

**PATTERNS AND ECOLOGICAL CONSEQUENCES OF EXOTIC PLANT INVASION  
IN CANADA'S ENDANGERED ANTELOPE-BRUSH ECOSYSTEM**

by

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## ABSTRACT

Exotic species invasion is a serious threat to ecosystem structure and function throughout the world. In an effort to understand and limit the future effects of invasion, recent research has focused on quantifying and predicting patterns of exotic plant invasion based on abiotic and biotic features, particularly native species diversity, over multiple spatial scales. I investigated native-exotic richness relationships (NERRs) and their scale-sensitivity and predictability within the antelope-brush (*Purshia tridentata* Pursh (DC)) shrub-steppe grasslands of the South Okanagan Valley, British Columbia, one of Canada's four most endangered ecosystems and a national hot spot of biodiversity and endemism. I applied for the first time the concept of focus, which describes one aspect of observational scale, to the NERR and built upon previous studies to determine how different components of scale influence the NERR. I found that the NERR was affected by changing the grain but not the focus or extent of analysis in the antelope-brush grasslands. Contrary to the prevailing hypothesis, I found a highly significant positive NERR at the finest grain and focus (i.e., 1 m<sup>2</sup>) that appeared to be influenced at least in part by preferential facilitation of exotic plants by antelope-brush shrubs. Also contrary to expectations from the literature, I found no association between exotic and native species richness at the broadest grain and focus (i.e., 1,000 m<sup>2</sup>), and that mean environmental conditions and variation in these conditions failed to account for significant variation in broad focus exotic species richness in this system. These unexpected results challenged me to re-examine my data in light of other possible hypotheses and to develop a novel interpretive framework that provides a theoretical explanation for all possible NERR results given a particular focus of analysis and study system. Although correlative, the patterns observed in this study may simplify the scope of exotic plant management in the antelope-brush grasslands, as they suggest that broad focus environmental heterogeneity has limited influence on species richness. However, the indication that biotic factors, particularly facilitation by antelope-brush shrubs, influence exotic species richness and abundance at fine focuses poses unique challenges to conservation efforts in this endangered ecosystem.

## **PREFACE**

With guidance from my supervisor, Dr. Jason Pither, I was responsible for the design, implementation, and analysis of the observational study described in Chapter 2 of this thesis. I was assisted with data gathering in the field and in the lab by research assistants. With guidance from Dr. Pither, I was also responsible for the writing of the entire thesis following the associated research. This thesis was reviewed by the following members of my supervisory committee, all of which are faculty at the University of British Columbia (Okanagan): Dr. Sylvie Desjardins, Dr. Bob Lalonde, and Dr. John Klironomos.

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## LIST OF ABBREVIATIONS

AN	antelope-brush / needle-and-thread grass (ecological community)
BGxh1	Bunchgrass biogeoclimatic zone, Okanagan Very Dry Hot variant
GIS	geographic information system
K-S test	Kolmogorov–Smirnov test
MAP	mean annual precipitation
MAT	mean annual temperature
NERR	native-exotic richness relationship
PCA	principal components analysis
PPxh1	Ponderosa Pine biogeoclimatic zone, Okanagan Very Dry Hot variant
$r_s$	Spearman's rank correlation coefficient
SR	species richness
TEM	terrestrial ecosystem mapping
UTM	Universal Transverse Mercator



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*To those who work to conserve our environment*

## **CHAPTER 1: GENERAL INTRODUCTION**

### **INTRODUCTION**

Exotic species are a growing concern in Canada's natural habitats and elsewhere in the world. These species, known also as "non-native," "alien," or "introduced," threaten ecosystem structure and function and can have devastating effects on endangered habitats and their associated organisms (di Castri 1989, Wilcove et al. 1998, Mack et al. 2000). Exotic species can also have staggering economic consequences, with annual losses estimated in the range of \$137 billion in lost productivity and management costs in the United States alone (Pimentel et al. 2000). In an effort to understand and limit the future effects of exotic species invasion, much research has focused on identifying why some exotic species are so successful at invading natural habitats, and whether this success is related to characteristics of the invading species, the receiving habitat, or both (Chesson 2000, Catford et al. 2009). Recent research has also focused on quantifying and predicting patterns of exotic plant invasion based on abiotic and biotic features, particularly native diversity, over multiple spatial scales (Levine and D'Antonio 1999, Fridley et al. 2007). Identifying where exotic species are located is a critical step in their control and eradication (Sakai et al. 2001), especially in an endangered ecosystem.

Exotic plant invasion consists of four main phases: transport and introduction to a new environment, establishment within that new environment, spread from the point of establishment, and impact or alteration of the novel range (Levine et al. 2004, Catford et al. 2009). Most long-distance transport and introduction of exotic species is directly related to anthropogenic activities, either deliberate (e.g., agricultural crops, ornamentals) or accidental (e.g., crop seed impurities, contaminated ballast water) (Sakai et al. 2001). Human movement corridors particularly facilitate the spread of exotic plants by acting as both vectors for propagule dispersal and agents of disturbance that create habitats ideally suited for exploitation by exotic plants (Gelbard and Belnap 2003). Many more exotic species are transported to new environments than the number of exotic species that actually establish in these new environments. Likewise, of the species that establish and manage to survive the receiving habitat's biological and environmental conditions, only a few are able to spread sufficiently to become invasive or noxious in their novel range (Williamson and Fitter 1996). Understanding the processes that influence invader success and their relation to community ecology is critical to predicting the effects of exotic species in invaded ecosystems.

Patterns of exotic plant invasion have not yet been quantified or predicted in the antelope-brush (*Purshia tridentata* (Pursh) DC) grasslands of the South Okanagan Valley, British Columbia, Canada. These habitats comprise one of Canada's four most endangered ecosystems and are critical to the biodiversity of this region, which is thought to support more plant and animal species than most other regions in the country (Schluter et al. 1995, British Columbia Ministry of Environment Lands and Parks 1998). Although never historically abundant, much of British Columbia's antelope-brush grasslands have been lost in the last two centuries due to anthropogenic disturbances, including agricultural and urban development. Many of the remaining habitats are in an early seral stage and, according to preliminary observations, are highly invaded by exotic plants (British Columbia Ministry of Environment Lands and Parks 1998, Lea 2008). The ecological consequences of these exotic plants on the native species and ecosystem processes in this habitat are likely vast, as inferred from research in similarly invaded grasslands throughout western North America (Tisdale 1947, Mack 1981).

This opening chapter of the thesis first places antelope-brush grasslands within the context of other grasslands in western North America, describing in detail their disturbance and invasion history as well as the known ecological effects of exotic plants in antelope-brush grasslands in the South Okanagan Valley. Next, using examples from antelope-brush grasslands where possible, the main hypotheses used to explain why exotic plants can be so successful in their novel ranges are summarized, and these hypotheses are then used to generate predictions about the expected relationship between exotic and native plant diversity at different spatial scales. Finally, an overview of the remaining chapters of this thesis, including the main research objectives and predictions, is provided.

## **ANTELOPE-BRUSH GRASSLANDS**

Grassland regions are scattered throughout British Columbia, from the Georgia Depression on Vancouver Island in the west to the Eastern Kootenay region, and from the Northern Boreal Mountains to the Southern Interior. The Okanagan grassland region of British Columbia extends southward from Vernon to the United States border, predominately within the lower elevations the Okanagan Valley, Similkameen Valley, and Kettle Valley systems, and connects to the Southern Thompson Uplands grasslands to the northwest (Grasslands Conservation Council of British Columbia 2011). These grasslands form the northernmost extension of the Pacific Northwest Bunchgrass grassland, which extends southward to northeastern Oregon and western Idaho in the United States (Tisdale 1947). Grasslands cover approximately one quarter of the South Okanagan Valley landscape and are divided

into two types, bunchgrass and shrub-steppe, the latter of which is further separated into big sagebrush (*Artemisia tridentata* Nutt.) shrub-steppe and antelope-brush (i.e., antelope bitterbrush, greasewood) shrub-steppe (British Columbia Ministry of Environment Lands and Parks 1998).

The antelope-brush shrub-steppe grasslands predominately exist in Canada at low elevations (280 to 760 m above sea level) between Penticton to the north and the United States border, and are the most endangered of the South Okanagan Valley grassland types (Lea et al. 2004). These grasslands exist in the driest, most nutrient poor soil regimes of the Okanagan Very Dry Hot variants of the Bunchgrass (BGxh1) and adjacent Ponderosa Pine (PPxh1) biogeoclimatic zones, the hottest and driest zones in British Columbia (Lloyd et al. 1990, Iverson and Haney 2006). The climate of these zones is primarily influenced by the intense rainshadow of the Coast Mountains to the west, particularly at the valley bottoms where hot dry summers and moderately cold winters with little precipitation are the norm (Nicholson et al. 1991). Antelope-brush grasslands are characterized mainly by gentle slopes of all aspects, underlain by rapidly draining, coarse textured soils (e.g., sandy, sandy gravelly) derived from glaciofluvial parent materials (Lloyd et al. 1990, Iverson and Haney 2009). The prevailing soil and climatic conditions contribute to the drought-stressed, semi-desert nature of the antelope-brush grasslands.

Five ecological communities in the South Okanagan Valley contain antelope-brush as a dominant feature (Table 1.1, Iverson and Haney 2009), although the antelope-brush / needle-and-thread grass (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) (AN) ecological community occupies the largest spatial area. This endangered community is characterized by a moderately dense shrub layer dominated by antelope-brush with some common rabbit-bush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird); the herb layer is typically dominated by needle-and-thread grass, brittle prickly-pear cactus (*Opuntia fragilis* (Nutt.) Haw.), and sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), with a high cover of the exotic cheatgrass (*Bromus tectorum* L.) at some sites (Lea et al. 2004). Communities approaching climax have a greater cover of bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) and junegrass (*Koeleria macrantha* (Ledeb.) Schult.), and a well developed cryptogam layer composed of numerous moss and lichen species (Lea et al. 2004). This fragile cryptogam layer is particularly important for soil moisture retention, which promotes plant growth and survival in the antelope-brush grasslands (Atwood and Krannitz 1999). The AN community typically lacks a prominent tree layer, although scattered ponderosa pine (*Pinus ponderosa* C. Lawson) may be present. Communities that were

historically AN but that have now been encroached upon by pines due to disruption of natural fire regimes (described below) are identified within the ponderosa pine / antelope-brush / red-three awn (*Aristida purpurea* Nutt.) ecological community (Iverson and Haney 2009).

**Table 1.1** Ecological communities containing antelope-brush habitat in the South Okanagan Valley. Descriptions follow Iverson and Haney (2009).

Ecosystem Unit	Code	Description
Antelope-brush / Needle-and- thread grass	AN	Level and gently sloped coarse-textured glaciofluvial sites in the BGxh1 and lower elevations of the PPxh1; dominated by antelope-brush and bunchgrass; lacking prominent tree overstory
Ponderosa pine / Antelope-brush / Red three-awn	PA	Level and gently sloped coarse-textured glaciofluvial sites in the BGxh1 and lower elevations of the PPxh1; open ponderosa pine overstory with antelope-brush and mixed bunchgrass dominated understory
Antelope-brush / Selaginella	SA	Gently sloped rocky sites with medium-textured, shallow soils in the BGxh1 and PPxh1; dominated by scattered shrubs (including antelope-brush), bunchgrasses, and lichens growing in rock features
Selaginella / Bluebunch wheatgrass rock outcrop	SB	Gently sloped sites with very shallow soils and exposed bedrock in the BGxh1 and PPxh1; dominated by selaginella, bluebunch wheatgrass and other bunchgrasses, mosses, lichens, and scattered shrubs (including antelope-brush); lacking prominent tree overstory
Bluebunch wheatgrass / Selaginella	WS	Gently sloped medium-textured sites with shallow morainal, colluvial, or glaciofluvial soils in the BGxh1; dominated by mixed big sagebrush and antelope-brush with bunchgrasses and selaginella

The antelope-brush grasslands of the South Okanagan Valley are considered a national hotspot of biodiversity and endemism. Located between the Canadian boreal forests to the north and the Great Basin deserts to the south, this ecosystem hosts many species that are at their northern or southern range limits, potentially representing genetically diverse and important populations for species survival during environmental change (British Columbia Ministry of Environment Lands and Parks 1998). As of 2003, 58 provincially extirpated, endangered, or threatened (i.e., red-listed) species and 30 species of special concern (i.e., blue-listed) occurred in this ecosystem, including 18 federally listed species (Dyer and Lea 2003, British Columbia Conservation Data Centre 2010). Notable examples include western

rattlesnake (*Crotalus oregonus* Holbrook), gopher snake (*Pituophis catenifer* Blainville), lark sparrow (*Chondestes grammacus* Say), pallid bat (*Antrozous pallidus* LeConte), Nuttall's cottontail (*Sylvilagus nuttallii* Bachman), bighorn sheep (*Ovis canadensis* Shaw), Columbia carpet moss (*Bryoerythrophyllum columbianum* (Herm. & Lawt.) Zand.), and Grand Coulee owl-clover (*Orthocarpus barbatus* Cotton) (Lea 2008, British Columbia Conservation Data Centre 2010). The antelope-brush grasslands are also a hotspot of invertebrate biodiversity: 104 rare invertebrate species (most not formally listed) are restricted to this ecosystem in the South Okanagan Valley (Dyer and Lea 2003), including Behr's hairstreak (*Satyrium behrii columbia* McDunnough), which obligately uses antelope-brush shrubs as its larval host plant and is a focal species for the conservation of British Columbia's antelope-brush grasslands (Southern Interior Invertebrates Recovery Team 2008).

Previous research into exotic plant patterns and ecological effects within the antelope-brush grasslands of the South Okanagan Valley has been limited in scope. Much of the available information is present in the "grey literature," consisting primarily of small scale government funded projects or technical reports (e.g., Schluter et al. 1995, British Columbia Ministry of Environment Lands and Parks 1998, Dyer and Lea 2003, Lea et al. 2004). Pam Krannitz of the Canadian Wildlife Service completed most of the limited published research, which was primarily focused on the effects of livestock grazing on antelope-brush shrubs (e.g., Krannitz 1997, Krannitz and Hicks 2000, Krannitz 2008), although one study (Clements et al. 2007) investigated the response of the seed banks of several exotic species to grazing history and environmental conditions in this system. The research presented in this thesis appears to represent the first rigorous assessment of exotic plant invasion at the landscape level within the antelope-brush communities of the South Okanagan Valley, and elsewhere in the antelope-brush range.

## **DISTURBANCE AND INVASION HISTORY**

Most exotic species introductions are related either directly or indirectly to anthropogenic activities that result in habitat fragmentation and disturbance (Sakai et al. 2001). Prior to European settlement in the Okanagan Valley, natural disturbance in the form of minimal native ungulate grazing and frequent, low intensity fires played a critical role in grassland maintenance (Gayton 2003). Pre-settlement First Nations peoples were also known to set fires within these habitats to improve wildlife grazing and plant food availability (Grasslands Conservation Council of British Columbia 2011). With the advent of European settlers, however, came an unprecedented amount of anthropogenic disturbance. The earliest settlers in the Okanagan Valley were recorded in the early 1800s, and cattle first arrived in

the 1830s (Tisdale 1947, Gayton 2003). In conjunction with the Cariboo Gold Rush of the late 1850s, large cattle herds were driven northward annually through the Okanagan Valley from the United States to supply beef, and large scale ranching operations became established (Gayton 2003, Grasslands Conservation Council of British Columbia 2011). This unregulated, year-round livestock use led to heavily overgrazed areas, particularly in low elevation grasslands (Tisdale 1947, Gayton 2003). Permanent settlement increased in the Okanagan Valley throughout the latter half of that century and into the next as agricultural activities were expanded to include commercial fruit crops, namely apple orchards and vineyards (Tisdale 1947, Lea 2008).

With the arrival of Europeans to the Okanagan Valley came other non-indigenous species: exotic plants. Second only to irreversible habitat loss, exotic plant invasion is thought to be one of the greatest threats to Okanagan Valley grasslands (Cannings et al. 1998). The highly invasive cheatgrass arrived in British Columbia around 1889, likely as a contaminant of agriculturally grown wheat (Mack 1981). Widespread agricultural practices and the completion of the northwest railway system facilitated the extensive spread of this (and likely other) invasive species such that cheatgrass was a dominant weed in the Columbia Basin by 1915 and present throughout its current range by 1930 (Mack 1981). Cheatgrass and Canada thistle (*Cirsium arvense* (L.) Scop.) were the first recorded exotic plants in the Okanagan Valley in 1912 and 1913, respectively (Cannings et al. 1998). Based on provincial herbarium specimens, these species were soon joined by the exotic plants common hound's-tongue (*Cynoglossum officinale* L.) in 1922, diffuse knapweed (*Centaurea diffusa* Lam.) in 1939, sulphur cinquefoil in 1940 (*Potentilla recta* L.), and Dalmatian toadflax (*Linaria genistifolia* (L.) Mill.) in 1952 (Cannings et al. 1998). All of the above-listed species are designated as provincially or regionally noxious in the Regional District of Okanagan-Similkameen under the *British Columbia Weed Control Act* (Cranston et al. 2005) and continue to be problematic in the South Okanagan Valley.

As a result of anthropogenic disturbance and subsequent exotic plant invasion, antelope-brush grasslands are now one of Canada's four most endangered ecosystems (Schluter et al. 1995). Never historically abundant, over 61% of the spatial extent of this ecosystem in British Columbia has been permanently lost in the last two centuries and habitat destruction continues at an unprecedented rate of 2% per year (Dyer and Lea 2003). Less than 3,386 hectares of antelope-brush grassland habitat remain (as of 2001), the vast majority of which are located on the Osoyoos Indian Reserve (59%); remaining habitat occurs on private land (28%) and crown land (13%) (Dyer and Lea 2003). Overall, less than 18% of this habitat is



situated in designated conservation areas (Dyer and Lea 2003). Livestock grazing and crop production continue to be major economical activities in the South Okanagan Valley that, along with residential development and recreational use, contribute to grassland loss, degradation, and plant invasion (Lea et al. 2004). Sulphur cinquefoil and Dalmatian toadflax are of particular concern in Okanagan Valley grasslands due to their aggressive nature and rapid expansion over the last two decades (Cannings et al. 1998).

## **ECOLOGICAL EFFECTS OF INVASION**

The ecological consequences of exotic plant invasion are diverse, ranging from whole ecosystem effects to both negative and positive interactions with individual species. Invading plants can cause large alterations to natural ecosystem processes such as changes to natural disturbance regimes and soil nitrogen cycling (D'Antonio and Hobbie 2005). One of the best documented cases is the alteration of natural fire regimes in western North America grasslands by exotic grasses, particularly *Bromus* L. species. These exotic grasses increase both the frequency and intensity of fires by altering available fuel properties, which can result in a positive feedback loop if fire regime alteration leads to a subsequent increase in exotic species establishment, further exacerbating restoration efforts (Brooks et al. 2004). It is estimated that 40 million hectares of western North America are affected by cheatgrass invasion and associated fire regime alteration (Whisenant 1990). These ecosystem scale effects also impact the survival of individual species; for example, 14% of imperilled species in the United States are thought to be threatened by habitat loss or degradation associated with the alteration of natural fire regimes (Wilcove et al. 1998).

Fire is required to maintain grasslands by preventing encroachment of woody trees and shrubs. The Okanagan Valley grasslands historically experienced frequent, low-intensity fires that controlled woody plant densities (Gayton 2003). However fire suppression activities since the 1940s and livestock grazing, which creates opportunities for exotic grass invasion, have led to changes in the historical fire regime in this region (Gayton 2003). While fire suppression results in less frequent fires, when fires do occur they are often more intense due to higher fuel loads from encroaching fire-intolerant shrubs such as antelope-brush (Gayton 2003). Fire intensity is also augmented by large densities of the highly flammable exotic cheatgrass, a species that rapidly spreads fire between senescing shrubs. This species also recovers quickly following fire and can out-compete and prevent the establishment of native grasses and antelope-brush seedlings (Holmgren 1956, D'Antonio and Vitousek 1992). The disturbed, open areas created by fire can then be invaded by other exotic species, further aggravating the effects of exotic plants on ecosystem processes.

Exotic plant species can also have important ecological effects on individual species, particularly those that are imperilled. Within the United States, and likely true in much of Canada, exotic invasion is thought to be the second greatest known threat to species at risk, affecting 49% of the imperilled species across all taxa and preceded only by habitat loss and degradation (Wilcove et al. 1998). These authors noted, however, that the invasion threat is likely increasing due to the continued arrival of new exotic species through time. Exotic species can adversely affect at-risk species either directly through biotic interactions or through indirect effects such as modifications to natural habitats or ecosystems processes. For example, exotic plants, particularly cheatgrass, are considered a primary threat to the federally endangered antelope-brush grassland species Grand Coulee owl clover, potentially due to competitive interactions with this native plant (Southern Interior Rare Plants Recovery Team 2007). Exotic plants may also threaten Columbia carpet moss, another at-risk species inhabiting antelope-brush grasslands, particularly in disturbed habitats such as those grazed by livestock (British Columbia Bryophyte Recovery Team 2010). The exotic plant sulphur cinquefoil may indirectly affect the federally threatened Behr's hairstreak by forming monocultures that outcompete both this butterfly's native nectar resources and its larval host plant seedlings (Southern Interior Invertebrates Recovery Team 2008).

In contrast, some exotic plants can actually benefit species at risk through facilitative interactions. For example, cheatgrass invasion is thought to have led to larger, more stable populations of the provincially red-listed Great Basin pocket mouse in Washington shrub-steppe grasslands through increased reproductive success, as cheatgrass is a primary food source for this rodent (O'Farrell et al. 1975). Exotic plant species are also known to facilitate butterfly populations; some exotic plant interactions in California have led to butterfly population increases, range expansions, longer flight seasons, increased survivorship in urban or otherwise altered landscapes, and protection from native host extinction (Graves and Shapiro 2003). Within the antelope-brush grasslands, for example, Behr's hairstreak is known to successfully nectar on the exotic plants alfalfa (*Medicago sativa* L.), clover (*Melilotus* Mill. spp.), Canada thistle, and baby's breath (*Gypsophila paniculata* L.) (St. John and Bunge 2003). While positive interactions with exotic plants are possible, adverse effects to at-risk species are much more frequently reported in the literature (Wilcove et al. 1998).

### **INVASION ECOLOGY THEORY**

Much research has focused on identifying why some exotic species are so successful in invaded natural habitats while other species are not (Chesson 2000, Catford et al. 2009). The invasibility of a particular species is related to characteristics both of the arriving exotic

species and of the receiving environment (Hufbauer and Torchin 2007). Numerous ecological hypotheses have been proposed to explain how exotic species invade novel habitats and thorough accounts are provided in Mitchell et al. (2006), MacDougall et al. (2009), and Catford et al. (2009). The authors of the latter report noted that there is much overlap and redundancy between existing hypotheses. Scale is a critical factor in determining which invasion hypotheses are relevant to a given system, as biotic interactions (e.g., competition, facilitation, herbivory) typically drive processes at fine scales, while abiotic factors take precedence at large scales (Pauchard and Shea 2006, Stohlgren et al. 2006, Fridley et al. 2007). Table 1.2 lists the main invasion ecology hypotheses in the literature, including whether the hypothesis predicts a positive or negative effect on invasion success and the scale at which the hypothesis is relevant. These hypotheses are described in more detail below.

**Table 1.2** Main invasion ecology hypotheses used to explain invader success and native-exotic richness relationships (NERRs) at different scales. Each hypothesis predicts either a positive or negative effect on invader success, and whether the NERR is positive or negative. See text for further explanation. Partially adapted from Mitchell et al. (2006), Fridley et al. (2007), and Catford et al. (2009).

Hypothesis	Invader Success	NERR	Scale
Pre-adaptation	+	-	fine
Novel weapons	+	-	fine
Enemy release or reduction	+	-	fine
Empty niche / Invasion windows	+	+	fine
Biotic resistance	-	-	fine
Mutualist facilitation / Facilitation	+	+	fine
Invasion meltdown	+	-	fine
Fluctuating resource availability	+	- / +	fine / broad
Biotic acceptance	+	+	broad
Spatial heterogeneity	+	+	fine / broad

The *pre-adaptation hypothesis* proposes that some exotic species are inherently more competitive than their native counterparts in novel ranges (Sax and Brown 2000). The explanation for this superiority is often related to anthropogenic disturbance: exotic species originating from areas with historically high disturbance (e.g., Eurasia) may be better adapted to and therefore better able to exploit disturbances compared to native species from novel ranges with historically less human-related disturbance (e.g., North America) (di Castri 1989, Sax and Brown 2000). A related proposition, the *novel weapons hypothesis*, suggests

that some exotic species have special adaptations such as biochemical root exudates that, while relatively ineffective in their natural range, are inhibitory to native plants or associated soil microbes in the invader's novel range (Callaway and Ridenour 2004). These range-dependent effects are thought to be due to differences in the regional coevolution trajectories of both ranges, where the plants of the exotic species' natural range are adapted to the allelopathic weapon but the plants of the novel range are not (Callaway and Ridenour 2004). Much of the initial evidence to support this hypothesis was derived from work with diffuse knapweed (Callaway and Aschehoug 2000), a noxious weed in the Okanagan Valley and throughout western North American grasslands. However other exotics species also support this hypothesis, including garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande), a highly invasive plant also present in the Okanagan Valley that is known to disrupt native plant mutualisms with mycorrhizal fungi in its novel range (Stinson et al. 2006, Callaway et al. 2008, Wolfe et al. 2008).

The *enemy release hypothesis* also focuses on differences between an invader's natural and novel ranges. Under this hypothesis, invaders are successful in their novel range because they are free from regulation by the natural "enemies" (e.g., specialized herbivores, parasites, pathogens) of their natural range, and are therefore better able to allocate their resources to growth and spread in their novel range (Keane and Crawley 2002, Colautti et al. 2004). This hypothesis predicts that although the invaders may still be attacked by generalist enemies in the novel range, these enemies will have greater adverse effects on the native residents in addition to the residents' specialist enemies (Keane and Crawley 2002). Similarly, the *enemy reduction hypothesis* posits that a reduction in enemy regulation, rather than a complete release, is enough to give an exotic species a competitive advantage in the novel range (Colautti et al. 2004). This hypothesis is the basis of exotic species management using biological control where the natural enemies of a particularly invasive weed are deliberately introduced to the novel range to regulate the spread of that species (Mack et al. 2000).

The *pre-adaptation*, *novel weapons*, and *enemy release/reduction* hypotheses all suggest that exotic species are somehow competitively dominant to the resident species in the novel habitat. In contrast, the *empty niche hypothesis* proposes that exotic species are able to invade novel habitats because there is unused or empty niche space present that is not filled by the existing resident species (Elton 1958, MacArthur 1970, Hierro et al. 2005). This hypothesis is related to the *invasion windows hypothesis*, which suggests that niche availability fluctuates spatially and temporally providing invaders with discrete opportunities

to colonize (Catford et al. 2009), and is essentially the inverse of the *biotic resistance hypothesis*. This later hypothesis contends that highly diverse communities are less susceptible to exotic species invasion because they more fully utilize the resources available (i.e. they fill the available niche space) and are therefore better able to competitively exclude potential invaders compared to species-poor communities (Elton 1958, Levine et al. 2004). These latter hypotheses highlight the importance of considering the characteristics of the invaded community as well as of the invader when predicting exotic success.

The *fluctuating resource availability hypothesis* proposes that opportunities for exotic species invasion emerge when unused resources (i.e., water, nutrients, light, space) become temporally available through either a pulse in resource availability or a reduction of competitive availability by existing native species (Davis et al. 2000). This hypothesis is strongly linked to disturbance, both natural and anthropogenic, which can decrease inter-specific competition by simultaneously creating empty niches and damaging existing native species to increase resource availability (Davis et al. 2000, Seabloom et al. 2003). Resource pulses can occur due to broad scale (e.g., volcanic eruption, fire, livestock grazing) or fine scale (e.g., animal burrows, ungulate grazing) disturbances, or may be unrelated to disturbance. For example, particularly wet growing seasons can increase water availability and therefore community invasibility (Hobbs and Mooney 1991). This hypothesis integrates several of the preceding invasion ecology hypotheses, including the *empty niche* and *invasion windows* hypotheses, and has also been combined with the *enemy release hypothesis* (together, the *resource-enemy release hypothesis*) to describe accelerated or increased invasion (Blumenthal 2006).

The preceding hypotheses primarily involve negative biotic interactions between exotic and native species. With the exception of the *biotic resistance hypothesis*, all of the described hypotheses explain how invaders benefit in their new environments at the expense of resident species (Table 1.2). However, positive biotic interactions between exotic and native plants and their associates are also possible (Mitchell et al. 2006). The *mutualist facilitation hypothesis* posits that plant invasion success is dependent on the formation of new mutualist relationships between exotic species and generalist pollinators, seed dispersers, and fungal associations in the novel range (Richardson et al. 2000). This hypothesis is related to the *invasion meltdown hypothesis* of invasion plant success, which suggests that positive interactions between only exotic species in their novel range lead to greater invasibility of that range and therefore greater potential for accelerated or compounding ecological effects (Simberloff and Von Holle 1999). However, exotic species can also be facilitated by native

species in the novel range. Facilitative interactions are especially common in stressful environments such as deserts where shrubs or adult plants can facilitate the establishment and growth of exotic seedlings through increased seed and nutrient trapping, reduced water stress through shading, and ameliorated protection from herbivory (Holzapfel and Mahall 1999, Flores and Jurado 2003). For example, and of particular relevance to the present study, both antelope-brush and big sagebrush have been shown to facilitate cheatgrass establishment and fecundity by creating more favourable microhabitats beneath the shrub canopy when compared to intershrub spaces (Griffith 2010).

At broad scales, the *biotic acceptance* (i.e., *favourable conditions*) *hypothesis* proposes that areas that support high native biodiversity also preferentially support high exotic biodiversity due to favourable mean environmental conditions (e.g., high resource availability) that similarly benefit both native and exotic species (Levine and D'Antonio 1999, Stohlgren et al. 2003, Stohlgren et al. 2006). While this hypothesis appears to oppose the *biotic resistance hypothesis*, these two hypotheses are actually not mutually exclusive as they function at different scales and are based on abiotic and biotic interactions, respectively. The *biotic acceptance hypothesis* does not appear to be well supported, as little theoretical or experimental evidence supports a positive relationship between mean resource availability and species richness at broad scales (Davies et al. 2005). The competing *spatial heterogeneity hypothesis* suggests that invasion success may occur due to high variation in (rather than mean) environmental conditions, leading to spatial heterogeneity in both exotic and native species composition (Davies et al. 2005, Melbourne et al. 2007). This hypothesis is a spatial analogue to the *fluctuating resource availability hypothesis* at broad scales (Fridley et al. 2007).

Potentially to the detriment of the subject, most generalizations in invasion ecology theory have been developed exclusive of community ecology theory despite widespread similarities in processes (Davis et al. 2001, Catford et al. 2009). Several recent publications have attempted to unite part or all components of several of these hypotheses, listed in parentheses below, under simplified frameworks based on characteristics of both the exotic species and the invaded environment. For example, Shea and Chesson (2002) developed a community ecology-based framework that relates exotic species establishment success and local spread to three characteristics of the novel habitat: resource availability (e.g., *biotic resistance*, *empty niche*, *fluctuating resource availability*), natural enemies (e.g., *enemy release/reduction*), and physical environment (e.g., *pre-adaptation*). The response of an

exotic species to these characteristics defines whether there is a niche opportunity for that invading species, that is, whether the community can be invaded (Shea and Chesson 2002).

Independently, niche theory supports how exotic species are able to invade communities with functionally different residents, but it does not explain how exotic species are able to invade communities with functionally similar residents (MacDougall et al. 2009). Further, why some exotic species are able to become dominant and exert large influences over their novel community is not explained, as according to niche theory, functionally similar species should not be able to invade and functionally different species should have minimal interaction (MacDougall et al. 2009). To resolve these issues, MacDougall et al. (2009) applied both niche theory and the more recent coexistence theory (*sensu* Chesson 2000) to invasion ecology using a framework based on both niche (e.g., *empty niche*, *biotic resistance*) and fitness (e.g., *novel weapons*, *enemy release/reduction*) differences between exotic and native species. According to this framework, niche differences facilitate coexistence by allowing a rare invader with a dissimilar niche from competing resident species to establish in a novel community despite a lower average fitness. In contrast, fitness differences promote competitive exclusion by allowing an invader with higher fitness to competitively dominate residents in the novel habitat, or vice versa, independent of species rarity. When applied to invaded communities at fine scales, this framework explains theoretically how both exotic and native species are able to coexist at low densities regardless of fitness levels where they have different niches, and how exotic species are able to adversely dominate communities where they have overlapping niches but higher fitness than native species.

Catford et al. (2009) also used a single framework to synthesize their review of 29 invasion ecology hypotheses. These authors related invasion success to four broad factors that vary in strength of influence with time and space: propagule pressure, abiotic characteristics of the novel habitat (e.g., *spatial heterogeneity*, *fluctuating resource availability*), biotic characteristics of both the invader (e.g., *novel weapons*, *empty niche*) and novel habitat (e.g., *biotic resistance*, *invasion meltdown*), and human influence (e.g., *fluctuating resource availability*) on each of these factors. Central to this framework is the inclusion of propagule pressure, part of the transport and introduction phase of invasion, as most hypotheses consider this to be a prerequisite rather than a driver of invasion (Catford et al. 2009). Propagule pressure is an important component of this framework because it affects the continued success of the invader by increasing genetic diversity and facilitating exotic

population survival during unfavourable conditions (Sax and Brown 2000, Catford et al. 2009).

### **NATIVE-EXOTIC RICHNESS RELATIONSHIPS**

Describing and predicting patterns of exotic species diversity in invaded ecosystems are both primary focuses of the invasion ecology literature (Levine and D'Antonio 1999, Fridley et al. 2007). In particular, the role of native species diversity as a predictor of invasion success has been widely investigated (e.g., Palmer and Maurer 1997, Stohlgren et al. 1999a, Naeem et al. 2000, Stohlgren et al. 2003). To date, the results of this research are seemingly contradictory, as both positive and negative native-exotic richness relationships (NERRs) have been observed in various systems (Levine and D'Antonio 1999, Fridley et al. 2007). Scale has recently been recognized as a critical factor in predicting the direction and magnitude of the NERR and the processes that govern this relationship (Shea and Chesson 2002, Stohlgren et al. 2006). In general, biotic interactions between exotic and native species are thought to exclusively explain NERRs at fine scales (typically  $<1 \text{ m}^2$ ), while NERRs at broad scales (typically  $>1 \text{ km}^2$ ) are influenced by abiotic factors that covary with species diversity, rather than due to diversity directly (Fridley et al. 2007).

The invasion success hypotheses described in the previous section can each be applied to predict the direction of the relationship between exotic and native species richness, as summarized in Table 1.2. The *biotic resistance hypothesis* is the most often cited hypothesis to predict a negative NERR at fine scales, where high native diversity confers community resistance to invasion and low native diversity allows opportunities for invaders (Elton 1958, Fridley et al. 2007). Competition from native species is generally assumed to be the dominant mechanism underlying biotic resistance, however other biotic interactions including herbivory and disease may be equally effective in controlling the invasibility and increasing the resistance of a community (Levine et al. 2004). As such, the hypotheses that predict either a competitive advantage for exotic species (i.e., *pre-adaptation*, *novel weapons*) or a reduction in herbivory or disease (i.e., *enemy release/reduction*) relative to native species will indirectly also lead to a negative NERR at fine scales by predicting opportunities for invaders at the cost of native species. A negative NERR is also the logical null expectation at fine scales due to physical constraints on the total number of individuals and thus species that can be present in a small area based on their size (Fridley et al. 2004, Daleo et al. 2009).



A positive fine scale NERR may be predicted in systems that promote coexistence, that is, where strong competitive interactions between exotic and native species are absent and one species group is not favoured over the other. For example, the *mutualist facilitation hypothesis* indirectly predicts a positive NERR in systems where there are mutualisms with both exotic and native species such that the diversity of both species groups is promoted. A positive NERR may also result where high native diversity increases the establishment success of exotic species, or where the presence of a single, strong community-structuring species facilitates that establishment of both exotic and native species (Bruno et al. 2003, Fridley et al. 2007). In contrast, the *invasion meltdown hypothesis* predicts a negative NERR at fine scales because in this case, facilitative interactions only occur between exotic species such that the presence of one exotic species promotes the establishment of only other exotic species, at the expense of native species (Fridley et al. 2007).

The *fluctuating resource availability hypothesis* integrates several of the described hypotheses, and thus supports both positive and negative NERRs and operates at both fine and broad scales depending on the system and type of resource pulse. If resources become temporally available through a fine scale pulse in resources (e.g., mortality of mature canopy plant leading to increased light availability), opportunities for both exotic and native species may exist, leading to an increase in both species groups and a positive NERR in the absence of competitive interactions. Similarly, the *empty niche hypothesis* and *invasion windows hypothesis* also predict a positive fine scale NERR if exotic species are able to take advantage of increased resources without competing with native species. If resources become available in a system due to a decrease in native species competitive ability, however, for example as a result of fine scale disturbance, the *fluctuating resource availability hypothesis* predicts a negative NERR, as exotic species will be favoured over native species by the disturbance. At the landscape scale, the NERR is primarily driven by abiotic rather than biotic interactions, so this same hypothesis predicts a positive NERR following a broad scale resource pulse (e.g., atypically high rainfall in an arid system) that favours both exotic and native species.

Both the *biotic acceptance hypothesis* and *spatial heterogeneity hypothesis* predict positive NERRs at broad scales as a result of abiotic factors (i.e., high mean or high heterogeneity in resource availability) that can sustain higher diversities of both exotic and native species (Davies et al. 2005, Fridley et al. 2007). The latter hypothesis may also work at fine scales: for example, systems with varying soil conditions or containing species with strong community structuring effects may exhibit sufficient environmental variation at fine scales as

to invoke the *spatial heterogeneity hypothesis* (Davies et al. 2005). An implicit assumption of broad scale positive NERR predictions is that exotic and native species diversity are primarily influenced by variation in abiotic factors (Fridley et al. 2007). As such, it follows that positive NERRs would not be expected in systems that are homogeneous at broad scales. Davies et al. (2005) suggest that the scaling terms “fine” and “broad” should be related to the scale of heterogeneity within a system rather than to the spatial area of analysis.

## **RESEARCH OVERVIEW AND OBJECTIVES**

The interactions between exotic species and their novel habitat are complex, as evidenced by both the array of hypotheses to explain successful invasion and the range of ecological effects. To better understand ecosystem invasibility, there is a need for more multivariate studies that simultaneously examine the influence of both biotic and abiotic factors on exotic species diversity (Fridley et al. 2007, Eschtruth and Battles 2009). Antelope-brush habitats have been extensively studied throughout their North American range, yet few studies have focused on community characteristics at the landscape level, particularly in relation to exotic species invasions (although see Clements et al. 2007, Griffith 2010). The endangered antelope-brush grasslands of the South Okanagan Valley offer a unique opportunity to study exotic plant patterns, underlying processes, and potential ecological consequences in an arid, highly stressed environment that has high conservation value. The purpose of the research described in this thesis was to investigate patterns and ecological consequences of exotic plant invasion in this ecosystem with the following specific objectives:

- (1) Inventory the plant species in antelope-brush grasslands using a stratified random sampling approach to characterize exotic plant invasion within this ecosystem;
- (2) Determine the relationship between exotic and native plant diversity in this ecosystem and compare the observed relationship to analogous studies in other systems;
- (3) Develop models to determine the relative importance of biotic and abiotic variables in describing and predicting patterns of exotic plant diversity;
- (4) Investigate the role of scale in applying hypotheses and making predictions about exotic plant invasion in this ecosystem; and,

- (5) Integrate the existing invasion ecology and NERR hypotheses into a concise framework that explains exotic plant invasion and the relationship between exotic and native species richness at both fine and broad scales.

Based on preliminary fieldwork (data not shown), it appears that antelope-brush communities in the South Okanagan Valley are not saturated with plant individuals as evidenced by the high percent cover of exposed soil; this may be due to historical intensive grazing and a slow to recover cryptogam layer (Krannitz 2008). This undersaturation may render competitive interactions between exotic and native species sufficiently weak in this system, particularly at lower and presumably drier elevations, such that native diversity has little or no effect on invader establishment success. Nurse-protégé facilitative interactions may also be occurring in the South Okanagan Valley due to its arid nature (e.g., Griffith 2010). As such, a prediction for this system was that there would be a positive NERR at fine spatial scales due to facilitative interactions in the antelope-brush grasslands, although this relationship might decrease in significance with increasing elevation as both competition and facilitative interactions may change in importance along environmental stress gradients (Pugnaire and Luque 2001, Callaway et al. 2002).

At broad scales, the prediction for this system was also a positive NERR, but that this relationship would be due to either mean or spatial heterogeneity in abiotic features, showing that scale does influence the processes that underlie patterns of exotic plant invasion. Based on the invasion ecology hypotheses, resource availability and anthropogenic disturbance were likely predictors of exotic plant invasion in the antelope-brush grasslands (Davis et al. 2000, Fridley et al. 2007, Catford et al. 2009). As such, predictions for this system were that areas with higher mean resource availability would favour both exotic and native species and would be more highly invaded than areas with lower resource availability, and that areas with higher disturbance would also be more highly invaded than areas with lower disturbance, but with disturbance influencing exotic and native species in opposing ways (e.g., Lilley and Vellend 2009). A separate prediction was that areas with high spatial heterogeneity in environmental conditions would favour both exotic and native species and would be more highly invaded than areas with low spatial heterogeneity.

Chapter 2 of this thesis is the main data chapter that addresses the above-listed research objectives (1 through 4) and predictions. This research is correlative and therefore cannot establish cause and effect relationships between variables. However, it nonetheless may reveal patterns that, when evaluated against existing and proposed hypotheses, may offer

useful insights into exotic species invasion. Despite this caveat, it is important to emphasize that observational studies are often the first step towards identifying potential causal relationships between species and environmental conditions, particularly at the landscape level where experimental studies are not feasible. Chapter 3 of this thesis provides a general discussion of this research including conservation implications for the South Okanagan Valley antelope-brush grasslands in light of the resulting patterns of exotic plant invasion in this ecosystem. This concluding chapter also provides a proposed general framework for the integration of fine and broad scale invasion ecology and NERR theory (objective 5), assumptions and limitations of the research, and suggestions for future research.

## CHAPTER 2: PREDICTING PATTERNS OF EXOTIC PLANT INVASION ACROSS SPATIAL SCALES IN CANADA'S ENDANGERED ANTELOPE-BRUSH ECOSYSTEM

### INTRODUCTION

Exotic species invasion is a serious threat to ecosystem structure and function throughout the world (Wilcove et al. 1998, Mack et al. 2000). In order to better understand the establishment and spread of exotic species, much research effort has been devoted to describing and predicting patterns of exotic species diversity in invaded ecosystems (Levine and D'Antonio 1999, Fridley et al. 2007). In particular, the role of native species diversity as a biotic predictor of invasion success has been a focus of many studies (e.g., Palmer and Maurer 1997, Stohlgren et al. 1999a, Naeem et al. 2000, Stohlgren et al. 2003, Davies et al. 2005, Lilley and Vellend 2009, Chen et al. 2010). Recent studies have also focused on abiotic factors as alternative or additional predictors of exotic diversity at the landscape scale (e.g., Bashkin et al. 2003, Eschtruth and Battles 2009, Lilley and Vellend 2009). However, multivariate studies that simultaneously examine the roles of both biotic and abiotic predictors of exotic species invasion are rare (Fridley et al. 2007, Eschtruth and Battles 2009), and may help to improve our understanding of the processes governing invasion success.

The role of native species diversity as a predictor of invasion success is at the centre of what is aptly termed the "invasion paradox," as both positive and negative native-exotic richness relationships (NERRs) have been observed in various systems (Levine and D'Antonio 1999, Fridley et al. 2007). Scale has recently been recognized as a critical factor in predicting the direction and magnitude of the NERR and the processes that govern this relationship (Shea and Chesson 2002, Stohlgren et al. 2006, Fridley et al. 2007). At fine scales (typically  $<1 \text{ m}^2$ ), biotic interactions are thought to govern NERRs as all individuals have the potential to interact with one another and environmental variation is generally limited within this small area (Fridley et al. 2007). Following the *biotic resistance hypothesis* (Elton 1958), highly diverse communities are thought to be less susceptible to exotic species invasion because they more fully utilize the resources available and are therefore better able to competitively exclude potential invaders compared to species-poor communities. This hypothesis forecasts a negative relationship between exotic and native species, although positive NERRs are also possible at fine scales as a result of biotic interactions such as mutualism and facilitation (Bruno et al. 2003, Mitchell et al. 2006, Fridley et al. 2007).

Positive NERRS are typical of broad scales (typically >1 km<sup>2</sup>) and are generally related to environmental conditions that covary with native diversity, as most individuals do not directly interact over these large areas (Levine and D'Antonio 1999, Stohlgren et al. 2006, Fridley et al. 2007, but see Lilley and Vellend 2009). Two main hypotheses underlie this prediction. The *biotic acceptance hypothesis* proposes that areas with abundant resources and/or mean favourable environmental conditions lead to increases of both native and exotic diversity (Levine and D'Antonio 1999, Stohlgren et al. 2006). In contrast, the *spatial heterogeneity hypothesis* contends that it is actually heterogeneity in species composition as a result of variation in environmental conditions that leads to a positive broad scale NERR (Davies et al. 2005, Melbourne et al. 2007). Abiotic factors that are thought to influence the NERR at broad scales include soil chemistry and texture (Huenneke et al. 1990, Bashkin et al. 2003, Davies et al. 2005), soil depth (Davies et al. 2005, MacDougall et al. 2006), topography (Davies et al. 2005, MacDougall et al. 2006), climate (Lilley and Vellend 2009), and disturbance (Gelbard and Belnap 2003, Eschtruth and Battles 2009, Lilley and Vellend 2009).

Several studies have attempted to deconstruct the relationship between spatial scale and the NERR using a multi-scale approach (e.g., Stohlgren et al. 1999a, Davies et al. 2005, Stohlgren et al. 2006, Chen et al. 2010, Tanentzap et al. 2010), yet few studies explicitly state which aspect of scale was manipulated. Following Scheiner et al. (2000), scale in relation to research on species richness actually consists of four components: sampling unit, grain, focus, and extent. They defined sampling unit as the spatial and temporal unit of data collection, grain as the standardized sampling unit used in the data analysis such that data from different sampling units are comparable, and extent as the spatial area, timeframe, or biological domain over which data are collected. A recent analysis by Sandel and Corbin (2010) highlighted the importance of both grain and extent when making NERR predictions. Scheiner et al. (2000) additionally defined focus, which is the component of scale at which the sampling grains are aggregated and which is equal to the number of replicates in the study. Depending on the analysis design, grain size may or may not be equal to the study focus, and this can have important implications for the interpretation of process from species richness patterns. To my knowledge, this issue has yet to be considered within the NERR literature.

Here I investigated NERRs and their scale sensitivity within the antelope-brush (*Purshia tridentata* Pursh (DC)) shrub-steppe grasslands of the South Okanagan Valley, British Columbia. These grasslands are one of Canada's four most endangered ecosystems due to

extensive anthropogenic disturbance and many of the remaining habitats are in an early seral stage and are highly invaded by exotic plants (Schluter et al. 1995, Lea 2008). These arid, hot grasslands are also part of Canada's only semi-desert ecosystem; as such, water is likely a limiting factor in the establishment and spread of both native and exotic plant species in this system. Water availability is typically affected by topographical features such as aspect, slope, and elevation, which in turn influence local temperature and precipitation patterns. Water availability within this system is also likely influenced by soil texture, as well as antelope-brush shrub density, which can facilitate herbaceous plants by reducing water stress through shading (e.g., Flores and Jurado 2003, Griffith 2010). Within this highly fragmented ecosystem, plant diversity patterns may also be influenced by anthropogenic disturbances such as roadways, which can facilitate the establishment and spread of exotic plant species at the cost of native diversity (Davis et al. 2000, Gelbard and Belnap 2003). It seems plausible, then, that some or all of these factors could be predictors of plant diversity patterns in this ecosystem.

Identifying where exotic species are located is a critical step in their control and eradication (Sakai et al. 2001), particularly in an endangered ecosystem. In this study, I evaluated the relative importance of biotic and abiotic factors in explaining patterns of exotic plant invasion in the antelope-brush grasslands using multiple linear regression. I also applied for the first time the concept of focus to the NERR and built upon previous studies to determine how different components of scale influence the NERR using a multi-scale approach. I found that the NERR in the antelope-brush grasslands was affected by changing the grain but not the focus or extent of analysis, and that variation in exotic species richness was not readily accounted for by abiotic factors at the broadest focus. In contrast to the prevailing hypothesis, however, I found a highly significant positive NERR at the finest focus that appeared to be influenced at least in part by preferential facilitation of exotic plant diversity by antelope-brush shrubs. These exotic invasion patterns have potentially important implications for the conservation of both this endangered ecosystem and its many dependent species at risk.

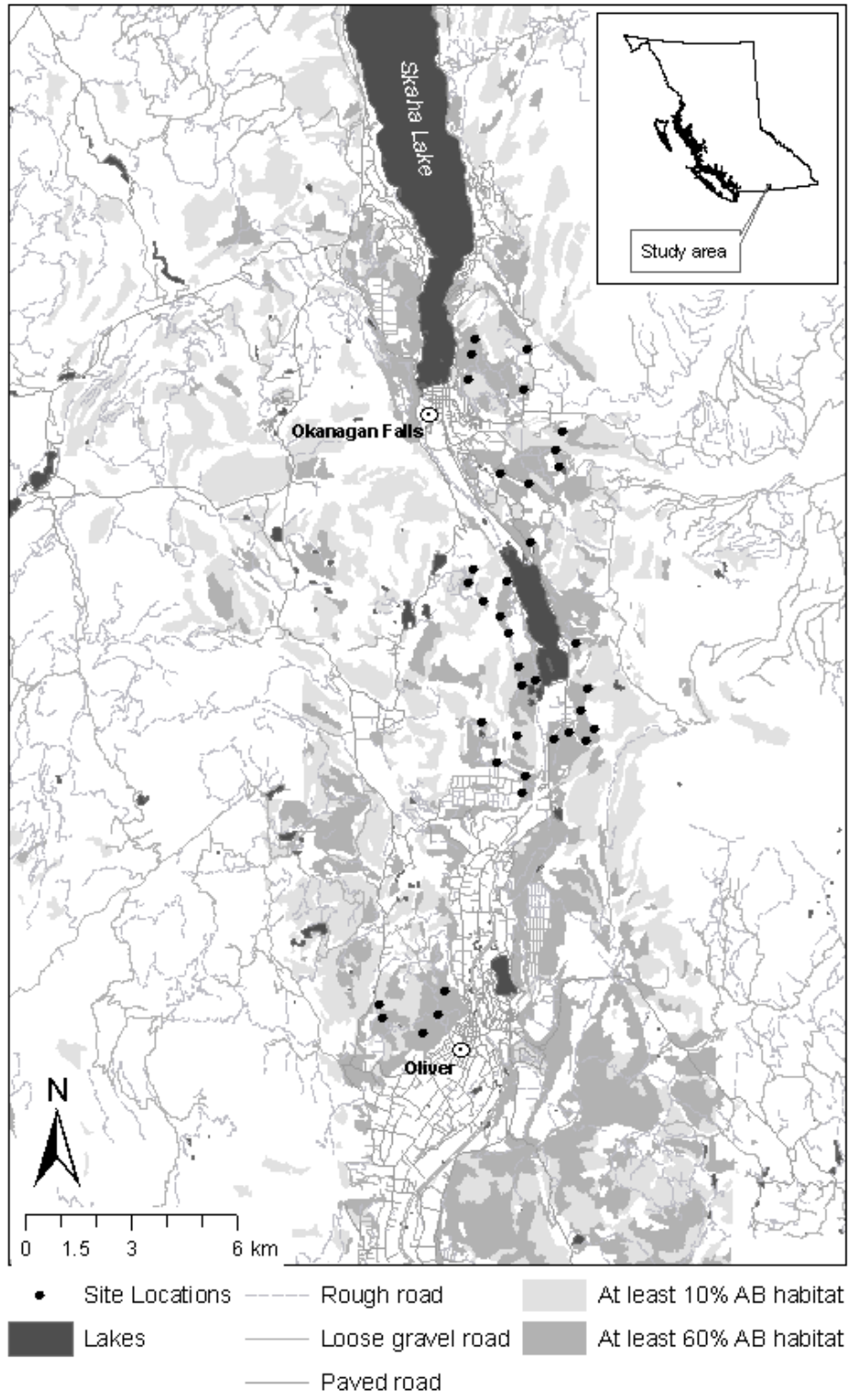
## **METHODS**

### **Study Area**

This study was conducted in remnant patches of antelope-brush grassland in the South Okanagan Valley, British Columbia, Canada (Figure 2.1). Within the study area, the antelope-brush / needle-and-thread grass (*Hesperostipa comata* (Trin. & Rupr.) Barkworth)

ecological community comprises the majority of the antelope-brush habitat present. This globally imperilled community typically occurs on gentle middle to lower slopes of all aspects on coarse well-drained soils, and is restricted to the lower elevations (280 to 760 m above sea level) of the Okanagan Valley south of Penticton in British Columbia, to eastern Washington and Oregon, and to the Columbia Basin and Owyhee Uplands in western Idaho in the United States (Lea et al. 2004). As one of Canada's biodiversity and endemism hotspots, 88 provincial and 18 federal species at risk rely on the antelope-brush grasslands for survival (Schluter et al. 1995, Dyer and Lea 2003). Although never historically abundant, over 61% of the spatial extent of these grasslands have been lost in the last two centuries (Lea 2008). Major threats to this ecosystem include orchard and vineyard development, residential development, livestock grazing, recreational use, roadway development, sand and gravel extraction, and likely climate change (Lea et al. 2004).





**Figure 2.1** Locations of sample sites (N = 37) within the antelope-brush (AB) grasslands of the South Okanagan Valley, British Columbia, Canada.

## Site Selection

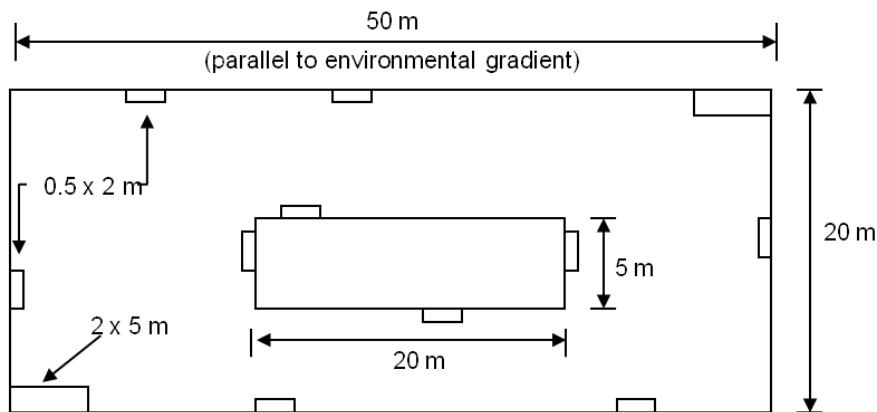
The likely presence of antelope-brush grassland habitat within the South Okanagan Valley was determined using available digital 1:15,000 terrestrial ecosystem mapping (TEM) (Iverson and Haney 2006). Within the TEM geo-dataset, each mapped ecosystem polygon consists of up to three ecological communities with their associated modifiers and structural stages. Five communities potentially contain antelope-brush habitat within the study area (Table 1.1, Iverson and Haney 2009). The sampling frame of the study consisted of ecosystem polygons comprising at least 60% of one or more of these five community types (see Figure 2.1). Site selection was limited to properties for which access permission could be obtained, which necessitated deviation from a truly stratified random sample design for all antelope-brush habitats. As such, inferences drawn from this study should be used with caution as they may be limited to the sampled population (i.e., primarily from conservation areas) and not applicable for all antelope-brush grasslands in the South Okanagan Valley.

Covering an area of approximately 112 km<sup>2</sup>, the sampling frame exhibited a range in elevation, aspect, and slope. Especially within a semi-arid ecosystem, slight shifts along these three physiographic gradients can have profound effects on microclimate and soil moisture, which in turn have been implicated as drivers of exotic plant species distributions and abundances (Padien and Lajtha 1992, MacDougall et al. 2006, Lilley and Vellend 2009). Using ArcGIS Version 9.3, a sampling strategy was therefore employed that randomly selected sites (i.e., point locations) within the sampling frame while maximizing variation along these gradients. Thirty sets of 50 randomly selected sites were generated; the set that best satisfied the sampling criteria (assessed by graphical analysis) was chosen.

Of the 50 sites in the chosen set, 15 sites were not used because they either did not actually contain antelope-brush upon field verification, they were physically inaccessible, or they were not feasible to sample due to remoteness from other sites. Two additional sites were added in areas that were geographically underrepresented during the fieldwork, resulting in a total of 37 sample sites. There is no evidence that the inclusion of these two non-randomly placed sites biased the results of this study in any way, as all of the regression and correlation results presented herein remained qualitatively identical when the entire analysis was completed with these two sites removed. Topographical information for each sample site is provided in Table A.1 in the Appendix. None of the final sites sampled were recently burned.

## Data Collection

Plant species data were collected at four spatial grains using the modified-Whittaker plot design developed by Stohlgren et al. (1995), which consists of ten 1 m<sup>2</sup> (0.5 m x 2 m) subplots, two 10 m<sup>2</sup> (2 m x 5 m) subplots, and one 100 m<sup>2</sup> (5 m x 20 m) subplot, all nested within a 1,000 m<sup>2</sup> (20 m x 50 m) plot (Figure 2.2). The rectangular plot design of each grain reduces size-shape interactions and covers more heterogeneous habitat, particularly when oriented parallel to the dominant environmental gradient, than either circular or square plots of equivalent areas due to an increased perimeter to surface area ratio (Stohlgren et al. 1995). Subplot placement within this design also minimizes spatial non-independence, with no overlap between subplots and only a 13% overlap between the nested subplots and the 1,000 m<sup>2</sup> plot (Stohlgren et al. 1995). These factors combine to increase the effectiveness of this design in assessing plant species diversity and detecting locally rare species compared to other commonly used vegetation sampling methods (Stohlgren et al. 1998, Korb et al. 2003), the latter of which is also important for early detection of exotic species invasions.



**Figure 2.2** Diagram of modified-Whittaker plot showing locations of subplots (black rectangles). Modified from Stohlgren et al. (1995) and Bashkin et al. (2003).

The species richness (i.e., total number of species per plot) and foliar cover of vascular plants were determined in each of the ten 1 m<sup>2</sup> subplots per site using a rectangular quadrat divided into ten 0.5 m x 0.2 m (i.e., 10%) cells, with one cell further divided into 0.2 m x 0.05 m (i.e., 1%) increments (Bashkin et al. 2003). Species that occupied <1% of a subplot were recorded as 0.5%. The percent cover of litter (i.e., dead detached plant material), duff (i.e., dead attached plant material), wildlife and cattle dung, cryptogam crust, and exposed ground (i.e., bare soil and rock) were also visually estimated within each 1 m<sup>2</sup> subplot. Plant

species richness was then determined through systematic searches in each of the 10 m<sup>2</sup>, 100 m<sup>2</sup>, and 1,000 m<sup>2</sup> plots until no further species could be recorded.

Plants that could not be immediately identified in the field were collected, assigned a morphospecies name, and later identified using regional taxonomic keys. Approximately 10% of all plants observed in the field could not be identified to species due to missing floral parts and were excluded from the analysis. At the 1 m<sup>2</sup> subplot grain, unidentified species accounted for less than 1.5% of the total cover of vascular plants across all sites. All plant species' common names, scientific names, and conservation statuses follow British Columbia Conservation Data Centre (2010), which lists the most current conventions in the province. Voucher plant specimens used to confirm identification are stored at the Biodiversity and Landscape Ecology Research Facility at UBC Okanagan and are available for viewing upon request. Each site was sampled once in the spring and once in the summer of 2010 to encompass the majority of the growing season, with each sampling period spanning 2.5 weeks and lower elevation sites sampled first to minimize phenological differences among sites.

Especially in arid ecosystems, shrubs can facilitate the seedling establishment and growth of both exotic and native species through increased seed and nutrient trapping, reduced water stress through shading, and ameliorated protection from herbivory (Flores and Jurado 2003). Antelope-brush shrub density was therefore also recorded within each 100 m<sup>2</sup> subplot. This species was by far the most abundant and widespread shrub in the study area, although other shrubs may also have facilitative roles in this system. Antelope-brush density from the 100 m<sup>2</sup> subplots and antelope-brush foliar cover from the 1 m<sup>2</sup> subplots were included in the applicable regression models as potential predictors of exotic plant diversity (see Data Analysis).

Site coordinates and elevation were estimated and recorded in the field using a Trimble GeoXT global positioning system. Aspect and slope angle were obtained using a compass and clinometer, respectively. Scale-free annual and season climate data were generated for each site based on its coordinates and elevation using climate normals from 1971-2000, the most recent time period available, in Climate BC Version 3.2 (Hamann and Wang 2005, Wang et al. 2006). All annual and seasonal climate variables were strongly correlated ( $|r_S| > 0.74$ ) with either mean annual temperature (MAT) or mean annual precipitation (MAP), which were not correlated ( $r_S = 0.138$ ,  $P = 0.416$ ) and were therefore included as separate terms in the applied abiotic predictive models (see Data Analysis). Elevation was strongly

correlated with MAT ( $r_S = -0.921$ ,  $P < 0.001$ ) and so was not included in the applicable predictive models.

Road density, which measures the average spatial patterns of a given area, is positively correlated with disturbance level and human access (Forman and Alexander 1998), both of which are biologically relevant to the establishment of exotic plant species. Surrounding road density ( $\text{m}/\text{m}^2$ ) was calculated using ArcGIS Version 9.3 as the total road length within a 500 m buffer radius around each site based on freely available digital road atlas data (Province of British Columbia 2010). Road density was included in the applied abiotic predictive models (see Data Analysis) using this buffer radius to facilitate comparisons with previous studies, which also used a 500 m buffer (e.g., Lilley and Vellend 2009, Tanentzap et al. 2010).

Information about soil conditions at the landscape scale was derived for each site from a detailed soil survey available in digital (i.e., geographic information system (GIS)) format for the South Okanagan Valley (Canadian Soil Information Service 2010). From this extensive data set, only native soils from the A and B horizons of the first component of each soil polygon in which a site was located were used; the second component was used if the first was identified as rock face. Principal components analysis (PCA) was then used to reduce the high number of soil variables (e.g., percent by weight sand, water retention) to the first two principal components, which collectively explained 73.8% (54.9% and 18.9%, respectively) of the variation in the soil data. The first PCA axis was strongly correlated with MAT ( $r_S = -0.697$ ,  $P < 0.001$ ), and the second PCA axis was weakly correlated with MAP ( $r_S = 0.346$ ,  $P = 0.036$ ) and slope ( $r_S = 0.393$ ,  $P = 0.016$ ). As such, the soil PCA axes were not included in the applied abiotic predictive models (see Data Analysis).

## **Data Analysis**

### *Species Composition*

All statistical analyses were conducted using R Version 2.11.1 (R Development Core Team 2010); a complete script of all analyses is available upon request. To characterize the species composition of the study area, the mean (and standard deviation, hereafter) exotic and native species richness were calculated at each of the four sampling grains and the mean foliar cover for each species group was calculated at the  $1 \text{ m}^2$  grain. Sign tests were used to determine if, at the finest grain and focus (i.e.,  $1 \text{ m}^2$ ), the median differences in exotic and native species richness ( $N = 357$ ) and foliar cover ( $N = 363$ ) were significantly different from zero in the study area; sample sizes for these two tests were smaller than the

total sample size because subplots with no difference between exotic and native diversity were removed from the analysis (Whitlock and Schluter 2009). The number of sites occupied and the mean foliar cover across the study area were also calculated for each species. Sample-based species accumulation curves with 1,000 permutations were generated for both exotic and native species using species data from the 1,000 m<sup>2</sup> grain. While these curves actually represent species density (i.e., number of species per unit area) rather than species richness (Gotelli and Colwell 2001), the term species richness is used throughout this thesis to remain consistent with previously published NERR literature. The extrapolated species richness in the exotic and native species pools were estimated using the non-parametric first-order jackknife estimator (Palmer 1990) to qualify completeness of sampling. Exotic and native site occupancy rates were compared using a Kolmogorov–Smirnov (K-S) test. Mean percent covers of cryptogam, bare soil, rock, and total plants were also calculated and were used to quantify environmental variation in the study area.

#### *Native-Exotic Diversity Associations*

The spatial scale of analysis determines the likely mechanism (i.e., biotic or abiotic) governing the NERR (Fridley et al. 2007). As such, correlation analysis was used to investigate whether (i) exotic and native species richness (i.e., the NERR) and (ii) exotic and native foliar cover were associated across multiple scales in the antelope-brush grasslands. For all bivariate analyses, non-linear associations necessitated the use of Spearman's rank correlation analysis over Pearson correlation analysis.

Firstly, the NERR was analyzed at four sampling grains, two main focuses, and two extents to determine the sensitivity of the direction and magnitude of this association to each component of scale. To evaluate the sensitivity of the NERR to changes in spatial grain, this association was determined across all sites (N = 37) at each of the following sampling grains while keeping the extent constant as the entire study area: 1,000 m<sup>2</sup>, 100 m<sup>2</sup>, 10 m<sup>2</sup>, and 1 m<sup>2</sup>. The NERR at the 1,000 m<sup>2</sup> grain was determined using the species richness data from the one 1,000 m<sup>2</sup> plot per site, therefore the focus of analysis was equal to the grain of analysis. Similarly, the NERR at the 100 m<sup>2</sup> grain was determined from the one 100 m<sup>2</sup> subplot per site, with focus again equal to grain. The NERR at the 10 m<sup>2</sup> grain was determined using the average species richness data from the two 10 m<sup>2</sup> subplots per site (i.e., 1,000 m<sup>2</sup> focus), and the NERR at the 1 m<sup>2</sup> grain was determined using the average species richness data from the ten 1 m<sup>2</sup> subplots per site (i.e., 1,000 m<sup>2</sup> focus).

To evaluate the sensitivity of the NERR to changes in spatial focus, the average 1 m<sup>2</sup> NERR (i.e., 1,000 m<sup>2</sup> focus) was then compared to a finer (i.e., 1 m<sup>2</sup>) focus NERR, which was determined using the species richness data from all of the 1 m<sup>2</sup> subplots individually (N = 370). The resulting  $r_s$  value for each focus was transformed using the Fisher's  $Z$  transformation to allow for comparison using a  $Z$  test (Zar 1999). Consistent with previous studies using the modified-Whittaker plot (e.g., Stohlgren et al. 1999a, Stohlgren et al. 1999b), the 1 m<sup>2</sup> focus analysis did not take into account the potential for spatial non-independence between the ten 1 m<sup>2</sup> subplots per site when analyzed individually.

The association between exotic and native species richness was also investigated within each individual site to evaluate the sensitivity of the NERR to changes in spatial extent (i.e., site versus study region). At this fine extent, the NERR of each site was characterized by the Spearman's rank correlation coefficient ( $r_s$ ), which was calculated using the exotic and native species richness data from the ten 1 m<sup>2</sup> subplots per site. A sign test was then used to assess whether the median of the resulting  $r_s$  values (one for each site) was equal to the null hypothesized median of zero across the entire study area. This analysis was essentially a meta-analysis of the trends at the broad study area extent based on 37 separate analyses of data from the fine extent of an individual site. Only 35 sites were actually included in this test because no exotic species were observed in the 1 m<sup>2</sup> subplots at one site, and because the  $r_s$  value of another site was equal to the null median (zero) so was removed from the analysis (Whitlock and Schluter 2009). This approach to evaluating the consistency of the NERR at fine extents does not appear to have been previously employed.

Secondly, the association between exotic and native foliar cover was investigated using Spearman's rank correlation to determine if this association was scale dependent in the antelope-brush grasslands. Foliar cover data were only collected in the 1 m<sup>2</sup> subplots; as such, the association between exotic and native foliar cover was investigated only at this single grain. To evaluate its sensitivity to changes in spatial focus, this association was determined using both the average foliar cover data from the ten 1 m<sup>2</sup> subplots per site (N = 37; 1,000 m<sup>2</sup> focus) and the foliar cover data from all of the 1 m<sup>2</sup> subplots individually (N = 369; 1 m<sup>2</sup> focus). Foliar cover was not recorded at one of the subplots, which was excluded from this and other applicable analyses. The association between exotic and native foliar cover was also investigated at the fine extent of an individual site to evaluate the sensitivity of this association to changes in spatial extent, following the same methods as for species richness at this extent (see above). Only 36 sites were included in the foliar cover sign test because no exotic species were observed in the 1 m<sup>2</sup> subplots at one site.

### *Predicting Fine Focus Diversity from Biotic Factors*

Biotic interactions are thought to govern NERRs and be the main determinants of species richness at fine focuses (Mitchell et al. 2006, Fridley et al. 2007). To evaluate this hypothesis in the antelope-brush grasslands, the relationships between exotic species richness and biotic factors at the finest grain and focus (i.e., 1 m<sup>2</sup>) were assessed. At least two variables other than native species richness may covary with exotic species richness and thereby confound interpretations of NERRs: total foliar cover (which could be considered a proxy for local productivity or carrying capacity) and antelope-brush cover. Species richness cannot be high at very low values of foliar cover, but it can be high or low at high values of foliar cover. Thus, on average, a positive association between species richness and foliar cover is expected, at least across low values of foliar cover. Antelope-brush is known to serve as a nurse plant for herbaceous species within arid ecosystems (e.g., Griffith 2010), and therefore canopy cover from this species may ameliorate local conditions for either exotic species, native species, or both.

A full multiple regression model was constructed to determine if an association remained between fine focus exotic and native species richness after accounting for total foliar cover and antelope-brush cover. Spatial non-independence between 1 m<sup>2</sup> subplots may again be a feature of this dataset, but consistent with previous studies (e.g., Stohlgren et al. 1999a), its influence was not explicitly considered. All explanatory variables were entered simultaneously (i.e., a “forced entry” model). While full models rarely are the best model for the data because they include non-significant predictors, stepwise regression procedures, which are commonplace in NERR research (e.g., Stohlgren et al. 1999a, Bashkin et al. 2003, Lilley and Vellend 2009), are not recommended for building predictive models due to problems with parameter bias and inflated Type I errors (James and McCulloch 1990, Whittingham et al. 2006, Mundry and Nunn 2009). The importance of the predictor variables in the model was assessed by comparing the magnitudes of their standardized regression coefficients. This method works well when the independent variables are uncorrelated, but may misrepresent their relative contributions when they are correlated (Murray and Conner 2009), thus investigations of bivariate associations between predictor variables using Spearman’s rank correlation also informed this analysis.

### *Predicting Broad Focus Diversity from Abiotic Factors*

Abiotic interactions are thought to govern NERRs and be the main determinants of species richness at broad focuses (Davies et al. 2005, Stohlgren et al. 2006, Fridley et al. 2007). Two approaches were taken to validate this hypothesis in the antelope-brush grasslands.



Firstly, from a primarily applied perspective, the relationships between species richness and readily accessible abiotic factors were assessed at the broadest grain and focus (i.e., 1,000 m<sup>2</sup>) using a forced entry full multiple regression model. The purpose of this analysis was to determine if variation in exotic and native species richness could be accounted for by (mean) abiotic variables that were either freely available or relatively easy to quantify in the field, such that any significant results from this analysis could be used by land managers to predict areas with high exotic plant invasion at non-sampled antelope-brush grassland sites without cost-prohibitive field sampling. The exotic species model contained the following six uncorrelated ( $P > 0.05$ ) abiotic predictor variables: slope, aspect, MAT, MAP, antelope-brush density, and road density. The importance of the predictor variables within the model was assessed by comparing the magnitudes of their standardized regression coefficients. One site was identified as a potential outlier due to high leverage (Cook's distance = 0.283) in the exotic model and so was excluded from this analysis (N = 36). Based on the NERR results, a separate model containing the same six abiotic variables was constructed for native species richness at this broad focus (N = 37).

The second approach aimed to validate the theoretical role of abiotic factors as determinants of species richness in this system by comparing the importance of differences in mean environmental conditions between sites to the importance of differences in within-site heterogeneity in environmental conditions between sites using a forced entry full multiple regression model with species richness at the broadest grain and focus (i.e., 1,000 m<sup>2</sup>) as the dependent variable. This analysis tested the relevancy of the *biotic acceptance* and *spatial heterogeneity* hypotheses, respectively, to this system (Melbourne et al. 2007). The mean environmental conditions of each site was estimated as the sum of the scaled means (based on measurements in the ten 1 m<sup>2</sup> subplots per site) of each of the following seven variables: percent bare soil cover, percent rock cover, percent cryptogam cover, percent litter cover, percent duff cover, percent antelope-brush cover, average soil depth, and maximum vegetation height. Although technically a biotic factor, antelope-brush cover was included here for its habitat structuring role in this system. The within-site heterogeneity in environmental conditions of each site was estimated as the sum of the scaled variances in each of the same seven variables. The importance of the predictor variables in the model was assessed by comparing the magnitudes of their standardized regression coefficients. Separate models were constructed for exotic and native species richness. Two sites in the exotic model and one site in the native model were identified as outliers due to high leverage (Cook's distance = 0.559, 0.995, and 0.578, respectively) and were excluded from the models (N = 35 and N = 36, respectively).

### *Predicting Individual Exotic Species Patterns*

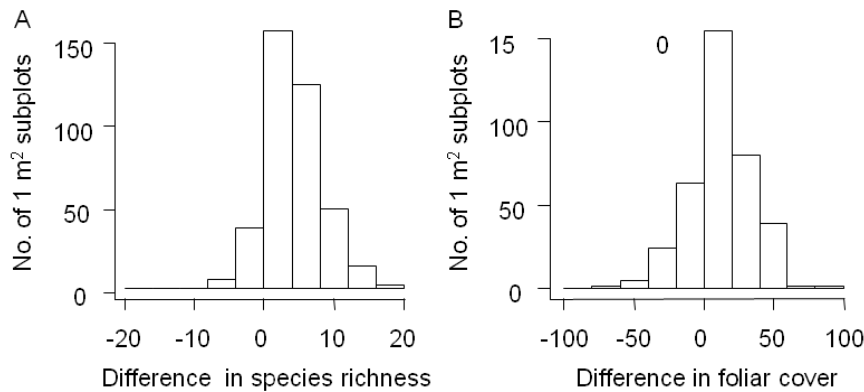
The aforementioned analyses of the associations between exotic and native species diversity, as well as the associations between species richness and both biotic and abiotic factors, addressed gaps in the NERR and invasion ecology literature and were primarily academic in focus. From a management perspective, however, it is also valuable to determine predictors of individual invasive or otherwise troublesome exotic species, particularly in an endangered ecosystem. At fine focuses, antelope-brush cover may be an important determinant of individual exotic species distributions due to its potential facilitative role in this system. Spearman's rank correlation was used to determine if exotic foliar cover of individual species was associated with antelope-brush cover for all abundant species (i.e., with a mean foliar cover of at least 1% of the landscape), widespread species (i.e., occupied at least 90% of the sites), and noxious species occupying at least 0.1% of the landscape. This included cheatgrass (*Bromus tectorum* L.), sulphur cinquefoil (*Potentilla recta* L.), Dalmatian toadflax (*Linaria genistifolia* (L.) Mill.), blue forget-me-not (*Myosotis stricta* Link ex Roem. & Schult.), common draba (*Draba verna* L.), and yellow salsify (*Tragopogon dubius* Scop.). At broad focuses, the same abiotic variables previously rationalized as applied predictors of exotic species richness (i.e., slope, aspect, MAT, MAP, antelope-brush density, and road density) may also be predictors of the foliar cover of individual exotic species. A forced entry full multiple regression model was used to determine the relationship between the average 1 m<sup>2</sup> grain foliar cover per site (i.e., 1,000 m<sup>2</sup> focus) of the same individual exotic species and the six uncorrelated abiotic variables.

## **RESULTS**

### **Species Composition**

A total of 162 plant species were identified among the 37 sample sites, including 124 native species and 38 exotic species; all species are listed with their conservation statuses in Table A.2 in the Appendix. The study area exhibited a wide range in species richness, from 29 to 75 species per site (Table A.1) and from 0 to 28 species per 1 m<sup>2</sup> subplot. Total foliar cover within the 1 m<sup>2</sup> subplots ranged from 0% to 88.5%, with up to 61% exotic foliar cover and 83% native foliar cover. Both the median fine focus richness (sign test; N = 357; positive tests = 330;  $P < 0.001$ ) and median foliar cover (sign test; N = 363, positive tests = 276,  $P < 0.001$ ) of native species were significantly greater than the corresponding median exotic species values (Figure 2.3). Exotic species consistently made up approximately 23% of the

total species list generated at each of the four sampling grains. Table 2.1 provides the mean exotic and native species richness and foliar cover for the study area at each sampling grain.



**Figure 2.3** Frequency distributions of the differences between native and exotic plant species richness (A) and foliar cover (B) based on data from the finest focus (i.e., 1 m<sup>2</sup>) within the study area extent. The median differences between species richness (sign test; N = 357; positive tests = 330;  $P < 0.001$ ) and foliar cover (sign test; N = 363, positive tests = 276,  $P < 0.001$ ) were significantly different from zero, favouring native species in each case.

**Table 2.1** Mean (standard deviation) species richness and foliar cover of exotic and native plants at each sampling grain within the study area extent.

Status	Species Richness				Foliar Cover
	1,000 m <sup>2</sup>	100 m <sup>2</sup>	10 m <sup>2</sup>	1 m <sup>2</sup>	1 m <sup>2</sup>
Exotic	13.7 (3.7)	9.0 (3.1)	5.8 (2.6)	3.7 (2.3)	9.9 (13.0)
Native	41.7 (9.2)	24.6 (7.0)	15.0 (4.9)	8.4 (4.2)	21.6 (16.6)

Of the identified plants, ten species were widespread, occurring in at least 90% of the sites (Table 2.2), while 113 species occurred in fewer than half of the sites. Forty-three (43) species were regionally rare, defined here as those species occupying less than four sites (i.e., 10% of sites sampled), and 19 species were singletons, occurring in only one site. Only seven species covered greater than 1% of the landscape (Table 2.2); together these species accounted for 61.4% of the total identified plant cover in the study area. By far the most common species was the exotic cheatgrass, which alone accounted for 20.1% of the total identified plant cover in the study area. Vascular plants only covered a mean of 32.0% (20.4) of the landscape based on the 1 m<sup>2</sup> subplots, while cryptogams, bare soil, and rock covered means of 21.7% (22.5), 10.0% (14.2), and 7.2% (14.0), respectively (N = 369). One regionally noxious and five provincially noxious weeds were recorded in the study area

(Table 2.3). No plant species listed provincially or federally as either endangered, threatened, or of special concern were observed.

**Table 2.2** Summary of common exotic (A) and native (B) plant species in the study area. Abundant species having a mean (standard deviation) foliar cover of at least 1% of the landscape based on the 1 m<sup>2</sup> subplots (N = 369) and widespread species occupying at least 90% of the sites (N = 37) are included.

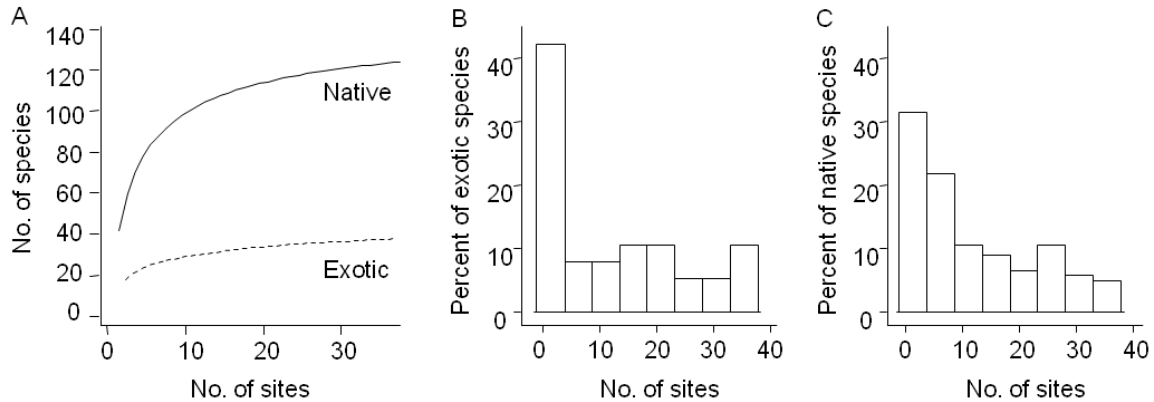
Common Name	Scientific Name	Cover	Sites
(A) Common exotic species			
Cheatgrass	<i>Bromus tectorum</i> L.	6.3 (11.0)	100
Blue forget-me-not	<i>Myosotis stricta</i> Link ex Roem. & Schult.	0.4 (0.8)	92
Common draba	<i>Draba verna</i> L.	0.2 (0.3)	95
Yellow salsify	<i>Tragopogon dubius</i> Scop.	0.1 (0.3)	97
(B) Common native species			
Bluebunch wheatgrass	<i>Pseudoroegneria spicata</i> (Pursh) A. Löve	3.8 (7.5)	100
Arrow-leaved balsamroot	<i>Balsamorhiza sagittata</i> (Pursh) Nutt.	2.6 (7.1)	76
Antelope-brush	<i>Purshia tridentata</i> Pursh (DC)	2.2 (7.7)	100
Needle-and-thread grass	<i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth	1.9 (5.7)	76
Sand dropseed	<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	1.3 (4.2)	73
Sandberg's bluegrass	<i>Poa secunda</i> J. Presl	1.3 (2.7)	100
Yarrow	<i>Achillea millefolium</i> L.	0.4 (1.7)	95
Small-flowered blue-eyed Mary	<i>Collinsia parviflora</i> Lindl.	0.3 (0.5)	97
Thread-leaved phacelia	<i>Phacelia linearis</i> (Pursh) Holz.	0.1 (0.6)	92

**Table 2.3** Mean (standard deviation) percent foliar cover and percentage of sites occupied by regionally (R) or provincially (P) noxious exotic plant species in the study area.

Common Name	Scientific Name	Status	Cover	Sites
Sulphur cinquefoil	<i>Potentilla recta</i> L.	R	0.8 (3.9)	62
Dalmatian toadflax	<i>Linaria genistifolia</i> (L.) Mill.	P	0.3 (1.3)	73
Diffuse knapweed	<i>Centaurea diffusa</i> Lam.	P	<0.1 (0.4)	62
Common hound's-tongue	<i>Cynoglossum officinale</i> L.	P	<0.1 (0.1)	11
Perennial sow-thistle	<i>Sonchus arvensis</i> L.	P	<0.1 (<0.1)	3
Canada thistle	<i>Cirsium arvense</i> (L.) Scop.	P	0 (0)	3

The species accumulation curves for exotic and native species each approached an asymptote; approximately 87% and 91%, respectively, of the extrapolated available exotic

and native species pools were sampled (Figure 2.4A). Site occupancy rates were similar between exotic and native species (Figure 2.4B-C; K-S test;  $N = 162$ ;  $D = 0.107$ ;  $P = 0.896$ ), even when the regionally rare species were excluded from the analysis (K-S test;  $N = 107$ ;  $D = 0.148$ ,  $P = 0.734$ ).



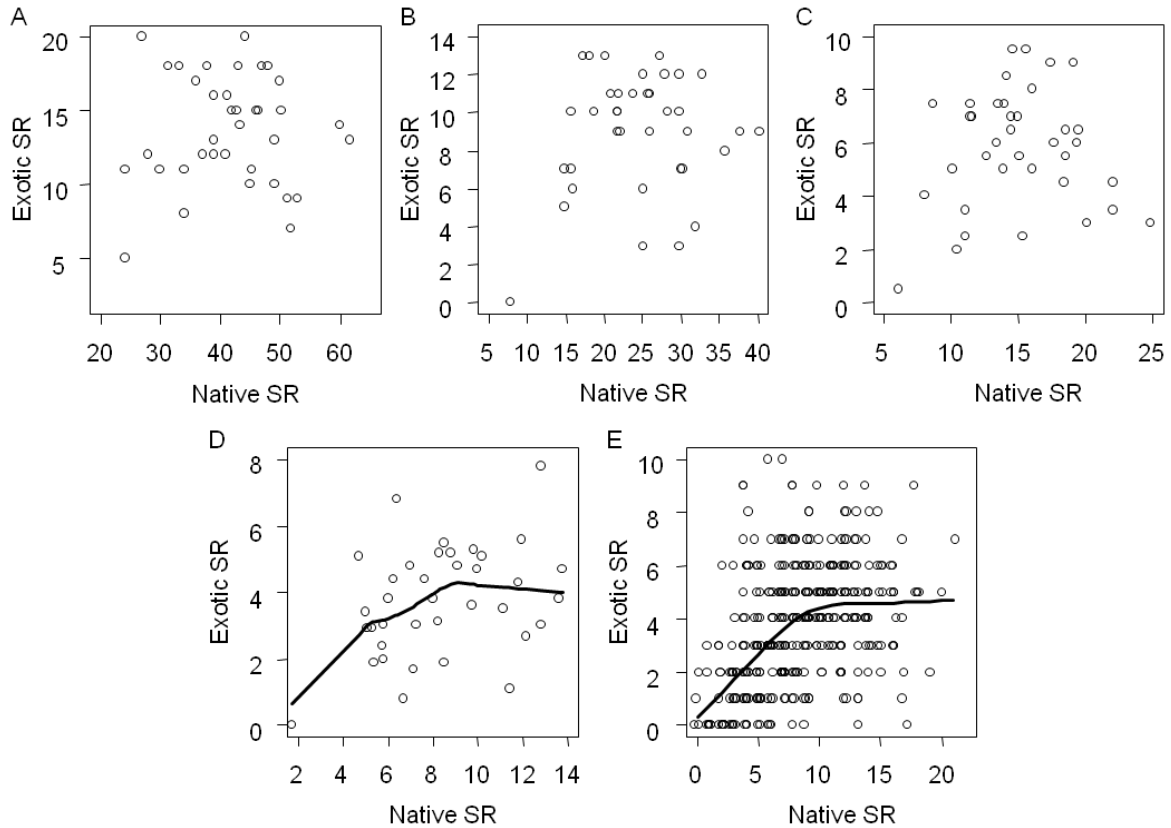
**Figure 2.4** Species accumulation curves (A) and species occupancy histograms for exotic (B) and native (C) plant species richness based on data from the broadest grain and focus (i.e., 1,000 m<sup>2</sup>) across the study area extent.

### Native-Exotic Diversity Associations

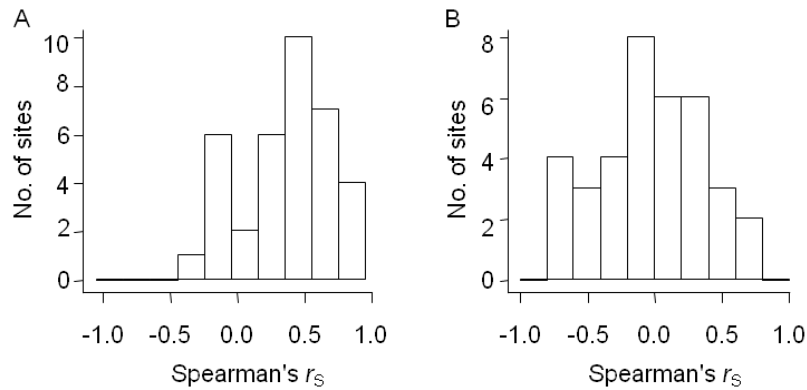
At the broad extent of the study area, there was no significant association between exotic and native species richness at the three largest grains (1,000 m<sup>2</sup>, 100 m<sup>2</sup>, 10 m<sup>2</sup>) (Table 2.4A, Figure 2.5A-C). At the 1 m<sup>2</sup> grain, however, there was a significant positive NERR when the focus was the 1,000 m<sup>2</sup> plot and a highly significant positive NERR when the focus was the 1 m<sup>2</sup> subplot (Table 2.4A, Figure 2.5D-E). The  $r_s$  values for these two focuses were not significantly different in magnitude ( $Z = 1.371$ ;  $P = 0.171$ ). When the analysis was conducted using each individual site as the extent, 11 of the 37 sites had a significantly positive within-site NERR ( $r_s$ ,  $\alpha = 0.05$ ) and none of the sites had a significantly negative NERR based on the ten 1 m<sup>2</sup> subplots per site (data not shown). Across the study area, the  $r_s$  values for the within-site NERRs were greater than zero (i.e. the NERR was positive) significantly more often than expected by chance (Figure 2.6A; sign test;  $N = 35$ ; positive tests = 29;  $P < 0.001$ ).

**Table 2.4** Association between exotic (dependent variable) and native (independent variable) plant species richness (A) and foliar cover (B) at four different grains and two main focuses within the study area extent. Significant ( $P < 0.05$ ) associations are bolded.

N	Sampling Unit	Grain	Focus	$r_s$	$P$
<b>(A) Exotic and native species richness</b>					
37	1,000 m <sup>2</sup>	1,000 m <sup>2</sup>	1,000 m <sup>2</sup>	-0.059	0.730
37	100 m <sup>2</sup>	100 m <sup>2</sup>	100 m <sup>2</sup>	0.008	0.964
37	10 m <sup>2</sup>	10 m <sup>2</sup>	1,000 m <sup>2</sup>	0.034	0.840
37	1 m <sup>2</sup>	1 m <sup>2</sup>	1,000 m <sup>2</sup>	<b>0.350</b>	0.034
370	1 m <sup>2</sup>	1 m <sup>2</sup>	1 m <sup>2</sup>	<b>0.438</b>	< 0.001
<b>(B) Exotic and native foliar cover</b>					
37	1 m <sup>2</sup>	1 m <sup>2</sup>	1,000 m <sup>2</sup>	0.021	0.900
369	1 m <sup>2</sup>	1 m <sup>2</sup>	1 m <sup>2</sup>	0.080	0.123



**Figure 2.5** Native-exotic richness relationships (NERRs) across multiple grains and focuses within the study area extent. No association was present when the 1,000 m<sup>2</sup> plot was both the grain and the focus (A), when the 100 m<sup>2</sup> subplot was both the grain and the focus (B), or when the 10 m<sup>2</sup> subplot was the grain and the 1,000 m<sup>2</sup> plot was the focus (C). A positive association was present when the 1 m<sup>2</sup> subplot was the grain at both the 1,000 m<sup>2</sup> (D) and 1 m<sup>2</sup> (E) focuses. Individual data points are jittered horizontally to improve visibility. Locally weighted scatter plot smoothing lines are shown where associations were significant.



**Figure 2.6** Frequency distributions of Spearman's rank correlation coefficients ( $r_s$ ) for fine (1 m<sup>2</sup>) grain within-site native-exotic diversity relationships for all sites across the study area extent. Within-site NERRs were positive (i.e.  $r_s > 0$ ) significantly more often than expected by chance (A; sign test;  $N = 35$ ; positive tests = 29;  $P < 0.001$ ). The sign test failed to reject the null hypothesis that positive and negative native-exotic foliar cover relationships occurred with equal probability (B;  $N = 36$ ; positive tests = 17;  $P = 0.868$ ).

With the study area as the extent, there was no association between exotic and native foliar cover regardless of whether the 1 m<sup>2</sup> subplot data were averaged across sites or analyzed individually (Table 2.4B). In general, this lack of association remained when the individual site was the extent: the within-site  $r_s$  values were centred on zero (Figure 2.6B), and a sign test failed to reject the null hypothesis that positive and negative native-exotic foliar cover relationships occurred with equal probability ( $N = 36$ ; positive tests = 17;  $P = 0.868$ ).

### Predicting Fine Focus Diversity from Biotic Factors

The full regression model containing biotic predictor variables was highly significant, and explained 22.0% of the variation in fine focus exotic species richness in the study area. Both native species richness and total foliar cover were highly significant predictors of exotic species richness and were comparable in their importance, as indicated by the similar magnitudes of their standardized coefficients (0.321 and 0.267, respectively; Table 2.5). Antelope-brush cover was not significant within the multiple regression, perhaps in part because it covaried with total foliar cover ( $r_s = 0.296$ ,  $P < 0.001$ ). Native species richness was also weakly associated with total foliar cover ( $r_s = 0.327$ ,  $P < 0.001$ ), particularly at low foliar cover as expected (see Data Analysis).



**Table 2.5** Multiple regression results for potential biotic predictors of exotic plant species richness (dependent variable) at the finest focus (i.e., 1 m<sup>2</sup>) within the study area extent. Significant ( $P < 0.05$ ) independent variables within the model are bolded.

Biotic Variable	Coefficient	Standardized Coefficient	$P$
Exotic species richness (N = 369, $F_{3,365} = 35.6$ , $R^2_{adj} = 0.220$ , $P < 0.001$ , SE = 2.012)			
Constant	1.321	<b><math>3.820 \times 10^{-4}</math></b>	< 0.001
Native species richness	0.174	<b>0.321</b>	< 0.001
Total foliar cover	0.030	<b>0.267</b>	< 0.001
Antelope-brush cover	$-5.224 \times 10^{-4}$	-0.003	0.950

Total foliar cover was separated by species group to deconstruct its association with antelope-brush cover using bivariate analyses. Exotic foliar cover, as well as exotic species richness, were significantly associated with antelope-brush cover (Table 2.6). High amounts of exotic foliar cover could reflect contributions of many different exotic species, or alternatively the contributions of one or a few dominant species. In the latter case, removing the contributions of the dominant species to total foliar cover may yield a different relationship between foliar cover and antelope-brush cover. To explore this possibility, the analysis was repeated after removing the contribution of cheatgrass, the most abundant species in the study area. The association between exotic foliar cover and antelope-brush cover was still highly significant ( $r_s = 0.207$ ,  $P < 0.001$ ), however, the  $r_s$  value was significantly smaller in magnitude ( $Z = 2.636$ ;  $P = 0.008$ ). In sharp contrast with these exotic species results, native foliar cover and species richness were both not associated with antelope-brush cover (Table 2.6).

**Table 2.6** Association between plant species diversity (dependent variable) and antelope-brush cover (independent variable) at the finest focus (i.e., 1 m<sup>2</sup>) within the study area extent. Significant ( $P < 0.05$ ) associations are bolded.

Dependent Variable	N	$r_s$	$P$
Exotic species richness	370	<b>0.179</b>	< 0.001
Exotic foliar cover	369	<b>0.389</b>	< 0.001
Native species richness	370	-0.028	0.594
Native foliar cover	369	0.081	0.118

### Predicting Broad Focus Diversity from Abiotic Factors

The full regression model containing applied abiotic predictor variables failed to explain a significant amount of variation in exotic species richness at the broadest focus (i.e., 1,000

m<sup>2</sup>) (Table 2.7A). Similarly, the same full regression model failed to explain a significant amount of variation in native species richness at the broadest focus (Table 2.7B).

**Table 2.7** Multiple regression results for potential applied abiotic predictors of exotic (A) and native (B) plant species richness (dependent variable) at the broadest focus (i.e., 1,000 m<sup>2</sup>) within the study area extent. Significant ( $P < 0.05$ ) independent variables within each model are bolded.

Abiotic Variable	Coefficient	Standardized Coefficient	<i>P</i>
(A) Exotic species richness (N = 36, $F_{6,29} = 1.702$ , $R^2_{adj} = 0.108$ , $P = 0.156$ , SE = 3.276)			
Constant	-15.400	<b><math>6.073 \times 10^{-16}</math></b>	0.351
Slope	0.144	0.330	0.053
Aspect	-0.003	-0.100	0.571
MAT	1.869	0.176	0.337
MAP	0.038	0.211	0.225
Antelope-brush density	0.239	0.308	0.081
Road density	-125.000	-0.093	0.613
(B) Native species richness (N = 37, $F_{6,30} = 1.527$ , $R^2_{adj} = 0.081$ , $P = 0.203$ , SE = 8.775)			
Constant	127.390	<b><math>5.806 \times 10^{-17}</math></b>	0.004
Slope	0.193	0.168	0.315
Aspect	0.018	0.201	0.262
MAT	-6.211	-0.225	0.225
MAP	-0.129	-0.282	0.116
Antelope-brush density	-0.164	-0.080	0.644
Road density	278.806	0.078	0.667

The full regression model containing theoretical abiotic predictor variables (i.e., mean and variation in environmental conditions) failed to explain a significant amount of variation in exotic species richness at the broadest focus (Table 2.8A). Similarly, the same full regression model failed to explain a significant amount of variation in native species richness at the broadest focus (Table 2.8B). The difference in mean environmental conditions between sites and the difference in within-site heterogeneity in environmental conditions between sites were each insignificant predictors of species richness in both models.

**Table 2.8** Multiple regression results for potential theoretical abiotic predictors of exotic (A) and native (B) plant species richness (dependent variable) at the broadest focus (i.e., 1,000 m<sup>2</sup>) within the study area extent. Significant ( $P < 0.05$ ) independent variables within each model are bolded.

Abiotic Variable	Coefficient	Standardized Coefficient	$P$
(A) Exotic species richness (N = 35, $F_{2,32} = 0.363$ , $R^2_{adj} = -0.039$ , $P = 0.699$ , SE = 3.429)			
Constant	12.954	<b>1.022 x 10<sup>-16</sup></b>	< 0.001
Mean	4.362	0.112	0.534
Variance	1.514	0.125	0.491
(B) Native species richness (N = 36, $F_{2,33} = 1.273$ , $R^2_{adj} = 0.015$ , $P = 0.293$ , SE = 8.705)			
Constant	40.066	<b>1.477 x 10<sup>-16</sup></b>	<0.001
Mean	-21.859	-0.250	0.145
Variance	3.019	0.102	0.550

### Predicting Individual Exotic Species Patterns

Analyses of the individual foliar covers of the six most common exotic species confirmed that cheatgrass, Dalmatian toadflax, and yellow salsify were significantly associated with antelope-brush cover but that sulphur cinquefoil, blue forget-me-not, and common draba were not (Table 2.9). The full regression models containing applied abiotic predictor variables failed to explain a significant amount of variation in the individual foliar covers of any of these exotic species (data not shown), though violations of normality and homoscedasticity regression assumptions precluded reliable interpretations of all but the cheatgrass predictive model.

**Table 2.9** Association between individual exotic plant species foliar cover (dependent variable) and antelope-brush cover (independent variable) at the finest focus (i.e., 1 m<sup>2</sup>) within the study area extent. Significant associations are bolded and are significant at Bonferroni-adjusted alpha levels ( $P < 0.05 / 6$  or  $8.3 \times 10^{-3}$ ).

Dependent Variable	N	$r_s$	$P$
Cheatgrass foliar cover	369	<b>0.391</b>	< 0.001
Sulphur cinquefoil foliar cover	369	0.120	0.035
Dalmatian toadflax foliar cover	369	<b>0.183</b>	< 0.001
Blue forget-me-not foliar cover	369	0.050	0.342
Common draba foliar cover	369	-0.070	0.178
Yellow salsify foliar cover	369	<b>0.138</b>	0.008

## DISCUSSION

These results show that the NERR in the antelope-brush grasslands was affected by changing the grain but not the focus or extent of analysis. Contrary to the prevailing hypothesis, a highly significant positive NERR was observed at the finest grain and focus (i.e., 1 m<sup>2</sup>) that appeared to be influenced at least in part by preferential facilitation of exotic plant diversity by antelope-brush shrubs. Also contrary to expectations from the literature, there was no association between exotic and native species richness at the broadest grain and focus (i.e., 1,000 m<sup>2</sup>). Abiotic factors, including mean and variation in environmental conditions per site, failed to account for significant variation in exotic species richness in this system. Although correlative, my results have potentially important practical implications for the mitigation of exotic species invasion in the antelope-brush grasslands.

### Importance of Grain, Focus, and Extent

Changing the scale of analysis clearly altered the direction and the magnitude of the NERR in the antelope-brush grasslands. Although not statistically significant, the  $r_s$  values for the NERRs were increasingly positive with decreasing grain and focus (Table 2.4). These results contrast with the general trend of a concurrent increase in NERR direction and magnitude with focus size supported by previous work (e.g., Davies et al. 2005, Stohlgren et al. 2006) and summarized in Fridley et al. (2007). The only statistically significant NERR in this study occurred at the finest grain (i.e., 1 m<sup>2</sup>) of analysis and persisted regardless of the focus. Also contrary to recent work (e.g., Sandel and Corbin 2010) and emerging theory (Shea and Chesson 2002), changing the extent of the fine focus analysis from a single site (1,000 m<sup>2</sup>) to the entire study area (~112,000 m<sup>2</sup>) did not alter the positive direction of the NERR in this system.

Differentiating between grain and focus can be critical to inferring process from observed NERR patterns. A typical usage of the scale descriptors “fine” and “broad” is to describe either (i) the amount of environmental heterogeneity in or (ii) the spatial size of the grain used (Davies et al. 2005, Fridley et al. 2007). Herein lies the potential for misinterpretation, however, as the environmental heterogeneity encountered in a study area actually relates to the focus of analysis, not the grain, and the amount of heterogeneity within a focus of a given spatial area is system-specific. Using this study as an example, when the 1 m<sup>2</sup> subplot was both the grain and focus of the analysis, the analysis was truly “fine,” assuming that within-focus environmental heterogeneity is limited within this spatial area such that biotic interactions dominate processes. Likewise, when the 1,000 m<sup>2</sup> plot was both the grain and focus of the analysis, the analysis was “broad,” assuming that most individuals cannot

interact and that within-focus heterogeneity in abiotic factors is sufficient to influence the number of species present. When the 1 m<sup>2</sup> subplot was the grain and 1,000 m<sup>2</sup> plot was the focus, however, the analysis was again “broad” despite a “fine” grain of analysis as, based on the previous assumptions, heterogeneity between the ten 1 m<sup>2</sup> subplots per site has now been incorporated into the analysis. NERR predictions may be inaccurate if either the focus and grain differ in size but the grain size is used to rationalize processes affecting the NERR, or if the system-specific assumptions made about the level of heterogeneity in a spatial area are not met (see Chapter 3).

The inconsistency in NERR results at different grains, focuses, and extents in different study systems clearly underscores the importance of considering all components of scale when synthesizing NERR patterns in the literature. Moving forward, it is important that future research be consistent in the terminology used to describe scale in order to facilitate meta-analyses and comparisons across studies (Scheiner et al. 2000). The terms “fine scale” and “broad scale” are often misinterpreted or ambiguously used in practice in invasion ecology studies, as these terms can be equivocally applied to all of the grain, focus, and extent of the analysis, and as these terms may apply to spatial area without consideration of the level of environmental heterogeneity within that area. As such, it is recommended instead that the component of scale under analysis be explicitly stated (e.g., fine grain, broad focus, broad extent), and that these terms be relative to other studies in the literature, rather than relative to other grains, focuses, or extents used within a single study. Such a strategy would likely facilitate interpretations of NERRs and generalizations across future studies.

### **Explaining Fine Focus Diversity Patterns**

Both native species richness and total foliar cover were strongly positive predictors of exotic species richness at the finest (i.e., 1 m<sup>2</sup>) focus that, along with antelope-brush cover, collectively explained 22.0% of the variation in exotic species richness (Table 2.5). The result of a positive fine focus NERR opposes that predicted by the *biotic resistance hypothesis* or other hypotheses that support the competitive dominance of one species group over the other (i.e., most of the negative NERRs in Table 1.2). While previously ignored in favour of negative biotic (e.g., competition, predation) and abiotic interactions, recent work has brought to the forefront the equal importance of positive interactions such as facilitation in structuring ecological communities (Bertness and Callaway 1994, Bruno et al. 2003). When related to niche space, these positive interactions have the potential to increase the spatial extent of the realized niche of a species, exotic or native, relative to its fundamental niche such that that species is able to survive in areas where it would not be

able if it was alone (Bruno et al. 2003). Facilitation is one hypothesis that supports a positive fine focus NERR whereby high native diversity increases the establishment success of exotic species, or where the presence of a single, strong community-structuring species (e.g., large perennial herbs, shrubs, trees) facilitates the establishment of both exotic and native species (Bruno et al. 2003, Fridley et al. 2007). Plant communities are often structured by both positive and negative interactions, however, with only the net result of these interactions apparent in an observational study (Callaway 1995).

Facilitative interactions between plants are most commonly reported from arid and semi-arid environments, but have been observed in a range of ecosystems (Bertness and Callaway 1994, Holmgren et al. 1997). In general, the role of facilitation in structuring communities is thought to increase with environmental stress and vary inversely with competition (Callaway et al. 2002). Facilitative interactions between shrubs and other plants, commonly called nurse-protégé interactions, have been well documented in stressful, arid environments (Callaway 1995, Flores and Jurado 2003). Specifically, antelope-brush shrub facilitation of several individual exotic species in arid environments has been previously reported. For example, Griffith (2010) demonstrated a positive spatial association between antelope-brush and both cheatgrass density and reproductive potential compared to intershrub spaces. Consistent with facilitative interactions, this author also found that areas beneath the shrub canopy had higher soil fertility and less extreme microclimates compared to intershrub spaces. Within the present study area, Krannitz (2008) also found that cheatgrass, as well as diffuse knapweed, had marginally higher foliar cover but similar densities under shrubs compared to intershrub spaces. Processes by which shrubs may facilitate smaller plants include reducing environmental stress, augmenting resource availability, and providing protection from herbivory (Callaway 1995).

The association between antelope-brush canopy cover and plant species diversity was investigated to elicit the potential role of nurse-protégé interactions in this system. The dominant shrub species in the study area, antelope-brush, may facilitate other plant species by providing shade to reduce heat and therefore water stress, by increasing nutrient availability beneath the shrub canopy, and by providing refuge from livestock and native ungulate herbivores (e.g., Griffith 2010). The results of this study are consistent with a role of antelope-brush shrubs as facilitators of exotic species diversity, as both exotic species richness and foliar cover were positively associated with antelope-brush cover at fine focuses in the study area (Table 2.6). This association persisted even when cheatgrass, which made up approximately one fifth of total plant cover, was excluded from the foliar

cover analysis, although the magnitude of the association was significantly smaller. This result indicates that shrub cover primarily facilitates this dominant exotic species but also facilitates other exotic species. In contrast, however, neither native species richness nor foliar cover was associated with antelope-brush cover (Table 2.6).

In stressful, arid environments, plant establishment is thought to occur only where there is a pulse of water resources to the entire system (i.e., during wetter than average seasons) or where the microhabitat is sufficiently ameliorated by nurse plants that shade the substrate, thereby augmenting soil moisture and reducing transpiration rates to decrease drought stress (Davis et al. 2000, Flores and Jurado 2003). A speculation for this system, based on the literature, is that exotic species in the study area may preferentially occupy microhabitats beneath shrubs to take advantage of these less stressful environments; in effect, the antelope-brush shrubs may be acting as refugia and possibly stepping stones for exotic plant spread in invaded areas during particularly stressful (i.e., dry) years (see also Griffith 2010). Further, less stressful conditions such as cooler, wetter spring and summer seasons (e.g., during La Niña years) may allow exotic species to spread out from these refugia into other areas in the landscape. In contrast, shrubs may not facilitate native plants in the same way because these plants are specifically adapted to dry, desert-like conditions and therefore can just as easily grow between versus under shrubs.

Shrub facilitation alone, although suggestive, paints an incomplete picture of how a positive NERR would arise at fine focuses in the study area, as antelope-brush shrubs appear to facilitate only exotic and not native species. It may be that this positive NERR results from facilitative interactions between exotic species and other native species, in addition to antelope-brush, such that the richness of one species group ameliorates the habitat, and therefore the establishment, of the other group. Many of the common native species in the study area (see Table 2.2) are relatively large bunchgrasses and asters that may produce enough shade to decrease heat and drought stress, or may perform some other facilitative role (e.g., protection from herbivory, nutrient catching) to invader richness in the study area. As there was no association between exotic and native foliar cover, these native plants may facilitate the initial establishment of exotic species, but not necessarily their spread. An alternative but related hypothesis that supports a positive NERR at fine focuses is that exotic and native species in antelope-brush grasslands are facilitated by generalist mutualisms (e.g., pollinators, seed dispersers, fungal associations) in the environment that augment the richness of both species groups (i.e., *mutualist facilitation hypothesis*, Table 1.2); testing for such associations was not within the scope of this study.

While the results of this study are indicative of some type of facilitative interaction, they are also correlative and should thus be considered in light of other hypotheses that could support a positive NERR at fine focuses (Table 1.2). The *spatial heterogeneity hypothesis*, while developed for broad focuses, may also hold true at fine focuses in systems where there is sufficient environmental variation to influence species richness (Davies et al. 2005). As shown in this study, variation in within-site environmental conditions across the study area failed to explain a significant amount of variation in exotic or native species richness. However, it may be that spatial heterogeneity occurs at a finer level than that assessed. For example, antelope-brush shrubs appeared to have strong community structuring effects in this system. These shrubs may contribute to microhabitat variation at fine focuses due to differences in light or moisture availability and therefore a subsequent increase in species richness (Alpert and Mooney 1996). Future research could explore this possibility by quantifying fine focus heterogeneity.

As summarized in Table 1.2, the *invasion windows*, *empty niche*, and *fluctuating resource availability* hypotheses can each also support a positive fine focus NERR. An implicit assumption of the NERR under these hypotheses, however, is that exotic species richness is able to increase due to fine grain availability of resources without directly competing with native species. The high amount and variation of bare soil in the study area could suggest that the antelope brush ecosystem is naturally undersaturated, which on one hand would potentially lower the frequency of competitive interactions between exotic and native species, and on the other would present opportunities for invasion. However, high bare soil cover is correlated with fine scale disturbance from livestock grazing in the study area (Krannitz 2008), which could reduce the competitive ability of native species while creating empty niches for disturbance-adapted exotic species (*sensu* Davis et al. 2000), subsequently leading to a negative fine focus NERR. It is therefore possible that the observed positive NERR could also be due to disturbance creating niches for exotic species that are competing with native species but that have not yet caused the widespread local extirpation of native species. This would create an artificial positive NERR in the system during the time lag between exotic invasion and native extirpation, that is, until the extinction debt in the antelope-brush grasslands was paid, at which point a negative NERR would be expected (Malanson 2008).

### **Explaining Broad Focus Diversity Patterns**

Contrary to the prevailing prediction of a positive NERR (Fridley et al. 2007), there was no association between exotic and native species richness at broad grains and focuses in the



study area. The question of whether biotic or abiotic interactions are prevalent at spatial focuses between 1 m<sup>2</sup> and 1 km<sup>2</sup> is unclear in NERR theory (Fridley et al. 2007). One possible explanation for the lack of a significant NERR is that it represents the net result of the opposing effects of biotic and abiotic interactions occurring at these intermediary focuses; in this case, however, a positive relationship would still be expected in this system given the highly significant positive NERR demonstrated at the 1 m<sup>2</sup> focus. As most individuals likely do not interact in this herb-dominated ecosystem at the broader grain sizes, it seems reasonable to assume that abiotic factors are the main drivers of plant diversity at these grains in the study area. However, this assumption was not supported by the applied abiotic predictive models (Table 2.7) in which none of the abiotic variables, specifically selected due to their known influences on plant diversity in other systems (e.g., Davies et al. 2005, MacDougall et al. 2006, Lilley and Vellend 2009, Griffith 2010), were significant predictors of either exotic or native species diversity at the broadest focus (i.e., 1,000 m<sup>2</sup>), despite a substantial range in species richness and environmental conditions in this system (see Table A.1).

Positive broad focus NERRs are thought to be either the result of landscape variation in either mean (i.e., *biotic acceptance hypothesis*) or heterogeneity of (i.e., *spatial heterogeneity hypothesis*) environmental conditions (Davies et al. 2005, Stohlgren et al. 2006, Fridley et al. 2007). As shown in this study, neither of these factors was positively associated with species richness at the broadest grain and focus (Table 2.8). However, should a positive broad focus NERR be expected in all ecosystems? The antelope-brush grasslands demonstrated high variation in fine grain cover of cryptogam, bare soil, and rock cover, yet within-site heterogeneity was not associated with either exotic or native species richness across the study area. A speculation for this system is that while relatively high in site-level variation, the study area could be relatively homogenous across sites in this variation; that is, the number of unique habitat opportunities at a given site is relatively similar throughout the entire study area. This may have occurred because this study investigated only a single ecosystem type, though it did encompass over one half of the Canadian distribution and five different ecological communities within the antelope-brush grasslands. Previous studies documenting positive broad focus NERRs typically spanned multiple ecosystems or much broader spatial extents NERRs (e.g., Stohlgren et al. 2003, Stohlgren et al. 2006).

## **Management Implications**

Predictive models can be useful tools for land managers tasked with managing exotic species in conservation areas, particularly when the resources necessary for extensive field inventories are limited. Significant predictive models explain exotic species diversity and distribution patterns based on known (or readily acquired) native diversity or environmental variables, and have been used successfully to forecast where highly invaded areas are in many national parks and other conservations areas (e.g., Tyser and Worley 1992, Stohlgren et al. 1999a, Pysek et al. 2002, Bashkin et al. 2003, Underwood et al. 2004, Allen et al. 2009). The results of such models can then be used to focus control, eradication, and restoration activities in these ecologically valuable areas in the absence of primary field surveys. In the antelope-brush grasslands of the South Okanagan Valley, however, broad focus exotic plant diversity patterns were not readily explained by native diversity or by available topographical, climatic, or disturbance factors, despite a range in exotic richness from 5 to 20 species per site.

These findings potentially complicate the management of exotic plants and their ecological consequences to the extent that predicting where highly infested areas are within this ecosystem appears challenging. In the absence of additional information, it may therefore be advisable for land managers to target the acquisition and restoration of remaining parcels of antelope-brush grassland habitat based on other conservation values (i.e., proximity to other conserved areas, known habitat for species at risk). The role of facilitation by shrubs in this system, and specifically antelope-brush, deserves further study from both academic and applied standpoints. If antelope-brush shrubs ameliorate conditions for exotic species and their spread, as Griffith (2010) has shown and as the results of the current study suggest, then management efforts might benefit from targeting shrub understoreys. However, the effectiveness of different management activities (e.g., targeted hand removal, mowing, or herbicide application) and the potential consequence for species at risk and other native species, particularly the shrubs themselves, should first be assessed in this habitat through experimentation.

## **CHAPTER 3: CONCLUSION**

### **GENERAL DISCUSSION**

Exotic plant invasion is a serious threat to the endangered antelope-brush grasslands of the South Okanagan Valley. However, patterns of exotic plant diversity had not been previously researched in this ecosystem using a statistically rigorous sampling approach at multiple scales. In an effort to identify and predict where exotic plant invasion occurred in this ecosystem, this research investigated the relationship between exotic plant diversity and both biotic and abiotic variables including native species richness, slope, aspect, mean annual temperature (MAT), mean annual precipitation (MAP), antelope-brush density, and road density. These variables were specifically chosen because they were known predictors of exotic plant invasion in other similar systems and they were either freely available or relatively easy to quantify in the field. This was done so that the results of this study could be easily interpolated and extrapolated throughout the entire Canadian range of the antelope-brush grasslands to predict areas with high exotic plant invasion. The original intention was to provide a management tool that could be easily used by government officials and land managers to inform restoration and acquisition efforts in this ecologically valuable ecosystem.

As shown by the results in Chapter 2, however, geographical variation in the species richness and foliar cover of exotic plants was not readily explained in the antelope-brush grasslands. In particular, available abiotic variables were not significant predictors of exotic (or native) species richness at the broadest grain and focus (i.e., 1,000 m<sup>2</sup>), which was the most relevant to regional or habitat-based exotic plant management. Although it may seem intuitive that, for example, habitats with higher surrounding road density or at lower elevations corresponding to higher anthropogenic development should be more highly invaded by exotic plants, the results of this stratified random sampling design of available antelope-brush habitats showed that this was not the case. These results should not be taken to mean that exotic plant invasion is uniform throughout the study area, but rather that areas of particularly high invasion in the landscape cannot be predicted by easily obtainable environmental variables. This study had a primarily academic focus of predicting patterns of exotic plant diversity and their scale sensitivity rather than of predicting the ecological impacts of specific exotic species in this ecosystem. However, as shown in Chapter 2, the assembled abiotic model also failed to account for variation in the foliar cover of cheatgrass, sulphur cinquefoil, and Dalmatian toadflax, which were the most noxious exotic species observed in the study area.

Exotic species richness was found to be significantly associated with both native species richness and foliar cover at the finest grain and focus (i.e., 1 m<sup>2</sup>). From a management perspective, a positive fine focus relationship between exotic and native species richness is a poor management tool, as arguably more resources, and certainly not less, would be required to inventory native diversity in order to predict exotic species richness, rather than to simply inventory exotic species richness in the first place. However, the investigation of this relationship defines this research as a NERR study and further informs this literature with results from a previously unknown ecosystem. Interestingly, few if any previous studies included total foliar cover as a covariate when predicting exotic from native species richness, as done in this study. Yet, this is essential for ascertaining whether native species richness can account for a significant amount of variation in exotic species richness over and above the inevitable influence of total area occupied by plants, particularly in an unsaturated system.

The majority of the 37 sample sites in the current study were located in areas designated for conservation and therefore likely represent some of the highest quality remaining antelope-brush grasslands in Canada. However, this research confirms that these areas are highly invaded by exotic plants including several noxious species. What does the presence of the observed exotic plants mean for the species at risk that use these endangered habitats? No plant species listed provincially or federally as either endangered, threatened, or of special concern were observed during this study; this result does not necessarily mean that these species were absent from the study area as by definition these species are regionally rare and may have been missed by the sample sites. However, incidental observations during the fieldwork confirmed antelope-brush grassland use by several animal species at risk, including the federally threatened Lewis's woodpecker (*Melanerpes lewis* Gray), Behr's hairstreak, western rattlesnake, and gopher snake, and the provincially blue-listed bighorn sheep.

Exotic plant invasion can have a wide range of ecological effects on species at risk and research investigating patterns of exotic plant invasion can help inform land managers of these effects. Within the antelope-brush grasslands, for example, this study addressed some of the research gaps identified in the recovery strategy for the lycaenid butterfly Behr's hairstreak, the focal species for the conservation of these grasslands (Southern Interior Invertebrates Recovery Team 2008). Specifically, the recovery strategy identified a need for research that determined the impacts of exotic plants on this butterfly's larval host plants (i.e., antelope-brush shrubs) and if there were correlations between antelope-brush and

exotic plant densities or specific species. As the current study shows, antelope-brush shrub cover was positively associated with both exotic plant species richness and foliar cover, as well as with the foliar cover of cheatgrass, Dalmatian toadflax, and yellow salsify. These results suggest net positive interactions between shrubs and exotic species, although negative interactions (e.g. competition for water resources) may also be occurring. Additional experimental tests would be required to deconstruct these relationships in the study area. As observed, however, exotic plants do not appear to be adversely affecting this butterfly's larval host plant in the study area.

Six regulated noxious weeds were observed in the study area. Of these exotic species, four occupied <0.1% of the landscape and therefore likely have little individual ecological impacts on the antelope-brush grasslands. Both perennial sow-thistle and Canada thistle were only present at one site each. Given the long history of Canada thistle in the South Okanagan (Cannings et al. 1998), it is likely that the record of this species in the antelope-brush grasslands does not represent a new introduction but rather that this species is rare in this arid environment; the site that this species was observed at was located adjacent to an ephemeral stream, which likely results in more mesic soil conditions compared to those observed at the other sites. Despite the fact that diffuse knapweed and common hound's-tongue also occupied <0.1% of the landscape, these noxious species were much more widely distributed throughout the landscape. Both sulphur cinquefoil and Dalmatian toadflax have been identified as of particular concern in South Okanagan Valley grasslands due to their aggressive nature and rapid expansion in the last two decades (Cannings et al. 1998); these two species were widespread throughout the majority of the study area, suggesting that eradication at this point may be challenging.

As expected, most of the recorded species in the antelope-brush grasslands were locally rare. As shown by the species accumulation curves (Figure 2.4A), sampling was relatively complete, despite the fact that the sample sites only covered a small fraction (i.e., 0.002%) of the potential sampling area. This suggests that the remaining species not observed are very locally or regionally rare and are patchily distributed. The species accumulation curves also showed that the species pool for native plants was much larger than that of their exotic cohorts. As shown by the species occupancy histograms (Figure 2.4B-C), however, common exotic species (i.e., those occupying at least 10% of sites sampled) occupied, on average, the same number of sites as common native species. This suggests that (i) the exotic species present in the antelope-brush grasslands are reasonably well adapted to the semi-arid environmental conditions found throughout this system, and that (ii) propagule

pressure is not a limiting factor for many species in this system. As these grasslands continue to undergo disturbance through livestock grazing, vineyard development, recreational use, and other anthropogenic activities, the potential for exotic plant introductions and establishment will likely increase.

This study employed a relatively novel approach to investigating NERR patterns by simultaneously examining multiple biotic and abiotic variables (Fridley et al. 2007, Eschtruth and Battles 2009), and more specifically the role of anthropogenic disturbance (Lilley and Vellend 2009), in describing and predicting patterns of exotic plant diversity. Although exotic plant diversity patterns have been studied in a variety of shrub-steppe habitats (e.g., Bashkin et al. 2003, Stohlgren et al. 2005, Stohlgren et al. 2006), no such research appears to have been completed to date in antelope-brush grasslands or in shrub-steppe communities as far north as Canada. The NERR in the antelope-brush grasslands was found to be affected by changing the grain but not the focus or extent of analysis. This inconsistency in NERRs at different components of scale and between different study systems clearly underscores the importance of considering all components of scale when synthesizing NERRs across the literature. The inclusion of the scaling term “focus” in relation to the NERR is neither meant to demand the re-evaluation of previous studies nor to revolutionize future NERR studies. This study simply draws attention to the applicability of this component of scale in invasion ecology and specifically in NERR studies. As Scheiner et al. (2000) identified in the community ecology context, and which appears to be true in NERR studies, altering the focus of analysis may change the relative importance of the ecological processes dictating the observed pattern.

## **A PROPOSED NERR FRAMEWORK**

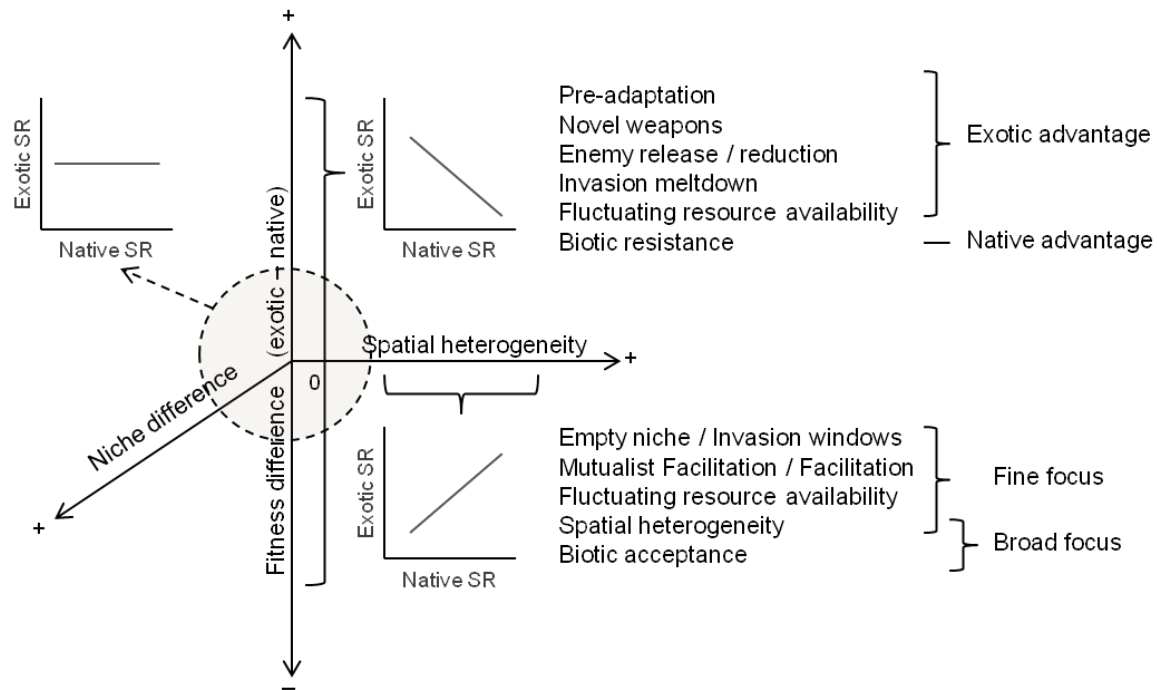
The results of this study were unexpected based on the prevailing NERR hypotheses. I was therefore challenged to re-examine the data in light of other possible hypotheses. Numerous hypotheses have been proposed to explain how exotic species are able to invade novel habitats and several recent publications have attempted to unite all or part of these hypotheses under simplified frameworks based on community ecology theory (e.g., Shea and Chesson 2002, Catford et al. 2009, MacDougall et al. 2009). As summarized in Fridley et al. (2007), some of these hypotheses have been previously invoked to interpret NERRs at both fine and broad spatial focuses. However, evidence to date indicates that NERRs can take on any form (i.e., negative, positive, no relationship) at any observational scale, although some forms appear more common at particular scales (see Figure 1 in Fridley et al. (2007)). This variation is not easily reconciled with existing theoretical frameworks.

Particularly desirable would be a framework that (i) draws upon the existing, simplified frameworks for understanding invasion biology founded in community ecology theory, and (ii) is able to accommodate NERRs that vary in form and strength across observational scales. Here such a framework is proposed, extended largely from MacDougall et al.'s (2009) work, which has not yet been directly applied to NERR theory despite its obvious application.

As described in the introductory chapter of this thesis, MacDougall et al. (2009) applied both niche and coexistence theory to explain exotic species dominance over, repulsion by, and coexistence with native species based on both niche and fitness differences between the two species groups. These authors' framework was illustrated using a schematic diagram that included two axes (see Figure 1 in MacDougall et al. (2009)): fitness difference (invader minus resident) along the *y*-axis and niche difference along the *x*-axis. As formulated, MacDougall et al.'s (2009) framework can be used to explain both negative NERRs and situations where there is no relationship between exotic and native species richness at fine focuses. Assuming that (i) variation in environmental conditions is limited at fine focuses, such that there is a small number of niche opportunities at each sample site within a study system, and (ii) biotic interactions dominate community diversity patterns, a strongly negative NERR would result if numerous exotic species were each competitively dominant (i.e., had higher average fitness) compared to resident native species from similar niches within a community, and vice versa. Incorporating the hypotheses presented in Table 1.2, invader dominance would occur if the exotic species had higher average fitness due to *pre-adaptation*, *novel weapons*, *enemy release/reduction*, or exclusive facilitative interactions (i.e., *invasion meltdown*). Invasion resistance would occur if the native species had higher average fitness (i.e., *biotic resistance*). In order for a negative NERR to emerge, variation in fitness differences between exotic and native species is required (i.e., observed fitness differences must span a broad range of the fitness difference axis, from positive to negative fitness differences), otherwise no relationship would result. Also, no relationship between exotic and native species richness would emerge if niche differences prevented competition between these two species groups such that one species group was not able to dominate the other group.

The framework in MacDougall et al. (2009) is limited in its applicability to NERRs in that (i) it applies exclusively to fine focus NERRs within sites of limited environmental variation, (ii) it explains invasion solely based on characteristics of exotic and native species and not of the invaded environment, and (iii) it fails to explain how positive fine focus NERRs could occur.

The framework proposed here, illustrated in Figure 3.1, attempts to address these shortfalls. The key adjustment of MacDougall et al.'s (2009) framework is the inclusion of a third axis that represents the number of unique niche or habitat opportunities, or for simplicity, the spatial heterogeneity in the system.



**Figure 3.1** Proposed native-exotic richness relationship (NERR) framework based on fitness differences between exotic and native species, niche differences between these species, and spatial heterogeneity in the invaded environment. Fine focus relationships between exotic and native species richness (SR) are a function of all three axes, while relationships at broad focuses are based primarily on the spatial heterogeneity axis as most individuals are not able to interact at these scales. Negative NERRs primarily occur as a result of variation in fitness differences between exotic and native species. Positive NERRs primarily occur as a result of variation in the spatial heterogeneity of the environment, assuming heterogeneity and species diversity are positively related. Invasion biology hypotheses related to both negative and positive NERRs (see Table 1.2) are provided. See text for further explanation. Adapted from Figure 1 in MacDougal et al. (2009).

With this axis in place, a positive fine focus NERR could result where there were large niche differences between most plants (i.e., exotic and native species are not competing) in a study system that, across sample sites, exhibited variation in the number of niche opportunities available. At sites with few unique niche opportunities, the diversity of both exotic and native species would be low. However, sites with abundant unique opportunities would be able to support high diversity of both species groups, provided both groups



benefited similarly from and were able to take equal advantage of increased niche opportunities. In order for a positive NERR to emerge, sufficient variation in the number of unique niches within the system is required (i.e., observations must span a broad range of the spatial heterogeneity axis). At fine focuses, these differences could arise through varied soil conditions or varied amounts of cover of species with strong community structuring effects (*sensu* Davies et al. 2005). This last point incorporates several of the hypotheses in Table 1.2. For example, areas with facilitation by one or a group of species, although technically a biotic interaction, could behave abiotically by creating new microhabitats and therefore more unique niche opportunities compared to areas with no or weaker facilitation (i.e., *mutualist facilitation*). A localized resource pulse could also create new unique niche opportunities (i.e., *fluctuating resource availability, empty niche, invasion windows*) and support a fine focus positive NERR provided that native species are not adversely impacted. At fine grains that are truly homogeneous and thereby present little variation in the number of unique niche opportunities per site, the spatial heterogeneity axis is irrelevant, and the NERR is determined exclusively from the fitness differences and niche differences axes, which is the common assumption of fine focus NERR predictions.

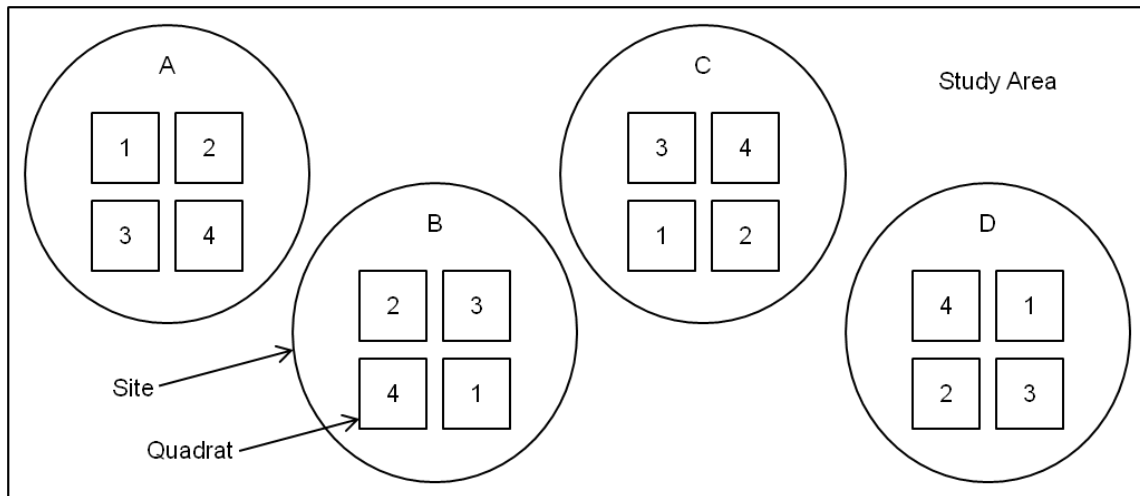
The inclusion of the spatial heterogeneity axis in the proposed framework also allows integration of broad focus invasion ecology hypotheses and NERR patterns. As abiotic factors tend to take precedence over biotic interactions at broad focuses, the fitness difference and niche difference axes are irrelevant; the magnitude and direction of the NERR is determined solely by the spatial heterogeneity axis. As at fine focuses, variation in the number of unique habitats within the system is required in order for a positive broad focus NERR to emerge (i.e., observations must span a broad range of the spatial heterogeneity axis). In contrast, no broad focus NERR would result in a system with little variation in the number of unique habitats (i.e., all sites lie at similar positions along the spatial heterogeneity axis). This point relates to both the *biotic acceptance hypothesis*, as diversity would be constant if all habitats were equally “good” for exotic and native species, as well as the *spatial heterogeneity hypothesis*, where heterogeneity and species diversity are positively related (Davies et al. 2005, Melbourne et al. 2007). Negative broad focus NERRs are rarely observed in practice (Fridley et al. 2007) and are more difficult to reconcile with the proposed framework. In contrast to most published studies, Lilley and Vellend (2009) observed a negative broad focus NERR, for which they provided an evolutionary explanation: exotic and native species respond differently to abiotic heterogeneity in climatic and disturbance conditions due to the separate evolutionary histories of each species group. The proposed framework can accommodate these unusual findings because, despite

drawing upon evolutionary explanations, they nonetheless invoke fitness differences between exotics and natives as the proximate mechanism. However, one would need to place the fitness difference axis within a broader spatial context than is usually done.

Clearly, the magnitudes of the NERRs in the examples provided above are extremes and a range of different strength negative and positive NERRs are possible as a result of the collective interactions between exotic and native species with varying fitness and niche differences, as well as interactions between these species and the degree of variation in their environment. The strength of the proposed framework is that it provides a theoretical explanation for all possible NERR results given a particular study system based on the existing invasion biology hypotheses. This framework is based on the underlying assumptions that (i) both exotic and native propagule pressure are equal and neither is a limiting factor within a system, and that (ii) both exotic and native species richness are positively related to variation in the environment such that an increase in the number of unique niches (or habitats) corresponds to a concomitant increase in species richness (Scheiner et al. 2000).

The proposed NERR framework in Figure 3.1 can be applied to explain the results in Chapter 2 of this thesis as an example. The observed positive fine focus NERR could have occurred as a net result of large niche differences but minimal fitness differences (i.e., reduced competitive interactions) between most exotic and native species in a landscape with substantial variation in unique niche opportunities at the fine focus (i.e., 1 m<sup>2</sup>). Evidence to support this explanation comes from the arid, stressful nature of the antelopebrush grasslands, as competitive interactions are thought to vary inversely with environmental stress (Callaway et al. 2002) and therefore may have had a reduced role in community assembly in this system. Both shrubs and large perennial bunchgrasses have been shown to increase variation in soil nutrient levels and other parameters (i.e., increase number of unique niches) at scales of less than 1 m<sup>2</sup> in other semi-desert shrub-steppe grassland systems (Jackson and Caldwell 1993, Schlesinger et al. 1996). Fine focus variation in the number of niche opportunities in the study area could also have resulted from the high inconsistency in cryptogam, rock, and bare soil cover. These factors could have increased the degree of variation in heterogeneity at the finest focus, as subplots located between community structuring plants would have had a low number of unique niches but subplots located under these plants would have had a high number of unique niches (especially for small plants; see Aarssen et al. 2006), resulting in a positive fine focus NERR. In contrast, the result of no relationship between exotic and native species richness at the

broad focus (i.e., 1,000 m<sup>2</sup>) could have occurred if the study area exhibited limited variation in the degree of heterogeneity encompassed by a site, such that each site across the study area had approximately the same number of niche opportunities. For example, the antelope-brush shrub canopy covered a mean area of 5.42 (6.07) m<sup>2</sup> per shrub in the study area, suggesting that the broadest focus would have been sufficiently large enough to each encompass the heterogeneity found both under and between these shrubs. Figure 3.2 is a conceptualized diagram to help explain the possible variation in the degree of heterogeneity in a study area depending on the focus of analysis.



**Figure 3.2** Conceptual diagram of the scale dependency of the variation in degree of heterogeneity in a hypothetical study area. Each circle (A-D) represents a site, each containing four square quadrats. The number in each quadrat is the number of unique niches present in that quadrat and, for simplicity, quadrats sharing the same number represent the same habitat type. If the focus of analysis is the quadrat (N = 16), fine focus spatial heterogeneity ranges from one to four unique niches and results in a positive NERR across the study area. In contrast, if the focus of analysis is the site (N = 4), broad focus spatial heterogeneity is consistent at four habitats (or ten niches) per site and results in no NERR across the study area. Exotic and native species richness are assumed to vary similarly and positively with spatial heterogeneity, as well as with some stochastic variation.

### ASSUMPTIONS AND LIMITATIONS

The design and implementation of this research had several limitations common to many landscape scale studies. The locations of the sampling sites were limited by the availability of known, accessible antelope-brush habitat within the South Okanagan Valley, which were identified using the most recently completed TEM available at the start of this research (Iverson and Haney 2006). This mapping was completed at a 1:15,000 scale with a maximum of three ecological communities per ecosystem polygon, therefore small patches

of antelope-brush in the study area may have been excluded from the potential sampling area. Of the approximately 3,386 ha of antelope-brush grassland remaining, 59% of this habitat is located on Indian Reserve (Dyer and Lea 2003) and was not included in the potential sampling area due to data publishing restrictions. The results of this study may not be applicable to the Indian Reserve, despite its proximity, due to differences in land management practices including grazing regime.

The number of sample sites within the sampling area was limited by the intensity of the multi-scale sampling design, as each site took between three and five hours to sample in addition to the time required to access each site, and each sampling period was limited to 2.5 weeks to minimize phenological variation among sites. Additional sample sites would have increased the power of the predictive model at the broadest focus, particularly in light of the high number (i.e., six) of non-correlated, ecologically relevant, potential predictor variables included in the model. Although there was sufficient sampling power at the finest sampling focus, a potential limitation of these results is that this analysis did not take into account spatial autocorrelation between the ten 1 m<sup>2</sup> subplots within a site compared to similarly sized subplots throughout the study area. However, other published studies using the modified-Whittaker plot design also did not take spatial autocorrelation into account (e.g., Stohlgren et al. 1999a, Stohlgren et al. 2005), so the current research is comparable with these studies.

Plant species identification was limited by the skills of the data collectors. While all efforts were made to accurately identify each plant to species using field identification guides, field photos, collected specimens, provincial identification guides, local expert advice, and both regional and habitat-specific species lists, some species may have been misidentified. Morphologically similar species likely had a higher probability of being unintentionally grouped together rather than distinguished as separate species. Smaller, less showy species also likely had a higher probability of being missed at the three largest sampling grains compared to their larger, showier counterparts; this was likely not a significant source of error at the 1 m<sup>2</sup> sampling grain. This study was designed to sample during both peak flowering phenology and peak biomass; as such, some very early spring, late summer, and fall bloomers may have also been unavoidably missed during data collection. The plant species identified in this study may also have been influenced by the atypically wet weather conditions present during the second of the two sampling periods.

The abiotic regression analyses were affected by the limitations of the source data. Based on visual comparisons within the GIS between the available digital road atlas and recent

orthophotos, for example, some roads were missing or misaligned in the road atlas, which may have influenced the surrounding road density calculation. Further, although the digital road atlas did distinguish between paved, loose, and rough roads, these classifications were not linked to any compositional attributes (e.g., age, amount of use, width), which are commonly measured to infer the effects of roadway disturbance on exotic plant patterns (Forman and Alexander 1998, Christen and Matlack 2009). In addition, due to prohibitive costs, the climate data were calculated for each site based on its coordinates and elevation using climate normals rather than site-specific measurements. Despite these limitations, these data were used because they were the best freely accessible data available for the study area and therefore the most useful for extrapolation by land managers throughout the study area.

Finally, the abiotic variables included in the predictive models were assumed to be the most relevant to exotic species diversity patterns in the study area for the reasons described in the introduction of Chapter 2 of this thesis. However, other abiotic variables may also be important for community assembly in this system. Grazing history is one disturbance factor that was not included in the predictive models but that likely influences exotic diversity patterns. Prior to European settlement, antelope-brush grasslands were grazed at a low intensity by native ungulates (Lea et al. 2004), but beginning in the 1850s these grasslands were intensively grazed during northward annual cattle drives through the valley bottom (Mack 1981). Livestock grazing can have particularly detrimental effects in this system due to the absence of large hoofed mammals throughout much of its evolutionary history: the characteristic bunchgrasses lack herbivore-adapted traits and trampling hooves can permanently destroy the fragile cryptogam layer between the bunchgrasses, providing sites for exotic plant establishment (Mack and Thompson 1982). Many of the antelope-brush habitats continue to be grazed despite their conservation status, as active cattle grazing was observed at nine of the sampled sites and grazing may have also occurred at nine additional sites that were not fenced from adjacent grazing areas. Remnants of fences and other structures were prevalent throughout most of the study area, betraying its grazing history. Despite its likely influence, grazing intensity could not be effectively quantified at all of the sample sites due to the absence of published information, and so was excluded from the abiotic predictive models.

## **SUGGESTIONS FOR FURTHER RESEARCH**

The results of this research suggest several possible avenues for future research. A highly significant positive NERR was observed at the finest focus in this study; however, the

mechanism for this association could not be confirmed as observational studies cannot indicate cause and effect relationships between variables. Although suggestive of facilitative interactions, other hypotheses support a fine focus positive NERR and may be applicable to the studied system as described in the discussion of Chapter 2. Competitive and other adverse biotic interactions could also be occurring in this system, with only the net outcome apparent in an observational study (Callaway 1995). Future research could experimentally test these alternative hypotheses and disentangle positive from negative and biotic from abiotic interactions in this system to determine the mechanism responsible for the positive NERR. To more directly examine the role of antelope-brush shrubs in preferentially facilitating exotic over native species diversity, plant diversity assessments directly beneath shrubs could be compared to adjacent intershrub spaces of similar areas (e.g., Lopez et al. 2009). Future research could also investigate the speculation that antelope-brush shrubs provide unique, less stressful microhabitats by investigating both the mean of and variation in fine focus abiotic variables such as soil moisture, soil temperature, nutrient availability, and seed caching under shrub canopies compared to intershrub spaces in this system. The current research focused primarily on exotic plant diversity patterns rather than on the specific exotic plants present in the antelope-brush grasslands. Further analysis could be conducted on the existing data to determine what functional roles the existing exotic species take on in their novel environment, how these roles parallel or compete with those of native resident plants, and what the ecological consequences of these interactions are for species at risk in the endangered antelope-brush grasslands.

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## APPENDIX

**Table A.1** Location and plant species richness data for all 37 sites sampled in the study area. The easting and northing are provided for the centre of each site using the Universal Transverse Mercator (UTM) coordinate system (Zone 11). Elevation (m above sea level), slope (degrees), and aspect (degrees) were measured from the bottom right corner of each site. The species richness (SR) of exotic and native plants from the 1,000 m<sup>2</sup> plot at each site is also provided.

Site No.	Site Name	Easting	Northing	Elevation	Slope	Aspect	Exotic SR	Native SR
1	Kennedy West	316388	5459310	321	2	240	12	28
2	Kennedy Centre	316826	5459470	335	1	240	13	39
3	Kennedy East	317287	5459230	355	2	240	5	24
4	Kennedy Ridge	317519	5459600	435	20	240	18	48
5	Leir	315711	5464860	340	12	230	18	31
6	Allendale West	314878	5466780	404	2	230	15	42
7	Allendale East	315690	5466510	435	4	230	20	27
8	McLean Creek Road Centre	315625	5470270	471	8	240	17	50
9	McLean Creek Road South	315556	5469130	460	12	210	18	33
10	Allendale Lake Road	316637	5467980	523	2	320	15	46
11	Weyerhauser Pasture	316532	5466970	511	25	105	18	38
12	Weyerhauser Road	316441	5467440	477	15	340	14	43
13	Scudder House	317012	5462010	385	25	255	20	44
14	Fairview Southwest	311558	5451420	507	25	200	11	34
15	Fairview Northwest	311454	5451830	565	17	265	9	53
16	CWS by River	315849	5460970	332	8	60	12	39
17	CWS by Pipeline	315375	5461360	401	6	345	13	49
18	CWS Southwest	315497	5460810	356	7	40	15	43
19	CWS Centre South	315120	5462300	402	7	40	10	49
20	CWS Centre North	314897	5462760	411	22	340	10	45
21	CWS North	315076	5463740	341	18	20	18	43
22	Oliver Mountain Quarry	313332	5452210	464	21	70	14	60



Site No.	Site Name	Easting	Northing	Elevation	Slope	Aspect	Exotic SR	Native SR
23	Oliver Mountain Centre	313143	5451530	479	6	265	12	41
24	Oliver Mountain South	312674	5451010	526	14	290	15	46
25	Peach Bluff North	313980	5469440	451	18	265	18	47
26	Peach Bluff South	314168	5470580	527	20	125	11	24
27	Peach Bluff Centre	314060	5470120	429	0	5	11	30
28	See Ya Later Winery South	314426	5463190	600	2	50	11	45
29	See Ya Later Winery Centre	313964	5463730	614	9	330	13	62
30	See Ya Later Winery North	314125	5464090	601	8	315	9	51
31	McIntire Bluff	315363	5459390	598	9	340	7	52
32	McIntire Lake	314373	5459760	565	20	180	16	41
33	McIntire South	314759	5458620	435	19	80	15	50
34	McIntire Bluff Bottom	315596	5458250	411	8	190	16	39
35	Covert Farm East	315478	5457760	405	0	205	12	37
36	Pinehaven	317318	5460700	455	18	180	17	36
37	Pinehaven South	317134	5460120	410	4	250	8	34

**Table A.2** Taxonomic and abundance data for the 162 plant species identified in the study area. Names and conservation statuses (i.e., native (N) or exotic (E)) follow British Columbia Conservation Data Centre (2010) which lists the most current data used in British Columbia, Canada. Mean (standard deviation) percent foliar cover from the 1 m<sup>2</sup> subplots (N = 369) and the percentage of sites occupied (N = 37) by each species are provided. Species with foliar covers listed as not available (NA) were not recorded in the 1 m<sup>2</sup> subplots, which was the grain size at which foliar cover data was collected.

Family	Scientific Name	Common Name	Status	Cover	Sites
Amaranthaceae	<i>Chenopodium album album</i>	lamb's-quarters	E	<0.01 (0.03)	37.8
Amaranthaceae	<i>Salsola tragus</i>	Russian thistle	E	NA	5.4
Anacardiaceae	<i>Rhus glabra</i>	smooth sumac	N	<0.01 (<0.01)	13.5
Apiaceae	<i>Lomatium ambiguum</i>	swale desert-parsley	N	0.01 (0.06)	18.9
Apiaceae	<i>Lomatium dissectum multifidum</i>	fern-leaved desert-parsley	N	0.05 (0.17)	54.1
Apiaceae	<i>Lomatium geyeri</i>	Geyer's desert-parsley	N	0.05 (0.16)	73.0
Apiaceae	<i>Lomatium macrocarpum</i>	large-fruited desert parsley	N	0.01 (0.13)	16.2
Apiaceae	<i>Lomatium triternatum triternatum</i>	nine-leaved desert-parsley	N	0.03 (0.13)	32.4
Apiaceae	<i>Perideridia gairdneri</i>	Gairdner's yampah	N	<0.01 (0.03)	10.8
Apocynaceae	<i>Apocynum androsaemifolium</i>	spreading dogbane	N	NA	2.7
Apocynaceae	<i>Asclepias speciosa</i>	showy milkweed	N	0.01 (0.06)	13.5
Asteraceae	<i>Achillea millefolium lanulosa</i>	yarrow	N	0.35 (1.65)	94.6
Asteraceae	<i>Agoseris glauca dasycephala</i>	short-beaked agoseris	N	0.02 (0.11)	45.9
Asteraceae	<i>Agoseris heterophylla heterophylla</i>	annual agoseris	N	NA	8.1
Asteraceae	<i>Antennaria dimorpha</i>	low pussytoes	N	0.03 (0.29)	51.4
Asteraceae	<i>Antennaria pulcherrima pulcherrima</i>	showy pussytoes	N	<0.01 (<0.01)	8.1
Asteraceae	<i>Antennaria umbrinella</i>	umber pussytoes	N	0.18 (0.99)	43.2
Asteraceae	<i>Arnica fulgens</i>	arnica	N	0.01 (0.06)	10.8
Asteraceae	<i>Artemisia campestris pacifica</i>	northern wormwood	N	0.01 (0.13)	8.1
Asteraceae	<i>Artemisia dracunculus</i>	tarragon	N	<0.01 (0.05)	5.4
Asteraceae	<i>Artemisia frigida</i>	prairie sagewort	N	0.05 (0.47)	29.7
Asteraceae	<i>Artemisia tridentata tridentata</i>	big sagebrush	N	0.56 (3.48)	27.0
Asteraceae	<i>Balsamorhiza sagittata</i>	arrow-leaved balsamroot	N	2.58 (7.11)	75.7

Family	Scientific Name	Common Name	Status	Cover	Sites
Asteraceae	<i>Centaurea diffusa</i>	diffuse knapweed	E	0.03 (0.37)	62.2
Asteraceae	<i>Chaenactis douglasii douglasii</i>	hoary false yarrow	N	NA	10.8
Asteraceae	<i>Cirsium arvense</i>	Canada thistle	E	NA	2.7
Asteraceae	<i>Cirsium undulatum</i>	wavy-leaved thistle	N	<0.01 (0.03)	10.8
Asteraceae	<i>Crepis atribarba originalis</i>	slender hawksbeard	N	0.08 (0.49)	70.3
Asteraceae	<i>Ericameria nauseosa speciosa</i>	common rabbit-bush	N	0.15 (1.35)	59.5
Asteraceae	<i>Erigeron compositus glabratus</i>	smooth cut-leaved daisy	N	<0.01 (0.04)	2.7
Asteraceae	<i>Erigeron corymbosus</i>	long-leaved fleabane	N	NA	29.7
Asteraceae	<i>Erigeron filifolius filifolius</i>	thread-leaved fleabane	N	<0.01 (<0.01)	13.5
Asteraceae	<i>Erigeron linearis</i>	linear-leaved daisy	N	<0.01 (0.05)	13.5
Asteraceae	<i>Erigeron pumilus intermedius</i>	shaggy daisy	N	<0.01 (<0.01)	32.4
Asteraceae	<i>Erigeron subtrinervis conspicuus</i>	triple-nerved fleabane	N	<0.01 (0.03)	18.9
Asteraceae	<i>Gaillardia arstata</i>	brown-eyed Susan	N	0.01 (0.08)	64.9
Asteraceae	<i>Heterotheca villosa villosa</i>	golden-aster	N	<0.01 (<0.01)	21.6
Asteraceae	<i>Hieracium scouleri</i>	Scouler's hawkweed	N	0.01 (0.11)	13.5
Asteraceae	<i>Lactuca serriola</i>	prickly lettuce	E	0.01 (0.05)	56.8
Asteraceae	<i>Madia glomerata</i>	clustered tarweed	N	NA	18.9
Asteraceae	<i>Sonchus arvensis</i>	perennial sow-thistle	E	<0.01 (0.03)	2.7
Asteraceae	<i>Taraxacum officinale</i>	common dandelion	E	0.16 (1.14)	81.1
Asteraceae	<i>Tragopogon dubius</i>	yellow salsify	E	0.09 (0.33)	97.3
Berberidaceae	<i>Mahonia aquifolium</i>	tall Oregon-grape	N	0.01 (0.10)	18.9
Betulaceae	<i>Betula occidentalis</i>	water birch	N	NA	2.7
Boraginaceae	<i>Cynoglossum officinale</i>	common hound's-tongue	E	0.01 (0.10)	10.8
Boraginaceae	<i>Lappula occidentalis</i>	western stickseed	N	0.01 (0.08)	21.6
Boraginaceae	<i>Lithospermum arvense</i>	corn gromwell	E	0.03 (0.14)	45.9
Boraginaceae	<i>Lithospermum incisum</i>	yellow gromwell	N	0.01 (0.11)	18.9
Boraginaceae	<i>Lithospermum ruderales</i>	lemonweed	N	0.09 (0.78)	62.2
Boraginaceae	<i>Myosotis stricta</i>	blue forget-me-not	E	0.37 (0.82)	91.9

Family	Scientific Name	Common Name	Status	Cover	Sites
Boraginaceae	<i>Phacelia hastata hastata</i>	silverleaf phacelia	N	0.03 (0.32)	13.5
Boraginaceae	<i>Phacelia linearis</i>	thread-leaved phacelia	N	0.13 (0.62)	91.9
Brassicaceae	<i>Arabis holboellii</i>	Holboell's rockcress	N	0.01 (0.12)	62.2
Brassicaceae	<i>Descurainia sophia</i>	flixweed	E	0.01 (0.06)	43.2
Brassicaceae	<i>Draba verna</i>	common draba	E	0.20 (0.31)	94.6
Brassicaceae	<i>Lepidium densiflorum</i>	prairie pepper-grass	N	NA	5.4
Brassicaceae	<i>Physaria douglasii</i>	Columbia bladderpod	N	NA	2.7
Brassicaceae	<i>Sisymbrium altissimum</i>	tall tumble-mustard	E	0.22 (1.78)	59.5
Brassicaceae	<i>Sisymbrium loeselii</i>	Loesel's tumble-mustard	E	<0.01 (0.06)	13.5
Cactaceae	<i>Opuntia fragilis</i>	brittle prickly-pear cactus	N	0.46 (1.72)	78.4
Caprifoliaceae	<i>Symphoricarpos albus laevigatus</i>	common snowberry	N	0.19 (1.52)	43.2
Caryophyllaceae	<i>Arenaria serpyllifolia</i>	thyme-leaved sandwort	E	NA	48.6
Caryophyllaceae	<i>Holosteum umbellatum</i>	umbellate chickweed	E	0.18 (0.35)	81.1
Caryophyllaceae	<i>Silene antirrhina</i>	sleepy catchfly	N	NA	35.1
Caryophyllaceae	<i>Silene douglasii douglasii</i>	Douglas' campion	N	<0.01 (0.04)	16.2
Caryophyllaceae	<i>Silene latifolia alba</i>	white cockle	E	NA	2.7
Clusiaceae	<i>Hypericum perforatum</i>	common St. John's-wort	E	NA	2.7
Crassulaceae	<i>Sedum lanceolatum lanceolatum</i>	lance-leaved stonecrop	N	<0.01 (0.04)	5.4
Cupressaceae	<i>Juniperus scopulorum</i>	Rocky Mountain juniper	N	0.08 (1.56)	2.7
Cyperaceae	<i>Carex petasata</i>	pasture sedge	N	0.05 (0.78)	24.3
Cyperaceae	<i>Eleocharis palustris</i>	common spike-rush	N	0.10 (1.58)	5.4
Dryopteridaceae	<i>Woodsia scopulina</i>	mountain cliff fern	N	0.02 (0.12)	56.8
Ericaceae	<i>Arctostaphylos uva-ursi</i>	kinnikinnick	N	0.04 (0.53)	8.1
Fabaceae	<i>Astragalus collinus collinus</i>	hillside milk-vetch	N	<0.01 (0.05)	16.2
Fabaceae	<i>Astragalus miser serotinus</i>	timber milk-vetch	N	0.16 (0.78)	43.2
Fabaceae	<i>Astragalus purshii glareosus</i>	woollypod milk-vetch	N	<0.01 (<0.01)	24.3
Fabaceae	<i>Lotus denticulatus</i>	meadow birds-foot trefoil	N	0.01 (0.10)	8.1
Fabaceae	<i>Medicago sativa sativa</i>	alfalfa	E	0.01 (0.17)	21.6

Family	Scientific Name	Common Name	Status	Cover	Sites
Fabaceae	<i>Melilotus officinalis</i>	yellow sweet clover	E	<0.01 (0.03)	10.8
Fabaceae	<i>Vicia villosa villosa</i>	hairy vetch	E	<0.01 (0.04)	8.1
Geraniaceae	<i>Erodium cicutarium cicutarium</i>	common stork's-bill	E	<0.01 (<0.01)	5.4
Grossulariaceae	<i>Ribes cereum cereum</i>	squaw currant	N	0.34 (2.98)	51.4
Hydrangeaceae	<i>Philadelphus lewisii</i>	mock-orange	N	0.47 (3.97)	27.0
Liliaceae	<i>Asparagus officinalis</i>	garden asparagus	E	<0.01 (<0.01)	2.7
Liliaceae	<i>Calochortus macrocarpus macrocarpus</i>	sagebrush mariposa lily	N	0.12 (0.23)	75.7
Liliaceae	<i>Fritillaria affinis affinis</i>	chocolate lily	N	<0.01 (0.06)	10.8
Liliaceae	<i>Fritillaria pudica</i>	yellow bell	N	0.01 (0.06)	45.9
Liliaceae	<i>Maianthemum stellatum</i>	star-flowered false Solomon's-seal	N	<0.01 (<0.01)	2.7
Liliaceae	<i>Zigadenus venenosus venenosus</i>	meadow death-camas	N	0.12 (0.58)	78.4
Onagraceae	<i>Epilobium angustifolium</i>	fireweed	N	0.02 (0.27)	2.7
Onagraceae	<i>Epilobium brachycarpum</i>	tall annual willowherb	N	NA	51.4
Orobanchaceae	<i>Orobanche fasciculata</i>	clustered broomrape	N	NA	5.4
Pinaceae	<i>Pinus ponderosa</i>	ponderosa pine	N	0.17 (1.27)	83.8
Pinaceae	<i>Pseudotsuga menziesii glauca</i>	Rocky Mountain Douglas-fir	N	0.09 (1.58)	32.4
Plantaginaceae	<i>Plantago lanceolata</i>	ribwort plantain	E	<0.01 (<0.01)	10.8
Plantaginaceae	<i>Plantago patagonica</i>	woolly plantain	N	0.02 (0.10)	67.6
Poaceae	<i>Achnatherum occidentale pubescens</i>	stiff needlegrass	N	0.13 (2.11)	21.6
Poaceae	<i>Aristida purpurea longiseta</i>	red three-awn	N	0.24 (1.29)	54.1
Poaceae	<i>Bromus briziformis</i>	rattlesnake grass	E	NA	10.8
Poaceae	<i>Bromus commutatus</i>	meadow brome	E	NA	64.9
Poaceae	<i>Bromus racemosus</i>	smooth brome	E	NA	10.8
Poaceae	<i>Bromus tectorum</i>	cheatgrass	E	6.31 (11.00)	100
Poaceae	<i>Calamagrostis rubescens</i>	pinegrass	N	0.02 (0.28)	8.1
Poaceae	<i>Dactylis glomerata</i>	orchard-grass	E	0.01 (0.19)	2.7
Poaceae	<i>Danthonia unispicata</i>	one-spike oatgrass	N	0.05 (0.63)	5.4
Poaceae	<i>Elymus repens</i>	quackgrass	E	NA	5.4

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Poaceae	<i>Festuca campestris</i>	rough fescue	N	0.18 (2.34)	5.4
Poaceae	<i>Festuca idahoensis</i>	Idaho fescue	N	NA	2.7
Poaceae	<i>Festuca occidentalis</i>	western fescue	N	0.74 (3.78)	32.4
Poaceae	<i>Hesperostipa comata comata</i>	needle-and-thread grass	N	1.92 (5.74)	75.7
Poaceae	<i>Koeleria macrantha</i>	junegrass	N	0.03 (0.25)	45.9
Poaceae	<i>Panicum capillare</i>	common witchgrass	N	0.06 (0.48)	37.8
Poaceae	<i>Phalaris arundinacea</i>	reed canarygrass	N	<0.01 (<0.01)	5.4
Poaceae	<i>Poa bulbosa vivipara</i>	bulbous bluegrass	E	0.88 (4.11)	35.1
Poaceae	<i>Poa pratensis</i>	Kentucky bluegrass	E	0.20 (2.11)	35.1
Poaceae	<i>Poa secunda secunda</i>	Sandberg's bluegrass	N	1.25 (2.70)	100
Poaceae	<i>Pseudoroegneria spicata inermis</i>	bluebunch wheatgrass	N	3.79 (7.51)	100
Poaceae	<i>Sporobolus cryptandrus</i>	sand dropseed	N	1.30 (4.21)	73.0
Poaceae	<i>Vulpia octoflora</i>	six-weeks grass	N	0.13 (0.95)	67.6
Polemoniaceae	<i>Collomia grandiflora</i>	large-flowered collomia	N	NA	2.7
Polemoniaceae	<i>Collomia linearis</i>	narrow-leaved collomia	N	0.01 (0.05)	5.4
Polemoniaceae	<i>Ipomopsis aggregata aggregata</i>	scarlet gilia	N	<0.01 (<0.01)	8.1
Polemoniaceae	<i>Linanthus pungens</i>	prickly phlox	N	<0.01 (<0.01)	5.4
Polemoniaceae	<i>Microsteris gracilis humilior</i>	pink twink	N	0.11 (0.26)	81.1
Polemoniaceae	<i>Phlox longifolia</i>	long-leaved phlox	N	0.25 (1.22)	45.9
Polygonaceae	<i>Eriogonum heracleoides angustifolium</i>	parsnip-flowered buckwheat	N	0.04 (0.33)	48.6
Polygonaceae	<i>Eriogonum niveum</i>	snow buckwheat	N	0.19 (0.91)	67.6
Polygonaceae	<i>Fallopia convolvulus</i>	black bindweed	E	<0.01 (0.05)	13.5
Polygonaceae	<i>Polygonum douglasii</i>	Douglas's knotweed	N	0.02 (0.10)	86.5
Polygonaceae	<i>Rumex acetosella</i>	sheep sorrel	E	0.01 (0.11)	10.8
Portulacaceae	<i>Claytonia rubra</i>	redstem springbeauty	N	0.31 (1.44)	59.5
Portulacaceae	<i>Lewisia rediviva</i>	bitterroot	N	0.02 (0.11)	37.8
Portulacaceae	<i>Montia linearis</i>	narrow-leaved montia	N	0.04 (0.14)	37.8
Primulaceae	<i>Dodecatheon pulchellum cusickii</i>	pretty shootingstar	N	<0.01 (0.04)	18.9

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Ranunculaceae	<i>Clematis ligusticifolia ligusticifolia</i>	white clematis	N	NA	2.7
Ranunculaceae	<i>Delphinium nuttallianum</i>	upland larkspur	N	0.02 (0.11)	54.1
Ranunculaceae	<i>Ranunculus glaberrimus ellipticus</i>	sagebrush buttercup	N	0.20 (0.45)	70.3
Rhamnaceae	<i>Ceanothus velutinus velutinus</i>	snowbrush	N	<0.01 (0.03)	5.4
Rosaceae	<i>Amelanchier alnifolia</i>	Saskatoon	N	0.20 (1.48)	81.1
Rosaceae	<i>Geum triflorum triflorum</i>	old man's whiskers	N	0.02 (0.30)	18.9
Rosaceae	<i>Potentilla glandulosa pseudorupestris</i>	sticky cinquefoil	N	0.02 (0.27)	13.5
Rosaceae	<i>Potentilla recta</i>	sulphur cinquefoil	E	0.83 (3.94)	62.2
Rosaceae	<i>Prunus virginiana melanocarpa</i>	choke cherry	N	<0.01 (0.06)	13.5
Rosaceae	<i>Purshia tridentata</i>	antelope-brush	N	2.17 (7.69)	100
Rosaceae	<i>Rosa woodsii ultramontana</i>	prairie rose	N	0.04 (0.53)	18.9
Rosaceae	<i>Rubus idaeus strigosus</i>	red raspberry	N	<0.01 (0.03)	2.7
Rosaceae	<i>Spiraea betulifolia lucida</i>	birch-leaved spirea	N	0.02 (0.31)	13.5
Rubiaceae	<i>Galium aparine</i>	cleavers	N	0.23 (1.06)	67.6
Salicaceae	<i>Populus balsamifera trichocarpa</i>	black cottonwood	N	0.02 (0.37)	2.7
Santalaceae	<i>Comandra umbellata</i>	pale comandra	N	0.01 (0.13)	64.9
Saxifragaceae	<i>Heuchera cylindrica</i>	round-leaved alumroot	N	0.06 (0.43)	32.4
Saxifragaceae	<i>Lithophragma parviflorum parviflorum</i>	small-flowered fringe-cup	N	0.27 (1.02)	81.1
Saxifragaceae	<i>Saxifraga nidifica nidifica</i>	meadow saxifrage	N	0.07 (0.66)	21.6
Scrophulariaceae	<i>Castilleja hispida hispida</i>	harsh paintbrush	N	<0.01 (<0.01)	2.7
Scrophulariaceae	<i>Castilleja thompsonii</i>	Thompson's paintbrush	N	NA	5.4
Scrophulariaceae	<i>Collinsia parviflora</i>	small-flowered blue-eyed Mary	N	0.34 (0.49)	97.3
Scrophulariaceae	<i>Linaria genistifolia dalmatica</i>	Dalmatian toadflax	E	0.32 (1.31)	73.0
Scrophulariaceae	<i>Penstemon confertus</i>	yellow penstemon	N	NA	10.8
Scrophulariaceae	<i>Penstemon fruticosus scouleri</i>	shrubby penstemon	N	0.02 (0.28)	8.1
Scrophulariaceae	<i>Penstemon pruinus</i>	Chelan penstemon	N	0.04 (0.58)	13.5
Scrophulariaceae	<i>Verbascum thapsus</i>	great mullein	E	0.02 (0.26)	43.2