The Drivers of Invasive Species Establishment and Impact on Ecological and Evolutionary Aspects of Resident Plant Communities

by

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Abstract

Invasive species can have important ecological and evolutionary impacts on resident species. Yet, we still lack a broad understanding of the conditions that determine invasive species establishment, performance and impact on ecological and evolutionary aspects of communities. In this thesis, I first determined the drivers of the strength of biotic resistance to invasion by integrating a meta-analysis and remote-sensing data. I found that the magnitude of biotic resistance to invasion increased with temperature and precipitation, while productivity was a poor predictor. Second, I focused on the invader *Bromus inermis* (Leyss.) to determine the drivers of invasive species impact on different aspects of community structure and function, as well as whether an invasive species can lead to the establishment of alternative community states by altering and homogenizing communities where they invade. *B. inermis* is a perennial grass considered one of the most widespread and serious invasive species in North America. I performed a survey across eight sites and used space-for-time substitutions and time-series to quantify *B. inermis'* impact on different aspects of the resident communities. I found that *B. inermis* impact on community structure and function was consistently negative within and across sites, yet stronger in warm, species-rich and productive sites. However, although *B. inermis'* impact on native species richness was consistently negative, its impact on exotic species richness was highly variable. This can have important management consequences, potentially resulting in secondary invasions or an even greater impact on native species diversity. *B. inermis* was also found to rapidly alter resident communities, reducing native species diversity, changing species composition, altering ecosystem function and homogenizing communities. In doing so, *B. inermis* led to the establishment of a potentially persistent alternative community state.

Due to its impact on resident species and ecosystem function, *B. inermis* has the potential to act as a selective agent on co-occurring individuals, through direct or soil-mediated effects.

Further, the adaptive responses to the invader, such as increased tolerance or suppression, can be only against the invader or generalized strategies, which remains unknown. Therefore, I evaluated whether previous maternal experience and soil conditions alter individuals' ability to tolerate or suppress *B. inermis*, as well as conspecifics, in three species. Results indicated no evidence of an adaptive response to coexist with *B. inermis*. Instead, I found that previous maternal experience interacting with *B. inermis* resulted in a decreased ability to suppress *B. inermis* performance, while tolerance was dependent upon soil conditions and not on previous maternal experience. Interestingly, these responses appear to be *B. inermis*-specific, as no effect of soil conditions or maternal experience were observed when interacting with conspecifics. These results highlight the need to better understand the conditions that facilitate or prevent species adaptation to invaders. Hence, I developed and proposed a theoretical model on how spatial patterns of invasion can be used to predict native species adaptation to invaders. If large, dense and well-connected invaded patches result in greater strength of selection and increased gene flow from other invaded areas (i.e. reinforcing gene flow), this would result in greater likelihood of an adaptive response to invaders. I highlight how this knowledge could be used to complement current management practices.

Overall, this thesis' results indicate that invaders can be important biotic forces structuring communities, altering ecological and evolutionary dynamics. Further, result from this thesis suggest that a better understanding of the conditions that determine the establishment, as well as the impact of invasive species on different aspects of resident communities, can help us design better management strategies to prevent further losses in biodiversity.

Preface

Chapter 2 of this thesis has been published as “Stotz GC, GJ Pec, JF Cahill (2016) Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis” at *Basic and Applied Ecology*. I was responsible for data collection, analysis and writing the manuscript. GJ Pec helped collect the data and revise the manuscript. JF Cahill was the supervisor author and was involved in the idea and concept development, and helped write the manuscript.

Chapter 3 of this thesis has been submitted as “Stotz GC, E Gianoli, MJ Patchell, JF Cahill. Differential responses of native and exotic plant species to an invasive grass are driven by variation in biotic and abiotic factors” to *Journal of Vegetation Science*. I was responsible for data collection, analysis and manuscript writing. MJ Patchell helped with data collection and revising the manuscript. JC Cahill and E Gianoli were involved in the idea and concept development and helped write the manuscript.

Chapter 6 of this thesis has been published as “Stotz GC, E Gianoli, JF Cahill (2016) Spatial pattern of invasion and the evolutionary responses of native plant species” at *Evolutionary Applications*. I was responsible for writing the manuscript and developing the conceptual model, which was done with help from JF Cahill and E Gianoli. JF Cahill and E Gianoli also helped write the manuscript.

Dedication

To my partner Gian Carlo D’Ottone and my family.

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Chapter 1: Introduction

Invasive plant species are one of the biggest threats to biodiversity (Wilcove et al. 1998, Vilà et al. 2011, Pyšek et al. 2012), but also provide unique systems where to study the mechanisms and drivers of species interactions and community assembly (Callaway and Maron 2006). Invasive species, by definition, are abundant, widespread, generally dominant species that have a negative effect on the environment, the economy or human health (Richardson et al. 2000, Lockwood et al. 2013). Although native species can also become invasive, most invaders are exotic species (Simberloff et al. 2012b). Exotic species are those moved across biogeographic barriers by human or human activities (considering only species introduced after 1942 in Europe or after European colonization in other parts of the world) (Richardson et al. 2000). Although many introductions are accidental, some species have been intentionally introduced due to their value as forage, crop or ornamental species. Although only about one in ten exotic species becomes invasive (Vilà et al. 2010), those that do, tend to decrease species diversity and alter ecosystem function (Ehrenfeld 2010, Vilà et al. 2011).

Invasion is a widespread phenomenon, with over 13,000 naturalized exotic species recorded across the world (van Kleunen et al. 2015), yet predicting which species become invasive and the conditions that determine their establishment, growth and impact is still a challenge (Gurevitch et al. 2011, Simberloff et al. 2012a, Hulme et al. 2013). Invasive species can have important ecological and evolutionary consequences for resident species (Strauss et al. 2006b, Vilà et al. 2011). Although evolutionary responses by native species to invaders have been documented (Strauss et al. 2006b, Oduor 2013) and can have important conservation and management implications (Schlaepfer et al. 2005, Leger and Espeland 2010, Carroll 2011a), our understanding of the drivers and consequences of evolutionary responses to invasion is fairly limited. In this thesis I aim at integrating different ecological and evolutionary hypotheses to extend our current understanding of the potential mechanisms determining invasion success, as well as the ecological and evolutionary consequences of invasion on resident species.

1.1 Mechanisms and consequences of invasion

The establishment, growth and impact of invasive species is determined by characteristics of the invader, the surrounding plant community, and other biotic and abiotic factors (Theoharides and Dukes 2007, Catford et al. 2009). Although multiple hypotheses exist, one that receives great attention is biotic resistance, which is the ability of the resident community to limit the establishment and growth of invasive species (Levine et al. 2004). Different components of the resident community are thought to confer greater biotic resistance, such as greater species (Elton 1958, Naeem et al. 2000, Kennedy et al. 2002) functional (Hooper and Dukes 2010) and phylogenetic (Strauss et al. 2006a, Gerhold et al. 2011) diversity of the resident plant community. However, results are mixed, with studies showing positive, negative or no association between biotic resistance and diversity (Stohlgren et al. 2003, Cully et al. 2003, Smith et al. 2004, Bennett et al. 2014). Thus, there may be other factors mediating the strength of biotic resistance.

Productivity and abiotic conditions have been proposed to be important predictors of plant-plant interactions (Grime 1973, Bertness and Callaway 1994) but rarely used to predict invasive species establishment or impact (but see MacDougall et al. 2006, Chambers et al. 2007, von Holle 2013, Reisner et al. 2015). Competitive interactions are thought to be weak in environmentally stressful and low productive areas (Grime 1973, Bertness and Callaway 1994), likely resulting in low biotic resistance to invasion, but also in low invasive species impact.

Broad scale studies across a range of conditions are necessary to test for the role of biotic and abiotic factors determining invasive species establishment, growth and impact. This knowledge is important to better design management strategies (D'Antonio et al. 2004). In this thesis, I focus on different abiotic and biotic factors as predictors of biotic resistance and invasive species performance, and impact on different groups of species.

Invasive species interact with both native and exotic species where they invade. Most studies have focused on invasive species impact on native or total species richness, while the interaction between invasive or exotic species has been generally understudied (Kuebbing et al. 2013). However, the magnitude and direction of invasive species impact on exotic species richness can also have important consequences for restoration and conservation efforts (Kuebbing et al. 2013). Positive, negative and neutral interactions among exotic species have been documented (Kuebbing and Nuñez 2015), with different implications for the native community (Simberloff and Von Holle 1999, Truscott et al. 2008, Ortega and Pearson 2010). A negligible or positive impact of invaders on exotic species can result in greater negative impact on native species richness and a positive effect on new invaders establishment (Gooden et al. 2009, Bernard-Verdier and Hulme 2015). On the other hand, a negative impact of an invader on exotic species can lead to secondary invasions upon invader dominance decay or removal (Ortega and Pearson 2010). Understanding the conditions under which invasive species reduce, or facilitate, native and exotic species richness may help design management strategies to minimize the impact on native species, while preventing the establishment of new exotic or invasive species.

Restoring invaded communities is difficult, as besides reducing species diversity, invasive species can alter community dynamics and ecosystem function (Ehrenfeld 2003, 2010, Wilsey et al. 2014), leading to the establishment of alternative and potentially persistent stable states (Suding et al. 2004, Martin and Wilsey 2014). The transition between community states following invasion may be gradual or rapid, which remains largely unknown. Invasive species may also create positive soil-feedbacks (Klironomos 2002, Ehrenfeld 2010) and suppress diversity-enhancing mechanisms (Fukami et al. 2013), thus facilitating the persistence of communities in an invaded state (Suding et al. 2004). Further, although most studies focus on diversity changes at the local scale, invasion may have important consequences for diversity at broader scales by potentially homogenizing communities (McKinney and Lockwood 1999), although results are mixed (McKinney 2004a, b, Lososová et al. 2012, Martin and Wilsey 2015). Homogenization results from the extirpation of native species from local communities as well as from the accumulation of widespread exotic species (Olden and Poff 2003, Olden and Rooney 2006). Broad scale, multi-year studies are needed to quantify the rate at which invasive species alter community and ecosystem properties and thus lead to the establishment of alternative community states (Suding et al. 2004). This is one of the goals of the present thesis.

1.2 Evolutionary consequences of invasion

Due to their impact and ability to alter the properties and dynamics in invaded areas, invasive species may select for particular traits in neighboring species (Strauss et al. 2006b, Thorpe et al. 2011). Accordingly, evidence is accumulating on native species adaptations to interact with invaders (Strauss et al. 2006b, Oduor 2013). The interaction with invasive species has resulted in native species increased tolerance to (Callaway et al. 2005, Leger 2008, Rowe and Leger 2010, Goergen et al. 2011, Fletcher et al. 2016) or suppression of (Rowe and Leger 2010, Goergen et al. 2011) the invader. However, whether the increased tolerance and suppression are only against the invader, or generalized strategies, remains largely untested. Evaluating which type of strategy evolves in response to the interaction with invaders, as well as whether adaptation is a specialized or generalized response, can have important implications for the long-term coexistence of these species.

However, not all species or populations adapt to compete or coexist with invasive species (Mealor and Hild 2007, Goergen et al. 2011, Dostál et al. 2012). Hence, we need to understand under which conditions species are more likely to persist in invaded areas; an area that remains largely unexplored (but see Strauss et al. 2006b). Two main drivers of adaptive evolutionary responses are gene flow and the strength of selection (Kawecki and Ebert 2004, Futuyma 2013). Understanding how these processes vary across invaded areas can help us predict and potentially manage native species ecological and evolutionary responses to invasion (Carroll 2007, 2011b).

1.3 *Bromus inermis* invasion into Canadian grasslands

In Canada, approximately 30% of vascular plant species are exotic, of which 40% are listed as invasive species (Canadian Food Inspection Agency 2008). Smooth brome (*Bromus inermis* Leyss.) is one of the most serious invasive exotic plant species threatening habitats in Canada (Catling and Mitrow 2005). Its broad distribution, strong impact on community diversity and ecosystem function, and economic importance, make it a good species/system to test for the drivers and consequences of invasion. *B. inermis* was intentionally introduced as a forage species to North America in the late 1800s from eastern Europe (Otfinowski et al. 2007). Two strains are thought to have been initially introduced to Canada, which were referred to as northern and southern varieties (Otfinowski et al. 2007). Since then, different cultivars have been bred and planted in Canada, such as the Carlton (1961), Magna (1968) and Signal (1983) cultivars (Alderson et al. 1994). *B. inermis* continues to be actively bred to increase its yield and growth under varying conditions (e.g. Coulman 2006) and planted for hay and pasture (Otfinowski et al. 2007).

However, *B. inermis* has escaped cultivated areas. It is currently found invading every Canadian province and most of the United States (Grace et al. 2000, Otfinowski et al. 2007, Ellis-Felege et al. 2013) and it continues to spread (Sinkins and Otfinowski 2012, Ellis-Felege et al. 2013). Where it establishes, *B. inermis* tends to form dense patches where plant species diversity is reduced by up to 70% (Otfinowski et al. 2007), but exotic species appear to be able to persist in *B. inermis*-invaded areas (Bennett et al. 2014). Although *B. inermis* establishes across a broad range of conditions, it is unknown whether its performance and impact on both native and exotic species richness varies depending on local biotic and abiotic conditions. Hence, a broad-scale study of *B. inermis* impact and invasion is necessary to determine the biotic and abiotic drivers, and the large-scale consequences, of its invasion.

B. inermis typically occupies nutrient-rich, moist sites (Blankespoor and Larson 1994, Blankespoor and May 1996, McClay et al. 2004) and its invasion is generally favored by disturbance (Larson 2003, Gendron and Wilson 2007). However, its deep root system confers *B. inermis* a high drought resistance capacity (Cook 1943, Dong et al. 2014). As a result, some studies suggest that although *B. inermis* is a stronger competitor under high moisture and nutrient availability, it remains a strong competitor, compared to native species, under low moisture or nutrient conditions (Nernberg and Dale 1997, Gendron and Wilson 2007, Holub et al. 2012). *B. inermis* may also facilitate its own performance by increasing nutrient availability where it invades (Mahaney et al. 2015, Piper et al. 2015b) through its high rate of litter production, faster litter decomposition rate (Vinton and Goergen 2006) and by altering soil microbial communities and their activity (Piper et al. 2015a, b). This greater nutrient availability in invaded areas is thought to result in an advantage for the invader over native species, and facilitate *B. inermis* persistence and expansion (Vinton and Goergen 2006).

By altering abiotic and biotic conditions in invaded areas, *B. inermis* may act as a biotic filter, selecting or systematically excluding certain species (Bennett et al. 2014). In doing so, *B. inermis* may not only reduce species diversity, but also result in the homogenization of plant communities within and across sites. Accordingly, Bennett et al. (2014) found shade-tolerance to be an important attribute facilitating species persistence in *B. inermis* invaded areas. *B. inermis* may, however, not only selectively exclude species, but also individuals with certain traits or trait values, thus acting as a selecting agent driving co-occurring species adaptation. Species adaptation to coexist with *B. inermis* can help maintain diversity in invaded areas; however, mal-adaptations can result in a greater invasive species expansion and impact on community structure.

1.4 Objectives and thesis outline

The objectives of this thesis are to evaluate the drivers of invasive species establishment and their impact on ecological and evolutionary aspects of communities. In chapter 2, I perform a meta-analysis to determine the drivers of the strength of biotic resistance to invasion. In Chapter 3, I determine *B. inermis* impact across multiple sites to determine whether biotic and abiotic conditions determine the direction and strength of its impact on native and exotic species richness. In Chapter 4, I evaluate whether *B. inermis* invasion homogenizes communities within and across sites, as well as the transition from a native-dominated to a *B. inermis*-dominated, homogeneous community, with differing species composition, nutrient availability and species dynamics. Since *B. inermis* strongly suppresses resident species and modifies conditions where it invades, in Chapter 5 I test whether previous maternal experience interacting with *B. inermis* and living under *B. inermis*-modified soil conditions, alters resident species ability to tolerate and/or suppress *B. inermis*. I also evaluate whether these responses are generalized or specific to the interaction with *B. inermis*. In Chapter 6, I propose a conceptual model based on invasive species spatial patterns to predict when native species adaptation to invasion is more likely to ensue. Further, I propose how this knowledge could be used to complement current invasive species management strategies. The general findings of my thesis are synthesized and discussed in Chapter 7.

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Chapter 2: Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis

2.1 Introduction

Biotic resistance is the ability of a resident community to limit recruitment and growth of invasive species (Levine et al. 2004). As such, when looking at biotic resistance we tend to assume that the resident community will have a negative effect on invasive species (i.e. competition) (Levine et al., 2004). However, resident communities may also facilitate invasive species establishment, growth and spread (Badano, Villarroel, Bustamante, Marquet, & Cavieres, 2007). The processes where native species facilitate exotic species has been termed biotic assistance (Inderjit & Cahill, 2015). Biotic resistance or assistance may result from both direct as well as indirect interactions (Bever, 2003; Inderjit & Cahill, 2015; Levine et al., 2004). Consequently, the outcome of the interaction between native communities and invasive species may range from biotic resistance to assistance (Figure 2-1).

The effectiveness of native communities at limiting invasion varies (Lonsdale, 1999), and this variation has been partly explained through changes in species richness and phylogenetic diversity within the native community (Dukes, 2001; Gerhold et al., 2011; Kennedy et al., 2002; Strauss, Webb, & Salamin, 2006). Absent, however, is a broad analysis across species and systems, investigating how habitat productivity and environmental conditions influence the ability of the resident communities to resist, or potentially facilitate invasion (Figure 2-1). This is particularly surprising as substantial theory suggests that the intensity and outcomes of plant-plant interactions are dependent upon primary productivity and environmental stress (Bertness &

Callaway, 1994; Grime, 1973). The same may be true for invasive species' effect on the resident community with the strength and direction of this effect varying depending on the habitat's productivity and/or environmental conditions (Figure 2-1) (e.g. MacDougall, Boucher, Turkington, & Bradfield, 2006).

Plant ecologists have long focused on the relationship between competition and productivity. It has been proposed that competition becomes stronger and influences community assembly as productivity increases, while stressful conditions are more important for assembly at low productivity (Grime, 1973). A slightly different model, the stress gradient hypothesis (Bertness & Callaway, 1994) proposes that competition is predominant in environments of intermediate productivity, while facilitation occurs more frequently in both highly stressful and highly productive environments. In contrast, an alternative theory proposes that competition is important across a productivity gradient, with different resources being limiting at both ends of this gradient (Tilman, 1988). Further, two meta-analyses suggest a general decline in competition with increased productivity and decreased stress (Goldberg, Rajaniemi, Gurevitch, & Stewart-Oaten, 1999; Maestre, Valladares, & Reynolds, 2005). However, these theories have rarely been tested in the context of invasion and biotic resistance (Chambers, Roundy, Blank, Meyer, & Whittaker, 2007; Harrison, Cornell, & Grace, 2015; Lortie & Cushman, 2007; Reisner, Doescher, & Pyke, 2015; von Holle, 2005, 2013).

Evidence suggests that environmental conditions and productivity may be important in determining invasion success. For example, invasive species are commonly found invading productive environments with greater resource availability (Foster, Smith, Dickson, & Hildebrand, 2002; Stohlgren et al., 1999), however, this is not always the case, as invasive species can also be found invading stressful habitats (Badano et al., 2007; Lortie & Cushman, 2007). Although invasive species performance tends to increase under benign, fertile conditions

(Chambers et al., 2007; Dukes & Mooney, 1999; Gerhardt & Collinge, 2007; Goldstein & Suding, 2014; Harrison et al., 2015), this advantage can be offset or decreased by the presence of a more resistant community in those areas (Chambers et al., 2007; Eskelinen & Harrison, 2014; Harrison et al., 2015). Thus, biotic resistance may be greater in benign and productive areas, while under stressful conditions, the resident community has been shown to facilitate, rather that resist invasion (Badano et al., 2007; Lortie & Cushman, 2007; Reisner et al., 2015; von Holle, 2005). Further, the susceptibility of communities along productivity or environmental gradients may depend upon the invader's functional group (Gómez-Aparicio, 2009), with some functional groups (e.g. trees and shrubs) being more dependent upon facilitation for establishment (Gómez-Aparicio, 2009; Mendoza, Gómez-Aparicio, Zamora, & Matías, 2009). By evaluating the effect of productivity and environmental stress on the strength and direction of the interaction between native communities and invasive species, we may be able to predict under which conditions communities are more or less susceptible to different invaders.

Here, we focus on testing the effect of resident communities on invaders along different environmental gradients. To evaluate this, we performed a meta-analysis, which allows us to include results from multiple systems across a broad geographical range. Further, we integrated these results with environmental data obtained from remote sensing databases to evaluate the effect of productivity and environmental stress on net neighbor effect on invasive species among sites. We specifically evaluated (1) the effect of native communities on invasive species performance (2) the frequency of facilitation and competition as outcomes of those interactions and (3) whether the strength and direction of the interaction is dependent upon the habitat's productivity and/or environmental conditions and (4) whether the dependence upon productivity and/or environmental conditions varied depending on an invaders' functional group.

2.2 Material and methods

2.2.1 Literature criteria and dataset construction

An ISI Web of Science search was conducted to retrieve relevant publications to include in the meta-analysis. We used – invasi* OR exotic* OR alien* OR introd* - as key words, given the number of terms used to define similar concepts (Richardson et al., 2000). We then refined the results to all articles included within the research areas of Ecology, Plant Sciences and Forestry, and to articles published between 1995 and 2015, as environmental data are not available for previous years (Appendix 1-1). This search resulted in 506,678 studies screened. To minimize the likelihood of relevant studies missed in our initial search, we further cross-referenced each of the articles for pertinent articles to potentially include. All resultant publications were screened to meet the following criteria: (1) studies needed to compare the performance of an invasive species in an area with and without the resident community present, (2) studies needed to be under field conditions, (3) the resident community needed to be native to its area and (4) means, standard error and sample sizes for treatments and the control needed to be available. If in graphical form, graphs were digitized and data points were extracted using the software Engauge Digitizer v.2.12 (http://digitizer.sourceforge.net). Including only experimental tests of biotic resistance (resident community intact vs. removed) limited the number of studies in our dataset, but allowed us to directly calculate the strength of interaction among resident communities and invasive species. We treated publications where investigators subjected different invasive species or the same invader to different communities as separate studies (Gurevitch & Hedges, 1993). If a study included various levels of vegetation or neighbor removal, we used data from the most severe treatment.

2.2.2 Response and explanatory variables

From each study, data were collected on invasive species performance with the resident community intact vs. removed. We classified the response variables into 4 categories: emergence, plant size, reproduction and survival. Evaluating different response variables may be important, as some interactions may comprise both competition and facilitation depending on the life stage or the response variable measured in the target species (Callaway & Walker, 1997). Further, to look at the direct effect of environmental conditions and productivity on performance, we used data on percent survival and emergence in absence of competition. Survival and emergence were calculated based on total seeds added or number of initially planted seedlings when metrics were not reported as a percentage. We also extracted information on the exact location of the experiments to obtain data for the following explanatory environmental variables: net primary productivity (NPP), normalized difference vegetation index (NDVI), precipitation and temperature. NPP, NDVI, precipitation and temperature were obtained from the Advances Very High Resolution Radiometer (AVHRR) and the Moderate Resolution Imaging Spectroradiometer (MODIS) remote sensing databases (see Appendix 1-1).

2.2.3 Data Analysis

We calculated Hedge's effect size *d* (Gurevitch & Hedges, 1993), which is the standardized mean difference between the control group (neighbor intact) ($\overline{X}_C$) and the experiment group (neighbor removal)($\overline{X}_E$) for plant size, emergence, reproduction and survival, separately using the following equation:.

$$d = \frac{\overline{X}_E - \overline{X}_C}{SD_{pooled}} J$$

A positive effect size *d* indicates a negative effect of neighbors on invasive species performance (competition) while a negative effect size *d* indicates a positive effect of neighbors on invasive species performance (facilitation). J was calculated to correct for small sample bias (Borenstein, Hedges, Higgins, & Rothstein, 2009) using the following equation:

$$J = 1 - \frac{3}{4\left(n_C + n_E - 2\right) - 1}$$

We conducted a random-effects meta-analysis, which is a meta-analysis model (different from a random effect linear model) that allows for variation between study effects in contrast to a fixed-effect model that assumes variance among study effects are known. Between study heterogeneity was assessed by calculating and testing for the significance of Q (see Appendix 1-2 for more details). Analyses were done using weighted linear models, where the models were weighted by the study's precision (W*) using the function *rma*, from the *metafor* package (Viechtbauer, 2010) in R (v.2.15.3, R Core Team, 2013). W* was calculated for each study as the inverse of the variance,

$$W_i^* = \frac{1}{V_{yi}^*}$$

where V_{yi}^* is the within-study variance plus the between-studies variance. Methods for meta-analysis followed those presented in (Borenstein et al., 2009). Publication bias, before the inclusion of moderator variables, was assessed through a funnel plot and the trim and fill method (Appendix 1-2 for more details).

Linear models were performed to test for the direct effects of environmental conditions on invasive species performance using percent emergence and survival in the absence of neighbors as response variables. Linear mixed effect models were used when testing for the effect of NPP and NDVI, where data source (MODIS or AVHRR) was added as a random effect to control for differences between the two sensors (see Appendix 1-1). Effects of environmental variables and productivity on the neighbor effects on invasive species performance were tested for using meta-regressions. A meta-regression is a meta-analysis that includes, in this case, a continuous variable to describe variation among study effects (moderator) (Borenstein et al., 2009). Each explanatory variable or moderator was tested for individually, in separate models, due to small sample size. In models including NPP and NDVI, data source (MODIS or AVHRR) was added as a random effect; however no random effect was added when evaluating the effect of temperature or precipitation. All meta-regressions were run using the *lm* function (for linear model) in the *stats* package and *lme* function (for linear mixed models) in the *nlme* package in R, with effect size *d* as the response variable and weighted by W* (Koricheva, Gurevitch, & Mengersen, 2013). To test for the robustness of our results (Koricheva & Gurevitch, 2014) and because of the significant heterogeneity between studies (see Appendix 1-2) we ran separate models for different invasive functional groups (i.e. forb, shrub, grass and tree, Appendix 1-3) when the number of replicates per functional group allowed for it (minimum of 6 replicates). Among all sites included in this study, there was no correlation between precipitation and temperature (r^2 = -0.07, P = 0.69). Neither temperature nor precipitation correlated with NPP (r^2 = -0.12, P = 0.544; r^2 = -0.1, P = 0.615, respectively) or NDVI (r^2 = -0,06, P = 0.74; r^2 = -0.03, P = 0.873, respectively). NPP and NDVI were strongly correlated (r^2 = 0.87, P < 0.01) and therefore, we only report results for NPP from now on, as results are very similar (not shown).

2.3 Results

We found a total of 23 publications that met our criteria (see Appendix 1-3), of which most included more than one invasive species or multiple study sites (treated as different studies).

In total, emergence of invasive species was evaluated in 21 studies, plant size in 27, reproduction in 11 and survival in 21. Further, 26 studies included a measure of invasive species survival and 21 studies of emergence reported, or could be calculated, as a percentage. Sites included in our analyses range in temperature and precipitation covering drier areas with high and low temperatures, as well as wetter ones with low temperatures (Figure 2-2). Wetter sites with low temperatures are under-represented in most of our analyses, except when looking at the impact of the resident community on invader's size (Figure 2-2B). Thus, our results are applicable to systems with those climatic conditions.

2.3.1 Native community's impact on invasive species performance

On average, native communities reduced invasive species emergence, size, reproduction and survival, indicating biotic resistance was common (Figure 2-3).

Biotic assistance was rare with only one case of net facilitative effects found when looking at the effect on size and one when looking at survival (see Appendix 1-4). The lack of evidence for biotic assistance is not an artifact of publication bias since the assessment of publication bias through funnel plots revealed that the overall effect size did not change after controlling for it. The trim and fill method revealed three studies missing from the right hand side of the funnel (i.e. those reporting biotic resistance) when evaluating survival (see Appendix 1-2). We also found significant heterogeneity between studies for three of the four response variables analyzed (size, reproduction and survival) (Appendix 1-2). Significant heterogeneity was expected and further justifies the need to explore other moderator variables to explain the variance between studies.

2.3.2 The effect of productivity, precipitation and temperature on invasive species performance

We found no direct effect of habitat productivity or environmental conditions on invasive species survival and germination in the absence of the resident community (Table 2-1).

2.3.3 The effects of productivity, precipitation and temperature on native community effects on invasive species performance

In general, productivity was not related to the effect of native communities on invasive species performance (Figure 2-4A-D, Appendix 1-5), while temperature and precipitation were significant predictors of the interaction outcome and strength (Figure 2-4F,I, Appendix 1-5). Temperature was positively associated with the neighbor effect on invasive species size, indicating more biotic resistance in warmer locations. However temperature did not affect biotic resistance for emergence, reproduction or survival (Figure 2-4E-H, Appendix 1-5). Precipitation was positively associated with the neighbor effect on invasive species emergence and size, indicating more biotic resistance in wetter locations, but had no effect on the invader reproduction or survival (Figure 2-4I-L, Appendix 1-5). Although the addition of moderator variables reduced the heterogeneity between the studies looking at the effect of neighbors on invasive species' size, the remaining heterogeneity was still significant (Appendix 1-2). This indicates that although moderators were significant, much of the variation remains unexplained, which may be due to the scale at which moderator variables were measured (Appendix 1-1).

When analyzing different invader functional groups separately our results remain quite consistent with our previous results (Figure 2-4, Appendix 1-5). NPP was not a significant predictor of neighbor effects on emergence, size or survival of invasive forbs, emergence of invasive shrubs or size of invasive grasses (Appendix 1-6). Temperature was positively associated with neighbor effect on the size of invasive forbs, but not the size of invasive grasses (Appendix 1-6). This indicates that the relationship we observed between temperature and neighbor effect on size is mainly driven by invasive forbs. Consistent with Figure 2-4, temperature was not related to emergence or survival, independent of functional group. Precipitation was positively associated with neighbor effect on invasive forb and shrub emergence as well as on the effect on the size of invasive forbs (Appendix 1-6). Interestingly, when looking at different functional groups, precipitation was negatively associated with neighbor effect on invasive forb survival (Appendix 1-6). The relationship between productivity and environmental conditions on invader's reproduction could not be assessed by functional group due to small sample size.

2.4 Discussion

We found a consistent pattern of change in net neighbor effect along precipitation and temperature gradients. This is in spite of having found a limited number of case studies that experimentally manipulated the presence of neighbors to evaluate their effects on invasive species (Appendix 1-3), which reflects an important hole in our knowledge about invasive species and their interaction with native species. Overall, we found that native communities have a negative impact on invasive species at all measured life stages, indicating biotic resistance (Figure 2-3), while examples of biotic assistance were uncommon (Appendix 1-4: Figure 2-1). However, we found significant heterogeneity between studies (Appendix 1-2) which highlights the limitations of comparing the effect of different community types on invaders and further stresses the need explain the variation between studies by including, for example, environmental variables. We found that the strength of the interaction was partly explained by the habitat's temperature and precipitation, but not by productivity (Figure 2-4). Our results support the stress gradient hypothesis (Bertness & Callaway, 1994; Maestre, Callaway, Valladares, & Lortie, 2009) indicating that net neighbor effects are dependent on abiotic conditions (Figure 2-1): stronger suppression of invasive species under warmer and wetter conditions and neutral to facilitative interactions under more stressful conditions. We found no support for a relationship between the strength and/or direction of the interaction and productivity as proposed by Grime (1973) (Figure 2-1).

Facilitation seems to be a common outcome of plant-plant interactions among native plants (Brooker et al., 2008; Venail et al., 2014). Venail et al. (2014) found, when reviewing -mostly observational- studies testing Darwin's naturalization hypothesis, that facilitative interactions were almost as common as competitive interactions. However, this does not seem to be the case for the interaction between native communities and invasive species. Further, when evaluating the effect of neighbors on species' survival, studies have found that neighbors tend to have neutral to positive effects, while negative effects are commonly found on plant growth (Howard & Goldberg, 2001; Maestre et al., 2009). In our meta-analysis, this was not found when looking at the interaction between native communities and invasive species. Although the overall negative effect on survival was not as strong as on the other response variables (Figure 2-3), facilitation was rare (Appendix 1-4: Figure 2-1). Invasive species facilitation may be uncommon because of their strong competitive ability (Levine et al., 2003; Vila & Weiner, 2004), or potentially because they invade areas close to their ecological optimum (Reisner et al., 2015); both being good predictors of facilitation (Brooker & Callaghan, 1998; Liancourt, Callaway, & Michalet, 2005). Although negative impacts on facilitator species are known to occur even within native species (Schöb et al., 2014) they are thought to destabilize or select against facilitation

(Bronstein, 2009). The lack of evidence for facilitation may also be a result of the experimental designs included in our analyses. Venail et al. (2014) reviewed mostly observational studies, in contrast to the experimental studies included in our meta-analysis. Both observational and experimental studies have been commonly used to measure facilitation, but greater evidence for facilitation comes from observational studies (Maestre et al., 2005).

Stressful habitats are generally assumed to be less susceptible to invasion, although in our meta-analysis we found no direct effect (in the absence of the native community) of environmental conditions on invasive species performance. This is potentially driven by the fact that we are evaluating different species, each potentially invading areas with climatic conditions to which they are adapted. In fact, modeling invasive species climatic niches has been one of the tools used for predicting invasions (Nuñez & Medley, 2011; Thuiller et al., 2005). However, when looking at individual species responses, they have been shown to respond to biotic and abiotic gradients (Chambers et al., 2007; Gerhardt & Collinge, 2007; Harrison et al., 2015). Environmental conditions did nonetheless affect the interaction between native communities and invasive species. The relationship between temperature and precipitation and the effect of neighbors on invasive species' performance is consistent with the stress gradient hypothesis (Bertness & Callaway, 1994; Maestre et al., 2009). Under more stressful conditions (lower average temperature and precipitation) the effects of the resident communities on the invaders were found to be weaker or slightly positive (though not significant) (Figure 2-4, Appendix 1-4). Although stressful conditions may be a relative term (Körner, 2003), we found temperatures of around 9-15 °C or precipitation of 0–50 mm per month to result in weaker effects of the resident community on the emergence and size of invaders (Figure 2-4). Abiotic conditions seem therefore to at least partially determine whether the effect of resident communities on invasive species results in biotic resistance or assistance, and the strength of the positive or negative effect

(Figure 2-1). However, significant variation remained across studies (Appendix 1-2). Measuring environmental variables at more local scales and accounting for other potentially important abiotic factors (e.g. nutrients) may help better explain the variation in the effect of neighbors on invasive species (Figure 2-1). Similar results were found at a within-community scale by (von Holle, 2005, 2013), where the native community had a negative effect on invasive species under more favorable conditions, but not under stressful conditions.

In general, when separating invasive species by their functional groups, we find similar results to those in Figure 2-4, supporting the stress gradient hypothesis (Appendix 1-6). The one exception to the stress gradient hypothesis in our results was observed in the lack of a negative effect on invasive forbs' survival in the more moist environments (Appendix 1-6), however, this was only observed for invasive forbs, but not shrubs (Appendix 1-6). Overall, invasive forbs were more responsive to the effect of neighbors along precipitation and temperature gradients, while the contrary seems to be true for invasive grasses (Appendix 1-6). This may be explained by a higher root to shoot ratio in invasive grasses which may make them stronger competitors and less susceptible to environmental stressors (Caldwell & Richards, 1986; Gordon, Menke, & Rice, 1989; Hoekstra, Suter, Finn, Husse, & Luescher, 2015; Pywell et al., 2003).

Productivity, as measured here at broad scales, seems to have no impact on species interactions. Although the inclusion of more studies, across a broader range of productivity values is needed to assess the role of productivity on plant-plant interactions, our results are consistent with the growing body of evidence suggesting that productivity is not a strong proxy for competition strength (Figure 2-1, Bennett & Cahill, 2012; Goldberg et al., 1999; Maestre et al., 2005). The way productivity is measured may be inadequate as we tend to ignore belowground biomass which may represent up to 80% of the total biomass of a community (Lamb & Cahill, 2006). Alternatively, competition may not depend on community attributes, such as productivity, but rather on the balance of resource supply and demand (Davis, Grime, & Thompson, 2000; Davis, Wrage, & Reich, 1998). Our results also show that temperature and precipitation, within the ranges of included studies (Figure 2-2), are better predictors of competition, however the mechanisms behind their impact on species interactions needs to be further explored. Maestre et al., (2009) suggested that facilitation is more probable when stress is caused by a non-resource-related environmental factor such as salinity or pH, while competition is more probable under resource-related stress. However, temperature and precipitation can have mixed effects. They are not only a measure of non-resource stress, but also are related to resource availability. Both precipitation and temperature are related to water availability and can alter microbial activity and nutrient cycling in the soil affecting the amount of resources available to plants (Brady & Weil, 2007). Further research is needed to disentangle the mechanisms behind the effects of environmental conditions on plant-plant interactions.

2.4.1 Conclusion and synthesis

Combining meta-analysis and remote sensing data enabled us to test hypotheses among, instead of just within, sites allowing for broader generalizations; however, the use of remote sensing data measured at broad scale is not without limitations. Moreover, we wish to use this article to emphasize the necessity of more experimental studies to be performed in different geographic locations and community types to better understand the interaction among native communities and invasive species. We found that native plant communities resisted invasion, which limited the emergence, growth, reproduction and survival of invasive species. Although there is variation in the effect on invasive species, facilitation was not found to be a common outcome. The variation in the strength of the interaction could not be explained by the habitat productivity, but in part, by temperature and precipitation. Understanding why some communities are more susceptible to invasion than others is important not only to target invasive species management strategies, but also to understand the mechanisms behind invasion, species interactions and overall community assembly.

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Table 2-1. Direct effect of productivity, temperature and precipitation on invasive species performance

The effect of productivity, temperature and precipitation on emergence and survival of invasive plant species in the absence of the native resident community

		Emergence (n=21)	Survival (n=26)
NPP	Estimate	-0.006	0.033
	F-value	0.833	0.833
	p-value	0.374	0.374
Temperature	Estimate	-0.003	-1.911
	F-value	3.487	2.128
	p-value	0.08	0.158
Precipitation	Estimate	-0.074	0.118
	F-value	0.026	3.099
	p-value	0.872	0.091

Figure 2-1: Conceptual diagram of the different hypotheses on the relationship between abiotic conditions and productivity on net neighbor effect on invaders. The effect of neighbors on exotic species (net neighbor effect), as well as the impact of exotic species on the resident communities, may be dependent upon the habitats' productivity and abiotic conditions. The net neighbor effect on invaders may range from negative (competition) to positive (facilitation). The negative effect of neighbors on exotic species is a process generally known as biotic resistance. However, the net neighbor effect can also be positive (where the resident communities facilitate invasive species), a process identified as biotic assistance. Evidence and hypotheses vary in their predictions on how the strength and direction of the interaction vary along stress (left graph) or productivity (right graph) gradients.

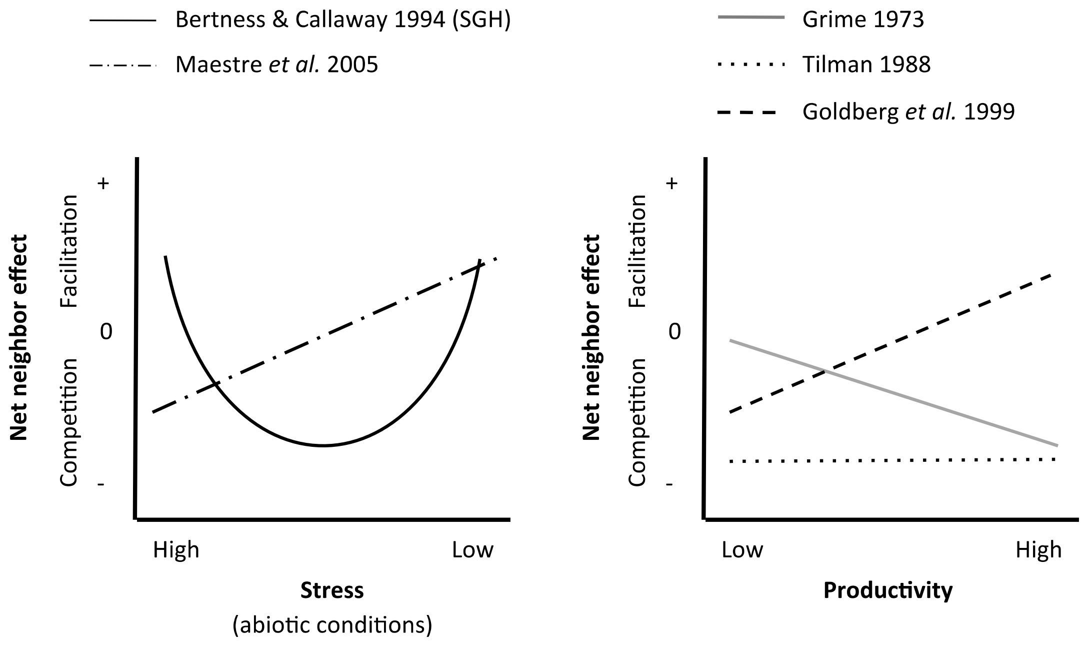


Figure 2-2: Relationship between precipitation and temperature for all sites included in the analyses. Temperature and precipitation were averaged for the growing season or duration of the experiment. Since different studies varied in the invaders response variable measured, the sites and therefore, the range of conditions in the analysis of each of the response variables are shown separately: (A) Total (B) emergence, (C) size, (D) reproduction and (E) survival.

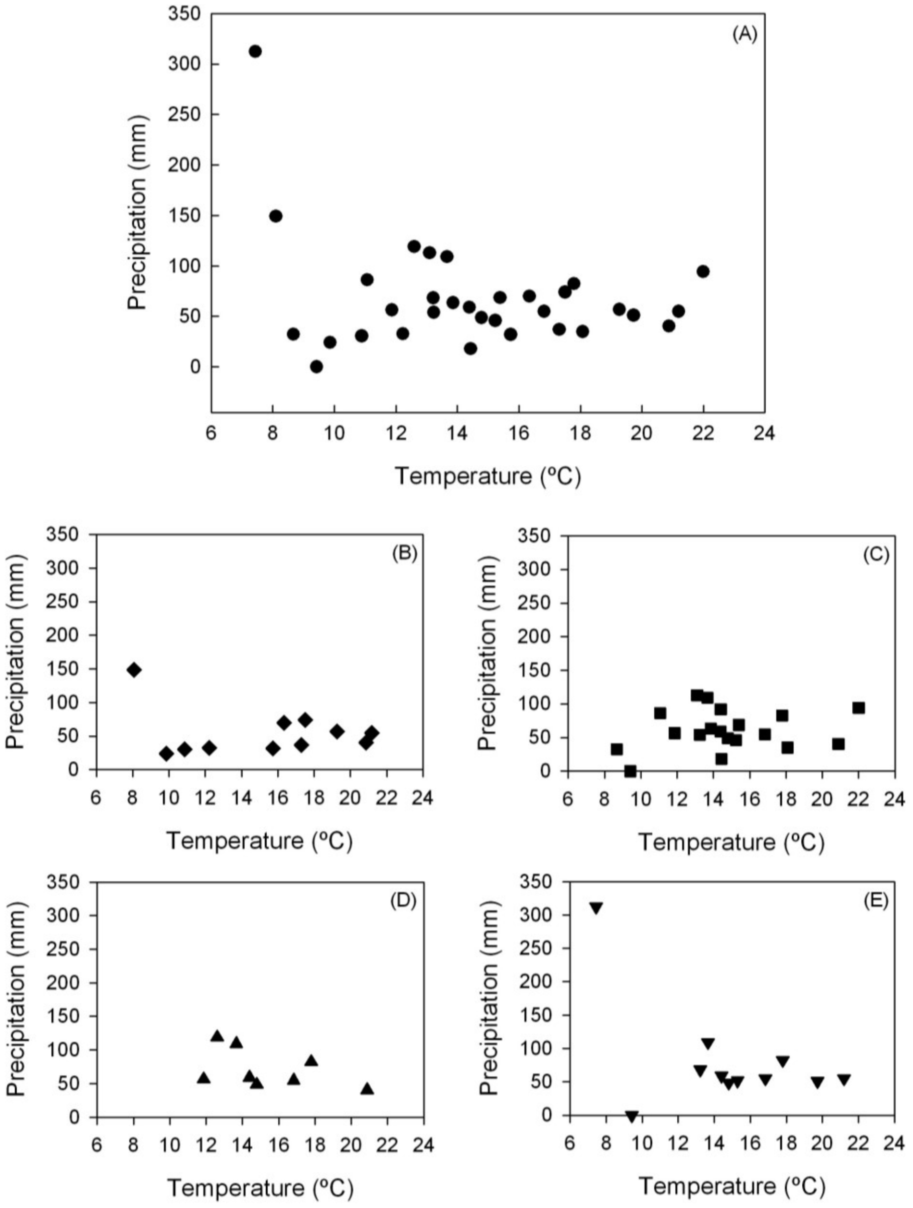


Figure 2-3: Net effect of the resident native community on invader seedling emergence, size, reproduction and survival. Mean ± 95% confidence intervals. Positive values indicate competition and negative values indicate facilitation. Larger values indicate stronger effects.

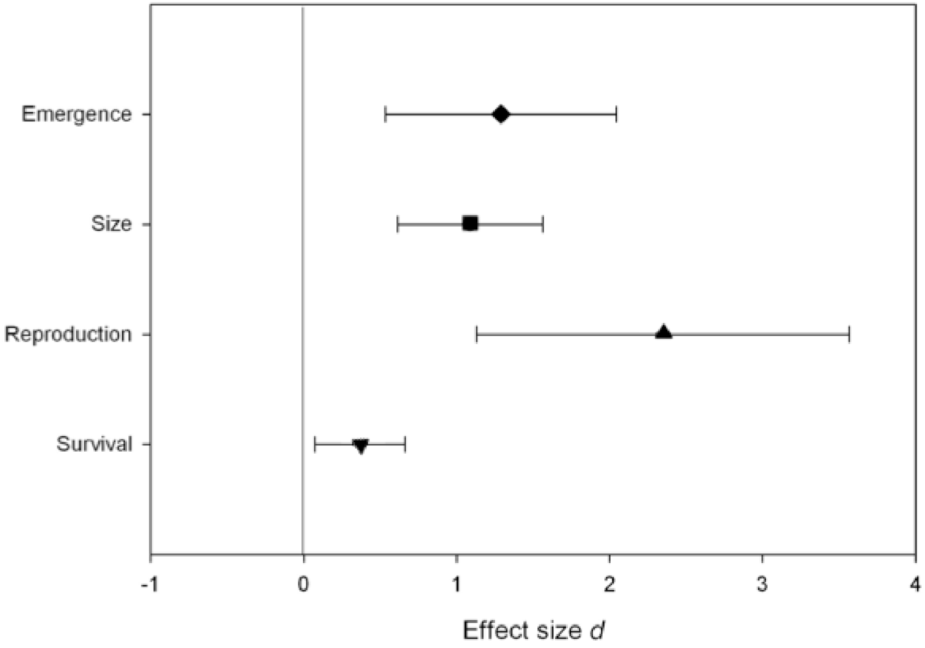
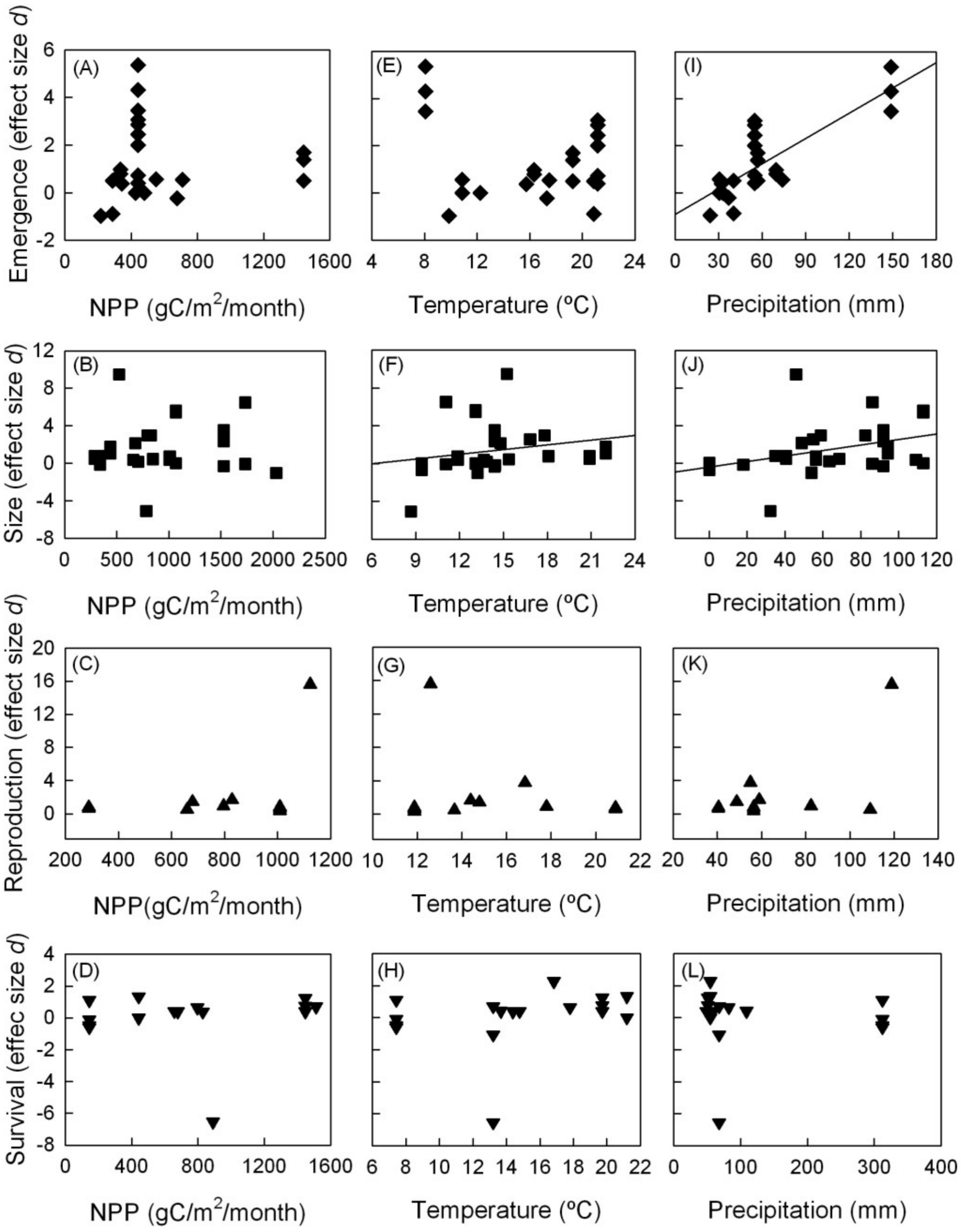


Figure 2-4: Effect of productivity, temperature and precipitation on the net neighbor effect (effect size *d*) on invasive species emergence (A,E,I), plant size (B,F,J), reproduction (C,G,K) and survival (D,H,L). Positive effect size *d* indicates negative effect of neighbors on invasive species' performance (competition) while a negative effect size *d* indicates a positive effect of neighbors on invasive species' performance. NPP, temperature and precipitation were averaged for the growing season or duration of the experiment.



Chapter 3: Differential responses of native and exotic plant species to an invasive grass are driven by variation in biotic and abiotic factors

3.1 Introduction

Invasive plant species reduce species diversity and alter the functioning of ecosystems (Vilà et al. 2011; Gaertner et al. 2014), yet we are still unable to predict their impact (Hulme et al. 2013). Invasive species impact on resident communities can be highly variable in both magnitude and direction (Vilà et al. 2006; Vilà et al. 2011; Hulme et al. 2013). Different biotic and abiotic factors can limit invasive species establishment and growth (Theoharides & Dukes 2007) which may help predict their impact on resident communities. If biotic and abiotic factors vary across sites, invasive species impact on community structure and function is also expected to vary (Vilà et al. 2006). Hence, we need large-scale studies that incorporate the variation across the invaded area to better understand the impact of invasive species on community structure and design effective management strategies (D'Antonio et al. 2004). Effective management strategies may allow us to take advantage of the services invasive species provide (Davis et al. 2011) while reducing their impact. Smooth brome (*Bromus inermis* Leyss.) is an important forage crop (Otfinowski et al. 2007), while also one of the worst invasive species in Canada (Catling & Mitrow 2005). However, although widely distributed (Grace et al. 2000; Otfinowski et al. 2007), it is unknown how its impact varies depending on different biotic and climatic factors.

Different hypotheses predict the conditions under which the resident community (i.e. biotic resistance, Levine et al. 2004) and abiotic conditions (i.e. abiotic resistance, Rejmanek 1989) limit the establishment and growth of invasive species. Greater species richness (Elton 1958; Levine et al. 2004) and community productivity (Cleland et al. 2004; Harrison et al. 2015, but see Stotz et al. 2016) tend to increase biotic resistance. Biotic resistance was also found to be stronger under warm, moist environments (Stotz et al. 2016), but these conditions can also result in greater invasive species impact (Castro-Díez et al. 2014). Temporal variation in environmental conditions can also facilitate invasive species, creating opportunities for invasion by temporarily suppressing native species or releasing resources (Johnstone 1986; Davis et al. 2000). Testing these hypotheses can help us predict invasive species impact on resident communities.

Invasive species may differ in their impact on native and exotic species (Bernard-Verdier & Hulme 2015), yet few studies evaluate the interaction of invaders with exotic species, which may be just as important when designing management strategies (Kuebbing et al. 2013; Kuebbing & Nuñez 2015). Although not all exotic species are invasive (dispersing across the invaded range and altering resident communities), about one in ten may be, or become, invasive (Vilà et al. 2010). Ecological differences between native and exotic species have been recognized, beyond different evolutionary histories with local communities (Callaway & Aschehoug 2000). Exotic plants are not a random subset of species, but those closely associated with human activities and altered landscapes, adapted to a broad range of conditions, and with high dispersal rates (Firn et al. 2011; Stohlgren et al. 2011; Seabloom et al. 2013; Buckley & Catford 2016). These characteristics may result in an advantage for exotic species when interacting with invasive species (Ehrenfeld 2003; Vila & Weiner 2004; Seabloom et al. 2013). Predicting if, and under which conditions invaders suppress or facilitate exotic species can have important management implications (Pearson & Ortega 2009; Kuebbing & Nuñez 2015). Negative interactions between invaders and exotic species can result in secondary invasions (Ortega & Pearson 2010), while positive interactions can result in the accumulation of exotic species and further suppression of native species (Simberloff & Von Holle 1999; Flory & Bauer 2014).

Predicting invasive species impact on community structure and their interaction with both native and exotic species can help plan management, as well as planting strategies for economically-important invasive species (Smith et al. 2006; Barney 2014). Smooth brome is a forage species actively bred and regularly sown (Romo & Grilz 1990; Coulman 2006; Otfinowski et al. 2007), while also a widely-distributed, harmful invasive species (Otfinowski et al. 2007; Grace et al. 2000; Sinkins & Otfinowski 2012; Ellis-Felege et al. 2013). Although smooth brome is known to have a negative impact on resident plant species diversity (Fink & Wilson 2011; Bennett et al. 2014) it is unknown whether its impact varies across sites. Hence, a broad assessment of smooth brome's impact across different environmental conditions is largely missing.

Our study fills important research gaps by specifically addressing the drivers of smooth brome impact, over a large-scale area including 8 undisturbed grassland sites in Alberta, Canada. Our main questions are (1) whether smooth brome has a consistent impact on community structure (species richness, evenness, composition and biomass) and function (productivity), (2) which biotic and climatic conditions are associated with smooth brome's impact on resident communities and (3) whether smooth brome has a similar impact on native and exotic species, and which biotic or climatic factors are associated with smooth brome impact on native and exotic species. If smooth brome's impact on community structure and function varies across sites, we could target management to areas where it poses a greater risk for biodiversity, and use areas of lower or no impact to cultivate smooth brome as a forage species.

3.2 Methods

3.2.1 Study system

To study smooth brome's impact across a range of conditions we focused on smooth brome invasion in the grassland area of Alberta (Otfinowski et al. 2007), with sites as far as about 850 km apart (Figure 3-1). These sites vary in species richness and climatic conditions ranging from a semi-arid Mixed grassland to the to the Aspen Parkland Ecoregion. The Mixed grassland has a mean annual precipitation of 250-350 mm, brown Chernozemic and Solonetzic soils, and is dominated by grasses such as *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Pascopyrum smithii* (Rydb.) Á. Löve and *Koeleria macrantha* (Ledeb.) Schult. The Aspen Parkland Ecoregion has a mean annual precipitation of 350-500 mm, black and dark brown Chernozems soils and is characterized by a mosaic of trembling aspen (*Populus tremuloides* Michx.) interspersed with rough fescue (*Festuca hallii* (Vasey) Piper) grassland (Shorthouse 2010). Across this area, we set up 135 transect in 8 sites, trying to maximize the variation in conditions both within and across sites (Figure 3-1, Appendix 2-1). The names and general description of the 8 sites sampled can be found in Appendix 2-1.

3.2.2 Measuring brome's impact on community structure and function and the potential biotic and abiotic drivers

To quantify smooth brome's impact on community structure and function we used a space-for time substitution, where invaded areas are compared to adjacent uninvaded areas. This method is commonly used in invasion studies (Vilà et al. 2006; Hejda & Pyšek 2006; Hejda et al. 2009; Powell et al. 2013; Kumschick et al. 2015) and is of great value to investigate long-term dynamics of invasion (Strayer et al. 2006; Kumschick et al. 2015) when pre-invasion data are not available. Smooth brome invasion offers a particularly suitable system for this approach because it forms dense and well defined patches (as indicated by a sharp drop in smooth brome cover over a short distance) (Bennett et al. 2014) and its invasion is ongoing, with patches continuously and rapidly encroaching into adjacent uninvaded areas (Otfinowski & Kenkel 2008; Bennett et al. 2014). This makes it unlikely that uninvaded areas are fundamentally different from invaded areas, which is a common limitation when using space-for-time substitutions (Pickett 1989).

To determine smooth brome's impact on community structure and function within and across sites, we set up 15 – 20 transects per site for a total of 135 transects in 2013 (i.e. at transect level n = 135, and at the site level n = 8) When performing site level analyzes, changes in community structure and function were averaged per site. Each transect was 4 m long, running perpendicular to the invasion edge, with 2 m into the invaded areas and 2 m into the uninvaded areas (similar to Bennett et al. 2014). We recorded the presence of each species using a line intercept method, recording species presence at each cm along the transect (Sutherland 1996). Impact was estimated as the difference between the 1.5 m at both ends of the transect (i.e. invaded vs. uninvaded areas). We excluded the 1 m at the invasion edge, to avoid the transition area between invaded and uninvaded where smooth brome invasion may be more recent or just occurring (Bennett et al. 2014).

As a measure of impact on community structure we calculated the change in species richness, evenness and non-brome biomass, while impact on community function was calculated as the change in community productivity (measured as total standing biomass). Species richness, and evenness were calculated for the invaded and uninvaded areas, using the number of cm at which species are found as a measure of abundance. Smooth brome was not included into the calculations (Thomsen et al. 2016). Species richness was also separated into native and exotic species. Two species that could not be identified were excluded from the analyses on native and exotic species richness. Evenness was estimated as J = *H'*/log(*S*), where *H'* is Shannon diversity index and S is total species richness. Smooth brome, litter and non-brome biomass were also measured in all transects. Biomass was clipped at peak biomass in three 10x100 cm plots placed perpendicular to transects, at each end of the transect (invaded and uninvaded areas). In each plot we clipped biomass and separated it into litter, smooth brome, and resident species biomass. All samples were dried at 70°C for 72 hours and weighed.

The change between uninvaded and smooth brome-invaded areas in community structure and function, was estimated as the log response ratio (lnRR) of smooth brome invaded areas relative to the adjacent uninvaded community (ln(invaded/native)). A negative lnRR reflects a lower value in invaded areas compared to uninvaded areas (i.e. negative impact), while the opposite is true for positive values. Change in species composition was calculated as the Bray-Curtis dissimilarity index between invaded and uninvaded areas per transect, obtained using the *vegdist* function from the *vegan* package in R (v.2.15.3, R Foundation for Statistical Computing, Vienna, AT). The Bray-Curtis index is bound between 0 and 1, where 0 indicates that invaded and uninvaded areas have the same species compositions, while 1 indicates the two areas have no species in common. We multiplied the Bray-Curtis index by -1 to reflect a negative impact when there is a greater difference in species composition.

3.2.3 Potential biotic and abiotic drivers of smooth performance and impact on community structure and function

To predict smooth brome's impact on community structure and function we measured different biotic and abiotic predictors: pre-invasion productivity (measured as total standing biomass) and species richness, measured in each transect (see above), as well as climate data.

Climate data were obtained from the Alberta Agriculture and Rural development AgroClimatic Information Service (ACIS) (at http://agriculture.alberta.ca/acis/, accessed October 2015). We used weather data from the stations no farther than 20 km from each site (Appendix 2-1). We obtained data on the accumulated precipitation and average temperature for the year before sampling, but also obtained historic precipitation records (available since 1961 for the growing season: April to September) to calculate the coefficient of variation (CV) in precipitation for each site, as the standard deviation divided by the mean. Historic temperature data are not available. Precipitation and temperature were also obtained for other time periods (e.g. growing season precipitation and last 2, 3 and 30 years), but their explanatory power was not better than that of the sampling year data (data not shown).

To determine the independence of the climatic variables as predictors, we tested for their correlation. Average temperature and accumulated precipitation were not correlated ($r^2 = 0.42$, $P = 0.29$). However, precipitation and the variation in precipitation (CV) were positively associated, with sites with higher precipitation having also the highest variation ($r^2 = 0.74$, $P = 0.03$). Although correlated, we evaluated the predictive effect of both variables, as they represent different system properties and their explanatory power differs (see below).

3.2.4 The effect of brome on community structure and function

To determine smooth brome's impact on community structure and function, we compared species richness, evenness, total biomass and non-brome biomass between invaded and uninvaded areas using linear mixed models. We ran an overall model, as well as separate models for each site with transect within site, or just transect as random effects, respectively. Mixed models were run using the *lme* function from the *nlme* package (Pinheiro et al. 2016). To test for differences in species composition between invaded and uninvaded areas we ran permutational ANOVAs using the *adonis* function from the *vegan* package (Oksanen et al. 2016). As above, we ran an overall model for all sites, as well as separate models per site, with site or transect as *strata* to account for the nested structure of the data.

To test whether smooth brome was associated with the changes observed, we evaluated the effect of smooth brome and litter biomass on the change in community richness, evenness, composition, total biomass and non-brome biomass. Litter biomass reflects past growth and can be an important driver of invasion impact by suppressing neighbors' establishment and growth (Farrer & Goldberg 2009; Loydi et al. 2015). Although litter biomass was not separated by species, visual inspections indicated that most of the litter present in the invaded areas was smooth brome litter. Further, smooth brome biomass was found associated with litter biomass in the invaded areas (glm: $\beta = 0.014$, $F = 20.35$, $P = 0.001$) and with the difference in litter biomass between uninvaded and invaded areas (glm: $\beta = 0.005$, $F = 5.41$, $P = 0.021$).

3.2.5 Biotic and abiotic predictors of brome performance and impact

We determined whether brome performance (smooth brome and litter biomass) and the changes associated with smooth brome invasion were dependent upon biotic and abiotic conditions. We only focused on three response variables: change in total species richness, non-brome biomass and species composition. We chose to only focus on these three response variables because evenness was not observed to change in most sites (Figure 3-2) and total biomass in the invaded areas was strongly driven by smooth brome biomass (F-value = 46.78, p-value < 0.0001). Linear mixed models were used to test for the effect of species richness and productivity at the transect level, with site as a random factor. Linear models were used to test for the effect of temperature, precipitation and the variation (CV) in precipitation (at the site level) on smooth brome's impact on species richness, non-brome biomass and species composition. Each predictor variable was analyzed separately due to low sample size at the site level.

3.2.6 The effect of smooth brome on native and exotic species, and the drivers of their interaction

To evaluate whether native and exotic species differ in their response to smooth brome invasion we ran linear mixed models, with change in species richness as the response variable, species origin (native vs. exotic) as fixed effect and transect within site as a random effect. We also tested for differences between invaded and uninvaded areas in native and exotic species richness in an overall model, as well as per site, as above. To evaluate whether exotic species richness was associated with a greater decrease in native species richness, we tested for the correlation between native and exotic species richness in invaded and uninvaded areas, as well as whether exotic species richness in invaded areas was associated with the change in native species richness. As above, we also tested whether smooth brome was the driver of the changes in native and exotic species richness with smooth brome and litter biomass as fixed effects.

To determine whether the response of native and exotic species to smooth brome was dependent upon biotic and abiotic conditions, we first tested for the effect of biotic and abiotic factors on the change in native and exotic species richness. Further, to evaluate whether exotic and native species differential response to smooth brome was context-dependent, we tested for the interaction between species origin (native vs. exotic) and biotic and/or abiotic factors on the change in species richness. A significant interaction between species origin and biotic and/or abiotic factors would indicate that the difference in response by native and exotic species is dependent upon such conditions.

3.3 Results

3.3.1 The effect of brome on community structure and function

Smooth brome invasion was associated with changes in community structure and function (Figure 3-2) including a relatively consistent reduction in species richness (Figure 3-2A) and non-brome biomass (Figure 3-2D) in smooth brome-invaded areas, compared to uninvaded within and across sites (Figure 3-2). More than 75% of transects fell below the no-impact line (Appendix 2-2). Smooth brome's impact on species richness was also reflected as a significant change in species composition (Appendix 2-3). Species evenness was similar in uninvaded and invaded areas, with the exception of one site (Kinsella), where evenness was significantly lower in smooth brome-invaded areas (Figure 3-2B). Total biomass was consistently higher in smooth brome-invaded areas in contrast to native areas both within and across sites (Figure 3-2C, Appendix 2-2).

Supporting the role of smooth brome as a driver of the change in community structure and function, smooth brome live and litter biomass were significantly associated with the changes in community structure and function observed (Table 3-1). There was a greater reduction in non-brome biomass, a greater change in species composition and a greater increase in total biomass in areas with greater smooth brome and litter biomass (Table 3-1). Change in species evenness was not associated with smooth brome or litter biomass (Table 3-1).

3.3.2 Biotic and abiotic predictor of brome performance and impact

Biotic and abiotic conditions were associated with smooth brome's performance, as well as with smooth brome's impact on community structure and function (Table 3-2, Figure 3-3). Smooth brome living biomass was greater in warmer sites (F-value = 7.74, P-value < 0.05), while litter biomass was greater in more productive sites (F-value = 24.24, P-value < 0.01) and sites with higher precipitation (F-value = 8.48, P-value < 0.05) or greater variation in precipitation (F-value = 10.61, P-value < 0.05). The proportional reduction in species richness in smooth brome-invaded areas was greater in species-rich communities (Figure 3-3A), while the change in species composition was not found associated with any biotic or abiotic factor measured (Table 3-2, Figure 3-3). Smooth brome was associated with a greater reduction in non-brome biomass in more productive (Figure 3-3F), variable (CV precipitation) (Figure 3-3I) and warmer (Figure 3-3O) sites.

3.3.3 The effect of smooth brome on native and exotic species, and the drivers of their interaction

Smooth brome-associated changes in species richness were dependent upon species origin (glm: $\beta = -0.189$, $F = 19.32$, $P = < 0.001$). Native species richness was consistently lower in smooth brome-invaded areas compared to uninvaded areas within (Appendix 2-2), as well as across sites (Figure 3-2E). The change in exotic species richness was, in contrast, highly variable, being lower in smooth brome-invaded areas in only two sites (PO and WoS; Figure 3-2F). We also found greater smooth brome biomass to be associated with a greater reduction in native species richness and not with the change in exotic species richness (Table 3-1). The opposite was true for litter biomass, which was associated with a greater reduction in exotic, but not native species richness (Table 3-1).

We found no evidence that the presence of exotic species resulted in a greater reduction in native species richness. Although native and exotic species richness were negatively correlated in uninvaded (r^2 = -0.37, $P < 0.001$) and invaded (r^2 = -0.27, $P = 0.001$) areas, exotic species richness in the invaded areas had no effect on the change in native species richness (glm: β = 0.01, F =0.09, $P = 0.76$).

Native and exotic species richness responded differently to smooth brome invasion depending on biotic and abiotic conditions (Figure 3-4). Native species richness was more greatly reduced in smooth brome-invaded areas in species-rich communities compared to species-poor areas (Figure 3-4A). A greater reduction in exotic species richness was observed in sites with a greater variation in precipitation (Figure 3-4C). Consequently, there was a significant interaction between species origin (native vs. exotic) and both species richness (glm: β = -0.03, F = 9.30, P = 0.003) and the variation in precipitation (lm: β = 2.18, F = 8.41, P = 0.013). No other factors or interactions were found to be significant (Figure 3-4).

3.4 Discussion

Overall, smooth brome reduced species richness and non-brome biomass across sites (Figure 3-2); however, the magnitude of the impact was at least partly dependent upon characteristics of the pre-invasion community and climatic conditions (Figure 3-3). We found a negative effect of species richness and productivity on biotic resistance (Figure 3-3), which is contrary to what has been proposed (i.e. greater biotic resistance in diverse and productive communities) (Elton 1958; Levine et al. 2004). However, we did find evidence of abiotic resistance (Rejmanek 1989). More importantly, we found a greater loss in native, compared to exotic species richness in invaded areas (Figure 3-2), with their response to invasion being driven by different factors. The factors driving the magnitude and direction of the effect of an invader on exotic species have rarely been tested (Kuebbing & Nuñez 2015). This information can provide insight into invasive species impact and help predict the possibility of an invasional meltdown and/or secondary invasions (Kuebbing & Nuñez 2015). Since secondary invasions are more likely when invaders are suppressing other exotic/invasive species (Kuebbing & Nuñez 2015), we predict they are more likely to occur in sites with a greater variation in precipitation.

3.4.1 The effect of smooth brome on community structure and function

Smooth brome was associated with changes in community structure and function within (Appendix 2-2) and across (Figure 3-2) sites. These results are in accordance with the findings of other studies on the negative effect of smooth brome on resident communities (Otfinowski et al. 2007; Fink & Wilson 2011; Bennett et al. 2014). However, no study had evaluated smooth brome's effect on resident communities across different environmental conditions. Broad scale studies like this are necessary to design management strategies at the landscape scale (D'Antonio et al. 2004). Smooth brome's consistent impact on community structure and function (Figure 3-2) is consistent with previous studies indicating that although smooth brome is a better competitor under moist and high nutrient conditions, it remains a strong competitor under less favorable conditions (Nernberg & Dale 1997; Gendron & Wilson 2007; Holub et al. 2012; Carrigy et al. 2016).

Smooth brome's ability to grow and compete under different conditions may be a consequence of being a forage species that has been selected for fast and high-density growth under different environments (Cook 1943; Alderson et al. 1994; Wilkins & Humphreys 2003). Selecting for environment-specific cultivars may help decrease forage species invasive potential (Jakubowski et al. 2011), while still maximizing their yield. However, a higher genetic diversity through the introduction of different cultivars can also increase the invasive potential of forage species (Lavergne & Molofsky 2007). For these reasons, it is being increasingly recognized that many forage species may pose a risk to biodiversity (Lonsdale 1994; Driscoll et al. 2014; Scasta et al. 2015). This highlights the need to quantify the invasive potential of forage species, before breeding and/or introducing them into potentially susceptible areas (Davis et al. 2010; Barney 2014; Driscoll et al. 2014).

3.4.2 Biotic and abiotic predictor of smooth brome performance and impact

We found productivity and species richness to be positively associated with smooth brome's impact on community structure (Figure 3-3), which is contrary to what is expected based on the biotic resistance hypothesis (Elton 1958; Levine et al. 2004); similar results were found by Vilà et al. (2006). The same conditions resulting in high species richness and productivity, such as high nutrient availability, potentially result in greater invader performance (Shea & Chesson 2002). Our results indicate greater invader performance in productive communities, compared to more arid, less productive communities (Rejmanek 1989; Thomsen, D'Antonio, et al. 2006). Biotic resistance may be stronger in moist and warm sites (Stotz et al. 2016), but once established, invasive species have a stronger effect on the resident community under those conditions (Castro-Díez et al. 2014). Consequently, preserving healthy resident communities and avoiding anthropogenic disturbances may prevent invasive species impact by limiting their establishment (Jauni et al. 2015). We also found support for Davis et al. (2000) model, which predicts that greater variation in resources or conditions facilitate invasive species establishment, growth and impact on community structure: these windows of opportunity give the invader a temporary advantage over native species (Johnstone 1986; Davis et al. 2000; Shea & Chesson 2002).

3.4.3 The effect of smooth brome on native and exotic species, and the drivers of their interaction

Smooth brome was consistently associated with a reduction in native species richness, while its effect on exotic species was highly variable (Figure 3-2, Appendix 2-2). Other studies have shown similar results (Gooden et al. 2009; Bernard-Verdier & Hulme 2015), yet the mechanisms behind the different response by native and exotic species remain largely unknown. A lower impact on exotic species may come from a greater number of exotic species adapted to human-altered landscapes, their coexistence with forage species and/or their growth in fertilized areas (Foster et al. 2002; Thomsen, Corbin, et al. 2006; Buckley & Catford 2016), since nutrient availability is higher in smooth brome-invaded areas (Fink & Wilson 2011; Piper et al. 2015). Exotic species may also be better competitors than native species (Vila & Weiner 2004), or more functionally different from smooth brome, which is thought to result in lower competitive suppression (Fargione et al. 2003). We found no evident functional difference between native and exotic species, as both groups have similar proportion of grasses (~20%) and are composed mainly of perennial species (>95%) (Appendix 2-4). A detailed study of competitive ability and functional differences is needed.

The different response by native and exotic species to smooth brome was, however, not consistent across sites (Figure 3-4). This may be the result of certain habitat conditions filtering/selecting for similar functional characteristics regardless of species origin (Gross et al. 2013). Further, the interaction of native and exotic species with smooth brome was driven by different factors (Figure 3-4). Although exotic species establishment is thought to be facilitated by the variation in conditions (Davis et al. 2000), we found the opposite (Figure 3-4), potentially because the variation conditions resulted in a greater advantage for smooth brome over other exotics.

Knowing the direction and strength of the impact of smooth brome on native and exotic species richness can help preserve native diversity and prevent further invasions (Kuebbing et al. 2013; Kuebbing & Nuñez 2015). Since smooth brome had a consistent effect on native species richness, the strategy used should focus on its effect on exotic species. Management of areas where smooth brome has a positive or neutral effects on exotic species can prevent further biodiversity losses and new foci of invasion (Simberloff & Von Holle 1999), especially since some of the exotic species found in smooth brome-invaded areas are considered to be invasive (e.g. *Agropyron cristatum*, *Melilotus officinalis* and *Poa pratensis*). The presence of other exotic species in the invaded areas did not result in native species loss. Management of areas where smooth brome is suppressing exotic species can be aimed at preventing secondary invasions where exotic species take over the previously invaded areas if/once the invader abundance declines (Truscott et al. 2008; Ortega & Pearson 2010; Flory & Bauer 2014).

3.3.4 Conclusions and implications

We need to move past simply measuring invasive species impact on resident community structure into trying to predict under which conditions invasive species have a significant impact (Hulme et al. 2013; Kumschick et al. 2015). Targeting populations that pose a threat to biodiversity, rather than species, may be a more reasonable and manageable approach given the limited conservations funds. Further, there is a need to better understand the direction and magnitude of the interaction between exotic species, which would help forecast future invasions and design efficient and successful management strategies (Ortega & Pearson 2010; Kuebbing et al. 2013; Kuebbing & Nuñez 2015; Bernard-Verdier & Hulme 2015). An improved understanding of the drivers of invasive species impact on native and exotic species can help us improve management strategies to potentially take advantage of forage species, while preventing/reducing their impact on biodiversity (Davis et al. 2010; Barney 2014).

3.5 References

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Table 3-1: The association between brome biomass and litter biomass in invaded areas and the change in total species richness (S), diversity (H'), evenness (J), composition (Spp Comp), total biomass (Biomass), non-brome biomass and native (Native S) and exotic (Exotic S) species richness. Change was calculated as the log response ratio (lnRR) between invaded and uninvaded areas (ln(invaded/uninvaded)). *F-ratios* are shown (General linear mixed models), in bold if significant (* *p-value* < 0.05, ** *p-value* < 0.01).

	S	J	Spp Comp	Total biomass	Non-brome biomass	Native S	Exotic S
Brome biomass	3.75	2.13	**17.3****	**4.46***	**38.55****	**4.21***	0.78
Litter biomass	2.33	2.40	1.30	**5.79***	**18.15****	0.13	**5.66***

Table 3-2: The effect of species richness and productivity in the native areas, the long-term variation in precipitation (CV precipitation), precipitation and temperature on brome and litter biomass, as well on the change in total species richness (S), species composition (Spp comp), non-brome biomass and native (Native S) and exotic (Exotic S) species richness associated with brome invasion. Change was calculated as the log response ratio (lnRR) between invaded and uninvaded areas (ln(invaded/uninvaded)).

F-ratios are shown (General linear mixed models and linear models), in bold if significant (* *p-value* < 0.05, ** *p-value* < 0.01).

	Change in (lnRR)				
	S	Spp comp	Non-brome biomass	Native S	Exotic S
Species richness	**26.63****	0.01	1.95	**15.58****	0.01
Productivity	0.21	1.99	**6.15***	0.01	1.49
CV precipitation	5.46	0.11	**8.56***	1.74	**24.31****
Precipitation	1.63	0.07	2.25	0.80	4.53
Temperature	0.10	0.02	**14.02****	0.19	4.38

Figure 3-1: Study sites locations in a heat map of model predictions of smooth brome (*Bromus inermis* Leyss) relative abundance in Alberta, Canada.

Warmer colors indicate a higher predicted relative abundance of brome. The location of the eight study sites across used in this study are indicated (see Appendix 2-1 for site full name and description). Predictions of smooth brome relative abundance in Alberta were obtained from a model created by the Alberta Monitoring Institute: ABMI (2016). Awnless Brome (*Bromus inermis*). ABMI Species Website, version 3.2 (2016-03-18).

URL:http://species.abmi.ca/pages/species/vplants/BromusInermis.html

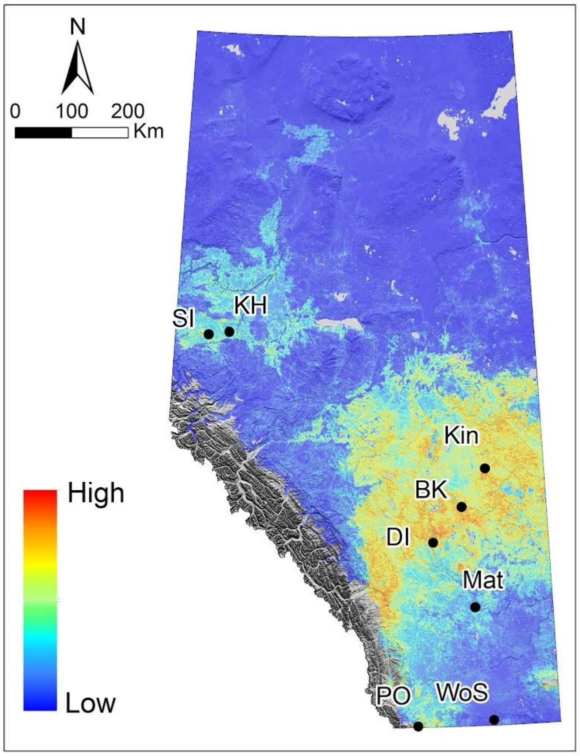


Figure 3-2: Change in species richness, diversity, evenness, total and non-brome biomass and native and exotic species richness between brome- invaded and uninvaded areas in each site. Sites are in the x-axis, and their full name and characteristics can be found in Appendix 2-1. Change was calculated as the log response ratio (lnRR) between invaded and uninvaded areas (ln(invaded/uninvaded)). Negative values of lnRR reflect lower values in invaded areas compared to uninvaded areas, while the opposite is true for positive values. General model results are in the upper right corner of each graph, and differences in each site are indicated in each column: * *p-value* < 0.05, ** *p-value* < 0.01.

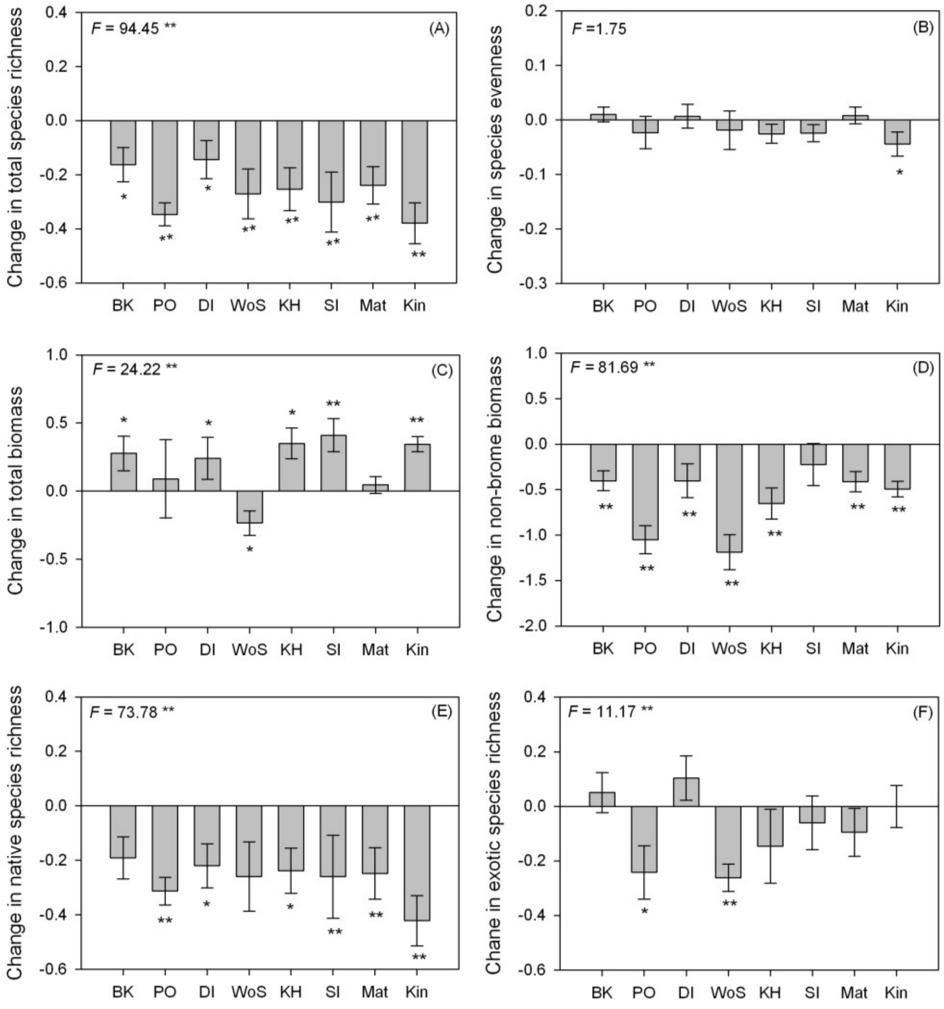


Figure 3-3: Change in total species richness, species composition and non-brome biomass between brome-invaded and uninvaded areas as a function biotic and abiotic factors. Change was calculated as the log response ratio (lnRR) between invaded and uninvaded areas (ln(invaded/uninvaded)).

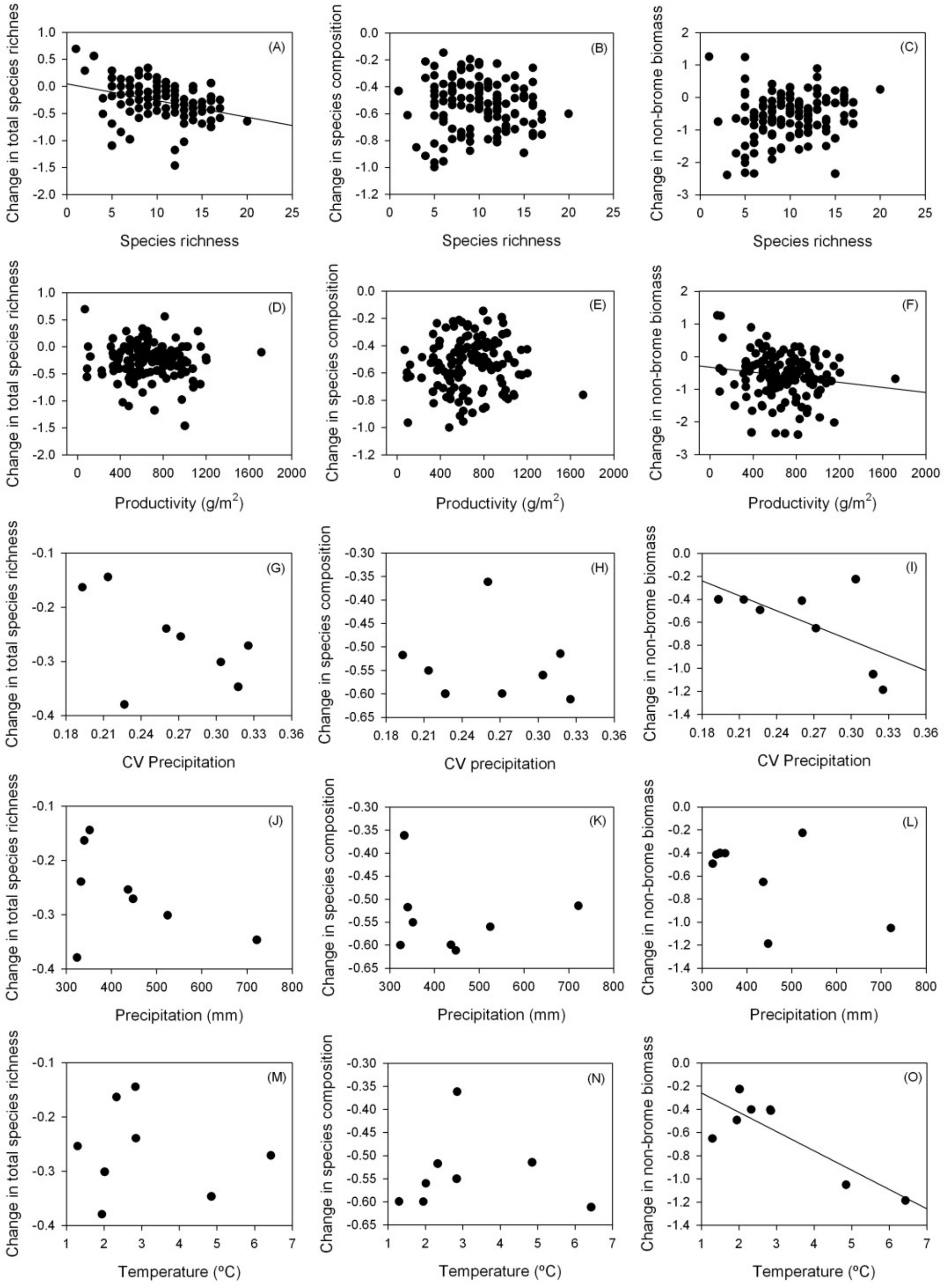
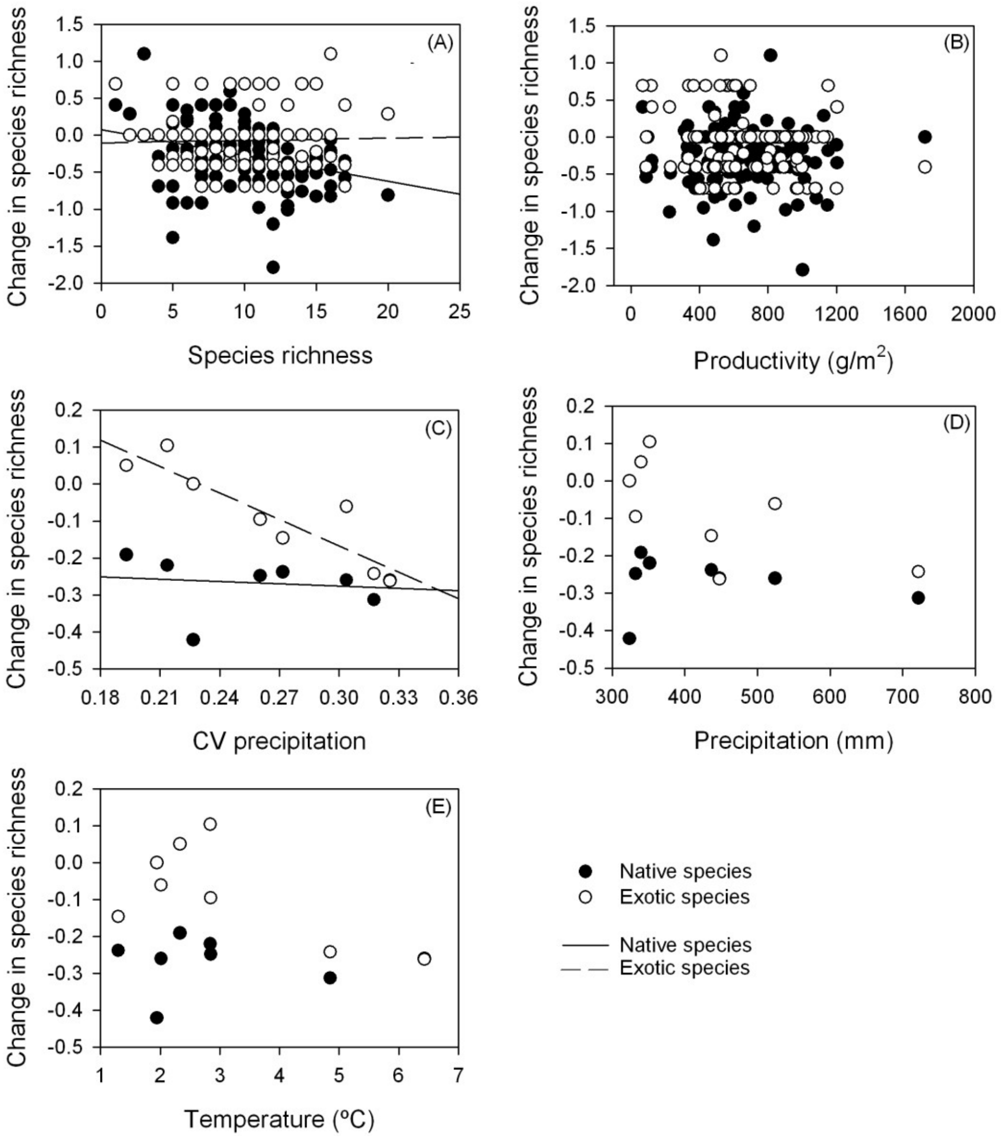


Figure 3-4: Change in species richness as a function of species origin (native vs. exotic) and biotic and abiotic factors.

Change was calculated as the log response ratio (lnRR) between invaded and uninvaded areas (ln(invaded/uninvaded)).



Chapter 4: *Bromus inermis* rapidly alters and homogenizes plant communities as it invades

4.1 Introduction

Invasive species may lead to the establishment of persistent, alternative community states in the landscape (Christian and Wilson 1999, Suding et al. 2004, Hobbs et al. 2006), altering the structure and functioning of communities (Ehrenfeld 2010, Vilà et al. 2011). Through changes in community structure and function, invaders may also increase the stability of these communities (Wilsey et al. 2014, Chisholm et al. 2015), increasing their resistance to restoration efforts (Suding et al. 2004). Studying invaded communities over space and time can help better understand their impact on community structure and function, the transition from a native-dominated to an invaded community and the persistence of invaded communities as an alternative state. The transition from a native-dominated to an invaded community state has rarely been studied in real time, and may occur as a slow, gradual transition, or as a rapid change following invader establishment (Scheffer et al. 2001, Hansen et al. 2013). Here, we evaluate the transition from a native to an invaded community state following invasion, and the potential mechanisms facilitating the persistence of the invaded community as an alternative state.

Different mechanisms can increase the stability and facilitate the persistence of invaded communities as alternative states (Scheffer et al. 2001, Suding et al. 2004), making them equally or more stable than native communities (Roscher et al. 2011, Wilsey et al. 2014). For instance, invasive species may establish self-reinforcing dynamics, which contribute to the stability, and therefore the persistence of alternative states (Suding et al. 2004). By altering ecosystem processes, such as nutrient cycling (Ehrenfeld 2010, Sardans et al. 2016), invasive species can facilitate their own growth and competitive ability (Davis and Pelsor 2001, Thomsen et al. 2006) thus creating a positive feedback. Further, through competition invasive species cannot only exclude species from invaded areas, but also limit their subsequent establishment (Yurkonis and Meiners 2004, Martin and Wilsey 2014), thus maintaining the community in a low-diversity, invaded state (Yurkonis and Meiners 2004, Martin and Wilsey 2014). However, the generally low species diversity in invaded communities can decrease community stability over time, as it may result in lower complementarity among species in their response to environmental change (Tilman et al. 1998, Loreau 2010, de Mazancourt et al. 2013).

Invasive species may not only reduce species diversity within invaded areas, but also among invaded areas, reducing species turnover across the landscape (i.e. beta-diversity) (Martin and Wilsey 2015). This would result in the biotic homogenization of communities across large spatial extents (McKinney and Lockwood 1999, McKinney 2004), with the potential reduction of overall community stability (Olden et al. 2004). The loss of species in invaded areas does not necessarily result in biotic homogenization (Olden and Rooney 2006, Smart et al. 2006); is the persistence of similar species in invaded areas across the range which result in greater similarity in species composition among invaded communities and thus in biotic homogenization (Olden and Poff 2003). In species-diverse communities, the establishment of species is determined, at least partly, by the interaction with different species (i.e. diffuse interactions) (Mitchley 1987). However, in highly dominated communities, such as those established by invaders, species establishment is determined mainly by their interaction with the invader (Stotz et al. 2016). If invaders act as non-random biotic filters, allowing only certain groups of species to establish or persist in invaded areas (e.g. Molinari and D’Antonio 2014, Bennett et al. 2014, Gooden and

French 2015), we would expect invasion to result in biotic homogenization (Olden and Poff 2003). Due to their generally broad distribution, invasive species may not only homogenize communities within sites, but also along their entire invaded range; although the likelihood of biotic homogenization due to invasion may vary depending on scale (Olden and Poff 2003).

At large scales, even if invaders act as strong biotic filters allowing only certain functional groups to persist in invaded areas, those functional groups may be represented by different species in different sites (Smart et al. 2006). This would result in the homogenization of invaded-areas within sites, but in a potential greater differentiation between sites (i.e. greater species turnover). On the other hand, it has also been proposed that the likelihood of detecting biotic homogenization due to invasion decreases at smaller scales (Olden and Poff 2003). This, because small scale heterogeneity in species distribution would increase the likelihood of detecting establishment and extinction of different species across sampling locations (within sites), while at larger scales (site level) each site would incorporate a greater breadth of conditions, thus increasing the likelihood of detecting similar species (Olden and Poff 2003, but see Martin and Wilsey 2015). If true, we may also expect homogenization to become apparent faster at larger scales, rather than at smaller scales. Overall, however, the homogenization of communities within and among sites would indicate that the invader establishes similar alternative community states across its invaded range.

Here, we provide real time evidence of the transition between community states following the invasion of smooth brome (*Bromus inermis* Leyss.), a widespread perennial grass that has been recognized as one of the worst invasive species in Canada (Catling and Mitrow 2005). Brome reduces species richness and alters nutrient availability where it invades (Fink and Wilson 2011, Bennett et al. 2014, Piper et al. 2015a). Further, its resistance to restoration efforts (Salesman and Thomsen 2011, Sinkins and Otfinowski 2012) may suggest brome-invaded areas are persistent community states. Although brome reduces local diversity where it invades (Otfinowski et al. 2007), it is unknown whether it results in the homogenization of communities, how fast it alters community state, and the mechanisms facilitating the persistence of communities in an invaded state. Specifically, in this study we test (1) whether species composition and nutrient availability change due to brome invasion, and the speed at which changes can be observed, (2) whether there is evidence of rapid biotic homogenization due to brome invasion within and across sites, and (3) whether species immigration, extinction and dynamics differ between brome- and native-dominated areas. The potential stability and persistence of invaded areas as alternative states are discussed in relation to potential positive feedbacks and the short-term temporal dynamics observed.

4.2 Methods

4.2.1 Study system

Brome (*Bromus inermis* Leyss) is a perennial grass intentionally introduced as a forage crop to North America in the late 1800s (Otfinowski et al. 2007). Brome has been widely planted across North America, but has escaped planted areas, invading natural, unseeded and undisturbed grasslands (Sather 1987, Grace et al. 2000, Otfinowski et al. 2007). Where it establishes, brome can form dense patches with a sharp edge, where brome cover drops from 60% to zero in less than a meter (Bennett et al. 2014). Brome disperses through seeds, but also through the vegetative growth of rhizomes, which is key to its invasiveness, increasing the density of patches and facilitating its expansion into adjacent native, uninvaded areas (Romo and Grilz 1990, Otfinowski et al. 2007, Otfinowski and Kenkel 2008). Brome is generally a strong competitor (Nernberg and

Dale 1997, Wang et al. 2010) reducing plant diversity by up to 70% where it invades (Fink and Wilson 2011, Bennett et al. 2014).

This study took place in eight undisturbed, unseeded sites distributed across Alberta, Canada. These eight sites cover a distance of 850 km and were chosen to be distributed throughout most of the grassland region in Alberta, where brome is commonly found invading (Otfinowski et al. 2007). The sites are located in different ecotypes (Shorthouse 2010): southern sites are located in the semi-arid Mixed grassland Ecoregion dominated by *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Pascopyrum smithii* (Rydb.) Á. Löve and *Koeleria macrantha* (Ledeb.) Schult, while northern sites are located in the Aspen Parkland Ecoregion, characterized by a mosaic of trembling aspen (*Populus tremuloides* Michx.) and grasslands dominated by *Festuca hallii* (Vasey) Piper and *Hesperostipa curtiseta* (Hitchc.) Barkworth. From south to north, the sites are: Police-Outpost provincial park (PP), Writing-on-Stone PP, the University of Alberta Mattheis ranch, Dry Island Buffalo Jump PP, Big Knife PP, the University of Alberta Roy Berg Kinsella ranch, Kleskun Hill Natural Area and Saskatoon Island PP. These sites vary in aboveground standing biomass from 54 to 90.4 g/m^2.

4.2.2 Sampling design

We sampled along transition zones between brome-invaded and native-dominated communities (Figure 4-1). These transition zones were used as space-for-time substitutions, where the conditions outside the brome-invaded areas are assumed to have been similar to those currently invaded (Pickett 1989). Further, since brome continuously and rapidly encroaches into adjacent uninvaded areas (Otfinowski and Kenkel 2008, Bennett et al. 2014) we also re-sampled the same areas after 1 and 2 years (Figure 4-1). This allowed us to quantify how conditions change following brome invasion.

In 2013 we set up 15-20 transects per site, for a total of 133 transects across all sites. Each transect was 4 m long, running perpendicular to the invasion edge, starting 2 m into the brome patch and ending 2 m into the native-dominated areas (Figure 4-1a). Within each transect, we focused on four positions (Figure 4-1): the area furthest into the brome patch (Position 1: 0 - 50 cm), the area at the inner edge of the invasional front (Position 2: 150-200 cm), the areas at the outer edge of the invasional front (Position 3: 200 – 250 cm) and the area farthest outside from the brome patch (Position 4: 350 – 400 cm). As brome encroached from 2013 to 2015 into the adjacent native-dominated areas, the area on the outer edge of the invasional front (position 3) became invaded (Figure 4-1). To validate our sampling design, initial differences in brome cover in the four positions, and how it changed from 2013 to 2015, were tested using general mixed models (Figure 4-1b).

At set up there was no more than 5% brome cover in the native-dominated areas in each transect. However, transects in three of the sites were set up in May, to give nutrient probes enough time for sampling (see below). This resulted in some encroachment of brome into native areas prior to sampling (peak season: June – July) (Figure 4-1b). More importantly, transects in which brome had invaded the area farthest outside from the brome patch (position 4) by 2015 were removed from our analyses, due to lack of a native area against which to compare the changes observed in brome invaded- and recently- invaded areas. This resulted in a total of 94 transects, with 8-14 transects per site. The removal of transects were brome is rapidly expanding from our analyses may have resulted in the underestimation of brome’s impact on community structure and function.

4.2.3 Community composition and nutrient availability

In each position we recorded the identity and abundance of all species present each year from 2013 to 2015, however we focused on 2013 and 2015 as the two most distant points in time. We used a line intercept method, recording every species touching the vertical line at each cm along the transect (Sutherland 1996). The line intercept method was specifically designed to quantify change in cover over time and has been found to be an efficient method in grassland communities (Mueller-Dombois and Ellenberg 1974, Caratti 2006). Abundance was estimated as the added number of cm at which a species was found within each position.

Nutrient availability was measured in 2013 and 2014 (unfortunately, nutrient data are not available for 2015) in a subset of transects, due to a limited number of nutrient-probes available: 10 transects per site, in 3 sites for a total of 30 replicates per position. The three sites were the Mattheis and Roy Berg Kinsella University of Alberta research stations, and Dry Island Buffalo Jump PP. We focused on nitrogen, phosphorus and potassium as they can be important drivers of plant communities' diversity, structure and productivity (Tripler et al. 2006, Elser et al. 2007, Vitousek et al. 2010, Peñuelas et al. 2013, Sardans and Peñuelas 2015). Nutrient availability was measured using Plant Root Simulator (PRS^{TM}) probes (Western Ag Innovation, Saskatoon, Saskatchewan) which are ion-exchange resin membranes. Transects in these three sites were set up in May 2013 to allow resins to absorb nutrients for two months: in both 2013 and 2014 PRS^{TM} probes were set up at the end of May and retrieved at the end of July.

4.2.4 Differences in composition and nutrient availability along a brome to native transition zone, and their change over time

To determine whether brome-invaded areas are different from native-dominated areas in their structure, function and dynamics, we tested for differences along the invasion gradient (i.e. among positions) in species composition and nutrient availability, as well as how they changed over time. Differences in composition were assessed through a perMANOVA (permutational multivariate analysis of variance), performed using the *adonis* function in the *vegan* package, with site as *strata* to account for the stratified nature of our data (Oksanen et al. 2016). The analyses were done using a Bray-Curtis distance matrix, because it is based on abundance, rather than presence/absence data. Pairwise differences between positions were also tested. Changes in species composition in each position from 2013 to 2015 were tested using the same analyses as above.

To test for differences in nutrient availability across positions we ran a general linear mixed model using the *lme* function in the *nlme* package (Pinheiro et al. 2016). We tested for differences in nitrogen, phosphorus and potassium, with position as the fixed factor and transects within sites as a random factor. The pairwise differences among positions were evaluated through Tukey contrasts using the *ghlt* function from the *multcomp* package (Hothorn et al. 2008). Similarly, the change in nutrient availability from 2013 to 2014 in each position was tested for using linear mixed models with year as a fixed factor and transects within site as a random factor.

4.2.5 Biotic homogenization within and between sites along a brome to native transition zone

To test for biotic homogenization of communities associated with brome invasion, we evaluated differences in beta-diversity across positions, within and among sites, and how it changed over time. Beta-diversity was estimated as the multivariate dispersion in species composition within each position (Anderson et al. 2006). This approach evaluates the distances of each replicate within group (in this case, within position) to the group's centroid, as a measure of dispersion (Anderson et al. 2006), with a greater distance among replicates indicating greater beta-diversity. We used the group's spatial median as the group's centroid as it is a more conservative approach than using the group's centroid.

We used the *betadisper* function in the *vegan* package to obtain the distances of each replicate to each groups' centroid and then used a linear (mixed) model to test for differences among positions. To test for differences within site, we calculated the distance of each transect to the group's (position) centroid, per site, and then used a mixed model, with site as a random factor, to test for differences among positions in their multivariate dispersion. To test for differences in beta-diversity among sites, we pooled species in each position per site, calculated the distance of each site to the position' centroid and then used a linear model to test for differences in dispersion among positions. Pairwise differences across positions were evaluated through Tukey contrasts, as above. We tested for differences in dispersion among positions in both years, as well as whether the dispersion changed from 2013 to 2015 in each position, at both spatial scales.

4.2.6 Differences in immigration, extinction and species dynamics along a brome to native transition zone

To evaluate the differences in species immigration and extinction along the invasion gradient, we tested for differences among positions in the number of species gained and lost from each plot, from 2013 to 2015. Differences among positions were tested using linear mixed models with positions as fixed effect and transect within sites as a random factor. We used Tukey contrasts, as above, for pairwise comparisons among positions.

We also tested for differences among positions in species re-ordering, by calculating the mean relative change in species rank abundances (Collins et al. 2008) in each position, from 2013 to 2015. To calculate the shift in species ranks, we used the *rank_shift* function from the *codyn* package (Hallet et al. 2016), and tested for differences across positions using a linear mixed model. Tukey contrasts were used to test for pairwise differences across positions. Further, to test whether the differences in rank shifts are a consequence of differences in average variation in species abundances among positions, we tested for differences in the average change in species absolute (not relative) abundances among positions. Change in species abundance was calculated as the natural log response ratio: ln(abundance in 2015/abundance in 2013), and we used a linear mixed model to test for differences across positions with transect within site as a random effect.

4.3 Results

We identified a total of 153 species across all sites, with 10 species present only in brome-invaded areas (positions 1 and 2), while 31 species (20%) were found only in recently or non-invaded areas (positions 3 and 4). Brome cover differed among positions (glm: $F = 933.38$, $P = < 0.001$) (Figure 4-1). More importantly, brome cover increased over time (2013 – 2015) in the areas immediately outside the brome patch (Figure 4-1) (Position 1: $F = 0.03$; $P = 0.86$; Position 2: $F = 3.22$, $P = 0.07$; Position 3: $F = 143.54$, $P < 0.001$). Also, as found in previous studies, species richness was lower in brome-invaded areas, compared to native areas ($F = 30.64$, $P = <0.001$) (Fink and Wilson 2011, Bennett et al. 2014).

4.3.1 Differences in composition and nutrient availability along a brome to native transition zone, and their change over time

Species composition was significantly different among positions in both years (2013: $F = 23.661$, $P = 0.001$; 2015: $F = 24.679$, $P = 0.001$) (Figure 4-2), with the greatest difference being between invaded (positions 1 and 2) and uninvaded areas (positions 3 and 4) (Figure 4-2, Appendix 3-1). Interestingly, in 2013 the positions on either side of the invasional front (position 2 and position 3) differed in species composition in spite of being spatially adjacent to each other on the inner and outer edges of the brome patch (Figure 4-1, 4-2) suggesting a sharp transition from brome-invaded to uninvaded areas.

Species composition was also found to change over time (2013 - 2015) although only in the positions outside the brome patch, while it remained unchanged in the invaded areas (Position 1: $F = 0.655$, $P = 0.63$; Position 2: $F = 0.972$, $P = 0.174$; Position 3: $F = 7.452$, $P = 0.001$; Position 4: F = 2.391, P = 0.001) (Figure 4-2). This suggests greater stability in species composition in invaded-areas compared to native-dominated areas. Results also indicate that brome-invasion led to rapid changes in species composition as the area that became invaded between 2013 and 2015 (position 3), became more different from the native-dominated areas and more similar in composition to brome-invaded areas (Figure 4-2, Appendix 3-1). On the contrary, we found no evidence of areas on the inner side of the invasional front (position 2) to become more similar to native, uninvaded areas (Figure 4-2, Appendix 3-1, Appendix 3-2).

Nutrient availability was significantly different among positions, though it varied among nutrients (Table 4-1, Figure 4-3). Nitrogen did not vary among positions in 2013 (Figure 4-2), however phosphorus and potassium were higher in brome-invaded areas (positions 1 and 2), compared to native-dominated areas (positions 3 and 4) (Figure 4-3). This difference suggests a sharp transition from brome-invaded to native-dominated areas in nutrient availability. Nutrient availability also changed from 2013 to 2014 and these differences appear to be driven partly by brome-invasion, but also by yearly differences (Figure 4-3). In 2014 nitrogen became higher in native- (position 4) as well as brome- dominated areas (position 1), while it did not change in more recently invaded areas (Figure 4-3a). Phosphorus was found to increase in the recently invaded areas (position 3) from 2013 to 2014, becoming as high as that in the brome-invaded areas (position 1 and 2) (Figure 4-3b). The change in potassium was likely driven by yearly differences, as it increased in all positions, independent of brome invasion (Table 4-1, Figure 4-3c).

4.3.2 Biotic homogenization within and among sites along a brome to native transition zone

Brome-invaded areas were more homogeneous in terms of species composition than native areas, as evidenced by a lower beta-diversity both within (Table 4-2, Figure 4-4a) and among sites (Table 4-2, Figure 4-4b). Beta-diversity did not change from 2013 to 2015 in brome-invaded areas (Position 1: $F = 0.174$, $P = 0.68$; Position 2: $F = 0.001$, $P = 0.97$), indicating a degree of species stability. However, beta-diversity decreased among years in both native and recently invaded areas (Position 3: $F = 9.449$, $P = 0.002$; Position 4: $F = 7.638$, $P = 0.006$). At the site level, recently invaded areas (position 3) became as homogeneous in their composition as invaded-areas (Figure 4-4b) suggesting a rapid change following brome-invasion. Although within site, the recently invaded areas (position 3) became more homogeneous, it remained higher than invaded areas (Figure 4-4a). Beta-diversity in the native areas (position 4) also decreased over time, but it remained significantly higher from invaded areas at both scales (Figure 4-4a,b).

4.3.3 Differences in immigration, extinction and species dynamics along a brome to native transition zone

Brome-invaded areas had lower species turnover and species rank shifts among years than native-dominated areas (Table 4-3, Figure 4-5). Fewer species were gained and lost in brome-invaded areas (position 1), compared to other positions (Table 4-3, Figure 4-5a,b). There were also fewer species rank shifts in brome-invaded areas, compared to recently- and non-invaded areas (Table 4-3, Figure 4-5c). This difference in species rank shift among positions appears to be the result of greater synchrony or asynchrony in species responses, rather than on differences in the average change in species abundance, which was not different among positions ($F = 0.819$, $P = 0.48$).

4.4 Discussion

Brome did not only change the state of communities, altering species composition and the availability of some nutrients (Figure 4-2, 4-3), but it also resulted in an overall reduction in the variation in invaded communities (Houseman et al. 2008). Brome invasion resulted in lower variation over time in species composition, with a lower number of species gained and lost from invaded areas (Figure 4-2, 4-5), as well as lower variation in space (Figure 4-4), establishing more homogeneous communities. Interestingly, these changes occurred rapidly, with communities differing significantly from a native state within only two years of brome invasion, which results in a sharp transition from native to brome-invaded communities. This rapid and sharp transition between community states emphasizes the rapid disruptive role invasive species can play in communities. Further, by altering soil conditions and limiting species recruitment, brome may facilitate the persistence of communities in an invaded state (Scheffer et al. 2001, Suding et al. 2004), making the restoration of these communities back to a native state difficult (Hobbs and Harris 2001, Hobbs et al. 2006).

4.4.1 Biotic homogenization of communities at different scales

The likelihood detecting biotic homogenization is thought to vary depending on scale (Olden and Poff 2003), although few studies have tested this hypothesis (Martin and Wilsey 2015). Martin and Wilsey (2015) found exotic communities to have higher beta-diversity than native communities at large scales, and lower at smaller scales. We found brome-invaded areas to have lower beta-diversity, evidencing biotic homogenization, at both larger (among sites) and smaller (within site) scales (Figure 4-4). However, biotic homogenization occurred faster at the site scale, compared to within sites, with recently invaded areas becoming as homogeneous as invaded areas in only two years (Figure 4-4). This pattern indicates that although different species persist in brome-invaded areas in different brome patches, they are the same across sites. One example is *Poa pratensis*, which co-occurs with brome in all sites, but only in about 70% of the transects. Overall, independent of scale, brome invasion was associated with the homogenization of communities (McKinney 2004, Lososová et al. 2012) which suggests that brome acts as non-random biotic filter allowing only certain species to persist or establish in invaded areas.

4.4.2 Existence and persistence of brome-invaded communities as an alternative state

Brome-invaded communities appear to be different from native-dominated communities in their state and overall stability (Houseman et al. 2008). Species richness is lower in brome-invaded compared to non-invaded areas (Fink and Wilson 2011, Bennett et al. 2014), and although we did not find a greater number of species being lost as brome invaded, we did see a rapid change in species composition, in only two years (Figure 4-2). Stein et al. (2016) also found transitions between different native and invaded community states to occur rapidly. More importantly, there are different types of state transitions: some can be dynamic and reversible (bi-directional), while others are more likely to occur in one direction and then persist in the new alternative state (Stein et al. 2016). Brome invasion seems to be an example of the latter, leading to the establishment of persistent alternative community states, as although transitions from native to an invaded community state were observed in all sites, there was no evidence of invaded areas returning to a native community state in the sites studied (Figure 4-2, Appendix 3-2).

Brome-invaded communities appear to also be generally more stable than native communities. Species composition did not change over time in invaded areas, while it did in native-dominated areas (Figure 4-2, Figure 4-5). Further, the lower number of species lost and gained from invaded areas seem to also indicate that brome-invaded communities are more stable, less dynamic communities, as does the lower variation in species relative abundances (Figure 4-5). Although it is generally thought that diverse communities are more stable (Tilman 1999, Tilman et al. 2006), studies have found invaded communities to be as stable as native communities, in spite of having lower species richness (Wilsey et al. 2014). This may be because dominant species tend to be more stable over time, compared to subordinate species; with the last ones representing a greater proportion in diverse communities (Roscher et al. 2011). However, the lower variation in species relative abundances or the synchrony among species in their change in abundance in brome-invaded areas may result in lower long-term stability, due to reduced compensation between species in response to external factors (Yachi and Loreau 1999, Tilman 1999, de Mazancourt et al. 2013). Longer-term datasets are necessary to further test for the stability and persistence of brome-invaded communities.

There was also greater nutrient availability in brome-invaded areas (Figure 4-3). We found, however, limited evidence of an increase in nutrient availability as brome encroached into native areas, which is not surprising considering we re-measured after only one year of brome's invasion. The greater nutrient availability in brome invaded areas may be driven by changes in microbial community composition and activity (Piper et al. 2015b, 2015a) and/or due to the greater volume and faster decomposition of litter in brome invaded areas (Vinton and Goergen 2006). This greater nutrient availability increases brome's performance (Gendron and Wilson 2007, DiAllesandro et al. 2013), thus creating a positive feedback which can increase the persistence of invaded-communities, and their resistance to restoration efforts (Hobbs and Harris 2001, Suding et al. 2004). However, positive feedbacks may be transient and deteriorate over time (Yelenik and Levine 2011, Yelenik and D'Antonio 2013). There is evidence of pathogen accumulation in brome invaded areas decreasing brome's performance (Vanterpool 1942, Myhr et al. 1966). However, whether this feedback will result in native species recovery (Yelenik and Levine 2011), remains unknown. No decline in brome's dominance or impact has yet been observed (Sinkins and Otfinowski 2012, Ellis-Felege et al. 2013).

The persistence of communities in an invaded-state may also be facilitated by mechanisms constraining species arrival and/or establishment in invaded areas (Martin and Wilsey 2014). Due to the short distance between positions (Figure 4-1), it is unlikely that propagule pressure differed between native and brome-invaded areas. However, competition from already established brome individuals and the greater litter biomass in brome-invaded areas (Fink and Wilson 2011) may be important factors limiting species establishment (Levine et al. 2003, Loydi et al. 2013, 2015). The lower number of species gained in invaded areas is consistent with what may be expected in saturated communities (Elmendorf and Harrison 2011). While native-dominated communities are rarely saturated (Cohen and Carlton 1998, Stohlgren et al. 2008, Harrison and Cornell 2008), invaded communities generally result in species loss and lower species establishment (Vilà et al. 2011, Fukami et al. 2013, Martin and Wilsey 2014). Consistently, Henriksson et al. (2016) found strong invaders (successful invaders with large impact on resident communities) to be also strong defenders, not allowing the establishment of new species, which is consistent with our results. Lower species immigration into invaded areas may be a driver of the lower number of species in brome-invaded areas (Yurkonis and Meiners 2004) and may constrain restoration efforts (Martin and Wilsey 2014).

4.4.3 Conclusions and implications

We found that invasive species, in this case smooth brome, can have important consequences for native communities, altering both alpha and beta-diversity and establishing persistent alternative community states (Suding et al. 2004, Hobbs et al. 2009). We also show that change can be quite rapid, following invasive species establishment. The processes behind this rapid change following brome invasion should be further investigated, as it can help inform the conditions needed to potentially restore the communities back to a native-dominated community state (Andersen et al. 2009, Hobbs et al. 2009, Hansen et al. 2013). However, these rapid changes also highlight the need for early detection and timely management strategies to prevent impact (Rejmánek and Pitcairn 2002, Norton 2009, Simberloff et al. 2013), as restoration in later invasion strategies may be costly and/or unsuccessful (Rejmánek and Pitcairn 2002, Suding et al. 2004). Advancing our understanding of the ecological mechanisms driving species invasion and impact is necessary for the development of more effective, science-based management strategies.

4.5 References

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Table 4-1: Differences in nutrient availability across positions along a brome-invaded to native transition area in 2013 and 2014. Position 1 is the area furthest inside brome patches, position 2 is the area at the inner edge of the invasional front, position 3 is the area at the outer edge of the invasional front and position 4 is the area outside the brome patch (i.e. uninvaded areas).

	df	*F*	*P*
2013			
Total nitrogen	3, 86	1.173	0.32
Phosphorus	3, 86	13.668	< 0.001
Potassium	3, 86	8.837	< 0.001
2014			
Total nitrogen	3, 86	5.88	0.001
Phosphorus	3, 86	4.55	0.005
Potassium	3, 86	1.355	0.26

Table 4-2: Beta-diversity as a function of positions along a brome-invaded to native transition area, within and across sites, in 2013 and 2015.

	df	*F*	*P*
2013			
Within site	3, 365	73.193	< 0.001
Across sites	3, 28	18.478	< 0.001
2015			
Within site	3, 365	32.679	< 0.001
Across site	3, 28	9.955	< 0.001

Table 4-3: Number of species gained, lost and shifts in species rank abundance order from 2013 to 2015 as function of position along a brome-invaded to native transition area.

	df	*F*	*P*
Species Gained	3, 279	9.662	< 0.001
Species Lost	3, 279	5.909	< 0.001
Rank shift	3, 279	36.447	< 0.001

Figure 4-1: Sampling design. (a) The transects were designed to encompass the transition between brome invaded areas (gray areas) to native-dominated areas (in white). Each transect was 4 m long, with the first 2 m into the brome-invaded area and last 2 m into the native-dominated area. Transects were divided into 4 areas of interested, which we refer to as positions (or Pos, in the diagram, (a)):

Position 1 is the area furthest inside brome patches, position 2 is the area at the inner edge of the invasional front, position 3 is the area at the outer edge of the invasional front and position 4 is the area outside the brome patch (i.e. uninvaded areas). Position 3 became invaded by brome between 2013-2015 (a), as evidence by a significant increase in brome cover (b).

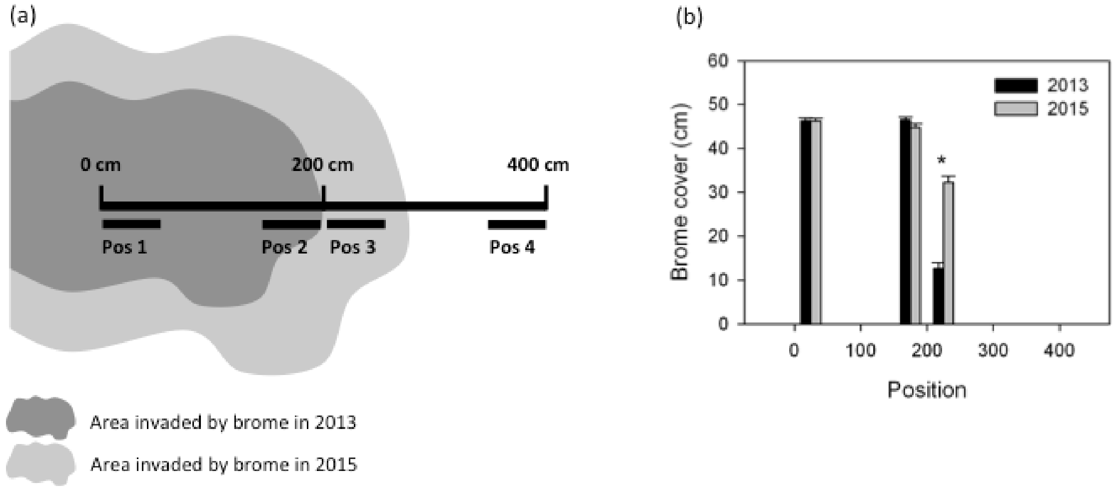


Figure 4-2: Change in species composition as a function of position along a brome-invaded to native-dominated transition area in 2013 and 2015.

An ordination including all sites was not possible. This ordination is for Big Knife Provincial Park and serves as an example, as trends were similar across sites (Appendix 3-2). Position 1 is the area inside brome patches (shown in red), position 2 is the area at the inner edge of the invasional front (shown in blue), position 3 is the area at the outer edge of the invasional front (shown in green) and position 4 is the area outside the brome patch (i.e. uninvaded areas) (shown in brown) (see Figure 1 for more details). Species composition in 2013 is shown with a continuous line, while the 2015 data is shown with a non-continuous line.

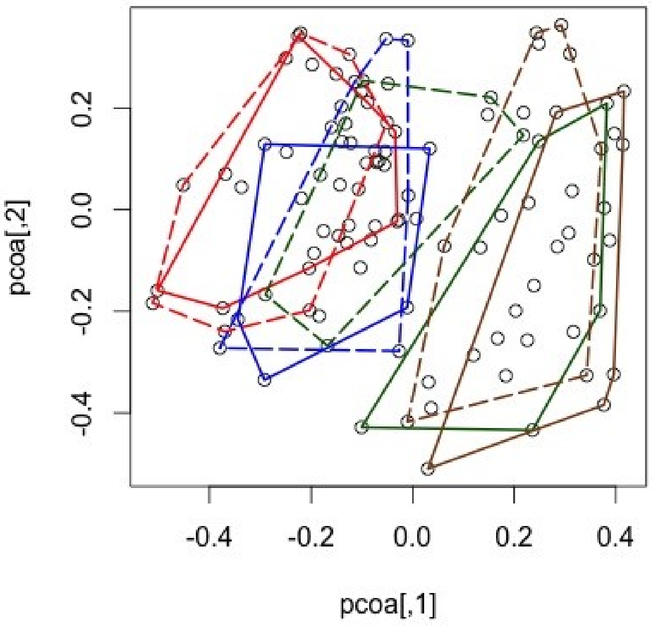


Figure 4-3: Mean total nitrogen (a), phosphorus (b) and potassium (c) availability (µm/10cm^2, measured over a 2 month period) as a function of position along a brome-invaded to native-dominated transition area, and year. The area between 0-50 cm (referred to as position 1) is farther into the brome invaded area, the area between 150-200 cm (position 2) is a more recently invaded area, the area between 200-250 cm (position 3) got invaded between 2013-2015, and the area between 350 and 400 cm (position 4) remained uninvaded (see Figure 1 for more details). Letters are used to indicate statistical differences, with lower-case letters and upper case letters indicating differences between positions in 2013 and 2014, respectively. Columns sharing a letter are not statistically different ($p > 0.05$). Bars indicate mean ± se.

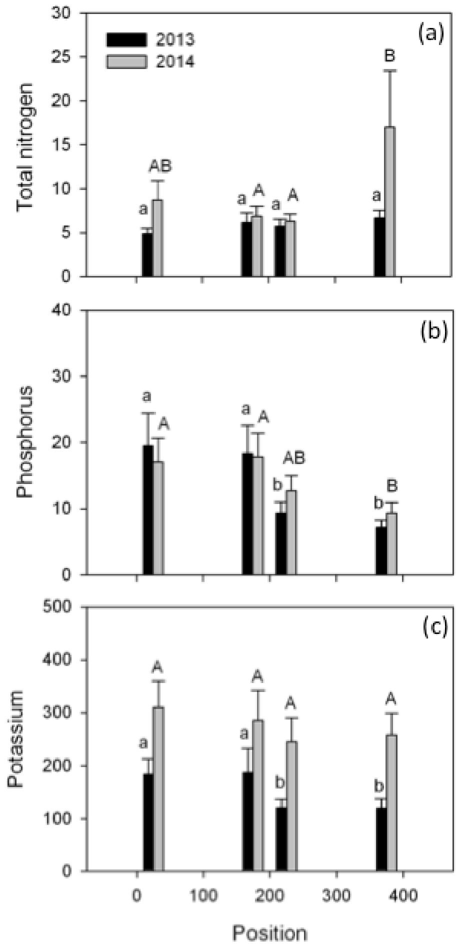


Figure 4-4: Beta-diversity (calculated as the average distance from the group's centroid), within (a) and across (b) sites in 2013 and 2015 along a brome-invaded to native-dominated transition area. The area between 0-50 cm (referred to as position 1) is farther into the brome invaded area, the area between 150-200 cm (position 2) is a more recently invaded area, the area between 200-250 cm (position 3) got invaded between 2013-2015, and the area between 350 and 400 cm (position 4) remained uninvaded (see Figure 4-1 for more details). Letters are used to indicate statistical differences, with lower-case letters and upper case letters indicating differences between positions in 2013 and 2015, respectively. Columns sharing a letter are not statistically different ($p > 0.05$). Stars (*) indicate statistical difference ($p < 0.05$) between years. Bars indicate mean ± se.

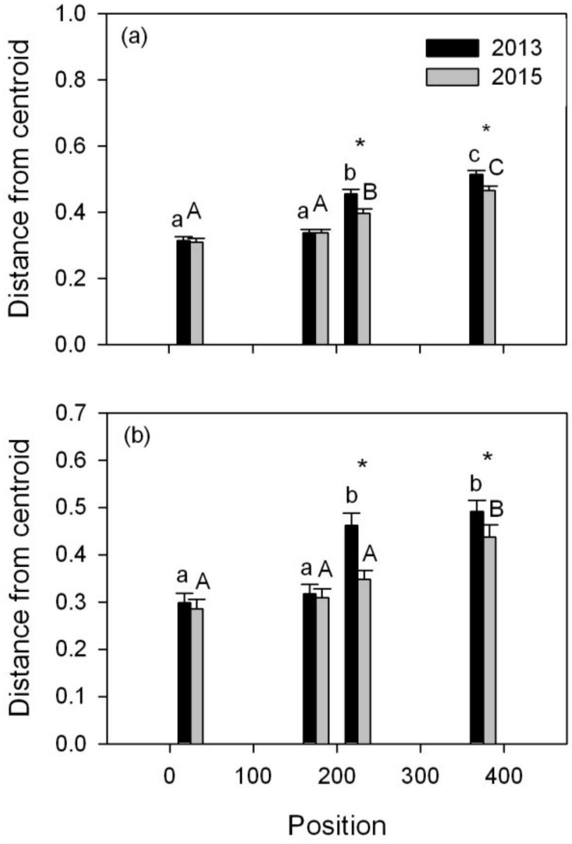
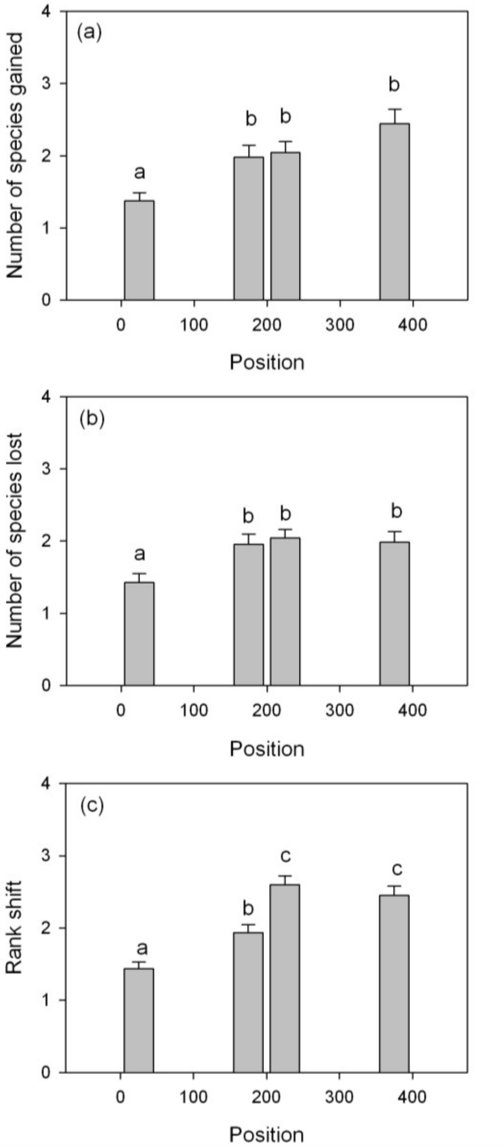


Figure 4-5: Number of species gained (a), lost (b) and shifts in species rank order (c) from 2013 to 2015 as a function of position along a brome-invaded to native-dominated transition area. The area between 0-50 cm (referred to as position 1) is farther into the brome invaded area, the area between 150-200 cm (position 2) is a more recently invaded area, the area between 200-250 cm (position 3) got invaded between 2013-2015, and the area between 350 and 400 cm (position 4) remained uninvaded (see Figure 4-1 for more details). Columns sharing a letter are not statistically different (*p* > 0.05). Bars indicate mean ± se.



Chapter 5: Maternal experience and soil conditions affect three species' tolerance to and suppression of the invader *Bromus inermis*, but not conspecifics

5.1 Introduction

Neighbors can have fitness consequences for co-occurring individuals (Keddy et al. 1998, 2002), therefore acting as selective agents (Callaway et al. 2005, Rowe and Leger 2010). Although diffuse interactions are expected in diverse and even communities (Wilson and Keddy 1986, Mitchley 1987), the strength of selection by a particular species is expected to increase with local dominance (Thorpe et al. 2011, Stotz et al. 2016). Highly dominated communities are common during invasions (Richardson et al. 2000) and hence some invasive species, due to their ability to suppress neighbors, have led to evolutionary responses by native species (Strauss et al. 2006, Oduor 2013). However, we still know little about the consequences of invasion on resident species adaptations (Stotz et al. 2016). Adaptation may be evidenced by individuals maintaining a higher performance in the presence of the invader and/or greatly reducing the invader's performance (Stotz et al. 2016). Invaders, instead, may be able to increase their fitness from selecting individuals unable to suppress or reduce invaders' performance. Understanding if and how plants respond or adapt to invasive species can help us understand the long-term consequences of invasion and the mechanisms behind coexistence (Stotz et al. 2016).

Evidence is accumulating on species adaptations to better tolerate (Callaway et al. 2005, Mealor and Hild 2007, Leger 2008, Fletcher et al. 2016) and/or suppress (Rowe and Leger 2010, Goergen et al. 2011) the invader (Stotz et al. 2016). These strategies may be independent of each other or evolve simultaneously, with species becoming better at both suppressing and tolerating neighbors (Wilson and Keddy 1986, Goldberg and Fleetwood 1987). More importantly, these strategies may be contingent upon neighbor identity (i.e. idiosyncratic) or consistent across neighbors, evolving as generalized strategies to the interaction with different neighbors (Goldberg 1996, Wang et al. 2010). If interaction were contingent upon neighbor identity, we would expect an increased ability to tolerate and/or suppress a neighbor to be evident only when interacting with that particular neighbor, rather than a generalized response when interacting with different neighbors. Interestingly, although studies have found native species becoming better at suppressing or tolerating invaders (Leger 2008, Goergen et al. 2011, Fletcher et al. 2016), whether this is a generalized or idiosyncratic response remains largely untested. Whether responses to neighbors are generalized or specialized strategies can have importantly implications, resulting in the evolution of overall stronger competitors or facilitating coexistence, respectively (Goldberg 1996).

Invasive species may also neighbor's performance through changes in soil conditions (Ehrenfeld 2010). Many species modify the nutrient availability and/or the soil communities around them (Ehrenfeld et al. 2005, Van der Putten et al. 2013), which can affect the strength and outcome of species interactions (Bever 1994, 2003). Thus, there is a growing body of evidence indicating that plants can adapt to grow and interact under particular soil conditions (Chanway et al. 1989, Johnson et al. 2010, Sherrard and Maherali 2012, Lankau 2013). Hence, to persist in invaded areas, individuals would benefit from adapting to interact with invaders under invader-modified soil conditions, especially since invasive species generally modify soil conditions to their own advantage (Klironomos 2002, Liao et al. 2008). However, if invaded soil results in a greater advantage for neighboring species over the invader, it would likely increase their ability to tolerate and/or suppress the invader (Yelenik and Levine 2011). Although a greater ability to tolerate or suppress the invader in invader-modified soil would facilitate persistence in invaded areas, it would also result in more contingent, less generalized strategies (Chanway et al. 1988, 1989, Lankau 2012).

In this study, we evaluated the effect of previous experience interacting with *Bromus inermis* and soil conditions on species tolerance to and suppression of *B. inermis*. *B. inermis* is an introduced perennial grass considered one of the most harmful invaders in Canada (Catling and Mitrow 2005). *B. inermis* reduces plant species diversity where it invades (Fink and Wilson 2011, Bennett et al. 2014), and it alters soil nutrient availability and microbial communities (Piper et al. 2015b, 2015a). We collected seeds from three species from *B. inermis*-invaded areas (experienced individuals) and from adjacent non-invaded areas (naïve individuals) as well as soil from both areas. We tested (1) for differences between offspring of naïve and experienced individuals in their ability to tolerate and/or suppress *B. inermis* and whether these differences were dependent upon soil type (invaded vs. native soil), (2) whether the individuals that suppress *B. inermis* the most, are also the most tolerant ones and (3) whether the differences between naïve and experienced individuals, in the two soil types, are also evident when interacting with conspecifics. If the difference between naïve and experienced individuals is only evident when interacting with *B. inermis,* it would indicate a specialized, rather than a generalized response.

5.2 Methods

5.2.1 Study species

Bromus inermis Leyss is a perennial cool-season grass intentionally introduced to North America in the late 1800s from Eurasia as a forage crop (Romo and Grilz 1990) and has since become one of the most invasive species in Canada (Catling and Mitrow 2005). *B. inermis* leads to a decline of up to 70% in native plant species diversity (Otfinowski et al. 2007, Fink and Wilson 2011, Bennett et al. 2014) and is spreading throughout North America (Grace et al. 2000, Sinkins and Otfinowski 2012, Ellis-Felege et al. 2013).

To test for the role of previous maternal experience on species interactions we selected three species from which we could collect seeds from individuals that had previous experience interacting with *B. inermis*, and from naïve individuals. Hence, we selected three perennial herbaceous species that are locally found in both *B. inermis*-invaded areas and adjacent uninvaded areas: *Symphyotrichum laeve* (L.) Á. Löve & D. Löve (Asteraceae), *Poa pratensis* L. (Poaceae) and *Melilotus officinalis* (L.) Lam (Fabaceae).

5.2.2 Seed and soil collection

Seeds of the three species and *B. inermis* were collected from the University of Alberta's Roy Berg Kinsella research station at Kinsella, Alberta, Canada (53°05'N, 111°33'W). This site is an unbroken, unseeded field located in the Aspen Parkland Ecoregion, a savannah type habitat with rough fescue (*Festuca hallii*) prairie interspersed with patches of aspen (*Populus tremuloides*) (Shorthouse 2010). Seeds were collected within a small area, with sampling locations no farther than 300 m of each other. For each species we collected 20 maternal families (those collected from the same mother plant) in brome-invaded areas (experienced individuals), as well as from adjacent non-invaded areas (naïve individuals). Seeds from 20 maternal families of *B. inermis* were also collected from the same general area.

Separating the effect of evolution and maternal effects is not possible when comparing the performance of offspring from individuals from invaded vs. uninvaded areas (e.g. Callaway *et al.* 2005; Goergen *et al.* 2011). Maternal environment can influence offspring performance through seed provisioning and/or epigenetic changes (Roach and Wulff 1987, Bonduriansky and Day 2009). Many of the reported maternal effects in plants have been through changes in seed size (Roach and Wulff 1987) and therefore, seeds from experienced and naïve individuals were weighed to test for maternal effects. Maternal effects not mediated by seed size were not tested for and cannot be ruled out.

Soil was collected from 10 paired native and *B. inermis*-invaded areas to a depth of 30 cm. After collection, soils were pooled by type and sieved (5 mm diameter sieve) to remove large roots. Homogenizing soils through mixing and sieving is a common practice, done to obtain representative soil conditions and ensure the same treatment is applied to all samples (Rodríguez-Echeverría et al. 2008, Dostál et al. 2013, Gundale et al. 2014, Baxendale et al. 2014, Cahill et al. 2016). Total and inorganic nitrogen concentrations were measured in both soil types to test for such differences in soil types. To extract and measure nitrogen availability we used a KCl extraction (Robertson *et al.* 1999), and then sent the samples to the Biogeochemical Analytical Service Laboratory at the University of Alberta for analysis.

5.2.3 Experimental design

To determine the effect of previous maternal experience and soil conditions on the ability of species to suppress, tolerate and/or avoid *B. inermis* we grew experienced and naïve individuals of *S. laeve*, *P. pratensis* and *M. officinalis*, in the two soil types and in different competition treatments. The competition treatments consisted of growing the plants alone, in competition with *B. inermis*, and under intraspecific competition. Growing plants alone, as well as with neighbors allows us to quantify their ability to suppress and tolerate neighbors by comparing the performance of the neighbors and focal plant when growing alone vs. with neighbors (see below). One maternal family per species per seed origin (experienced or naïve) was used in each treatment combination to control for potential differences among maternal families (i.e. genotypes).

Plants were grown in two soil treatments: soil from *B. inermis* invaded areas (brome soil) and from adjacent uninvaded areas (native soil). We used a whole soil approach, in contrast to using inoculums, in which field soil was mixed in a 1:1 ratio with potting soil (coarse sand, fine sand and topsoil in a 2:1:1 ratio). Inoculums are typically used to evaluate the effect of soil microbes on plant performance (Brinkman et al. 2010). However, as our focus was not on whether biotic or abiotic aspects of conditioning impact neighbor response, a whole soil approach is preferred. Further, *B. inermis* can alter both soil fertility and microbial communities where it invades (Piper et al. 2015b, 2015a), highlighting the need to include both aspects as potential influences on competitive dynamics.

5.2.4 Greenhouse experiment

We set up this experiment under controlled greenhouse conditions (daytime temperature of ~ 20°C, with natural and supplemented light: 16/8 light period). As stated above, we used one family per species per origin for each treatment combination, and therefore, we divided families in two, to germinate them in each soil type. Three weeks after sowing, seedlings were transplanted into 20 cm deep pots with the same soil types (brome or native soil) and randomly assigned to different neighbor treatments: alone, with *B. inermis*, or with a conspecific, for a total of six treatment combinations. *B. inermis* was also grown alone, to allow us to quantify its biomass response to neighbors (see below).

Pots were arranged into 20 replicate blocks with one pot of each treatment combination per block. Seedlings were grown for 4 months. At harvest, shoots and roots of each focal and neighbor plant were collected separately. Roots were washed, and then shoot and root biomass was dried at 70°C for 72 hours and then weighed.

5.2.5 Quantifying effect on and response to neighbors

To quantify the effect on and response to neighbors, we used competitive effect and response metrics (Cahill 1999), as they reflect the cost or gain in biomass when growing with a neighbor, relative to growing alone. The biomass response to neighbors was calculated as

$$\ln\left(\frac{F_N}{F_A}\right)$$

where F_N is the focal plant total biomass when growing with neighbors and F_A is the focal plant total biomass when growing alone. A lower response to neighbors in offspring from experienced individuals would indicate enhanced tolerance to growth with *B. inermis*, relative to offspring from naïve individuals.

The ability of a plant to suppress the biomass of neighbors was calculated as:

$$\ln\left(\frac{N_F}{N_A}\right)$$

where N_F is the neighbor plant total biomass when growing with the focal plant and N_A is the neighbor plant total biomass when growing alone.

5.2.6 Data analysis

To test whether offspring of experienced and naïve individuals differ in their ability to interact with *B. inermis*, and whether these differences were dependent upon soil conditions, we ran linear mixed models. The effect on and response to *B. inermis* were analyzed for separately, with species identity, experience and soil type as fixed effects and block as a random effect. Follow up models (i.e. posthoc tests) were ran to interpret the differences among treatment and treatment interactions, when necessary. A significant interaction between experience and soil type would indicate that the effect of maternal experience is contingent upon soil conditions. A significant species by treatment interaction would indicate that species respond differently to treatments, while absence of such interaction would indicate similar responses by the three species.

To evaluate whether the effect on and the response to *B. inermis* are associated, we tested for the correlation between competitive effect and response. We also tested whether different treatments or treatment combinations affected the association between them, using linear mixed models with block as a random factor.

We also evaluated whether the changes in individuals' ability to suppress and/or tolerate *B. inermis* were specialized (invader specific) or generalized responses. To do so we ran mixed effect models, as above, testing for the effect of experience and soil type on species ability to interact with conspecifics, with block as random factor. All analyzes were performed using the *lme* function in the *nlme* package (Pinheiro et al. 2016) in R (v.2.15.3, R Foundation for Statistical Computing, Vienna, AT).

5.2.7 Differences between invaded and uninvaded areas in species' seed size and soil nutrient availability

We evaluated the differences in seed weight between experienced and naïve individuals, which allowed us to test for potential maternal effects through seed provisioning. Differences in seed weight were tested using linear models, with species and maternal experienced as fixed effect. Further, if different, we also tested for the effect of seed size on total biomass when alone, as well as on the effect on and response to *B. inermis*.

We also assessed differences between native and brome soil in their nutrient availability, using linear models to test for differences in total and inorganic nitrogen concentration between soil types.

5.3 Results

5.3.1 Effect of maternal experience and soil type on their interaction with *B. inermis*

Counter to expectation, offspring from experienced individuals had a less suppressive effect on *B. inermis*, compared to offspring from naïve individuals (Table 5-1, Figure 5-1). Although there was a difference between species in their ability to suppress *B. inermis*, there was no interaction between species identity and maternal experience, indicating that the effect of experience was similar among species. Soil type, on the other hand, had no effect on species ability to suppress *B. inermis* (Table 5-1). There was a near significant interaction between experience and soil type in determining the ability to suppress *B. inermis* (Table 5-1), suggesting a greater difference between experienced and naïve individuals in brome soil, compared to native soil (Appendix 4-1).

The ability to tolerate *B. inermis* was not dependent upon maternal experience, but rather on soil conditions (Table 5-1). There was a significant species by soil-type interaction, where two of the three species (*P. pratensis* and *S. laeve*) were less suppressed by *B. inermis* on brome soil (*P. pratensis*: *F-value* = 8.23, *p-value* = 0.01; *S. laeve*: *F-value* = 8.65, *p-value* = 0.01), compared to native soil, while there was no difference in *M. officinalis* tolerance to *B. inermis* between soil types (*F-value* = 0.29, *p-value* = 0.59) (Table 5-1, Figure 5-2).

5.3.2 Association between response to and effect on neighbors

We found a positive association between tolerance and suppression of *B. inermis*, where individuals that suppress *B. inermis* more, were also less suppressed by it (correlation: $r^2 = -0.31$, *p-value* < 0.05). The relationship between tolerance and suppression was consistent across species (*F-value* = 0.19, *p-value* = 0.82), soil type (*F-value* = 0.91, *p-value* = 0.34) and maternal experience (*F-value* = 0.55, *p-value* = 0.46). However, there was an almost significant interaction between soil type and maternal experience (F-value = 3.42, p-value = 0.07) suggesting a stronger correlation between tolerance and suppression in experienced individuals, in native soil (Appendix 4-2).

5.3.3 Generalized vs. specialized effect on and response to neighbors

The ability to suppress and tolerate conspecifics was not dependent upon soil type, maternal experience or species identity (Table 5-2), suggesting that the differences between experienced and naïve individuals are a rather specialized response to the interaction with *B. inermis*.

5.3.4 Differences between invaded and uninvaded areas in species seed size and soil nutrient availability

There was a significant species by experience interaction for seed size (*F-value* = 6.78, *p-value* = 0.001). We found that seeds from experienced individuals were larger than those of naïve individuals in *M. officinalis* (*t-value* = -5.08, *p-value* = <0.001), but not in *S. laeve* (*t-value* = 1.144, *p-value* = 0.86) or *P. pratensis* (*t-value* = 0.16, *p-value* = 0.99). However, seed size was not found associated with total biomass of *M. officinalis* when growing alone (*F-value* = 0.18, *p-value* = 0.67), nor with its effect on (*F-value* = 2.21, *p-value* = 0.14) or response to (*F-value* = 0.109, *p-value* = 0.74) *B. inermis*.

Soil from *B. inermis* and adjacent native areas was found to differ in nitrogen content, with brome soil having a higher concentration of total and inorganic nitrogen than native soil (Total nitrogen: *F-value* = 11.259, *p-value* = 0.01; Inorganic nitrogen: *F-value* = 21.679, *p-value* = 0.002).

5.4 Discussion

We found that co-occurring with a dominant invader, such as *B. inermis*, does not necessarily result in an adaptive response (i.e. increased ability to suppress and/or tolerate the invader), but may instead result in mal-adaptive responses (Goergen et al. 2011, Dostál et al. 2012). We found offspring from experienced individuals to have a reduced ability to suppress *B. inermis*, compared to offspring from naïve individuals (Table 5-1, Figure 5-1), while tolerance was not dependent upon previous maternal experience (Table 5-1, Figure 5-2). Species ability to tolerate *B. inermis* was, instead, dependent upon soil conditions, with a greater tolerance in soil from invaded areas (Table 5-1, Figure 5-2). Interestingly, the effects of maternal experience and soil type on species ability to tolerate and suppress neighbors appear to be *B. inermis*-specific, as no such effects were observed when interacting with conspecifics (Table 5-2). Specialized responses may help facilitate coexistence, as it results in no genotype being able to optimally suppress and/or tolerate all other species or genotypes (Laird and Schamp 2006).

Although evidence of species adaptation to invaders is accumulating (Strauss et al. 2006, Oduor 2013), non- or mal-adaptive responses appear to also be common (Goergen et al. 2011, Dostál et al. 2012), though largely ignored (Schlaepfer et al. 2005). Goergen et al. (2011) found a range of responses by experienced individuals to the invader cheatgrass (*Bromus tectorum*) with maladaptive responses being as common as adaptive responses. Interestingly, the lower suppressive ability seems to be a specialized response to *B. inermis*, and not a generalized reduced competitive ability. Neighbor-specific responses indicate that different neighbors select for different traits/trait values (Proffitt et al. 2005, Baron et al. 2015). Selecting for individuals less able to suppress *B. inermis*, but not other species, may facilitate *B. inermis*' persistence, spread and/or impact (Levine 1999). Further, these results highlight the need to better understand the conditions under which species are more likely to adapt to coexist and/or compete with invaders, as we may be able to facilitate adaptive responses in native species and/or decide when they may be a valuable resource to manage invasive species (Stotz et al. 2016).

Different mechanisms may result in invasive species selecting for less suppressive individuals (Figure 5-1). Invasive species may more strongly suppress or exclude species that are able to suppress them, leaving only weak suppressors in invaded areas. *B. inermis* has been found to more strongly suppress common, over rare species (Bennett et al. 2014). One of the potential explanation for a stronger suppression of common species could be because they are generally better at acquiring resources and therefore, more likely to have a negative effect on *B. inermis* performance, while rare species are generally better at conserving resources being overall more tolerant species (Lavergne et al. 2004, Cornwell and Ackerly 2010, Dawson et al. 2012). Alternatively, *B. inermis* may limit neighbors resource acquisition, reducing their allocation to seeds and progeny (i.e. maternal effects) (Roach and Wulff 1987). However, we found no evidence of maternal effects through seed size (Roach and Wulff 1987, Germain and Gilbert 2014), and more importantly no consistent lower performance of offspring from experienced individuals, as there was no difference between offspring from naïve and experience individuals when interacting with conspecifics (Table 5-2). However, independent of the mechanism, previous experience interacting with *B. inermis* only affected species ability to suppress but not to tolerate the invader (Table 5-1, Figure 5-2).

Tolerance to *B. inermis* was greater in soil from invaded, compare to native areas in two of the three species (Table 5-1, Figure 5-2), potentially due the higher nutrient availability in brome soil. This result was rather surprising, as most invasive species studied have been found to modify soil conditions to their own advantage (Klironomos 2002, Liao et al. 2008, but see Nijjer et al. 2007, Scharfy et al. 2010). Overall, brome soil seems to give species an advantage over *B. inermis*, but not other species, as the greater tolerance was only observed when interacting with *B. inermis* but not when interacting with conspecifics (Table 5-2). The lower performance of *B. inermis* in its own soil is consistent with *B. inermis* lower recruitment in brome-invaded areas (Carrigy et al. 2016) and may be due to the accumulation of pathogens (Vanterpool 1942, Myhr et al. 1966). Although a negative effect of invaded soil on the invader may facilitate the coexistence of competitors and result in a reduced impact over time (Bever 2003, Yelenik and Levine 2011), no decline in *B. inermis* dominance or recovery of resident species diversity or abundance has been observed or documented so far (Sinkins and Otfinowski 2012, Ellis-Felege et al. 2013), though further studies are needed.

Overall, although positively correlated (Appendix 4-2), we found individuals tolerance and suppression of *B. inermis* to be determined by different factors: maternal experience and soil conditions, respectively (Table 5-1). This is consistent with other studies in which, when comparing experienced and naïve individuals, they found a change in either effect on or response to the invader, but not both (Leger 2008; Fletcher *et al.* 2016, but see Rowe & Leger 2010). Further, the lack of interaction between soil type and maternal experience indicate that although brome soil increases the tolerance of individuals to *B. inermis*, experienced individuals do not gain a greater advantage over naïve individuals, as has been found by others (Chanway et al. 1988, 1989). More studies on the role of soil conditions and maternal experience are needed, to better understand the ecological and evolutionary consequences of interacting with dominant and/or invasive species (Stotz et al. 2016).

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Table 5-1: The effect on and response to *Bromus inermis* as a function of species identity (*Symphyotrichum laeve*, *Poa pratensis* and *Melilotus officinalis*), maternal experience (seeds collected from *B. inermis* invaded areas or from adjacent uninvaded areas) and soil type (collected from *B. inermis* invaded areas or adjacent uninvaded areas).

	df	*F-value*	*p-value*
Effect on *B. inermis*			
Species	**2, 184**	**4.29**	**0.015**
Maternal experience	**1, 184**	**4.50**	**0.035**
Soil type	1, 184	0.001	0.971
Species * maternal experience	2, 184	0.88	0.416
Species * soil type	2, 184	0.78	0.458
Maternal experience * soil type	1, 184	3.27	0.072
Species * maternal experience * soil type	2, 184	0.55	0.580
Response to *B. inermis*			
Species	2, 167	0.59	0.557
Maternal experience	1, 167	0.02	0.89
Soil type	**1, 167**	**6.49**	**0.012**
Species * maternal experience	2, 167	0.72	0.486
Species * soil type	**2, 167**	**3.22**	**0.042**
Maternal experience * soil type	1, 167	1.85	0.175
Species * maternal experience * soil type	2, 167	2.53	0.082

Table 5-2: The effect on and response to intraspecific competition as a function of species identity (*Symphyotrichum laeve*, *Poa pratensis* and *Melilotus officinalis*), maternal experience (seeds collected from *B. inermis* invaded areas or from adjacent uninvaded areas) and soil type (collected from *B. inermis* invaded areas or adjacent uninvaded areas).

	df	*F-value*	*p-value*
Competitive effect			
Species	2, 154	1.35	0.262
Maternal experience	1, 154	0.71	0.402
Soil type	1, 154	0.01	0.937
Species * maternal experience	2, 154	2.77	0.066
Species * soil type	2, 154	0.99	0.374
Maternal experience * soil type	1, 154	0.03	0.844
Species * maternal experience * soil type	2, 154	2.24	0.110
Competitive response			
Species	2, 155	1.67	0.191
Maternal experience	1, 155	2.55	0.112
Soil type	1, 155	0.90	0.345
Species * maternal experience	2, 155	1.18	0.310
Species * soil type	2, 155	1.22	0.299
Maternal experience * soil type	1, 155	1.85	0.176
Species * maternal experience * soil type	2, 155	1.65	0.195

Figure 5-1: Effect of offspring from experienced and naïve individuals from three species (*Symphyotrichum laeve, Melilotus officinalis* and *Poa pratensis*) on *B. inermis* biomass.

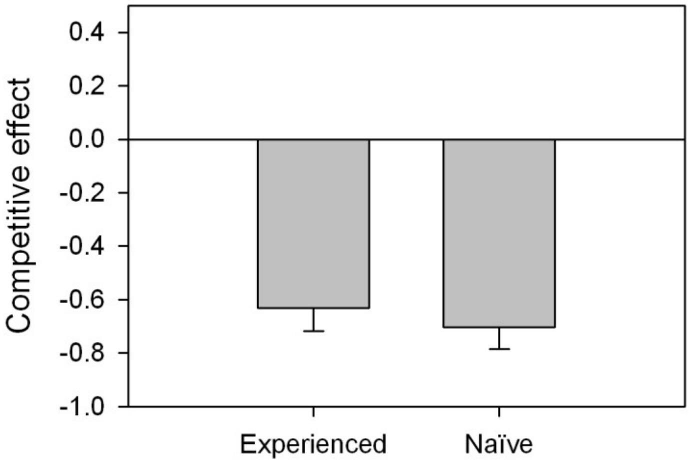
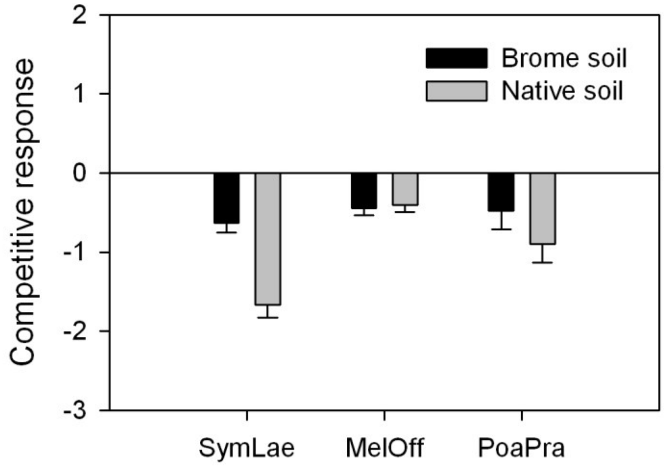


Figure 5-2: Response of *Symphyotrichum laeve* (SymLae), *Melilotus officinalis* (MelOff) and *Poa pratensis* (PoaPra) to the invader *Bromus inermis*, in two soil types (collected from *B. inermis* invaded areas or adjacent uninvaded areas).



Chapter 6: Spatial pattern of invasion and the evolutionary responses of native plant species

6.1 Introduction

Invasive species can strongly impact native species diversity (Vilà et al. 2011; Pyšek et al. 2012) and ecosystem function (Weidenhamer and Callaway 2010, Vilà et al. 2011, Pyšek et al. 2012, Strayer 2012). Great efforts are made to control and eradicate invasive species (Roques and Auger-Rozenberg 2006; Simberloff 2014), with both positive (Wotherspoon and Wotherspoon 2002; Hoffmann 2010) and negative outcomes (Rejmánek and Pitcairn 2002). In spite of their strong negative impact on native species, and our limited ability to eradicate them, invasive plant species have not led to the global extinction of many native species, but this is thought to be a matter of time (Gilbert and Levine 2013). The time lag between invasive species establishment and native species extinction risk gives native species a window of opportunity to evolve adaptive traits and thus persist within the newly structured community. There is growing evidence that some plant species can evolve in response to invasion (see Oduor 2013 for a meta-analysis on native species adaptation to invasion and Strauss, Lau, and Carroll 2006 for a review). Strauss et al. (2006) reviewed 33 examples of native species evolution in response to invasion and argued that understanding when native are more likely to evolve in response to invasion can help us understand the long-term impact of invasions. Native species evolutionary responses could facilitate the coexistence between native and invaders, therefore lessening the impact of invasive species on native plant populations (Strayer et al. 2006).

Taking advantage of evolutionary responses of native species to invaders may help manage the impact of invaders. Existing management strategies in response to invaders are diverse (Theoharides and Dukes 2007; Simberloff 2014) and can include the use of bio-control agents, promoting intact native communities, and species removal. We may be able to use evolutionary responses of native species to refine and complement these currently used strategies. Strategies of early control have been relatively effective at reducing long-term invasive species impact (Simberloff et al. 2013), and are generally more cost-effective (Harris and Timmins 2009) than control strategies in later stages of the invasion process. In contrast, efforts to control or eradicate long-established invasive species have been less successful (Simberloff et al. 2013; Rejmánek and Pitcairn 2002; Norton 2009; Pala 2008), and are typically more expensive (Rejmánek and Pitcairn 2002; Panetta 2009). It is particularly to those long-established, highly abundant invasive species that native species may adapt (Thorpe et al. 2011). Evolutionary ecology has been an important tool in addressing other aspects of global change, such as delaying evolution of resistance in pests and pathogens and adaptation to climate change (reviewed in Carroll et al. 2014). Likewise, it could also be a useful tool when trying to manage or control invasive species (Schlaepfer et al. 2005; Leger and Espeland 2010; Oduor, Yu, and Liu 2015).

Implementing the use of adapted genotypes of native species to complement current management strategies may help minimize the impact of long-established invasive species (Schlaepfer et al. 2005; Carroll et al. 2014; Strayer et al. 2006). Native species genotypes that have adaptations allowing increased coexistence with invaders could be used to increase the resistance of communities to further invasions (Schlaepfer et al. 2005), to minimize future extinction risks, to help manage the invader in already invaded communities, or to restore previously invaded areas. In order to implement this strategy it is necessary to first understand under which circumstances native species are more likely to show evolutionary responses to invaders.

Although many species are able to evolve in response to co-occurring invasive species (Oduor 2013), this is not always the outcome. Following the interaction with invasive species, some native species may evolve an increased ability to suppress the invader (Rowe and Leger 2010; Goergen, Leger, and Espeland 2011) or to better tolerate the presence of the invader through a reduction in competitive suppression (Callaway et al. 2005; Leger 2008; Rowe and Leger 2010), i.e. evolution of character displacement to reduce competition when in sympatry (Brown and Wilson 1956; Grant and Grant 2006). However, not all species are able to evolve in response to the interaction with a strong invader (Mealor and Hild 2007; Goergen, Leger, and Espeland 2011). For example, when testing for the adaptation of native species to the invasive cheatgrass, *Bromus tectorum*, it was found that native species were more tolerant to the invader in only two out of four populations (Goergen, Leger, and Espeland 2011). Identifying the conditions and processes influencing the likelihood of native species adaptation may help us manage these eco-evolutionary processes to improve our understanding of natural systems and complement current management strategies (Carroll 2011; Schlaepfer et al. 2005).

Although the integration of evolution into the management of invasive species has been suggested earlier (Carroll 2011; Schlaepfer et al. 2005; Leger and Espeland 2010; Oduor, Yu, and Liu 2015), a more detailed eco-evolutionary conceptual framework is needed to guide the development of both research and management practices for the control of invasive plant species. In this study we first explore the requisites for, and evidence of, rapid evolution of native plant species in response to invasion. We subsequently propose a framework that focuses on using the spatial distribution of invasive species to understand the conditions under which native species are more likely to adapt to the pressures exerted by invasive species. We also discuss species characteristics and conditions that may influence the potential to respond to selective pressures.

Finally, we outline potential management actions to promote rapid evolution, help control invasion, and prevent future extinctions due to invasion.

6.2 Factors affecting rapid evolutionary responses to invaders

Evolution may seem slow over long periods of time; however, when selection is strong and constant, evolution can be rapid (Thompson 1998; Gómez-González et al. 2011). Plants are generally capable of evolving rapidly in response to local conditions (Bone and Farres 2001; Leimu and Fischer 2008). However, the evolutionary responses of plants to the interaction with neighbors remains poorly studied, compared to their evolutionary responses to other biotic and abiotic factors (Bone and Farres 2001). As highlighted by Strauss et al. (2006) for plant-plant interactions to lead to an evolutionary response there are at least three requisites: competitors must have an impact on neighbor fitness, fitness effects must be non-random (i.e. some genotypes more strongly affected than others) and the adaptive traits must be heritable (Futuyma 2013; Strauss, Lau, and Carroll 2006). Yet, plant-plant interactions occur over small spatial scales, where gene flow is highly likely and may prevent adaptation (Kawecki and Ebert 2004). However, Turkington (1979) reported local adaptation of *Trifolium repens* to three different neighbors to have occurred not only over a short time period (10 years), but also over small spatial scales despite (highly likely) gene flow, which is possible when selection is strong enough (Richardson et al. 2014).

Many invasive species impose strong (and potentially novel) selective pressures on native species populations (Vilà et al. 2011). This may in part explain why most examples of rapid adaptation to neighbors come from interactions with invasive species (Strauss, Lau, and Carroll 2006; Oduor 2013; Lau 2008), as strong selection is thought to be the main promoter of rapid evolutionary responses (Hairston et al. 2005). However, only native species with high levels of genetic variability in adaptive traits will be able to adapt in response to invasive species (Strauss, Lau, and Carroll 2006). To coexist with invasive species, native plant species could evolve a higher impact on (competitive effect) or tolerance to (competitive response) the invader (Rowe and Leger 2010; Goergen, Leger, and Espeland 2011; Leger and Espeland 2010; Callaway et al. 2005). Both, competitive effect and response, may be genetically determined and vary between individuals/genotypes (Cahill, Kembel, and Gustafson 2005; Baron et al. 2015; Willis, Brock, and Weinig 2010; Johnson et al. 2008).

Different traits may determine individual competitive ability, and this may depend on the context under which the interaction takes place as well as on the particular species/genotypes involved in the interaction (Wang et al. 2010; Baron et al. 2015). Some of the traits associated with an increased ability to suppress or tolerate invaders are: earlier and faster growth, greater height, larger seed size, greater root growth or root-to-shoot ratio and increased resistance to allelochemicals (Leger 2008; Turkington 1979; Rowe and Leger 2010; Lankau 2012; Callaway et al. 2005; Mealor and Hild 2007; Goergen, Leger, and Espeland 2011). The network of genes underlying these traits may slow or decrease the likelihood of an evolutionary response (Kawecki 2008). The genetic correlation among traits may facilitate evolution if adaptive traits are positively correlated, but it can also constrain adaptation (Pigliucci 2003; Orr 2000; Etterson and Shaw 2001). Despite the potential complexity behind competition-related traits, many of these traits have shown rapid evolutionary responses (Bone and Farres 2001).

In spite of the growing body of evidence of rapid evolution in response to plant-plant interactions, there is still some reluctance to integrate it into current conservation strategies (Kinnison, Hendry, and Stockwell 2007). Although evolution is not always easy to detect, there are some indicators of which species/populations are more likely to evolve adaptations to persist in invaded areas. Linking evolutionary processes to observable ecological patterns and processes may: i) help bridge the gap between evolutionary ecology and conservation biology and ii) lead to the implementation of evolution-informed management practices. Here, we propose a framework where spatial patterns of invasion can be used to predict the likelihood of native species adaptation to invaders.

6.3 The spatial pattern of invasion

By definition invasive species are highly dominant (i.e. show high relative abundance and density) where they invade (Lowe et al. 2004; Richardson et al. 2000). Invasive species dominance is, however, not continuous across the landscape, as invaders may form patches or "islands" of invasion (Figure 6-1) (Lewis and Pacala 2000; Kolb et al. 2002). Their presence and dominance across the landscape may be limited, for example, by dispersal, disturbance, enemies or abiotic conditions, leaving areas between invaded patches where native species persist (Figure 6-1) (Huenneke et al. 1990; MacDougall and Turkington 2006; Kolb et al. 2002). This spatial variation in dominance by invasive species may result in concomitant spatial patterns in the evolutionary responses to invasion. If true, we could use characteristics of the spatial pattern of invasion to predict where native species are more likely to be adapted.

Characteristics of the spatial pattern of invasion, such as patch size and distance between invaded patches, may determine the likelihood of native species adaptation to invasion. Just as size and distance from immigrant source were found to be major determinants of ecological and evolutionary processes in islands (Island Biogeography Theory; Simberloff 1974; Simberloff and Wilson 1969; Losos and Schluter 2000), we believe that size and isolation of these "islands of selection" are important determinants of eco-evolutionary processes between native and invasive species (Leger and Espeland 2010). Likewise, size and isolation among areas with different selective pressures are key factors in the evolution of insecticide resistance in pests and pathogens (Carrière et al. 2004; Gould 2000; Sisterson et al. 2005). For example, because of the widespread use of *Bt*-crops (crops transformed to contain a transgene for an insecticidal protein) the evolution of resistance in pests and pathogens is a concern. One of the strategies used to prevent the evolution of resistance is to plant non-*Bt* cultivars as refuges for the survival of susceptible pests (Gould 1988; Roush 1994; Gould 2000), which has proven to be a successful approach (Tabashnik, Brévault, and Carrière 2013). Thus, short distances facilitate high gene flow between areas, and size or abundance of refuges allow for large-enough population size of susceptible pest genotypes (Carrière et al. 2004; Sisterson et al. 2005; Caprio, Faver, and Hankins 2004). Similarly, we propose that size and isolation of invaded areas may determine the likelihood of evolution of "resistance" in native species against invaders.

6.4 The influence of patch size and isolation on native species adaptation to invasion

The likelihood of an evolutionary response by native species to the invader will depend on the strength of selection, frequency of the interaction and gene flow (Kawecki and Ebert 2004; Strauss, Lau, and Carroll 2006). Here, we argue that the spatial pattern of invasion, particularly the size and isolation of the invaded patches, may influence these processes, therefore altering the potential for native species adaptation (Figure 6-2). Specifically, we propose that native adaptation is more likely to occur in large and well-connected invaded patches, while in smaller and isolated "islands" the selective pressure will be weaker and gene flow from non-invaded areas higher, thus decreasing the likelihood of adaptation by native species (Figures 6-1, 6-2).

6.4.1 Invaded patch size and the strength of selection

Invaded patch size, or population size, is often associated with the invader impact on native species (Davies 2011; Jackson, Ruiz-Navarro, and Britton 2014). Larger invaded patches will tend to have a higher density of invaders and reduced species diversity (Jackson, Ruiz-Navarro, and Britton 2014). This would increase the likelihood of adaptation by increasing interaction frequency and consistency (less diffuse interactions) (Connell 1980; Thorpe et al. 2011). Thus, in patches where a single invader becomes dominant any individual would interact mainly, if not only, with the invader (Figure 6-1). Larger patches, and a higher density of invaders will also result in a stronger negative impact on native species performance (Jackson, Ruiz-Navarro, and Britton 2014; Parker et al. 1999). Since the strength of selection increases with impact on fitness (Kingsolver et al. 2001), invasive species may exert stronger selection on native species in larger patches (Figure 6-2a). Therefore, provided that native species have genetic variation for the selected traits, and thus may show evolutionary responses to the selective pressures imposed by the invader (Strauss, Lau, and Carroll 2006), then the likelihood of native species adaptation and persistence will be higher in larger and denser invaded patches (Figure 6-2d) (Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007).

6.4.2 Invaded patch isolation and gene flow

Native species adaptation will also depend on gene flow (Kawecki and Ebert 2004). Since invaded patches are often surrounded by a matrix of native species, gene flow among these areas is probable (Figure 6-1). Gene flow can facilitate or hinder local adaptation, depending on its strength and origin (Kawecki and Ebert 2004; Strauss, Lau, and Carroll 2006). Gene flow tends to increase variation within populations, which is necessary for natural selection to occur.

However, it may also reduce (or even prevent) selective processes in the population when individuals/genes arrive from areas with different selective pressures (Figure 6-1) (Riechert 1993; Nosil 2009). In this case, if homogenizing gene flow from native areas is strong, it would limit or prevent adaptation of native individuals within the invaded patches. However, local adaptation can occur in the face of high gene flow, provided that the strength of selection is greater than the homogenizing effect of gene flow (Kawecki and Ebert 2004; Fitzpatrick et al. 2015). For example, Fitzpatrick et al. (2015) found that adaptive phenotypic divergence of Trinidadian guppies in response to predators was maintained even after extensive gene flow. Similarly, local adaptation has been observed across small spatial scales, where gene flow is highly likely (reviewed in Richardson et al. 2014).

In contrast to homogenizing gene flow, reinforcing gene flow would facilitate local adaptation (Figure 6-2) (Urban 2011). Reinforcing gene flow is the arrival of individuals/genes from areas with similar selective pressures: in this case, from other invaded patches (Figure 6-1). The arrival of pre-adapted individuals/genes would facilitate adaptation of native species within invaded patches. Byars *et al.* (2009) found that genetic differences between high- and low-altitude populations of *Poa hiemata* were explained by biased gene flow: there was higher gene flow among populations at either altitude than across altitudes. Similarly, proximity among invaded patches would facilitate the arrival of pre-adapted individuals/genes (Thrall, Burdon, and Young 2001; Urban 2011) (Figure 6-2b). This reinforcing gene flow could facilitate the adaptation of native species populations to the invader in those patches (Figure 6-2c). Moreover, strong selection against mal-adapted immigrants (Ehrlich and Raven 1969; Lin et al. 2008) can restrict the number and quality of immigrants, further limiting homogenizing gene flow.

6.4.3 Spatial pattern of invasion and a mosaic of adaptation

We propose that the likelihood of native adaptation to invasion is higher in large, dense and well-connected patches than in small, isolated patches (Figure 6-2). In support of the importance of size and distance among interaction patches for evolutionary dynamics among species, studies on coevolution between pine trees and crossbills suggest that small, isolated forest areas tend to result in "cold spots" for coevolution (see below), probably due to weaker selective pressures and higher homogenizing gene flow (Benkman and Parchman 2009; Mezquida and Benkman 2010), while the contrary would be true for large, dense and well-connected forest patches. However, although the potential for adaptation may be higher in large, well-connected patches, the adaptive response of particular species will also depend on their genetic diversity, with a low genetic diversity potentially hindering an adaptive response (Figure 6-2e) (Strauss, Lau, and Carroll 2006).

The predictions of our model (Figure 6-2) result in patches with native plants adapted to the invader and patches where such adaptation does not occur, as found by Goergen, Leger, and Espeland (2011). This outcome is analogous to hot and cold spots for coevolution, as predicted by the Geographic Mosaic Theory of Coevolution (GMTC) (Thompson 2005). GMTC integrates spatial mosaics of selection, the occurrence of coevolutionary hot and cold spots, and gene flow among these areas (Thompson 2005). Viewing invaded areas as a mosaic of cold and hot spots for native species adaptation and/or coevolution could help us better understand the dynamics of adaptation in these systems. Although our model aims at predicting hot spots for adaptation, coevolution between native and invasive species is also possible and it is potentially more likely to occur in large, dense and well-connected patches (Leger and Espeland 2010; Lankau 2012; Turkington 1989). Greater connectivity among invaded patches may facilitate gene flow between invasive species populations/patches, potentially promoting their evolutionary potential (Leger and Espeland 2010). Further, if native species adapt to invaders more often in large, well-connected patches, it is in those patches where we could expect to see a reciprocal evolutionary response by the invader.

Invasive species often have a high evolutionary potential (Matesanz, Gianoli, and Valladares 2010; Richards et al. 2006), thus making coevolution a possible outcome. However, coevolution among native and invasive plant species has rarely been studied (Leger and Espeland 2010), and therefore convincing evidence has only been reported once (Lankau 2012). Lankau (2012) found that the invader garlic mustard (*Alliaria petiolata*) responded to high density of native competitors with an increased investment in sinigrin, a toxic allelochemical. In response, a native species, when co-occurring with high-sinigrin garlic mustard, was more tolerant to the allelochemical. However, a decline in garlic mustard's sinigrin production has also been documented (Lankau et al. 2009), potentially due to the evolution of resistance in native plants and microbes to the chemical, rendering it ineffective. As such, invasive species evolution, or the co-evolution between native and invasive species, may also facilitate coexistence among interacting species, and not necessarily lead to an escalating dynamic of increased "aggressiveness" between them (Oduor, Yu, and Liu 2015).

GMTC, rather than merely predicting the occurrence of hot spots for (co)evolution, focuses on how coevolutionary hot spots –which may differ due to selection mosaics- interact with each other and with coevolutionary cold spots through the remixing of adaptive traits, thus determining the outcome of the interaction across broader scales (Thompson 2005; Gomulkiewicz et al. 2007). This framework could be applied equally to the interaction between "adaptive" hot and cold spots. We know that selection differs between invaded and uninvaded areas, with individuals in invaded areas being selected for traits such as increased growth rate, advanced phenology, particular root architecture and tolerance to allelochemicals, among other traits (Callaway et al. 2005; Rowe and Leger 2010; Goergen, Leger, and Espeland 2011; Lankau 2012). However, as predicted by GMTC, selection may also vary between invaded patches due to different environmental conditions, interactions with other species and/or invasion history (Gómez 2003; Parchman and Benkman 2008; Salgado-Luarte and Gianoli 2012; Lankau 2012; Oduor, Yu, and Liu 2015). Since invasive species often are often distributed across broad geographic areas, selection mosaics are highly likely. For example, the invader cheatgrass (*Bromus tectorum*) increased nitrogen cycling when invading cool desert areas, but decreased it when invading arid grasslands (Ehrenfeld 2003), likely imposing different selective pressures on native species in those areas. Evaluation of this scenario is important for invasive species management as it may imply that there is no single genotype of native species that is able to resist and/or tolerate the invader, but rather that adaptations are context-dependent.

Because invasive species management occurs at the landscape level, it is important to underscore that variation in species interactions and selection at the local spatial scale can affect large scale population and community dynamics (Hartvigsen and Levin 1997; Gomulkiewicz et al. 2000). As models show, both the abundance and distribution of (co)-evolutionary hot spots across the landscape can determine the adaptation dynamics for the meta-population as a whole (Nuismer 2006; Hanski, Mononen, and Ovaskainen 2011; Gibert et al. 2013; Gomulkiewicz et al. 2000). Similar models could be used to predict the dynamics of adaptation of native species to invasive species.

6.5 Biotic and abiotic factors that may influence native species adaptive potential

Several characteristics of native and invasive species as well as environmental conditions may influence the likelihood of an adaptive response by native species to invasion. We briefly discuss below some characteristics that have been identified as important in determining the invasive species establishment and impact or species evolutionary dynamics in general (Catford, Jansson, and Nilsson 2009; Holsinger 2000; Reznick, Bryant, and Bashey 2002; Lavergne and Molofsky 2007), while suggesting possible links with the size and/or isolation of invaded patches. Other aspects of species, such as population size, generation time and other life history traits are also known to influence the rate of evolution, and have been discussed elsewhere (Rosenheim and Tabashnik 1991; Bousquet et al. 1992; Hartl, Clark, and Clark 1997; Andreasen and Baldwin 2001; Willi, Van Buskirk, and Hoffmann 2006; Smith and Donoghue 2008; Kostikova et al. 2013).

6.5.1 Mating system of native species

Self-pollination can be advantageous under stressful conditions (Horandl 2006; Barrett 1996). For individuals adapted to invaded areas, vegetative reproduction and self-pollination could assure reproduction in the absence (or low density) of sexual partners (Lloyd 1992; Morgan and Wilson 2005) and increase the probability of production of offspring well-adapted to persist in invaded areas (Antonovics 1968). In invaded patches, native plants that favor self-pollination over out-crossing would reduce homogenizing gene flow, thus further increasing the likelihood of adaptation (Antonovics 1968). Therefore, selfers could be more tolerant to the isolation in invaded patches. However, self-pollination may also lead to reduced fitness (inbreeding depression, Charlesworth and Charlesworth 1987), smaller effective population size and genetic diversity, thus reducing the likelihood of an evolutionary response to other stressors (e.g., disturbance, see below) and increasing population extinction risk (Holsinger 2000; Kamran-Disfani and Agrawal 2014; Gomulkiewicz and Holt 1995; Kinnison and Hairston 2007).

6.5.2 Common vs. rare native species

Common species have the advantage of larger initial population size, but a decrease in population size may have greater negative consequences on these species compared to rare species (Lankau and Strauss 2011). Rare species, with their lower population sizes, are likely to show lower genetic variation and inbreeding depression, which may limit their evolutionary potential and make them more prone to demographic stochasticity (Willi, Van Buskirk, and Hoffmann 2006; Reznick and Ghalambor 2001; but see Wares, Hughes, and Grosberg 2005; Avery and Hill 1977). However, rare species may be adapted to avoid pollen limitation and decreased reproductive output in low-density situations (Reznick, Bryant, and Bashey 2002; Lankau and Strauss 2011; Eckert et al. 2010; Kunin and Shmida 1997). Further, rare species may be better adapted to compete against inter- rather than intra-specific competitors, compared to common species (Shaw et al. 1995). This may explain why, in certain cases, invasive species have lower impact on rare species (Bennett, Stotz, and Cahill 2014; Powell, Chase, and Knight 2013). When facing the strong selection expected in large, dense invaded patches, which often leads to significant reductions in population size, rare species –unless in very low densities- could be less affected than common species.

6.5.3 Invader's genetic diversity and multiple introductions

Genetic variation and repeated introduction of invasive species are known to influence their evolutionary potential (Vellend et al. 2007; Lavergne and Molofsky 2007; Matesanz, Horgan-Kobelski, and Sultan 2014), but these factors may also affect the likelihood of native species adaptation. First, increased beta diversity of invader genotypes, over time and/or space, increases the variation of selective pressures on native species, potentially preventing an adaptive response (Aarssen and Turkington 1985; Willis, Brock, and Weinig 2010). Second, the presence of different invader genotypes across the landscape may decrease the rate of reinforcing gene flow (Figure 6-1), as native species' propagules from one invaded patch may be maladapted to establish/persist in another patch. The invader garlic mustard (*Alliaria petiolata*) varies in its levels of sinigrin (a toxic allelochemical) and therefore also in its selective pressure on native species: high-sinigrin garlic mustard populations select for a greater resistance to the loss of arbuscular mycorrhizal fungi colonization in a co-occurring native species (Lankau 2012), while no such selection was observed in low-sinigrin populations. These effects may be particularly detrimental for native species in isolated invaded patches, as the effective, functional distance among these islands will be far greater than the actual distance. In other words, multiple introductions of invasive plant genotypes could magnify the isolation effect. Although the arrival of new propagules of invasive species is generally regulated (Roques and Auger-Rozenberg 2006; Simberloff et al. 2013), this is not always the case for pasture and horticulture species, which are continuously bred and re-seeded in their introduced range (Driscoll et al. 2014; Lonsdale 1994; Reichard and White 2001).

6.5.4 Disturbance

Invasive species are often facilitated by, or active drivers of, disturbance (Sher and Hyatt 1999; Colautti, Grigorovich, and MacIsaac 2006; Mack and D'Antonio 1998). Disturbance may result in new sources of stress for native species, and in conjunction with invasion may constrain a timely adaptive response by native species (Byers 2002; Fenesi et al. 2015; Fakheran et al. 2010; Rolshausen et al. 2015). A recent meta-analysis found that disturbance benefits invasive species, while native species are generally unaffected by disturbance in the presence of invasive species (Jauni, Gripenberg, and Ramula 2015). In turn, native species that are affected by disturbance may be less likely to adapt to invasive species, because disturbance and competition may exert opposing selective pressures (Fakheran et al. 2010). Theory suggests that high and low frequency of disturbance select for a ruderals strategy and stronger competitive ability, respectively (Grime 1974). If highly competitive genotypes are eliminated from highly disturbed landscapes (Fakheran et al. 2010), the adaptation of native species to disturbance may constrain their adaptation to invasion and vice versa. In sum, disturbance would hamper adaptation of native species to invaders, seemingly regardless of the size and isolation of invaded patches.

6.5.5 Plant-soil feedbacks

Many invasive plant species are known to modify soil conditions where they invade, which can affect native species performance and competitive ability (Bever 1994; Bever 2003; Ehrenfeld 2010; Suding et al. 2013). Invader-driven changes in soil conditions have the potential to influence both the strength and direction of selection on native species, and their adaptive response (Chanway, Holl, and Turkington 1989; Chanway, Holl, and Turkington 1988; Ehlers and Thompson 2004). Further, these invader-driven changes in soil conditions may cancel out the local or home advantages that native species may have had over invasive species (Byers 2002), and further constrain their evolutionary responses (Gonzalez and Bell 2012). This would be particularly true in large patches of invaders, where their greater abundance or density will bring about greater changes in soil conditions.

6.5.6 Enemy release

Many invasive species escape their natural enemies, experiencing reduced damage in the introduced range (Keane and Crawley 2002; Agrawal et al. 2005). Native species able to persist in invaded patches may benefit from the association with invaders, and also experience reduced damage (i.e. associational resistance, Barbosa et al. 2009). This reduced damage may lead to the re-allocation of resources towards an increased competitive ability in native species, as with invasive species (Blossey and Notzold 1995) favoring the adaptation of native species to coexist or compete with an invader. For example, the increased competitive ability of *Solidago altissima* after being experimentally released from aboveground herbivores occurred within 12 years in its native range (Uesugi and Kessler 2013). The benefits of associational resistance for native species should be more evident in large patches of invaders, where natives would be more sheltered.

6.6 Management implications

As management practices move forward, it is important to understand the eco-evolutionary dynamics between native and invasive species. This information could improve current control strategies for invasive species. Testing whether native species are able to adapt to coexist, or resist, invasive species was a first step. Now that we know adaptation is possible, a second step is to identify the underlying mechanisms in order to determine under which conditions adaptation is more likely to occur. In order to do so, we need to identify under which conditions adaptation is more likely (which we propose doing based on characteristics of the invasive species spatial pattern) and which native species are more likely to adapt (based on characteristics of the native species). Knowledge of the conditions where adaptation is more probable and which species are more likely to adapt can allow managers to (1) increase the likelihood of native species adaptation, and (2) facilitate the gathering of adapted genotypes to increase resistance to invasion and restore invaded areas (Table 6-1).

Attempts could be made to facilitate native species adaptation (Leger and Espeland 2010) (Table 6-1). Modifying the spatial distribution of the invader may not be a realistic goal, but gene flow between invaded areas could be manipulated. Reinforcing gene flow could be increased through additions of adapted genotypes (seeds or whole plants) into invaded patches, particularly for self-incompatible species (Table 6-1). This procedure would be especially important in the more isolated patches. Many factors need to be considered when developing management strategies. If feasible, the complete removal of an invasive species is often desirable (but see Carroll 2011; Schlaepfer, Sax, and Olden 2011). However, for cases in which resources are not enough to eradicate all patches of an invasive species, we offer an additional tool to managers: we suggest starting by eliminating isolated patches, which would not only prevent establishment of new invasion foci but would also remove patches where adaptation of native species is unlikely (i.e. cold spots). Furthermore, identification of the traits underlying native species' increased resistance and/or tolerance to invasive plant species can help select traits to increase the resistance of native communities (Funk et al. 2008); this should target individuals in large, dense and well-connected invaded patches (Table 6-1). Information on which type of species (e.g., common vs. rare species, selfing vs. outcrossing species, annual vs. perennial) are more likely to adapt, may further advance our understanding of the conditions under which native species are likely to adapt.

Management practices could also reduce the evolutionary consequences of further introductions of new genotypes by regulating the planting of different/new genotypes of forage and horticulture species, as well as the movement of invasive species within the introduced range

(Driscoll et al. 2014; Reichard and White 2001; Oduor, Yu, and Liu 2015). Also, reducing the frequency of anthropogenic or novel disturbances in areas where adaptation of native species is likely (i.e. large, well-connected patches) would reduce the extinction risk of native species and potentially facilitate their adaptation. The reduction of disturbances may also include discontinuing the eradication of invasive species in certain areas to promote the adaptation of native species, as argued by Carroll (2011): he proposed protecting invasive plant populations in one region of Australia where selection resulted in the adaptation of a native insect to more effectively consume the invader seeds (Carroll et al. 2005). Those adapted insect populations could then be used to promote gene flow to poorly adapted insect populations in other regions of Australia to help control a recent and serious invasion of a closely related plant species.

We predict that native species are more likely to adapt to coexist or compete against invasive species in large, dense and well-connected invaded patches (Figure 6-2). If so, preference should be given to large and well-connected invaded patches when collecting propagules from adapted genotypes for management purposes (Table 6-1). Within these sites, preference should be given to native species with larger population sizes, as small populations may be still in the process of adaptation (Gomulkiewicz and Holt 1995). Besides implementing the use of adapted genotypes to complement management strategies, it is advisable to first evaluate the occurrence of a selection mosaic across the introduced range of invasive species, as predicted by the GMTC (Thompson 2005). Testing for selection mosaics implies comparing selection by the invader on key traits in similar-sized invaded patches along biotic and/or abiotic gradients across the invaded area. Invasive species may select for different traits or trait values depending on biotic or abiotic conditions. If there is evidence of a selection mosaic, the source of native species propagules should ideally match the biotic and abiotic condition of the area targeted for management (Table 6-1). It may be argued that selecting and using only a limited number of genotypes for management efforts can be disadvantageous because low genetic variation is associated with decreased fitness (Leimu et al. 2006) and increased susceptibility to new stress factors (Gonzalez and Bell 2012; Willi, Van Buskirk, and Hoffmann 2006; Frankham 1996). However, selected adapted genotypes may have a higher probability of survival in invaded areas, increasing population growth and the probability of population persistence (Reznick and Ghalambor 2001).

Native species adaptation in the invaded patches will partly depend on the abundance of and connectedness between cold and hot spots (Thompson 2005; Hanski, Mononen, and Ovaskainen 2011). We could modify the connectedness of invaded patches to facilitate adaptation, while preventing further expansion of the invader. This could be achieved by removing cold spots (an easier task, since those are the smaller patches), or by increasing reinforcing gene flow to increase the likelihood of cold spots becoming hot spots (Table 1). The more hot spots in the landscape, the higher the probability of cold spots becoming hot spots by extensive reinforcing gene flow (Shirley and Sibly 2001; Gibert et al. 2013; Hanski, Mononen, and Ovaskainen 2011).

Overall, by better understanding the conditions that facilitate native species' adaptation to invasion, and by being able to predict where native species are more likely to have adapted, we can take advantage of these eco-evolutionary processes to manage invaded ecosystems and complement current management strategies to control invasive plant species.

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Table 6-1: Predictions of the proposed framework, examples of methods that could be used to test the predictions, and management implications if predictions are verified.

Predictions	Methods	Management implications
Large, well-connected patches are more likely to result in native species adaptation to invaders	- Determining the strength of selection on key traits as a function of patch size - Molecular marker data could be used to infer gene flow among sub-populations of native species in invaded areas - Quantify adaptation across patches of different sizes and isolation to test for the individual and interactive effects of patch size and isolation	- Propagules to reclaim invaded areas or increase the resistance of communities to invasion should be collected from large, well-connected invaded patches - Studies on plant traits underlying resistance/tolerance to invasive plants should target native species individuals from large, well-connected areas - The size and isolation of patches could be managed to increase the likelihood of native species adaptation - Gene flow between invaded areas could be facilitated to increase the rate of reinforcing gene flow
Selection imposed by the invader on native species varies across the invaded range due to changes in biotic and abiotic conditions	- Quantifying selection on key traits in invaded patches changes along abiotic or biotic gradients - Test whether native species adapted to interact with the invader on one end of the abiotic or biotic gradient, show the same fitness advantage when on the other end of gradient	- Propagules from adapted native species should be used to reclaim or increase resistance in areas with similar biotic and/or abiotic conditions to the areas where they were collected
Abundance and distribution of hot spots determine the adaptation dynamics for the meta-population	- Create a model to predict meta-population dynamics of adaptation based on selection parameters estimated from the previously mentioned experiments and invasive species abundance and distribution	- The abundance and distribution of hot spots for adaptation could be managed to increase the scale of local adaptation. Cold spot abundance could be decreased by eradicating the invader from those areas or by promoting reinforcing gene flow to increase the chances of it becoming a hot spot

Figure 6-1: Conceptual diagram of the landscape pattern of invasion and the different kinds of gene flow affecting the adaptation of native species to invasion. Green areas symbolize invaded patches, the light-blue area represents the matrix of native habitat and blue individuals represent native species. As shown on the right part, a native individual in an invaded area interacts almost exclusively with the invader, while native individuals in native areas (the white matrix) interact with several species. Red arrows stand for homogenizing gene flow (source: native plants from native areas), while black arrows stand for reinforcing gene flow (source: native plants from other invaded areas). Continous-line arrows indicate high rates of gene flow, while dashed-line arrows indicate low rates of gene flow.

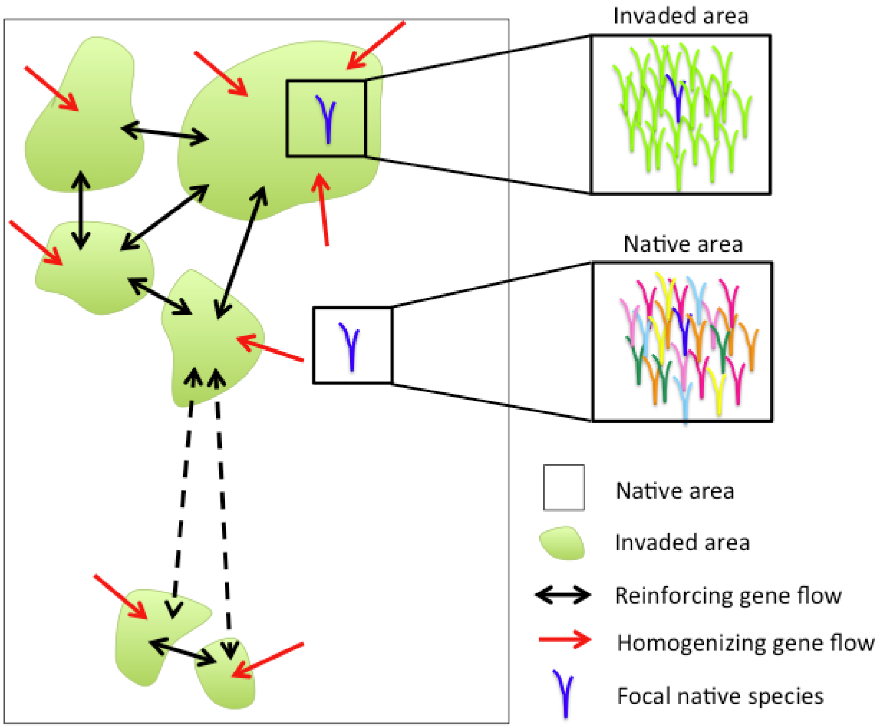
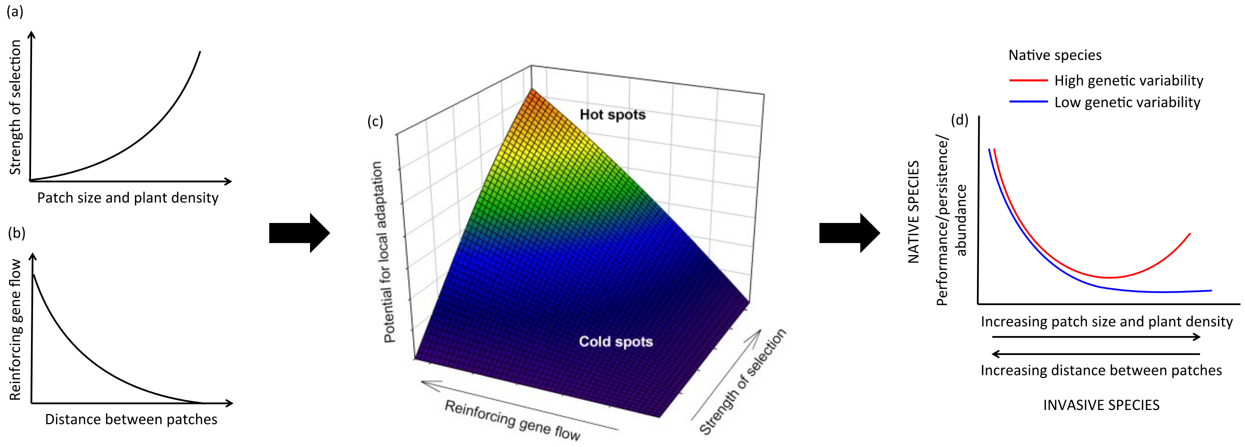


Figure 6-2: Conceptual model of eco-evolutionary dynamics between native and invasive species as a function of size and isolation of invaded patches.

The strength of selection is predicted to increase as a function of invasive species patch size and density (a). Reinforcing gene flow is predicted to decrease with distance between invaded patches (b). Consequently, the potential for native species adaptation would increase as patch size increases and the distance between patches decreases (c), resulting in cold and hot spots for the adaptation of native species to invasive species. If native species have the necessary genetic diversity to respond to selection, following an initial decrease of native species performance/abundance as the invasion process progresses (larger and closer invaded patches) there would be a recovery of those natives that succeed in adapting to the invasive species (d). However, if the genetic diversity of native species is too low, then an adaptive response to invasion and, therefore, the recovery of the population, is unlikely (d).



Chapter 7: Conclusion and future directions

The overall objective of this thesis was to evaluate the drivers of invasive species establishment and impact on ecological and evolutionary aspects of communities. I found that the strength of the resistance opposed by the resident plant community to invaders establishment and growth increased in warm, moist sites, while productivity was not found associated with the strength of biotic resistance (Chapter 2). *Bromus inermis* impact on community structure, although consistently negative, was also influenced by local biotic and abiotic conditions (Chapter 3). More importantly, *B. inermis* impact on species richness was dependent upon species origin, with a consistent negative impact on native species richness, but a highly variable impact on exotic species richness (Chapter 3), which can have important management implications (Kuebbing and Nuñez 2015, Bernard-Verdier and Hulme 2015). In general, we found *B. inermis* to rapidly alter resident communities, reducing native species diversity, changing species composition, altering ecosystem function, homogenizing communities and changing overall community dynamics (Chapters 3 and 4). In doing so, *B. inermis* creates a sharp transition between alternative community states (invaded and uninvaded), establishing potential self-reinforcing dynamics that facilitate the persistence of communities in an invaded state (Chapter 4).

B. inermis' strong impact on species diversity, composition and ecosystem function has the potential to result in an evolutionary response by resident species (Chapter 6, Strauss et al. 2006, Thorpe et al. 2011, Parachnowitsch et al. 2014). However, we found no evidence of an adaptive response to the impact of *B. inermis* in any of the three species tested (Chapter 5). In fact, we found a decrease in species ability to suppress *B. inermis* performance. This highlights the need to better understand under which conditions species are more likely to adapt to coexist with invasive species. Hence, in chapter 6 we reviewed the factors that are likely to determine native species adaptation and proposed a theoretical model on how a greater size of, and lower distance between, invaded patches may favor native species adaptation to invaders. If the size and density of, and distance between, patches are good predictors of native species adaptation, we could manage certain aspects of invasions to facilitate native species adaptation and/or use characteristics of invaded patches to study and collect well adapted genotypes to complement current restoration efforts.

7.1 Mechanisms and consequences of invasion

My results indicate that resident communities oppose a higher resistance to invasion, reducing invasive species performance, in sites with higher temperature and precipitation (Chapter 2). However, it is also under those generally benign conditions where, after established, invasive species have a greater impact on community diversity and function (Chapter 3) (Chambers et al. 2007, González-Moreno et al. 2014, Prevéy and Seastedt 2015). Overall, similar environmental conditions resulting in both greater biotic resistance to invasion and greater invasive species performance after establishment, support the idea that native and invasive species are not fundamentally different (Thompson et al. 1995, Corbin and D'Antonio 2010), but rather respond similarly to environmental variables (Pouteau et al. 2015). However, although *B. inermis* performance was associated to certain environmental conditions, we found that it was able to establish and alter resident communities structure and function across the range of sites and environmental conditions evaluated (Chapter 3, 4). Due its greater performance and impact on community structure under more benign environmental conditions *B. inermis* could be considered a “Master-of-some”, following (Richards et al. 2006). Yet it could also be argued that *B. inermis* is a “Jack-and-master”, as it has a greater performance under favorable environmental conditions, but it is also able to maintain fitness under less favorable conditions (Richards et al. 2006).

Invasive species performance is generally dependent upon local biotic and abiotic conditions. However, invasive species can also alter the environments they invade (Ehrenfeld 2003, 2010, Kulmatiski et al. 2008), thereby facilitating or reinforcing their dominance. In doing so, they may lead to the establishment of alternative persistent stable states in the landscape (Suding et al. 2004, Hobbs et al. 2006). Consistently, my results suggest that *B. inermis* may increase the persistence of communities in an invaded, alternative state by increasing nutrient availability in invaded areas, which in turn may facilitate its own growth and overall performance (Chapter 4). Further*, B. inermis* high standing and litter biomass limit species recruitment, constraining native species recovery and increasing the persistence of the community in a invaded, low diversity state (Chapter 4). Studies also suggest, however, that self-reinforcing invasion dynamics may break-down over time, eventually leading to native species recovery (Strayer et al. 2006, Lankau et al. 2009, Yelenik and D’Antonio 2013). Soil pathogens may accumulate in *B. inermis* invaded areas (Vanterpool 1942, Myhr et al. 1966) likely explaining *B. inermis* lower growth (Chapter 5) and recruitment (Carrigy et al. 2016) in soil from *B. inermis*-invaded areas, compared to soil from native-dominated areas. This may eventually result in *B. inermis* dominance decay and native species recovery. Further studies on the effects of soil microbial communities on *B. inermis*-invasion dynamics, as well as long-term studies of *B. inermis* dominance, and impact on community structure and ecosystem function, may be central to understand and manage *B. inermis* invasion.

Yelenik and D'Antonio (2013) found that although the impact of an invasive species on ecosystem function decreased over time, rather than leading to native species recovery, it led to the establishment of other exotic invasive species. Results from this thesis suggest that similar dynamics might be expected in *B. inermis*-invaded areas. Although the impact of *B. inermis* on exotic species was highly variable across sites, we found that exotic species were in general able to persist in invaded areas, while native species were consistently excluded (Chapter 3). Hence, if (or once) *B. inermis* dominance decays, exotic species are more likely to establish and grow in the previously invaded areas, compared to native species. Future studies investigating the interaction of *B. inermis* with other exotic species may be necessary to assess, and potentially prevent, secondary invasions (Ortega and Pearson 2010, Kuebbing and Nuñez 2015) and/or an invasional meltdown (Simberloff and Von Holle 1999). *B. inermis* may not only facilitate the establishment and persistence of exotic species, but may also enhance their competitive ability. In Chapter 5, however, I found no evidence of an increased ability to tolerate or suppress neither *B. inermis* nor conspecifics in the three species assessed, two of them being exotic species (*Poa pratensis* and *Melilotus officinalis*).

7.2 Potential evolutionary consequences of invasion

Results indicate that *B. inermis* patches are “islands” within the landscape, with a sharp transition between invaded and native-dominated areas (Chapter 4). *B. inermis*-invaded areas are generally less diverse, have a different species composition, loose and gain fewer species in time, have a higher productivity and greater nutrient availability, compared to native-dominated areas (Chapters 3 and 4). *B. inermis*, due to its impact on different abiotic and biotic factors where it invades, as well as its strong suppressive effect (Chapter 3, Wang et al. 2010), may act as a selective agent for neighboring species (Chapter 6). *B. inermis* invasion resulted in biotic homogenization within and across sites, indicating that only certain species were able to consistently persist in invaded areas, while most species were excluded (Chapter 4). Further, Bennett et al. (2014) found that shade-intolerant species were more strongly suppressed by *B. inermis*, compared to more shade-tolerant species. Yet, I found no evidence of an enhanced ability to suppress or tolerate *B. inermis* in offspring from individuals collected from invaded areas (experienced individuals), compared to offspring from individuals in native-dominated areas (naïve individuals) (Chapter 5). However, results did suggest that more suppressive individuals may be selected against, in *B. inermis*-invaded areas.

This lack of adaptation by resident species may be due to their own features and/or characteristic of *B. inermis'* invasion. Although strong selection is one of the main drivers of rapid adaptation (Chapter 6, Hairston et al. 2005), it can also have strong demographic effects, rapidly and/or greatly reducing population size and resulting in population extinction (Willi et al. 2006). Hence, *B. inermis* strong suppressive effect may greatly reduce neighboring species population size, preventing an adaptive response (Chapters 5 and 6). Further, as a forage species, different cultivars of *B. inermis* have been bred and released (Alderson et al. 1994, Coulman 2006). These repeated introductions may result in high genetic variation and diversity of genotypes in the landscape, increasing *B. inermis* evolutionary potential, and reducing the likelihood of native species adaptation (Chapter 6, Lavergne and Molofsky 2007, Vellend et al. 2007, Matesanz et al. 2014). Invaders' high genotypic diversity can reduce the likelihood of native species adaptation. This, because different genotypes may oppose different selective pressures (Baron et al. 2015), which would result in a lower rate of reinforcing gene flow (arrival of individuals/gene from areas with similar selective pressures) (Chapter 6) (Sexton et al. 2014).

Interacting with *B. inermis* did result in a lower ability to suppress *B. inermis*, but not conspecifics (Chapter 5). Although the usual focus in these studies has been on adaptive responses to invaders (Chapter 6, Strauss et al. 2006, Goergen et al. 2011, but see Schlaepfer et al. 2005), mal-adaptive responses by resident species to invaders should also be considered, as they can have important negative consequences for the resident species, while facilitating invader performance and expansion (Schlaepfer et al. 2005). Further, more studies testing whether species responses to invaders are specialized or generalized can shed light into the long-term consequences of invasion, as well as on how species coexist and communities assemble. A generalized lower suppressive ability could increase species likelihood of becoming going extinct, while a reduced suppressive ability that is invader-specific may result in greater invader impact and spread (Levine 1999); our results indicate specialized responses to the invader (Chapter 5).

7.3 Synthesis and implications

B. inermis is an important forage species that increases productivity, soil fertility and is well adapted to grow under different environmental conditions (Chaper 2 and 3, Otfinowski et al. 2007). However, *B. inermis* also has a consistent negative effect on native species diversity (Chapter 3 and 4) and is already a widespread invasive species in North America. Although forage species are important for food production (Godfray et al. 2010), the potential ecological and evolutionary consequences for native species should be evaluated and considered before introducing them (Driscoll et al. 2014). The introduction of new genotypes of already introduced and/or invasive species should also be carefully considered, as it can further increase species invasive potential and limit the possibility of native species adaptation to invasion (Chapter 6).

In the case of *B. inermis*, its planting should be avoided in areas where it may pose a greater threat to biodiversity, such as species-rich communities, as well as where it has the potential to facilitate the establishment and persistence of other exotic species (Chapter 3). Although exotic species are likely to accumulate in *B. inermis*-invaded areas, *B. inermis* may actually reduce their invasive potential by reducing their ability to suppress neighbors (Chapter 5). Unfortunately, the reduced suppressive ability appears to be a specialized response to *B. inermis*, and not a generalized response. Overall, we need more studies evaluating the ecological and evolutionary consequences of *B. inermis* on native and exotic species, as well its interplay with other invasive species.

7.4 References

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Appendices

Appendix 1

Appendix 1-1: Source of NPP, NDVI, precipitation and temperature data

NPP and NDVI were obtained from two sources, depending on the year. NPP and NDVI for the years 1995-2000 was obtained from the Advances Very High Resolution Radiometer (AVHRR) Global Production Efficiency Model (GloPEM) dataset (http://glcf.umd.edu/data/glopem/) at an 8-km spatial resolution for NPP and at an 1-km spatial resolution for NDVI. NPP and NDVI data for the years 2000-2012 was obtained from the Numerical Terra Dynamic Simulation Group (http://www.ntsg.umt.edu/project/mod17) using the MOD17 Moderate Resolution Imaging Spectroradiometer (MODIS) dataset at a 1-km spatial resolution. Precipitation data was obtained from the GPCC Global Precipitation Climatology Centre dataset, provided by NOAA/OAR/ESRL PSD (Boulder, Colorado, USA), with a spatial resolution of 0.5x latitude by longitude (Schneider et al., 2011). Air temperature data was obtained from the GHCN Gridded V2 dataset, provided by the NOAA/OAR/ESRL PSD (Boulder, Colorado, USA; http://www.esrl.noaa.gov/psd/), at a spatial resolution of 0.5x latitude by longitude. All explanatory variables were averaged for the duration of the experiment or the entire growing season with multiple year experiments being averaged over multiple growing seasons.

Appendix 1-2: Heterogeneity in effect sizes and publication bias

Heterogeneity in effect sizes

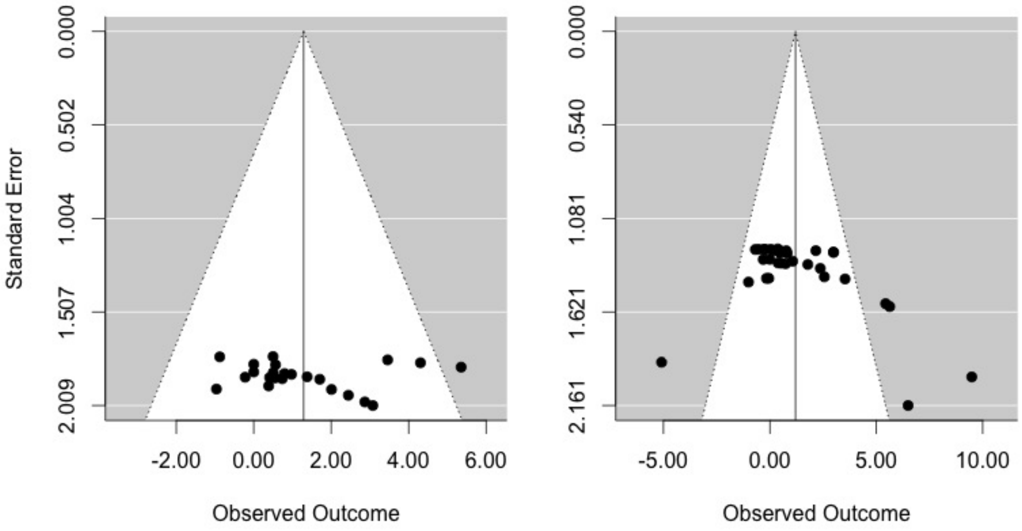
The heterogeneity in effect size was assessed by calculating Q, which is a measure of the heterogeneity of the meta-analysis (Borenstein et al., 2009). Q is tested against a chi-square distribution with degrees of freedom equal to k -1 (where k is the number of studies included). A significant p-value provides evidence that there is heterogeneity between studies.

When testing for the response variable emergence, we found no evidence of heterogeneity ($Q = 17.37$, p-value = 0.742). However, the other three variables evaluated do show significant heterogeneity between effect sizes (Size: $Q = 74.32$, p –value < 0.0001; Reproduction: $Q = 43.41$, p-value < 0.0001; Survival: $Q = 31.61$, p-value = 0.0477). Although moderator variables (temperature and precipitation) were significantly associated with the effect of neighbors on invasive species' size, and their addition reduced Q, Q remained significant (Size, temperature: $Q = 68.933$, p-value < 0.0001; precipitation = 61.3603, p-value = 0.0006).

Publication bias assessment

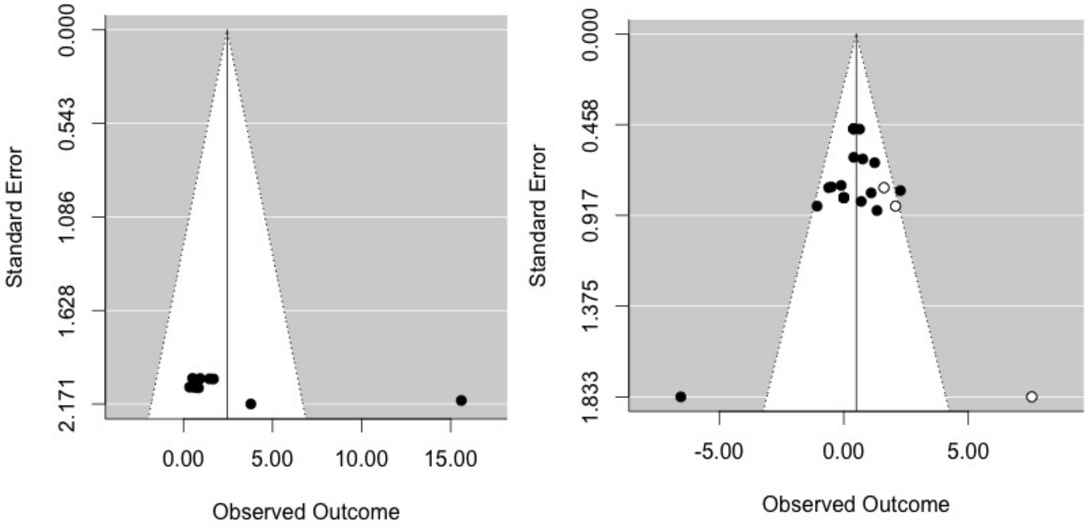
Publication bias (the greater possibility of publishing significant results) was assessed from visual inspection of a funnel plot (Borenstein et al., 2009). We further assessed publication bias by the trim and fill method (Duval & Tweedie, 2000), which estimates the number of missing studies due to publication bias. Analyses were carried out using the package *metafor* (Viechtbauer, 2010) in R (v.2.15.3, R Foundation for Statistical Computing, Vienna, AT).

Figure S1-2: Forest plots for (a) emergence, (b) plant size, (c) reproduction and (d) survival. Solid circles are the observed studies (original data) and open circles are the imputed studies (missing studies).



(a) Emergence

(b) Plant size



(c) Reproduction

(d) Survival

Citations

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Appendix 1-3: Studies included in the meta-analysis investigating the relationship between strength of biotic resistance in relation to the community's productivity and environmental conditions.

Alien species name, functional group, number of sites, time period of the experiment, number of replicates, site location, habitat and response variables reported for each study included in the meta-analysis.

Citation	**Alien species**	**Funct group**	**# sites**	**Start date**	**End Date**	**# reps**	**Site location**	**Habitat**	**Response variables**
Adair et al., 2008	*Bromus tectorum*	Grass	1	9/1/2003	7/1/2004	4	Colorado, USA	Grassland	Aboveground biomass
Badano et al., 2007	*Taraxacum officinalis*	Forb	3	12/1/2005	1/1/2006	40	Central Chile	Alpine	Aboveground biomass, survival
Badano et al., 2007	*Cerastium arvense*	Forb	3	12/1/2005	1/1/2006	40	Central Chile	Alpine	Aboveground biomass, survival
Bakker & Wilson, 2001	*Agropyron cristatum*	Grass	1	5/1/1995	9/1/1995	10	Saskatchewan Canada	Grassland	Survival
Barger et al., 2003	*Melinis minutiflora*	Grass	1	7/1/1996	6/1/1997	10	Caracas, Venezuela	Grassland	Aboveground biomass
Caño et al., 2008	*Senecio pterophorus*	Shrub	1	4/1/2005	1/1/2006	16	Barcelona, Spain	Grassland	Aboveground biomass, survival, reproduction

Erneberg, 1999	*Anthemis cotula*	Forb	1	6/1/1996	8/1/1996	10	Aarhus, Denmar	Grassland	Aboveground biomass
Eskelinen & Harrison 2014	*Centaurea solsticialis*	Forb	3	12/01/2011	07(01/2012	10	California, USA	Grassland	Total biomass
Eskelinen & Harrison 2014	*Aegilops triuncialis*	Grass	3	12/01/2011	10/01/2012	10	California, USA	Grassland	Total biomass
Garcia-Serrano et al., 2004	*Senecio inaequidens*	Shrub	4	5/1/2002	10/1/2002	4	Catalonia, Spain	Grassland	Survival
Garcia-Serrano et al., 2004	*Senecio pterophorus*	Shrub	3	5/1/2002	10/1/2002	4	Catalonia, Spain	Grassland	Survival
Going et al., 2009	*Avena barbata*	Grass	1	10/1/2005	5/1/2006	8	Santa Barbara, USA	Grassland	Aboveground biomass, reproduction
Going et al., 2009	*Bromus diandrum*	Grass	1	10/1/2005	5/1/2006	8	Santa Barbara, USA	Grassland	Aboveground biomass, reproduction
Going et al., 2009	*Hordeum murinum*	Grass	1	10/1/2005	5/1/2006	8	Santa Barbara, USA	Grassland	Aboveground biomass, reproduction
Greiling &	*Achillea millefolium*	Forb	1	4/1/1996	10/1/1996	5	Michigan, USA	Grassland	Emergence

Kichanan, 2002									
Greiling & Kichanan, 2002	*Hyperisum perforatum*	Forb	1	4/1/1996	10/1/1996	5	Michigan, USA	Grassland	Emergence
Grieshop & Nowierski, 2002	*Linaria genistifolia*	Forb	2	6/1/1997	8/1/1997	4	Montana, USA	Grassland	Emergence
Harrison et al. 2015	*Aegilops triuncialis*	Grass	1	11/01/2011	07/01/2012	108	California, USA	Grassland	Reproduction
Jesson et al., 2000	*Anthoxanthum odoratum*	Grass	1	2/1/1995	11/1/1995	5	South Island, New Zealand	Forest	Survival
Jesson et al., 2000	*Holcus lanatus*	Grass	1	2/1/1995	11/1/1995	5	South Island, New Zealand	Forest	Survival
Jesson et al., 2000	*Cerastium fontanum*	Forb	1	2/1/1995	11/1/1995	5	South Island, New Zealand	Forest	Survival
Jesson et al., 2000	*Hieracium pilosella*	Forb	1	2/1/1995	11/1/1995	5	South Island, New	Forest	Survival

							Zealand		
Har-Edom & Sternberg, 2009	*Conyza canadensis*	Forb	3	10/1/2005	4/1/2006	30	Israel	Scrubland	Aboveground biomass
Hierro et al., 2011	*Centaurea solsticialis*	Forb	4	variable	variable	45	California, USA & Santa Rosa, Argentina	Grassland	Aboveground biomass, survival, reproduction
Hill & Kotanen, 2012	*Solidago virgaurea*	Forb	3	variable	variable	10	Ontario, Canada	Grassland	Survival
Holmes et al., 2010	*Brachypodium sylvaticum*	Grass	1	04/01/2005	08/01/2008	4	Oregon, USA	Forest	Size
Meiman et al., 2009	*Centaurea diffusa*	Forb	1	9/1/2001	10/1/2002	3	Colorado, USA	Grassland	Emergence
Meiman et al., 2009	*Centaurea diffusa*	Forb	1	4/1/2002	10/1/2002	3	Colorado, USA	Grassland	Emergence
Pfeifer-Meister et al., 2008	*Lolium multiflorum*	Grass	1	3/1/2004	6/1/2004	4	Oregon, USA	Grassland	Aboveground biomass
Pfeifer-Meister et al., 2008	*Schedonorus arudinaceus*	Grass	1	3/1/2004	6/1/2004	4	Oregon, USA	Grassland	Aboveground biomass
Saccone et	*Acer*	Tree	3	3/1/200	11/1/20	4	Sablons,	Forest	Survival

al., 2010	*negundo*			4	05		France		
Sans et al., 2004	*Senecio inaequidens*	Shrub	1	3/1/1999	11/1/1999	20	Barcelona, Spain	Grassland	Aboveground biomass, reproduction, emergence
Sans et al., 2004	*Senecio pterophorus*	Shrub	1	3/1/1999	11/1/1999	20	Barcelona, Spain	Grassland	Aboveground biomass, reproduction, emergence
Sheley & James, 2010	*Taeniatherum caput-medusae*	Grass	1	04/01/2006	07/1/2009	4	Wyoming, USA	Grassland	Aboveground biomass
Vikane et al., 2013	*Picea sitchensis*	Tree	3	06/01/2010	09/01/2010	30	Island Lygra, Norway	Grassland	Emergence

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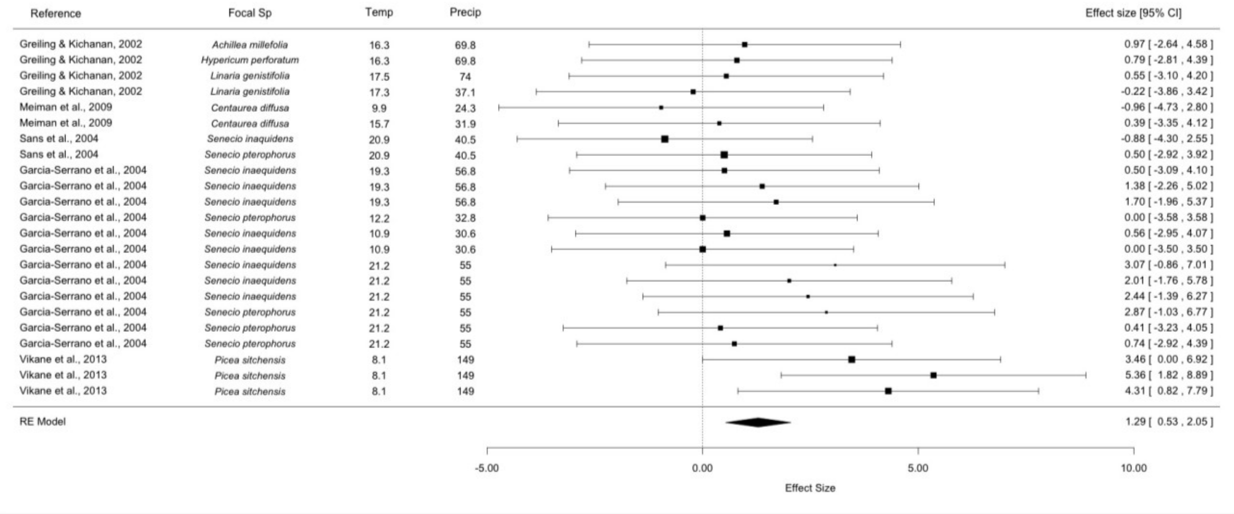
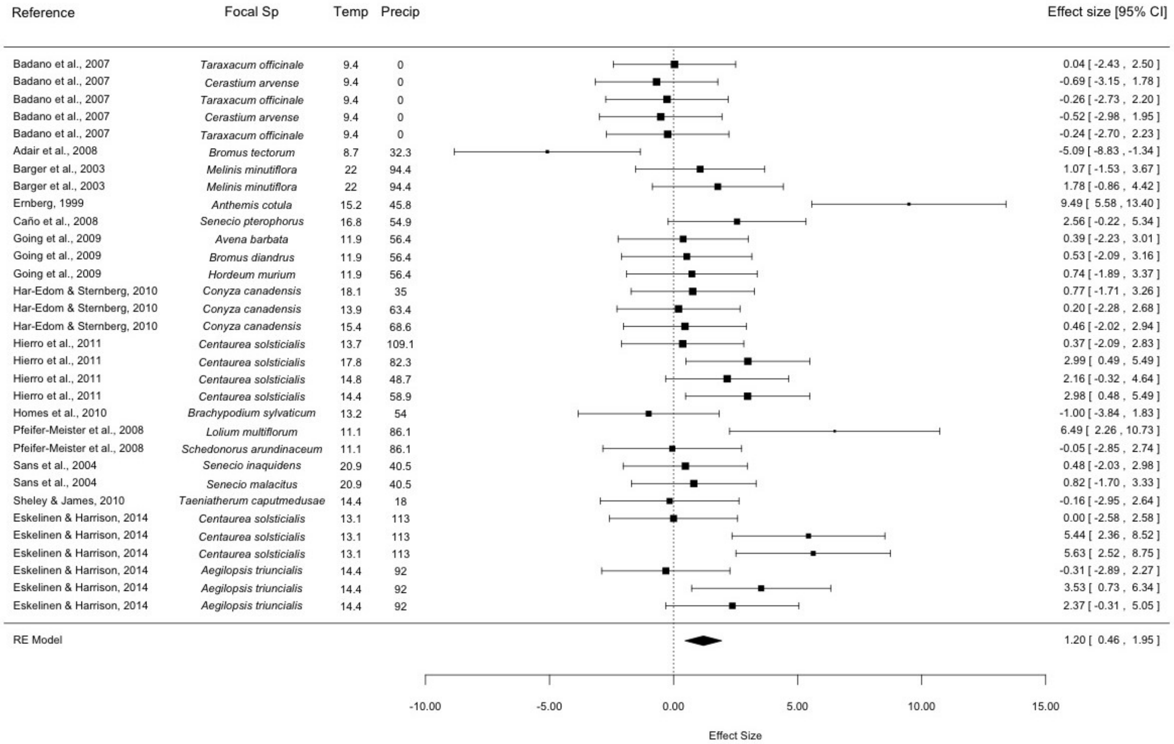
Appendix 1-4: Forest plots

Forest plots for the meta-analysis on net effects of neighbors on invasive species emergence, size, reproduction and survival. The name of the focal invasive species and the sites' temperature (Temp) and precipitation (Precip) are included. The size of the points is proportional to the sample size of each study. Negative effect sizes indicate facilitation and positive effect sizes indicate competition.

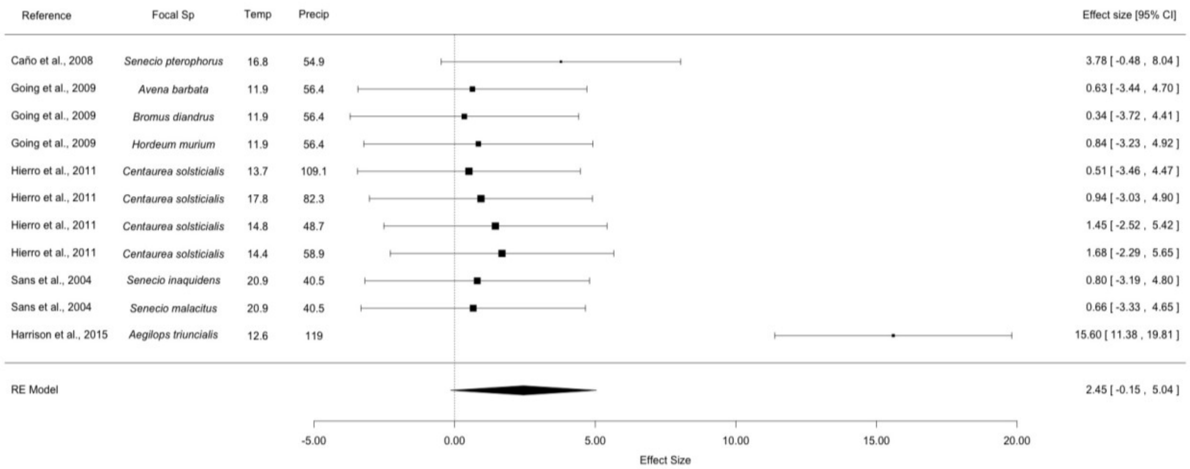
(a) – Response variable: emergence



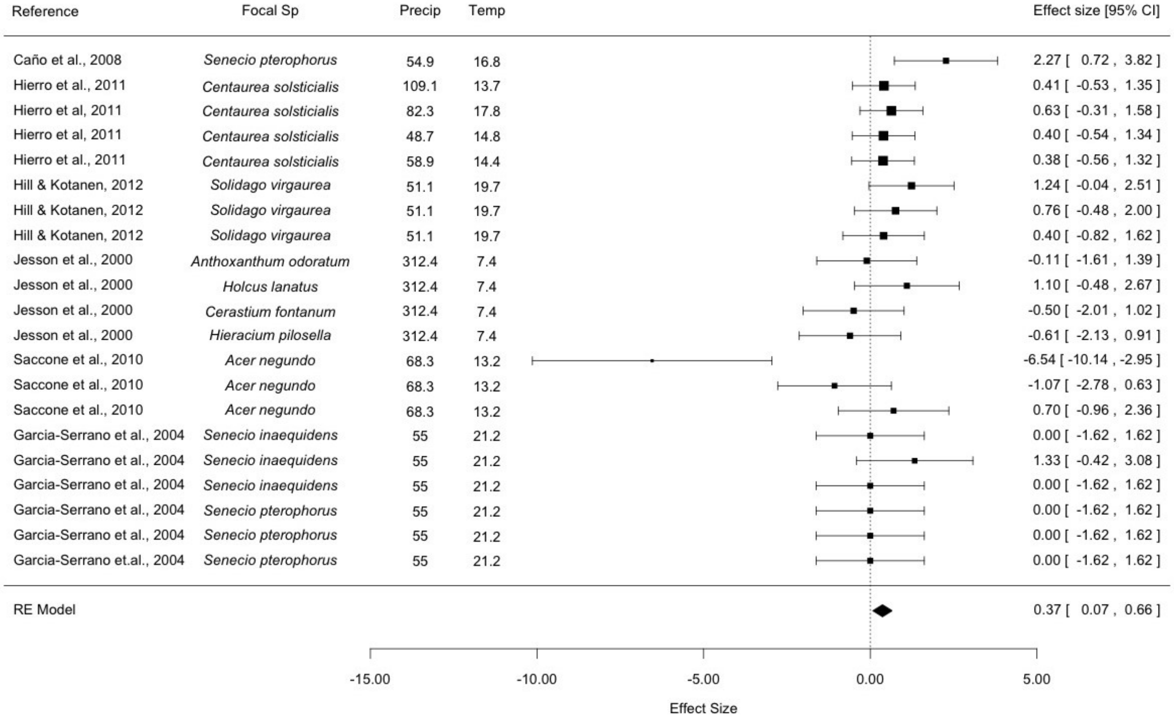
(b) Response variable: size



(c) Response variable: reproduction



(d) Response variable: survival



Appendix 1-5: The effect of productivity, temperature and precipitation on the strength of biotic resistance (hedges' *d*) on invasive plant species' performance. Performance was separated into emergence, size, reproduction and survival.

		Emergence	Size	Reproduction	Survival
		(n=23)	(n=32)	(n=11)	(n=21)
NPP	Estimate	0.331	0.002	-0.000	-0.002
	F-value	0.045	1.925	0.063	0.886
	p-value	0.833	0.179	0.810	0.361
Temperature	Estimate	-0.098	**0.947**	-0.003	0.045
	F-value	2.037	**4.258**	0.079	1.206
	p-value	0.168	**0.048**	0.786	0.286
Precipitation	Estimate	**0.036**	**0.024**	0.001	-0.695
	F-value	47.639	**6.338**	0.632	0.987
	p-value	<**0.001**	**0.017**	0.449	0.333

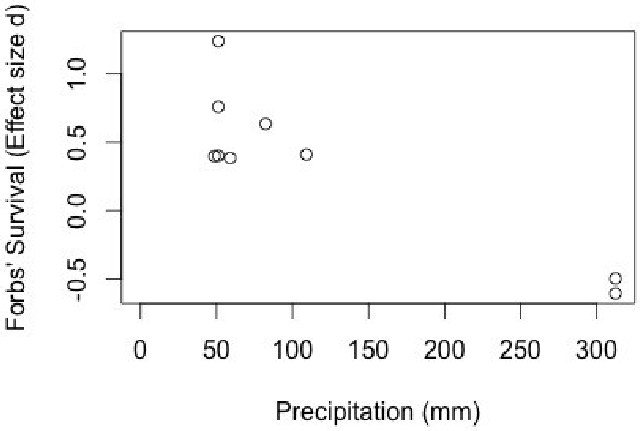
Appendix 1-6: Effect of productivity and environmental variables on the strength of biotic resistance by invasive species' functional group

Table S1-6: The effect of productivity, temperature and precipitation on the strength of biotic resistance (hedges *d*) on invasive plant species' performance by invasive species' functional group.

		Forb emerge (n=6)	Size (n=16)	Survival (n=13)	Shrub emergence (n=14)	Grasses size (n=13)
NPP	Estimate	-0.000	0.002	-0.001	-0.000	0.003
	F-value	0.021	0.275	2.060	0.036	2.928
	p-value	0.894	0.613	0.201	0.853	0.118
Temp	Estimate	0.188	**0.204**	0.193	0.114	-0.059
	F-value	4.648	**11.126**	2.615	2.381	1.532
	p-value	0.097	**0.005**	0.150	0.149	0.242
Precip	Estimate	0.027	**-0.012**	**-0.004**	**0.067**	0.045
	F-value	8.816	**8.742**	**15.819**	**7.567**	4.728
	p-value	0.041	**0.010**	**0.005**	**0.018**	0.052

Figure S1-6

Effect of precipitation on the net neighbor effect (effect size *d*) on invasive forbs' survival. Positive effect size *d* indicates negative effect of neighbors on invasive species' survival (competition) while a negative effect size *d* indicates a positive effect of neighbors on invasive species' survival.

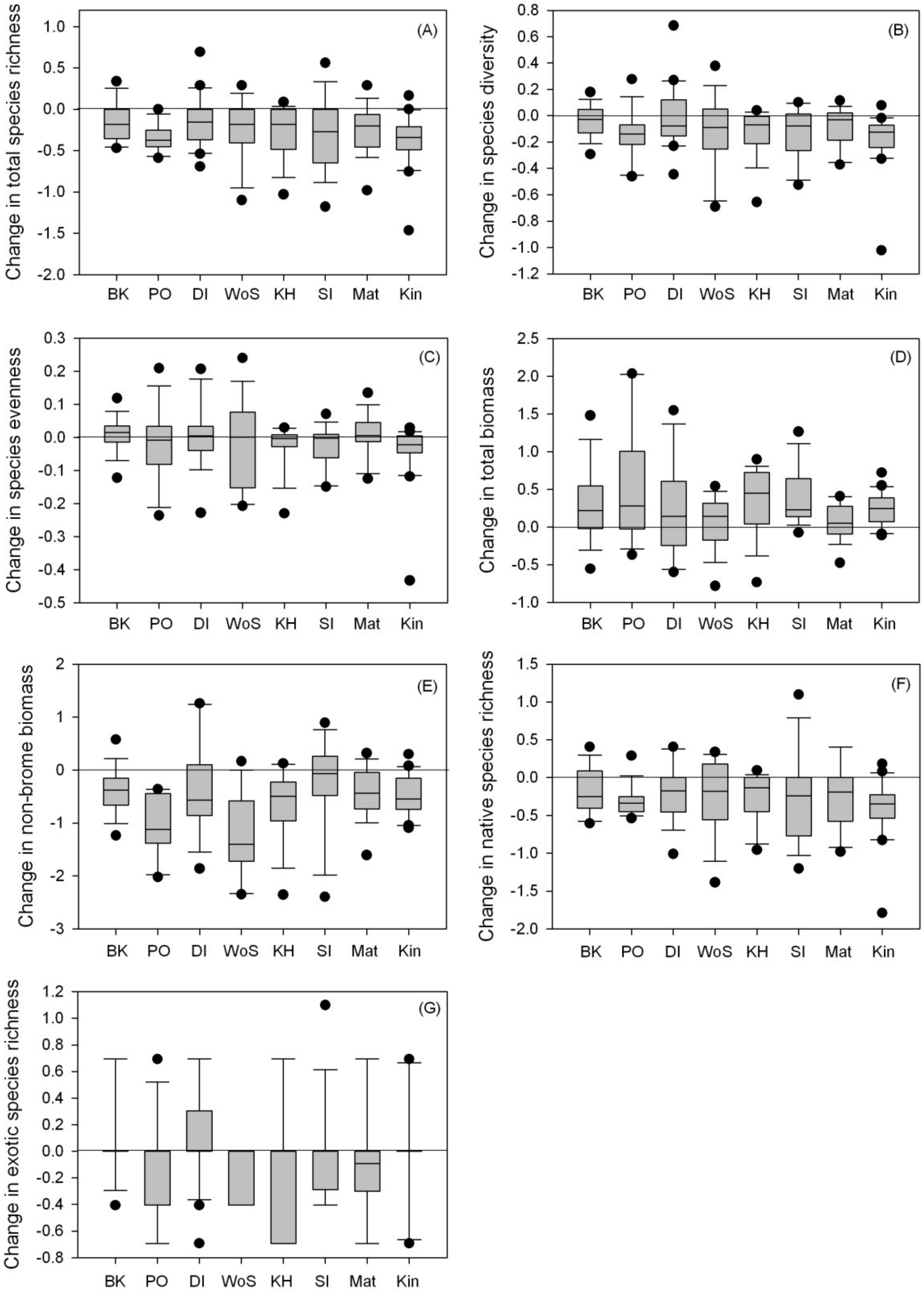


Appendix 2

Appendix 2-1: Study sites invaded by brome (*Bromus inermis*) across the grassland area of Alberta, Canada. We indicate for each site the abbreviated site name, closest weather station (distance to the site indicated in brackets), precipitation (mm) and productivity (g/m^2) (mean ± se).

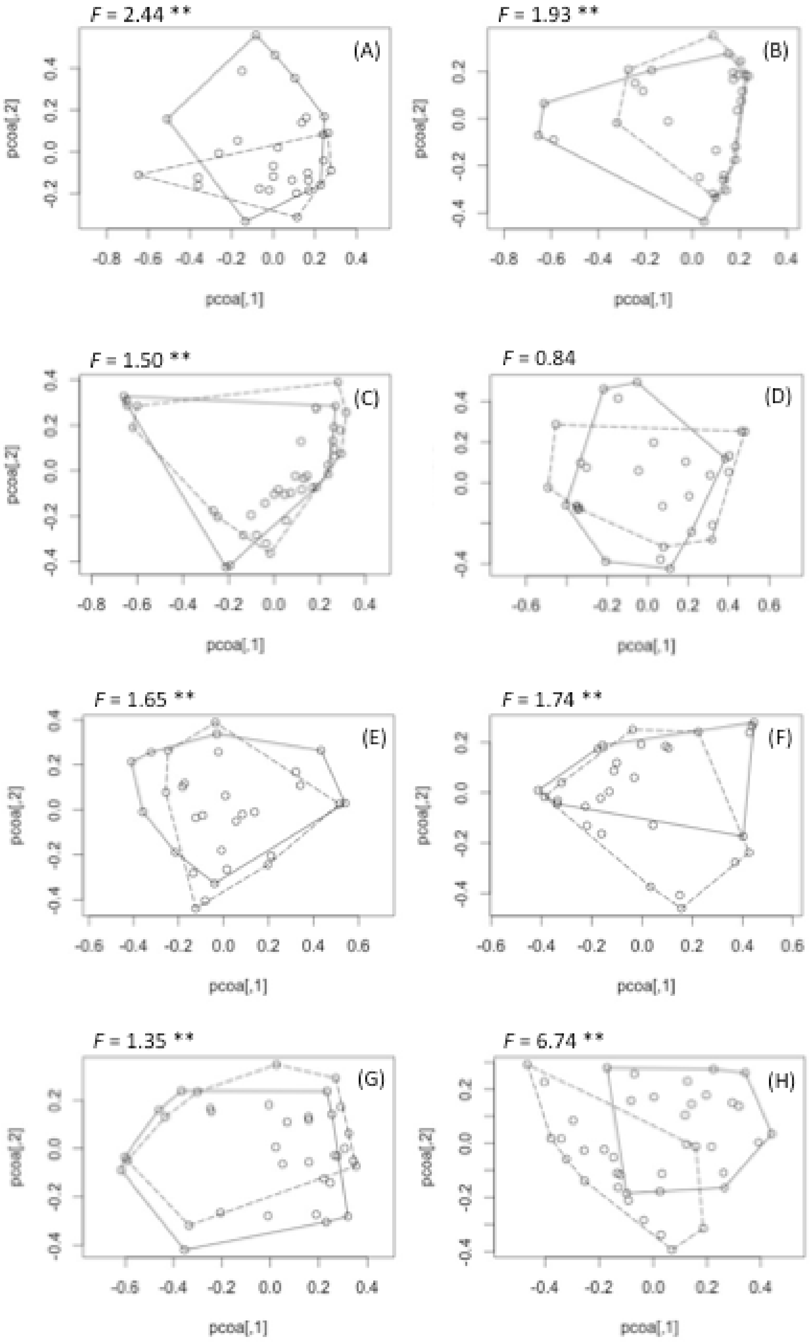
Site	Site abbrev	Weather station	Precipitation	Productivity
Big Knife	BK	Forestburg AGCM (9.5 km)	310.82	544.9 ± 60.3
Police-Outpost PP	PO	Lee Creek 99 (6 km)	423.03	561.4 ± 87.9
Dry Island Buffalo Jump PP	DI	Big Valley AGCM (13 km)	303.60	591.0 ± 60.9
Writing-on-Stone PP	WoS	Masinasin AGDM (6 km)	264.45	647.6 ± 53.9
Kleskun Hills PP	KH	Teepee Creek AGCM (12 km)	314.69	678.8 ± 91.5
Saskatoon Island PP	SI	Beaverlodge RCS (19 km)	292.21	681.2 ± 58.6
Mattheis	Mat	Rosemary IMCIN (12 km)	246.79	703 ± 46.9
Roy Berg Kinsella	Kin	Viking AGCM (16 km)	314.91	904.2 ± 37.9

Appendix 2-2: Boxplots if the change in total species richness, species diversity, evenness, total and non-brome biomass and native and exotic species richness between brome- invaded and uninvaded areas in each site. Sites are in the x-axis, and their full name and characteristics can be found in Appendix 1. Change was calculated as the log response ratio (lnRR) between invaded and uninvaded areas (ln(invaded/uninvaded)). Negative values of lnRR reflect lower values in invaded areas compared to uninvaded areas, while the opposite is true for positive values.


(A)
Change in total species richness
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
(B)
Change in species diversity
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
(C)
Change in species evenness
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
(D)
Change in total biomass
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
(E)
Change in non-brome biomass
2
1
0
-1
-2
-3
(F)
Change in native species richness
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
(G)
Change in exotic species richness
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
BK
PO
DI
WoS
KH
SI
Mat
Kin

Appendix 2-3: Difference in composition between brome- invaded (dashed line) and uninvaded (continuous line) areas in each site: (A) BK, (B) PO, (C) DI, (D) WoS, (E) KH, (F) SI, (G) Mat, (H) Kin.

Species composition in invaded and uninvaded areas was found differ across sites ($F = 4.63$ **). Differences within each site are indicated in each graph: * *p-value* < 0


F = 2.44 **
(A)
F = 1.93 **
(B)
F = 1.50 **
(C)
F = 0.84
(D)
F = 1.65 **
(E)
F = 1.74 **
(F)
F = 1.35 **
(G)
F = 6.74 **
(H)
pcoa[,1]
pcoa[,2]

Appendix 2-4: List of all species found in the 8 sites in brome (*Bromus inermis*) invaded and adjacent uninvaded areas.

Species name	**Biogeographic origin**	**Functional group**	**Life cycle**
Achnatherum richardsonii	native	grass	perennial
Achillea millefolium	native	forb	perennial
Agoseris aurantiaca	native	forb	perennial
Agoseris glauca	native	forb	perennial
Agropyron cristatum	alien	grass	perennial
Agropyron dasystachyum	native	grass	perennial
Agropyron repens	alien	grass	perennial
Agropyron trachycaulum	native	grass	perennial
Agrostis scabra	native	grass	perennial
Allium textile	native	forb	perennial
Amelanchier alnifolia	native	shrub	perennial
Anemone canadensis	native	forb	perennial
Anemone multifida	native	forb	perennial
Androsace septentrionalis	native	forb	annual/perennial
Antennaria anaphaloides	native	forb	perennial
Antennaria neglecta	native	forb	perennial
Antennaria parvifolia	native	forb	perennial
Antennaria rosea	native	forb	perennial
Arabis hirsuta	native	forb	annual/perennial
Arabis holboellii	native	forb	biennial/perennial
Arctostaphylos uva-ursi	native	shrub	perennial
Arnica chamissonis	native	forb	perennial
Artemisia campestris	native	forb	biennial/perennial
Artemisia cana	native	shrub	perennial
Artemisia frigida	native	forb	perennial
Artemisia ludoviciana	native	forb	perennial
Aster campestre	native	forb	perennial
Astragalus agrestis	native	forb	perennial
Astragalus bisulcatus	native	forb	perennial
Astragalus canadensis	native	forb	perennial
Astragalus cicer	alien	forb	perennial
Astragalus flexuosus	native	forb	perennial
Axyris amaranthoides	alien	forb	annual

Bouteloua gracilis	native	grass	perennial
Bromus japonicus	alien	grass	annual
Botrychium lunaria	native	forb	perennial
Calamagrostis canadensis	native	grass	perennial
Calamovilfa longifolia	native	grass	perennial
Campanula rotundifolia	native	forb	perennial
Carex aenea	native	sedge	perennial
Carex atherodes	native	sedge	perennial
Carex deweyana	native	sedge	perennial
Carex houghtoniana	native	sedge	perennial
Carex inops	native	sedge	perennial
Carex petasata	native	sedge	perennial
Carex praticola	native	sedge	perennial
Carex richardsonii	native	sedge	perennial
Carex scirpoidea	native	sedge	perennial
Carex siccata	native	sedge	perennial
Carex sprengelii	native	sedge	perennial
Carex stenophylla	native	sedge	perennial
Cerastium arvense	native	forb	perennial
Chenopodium album	alien	forb	annual
Cirsium arvense	alien	forb	perennial
Cirsium undulatum	native	forb	biennial/perennial
Cirsium vulgare	alien	forb	biennial
Collomia linearis	native	forb	annual
Comandra umbellata	native	forb	perennial
Danthonia californica	native	grass	perennial
Danthonia intermedia	native	grass	perennial
Deschampsia cespitosa	native	grass	perennial
Descurainia sophia	alien	forb	annual/biennial
Elaeagnus commutata	native	shrub	perennial
Elymus glaucus	native	grass	perennial
Equisetum laevigatum	native	forb	perennial
Erigeron caespitosus	native	forb	perennial
Erigeron glabellus	native	forb	biennial/perennial
Festuca hallii	native	grass	perennial
Festuca saximontana	native	grass	perennial
Festuca scabrella	native	grass	perennial
Fragaria virginiana	native	forb	perennial
Gaillardia aristata	native	forb	perennial
Galeopsis tetrahit	alien	forb	annual

Galium boreale	native	forb	perennial
Gaura coccinea	native	forb	perennial
Geranium viscosissimum	native	forb	annual/perennial
Geum triflorum	native	forb	perennial
Glycyrrhiza lepidota	native	forb	perennial
Hieracium umbellatum	native	forb	perennial
Hierochloe odorata	native	grass	perennial
Hedysarum alpinum	native	forb	perennial
Helianthus subrhomboideus	native	forb	perennial
Hesperostipa comata	native	grass	perennial
Hesperostipa curtiseta	native	grass	perennial
Heterotheca villosa	native	forb	perennial
Heuchera richardsonii	native	forb	perennial
Juncus balticus	native	-	perennial
Juniperus horizontalis	native	shrub	perennial
Koeleria macrantha	native	grass	perennial
Lactuca tatarica	native	forb	biennial/perennial
Lathyrus ochroleucus	native	forb	perennial
Liatris punctata	native	forb	perennial
Lilium philadelphicum	native	forb	perennial
Linum lewisii	native	forb	perennial
Linum perenne	alien	forb	perennial
Lithospermum incisum	native	forb	perennial
Lupinus lepidus	native	forb	perennial
Maianthemum stellatum	native	forb	perennial
Melilotus officinalis	alien	forb	annual/biennial/perennial
Monarda fistulosa	native	forb	perennial
Muhlenbergia cuspidata	native	grass	perennial
Muhlenbergia richardsonis	native	grass	perennial
Neslia paniculata	alien	forb	annual
Nassella viridula	native	grass	perennial
Oenothera nuttallii	native	forb	perennial
Orthocarpus luteus	native	forb	annual
Oxytropis monticola	native	forb	perennial
Pascopyron smithii	native	grass	perennial
Penstemon confertus	native	forb	perennial
Penstemon gracilis	native	forb	perennial
Penstemon procerus	native	forb	perennial
Phleum pratense	alien	grass	perennial
Poa cusickii	native	grass	perennial

Poa interior	native	grass	perennial
Poa palustris	native	grass	perennial
Poa pratensis	alien	grass	perennial
Poa sandbergii	native	grass	perennial
Polygonum douglasii	native	forb	annual
Populus tremuloides	native	tree	perennial
Potentilla arguta	native	forb	perennial
Potentilla concinna	native	forb	perennial
Potentilla fruticosa	native	shrub	perennial
Potentilla gracilis	native	forb	perennial
Potentilla hippiana	native	forb	perennial
Puccinellia cusickii	native	grass	perennial
Pulsatilla patens	native	forb	perennial
Ranunculus acris	alien	forb	perennial
Ranunculus cardiophyllus	native	forb	perennial
Ratibida columnifera	native	forb	perennial
Ribes oxyacanthoides	native	shrub	perennial
Rosa acicularis	native	shrub	perennial
Rosa arkansana	native	shrub	perennial
Solidago canadensis	native	forb	perennial
Solidago missouriensis	native	forb	perennial
Solidago multiradiata	native	forb	perennial
Solidago spathulata	native	forb	perennial
Sonchus arvense	alien	forb	perennial
Sphaeralcea coccinea	native	forb	biennial/perennial
Stachys palustris	alien	forb	perennial
Stellaria longifolia	native	forb	perennial
Stellaria longipes	native	forb	perennial
Stipa columbiana	native	grass	perennial
Symphyotrichum ericoides	native	forb	perennial
Symphyotrichum falcatus	native	forb	perennial
Symphyotrichum laeve	native	forb	perennial
Symphoricarpus occidentalis	native	shrub	perennial
Sisyrinchium montanum	native	forb	perennial
Taraxacum officinale	alien	forb	perennial
Thalictrum venulosum	native	forb	perennial
Thermopsis rhombifolia	native	forb	perennial
Tragopogon dubius	alien	forb	annual/biennial
Trifolium pratense	alien	forb	biennial/perennial
Trifolium repens	alien	forb	perennial

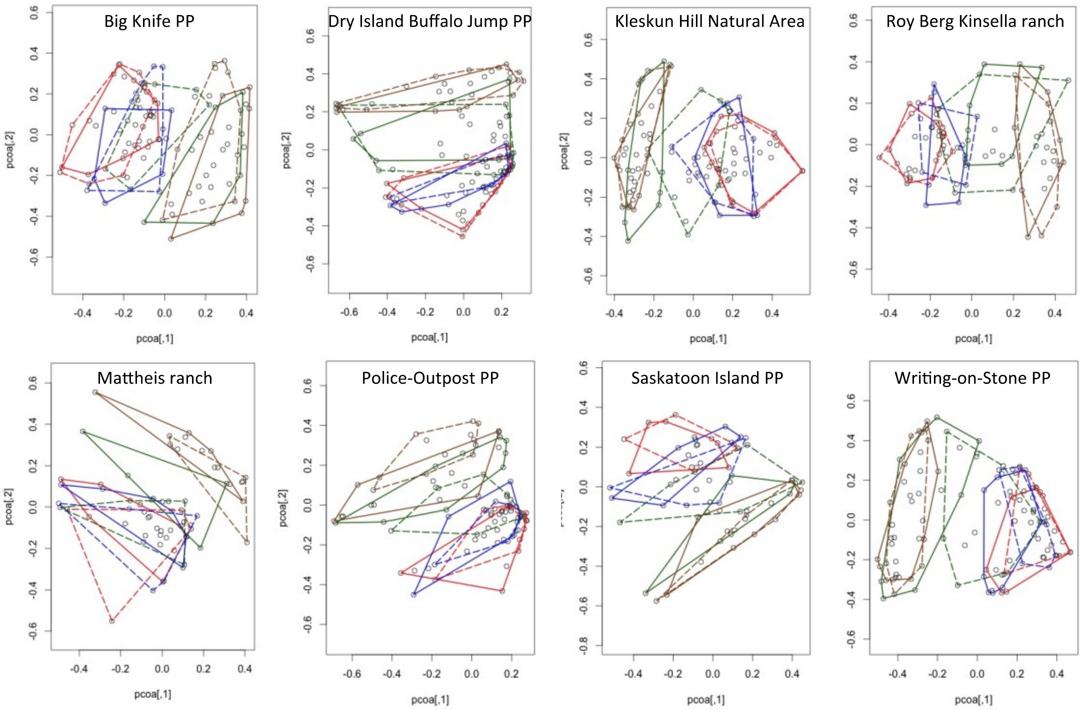
Vicia americana	native	forb	perennial
Viola adunca	native	forb	perennial
Zizia aptera	native	forb	perennial
Anemone multifida	native	forb	perennial
Geum aleppicum	native	forb	perennial
Festuca rubra	native	grass	perennial
* UnID Forb		forb	
* UnID grass		grass	

Appendix 3:

Appendix 3-1: Pairwise differences in species composition across positions. Position 1 is the area inside brome patches, position 2 is the area at the inner edge of the invasional front, position 3 is the area at the outer edge of the invasional front and position 4 is the area outside the brome patch (i.e. uninvaded areas).

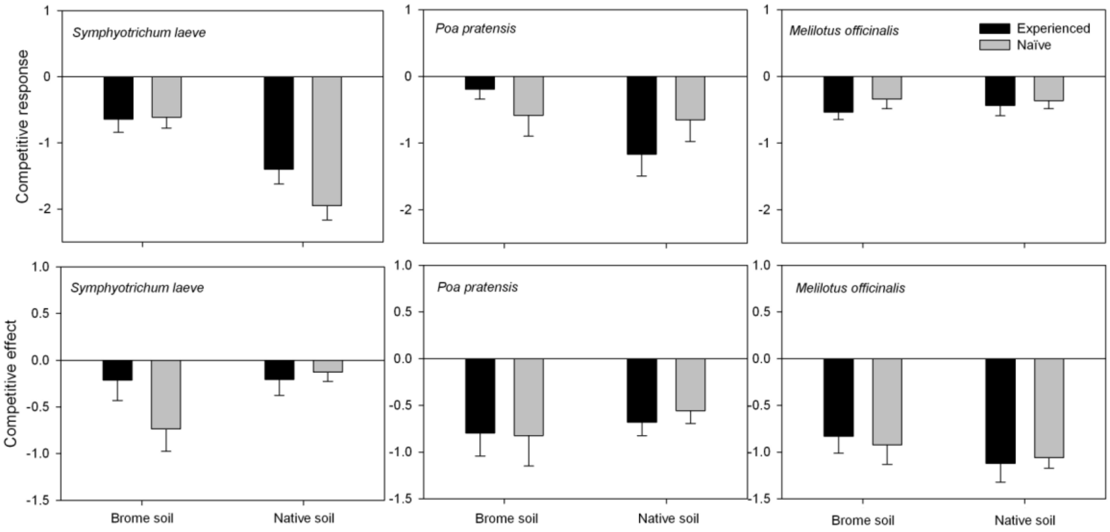
	2013		2015	
	F	*P*	*F*	*P*
Position 1 vs 2	1.922	0.003	2.579	0.002
Position 1 vs 3	30.285	0.001	11.499	0.001
Position 1 vs 4	46.886	0.001	56.013	0.001
Position 2 vs 3	21.805	0.001	5.055	0.001
Position 2 vs 4	36.07	0.001	40.414	0.001
Position 3 vs 4	3.56	0.001	20.23	0.001

Appendix 3-2: Change in species composition as a function of position along a brome-invaded to native-dominated transition area in 2013 and 2015, per site. Position 1 is the area inside brome patches (shown in red), position 2 is the area at the inner edge of the invasional front (shown in blue), position 3 is the area at the outer edge of the invasional front (shown in green) and position 4 is the area outside the brome patch (i.e. uninvaded areas) (shown in brown) (see Figure 4-1 for more details). Species composition in 2013 is shown with a continuous line, while the 2015 data is shown with a non-continuous line.



Appendix 4:

Appendix 4-1: Effect on (ability to suppress) or response to (ability to tolerate) *Bromus inermis* of offspring from experienced and naïve individuals of *Symphyotrichum laeve*, *Poa pratensis* and *Melilotus officinalis,* in two soil types: *B. inermis* invaded areas (brome soil) and adjacent uninvaded areas (native soil). Bars represent mean ± se.



Appendix 4-2: Association between the effect on and response to *Bromus inermis* by offspring from experienced and naïve individuals in two soil types (brome and native soil).