoebe* populations and the amount of bare ground did not change significantly over time or in response to treatments. While *C. stoebe* density and cover increased in some no treatment and previously uninvaded plots, *C. stoebe* density and cover remained constant or decreased in other no treatment and previously uninvaded plots. Together, these findings suggest that *C. stoebe* may not always rapidly invade sagebrush-grassland communities, in spite of intermediate natural and anthropogenic disturbance and persistent bare ground.

It is generally assumed that non-native plants exert negative impacts that justify their control and that after control actions are taken, desirable properties of the community will improve, typically unaided. However, it is increasingly recognized, particularly in natural areas and wildland ecosystems, that non-native plant control strategies often do not result in desirable long-term outcomes (D'Antonio et al. 2004; Reid et al. 2009). A lack of native species recovery and secondary invasion are common hindrances (e.g. Mason and French 2007; Turner et al. 2008; Rinella et al. 2009; Larson and Larson 2010; Kettenring and Adams 2011). Our results support the idea that "one size does not fit all" in terms of non-native plant management and that the existing conditions and potential future conditions need to be considered in the decision-making process (Seastedt et al. 2008). We do not advocate abandoning efforts to control *C. stoebe*. Rather, we suggest greater consideration of the actual impacts of *C. stoebe* and a weighing of this information against the costs and benefits of management (Rew et al. 2007). Because of ecological tradeoffs, such as those described in our study, there may be situations in which the benefits of herbicide treatment do not justify the costs. If the primary management objective is maximizing grass cover for forage, herbicide treatment of *C. stoebe* may be beneficial and cost-effective. However, this approach should be used cautiously in areas containing *B. tectorum* or other undesirable grass species; these may increase at least as much, if not more, than the desirable forage species. Monitoring unmanaged non-native plant populations in natural areas is a necessary component in this adaptive management process (Rew et al. 2007).

The loss of forbs incurred by herbicide treatment will be a consequence that must be weighed against management objectives (Rinella et al. 2009). Forbs are an important component of sagebrush-grassland habitats (Mueggler and Stewart 1980), providing food and habitat for organisms across all trophic levels including soil biota, insects, and small and large mammals (Viketoft et al. 2005; Torstenson et al. 2006; Vogel et al. 2007; Cook et al. 2011). These organisms play important roles in ecosystem processes, such as decomposition, nutrient cycling, and pollination. Based on our results, many native forbs in this region successfully co-exist with *C. stoebe*. Thus, typical sagebrush-grassland communities in natural areas (i.e one that retains a viable native plant component) that is being managed for biodiversity and conservation may benefit more from activities that promote the existing desirable vegetation than from *C. stoebe* removal. On the other hand, in communities harboring species of concern, such as the rare Mt. Sapphire rockress studied by Lesica and Shelly (1996), direct control of *C. stoebe* may be necessary for the conservation of rare plant populations.

In conclusion, we have highlighted several ecological tradeoffs to consider when managing non-native pants in natural areas. *C. stoebe* had negligible impacts on the cover and richness of native forbs and grasses in sagebrush-grassland communities examined in southwest Montana. Our experimental results indicate that it is possible for communities to maintain ecological value (i.e. native species, forage production, wildlife habitat) despite the presence of this ubiquitous non-native plant. We cannot say whether this lack of significant plant community impacts by *C. stoebe* would hold true in severely disturbed areas or significantly different climates. In our study system, the common herbicide used to control *C. stoebe* affected the plant community much more than *C. stoebe* itself, by decreasing the cover and richness of native forbs and increasing the cover of undesirable non-native grass. In natural areas and wildland ecosystems where, in addition to controlling non-native plants, management objectives include providing high-quality wildlife habitat, conserving biological diversity, and maintaining ecosystem services, careful consideration of the ecological and economic costs and benefits of non-native plant control is prudent. The loss of forbs and potential for secondary invasion may outweigh the benefits gained by reducing non-native plant abundance. Sound management decisions will consider these tradeoffs in relation to the quantified impacts of non-native plants themselves.

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List of Appendices

Appendix E. - Allometric Relationship between Size and Biomass for *P. spicatum* & *N. viridula*

Appendix F. - ANOVA for Pre-treatment Conditions

Appendix G. - Complete Mixed Model and ANOVA Output for Treatment Effects Over Time

Appendix H. - Effect Size of Treatments Estimated from Bootstrap Samples

Table 4.1. Results from one-way analysis of variance for variation in the proportional change in response variables from pre-treatment to three years post-treatment levels amongst treatments. Treatments: (1) no treatment, (2) manual *C. stoebe* removal, (3) disturbance, and (4) herbicide treatment. Only significant response variables shown ($p < 0.05$); complete results in Appendix G.

Response variable	Mean square	$F_{3,60}$	p
C. stoebe cover	22.41	7.98	< 0.001
Total non-native cover	21.80	4.04	0.011
Native forb cover	6.38	3.14	0.032
Native grass cover	0.63	3.01	0.043
B. tectorum cover	29.74	4.52	0.006

Table 4.2. One-way analysis of variance results for differences between treatment plots and uninvaded plots in vegetation response variables. Only significant response variables are shown ($p < 0.05$).

	Pre-treatment (2007)		3 Years post-treatment (2010)	
	$F_{4,77}$	P	$F_{4,77}$	P
Forb proportion	5.15	0.002	3.45	0.016
Native forb proportion	8.36	< 0.001	5.44	0.001
Grass proportion	5.15	0.002	3.53	0.015
Native grass proportion	3.62	0.013	1.17	0.339

Table 4.3. Percent of total vegetation cover (mean ± 1 SE) represented by growth form and origin groups pre-treatment (2007) and 3 years post-treatment (2010) for treated and uninvaded plots. Different letters denote statistical differences among treatments within growth form/origin and year ($p < 0.05$; Tukey's HSD test; uninvaded considered a treatment here). Results from ANOVA testing for differences between years within growth form/origin and treatment shown as '*p*-value for 2007 to 2010 change'. CON = no treatment; DIST = disturbed; REM = manual removal; HERB = herbicide; OUT = uninvaded.

The mean (± 1 SE) total vegetation cover per plot was 24.5% ± 2.7 in 2007 and 32.5% ± 4.07 in 2010.

	Forb		*p*-value for 2007 to 2010 change (df = 1, 16)	Grass		*p*-value for 2007 to 2010 change (df = 1, 16)
	2007	2010		2007	2010	
CON	18.7 ± 5.7^{a}	22.8 ± 6.4^{a}	0.395	81.3 ± 5.7^{a}	78.3 ± 6.7^{a}	0.533
DIST	20.8 ± 5.1^{a}	31.2 ± 6.2^{a}	0.64	79.2 ± 5.1^{a}	71.0 ± 6.8^{a}	0.175
REM	19.3 ± 4.5^{a}	26.4 ± 6.5^{a}	0.002*	80.7 ± 4.5^{a}	75.1 ± 7.0^{a}	0.375
HERB	24.0 ± 6.6^{a}	14.8 ± 5.4^{b}	0.186	76.0 ± 6.6^{a}	88.1 ± 5.6^{b}	0.010*
OUT	50.1 ± 7.1^{b}	46.2 ± 6.8^{a}	0.078	49.9 ± 7.1^{b}	54.4 ± 6.7^{a}	0.109
	Native forb		*p*-value for 2007 to 2010 change	Native grass		*p*-value for 2007 to 2010 change
	2007	2010		2007	2010	
CON	12.9 ± 3.8^{a}	13.1 ± 5.1^{a}	0.960	57.9 ± 4.7^{a}	54.6 ± 4.8^{a}	0.549
DIST	13.8 ± 3.5^{a}	17.3 ± 4.5^{a}	0.078	58.7 ± 5.2^{a}	55.7 ± 8.1^{a}	0.587
REM	11.5 ± 3.0^{a}	16.1 ± 5.1^{a}	0.231	55.5 ± 3.1^{a}	54.7 ± 6.5^{a}	0.876
HERB	18.1 ± 5.7^{a}	7.6 ± 3.7^{a}	0.030*	59.6 ± 6.4^{a}	62.0 ± 5.2^{a}	0.735
OUT	43.5 ± 6.2^{b}	38.2 ± 6.2^{b}	0.182	34.7 ± 7.3^{b}	43.4 ± 6.0^{a}	0.015*
	Non-native forb		*p*-value for 2007 to 2010 change	Non-native grass		*p*-value for 2007 to 2010 change
	2007	2010		2007	2010	
CONT	5.8 ± 2.3^{a}	8.6 ± 2.9^{a}	0.242	23.5 ± 5.3^{a}	23.7 ± 5.4^{a}	0.976
DIST	7.0 ± 1.9^{a}	11.7 ± 3.4^{a}	0.143	20.5 ± 3.9^{a}	15.3 ± 4.6^{a}	0.216
REM	7.9 ± 3.5^{a}	8.8 ± 3.7^{a}	0.821	25.1 ± 5.2^{a}	20.4 ± 4.9^{a}	0.278
HERB	6.0 ± 2.5^{a}	4.3 ± 2.1^{a}	0.388	16.4 ± 5.1^{a}	26.2 ± 6.1^{a}	0.117
OUT	6.7 ± 3.5^{a}	7.4 ± 2.8^{a}	0.827	15.2 ± 6.7^{a}	11.1 ± 5.8^{a}	0.0801

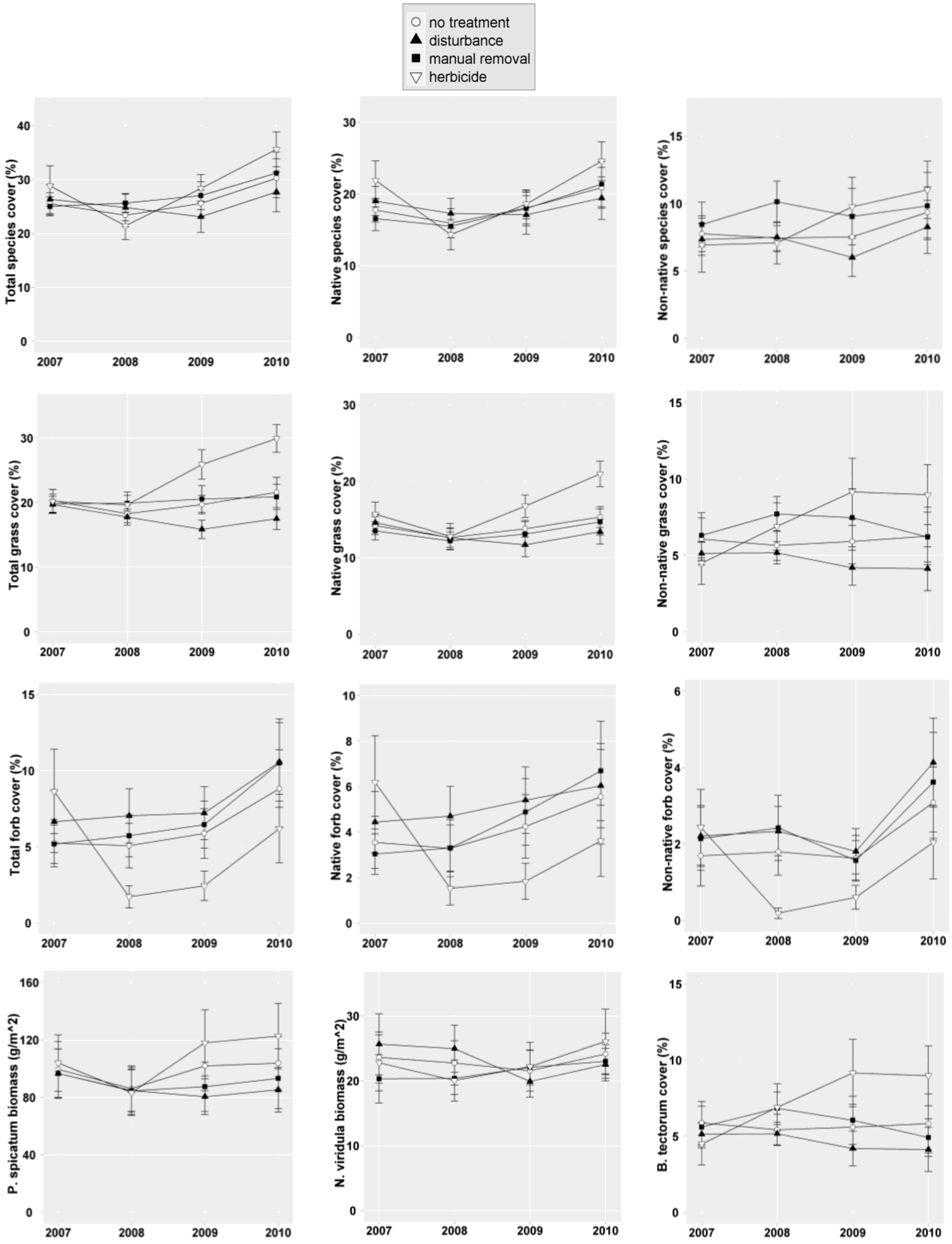

Figure 4.1. Mean (±1 SE) for response variables by treatment over time (n = 18 per treatment). 2007 values are pre-treatment. Note *C. stoebe* excluded from all metrics except *C. stoebe* cover and density.

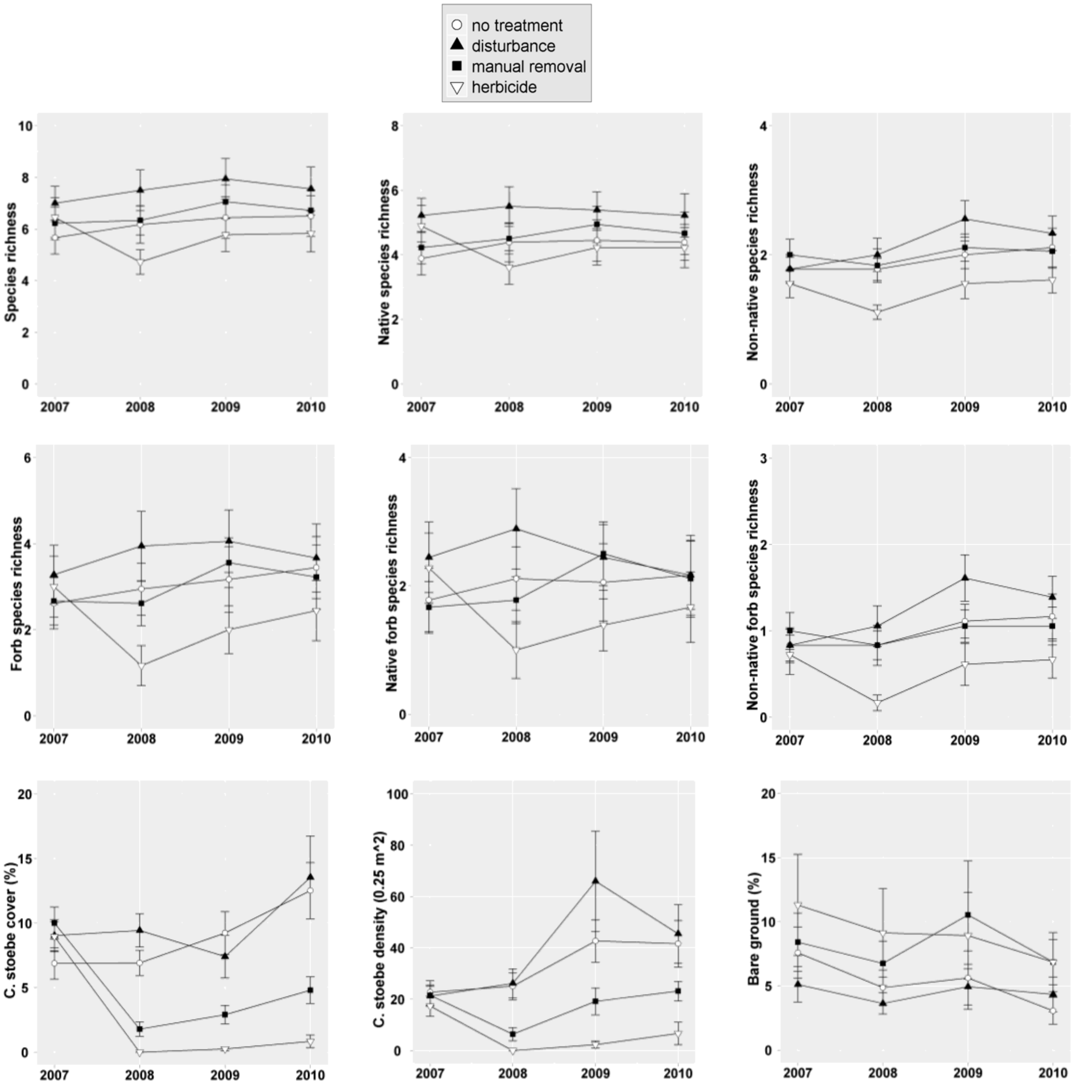

Figure 4.1 (Continued). Mean (±1 SE) for response variables by treatment over time (n = 18 per treatment). 2007 values are pre-treatment. Note *C. stoebe* excluded from all metrics except *C. stoebe* cover and density.

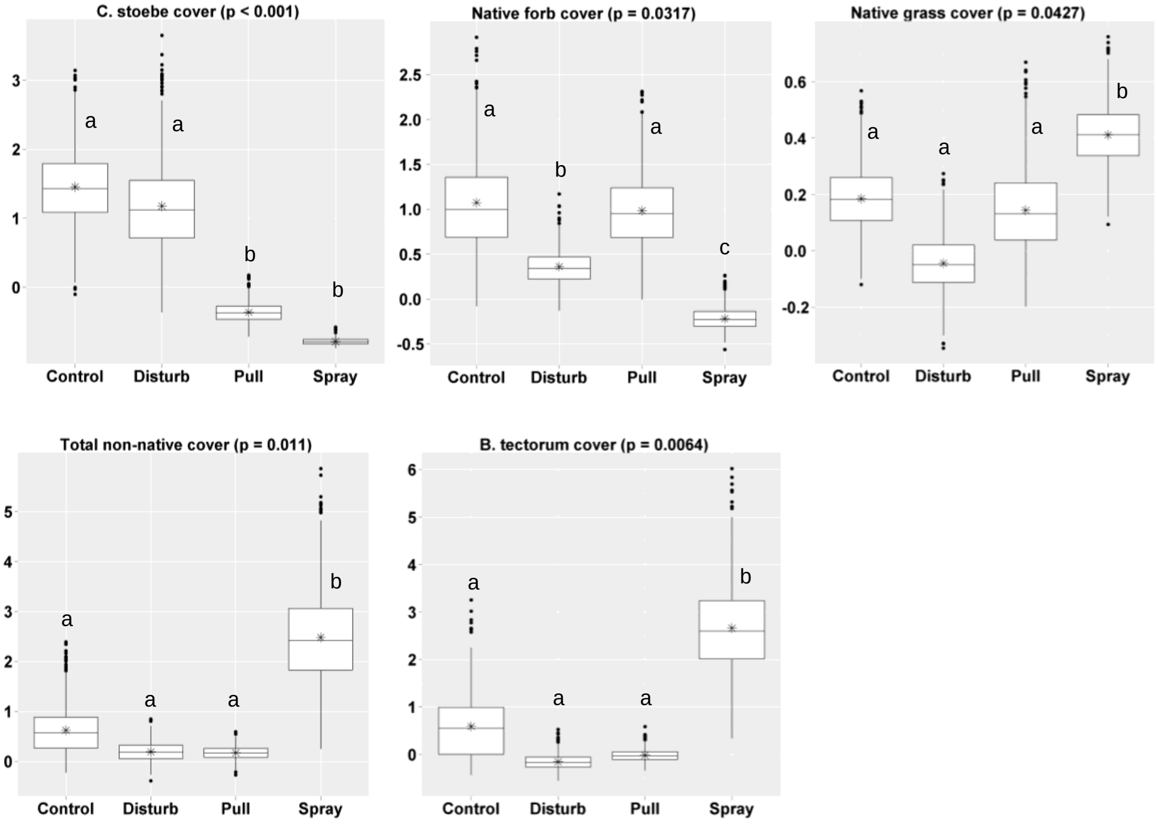

Figure 4.2. Distributions of treatment effect sizes estimated from 1000 bootstrap samples of the proportional change in the response variable from pre-treatment level to 3 years post-treatment = (2010 value – 2007 value)∕2007 value. Values on the y-axis correspond to the proportional change in the response variable; however, effect sizes are presented as a percent change in the text. Therefore, a mean effect size plotted as 1.0 indicates that the response variable increased, on average, by 100% from before treatment to 3 years after treatment. Negative values indicate an overall reduction in the response variable over time. Absolute values of response variables are shown in Fig. 4.1. *p*-values are from one-way analysis of variance examining differences in proportional change among treatments (Table 4.1 and Appendix G); only significant response values are shown here ($p < 0.05$). Note *C. stoebe* was excluded from the calculation of 'Total non-native cover'. Mean indicated by asterisk (✳). Different letters, a-c, denote significant differences among means ($p < 0.05$; Tukey's HSD test). Numerical values of mean effect sizes ± SE provided in Appendix D. 'Control' = no treatment, 'Pull' = manual removal, 'Disturb' = disturbance, 'Spray' = herbicide.

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CHAPTER FIVE

ABUNDANCE-IMPACT RELATIONSHIPS OF NON-NATIVE PLANTS: AN EXAMINATION OF *BROMUS TECTORUM* L. IN SOUTHWEST MONTANA SAGEBRUSH-GRASSLAND PLANT COMMUNITIES

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Abstract

Eradication of widespread non-native plant species is not possible; thus, management must focus on high priority areas where the risk of negative impact is greatest. If non-native plant abundance thresholds exist below which impacts are minimal, control efforts could target high-value areas where abundance exceeds this threshold. We examined impacts, and potential impact thresholds, of the non-native annual grass, *Bromus tectorum* L., in sagebrush-grassland communities of southwest Montana. We implemented three treatments (*B. tectorum* removal, small-scale disturbance, and untreated control) across a gradient of *B. tectorum* cover and quantified the response of native and non-native plant species cover and richness over three years. We hypothesized a negative relationship between *B. tectorum* cover and native species cover and richness, and a positive relationship between initial *B. tectorum* cover and the increase in these variables in response to removals. Before treatments, there were significant negative relationships between *B. tectorum* cover and total and native species cover and richness, with several non-linear relationships suggesting an impact threshold of 60% *B. tectorum* cover. After three years, *B. tectorum* cover had decreased significantly, and native cover and richness increased significantly, and to the same degree, across all treatments. There was a positive relationship between initial *B. tectorum* cover and the increase in non-native species richness in removal plots, suggesting *B. tectorum* may prevent the establishment of other non-native species. The lack of differences among treatments suggests that *B. tectorum* is not directly affecting native species abundance and diversity in these communities. Climate variability operating at larger spatial scales is more likely driving overall vegetation patterns.

Keywords: invasive plants; cheatgrass; impacts; thresholds; management; environmental variability

Introduction

Non-native plants are a threat to ecosystem integrity and biological diversity (Simberloff 2011; Vilà et al. 2011). The impacts of a non-native plant likely vary as a function of non-native plant abundance, with impacts increasing as a linear or non-linear function of non-native abundance (Parker et al. 1999; Thiele et al. 2010). Understanding these relationships is considered one of the most important research needs in invasion ecology; without this knowledge impact assessments can be grossly inaccurate (Thiele et al. 2010). Limited time, money, and personnel often make management of all non-native plant populations untenable. Therefore, tools for management prioritization are essential (Rew et al. 2007). Incorporating threshold concepts into natural resource management is one way to aid in prioritizing non-native plant populations for control efforts (Panetta and James 1999; Byers et al. 2002).

Thresholds have historically been developed and applied in agricultural systems to determine the appropriate level and timing of weed control strategies. Cousens (1987) defined three general types of thresholds applicable to weed containment strategies: (1) competition or damage threshold, which is the weed density at which yield loss begins to occur; (2) economic threshold or injury level, which denotes the point at which the cost of control measures equals the increased return on yield which would result; and (3) action or economic optimum threshold, which is the point at which control action should be initiated to avoid reaching the economic injury level. Applications of threshold concepts to wildland non-native plant management may derive basic principles from the agricultural setting, but must also address thresholds in the broader ecological context. From an ecological perspective, thresholds can be regarded as boundaries in space and time between two different states (Friedel 1991). Muradian (2001) defines thresholds as ecological discontinuities or sudden changes in any property of an ecological system that occur in response to monotonic and continuous change in an independent variable. When examining non-native plants, their colonization rates, and their potential impacts, it may be more appropriate to consider thresholds as regions or zones of transition in stochastic systems rather than discrete points (Wiens et al. 2002; Huggett 2005).

The ecological threshold concept originated from the idea that a community or ecosystem may exhibit multiple stable states or regimes (Briske et al. 2006; Groffman et al. 2006). Embedded in the ecological threshold concept is the idea of ecosystem resilience, which refers to the amount of disturbance or system modification required to move a community to a different state (Scheffer and Carpenter 2003; Briske et al. 2006). Understanding what forces may drive a system from a state to an undesirable desirable (or vice versa) and the rate at which these forces act, could be powerful information for a land manager (Suding and Hobbs 2009).

In general, transitions from one state to another may be driven by biotic or abiotic factors, or a combination of the two. The biotic mechanism is the most commonly considered, particularly in regards to non-native plants, wherein, for example, the presence of a non-native plant alters resource availability, which shifts competitive dynamics, eventually leading to a restructuring of the plant community. Abiotic mechanisms involve responses to long-term site modifications (i.e. climate change, water availability) and are more difficult to quantify due to the lag time in response (Briske et al. 2006). Applying threshold concepts to wildland non-native plant management could focus attention on communities that are moving towards an undesirable state, but for which this progression could be reversed (Panetta and James 1999; Suding and Hobbs 2009). Examining abundance-impact relationships is one important component of applying thresholds to non-native plant management (Thiele et al. 2010). A threshold of non-native plant impacts might be indicated by a non-linear relationship between non-native plant abundance and plant community metrics (i.e. species richness), exhibiting a sharp decline in the community response variable at a certain level of non-native plant abundance.

In this study, we assessed the impact, and the potential for impact thresholds, of the non-native annual grass, *Bromus tectorum* L. (cheatgrass, downy brome) on native and non-native plant species cover and richness in sagebrush-grassland communities of the Greater Yellowstone Ecosystem. *B. tectorum* is a winter annual grass that is native to Eurasia that was introduced to the western North America in the 1880s through contaminated crop seed and ship ballast (Mack 1986). A combination of anthropogenic and environmental factors enabled the rapid spread of *B. tectorum*, which is now established throughout much of the sagebrush-grassland habitat in the Intermountain west and Great Basin of western N. America (Mack 2011). *B. tectorum* has a high reproductive rate and can grow competitively in many conditions (Melgoza et al. 1990; Mazzola et al. 2008). Historically, *B. tectorum* impact studies have focused on alterations to ecosystem processes, such as increased size, frequency, and intensity of fires (Whisenant 1990; D'Antonio and Vitousek 1992; Brooks et al. 2004) and nutrient cycling (Sperry et al. 2006; Evans et al. 2001); inherent growth capabilities of *B. tectorum* (Rice et al. 1992; Svejcar 1990); and species-specific competitive effects of *B. tectorum* under controlled conditions (Harris 1967; Blank 2010; Ray-Mukherjee et al. 2011). Although it is speculated that *B. tectorum* displaces native grassland and sagebrush-steppe plant species and reduces species richness and diversity (Knapp 1996; Anderson and Inouye 2001), there is very little quantitative data from field-based experiments. Furthermore, although the importance of impact thresholds is increasingly recognized, functional relationships between *B. tectorum* abundance and plant community impacts have not been examined.

Our primary objectives in this study were to: (1) assess the impacts of *B. tectorum* on sagebrush-grassland plant communities by quantifying the response of native and non-native plant species to *B. tectorum* removal, and (2) assess if there were relationships between *B. tectorum* abundance and *B. tectorum* impacts. If the latter was true, we sought to determine the nature of these relationships (i.e. linear or non-linear), and thus whether thresholds of impact might exist.

Methods

Study Area

The experiment was conducted between May 2007 and July 2010 in the sagebrush-grassland habitat of southwest Montana. Field sites contained a mix of native and non-native plant species, and experienced moderate natural disturbance with no domestic grazing, but frequent wildlife use. Perennial grasses feature prominently, ranging between 40 to 60 percent canopy cover. Forb canopy cover typically ranges from 20 to 30 percent, and shrub canopy cover averages 5 to 10 percent. Average litter cover in these communities is 40 to 60 percent and bare ground 5 to 10 percent. Average temperatures in the study area are 19 °C in the summer and -4 °C in the winter. The average annual precipitation is 480 mm, with most falling in April, May, and June.

Experimental Design

Study sites were located between 45°31' N, 111°15' W; 45°17' N, 110°49' W; and 45°10' N, 110°51' W at elevations between 1515 and 1790 m. To examine the plant community impacts of *B. tectorum*, plots were established across a gradient in *B. tectorum* cover from < 2% to 82%, which resulted in 33 *B. tectorum* cover levels. Within each *B. tectorum* cover levels, three plots (each 0.5 × 0.5 m) were established, which were randomly assigned to one of three treatments: (1) manual removal of all *B. tectorum*; (2) ground disturbance (using hand tools) similar to that created in manual removal treatment, except with no vegetation removed; and (3) unmanipulated control. Thus, there were 33 plots per treatment that ranged from 2 to 82% *B. tectorum* cover, for an overall total of 99 plots. The ground disturbance treatment was used as a second control to allow a distinction between responses due to the absence of *B. tectorum* (in removal plots) from responses due to the ground disturbance created in the process of removing *B. tectorum*. Within *B. tectorum* cover level, plots were established to maximize the similarity among treatments in terms of canopy cover, percent bare ground, ratio of forbs to grasses, and species richness. Plots were separated by at least 1 m within populations (patches) of *B. tectorum*.

Data Collection

We visually estimated the canopy cover of each species for each plot in June 2007, after which treatments were implemented. Due to multi-layer canopies, total per-plot cover could exceed 100%. Individual species were subsequently categorized as native forb, non-native forb, native grass or non-native grass. We calculated the total summed cover of native forbs, non-native forbs, all forbs, native grasses, non-native grasses, and all grasses per plot. We calculated the species richness for each of the growth form/origin categories per plot as well. Percent cover data were collected annually from 2007 through 2010 between 20 June and 20 July. We compared the change in response variables among (1) no treatment, (2) manual removal, and (3) disturbance.

Data Analysis

The response variables examined were percent cover of: total, native, non-native, forb, native forb, grass, native grass, and litter; and richness of: total, native, non-native, and native forb species. *B. tectorum* was excluded from all response variable calculations.

Regression was used to identify relationships between the initial values (pre-treatment) of response variables and *B. tectorum* percent cover and to identify potential impact thresholds (i.e. a regression relationship in which a relatively flat relationship between *B. tectorum* cover and the response variable is followed by point (or zone) of steep increase or decrease in the response variable). Linear, quadratic and cubic models were examined and compared using Akaike Information Criterion (AIC) and residual error values. The model form with the lowest AIC value and residual error was considered the best fit. Initial cover values were square root transformed, and richness values log transformed, to meet parametric assumptions of normality and constant variance of errors among treatments. The overall analysis methodology follows a similar approach used by Gooden et al. (2009) and Drinnin (2005).

To assess the impacts of *B. tectorum*, and distinguish these impacts from those originating from the disturbance of removing *B. tectorum*, we used analysis of variance to test for differences among the three treatment groups within each year, 2007 and 2010. We also used ANOVA to determine whether there were differences in the change in the response variable from pre-treatment to three years post-treatment among the three treatments. Finally, we assessed potential impact thresholds based on the experimental manipulations by modeling the change in the response variable as a function of the initial *B. tectorum* percent cover. In this assessment of the change values, we again examined both linear and non-linear models, and determined the best fit using AIC and residual error values. Curves of the best model fit for each response variable showing a significant relationship were plotted against initial *B. tectorum* cover to identify the presence of zones where the response variable decreased dramatically, indicating potential thresholds (Drinnan 2005; Gooden et al. 2009).

Results

Initial Conditions and Relationships between Response Variables and *B. tectorum* Cover

At the beginning of the experiment (pre-treatment, 2007), there were no significant differences among the treatment groups for any response variables (Figure 5.2). Before treatment, there were significant negative relationships between *B. tectorum* percent cover and total species cover, native species cover, forb cover, native forb cover, grass cover, native grass cover, total species richness, native species richness, and native forb species richness (Figure 5.1). Linear regressions best described the decrease in cover of native species, forbs, native forbs, native grasses, and species richness of native forbs as *B. tectorum* cover increased, as indicated by the lowest AIC and residual error (Table 5.1). Although non-linear models were significant for the relationships between *B. tectorum* cover and total cover, grass cover, and total and native species richness, the differences in AIC values between the linear and cubic fits were minor (Table 5.1). Thus, the less parsimonious cubic models were not justified.

Response to Treatments

Three years after treatment, total vegetation cover and total, native, and non-native species richness had increased significantly compared to pre-treatment levels ($P \leq 0.01$) (Figure 5.2). However, there were no significant differences in the change in response variables from pre-treatment to three years post-treatment among the treatments for any response variable. The absolute values of response variables three years after treatment also were not significantly different among treatments, meaning that the response variables that increased from the beginning to the end of the experiment did so regardless of *B. tectorum* removal or ground disturbance (Figure 5.2). Native cover increased significantly over the three year period, but only with disturbance and no treatment (*P* = 0.017 and 0.041, respectively). Native forb richness increased significantly over the three year period, but only in the disturbance treatment (*P* = 0.025). Unexpectedly, *B. tectorum* cover decreased significantly from before treatment to three years after treatment equally across all treatments (*P* < 0.001; Figure 5.2).

Relationships between Change in Response Variables and *B. tectorum* Cover

Most of the significant negative relationships that were detected between *B. tectorum* cover and response variables before treatment (Table 5.1, Figure 5.1) were not maintained with the change in response variables from before treatment to three years after treatment (Table 5.2, Figure 5.3). The only response variables for which the change from pre-treatment to three years post-treatment was significantly related to *B. tectorum* cover were: total and non-native species richness in disturbance treatments (linear increase for total, *P* = 0.006; and cubic increase for non-native, *P* < 0.001 with sharp increases between 0 and 20% and beyond 60% *B. tectorum* cover; Figure 5.3) and non-native species richness in *B. tectorum* removal treatments (significant linear increase, *P* = 0.005). Approximately 22% of the variation in the change in total species richness in disturbance treatments, 23% of the variation in the change in non-native species richness for manual removal treatments, and 49% of the variation in the change in non-native species richness for disturbance treatments was explained by *B. tectorum* cover (Table 5.2).

Discussion

The significant negative relationships observed between *B. tectorum* cover and native and non-native species cover and richness at the outset of the experiment suggested that *B. tectorum* was having significant impact on plant community characteristics, and that these impacts were greater at higher *B. tectorum* cover.

Based on the hypothesis that *B. tectorum* negatively affects native plant cover and richness in sagebrush-grassland plant communities, we expected to see significant increases in these response variables in *B. tectorum* removal plots, particularly relative to the unmanipulated controls. Furthermore, based on the initial regression findings, we expected to see positive relationships between *B. tectorum* cover and the change in response variable three years after *B. tectorum* removal, which would provide causal evidence of density-dependent impacts and potential impact thresholds. Thus, it was surprising to find, three years after treatment, no significant differences in any response variables among treatments. Based on a common assumption that competitive non-native plants, such as *B. tectorum*, rapidly increase in abundance once they are established, it was particularly unexpected that *B. tectorum* cover decreased significantly, and to the same degree, across all treatments. Thus, as in the pre-treatment conditions, there were still no significant differences in *B. tectorum* cover among treatments at the end of the experiment. Several implications of these results are that, in these sagebrush-grassland communities, *B. tectorum* is not steadily and consistently increasing in abundance over time and, at the current, fluctuating cover levels, *B. tectorum* is not exerting significant impacts on most plant community characteristics.

The significant decrease in *B. tectorum* cover coincident with significant increases in total and native cover and native and non-native species richness indicate that *B. tectorum*, at this stage in these communities, is a passenger, rather than a driver, of the changes in plant community structure quantified in this experiment. Any local-scale community effects of *B. tectorum* are likely being swamped by biotic and abiotic factors and variability operating at broader spatial scales and, therefore, affecting the communities regardless of *B. tectorum* presence or abundance. The climate before and during the experiment may have been an important factor underlying the high *B. tectorum* cover in 2007, the significant decrease in *B. tectorum* cover by 2010, and the significant increases in native cover and richness over the course of the experiment. In 2006 and 2007, annual temperatures were 1.5° C warmer than average, precipitation was 10.5 mm less than average, and there were substantially more growing degree days (approximately 2100 compared with the 20th century average of 1620). Subsequently, 2008 through 2010 were cooler and wetter, with temperature close to average and higher than normal precipitation in 2008 and substantially higher precipitation in 2010 (470 mm compared to the 20th century average of 389 mm) (NOAA 2012). Decreased precipitation, particularly in the summer, has been linked to an increased likelihood of *B. tectorum* invasion and range expansion, and increased precipitation is linked to a decreased likelihood (Bradford and Lauenroth 2006; Bradley 2009).

Our findings highlight the fact that studies in natural plant communities are inevitably affected by climatic variability; thus, multi-year studies are imperative. While our study lasted only four years, this is actually relatively long for most non-native plant impacts studies (Kettenring and Adams 2011). By following the same study plots over the course of four years, we were able to document some of the plant community fluctuations that are, at least in part, a response to inter-annual climate variability. Observational studies using space-for-time substitution are the most common type of non-native plant impact study (Chapter 2) and this methodology will continue to be necessary due to the logistical constraints of longer-term experimental studies. However, that these studies are a snapshot in time (i.e. one-time sampling across a large spatial area) should be borne in mind in their interpretation, particularly when quantifying a relationship between vegetation patterns and non-native plant abundance. Had we relied solely on the relationships between *B. tectorum* cover and the cover and richness of the rest of the plant community observed in 2007 (a year marked by, and preceded by, above average temperatures and below average precipitation), we would have drawn dramatically different overall conclusions. The variation in population dynamics and episodic nature of non-native plant populations are several major obstacles to applying threshold concepts to non-native plant management in natural ecosystems (Panetta and James 1999).

Managing non-native plants has become a major component of biological conservation and ecosystem restoration programs. Effective and efficient non-native plant control strategies and restoration efforts require understanding the processes driving non-native plant impacts. An important factor in these processes is the relationship between non-native plant abundance and biologically significant impacts. Examining the functional form of these relationships can identify thresholds of impact, which can be useful information for initiating and targeting management efforts. If, in response to climate change and/or other promoting factors, *B. tectorum* steadily and consistently increases throughout the sagebrush-grasslands in this region, relationships between *B. tectorum* abundance and plant community response variables identified in our initial regression analyses may be useful for management.

At this late stage of *B. tectorum* invasion in western North America, eradication, or even control across a significant portion of the invaded range, is unrealistic. Thus, prioritization and optimization strategies are necessary to focus management efforts on areas of high conservation or production value that are most likely to experience significant impacts (Rew et al. 2007). Multi-year monitoring of impacts across a range of conditions, including non-native plant abundance, is crucial to developing these strategies.

There is growing evidence that native plant species of sagebrush and grassland habitats of western N. America can be competitive against non-native annual grasses (Seabloom et al. 2003; Corbin and D’Antonio 2004; Leger 2008; Goergen et al. 2011). It is also documented that non-native annual grasses, such as *B. tectorum*, have a low probability of establishing in relatively intact sagebrush-grassland communities (Anderson and Inouye 2001; Chambers et al. 2007). Furthermore, common herbicides used to control *B. tectorum* and other non-native annual grasses can cause significant undesirable non-target effects in native plant communities (Elseroad and Rudd 2011; Owen et al. 2011). Collectively, this knowledge underscores the need for consistent, long-term (i.e. > 2 years) field monitoring of non-native plant populations to determine whether, and in what context, non-native plants have biologically significant impacts and whether the outcomes of management actions will benefit the overall land management goals.

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Table 5.1. Linear and cubic regression model output for relationships between *B. tectorum* cover (%) and pre-treatment (2007) percent cover (total, native, non-native, forb, native forb, grass and native grass), species richness (total, native, non-native and native forb) and percent litter cover ($n = 99$). Values in bold denote the lowest Akaike Information Criterion (AIC) and residual error values and, thus, the model with the best fit. * indicates statistical significance ($P < 0.05$). Scatter plots of data and best fit regression line shown in Fig. 5.1. Note *B. tectorum* was excluded from all response variable calculations.

Response variable	Model type	
	Linear	Cubic
Total species cover (%)		
R^2	0.104	0.143
P	0.001*	0.002*
Residual error	1.34	1.31
AIC	340.45	340.16
Native species cover (%)		
R^2	0.104	0.136
P	0.001*	0.003*
Residual error	1.45	1.44
AIC	358.66	359.06
Non-native species cover (%)		
R^2	0.008	0.010
P	0.384	0.815
Residual error	1.48	1.50
AIC	363.00	366.80
Forb cover (%)		
R^2	0.043	0.043
P	0.039*	0.232
Residual error	1.86	1.88
AIC	407.57	411.48
Native forb cover (%)		
R^2	0.048	0.059
P	0.029*	0.118
Residual error	2.04	2.05
AIC	426.21	428.99

Table 5.1 Continued.	Linear	Cubic
Grass cover (%)		
R^2	0.086	0.131
P	0.003*	0.004*
Residual error	1.55	1.53
AIC	371.59	370.56
Native grass cover (%)		
R^2	0.067	0.074
P	0.009*	0.060*
Residual error	0.70	1.68
AIC	386.30	389.58
Litter cover (%)		
R^2	0.254	0.317
P	<0.001*	<0.001*
Residual error	13.52	13.07
AIC	800.55	795.85
Total species richness		
R^2	0.167	0.213
P	<0.001*	<0.001*
Residual error	0.43	0.42
AIC	118.81	117.15
Native species richness		
R^2	0.196	0.230
P	<0.001*	<0.001*
Residual error	0.46	0.45
AIC	130.82	130.52
Non-native species richness		
R^2	0.014	0.040
P	0.244	0.269
Residual error	0.28	0.28
AIC	35.40	36.73
Native forb species richness		
R^2	0.152	0.158
P	<0.001*	<0.001*
Residual error	0.67	0.68
AIC	206.16	210.11

Table 5.2. P-values from regression models for the relationship between *B. tectorum* cover (%) and the change in response variables from pre-treatment (2007) to three years post-treatment (2010) for each treatment. All values are from linear models unless otherwise noted. Values in bold denote the lowest AIC and residual error and, thus, the model with the best fit. * indicates statistical significance ($P < 0.05$). Scatter plots of data and best fit regression line shown in Fig. 5.3.

No treatment	Manual removal	Disturbance
Change in total cover (%)		
$P = 0.270$	$P = 0.26$	$P = 0.30$
Change in native species cover (%)		
$P = 0.654$	$P = 0.72$	$P = 0.48$
Change in non-native species cover (%)		
$P = 0.202$	$P = 0.17$	$P = 0.69$
Change in forb cover (%)		
$P = 0.458$	$P = 0.47$	$P = 0.89$
Change in native forb cover (%)		
$P = 0.484$	$P = 0.80$	$P = 0.97$
Change in grass cover (%)		
$P = 0.207$	$P = 0.23$	$P = 0.19$
Change in native grass cover (%)		
$P = 0.477$	$P = 0.84$	$P = 0.15$
Change in litter cover (%)		
$P = 0.227$	$P = 0.40$	$P = 0.90$
Change in total species richness		
$P = 0.435$	$P = 0.59$	linear: $P = 0.006$*, $R^2 = 0.22$, residual error = 2.17, AIC 151.54; cubic: $P = 0.016$, $R^2 = 0.30$, residual error = 2.22, AIC = 152.07
Change in native species richness		
$P = 0.773$	$P = 0.71$	$P = 0.219$
Change in non-native species richness		
$P = 0.359$	linear: $P =0.005$*, $R^2 = 0.23$, residual error = 1.09, AIC 104.08; cubic: $P = 0.02$, $R^2 = 0.29$, residual error = 1.09, AIC = 105.25	linear: $P < 0.001$*, $R^2 = 0.39$, residual error = 1.09, AIC = 103.09; cubic: $P < 0.001$*, $R^2 = 0.49$, residual error = 1.02, AIC = 100.97
Change in native forb species richness		
$P = 0.9876$	$P = 0.92$	$P = 0.47$

Vegetation cover (%)

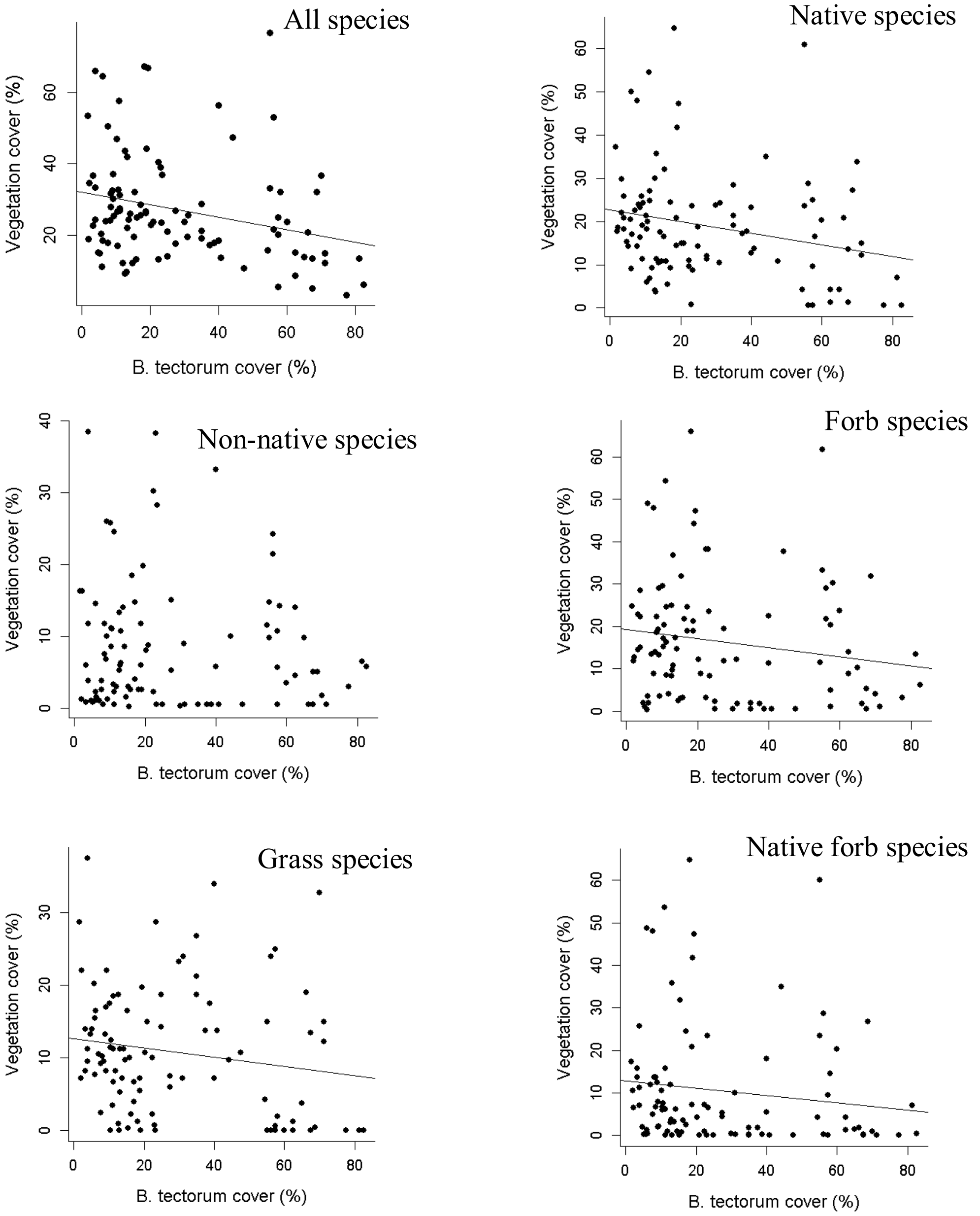
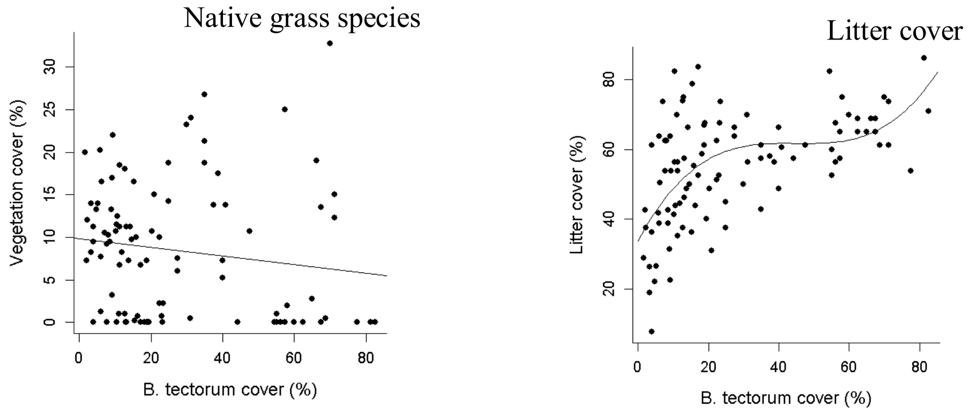


Figure 5.1. Relationships between initial levels of response variables (pre-treatment, 2007) and *B. tectorum* percent cover. Best fit regression lines based on model output in Table 5.1. Note *B. tectorum* was excluded from all response variable calculations.



Species richness

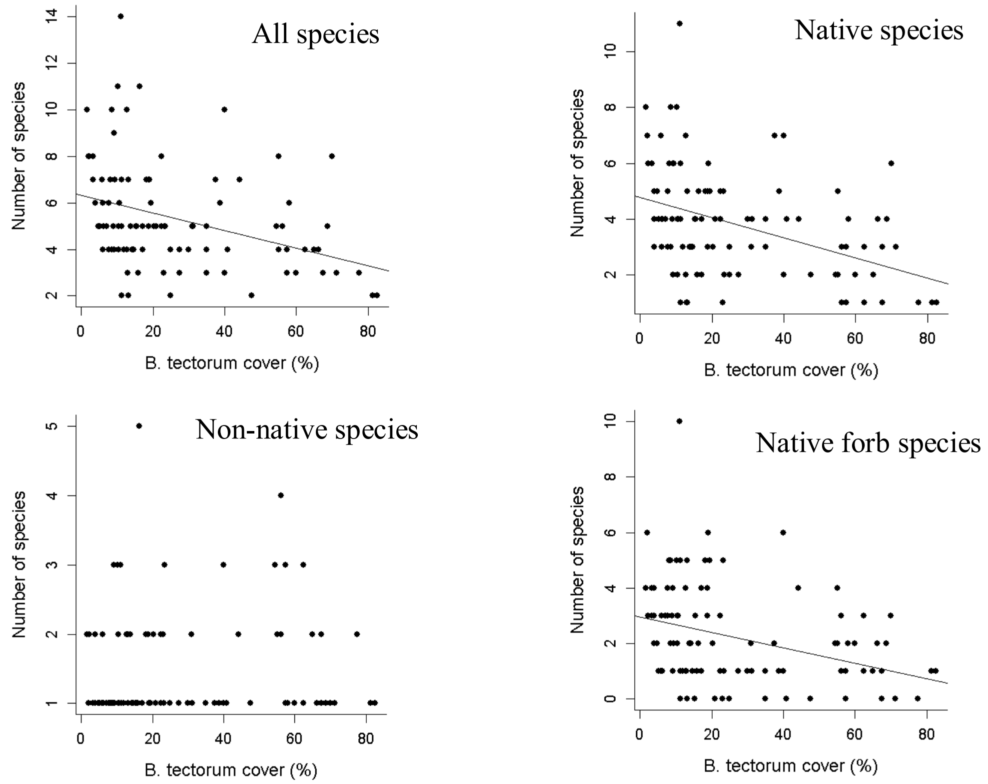


Figure 5.1 Continued.

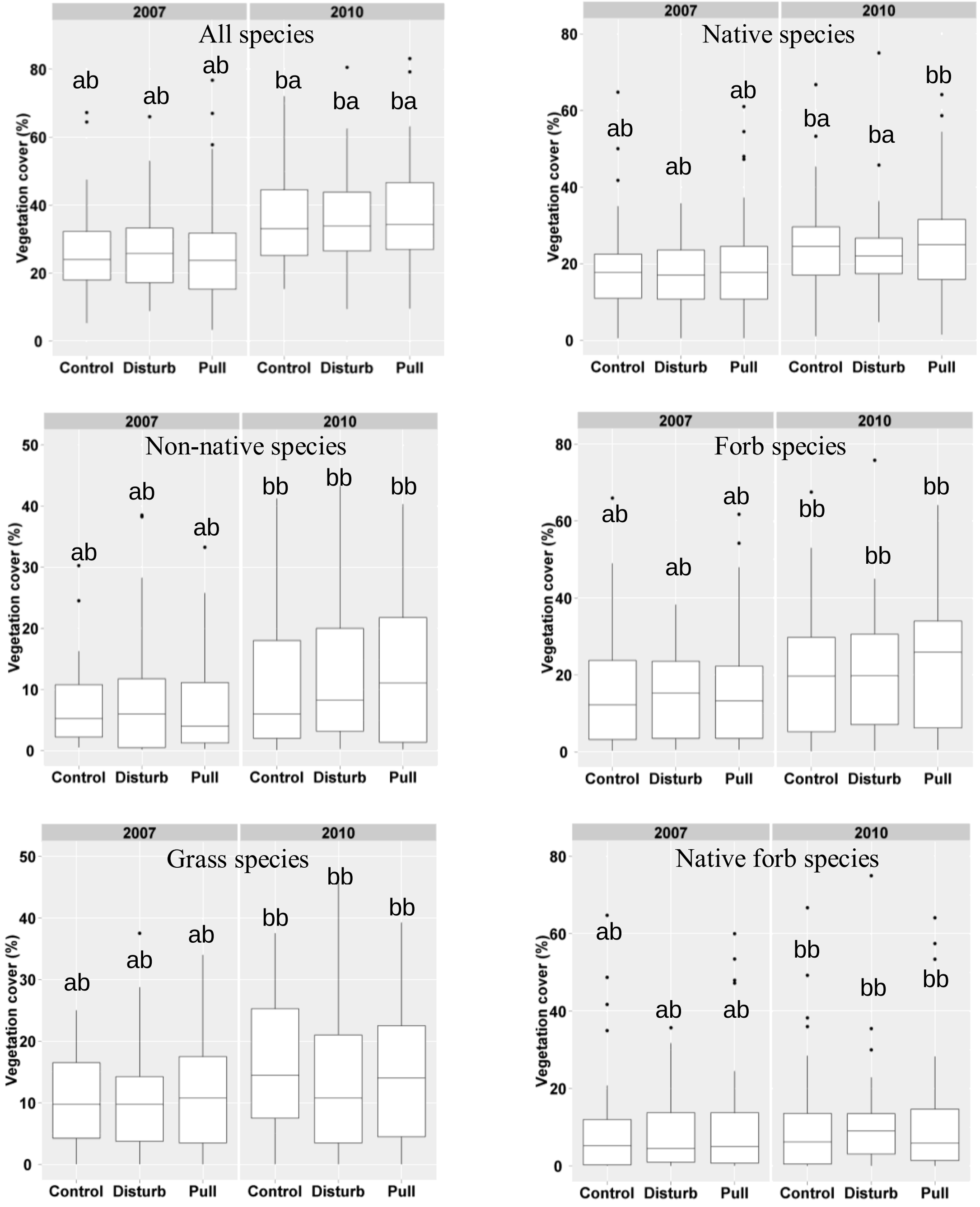


Figure 5.2. Distribution of absolute values of response variables by treatment and year. The first letter (*a* or *b*) denotes a significant difference ($P < 0.05$) among treatments within year. The second letter (*a* or *b*) denotes a significant difference between years within treatment (i.e. native cover in manual removal (pull) treatments in 2007 vs. native cover in manual removal treatments in 2010). There were no significant differences among treatments for the "change in" value (2010 value − 2007 value) for any response variables (data not shown). Note *B. tectorum* was excluded from all response variable calculations.

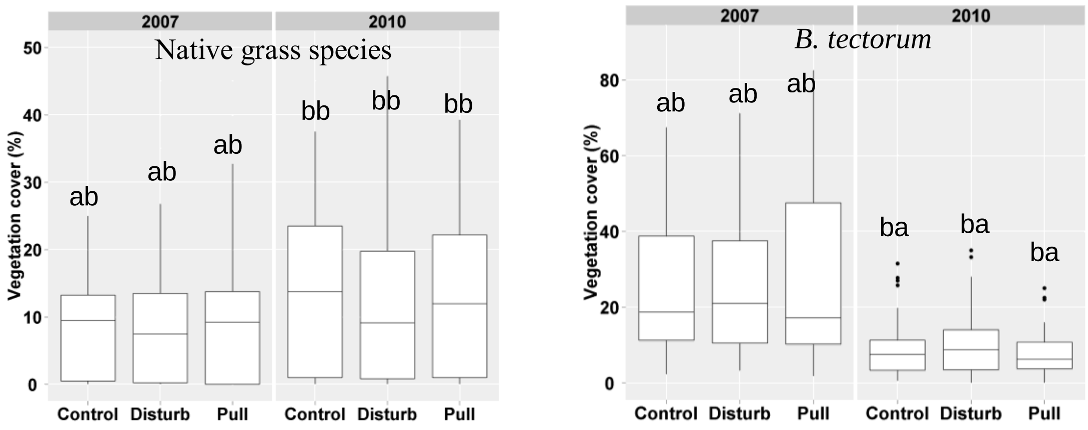


Figure 5.2 Continued.

Change in vegetation cover (%)

No treatment (○) ***B. tectorum*** **removed (△) Disturbance (+)**

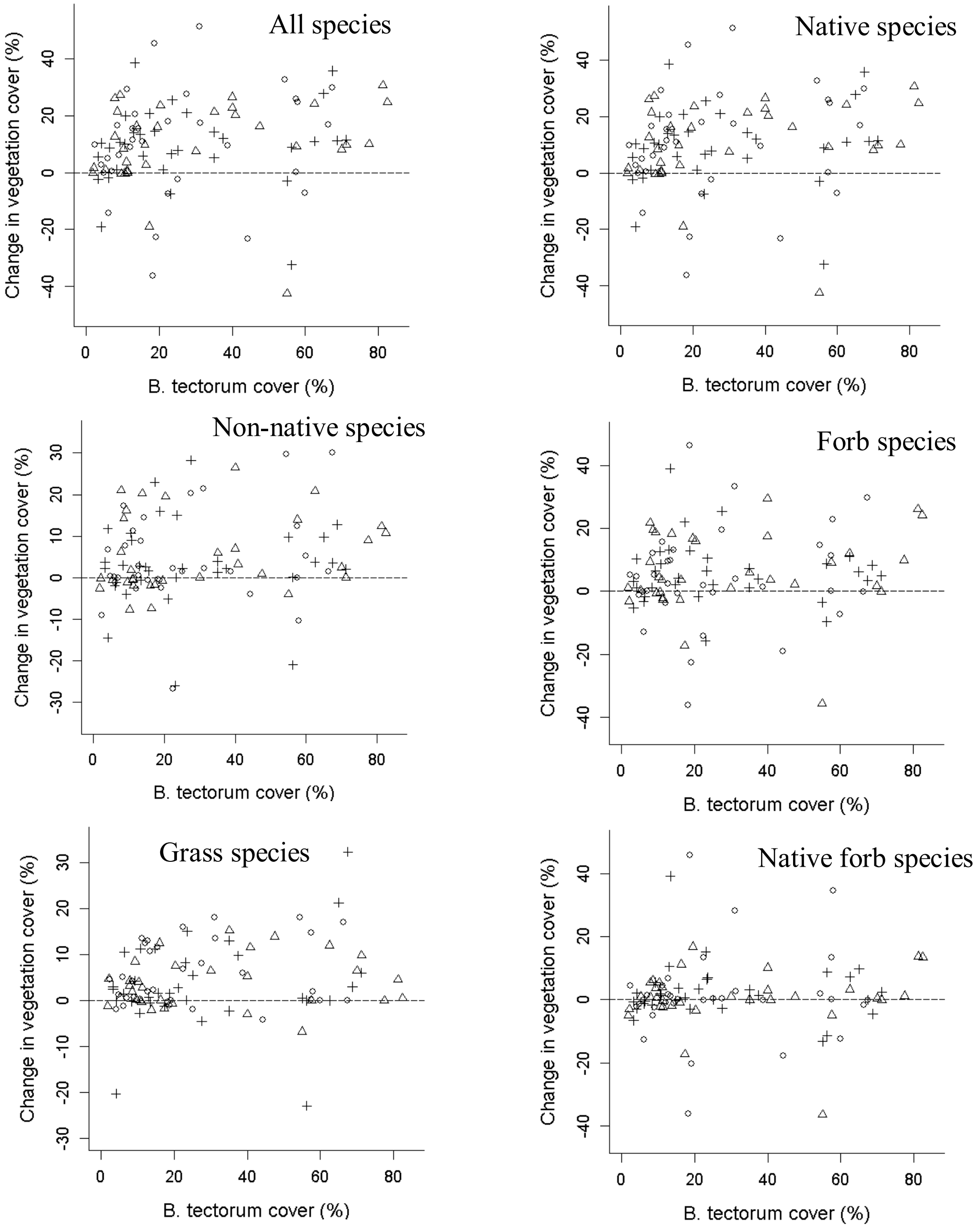
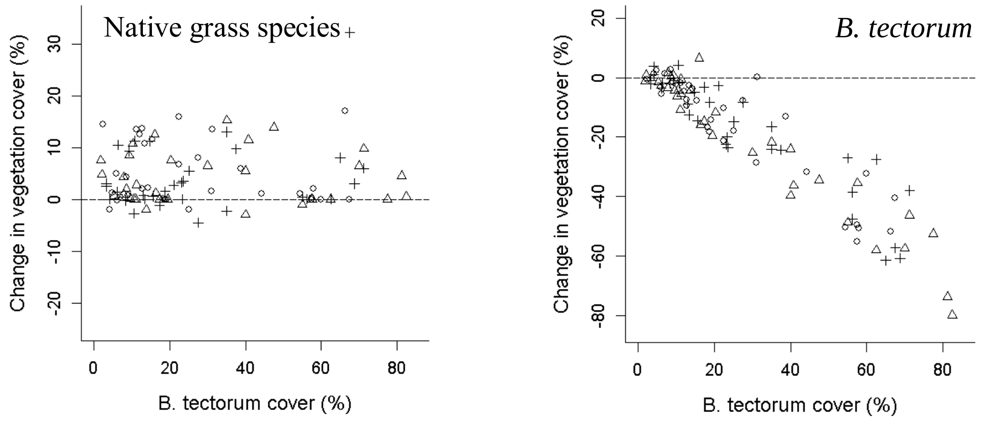


Figure 5.3. Relationships between the changes in response variables from pre-treatment levels (2007) to three years post-treatment as a function of initial *B. tectorum* percent cover.

No treatment (○) ***B. tectorum*** **removed (△)** **Disturbance (+)**



Species richness

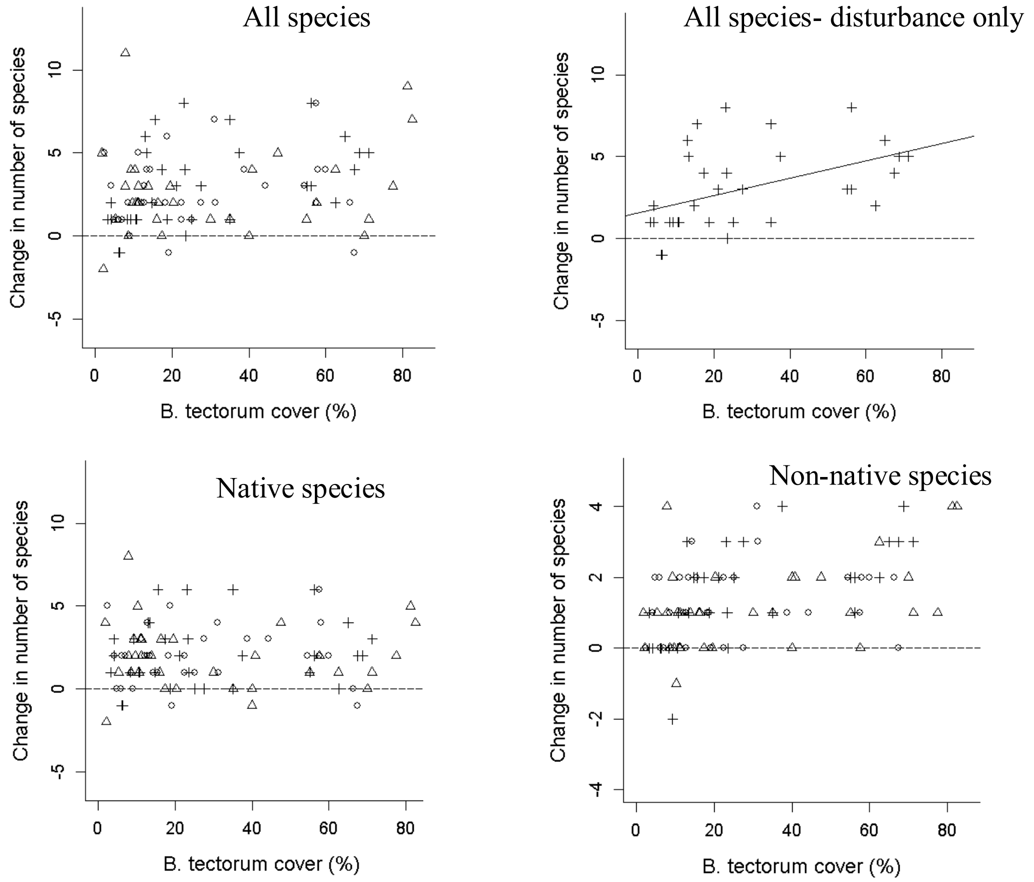


Figure 5.3 Continued.

No treatment (○) ***B. tectorum*** **removed (△)** **Disturbance (+)**

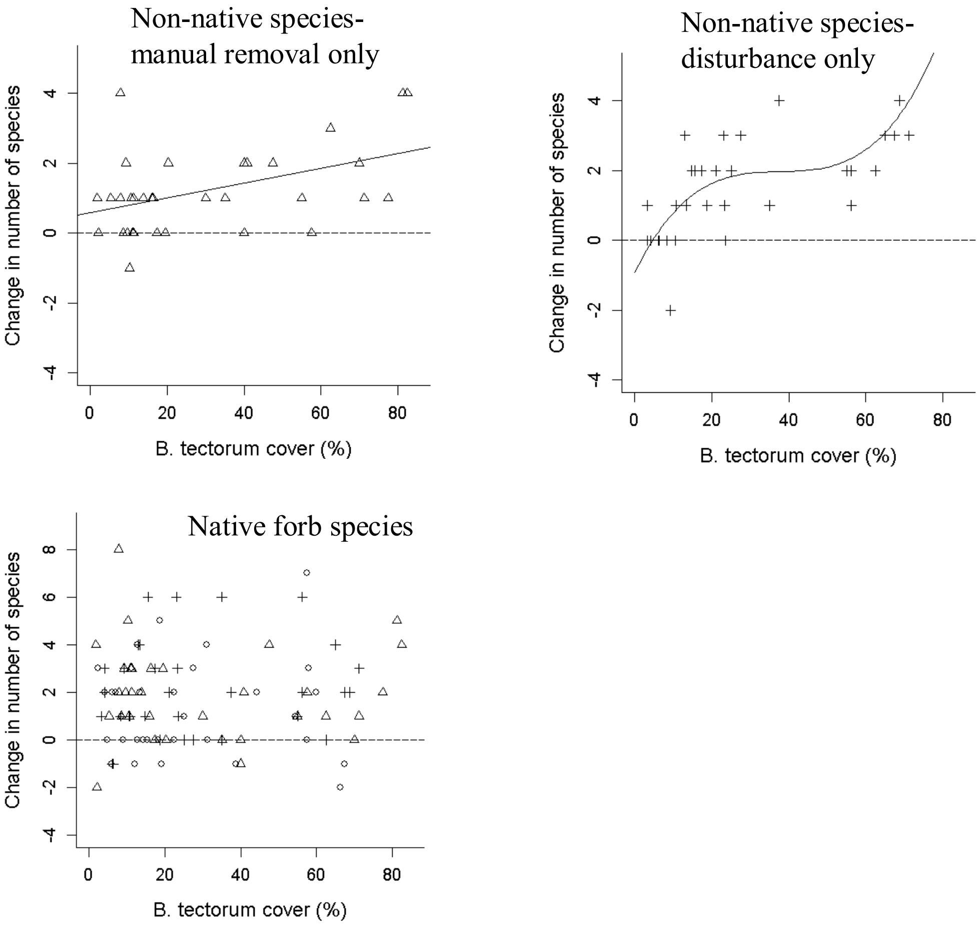


Figure 5.3 Continued.

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CHAPTER SIX

CONCLUSIONS

This dissertation has examined ecological impacts of non-native plants through a review and synthesis of previous experimental research, and field-based experiments in plant communities of the GYE. Below I outline the major findings from each chapter.

Chapter Two was an in-depth review and synthesis of ecological impacts of non-native plants based on experimental research from 2001 through 2010. One of the more significant findings of this review was the prevalence of context-specificity--not all non-native plant populations had significant impacts in all situations. In fact, only half of all experiments we reviewed (*n* = 696) showed significant effects of non-native plants, and at least 10% of these could be considered beneficial or facilitative outcomes. Impacts varied across different native and non-native species, environmental conditions and circumstances--a finding that can be very useful for management prioritization. Contrary to common assumptions, native plants often competed successfully against non-native plants, underscoring the importance of maintaining remnant native plant populations (Leger 2008). Removal experiments often led to secondary invasion by other undesirable non-native plant species. Thus, management of non-native plants can shift a community further from conservation goals than the presence of the non-native plants themselves. These findings are an excellent counterpart to a recent review of invasive plant control experiments (Kettenring & Adams 2011) that showed many control programs have been unsuccessful, and even counterproductive. Together, these two reviews forge a more complete picture of the consequences of non-native plants and their management.

Our review of non-native plant impacts provides support for the assertion that in many situations, reductions in native populations are driven by other environmental stressors, such as anthropogenic disturbance, rather than competition from non-native plants (Didham et al. 2005). Although impact assessment methodologies are improving, there are still very few attempts to distinguish the impacts of non-native plants from the effects of other drivers of environmental change. This will be a critical area for future research as the sources and extent of global change steadily increase. Land use change and disturbance history are inextricably linked to the invasion of non-native plants, and; therefore, without properly designed multi-factor experiments, the ultimate cause of ecological changes, such as reduced species diversity, will be confounded.

Chapter Three provided an updated appraisal (since Levine et al. 2003) of mechanisms underlying non-native plant impacts based on a thorough review of experimental research from 2001 through April 2011. Approximately half of all experimental non-native plant impact studies from this period included an explicit examination of mechanisms, resulting in an inclusion of 58 studies in our review. Significant advances have been made in experimental methods, particularly with designs enabling the important distinction between impacts caused by direct competition and those arising from non-trophic interactions, such as habitat modification. Contrary to common assumptions, direct competition for resources was not well-supported as a mechanism underlying non-native plant impacts. Rather, impacts were often the result of non-trophic interactions, such as altered light availability, temperature and litter dynamics. We detailed the methods and findings for a number of other commonly investigated mechanisms, including altered plant-pollinator interactions, allelopathy, apparent competition and nutrient dynamics. The integration of non-native plants into native plant-pollinator networks was frequently examined, but outcomes varied among studies. Although manual application of non-native pollen to native flowers typically reduced native plant reproduction, this amount of non-native pollen was rarely found under field conditions. Alteration of belowground communities by non-native plants was a driver of impacts on soil properties, native plant growth and invertebrate populations. In addition, experimental results provided some support for allelopathy and apparent competition, but also indicated that other suppressive mechanisms may be operating simultaneously.

Our review of mechanistic impact studies revealed that recruitment limitation is often the most significant barrier to native plant population growth, and that these limitations can be, but are not necessarily, associated with the presence of non-native plants. The evidence also indicates that non-native plants are not always superior competitors, but rather are better able to rapidly colonize disturbed areas and, due to rapid growth and high fecundity, can achieve densities much greater than those of native vegetation. Summarizing the latest research allowed us to identify several avenues for productive future research, such as whether altered ecosystem processes are a mechanism imapcting individual species and communities. The research described in our review of mechanisms could help move the discussion of non-native plant impacts, and impacts of disturbance more generally, from observation-based theories towards an empirically-derived framework.

In Chapter Four, the plant community impacts of *C. stoebe* were assessed and compared with the impacts of herbicide treatment of *C. stoebe* in a three-year experiment in sagebrush-grassland communities of southwest Montana. We found that the broadleaf herbicide, picloram, was highly effective at reducing *C. stoebe*, but also resulted in a significant loss of native forb cover and a significant increase in non-native grass cover, primarily *Bromus tectorum*. There was a significant increase in native forb cover in response to manual removal of *C. stoebe*, which would seem to indicate *C. stoebe* had been suppressing native forbs. However, there was an equivalent increase in native forb cover with no treatment. Thus, in some communities, *C. stoebe* appears to have a negligible effect on native forb and grass cover and richness. Depending on management objectives, the loss of native forb cover and potential secondary invasion may outweigh the benefits of reduced target non-native plant abundance. Thus, this study highlighted several ecological tradeoffs to consider when managing non-native pants in natural areas. The results indicate that it is possible for communities to maintain ecological value (i.e. native species, forage production, wildlife habitat) despite the presence of this ubiquitous non-native plant. In our study system, the common herbicide used to control *C. stoebe* affected the plant community much more than *C. stoebe* itself, by decreasing the cover and richness of native forbs and increasing the cover of undesirable non-native grass.

One of the important factors in whether and to what degree non-native plant populations will have a significant impact is their abundance. Identifying relationships between non-native plant abundance and impacts could help inform natural resource management and decision-making. In Chapter Five we continued our examination of non-native plant impacts, here with the additional inquiry of how impacts might be related to non-native plant abundance in natural plant communities and the possibility of detecting impact thresholds. In a three-year manipulative field experiment focused on the non-native annual grass *Bromus tectorum* L., we hypothesized a negative relationship between *B. tectorum* cover and native species cover and richness, and a positive relationship between initial *B. tectorum* cover and the increase in these variables in response to *B. tectorum* removal. Before treatments, there were significant negative relationships between *B. tectorum* cover and total and native species cover and richness. After three years, *B. tectorum* cover had decreased significantly, and native cover and richness increased significantly, and to the same degree, across all treatments. There was a positive relationship between initial *B. tectorum* cover and the increase in non-native species richness in *B. tectorum* removal plots, suggesting *B. tectorum* may prevent the establishment of other non-native species. The lack of differences among treatments suggests that *B. tectorum* is not directly affecting native species abundance and diversity in these communities. Climate variability over the four-year experiment was likely an important factor in the vegetation patterns and treatments responses we observed. From this multi-year examination of *B. tectorum* in natural plant communities, we concluded that assessments of impact and impact thresholds should not be based solely on single point-in-time observations of plant communities given the significant year-to-year variability. Furthermore, the abundance of non-native plants may be correlated with environmental variation, thereby confounding the relationship between invader abundance and impact. Thus, models estimating invader impacts should include not only invader abundance, but also potentially significant environmental covariates, such as slope, elevation, and habitat type (Thiele et al. 2010).

Overall this dissertation research shows that non-native plants often have minimal impacts, native plants are often competitive against non-natives, and non-native plant removal often leads to secondary invasion. Thus, management of non-native plants can shift a community further from conservation goals than the presence of the non-native. Furthermore, our findings support the assertion that in many situations, reductions in native populations are driven by other environmental stressors, such as anthropogenic disturbance, rather than competition from non-native plants. The context-dependent nature of impacts suggests that surrogate measures and observational approaches may not accurately characterize non-native plant impacts and underscores the need for experimental, multi-level studies. As non-native plants continue to establish and spread, the burden of managing invasions with finite resources increases. Prioritizing management and developing ecologically effective strategies requires an understanding of the variability and underlying mechanisms of impact (Levine et al. 2003; Smith et al. 2006). In addition, if management objectives include maintaining viable native populations, knowing what constrains their growth—and whether non-native plants play a role in this—would benefit conservation and restoration efforts (Didham et al. 2007). There is strong evidence from a number of studies, including those in this dissertation, that plant communities can remain relatively intact despite the presence of non-native plants. Thus, management actions must be approached cautiously to avoid the loss of important native components.

Future Directions

An important follow-up line of inquiry for impact assessment and identification of impacts thresholds is the need to conduct quantitative research across a range of environments. Ideally, if we can determine important biotic and abiotic factors underlying the variability in impacts, we can better predict where on the broader landscape impacts are likely to be the highest (Rew et al. 2007). While this was an original goal of this research, it was challenged by the current lack of non-native plant populations across sufficient gradients.

Finally, there is a growing recognition that in many situations non-native plants are not the underlying drivers of ecosystem change. Nevertheless, management generally remains focused on reducing or eliminating non-native plant populations. Appropriate, effective and efficient natural resource management will depend in large part on determining whether non-natives plants are a primary cause for native species decline, a contributing factor for a species already hindered by disturbance and/or recruitment limitation, or merely a passenger of other environmental changes (Hobbs and Humphries 1995; Gurevitch and Padilla 2004; MacDougall and Turkington 2005). While these concepts are slowly influencing the design of impacts research, future studies that include ecological context and interacting factors will further this goal.

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EPILOGUE

What a fascinating journey this has been. I am deeply grateful to my co-advisors, Bruce Maxwell and Lisa Rew, for giving me the opportunity and freedom to explore and be involved in so many different facets of plant ecology and invasive plant management. I still love science and ecology, my mind is filled with countless future research questions, I look forward to helping address future policy and management challenges, and am continuing on in the plant and invasion ecology field with a post doc position in Nevada. All of this, I believe, says a great deal about my advisors, the Invasive Plant Ecology Lab (a.k.a. WIPEM), MSU, and my PhD research and degree program. One of the characteristics that drew me to Bruce and Lisa's lab was the blend of basic and applied ecology. The majority of work conducted in the lab has direct management implications, with numerous collaborations with county, state, and federal land management agencies and private landowners. Conducting science relevant to public lands management was (and still is) very important to me, as someone returning to school after seven years of botanical and natural resource work for the US Forest Service and Park Service.

During my Ph.D. program, I had the opportunity to travel to Washington, D.C. as a recipient of an Ecological Society of America graduate student policy award. I appreciate that Bruce and Lisa allowed me to take time away from my research to participate and encouraged me to pursue my interest in policy. The ESA gives three to four of these awards each year and the recipients are sent to DC to participate in the Biological and Ecological Sciences Coalition Congressional Visits, together with the

Coalition on Funding Agricultural Research Missions. We spent several days on Capitol Hill meeting with Congressional staff and policy advisors to communicate the value of the National Science Foundation (NSF) and the US Department of Agriculture (USDA) research programs and the need for sustained funding. It was an exciting and educational experience, particularly because of the timing of my award—April 2009, just a few months into the new Obama administration. This was a time of high energy and optimism throughout the country, particularly on Capitol Hill, which buzzed with the prospect of fixing broken climate-change and environmental policy and enacting ambitious new programs that could address environmental issues and help rebuild the economy. As luck would have it, the time I was there coincided with hearings on the Waxman-Markey Bill, which, among other things, would have established an emissions trading program for heat-trapping gases with the ultimate goal of reducing global warming. During spare time, I sat in on some of the hearings before the Energy and Commerce Committee, which was so interesting to witness. At the risk of seeming gloomy, it is disheartening to look back to that time and see that, not only have we not moved forward with significant environmental policies (the Waxman-Markey bill died in the Senate), but now we are back to debating whether climate change actually exists, matters, and is related to human activities. Hopefully the pendulum will swing back before too long.

Regardless, the experience strengthened my interest in the science/policy interface and what might be done to help bridge the gap that persists. I feel that it is no longer enough to do high-quality research in relative isolation and hope or assume the results will fall into the right hands. More scientists must attempt, in any small part (newspaper article, web blog, letter to Congressional delegate) to disseminate the relevance and significance of their science. Although it is difficult to tell these days, many legislators do want to hear about policy-relevant scientific research, but they need to be provided with the information. They, and even their staffers, rarely seek out research findings—they use what comes to them and, historically, the majority of what comes to them is from National Institutes of Health and NSF research, and far less from USDA and other natural resource/ecology research programs.

Although not to the same degree as climate change, invasive species have become a high-profile, global environmental issue, and one too that, in my opinion, suffers from significant problems of perception. Unlike climate change, invasive species are assumed to be a severe threat and, thus, action to combat non-native species must strong and sustained. This, despite the fact that there is a large (and ever growing) body of research indicating that in many, if not most, cases, non-native species do not have significant impacts. One of the most interesting things I encountered during my Ph.D. research was the degree of resistance to the notion that non-native plants may not always exert significant impacts and the importance of knowing the actual impacts before implementing aggressive control strategies. This was evidenced by the reaction to a recent paper, “Don’t judge species on their origins” by Mark Davis and 18 other prominent ecologists (*Nature* 474, 153-154; 2011). This paper, which made a great deal of sense to me, simply stated that management of introduced species should be based on rational (i.e. quantified impacts) rather than emotive (fears and perceptions) reasons—sound empirical evidence and not on unfounded claims of harm caused by non-native species. There was a tremendous backlash to this paper, including a formal objection by 141 scientists (*Nature* 475, 36; 2011), as well as months of heated debate on ECOLOG, the prominent ecological listserve. The overall sentiment was that this paper and its message were reckless, irresponsible, and a threat to the future of invasive species management programs. Thus, it seems there will always be a segment of the scientific community (and therefore the general public) for which the perceived threats are simply too great to justify time spent monitoring and measuring impacts. How we address invasive species parallels other environmental issues in that the science is only one aspect of how we think about and respond to the problem. Psychology, sociology, economics and politics all play major roles in invasive species policy and management; thus, it is unrealistic to think that policy and management decisions will be based solely on scientific findings. Nevertheless, there is still a long way to go towards incorporating sufficient and appropriate science into policy and management. Thus, many great challenges lie ahead, making it a fascinating time to be an ecologist.

“The greatest enemy of truth is very often not the lie—deliberate, contrived and dishonest—but the myth—persistent, persuasive, and unrealistic” –John F. Kennedy

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APPENDICES

APPENDIX A

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APPENDIX B

METHODOLOGICAL ATTRIBUTES OF REVIEWED IMPACT STUDIES

Table B.1. Methodological attributes of reviewed experimental impact studies (*n* = 119)

Methodological attribute	Potential number of studies*	Actual number of studies that included this attribute (% of potential)
Quantified impacts on multiple (specific) response variables	119	96 (81%)
Tested mechanism(s) of impact	119	66 (55%)
Examined interaction between non-native plant impact(s) and covarying factor(s) (multifactor experiments) †	119	57 (48%)
Quantified impacts on multiple target species	106	43 (41%)
Conducted an observational study in addition to experimental	119	39 (33%)
Compared impact of non-native to impact of native ‡	119	28 (24%)
Assessed impacts at multiple ecological levels (individual species, community structure, ecosystem properties & processes)	119	25 (21%)
Conducted experiment at multiple sites	96	19 (20%)
Quantified the impacts of multiple non-native species (individually) on same response variables	119	11 (9%)

* Indicates the number of studies, out of the 119 that, based on the experimental methods and response variables, had the potential to include the attribute (e.g. studies comprised solely of greenhouse experiments did not have the potential to be conducted at multiple sites).

† Either additional treatments crossed with non-native plant presence (e.g. water level, nutrient additions), or multiple levels of a factor that the experiment was stratified across (e.g. non-native plant density)

‡ Three studies used native congeners

APPENDIX C

NON-NATIVE PLANT SPECIES AND ATTRIBUTES EXAMINED IN REVIEWED EXPERIMENTAL IMPACT STUDIES

Table C.1. Species name and attributes for the 103 non-native plant species examined in reviewed experimental impact studies from 2001 through April 2011 (n = 119). Composite studies examined the impact of multiple non-native species as a group, therefore results are not species-specific.

Species	Number of studies		Growth form	N-fixer	Longevity
	Species-specific studies	Composite studies			
Agropyron cristatum	1	-	C_3 grass	no	perennial
Agropyron repens	1	-	C_3 grass	no	perennial
Agrostis capillaries	-	1	C_3 grass	no	perennial
Ammophila arenaria	1	-	C_3 grass	no	perennial
Anthoxanthum odoratum	-	1	C_3 grass	no	perennial
Arundo donax	1	-	C_3 grass	no	perennial
Avena barbata	-	5	C_3 grass	no	annual
Brachypodium	-	1	C_3 grass	no	annual
Bromus diandrus	1	3	C_3 grass	no	annual
Bromus hordeaceus	-	3	C_3 grass	no	annual
Bromus inermis	2	1	C_3 grass	no	perennial
Bromus japonicus	-	1	C_3 grass	no	annual
Bromus madritensis	-	1	C_3 grass	no	annual
Bromus madritensis	2	1	C_3 grass	no	annual
Bromus racemosus	1	-	C_3 grass	no	annual
Bromus tectorum	-	1	C_3 grass	no	annual
Dactylis glomerata	-	2	C_3 grass	no	perennial
Festuca arundinacea	-	1	C_3 grass	no	perennial
Holcus lanatus	-	1	C_3 grass	no	perennial
Lolium arundinaceum	1	-	C_3 grass	no	perennial
Lolium rigidum	1	-	C_3 grass	no	annual
Nassella trichotoma	1	-	C_3 grass	no	perennial
Phalaris aquatica	-	1	C_3 grass	no	perennial
Phalaris arundinacea	2	-	C_3 grass	no	perennial
Phleum pratense	-	1	C_3 grass	no	perennial
Phragmites australis	1	-	C_3 grass	no	perennial
Poa pratensis	1	2	C_3 grass	no	perennial
Vulpia myuros	-	1	C_3 grass	no	annual
Andropogon virginicus	-	1	C_4 grass	no	perennial
Melinis minutiflora	-	1	C_4 grass	no	perennial
Melinis repens	1	-	C_4 grass	no	perennial

Table C.1 Continued.

Microstegium vimineum	9	-	C_4 grass	no	annual
Pennisetum ciliare	1	-	C_4 grass	no	perennial
Pennisetum setaceum	1	-	C_4 grass	no	perennial
Schizachyrium condensatum	-	1	C_4 grass	no	perennial
Acacia saligna	1	-	deciduous tree	yes	perennial
Acer platanoides	2	-	deciduous tree	no	perennial
Ailanthus altissima	1	-	deciduous tree	no	perennial
Cinchona pubescens	1	-	deciduous tree	no	perennial
Alstonia scholaris	-	2	evergreen tree	no	perennial
Cecropia obtusifolia	-	2	evergreen tree	no	perennial
Macaranga mappa	-	2	evergreen tree	no	perennial
Myrica faya	1	-	evergreen tree	yes	perennial
Pinus contorta	1	-	evergreen tree	no	perennial
Pinus elliottii	1	-	evergreen tree	no	perennial
Pinus nigra	1	-	evergreen tree	no	perennial
Pinus pinaster	-	1	evergreen tree	no	perennial
Pseudotsuga menziesii	1	-	evergreen tree	no	perennial
Psidium cattleianum	1	2	evergreen tree	no	perennial
Acroptilon repens	1	-	forb	no	perennial
Alliaria petiolata	7	-	forb	no	annual
Barbarea vulgaris	1	-	forb	no	biennial
Brassica nigra	1	-	forb	no	annual
Brassica tournefortii	1	-	forb	no	annual
Cakile maritime	-	1	forb	no	perennial
Carduus nutans	1	-	forb	no	perennial
Centaurea diffusa	1	-	forb	no	biennial
Centaurea maculosa	5	-	forb	no	biennial
Centaurea solstitialis	2	-	forb	no	annual
Chrysanthemum leucanthemum	1	-	forb	no	perennial
Daucus carota	1	-	forb	no	biennial
Elodea nuttallii	1	-	forb	no	perennial
Erodium cicutarium	1	-	forb	no	annual
Euphorbia esula	3	-	forb	no	perennial
Heracleum	1	-	forb	no	perennial
Hesperis matronalis	1	-	forb	no	perennial
Hieracium caespitosum	1	-	forb	no	perennial
Hieracium lepidulum	1	1	forb	no	perennial

Table C.1 Continued.

Hieracium pilosella	-	1	forb	no	perennial
Impatiens glandulifera	5	1	forb	no	annual
Linaria dalmatica	1	-	forb	no	perennial
Lythrum salicaria	6	-	forb	no	perennial
Medicago polymorpha	2	-	forb	yes	annual
Melilotus officinalis	1	-	forb	yes	annual
Mimulus guttatus	1	1	forb	no	perennial
Phacelia tanacetifolia	1	-	forb	no	annual
Potentilla recta	1	-	forb	no	perennial
Rumex acetosella	1	-	forb	no	perennial
Solanum elaeagnifolium	1	-	forb	no	perennial
Solidago gigantea	1	-	forb	no	perennial
Taraxacum officinale	5	-	forb	no	perennial
Trifolium hybridum	1	-	forb	yes	perennial
Trifolium pratense	1	-	forb	yes	perennial
Trifolium repens	1	-	forb	yes	perennial
Typha glauca	2	-	forb	no	perennial
Berberis thunbergii	1	-	shrub	no	perennial
Buddleja davidii	1	-	shrub	no	perennial
Carpobrotus spp	3	1	shrub	no	perennial
Cytisus scoparius	1	-	shrub	yes	perennial
Fallopia bohemica	1	-	shrub	no	perennial
Fallopia japonica	-	1	shrub	no	perennial
Hakea sericea	-	1	shrub	no	perennial
Ipomoea hildebrandtii	1	-	shrub	no	perennial
Lantana camara	2	-	shrub	no	perennial
Lonicera maackii	5	-	shrub	no	perennial
Lonicera tatarica	1	-	shrub	no	perennial
Melastoma	-	2	shrub	no	perennial
Rhamnus frangula	2	-	shrub	no	perennial
Rosa multiflora	1	-	shrub	no	perennial
Tamarix ramosissima	1	-	shrub	no	perennial
Delairea odorata	1	-	vine	no	perennial
Hedera helix	1	-	vine	no	perennial
Lonicera japonica	2	-	vine	no	perennial

APPENDIX D

EXPERIMENTAL STUDIES EXAMINING NON-NATIVE PLANT IMPACTS ON NATIVE PLANT-POLLINATOR INTERACTIONS

Table D.1. Experimental studies examining non-native plant impacts on native plant-pollinator interactions, 2001- April 2011. ‘Impact’ is the impact of the non-native plant(s), regardless of the experimental methods.↑*↓* and ↑↓ indicate a significant ($p < 0.01$ and $p < 0.05$, respectively) effect in the indicated direction, $\uparrow^{ns}\downarrow^{ns}$ indicate p = 0.05 - 0.1, and ‘Ø effect’ indicates $p > 0.1$. N = native, NN = non-native, obs = observational, wk = weeks, mo = months, yr = years, (+) = facilitation.

Reference	**Non-native (NN) species**	**NN growth form**	**Habitat & study location**	**Experimental method & duration**	**Response variable(s)**	**Results**	**Comments**
Aigner 2004	*Cakile maritime* (European sea rocket) and *Carpobrotus* spp. (sea figs)	annual/ perennial forb and perennial shrubs/ subshrubs	coastal sand dunes; southwest Channel Islands, southern California, USA	removal of NN flowers (3mo)	pollinator visits to and seed-set of *Dithyrea maritime* (rare co-occurring N perennial forb)	Ø impact on pollinator visits or seed-set	
Cariveau and Norton 2009	*Carduus nutans* (musk thistle)	biennial/ perennial forb	open grass meadow w/ pines; north-central Colorado, USA	mixed & monospecific assemblages of potted NN & N plants (3mo)	pollinator visits to, pollen counts on, and seed-set of *Monarda fistulosa* (co-occurring N perennial forb)	Ø effect on visits ↓ conspecific pollen ↑* NN pollen on native Ø effect on seed set	-examined effect of distance from non-native on visits to native; most effect at 1 – 5m, but observed ↓ visits up to 15m apart -increased NN pollen did not affect N reproduction
Jakobsson et al. 2008	*Carpobrotus* spp. (sea figs)	perennial shrubs	semi-natural grassland & dune environment; northeast Majorca, Spain	hand-pollination of N w/ conspecific, mixed, & NN pollen (2mo) (also obs study)	fruit/ seed set of *Asphodelus aestivus*, *Dorycnium hirsutum* & *Helichrysum stoechas* (co-occurring N forbs)	↓* fruit set (*A. aestivus*) ↓ seed set (*D. hirsutum*) ↓ seed set (*H. stoechas*)	-multiple N species -suggest NN unlikely to have negative impact because frequency of NN pollen on N flowers *in situ* is low

Table D.1 Continued.

Moragues and Traveset 2005	*Carpobrotus* spp. (seafigs)	perennial shrubs	rocky coast & dune; Mallorca Island, Spain	hand-pollination of N w/ conspecific, mixed, & NN pollen (3mo) (also obs study)	seed-set of *Cistus monspeliensis* & *C. slaviifolius* (co-occurring N forbs)	Ø effect on either spp.	-examined impact on multiple target N species -seed-set w/ NN pollen no different than open-pollinated -frequency of NN pollen on N flowers *in situ* is low
Montgomery 2009	*Euphorbia esula* (leafy spurge)	perennial forb	greenhouse; Michigan, USA	hand-pollination of N w/ conspecific & mixed NN/ N pollen (6mo) (also obs study)	fruit & seed-set of *Viola pedatifida* (co-occurring N forb)	Ø effect on fruit set (both yr) ↓* seed set (yr1) $\downarrow^{ns}$ seed set (yr2)	-repeated over 2 years -*in situ*, NN pollen was not associated with decreased N fruit or seed set. Also, N fruit set was higher in sites with NN despite increased NN pollen receipt, and seed set did not vary with the presence of NN. Thus, no evidence that competition for pollination reduces N fecundity
Nielsen et al. 2008	*Heracleum mantegazzianum* (giant hogweed)	perennial forb	riparian grasslands; Copenhagen, Denmark	(1) addition: N to NN stands (2) hand-pollination of N w/ NN pollen (2yr)	pollinator visits to & seed-set of *Mimulus guttatus* (co-flowering native)	impact of addition: ↑* pollinator visits (+) Ø effect on seed-set impact of hand-pollination: ↓* seed-set	- examined influence of distance to NN on impacts - no distance effect

Table D.1 Continued.

Bartomeus et al. 2010	*Impatiens glandulifera* (Himalayan balsam)	annual forb	riparian; southern Lower Saxony, Germany	addition: N to areas w/ & wo/ N (3wk)	pollinator visits to & reproductive effort of *Raphanus sativus* (N forb)	Ø effect on visits (overall) Ø effect on reproductive effort	-conducted at 14 sites along a gradient of decreasing natural land cover -land cover influenced overall pollinator density, but not impacts
Chittka and Schurkens 2001	*Impatiens glandulifera* (Himalayan balsam)	annual forb	river-bank; Germany	addition (duration not given)	pollinator visits to and seed-set of *Stachys palustris* (co-occurring N forb)	↓* pollinator visits ↓* seed set	
Lopezaraiza-Mikel et al. 2007	*Impatiens glandulifera* (Himalayan balsam)	annual forb	urban field; Bristol, U.K.	NN flower removal (3mo)	NN pollen abundance, pollinator abundance, richness and visits to N flowers	all ↑*	-NN pollen dominated the plant-pollinator network, but observed minimal NN pollen on N plant stigmas
McKinney and Goodell 2010	*Lonicera maackii* (Amur honeysuckle)	perennial shrub	mesic deciduous forest; central Ohio, USA	all NN biomass or flower removal + potted N addition (4mo over 2 seasons)	pollinator visits to, conspecific pollen load on & fruit & seed production of *Geranium maculatum* (co-occurring/ co-flowering N forb)	impact of whole plant: ↓* visits ↓ conspecific pollen ↓* fruits per flower ↓ seeds per plant impact of just flowers: Ø effect on any parameters	-observed little heterospecific pollen on N flowers -results indicate that N reproduction ↓ due to altered pollinator behavior in response to increased understory shading, not competition for pollinators

Table D. 1 Continued.

Brown et al. 2002	*Lythrum salicaria* (purple loosestrife)	perennial forb/ subshrub	wetland; northeast Ohio, USA	mixed & monospecific assemblages of potted NN & N (1yr)	pollinator visits to and seed-set of *Lythrum alatum* (N congener)	↓* pollinator visits ↓* seed set	-examined impact on congeneric N species
Da Silva and Sargent 2011	*Lythrum salicaria* (purple loosestrife)	perennial forb/ subshrub	constructed community (greenhouse); Ottawa, Canada	hand-pollination (2mo)	seed-set of *Decodon verticillatus* (co-flowering N forb/subshrub)	↓* seed set	-observed that N is not pollen-limited in invaded sites
Flanagan et al. 2010	*Lythrum salicaria* (purple loosestrife)	perennial forb/ subshrub	field; southeast Wisconsin, USA	mixed & monospecific assemblages w/ 2 NN densities (1.2yr)	pollinator visits to and seed-set of *Mimulus ringens* (co-flowering N forb)	↑ visits (+) ↓* seeds-set	-examined two NN densities -impacts were greater at higher NN density -↓ quality but not quantity of pollinator visits was mechanisms of impact
Totland et al. 2006	*Phacelia tanacetifolia* (lacy phacelia)	annual forb	boreal forest; Telemark County, southern Norway	NN addition (3mo?)	pollinator visits to and fruit-set of *Melampyrum pretense* (N forb)	↓* pollinator visitation rates Ø effect on fruit-set	-examined impacts in disturbed (logged) and undisturbed habitat (no difference found) -↑* visits to plots w/ NN added, but not to individual plants
Kaiser-Bunbury and Müller 2009	*Psidium cattleianum* (strawberry guava)	perennial tree/ shrub	heathland; southern Mauritius	NN flower removal (6mo) (also obs study)	pollinator visits, flower, fruit & seed-set, fruit size & weight of *Bertiera zaluzania* (co-occurring N shrub)	Ø effect on any parameters	

Table D.1 Continued.

Tscheulin et al. 2009	*Solanum elaeagnifolium* (silverleaf nightshade)	perennial forb/ subshrub	stony Mediterranean beach; Lesvos Island, Greece	hand-pollination of N w/ conspecific, NN & mixed pollen (2mo) (also obs study)	seed-set of *Glaucium flavum* (co-flowering N)	mixed pollen: Ø effect on seed-set pure exotic pollen: ↓* seed-set	-open pollinated flowers produced ↓* seeds than hand-pollinated w/ mixed pollen, suggesting pollen limitation *in situ* -observed ↓* pollinator visits to native where NN was present
Matsumoto et al. 2010	*Taraxacum officinale* (common dandelion)	perennial forb	urban fields; southern Japan	hand-pollination of N w/ mixed N/ NN pollen (2wk) (also obs study)	seed-set of *Taraxacum japonicum* (co-occurring N congener)	↓* seed-set	-sig.(+) relationship observed *in situ* between proportion of NN plants & ratio of NN pollen on N stigma -sig (-) relationship observed between ratio of NN pollen and N seed-set
Muñoz and Cavieres 2008	*Taraxacum officinale* (common dandelion)	perennial forb	alpine; central Chilean Andes	N + NN assemblages w/ 1:1 & 5:1 NN-to-N ratios (3mo) (also obs study)	rates & duration of pollinator visits to & seed-set of *Hypochaeris thrincioides* & *Perezia carthamoides* (co-occurring N forbs)	*H. thrincioides* (1:1) Ø effect on rates ↑ duration & seed-set (+) *H. thrincioides* (5:1) Ø effect on rates ↓ duration & seed-set *P. carthamoides* (1:1) Ø effects (5:1)↓ rates & seed-set Ø effect on duration	-examined two NN densities -multiple target species -impacts varied among target species -impacts only at high NN density

Table D.1 Continued.

Takakura et al. 2009	*Taraxacum officinale* (common dandelion)	perennial forb	grasslands; southcentral (Osaka) Japan	NN flower removal (2wk) (also obs study)	seed-set of *Taraxacum japonicum* (N congener)	↓ seed-set	-observed sig (-) relationship between proportion of NN & N seed set *in situ*
Kandori et al. 2009	*Taraxacum officinale* (common dandelion)	perennial forb	fields; central Japan	potted plant assemblages: NN/ N mixed & monospecific stands (2yr) (also obs study)	pollinator visits to & seed-set of *Taraxacum japonicum* (co-occurring N congener)	↓*pollinator visits ↓*seed set	-conducted experiment at 7 sites -no site x impact interactions

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APPENDIX E

ALLOMETRIC RELATIONSHIP BETWEEN SIZE AND BIOMASS FOR *P. SPICATUM* & *N. VIRIDULA*

Allometric relationships between size and biomass for two dominant perennial forage grasses.

Linear regression was used to calculate the relationship between plant basal diameter (cm), average height (cm) and aboveground biomass (g) for the native perennial bunchgrasses, *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass) and *Nassella viridula* (Trin.) Barkworth (green needlegrass).

Pseudoroegneria spicata **(Pursh) Á. Löve (bluebunch wheatgrass)**

Considered excellent forage for cattle, domestic sheep, elk, mule deer, white-tailed deer, pronghorn antelope and bighorn sheep

Biomass = (-6.8383) + 1.0278 (basal diameter) + 0.1599 (height), n = 122; r^2 = 0.842

Nassella viridula **(Trin.) Barkworth (green needlegrass);** ***n*** **= 71**

Considered good early-season forage for cattle, domestic sheep, bison and elk

Biomass = (1.8088) + 0.6546 (basal diameter) + 0.0865 (height); n = 71; r^2 = 0.903

APPENDIX F

ANOVA FOR PRE-TREATMENT CONDITIONS: IMPACTS OF *C. STOEBE* IN SAGEBRUSH-GRASSLANDS (CHAPTER 4)

Table F.1. One-way analysis of variance results for pre-treatment levels of response variables among treatment groups (no treatment, disturbance, manual removal, and herbicide). (√) = response variable was square root transformed. df = 3, 60.

Response variable	All Species		Native species		Non-native species	
	$F_{3, 60}$	p	$F_{3, 60}$	p	$F_{3, 60}$	p
Cover (√)	0.245	0.8649	1.048	0.377	0.506	0.6794
Forb cover (√)	0.450	0.7178	0.681	0.5666	0.079	0.971
Grass cover (√)	0.029	0.9998	0.510	0.7446	0.828	0.4832
Richness (√)	0.820	0.4876	1.518	0.2178	0.807	0.4944
Forb richness (√)	0.290	0.8328	0.585	0.6267	0.475	0.7005
C. stoebe cover (√)	1.478	0.2283				
C. stoebe density (√)	0.245	0.8645				
B. tectorum cover (√)	0.579	0.6309				
P. spicata biomass	0.035	0.991				
N. viridula biomass	0.278	0.8408				
Bare ground (√)	0.699	0.5557				
Litter cover (√)	1.342	0.2679				

Table F.2. Multivariate analysis of variance results for pre-treatment differences in species composition among treatment plots. Results based on 1000 permutations of Bray-Curtis dissimilarity matrices.

$F_{3,60}$	p
0.4359	0.986

APPENDIX G

COMPLETE MIXED MODEL AND ANOVA OUTPUT FOR TREATMENT EFFECTS OVER TIME: IMPACTS OF *C. STOEBE* IN SAGEBRUSH-GRASSLANDS (CHAPTER 4)

Table G.1. Model results for treatment effects over time (linear mixed effects models [MM]) and differences among treatments in the proportional change in response variables from pre-treatment to 3 years post-treatment (one-way ANOVA). In MM, *treatment* was a fixed effect and *year*, *population*, and *plot* were random effects; *plot* was a repeated measure through time and was nested in *population*. Proportional change = (2010 value - 2007 value) ⁄ 2007 value, abs val = absolute values of response variables, Trt = treatment, Yr = Year, (√) = absolute value was square root transformed.

Response variable and model factor	MM (abs val)	ANOVA (prop chg)	MM (abs val)	ANOVA (prop chg)	MM (abs val)	ANOVA (prop chg)
	p-value (treat × year)	$F_{3,60}$, *p*-value	*p*-value (treat × year)	$F_{3,60}$, *p*-value	*p*-value (treat × year)	$F_{3,60}$, *p*-value
Cover	All species (√)		Native species (√)		Non-native species (√)	
No Trt	0.0840	0.851, 0.471	0.0654	1.039, 0.381	0.6228	4.041, 0.011
Disturb	0.8449		0.7532		0.6805	
Pull	0.0507		0.0110		0.9011	
Spray	0.0004		0.0177		0.0004	
Yr × Trt	$p > 0.1$		$p > 0.1$		$p > 0.1$	
Forb cover	All species (√)		Native species (√)		Non-native species (√)	
No Trt	0.0366	1.894, 0.139	0.0278	3.143, 0.0317	0.0692	1.393, 0.252
Disturb	0.0226		0.2830		0.0195	
Pull	0.0018		0.0053		0.2321	
Spray	0.2930		0.0162		0.9867	
Yr × Trt	0.0249 (spray), $p > 0.01$ (all others)		0.0010 (spray)		$p > 0.1$	

Table G.1 Continued.

Grass cover	All species (√)		Native species (√)		Non-native species (√)	
No Trt	0.3960	3.275, 0.0262	0.2619	3.010, 0.0427	0.6515	4.36, 0.0076
Disturb	0.0541		0.0763		0.0239	
Pull	0.7525		0.5589		0.4573	
Spray	0.0000		0.0001		0.0000	
Yr × Trt	0.0477 (dist); 0.0002 (spray)		0.0393 (dist); 0.0262 (spray)		0.0006 (spray)	
Total richness	**All species (√)**		**Native species (√)**		**Non-native species (√)**	
No Trt	0.0576	1.653, 0.185	0.1349	2.027, 0.118	0.1800	0.95, 0.421
Disturb	0.2261		0.6966		0.0038	
Pull	0.1530		0.2304		0.7065	
Spray	0.5492		0.2100		0.1705	
Yr × Trt	0.0745 (spray)		0.0507 (spray)		p > 0.1 (all)	

APPENDIX H

EFFECT SIZE OF TREATMENTS ESTIMATED FROM BOOTSTRAP SAMPLES: IMPACTS OF *C. STOEBE* IN SAGEBRUSH-GRASSLANDS (CHAPTER 4)

Table H.1. Effect size of treatments estimated from 1000 bootstrap samples of the proportional change in the response variable = (2010 – 2007)/2007. Effect sizes were calculated only for response variables indicated as significant by analysis of variance of proportional change (Table 4.1 and Appendix G). A mean effect size of 1.0 indicates that the response variable increased, on average, by 100% from before treatment to 3 years after treatment. Negative values indicate an overall reduction in the response variable over that time.

Response × treatment	Mean effect size	SD	SE
Non-native cover			
No treatment	0.620	0.451	0.014
Disturbance	0.194	0.197	0.006
Manual removal	0.167	0.128	0.004
Herbicide	2.476	0.915	0.029
Native grass cover			
No treatment	0.185	0.113	0.004
Disturbance	-0.044	0.098	0.003
Manual removal	0.144	0.148	0.005
Herbicide	0.411	0.105	0.003
Non-native grass cover			
No treatment	0.688	0.699	0.022
Disturbance	-0.151	0.155	0.005
Manual removal	0.029	0.130	0.004
Herbicide	2.636	0.880	0.028
Native forb cover			
No treatment	1.074	0.505	0.016
Disturbance	0.361	0.192	0.006
Manual removal	0.984	0.412	0.013
Herbicide	-0.219	0.128	0.004
Native forb richness			
No treatment	0.317	0.142	0.004
Disturbance	-0.047	0.103	0.003
Manual removal	0.131	0.110	0.003
Herbicide	-0.099	0.129	0.004
B. tectorum cover			
No treatment	0.590	0.645	0.020
Disturbance	-0.155	0.157	0.005
Manual removal	-0.019	0.128	0.004
Herbicide	2.659	0.905	0.029

Table H.1 Continued.

Response × treatment	Mean effect size	SD	SE
C. stoebe cover			
No treatment	1.454	0.542	0.017
Disturbance	1.175	0.637	0.020
Manual removal	-0.364	0.143	0.005
Herbicide	-0.789	0.047	0.002

APPENDIX I

OVERVIEW MAP OF FIELD SITES

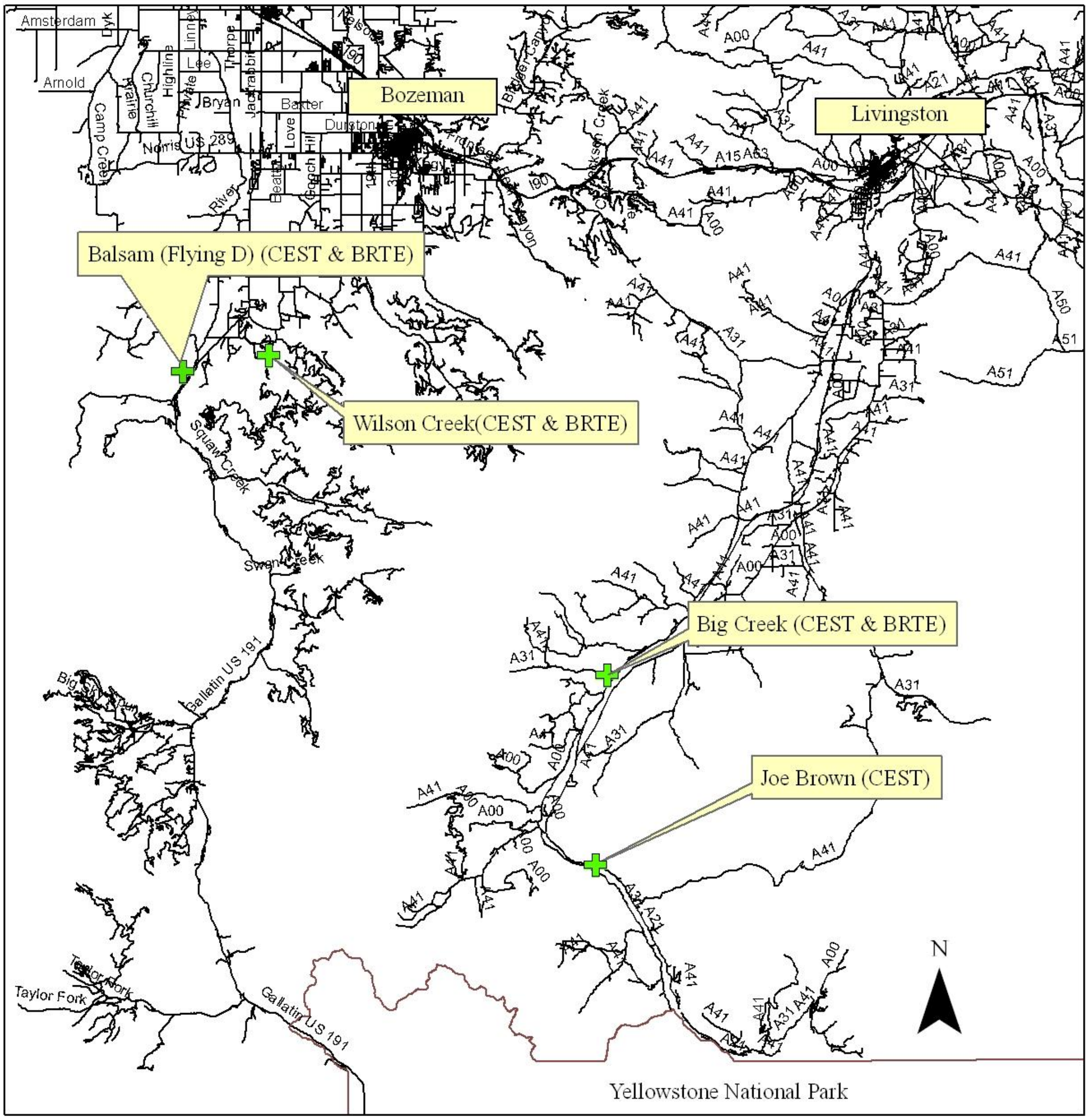

Figure I.1. Field site locations

APPENDIX J

LOCATION OF DATA, FIELD SITES, AND PHOTOS

Electronic version of this disseratation:

> Seedbank:\Theses\TSkurski

GPS and GIS data for locations of field sites and plots:

> Seedbank:\Experiments\Gallatin\Tanya_Gallatin & Paradise Valley Data\Field Sites & Plots Locations\Sites
>
> Seedbank:\Experiments\Gallatin\Tanya_Gallatin & Paradise Valley Data\Field Sites & Plots Locations\Plots\... Subfolders by field site (Balsam, Wilson Creek, Big Creek, and Joe Brown with corrected GPS points, shapefiles, and a table with lat/long for all plots

GPS polygons and GIS spatial data for *C. stoebe* populations (patches) 2007-2010:

> Seedbank:\Experiments\Gallatin\Tanya_Gallatin & Paradise Valley Data\Field Data\CEST Spatial Data

Field photos:

> Seedbank:\Experiments\Gallatin\Tanya_Gallatin & Paradise Valley Data\Field Photos

Field data:

> Seedbank:\Experiments\Gallatin\Tanya_Gallatin & Paradise Valley Data\Impacts\Field Data & Analysis… Subfolders 07Data, 07Analysis, 08Data, 08Analysis, 09Data, 09 Analysis, 10Data, 10Analysis, and 11FinalAnalysis! (These folders contain cover data for all species by plot per year, and *B. tectorum* and *C. stoebe* density count data)

C. stoebe seed count and germination data:

> Seedbank:\Experiments\Gallatin\Tanya_Gallatin & Paradise Valley Data\CEST Seeds

Complete table and Excel spreadsheet of reviewed impacts studies and findings (Chapters Two and Three):

> Seedbank:\Manuscripts\Impacts\Tanya_Impacts Review
>
> Seedbank:\Manuscripts\Impacts\Tanya_Mechanisms Review