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**ALIEN PLANT SPECIES IN PROTECTED AREAS AND THEIR MATRICES:
UNDERSTANDING INVASIONS AT MULTIPLE SCALES**

by

Aníbal Pauchard

Licenciate in Forestry Sciences, Universidad de Concepción

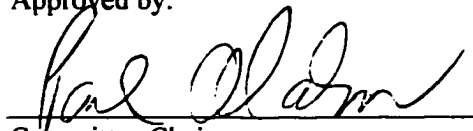
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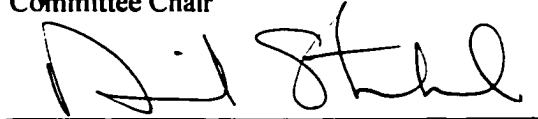
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Abstract

Aníbal Pauchard Ph.D., 2002, Forestry

Alien Plant Species in Protected Areas and Their Matrices: Understanding Invasions at Multiple Scales

Committee Chair Dr. Paul B. Alaback

PA

Alien plant invasions are an increasing threat to ecological processes and biological diversity. These human-caused invasions are affecting both human-disturbed landscapes and also natural reserves or protected areas even in remote areas with harsh climates. To understand invasions in the complex landscapes of protected areas, it is necessary to consider the surrounding landscape matrix. In chapter 1, I review evidence about the importance of assessing invasions at multiple scales. While most evidence about invasion is collected at the local scale, mechanisms that control invasions operate over a broad range of scales. Integrating observations from several scales may help to capture the complexity of these invasions. I studied the influence of elevation, landuse and landscape context in the distribution of alien species in Villarrica National Park, South Central Chile (chapter 2). I found that elevation is negatively associated with alien species richness and abundance. This response may be explained by changes in landuse, propagule pressure and microclimatic differences. I also studied the effects of edge type in determining edge effects on alien and native plant diversity in *Pinus contorta* forests around West Yellowstone, Montana, in the interface between Gallatin National Forest and Yellowstone National Park (chapter 3). Highways appeared as the only edge types with consistent presence of alien species. I conclude that propagule pressure is as important as edge effects in determining alien species distribution. In the same area, I studied the invasion of *Linaria vulgaris* using a multi-scale method (chapters 4 and 5). I determined that this perennial herb is colonizing both human and naturally disturbed areas, increasing its abundance at the local scale and extending its distribution at the landscape scale. However, significant annual variation associated with climatic fluctuations can be observed in *L. vulgaris* populations and the invaded plant community (chapter 5). This dissertation illustrates the importance of considering landscape processes, such as cross-boundary dispersal, when studying and managing plant invasions in protected areas. It also emphasizes the advantages of using multi-scale methods to address invasion processes in the complex landscapes of protected areas.

To my wife Paula

for all her support, help, advice, hard work and friendship

that helped to make this possible

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Overview

I started my dissertation thinking about the influence of the surrounding landuse on ecological processes in natural reserves. Evidence had shown that while protected areas were increasing in size and total coverage, the rapid development of the surrounding matrices was threatening the ecological integrity of the protected ecosystems.

These types of questions have been addressed in the emerging discipline of landscape ecology, with much emphasis in capturing patterns of landscape fragmentation and connectivity. However, I felt that there was still little connection between the theoretical models at the landscape scale with the diverse and complex ecological processes that were occurring across a broad range of scales in real landscapes.

On the other hand, biological invasion was becoming a topic of concern and interest for ecologists and managers. But few studies had been conducted in protected areas and surrounding matrices, even less have tried to understand invasions as landscape processes. Therefore, it seemed apparent that a combination of both landscape ecology and biological invasions would be an appropriate approach to my dissertation. Having the possibility of conducting research in two completely different study sites (and hemispheres), I decided to study similar invasion processes in both Villarrica National Park, Chile and Yellowstone National Park, Montana.

Chapter 1 reviews concepts of scale and its interaction with biological invasions. I found it extremely interesting how scale determines the driving mechanisms in ecology. This principle also applies to alien plant invasions, and to understand its basis may help to develop better tools to capture and manage invasions. In this Chapter, I have chosen to review elements of dispersal, disturbance, invasibility and ecological impacts that vary with scale.

Chapter 2 shows the results of my research in cross-boundary invasions in Villarrica National Park, Chile with emphasis in roadsides and road-forest edges. The results suggest that both elevation and landuse are major drivers of the presence of alien species along roadsides.

Also, it highlights the importance of roads as corridors of alien species into core areas of natural reserves. Even though, edges are recognized as facilitators of the percolation of alien species into interior habitats, in this study area, I found that most species tend to stay in the open environments along roadsides.

Chapter 3 presents the results of my study in edge effects and the interaction with edge type in determining alien and native plant species patterns. I compared highway, clearcut and burned areas forest edges in *Pinus contorta* forests of West Yellowstone, Montana. Most alien species occur in highway matrices and edges and only a few get to the interior. Burns and clearcut show a few exotic species that are not invasive. This suggest that propagule availability, and thereby landscape context is as important as physical changes in determining edge effects on alien plants.

Chapter 4 is dedicated to understanding the advantages of using a multi-scale method to assess plant invasions. I show the results for a perennial herb (*Linaria vulgaris*) that is invading natural and human disturbed sites in Yellowstone National Park and adjacent Gallatin National Forest. I found that the species is highly invasive in disturbed areas and shows rapid filling of colonized area, with wide distribution over the landscape. In the light of these results I discuss the implications for invasive species assessment in protected areas. I conclude that a multi-scale method is more efficient and useful than a single-scale method in capturing the patterns and mechanisms of invasions, especially in the complex protected area landscapes.

Chapter 5 illustrates the potential value of monitoring invasive species over longer time intervals. Based on the methods of Chapter 4, I monitored the population and stand dynamics during three growing seasons. I found significant annual variation in both *Linaria vulgaris* attributes and overall plant community attributes that was related to climatic variation. This study suggests that monitoring is needed to really understand the long-term implications of the process of invasion. As with multiple scales, monitoring also should be run at multiple temporal scales.

Chapter 6 summarizes my dissertation results, highlighting the major generalities that emerge from this work. Even though, West Yellowstone and Villarrica study areas represent complete different ecological and cultural systems, a few major trends in invasion processes can be observed in both cases. First, alien species are more abundant in the matrices of protected areas than in their interiors. Second, roads act as major corridors for the introduction of alien species into more pristine areas. Third, propagule dispersal appears as a constraint to invasion. These results emphasizes the importance of considering the landscape context of protected areas (their matrices) when studying and managing invasive species.

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CHAPTER I

ALIEN PLANT INVASIONS ACROSS SPATIAL SCALES: INTEGRATING PROCESSES

ABSTRACT

Alien plant invasions caused by human activities are affecting ecological processes and threatening biodiversity worldwide. The mechanisms and ecological impacts of alien plant invasion vary across spatial scales. The consideration of scale may help to understand the ecological processes of invasion. I review elements of invasion such as dispersion, disturbance, and invasibility and their relation to spatial scale and the importance of scale in assessing and controlling invasive species. Dispersion is greatly influenced by scale, with differential mechanisms controlling global, regional and local dispersal. The role of disturbance in invasions is also influenced by spatial and temporal scale and by other factors including causal agents. Community invasibility is in part determined by community attributes such as species diversity, but also by external factors such as propagule pressure and fertilization. The ecological effects of plant invasions are also scale-dependent, from altering local community diversity to changing biogeochemical cycles at the regional or global scale. Therefore, the study and control of invasions requires capturing and integrating invasion processes at multiple scales. A multi-scale approach is recommended to better understand the full suite of processes and their interactions that underlie the invasion process.

INTRODUCTION

Humans have increased the rate and success of biological invasions across the globe, creating new arrangements of animal and plant species. Since the beginning of human migrations, people have been important dispersal agents of non-native plants and animals into new environments (Lonsdale 1999; Mack and Lonsdale 2001). However, the exponential increase in movement of species over long distances, in many cases crossing continents and oceans, has been particularly sensitive to international trade and modern globalization (Mack et al. 2000). Impacts of these newly introduced species on native species and ecosystems are still a source of debate (Parker et al. 1999; McNeely et al. 2001). A growing body of evidence suggests that species that evolved in a different biotic and abiotic environment may disrupt ecosystem processes and native biological diversity, produce large agricultural losses, and even harm human health (Mack et al. 2000; Sala et al. 2000). In the United States, annual direct and indirect losses due to invasive species are estimated at over 138 billion dollars (Pimentel et al. 2000).

Invasions are constrained by both biotic and abiotic factors, which determine invasion success. As in all other ecological processes, invasions are affected by environmental heterogeneity (Milne 1991). From seed dispersal to production of new propagules, invasive plants face diverse ecological constraints that are scale-dependent, that is they vary in relation to the scale at which they occur. A comprehensive approach to capture the dynamic process of alien invasion across multiple spatial scales may contribute to our understanding of its ecological causes and effects, and to help us identify more efficient and effective control strategies (Mack 2000).

In this paper I address plant invasions in the context of scale. Briefly, I discuss some basic scale related concepts in ecology. Then, I review evidence of scale-dependent processes affecting biological invasion success, such as dispersal mechanisms, disturbance and community invasibility. In the final section, I discuss the implications of scale on ecological impacts of invasions, their assessment and control strategies.

WHY IS SPATIAL SCALE IMPORTANT IN PLANT INVASIONS?

For decades ecologists have been conscious of the importance of scale in ecological processes (Allen and Starr 1982). Human cultural and biological constraints make it difficult for us to conceptualize processes occurring at larger spatial scales. However, the study of processes at regional or global scales, coupled with powerful remote sensing and geographic information systems, have enhanced our understanding of the key role of scale in ecosystem dynamics. For example, scale has been recognized as an essential element in understanding biodiversity patterns, both because of its role in determining mechanisms at each scale and the difficulty to scale up or down the observed patterns (Willis and Whittaker 2002, Crawley and Harral 2001).

From hierarchy theory, it is clear that dominant processes can change across scale (O'Neill and King 1998). There is not only change associated with the relative sizes of processes, but with the phenomena themselves. Recently, Willis and Whittaker (2002) reviewed the effects of scale on species diversity, recognizing that richness (the number of species) is best explained by different variables depending on spatial scale.

Scale and level are concepts that tend to be used interchangeably without much further consideration of their ecological meaning. As defined by O'Neill and King (1998) "scale refers to physical dimensions of observed entities and phenomena". Therefore, when describing a scale, it should be possible to characterize its dimensions in specific measurement units. Scale is defined by its "grain" or resolution, and its "extent" or total dimensions.

Scale also reflects the observer's point of view, incorporating the spatial dimensions of an observation and influencing the observer conclusions about the system studied. In contrast, "level" refers to "level of organization in a hierarchically organized system" (O'Neill and King 1998). Levels are closely connected with processes (e.g. flows, interactions), and therefore they characterize system organization. The classic example to show the differences between scale and

level is the comparison of an elephant and an ant. Both are in the same level (individuals of a population), however the elephant is operating in a scale thousands of times larger than the ant.

Confusion arises because levels may occur at a specific scale and consequently, the scale at which processes are observed also determines the level that is captured. For example, to study population level in bacteria, the scale is microscopic, but at the scale it is impossible to study the population level of large mammals. Practical problems originate when combining data-sets taken at different scales and thereby assessing different levels of organization. The answer for a specific question may vary according to scale at which observations are taken. Thereby, ecologists must be careful in defining clearly the scale and level at which they want to make inferences in order to avoid confusing casual mechanisms.

Biological invasions as complex ecological processes occur at many temporal and spatial scales. From short distance seed shadows to inter-continental dispersion, plant invasion mechanisms are scale-dependent (Table 1). However, few studies have addressed the importance of scale in biological invasions (e.g. Stohlgren et al. 1999; DeFerrari and Naiman 1994). Most studies of invasions have focused at one spatial setting, and have failed to consider the effects of invasion processes across scales. Recently, with the increasing interest in landscape ecology and in long-term studies, researchers are trying to better describe and explain the process and implications of plant invasion across a range of scales.

DISPERSAL MECHANISMS ACROSS SCALES

Invasive alien species employ a wide set of scale-dependent dispersal strategies to colonize new environments, from global dispersion, mostly carried out by humans, to local short distance dispersal, by mostly natural mechanisms such as wind or animals. Mechanisms of dispersion and constraints for dispersal vary with scale (Nathan and Muller-Landau 2000). However, the ultimate result of dispersal strategies at any scale is basically the same, sending propagules to a new and safe environment to increase recruitment.

Dispersal is now recognized as probably the most important process determining invasion success, mainly because evidence suggests that given sufficient propagule pressure and adequate climate conditions, any ecosystem can be invaded by alien species (D'Antonio et al. 2001).

Even though stochasticity plays a major role in defining dispersion success, plants have developed specific mechanisms to maximize dispersal at each scale (Nathan and Muller-Landau 2000). For example, in wind-dispersed species, most seeds tend to fall close to the maternal plants due to gravity, but a small proportion of seeds is actually transported long distances due to the morphological structures of the seeds (e.g. wings, achenes). The success of an invasive species is determined at each of the scales at which dispersion occurs and therefore plants need a complete suite of dispersal strategies, from local to global scale.

Global Dispersion

Plant species moved around the globe long before humans became an important dispersal agent. Colonization of new islands in the Pacific Ocean by continental plants has caught ecologists' attention, particularly the dispersal mechanisms and the rate of invasion success (Fenner 1985). For example, the successful dispersal and establishment of one plant every 7,900 years would explain the accumulation of species in the Galapagos Islands flora; for the Hawaiian Islands once every 20,000-30,000 years (see review in Fenner 1985). Under natural conditions, most long distance dispersal is carried out by birds, with both internal and external transport, followed by drift and wind. Both transoceanic and continental global dispersion is highly constrained by physical and biological barriers. For example, Chile has a high level of floristic endemism that distinguishes it from other countries in South America (Arroyo et al. 1995), because few species were able to disperse over the topographic barriers of the Andes and the climatic barrier of the Atacama desert.

Recognizing the differences between natural and human dispersal processes is key to enhance the understanding and management of alien invasions. Natural and human global alien

plant dispersal processes differ in rate, intensity, mechanisms and scale. Humans, breaking natural barriers of dispersal, have served as dispersal agents for alien plants since the first human migrations and the beginning of agriculture and livestock domestication (Mack et al 2000; Mack and Lonsdale 2001). With the arrival of Europeans to the Americas, a new scenario for alien plant invasion was opened. Along with crop seed, came a number of alien species capable of colonizing this geologically isolated continent. In the last 200 to 500 years, a significant number of species have arrived, deliberately or accidentally, to the Americas. Species from the Americas have also become invasive in Europe, Africa and Asia (Williamson and Fitter 1996). Eurasia is recognized as the main source of alien invaders for all other continents. With only 4.4% of the total flora of the world, Eurasia contributes with 58.9% of naturalized alien species (Pysek 1998).

Human dispersal mechanisms of alien species at a global scale are much more efficient and effective than natural mechanisms. For example, in ocean waters the introduction of novel species in ballast water is a ongoing worldwide process. It is estimated that 10,000 species are transported daily around the world in ballast water of ships (Carlton 2000).

A probably less massive, but equally effective introduction, is carried out for plants in crop seed exchanged across countries and continents. Because of the continuous propagule flow, the rate of new introductions of vascular plants does not have a parallel in evolutionary history. It is not only the number of new species propagules introduced, but also the number of propagules introduced by each species and the times that they are introduced (D'Antonio et al. 2001). The larger the number of propagules, the higher the probability of a species to establish. For example, the introductions of new alien species in the Northwest of the United States are closely related to changes in transport and human activities (Fig. 1). The first large introduction wave was brought by agricultural and livestock development in the early 1900s. However, increased globalization of transport has raised the rate of intentional and unintentional introductions in the last three decades.

As described by the tens rule, 1 in 10 of all imported species appear in the wild, from those only 1 in 10 become naturalized and only 1 in 10 of those naturalized become invasive (Williamson and Fitter 1996). However, variation on the tens rule occur when there are repetitive introductions, intense propagule pressure (large number of propagules) or other factors such as life history traits or unique ecological conditions influenced the invasion process (Williamson and Fitter 1996; Sax and Brown 2000).

Regional Long Distance Dispersion

Once a population of an alien plant species is established in a new continent or region, regional dispersal mechanisms come into play allowing the species to expand its range of distribution. *Bromus tectorum* (cheatgrass), a European annual grass, is an aggressive invader of more than 200,000 km² in the United States Intermountain West and has extended to other areas of the United States *B. tectorum* was first detected in the United States in 1859 in Pennsylvania (Novak and Mack 2001). However, it entered presumably by multiple ports to the West Coast in 1875. By 1930, it had already reached its limits in the western United States. Using genetic markers, Novak and Mack (2001) found that cheatgrass populations are the result of various introductions and consequent terrestrial transport of seeds, from both east and west coasts across the continent.

The invasion of *B. tectorum* illustrates how regional long distance alien plant dispersal is driven by completely different mechanisms than global dispersion. In regional dispersion, humans continue to be the main dispersal agent, but the complexity of dispersion pathways increases with landscape heterogeneity. Propagule movement usually follows landscape corridors such as roads and rivers (Parendes and Jones 2000; Trombulak and Frissell 2000). Other natural factors such as wind and wild animals differentially enhance dispersal success (e.g. Parendes and Jones 2000).

Another well-studied example of regional dispersion is the invasion of *Tamarix* species in riparian habitats of the western United States. This species was introduced as an ornamental and erosion control agent in the early 1900s. Now, it occupies a large portion of riparian corridors, invading more than 370,000 ha in 15 states (Zabaleta 2000). Once established, *Tamarix* can disperse downwards by water and, in disturbed flood regimes such as reservoirs and dams, may disperse upwards (Lesica and Miles 2001). Regional dispersal mechanisms are complex, species-specific and influenced by the interplay between human and natural factors.

Local Dispersal Mechanisms

For a new population to become established it is necessary that at least one individual succeed in completing its life cycle. Short distance dispersion of this individual's propagules is the initial stage in the development of a new population. The dispersal mechanisms displayed in this stage differ from those in long-distance dispersion (Nathan and Muller-Landau 2000). First, in the majority of the cases, humans are not the primary agent of short distance dispersal, but they can modify the abiotic and biotic conditions enhancing invaders dispersion and the environmental conditions for survival. Second, the intensity and frequency of propagule pressure is higher just because the propagule source is closer. This is the case for most weed infestations, which after an initial introduction increase their density and extent by short distance dispersal of the propagules generated in the nuclei population (Sakai et al. 2001).

Most species disperse their seed following a dispersal curve, usually having the peak in seed dispersal at a short distance from the maternal plant (Fenner 1985; Nathan and Muller-Landau 2000). This short distance mechanism is promoted by wind and animal movement, which liberates seeds that tend to fall by gravity. By evolutionary adaptation, the distance at which the peak in seed rain occurs is usually related to the presence of a zone of safe sites for recruitment (Nathan and Muller-Landau 2000). This dispersal peak is an evolutionary response in life history traits to maximize reproductive success in environments with specific ecological constraints

(Willson and Traveset 2000). For example, plants that require unusual conditions to establish successfully will have a more distant peak in seed rain than those that suffer intense seed predation (Fenner 1985).

Wind tends to dominate dispersal mechanisms because most of invasive plants have evolved in early successional stages where animals are scarce and a great amount of seeds is required to colonize faster the disturbed environments (Sax and Brown 2000). However, some weedy shrubs and herbs need animals for dispersing their seed into more optimal environments. Animal dispersal mechanisms are not usually constrained to one particular scale. For instance, bird species with larger geographic ranges can carry seeds both short and long distances.

Dispersion can also occur via vegetative reproduction. Asexual reproduction is a common and successful mechanism of local dispersion for invasive plants (Bazzaz 1996). While, the species allocate part of the resources to long distance dispersion by seeds, a proportion is utilized in vegetative reproduction. The tradeoff between sexual and asexual reproduction is driven by the risk of having no recruitment from seeds (Bazzaz 1996). Therefore, by reproducing asexually the plant is reducing the risk of local extinction and increasing the potential for seed production for the next year. For example, *Linaria vulgaris*, a perennial invader of cold temperate climate and disturbed soils, can expand its populations by vegetative growth up to 2 m per year in barley crops due to its extensive root system (Nadeau et al. 1991).

Each of the scales at which invasion occurs is crucial for invasion success (Table 1). The failure of a dispersal mechanism on short, long or global scale may prevent a species from becoming invasive in a given environment. While global-scale dispersion is most influenced by human activity, the interaction of both natural and anthropogenic processes drives dispersion at other scales. Ultimately, understanding the influence of natural and human-caused factors in dispersion across scales will facilitate prevention and mitigation management of plant invasions.

Dispersal into protected areas: dispersal across scales

Invasions into protected areas illustrate the importance of multiple scales in the dispersal process. For an alien species to invade into a protected area it is necessary that the species first overcome long-distance intercontinental dispersal barriers. However, this first stage has usually occurred long before the actual invasion of the reserve, because most alien species usually are naturalized in adjacent heavily disturbed areas under human landuse types (See Chapter 2). In rare cases, where a large number of visitors are getting to a reserve, they also may act as vectors of intercontinental dispersal. For example, many species in the Northwest of United States were introduced into agricultural or urban landscapes in the late 1800s and early 1900s (Toney et al. 1998; Fig. 1). However, these species have taken longer to establish in parks and reserves due to their relative isolation at the regional scale. The invasion of reserves is also constrained by relative lower human transportation and disturbance, diminishing the chances of successful establishment. However, the presence of large herbivores (domestic or wild) may increase the rate of successful introductions, by acting as major seed vectors (See Chapter 2).

Lesica and Ahlenslager (1993) found a significant correlation between the number of visitors and the number of alien species in Glacier National Park. Using data from 52 parks from the United States and South Africa, Lonsdale (1999) found a similar positive correlation between the number of alien species and the number of visitors, even after correcting for park size. This relationship does not necessarily mean causality. Increasing visitor numbers is also related to increase development of surrounding areas and increasing overall human activities inside the reserve (Liu et al. 2001).

A species established in a reserve does not necessarily become invasive; local scale dispersal barriers may constrain the invasion. In Yellowstone National Park, most alien species that invade adjacent lands are able to cross the park boundary and establish in roadsides and other disturbed grounds. However, only a few become abundant or invade more pristine environments in the short term (Olliff et al. 2001; A. Pauchard and P. B. Alaback, unpublished data, See

Chapters 4 and 5). On the other hand, long term invasion success is difficult to predict and may depend heavily upon propagule production and genetic adaptations to the new environment (Sakai et al. 2000, Lee 2002).

DISTURBANCES AND SCALE: TYPE, EXTENT AND FREQUENCY

Ecologists have long recognized that disturbance promotes alien plant invasions. The role of disturbance in invasion has risen to the level of “dogma”, where disturbance is a requisite of any invasion (D’Antonio et al. 1999). However, the relative role of disturbance and propagule availability, as determinants of plant invasions, has not yet been clearly understood (e.g. Levine 2000). Few studies have addressed both components simultaneously and even less have monitored these processes over a long temporal scale (D’Antonio et al. 1999).

Disturbance has several definitions, but it implies the damage or killing of individuals and the consequent release of resources for other individuals (adapted from D’Antonio et al. 1999). Disturbance can occur at different temporal and spatial scales and may also vary in type, in reference to the causal agent. It has been widely reported that any type of disturbance increases the probability of alien plant invasions. Human-disturbed areas such as roads, clearcuts and agricultural crops usually contain the highest levels of richness and abundance of invaders (e.g. Parendes and Jones 2000; Spellerberg 1998; Heckman 1999; Hobbs 2000). Nonetheless, natural disturbances such as fire, hurricanes, volcanic events and native ungulate grazing provide a suitable environment for invasive plants (D’Antonio et al. 1999).

The mechanism for explaining the relation between disturbance and invasion is still poorly understood due to the complexity of factors involved in a disturbance event. The main hypothesis is that disturbance liberates resources that introduced plants can utilize faster than natives and thereby colonizing and outcompeting native plants (Sax and Brown 2000). However, as I will discuss later, variation in the type of disturbance and the communities involved, makes the usefulness of such simple generalizations questionable.

Disturbance is a scale-dependent process and therefore, its characteristics vary with scale. For discussing the role of disturbance in invasion at different scales, it is necessary to identify the three main characteristics of disturbance: type, extent and frequency (adapted from Walker and Willig 1999). Type is defined by the agent that produces the disturbance (e.g. natural or human). The spatial scale of disturbance is termed the extent. Finally, frequency is the number of times that a disturbance occurs over a given period.

Type of disturbance

The type of disturbance has been cited as the most critical factor influencing facilitation of plant invasions. Some ecologists tend to classify disturbances into natural and human disturbances. However, this coarse classification overlooks the multiple factors that influence disturbances and may obfuscate similarities or contrasts between these artificial categories. More useful classifications have taken into account the specific characteristic of the disturbance identifying a wide range of disturbance types. Walker and Willig (1999) identified six elements that may cause terrestrial disturbances: tectonic, air, water, fire, biota and humans. Each one may be subdivided in several categories. In most cases, disturbances trigger chains of processes involving more than one element. For example, fires increase the risk of windthrows in forest edges and higher dead biomass may increase the risk of insect outbreaks.

Among the natural disturbances that have been shown to increase invasion are volcanic eruptions, fires and over-grazing. Areas recently disturbed by volcanism are soon colonized by a wide variety of opportunistic alien invaders (review by Del Moral and Grishin 1999). Fire, of both natural and antropogenic origin, has been shown to increase the presence of pioneer alien species. For example, Turner et al. (1997) found in Yellowstone National Park that the abundance of alien species increased after fire. A similar trend was reported for *Carpobrotus edulis* in California maritime chaparral (D'Antonio et al. 1993).

D'Antonio et al. (1999) reviewed 25 studies, including study sites worldwide, where the effect of fire was reported on invasive species. A total of 21 studies documented some type of a promoting effect while only four showed either no effect or a negative effect on the invader. This evidence suggests that natural fires can be an important mechanism for invasion, and given sufficient propagule availability natural and human caused disturbances can have similar effects in plant invaders. The main difference may be that native species have evolved under unique natural disturbances, while Eurasian weeds have evolved in a human disturbed environment for at least a few thousands years, and strong selective pressure has operated to increase their capacity to resist and take advantage of disturbance (Sax and Brown 2000).

Extent of disturbance

Large-scale disturbances generally have a greater effect on ecosystem processes than small-scale disturbances (Foster et al 1998), thereby modifying resource availability to the potential advantage of pioneer invasive species. For example, small forest gaps should be less susceptible to invasion than large burn forests or forest-windthrow areas. Just by chance, large disturbed areas have a higher probability of being invaded, and their slower recovery rate also opens a wider temporal window for invasive plants (e.g. Foster et al. 1998). Propagules are more likely to find a safe site for initial establishment in large disturbances and from there start a rapid invasion of the area. However, evidence suggests that small-scale disturbance such as soil disturbances by rodents and ungulates may effectively promote invasion if sufficient propagules are available (review by D'Antonio et al. 1999). In Yellowstone National Park, *Linaria vulgaris* seems to be colonizing faster in gopher or bison disturbed soil than in adjacent undisturbed soil (A. Pauchard and B. D. Maxwell, personal observation).

The extent of disturbances also influences the array of invasive species that are able to colonize an area. Pioneer species, which account for most alien weeds, prefer areas without competition and large resource availability than late successional species (Sax and Brown 2000).

However, more tolerant-conservative species such as *Hedera helix* invade areas under small-scale disturbances like forest openings (Reichard 2000).

Frequency of disturbance

In spite of its fundamental role in maintaining alien invaders as dominant species in plant communities, the frequency of disturbance has occasionally been ignored in the literature. The extent and intensity of the disturbance effects are closely related to frequency. Most studies report invasions few years after the disturbance, but only a few include long-term monitoring of invasions (Mack 2000). If the disturbance is frequent enough to maintain a significant proportion of the landscape as a suitable environment for invasions, and therefore there is probably little chance for native species to outcompete invaders.

In areas with frequent disturbances invaders may become part of the system and in some cases promote the disturbance regime, perpetuating themselves as dominant species in the community in a positive feed-back cycle (Mack and D'Antonio 1998). The promotion of fire by invasive annuals in Hawaii, shrubs in South African fynbos and cheatgrass in western United States are well-documented examples of positive feedbacks between invasion and disturbance (reviewed in Mack and D'Antonio 1998).

Other frequent disturbances that occur over large scales such as herbivory may increase alien species invasion as well. There are documented cases in which herbivory has not prompted invasion (e.g. Stohlgreen et al. 1999b), however, most studies have shown that invasive species are favored by heavy herbivory (D'Antonio et al. 1999). Simply changing disturbance patterns may also enhance invader performance. This is the case for *Tamarix* (*Tamarix ramosissima*) and Russian Olive (*Elaeagnus angustifolia*) in Montana reservoirs. Both species are invading riverbanks, in areas with diminished seasonal riparian flooding and consequent reduced substrate erosion due to dam construction (Lesica and Miles 1999; Lesica and Miles 2001).

Ultimately, disturbance attributes such as type, extent and frequency interact with each other, modifying the biotic and abiotic conditions for plant invasions. The specific spatial and temporal scale of each disturbance creates a unique set of conditions that may favor a particular set of invasive species. Generalization about the effects of disturbance on invasive species should be carefully scrutinized with more “real-world” data. This is especially important in the presence of confounding factors such as differential propagule pressure.

INVASIBILITY: THE PERSPECTIVE OF INVADDED COMMUNITIES

Recently, ecologists have focused their efforts on answering two foundational and synthetic questions about invasions: 1) what characteristics determine the susceptibility of a plant community to invasion and 2) what are the functional characteristics of successful invaders (Levine and D’Antonio 1999; Sax and Brown 2000). The latter question is related with the autoecology and life history traits of the invaders, and has been widely discussed in the literature (e.g. Rejmanek and Richardson 1996). However, the first question addresses an interesting and relatively novel problem in ecology: finding the mechanisms for explaining why some communities are more susceptible to invasion than others (Mack et al. 2000). Disturbance, community diversity, nutrient availability and escape from biotic constraints have been cited as major factors for explaining differential community invasibility (Tilman 1997; Burke and Grime 1996; Mack et al. 2000 and Dukes 2001).

Are diverse communities less susceptible to invasion?

Community species richness is probably one of the most controversial factors in invasibility. Elton (1958) proposed that communities with higher species richness are more “stable” and less susceptible to invaders. This hypothesis is based on the premise that more niches are used and fewer niches are available for invaders in diverse communities (Levine and D’Antonio 1999; Mack et al. 2000). Resistance to invasion in natural communities may also be

driven by other factors (e.g. disturbance, nutrients) and may be affected by changes in scale. Tilman (1997), using experimental manipulations in grasslands, found that communities with higher species richness were more resistant to invasion (1m² scale). He hypothesized that more empty niches were available for invasion in the low diversity communities. In a different environment, *Centaurea solstitialis* grown in experimental microcosm plots of 315 cm² is less likely to invade more functionally diverse communities, being more capable of dominating and suppressing diversity in species-poor communities (Dukes 2001).

Other studies have shown no relation or an opposite relationship between diversity and invasibility (Levine and D'Antonio 1999). For example, Levine (2000) found that propagule pressure was more important than community diversity in the success of invaders in controlled tussocks of 350 cm² where he manipulated diversity and added seed of three invasive plants. Stohlgren et al (1999), looking at natural communities in a 1 m² scale, found that Central Great Plains prairies confirm the hypothesis that more diverse sites are less invasible, while forest and meadows sites in the Rocky Mountains contradict this pattern. However, when sampled at a larger scale (1000 m²), all forests and grasslands sites, showed a positive correlation between species richness and susceptibility to invasion. Stohlgren et al. (1999) concluded that invasibility may be more related to resource availability (e.g. nitrogen) than to species richness.

Shea and Chesson (2002) offer an explanation for the changes in responses of alien diversity to native diversity across scales. They postulate that a negative pattern of alien richness as a function of native diversity is obtained under similar extrinsic conditions (e.g. soil, climate). Under these constant conditions, a more diverse community would be less susceptible to invasion. However, at broader scales where physical factors dominate, the combination of different datasets of negative relationships may result in a positive relationship between alien and native diversity. At these larger scales, extrinsic factors vary and those factors that favor native diversity also favor alien diversity (e.g. latitudinal and elevation climate variation).

Nutrients as invasion driving factor

Nutrient availability has also been cited as a major factor for invasion success. Burke and Grime (1996) conducted an experiment to understand the relative importance of nutrient availability and disturbance, using an artificial gradient of fertility and disturbance in a grassland community in Derbyshire, United Kingdom. They found that alien species invaded in the presence of disturbance that created bare soils, but they were more aggressive in fertile soils. This pattern was also reported for serpentine grasslands in California (Huenneke et al. 1990). Serpentine grasslands occur under isolated poor nutrient soils, and are surrounded by alien annual grasses dominated communities. Huenneke et al. (1990) applied a fertilizer mix (e.g. N, P) to serpentine soils and measured the responses in productivity and diversity. They found that introduced grasses invaded the community in the second year of treatment, displacing even the most seed-productive species of native forbs.

Similar positive relationships between nutrient availability and invasions have been reported for Californian maritime communities dominated by *Lupinus arboreus* (Maron and Jefferies 1999). *L. arboreus*, a native nitrogen-fixer shrub, goes through natural cycles of advancement and die-off due to fluctuations in insect herbivory. After an intense period of *L. arboreus* mortality, an increase in nitrogen availability favors invasive annual grasses over native flora (Maron and Jefferies 1999). An estimated 25-year period is necessary for lowering nitrogen to a level suitable for the reintroduction of native species.

Scale and the effect of nutrients

Small-scale experiments on the effects of nutrient availability on invasibility may help to understand the effects of global processes such as human-caused increases in nitrogen deposition. Wedin and Tilman (1996) added nitrogen to grassland plots in Minnesota for a 12 year period. Nitrogen additions shifted composition towards alien C3 grasses over the native C4 grasses. In

Germany, nitrogen deposition has increased during industrial times by two orders of magnitude with consequent effects on the introduced flora (Scherer-Lorenzen et al. 2000).

The fertilizing effect of N may favor nonnative species with a faster rate of N assimilation, altering competitive balance in naturally N-limited communities and allowing invasion in undisturbed areas (Scherer-Lorenzen et al. 2000). However, it is necessary to be cautious when scaling up the results of small-scale experiments to regional or global scenarios. This is particularly important in biogeochemical cycles, in which process studies are performed in isolation or under controlled conditions which do not take into account complex interactions at large scales.

Elevated CO₂ concentration is also a potential factor for community invasibility, especially in the certainty that atmospheric CO₂ concentrations have continuously risen during the last century. Increases in CO₂ concentrations may differentially enhance species' water use efficiency and thereby alter competitive balance in natural communities (Dukes and Mooney 1999). This is particularly important in water-limited ecosystems such as Mediterranean and desert biomes. Smith et al. (2000) found that in communities dominated by the evergreen shrub *Larrea tridentata*, the introduced annual grass *Bromus tectorum* (Cheatgrass), increased more its biomass, seed output and density more than native annuals when exposed to elevated CO₂ levels (constant 550ppm in a FACE system). However, these results may not apply for all invasive species; other experiments have shown negative or no effects of CO₂ increases on invaders (review by Dukes and Mooney 1999). Many alien weeds are C4 species, so it is expectable that their competitive advantage against native C3 species may be reduced, but complex interactions limit our predictions (Dukes and Mooney 1999).

ECOLOGICAL IMPACTS OF INVASIONS: FROM LOCAL TO GLOBAL

Biological invasions may impact ecological processes differentially from the local-scale to the global-scale (Table 1). For plant invasions, small-scale impacts are related to changes in

native plant population dynamics, and community structure and diversity (Parker et al. 1999; Mack et al. 2000). Allen and Knight (1984) found that cover, density and richness per unit area of native species in sagebrush-grassland communities in Wyoming have been reduced by invasive annual alien species (*Salsola kali*, *S. collina*, *Sisymbrium altissimum* and *Bromus tectorum*). Similar results were found for Californian serpentine grassland, where invasive annual grasses displace native forbs in fertilized plots (Huenneke et al. 1990). Interactions with other introduced organisms may also influence population dynamics of native species. For instance, *Centaurea maculosa*, an aggressive weed of northwestern United States, reduces *Festuca idahoensis* seed outputs and root and shoot growth, especially after herbivory by an introduced biocontrol (*Trichoplusia*) in controlled environment (Callaway et al. 1999).

Recently, ecologists have recognized that invasion may cause genetic impacts on native populations. Hybridization of native and invasive species can have three main effects (Parker et al. 1999): 1) Creation of a new invasive hybrid, 2) Production of sterile hybrids and 3) Genetic pollution or introgression of invader's genes into native species. Genetic flows between invasive and native species can be particularly important when dealing with genetically modified organisms, which may carry harmful genes that can affect ecosystem processes (Williamson and Fitter 1996).

Invasive species may alter ecosystem processes by inducing large-scale changes. Initial changes in vegetation diversity and structure produced by invaders may directly or indirectly alter ecosystem structure, disturbance regimes and biogeochemical cycles (Mack et al. 2000; Parker et al. 1999; Mack and D'Antonio 1998). For example, *Melaleuca quinquenervia* (Australian paperbark tree) has increased its range in Florida at a rate of more than 20 ha per day, reaching about 160,000 ha (see Schmitz et al. 1997 in Mack et al. 2000). This alien tree has replaced cypress, sawgrass and other native species, providing poor habitats for native animals, using higher amounts of water and intensifying fire regime. Other similar cases included *Mimosa pigra* in Australia, *Chromolaena odorata* in Asia and Africa, and *Lantana camara* in East Africa

(reviewed in Mack et al. 2000). In south central Chile, *Acacia dealbata* and *Ulex europaeus* have escaped and invaded large areas modifying habitat structure and completely displacing native species (A. Pauchard, personal observation). Meanwhile plantations of introduced conifers (e.g. *Pseudotsuga menziesii*) have been shown to alter soil, understory vegetation and fauna in the same region (Frank and Finckh 1997).

Impacts of invasive species in disturbance regimes may contribute to larger indirect effects on invaded ecosystems. Positive feedback has been reported between disturbance and abundance of invasive species (Mack and D'Antonio 1998). For example, invasion of African grasses in the Amazon have increased fire frequency and intensity, and eventually may cause the conversion of tropical forest into savanna-like ecosystem (D'Antonio and Vitousek 1992). D'Antonio et al. (1999) found 58 studies that link invasion with changes in disturbance regimes, including plant and animals. Plant invaders may enhance fire by increasing dead biomass accumulation, thereby auto-perpetuating their populations. In other cases invasive species may suppress fire regimes, by reducing native fire adapted species (D'Antonio et al. 1999). Other invaders can modify geomorphological disturbances by changing riparian habitat dynamics, increasing runoff erosion or stabilizing disturbed substrates (review in D'Antonio et al. 1999).

Invasive species modify biogeochemical cycles by both direct and indirect mechanisms. Most invasive species are strong competitors with higher metabolism rates that require higher amount of water and nutrients. For example, *Centaurea solstitialis* increases evapotranspiration rates in invaded communities (Dukes 2001). The invasion of trees or shrubs in grassland ecosystem may also increase evapotranspiration (Mack et al. 2000). Rates of nutrient uptake may also increase with alien plant invasion and thereby reducing available pools for native species (Parker et al. 1999). In other cases, alien nitrogen fixers may increase nitrogen availability in nutrient-poor soils (e.g. Hawaiian volcanic soils in Vitousek 1990). Changes in carbon cycle dynamics with possible consequences in global climate may also be produced by an increase in

fire frequency and subsequent expansion in CO₂ production and reduction in organic fixed carbon (Mack et al. 2000).

THE NEXT STEP: UNDERSTANDING INVASIONS ACROSS SCALES

To enhance our understanding of the mechanisms of alien plant invasions scientists must consider a research approach that integrates the study of invasion across scales. While many studies have explored small-scale mechanisms of invasive plant species, and a few have examined large-scale patterns, there is a critical gap in understanding the interaction between these scales on the invasion processes. As demonstrated above, this is not a simple matter of scaling up, because most processes controlling invasion are scale-dependent. Without sufficient knowledge of invasion-driven processes at different scales it is difficult to understand, and therefore manage plant invasions. As Stohlgren et al. (1999) show, sampling scale influences the results obtained in studying the invasibility of plant communities. Assessing invasion at multiple scales may help to better understand the dynamics of invasion and its implications to ecosystem processes. For example, *Linaria vulgaris* in West Yellowstone has been dominant for at least one decade in clearcuts and disturbed areas, displacing native grasses and forbs. However, its potential impacts in the adjacent Yellowstone National Park were not recognized until its distribution across the landscape was considered (A. Pauchard and P. B. Alaback, unpublished data).

Scientists must also attempt to use a multi-scale approach to understand the dynamics of the systems exposed to plant invasions. This may provide a more useful ecological context for the study of the invader. Questions about the interactions between invasion and disturbance or community invasibility will only be realistically answered if there is sufficient understanding of the ecological processes affecting that system. For instance, more emphasis must be placed on the mechanisms by which disturbance increases alien species invasion, and the characteristics of disturbance that favor this process. Additionally, multiple interactions of the driving factors of

invasion should be addressed explicitly. For example, this has been proven to be particularly important for determining the specific role of propagule pressure, disturbance or species diversity in community invasibility (e.g. Levine 2000).

Temporal scales should also be more fully incorporated into invasion research (Table 1). Most studies only look at short periods of time (2-3 years), yet it is well known that invasions occur over much longer periods of time. Furthermore changes over time are rarely linear, as shown in the historical reconstruction of invasive species detection (Toney et al. 1998). Monitoring systems need to be implemented using a scientific design, which recognizes these multi-scale relationships. For example, small and medium size permanent plots, the most classical approach to temporal variation in vegetation, are necessary to understand long-term changes in plant communities (Mack 2000). In New Zealand, Wiser et al. (1998) were able to describe the advance of *Hieracium lepidulum* in *Nothofagus* forests using data from permanent plots established more than 20 years before.

Historical records of species distribution that can be monitored using Geographic Information Systems (GIS) also enhance the possibilities for a clear understanding of temporal scale in invasions (Mack 2000). For instance, Arroyo et al. (2000) analyzing herbarium data were able to reconstruct historical movement of invasive species in Chile. The advantage of georeferenced historical data is that invasions may be analyzed with respect to both temporal and spatial dimensions and their interactions. Monitoring invasion at multiple scales may help to understand the mechanisms driving invasions, while providing valuable information to optimize efficiency in the control of invasive species.

Finding the dominant elements that determine invasion success at each scale and directing control efforts at the appropriate scale could help increase the efficacy of invasive species control. For example, in protected areas where medium distance dispersal is essential for weed invasion, weed specialists may be able to attack the causes of such dispersal. This would include not only the dispersal mechanisms, but also the sources of propagules outside the

protected area. In other cases, global processes such as long distance dispersal may be more important for invasion prevention, especially in areas that still maintain a low number of invasive species.

Development of multi-scale conceptual frameworks for understanding evolutionary processes, disturbance processes, nutrient transport, and most recently biodiversity patterns have provided ecologists with a rich set of tools with which to address increasingly complex questions. The enormous challenge of managing an increasing number of invasive plant populations should also benefit from experimentation with an integrated multi-scale approach.

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Table 1. Conceptual framework for understanding the role of scale on plant invasion processes.

Element \ Scale	Global	Regional	Landscape	Local
Invasion Processes	Intercontinental introductions	Range expansion	Establishment of new patches	Infilling of infected areas, patch expansion
Temporal scale	Centuries to millenia	Decades-centuries	Decades	Years
Impacts	Increase in alien flora and homogenization of global flora	Changes in biochemical cycles and disturbance regimes, losses in agricultural production	Regional impacts concentrated over specific landscape elements (e.g. reserves, riparian zones)	Changes in community composition, competitive relationships and displacement of natives
Study methodology and Monitoring	Species lists, voucher specimens, first records. Search for "expected" aliens.	Georeference new invaded areas and monitor advances (e.g. counties, other political boundaries)	Determine infection centers, corridors and new patches, establish changes in biochemical and disturbance cycles.	Determine changes in plant communities, conduct population studies including control, disease and insect interactions
Control	Limit new introductions, early detection and rapid response	Concentrate efforts on rapid expansion fronts, watch lists.	Control new foci and local dispersal mechanisms, evaluate control priorities.	Direct control over alien populations

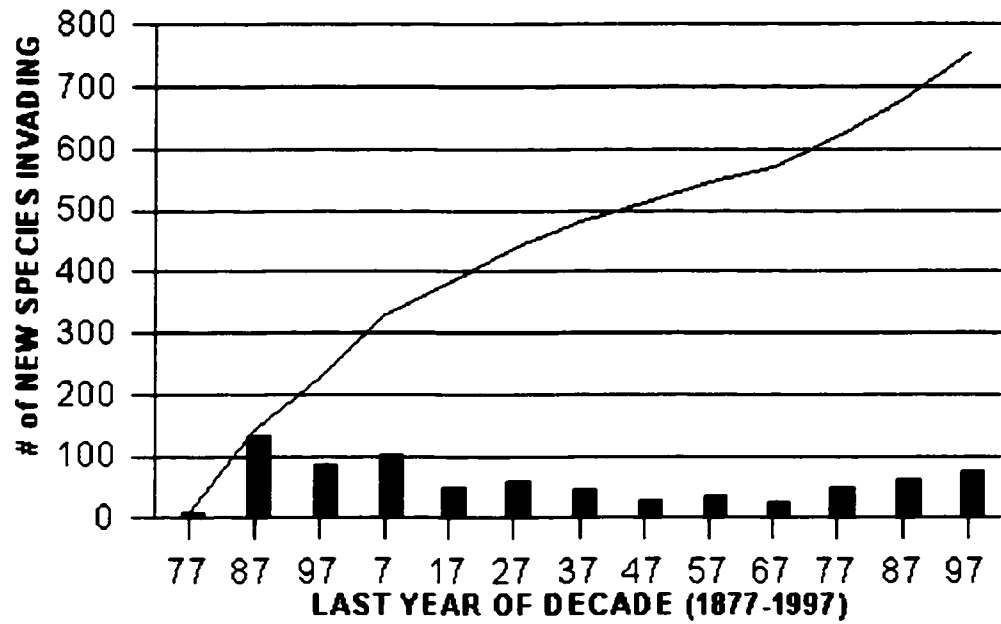


Fig. 1. New introductions of alien species by decades in five Northwest States in the United States. Bars indicate numbers per decade and the line indicate cumulative numbers. Taken with permission from Rice (2002).

CHAPTER 2

ROADS AS DISPERSAL CORRIDORS FOR ALIEN PLANTS IN PROTECTED AREAS OF SOUTH CENTRAL CHILE: HOW ELEVATION, LANDUSE AND LANDSCAPE CONTEXT INFLUENCE INVASION PATTERNS.

ABSTRACT

Alien plant species are a growing concern for protected areas, yet little information is available on the role of roads as corridors for alien species and the effects of elevation, landuse and landscape context in these invasions. These concerns are of particular interest in temperate zones of South America where protected areas have high concentrations of endemic species. We studied roadside alien plant communities and forest-road edges in Villarrica and Huerquehue national parks in the Andean portion of South-Central Chile. All alien species and their abundances were sampled along 21 km of roads inside parks and 22 km outside parks, using 500m roadside transects. We also sampled all plant species and abundance in 15 transects located perpendicular to forest-road edges in four forest types. Of the 66 total alien species encountered in roadsides, 61 were present outside parks and 39 inside parks. There was a significant negative correlation between elevation and alien species richness on roadsides ($R^2=0.56$, $p<0.001$). Elevation, landuse and their interaction explained 74% of the variation in alien species richness along roadsides ($p<0.001$). Transects located in pasture or disturbed secondary forests had a significantly higher number of alien species. We found no significant edge effect on native and alien species richness. Only few alien species percolate into forest interiors. We found no relationship between native and alien diversity in edge plots. Almost half of the alien species belong to 3 families and 85% originated in Eurasia. Our results suggest that alien species are moving into parks along road corridors and that elevation and landuse of the matrix influence these invasion processes. These findings corroborate the importance of early detection and control of invasive species in protected areas, and highlights the importance of considering surrounding matrix landuse in developing conservation strategies for reserves.

INTRODUCTION

Alien plants (*sensu* Richardson et al. 2000) are increasingly being recognized as a potential threat to the conservation of protected areas (e.g. McDonald et al. 1989; Lonsdale 1999; Mack et al. 2000). These plant invasions may ultimately decrease protected areas capacity to conserve biodiversity, because of their detrimental effects on native species and ecosystem processes (Mack et al. 2000) and the difficulty in controlling them in natural environments (McDonald et al. 1989).

Landuse, disturbance and climate are driving factors of alien plant invasion (Hobbs 2000, D'Antonio 1999; Lonsdale 1999). In temperate ecosystem, most alien species are invasive in human disturbed landscapes at low elevations mild climate (Hobbs 2000). However, accumulating evidence suggests that high elevation, pristine environments where most protected areas occur (Noss and Cooperrider 1994), can also be susceptible to invasion by alien plants (Stohlgren et al. 1999; Heckman 1999; DeFerrari and Naiman 1994).

Roads represent the primary corridors for the introduction of alien plant species into protected areas, especially for generalist species with rapid life cycles and high reproduction (Spellerberg 1998; Trombulak and Frissell 2000; Parendes and Jones 2000). Fortunately, most alien species growing in disturbed roadsides are incapable of colonizing less disturbed natural environments. Even so, roadsides still may serve as starting points for some species to percolate from the edges to the interiors of pristine or naturally disturbed environments (Murcia 1995; Cadenasso and Pickett 2001). Roadsides may also act as reservoirs of alien plant propagules that can be liberated in disturbance events (Parendes and Jones 2000).

Roads represent a priority for recognizing patterns of distribution of alien species along disturbed corridors and their potential for invasion into interior habitats (Trombulak and Frissell 2000). This is especially so in protected areas, which often are immersed in a human-disturbed landscape matrix and where ecological effects transgress administrative boundaries (Landres et al. 1998). Additionally, roadsides are useful sites to study the potential range of invaders at high

levels of soil disturbance, where climatic conditions and propagule availability are the main constraints (Spellerberg 1998; Milton and Dean 1998; Wilson et al. 1992; Tyser and Worley 1992; D'Antonio et al. 2001).

The South Central Chile region is of particular interest for studies of alien plant species because it contains a highly endemic and diverse flora that could be especially sensitive to invasions (Armesto et al. 1998; Arroyo et al. 2000; Armesto et al. 2001). Chile has approximately 690 naturalized alien species (15% of total flora); 381 of them occur in humid-seasonal-rainforest of Chile (Arroyo et al. 2000). Protected areas in this region are mostly located at high elevations and therefore do not appear to be significantly threatened by alien plant invasions (Arroyo et al. 2000; Pauchard and Alaback 2002). However, due to the increasing human disturbance and dispersal, alien species are moving from agricultural landscapes to natural environments. At the same time, new sets of species are arriving from overseas, increasing the susceptibility to invasion of the biogeographically isolated temperate forests of Southern Chile (Arroyo et al. 2000).

To better understand the susceptibility to invasion of protected areas it is necessary to understand the role of elevation, landuse and the spatial arrangement of landuse (landscape context) in patterns of distribution of alien species (D'Antonio et al. 2001). It is also important to assess the degree of percolation of alien species into more pristine environments (Cadenasso and Pickett 2001). In this study, we evaluated the influence of elevation, landuse and landscape context on alien species abundance and distribution along roadsides in two representative protected areas in South-Central Chile and their adjacent matrices. We also explored alien species distribution and abundance in park forest-road edges.

Study Sites

The study sites are comprised of two national parks and surrounding matrices, located in the Chilean South-central Andes: Villarrica National Park and Huerquehue National Park.

Villarrica National Park (63,000 ha) is located south of the towns of Pucón and Villarrica and extends to Lanín National Park in Argentina (ca. 39°W, 71°S). Elevation ranges between 600 and 3747 m. Three volcanoes shape its geomorphology: Villarrica (2,847 m), one of the most active volcanos in the Southern Andes (Casertano 1963), Quetrupillán (2,382 m) and Lanín (3,747 m). Huerquehue National Park (12,500 ha) is located 30 km north of Villarrica National Park near Caburgua Lake (39°W, 71°). This park shares a similar environment and natural history with Villarrica National Park but has been less affected by recent volcanic disturbances.

The climate in these areas is temperate with dry summers and cool and moist winters. Average annual precipitation ranges from 2,500 to 3,500 mm at high elevations. The mean annual temperature is 12°C with accumulations of up to 2 m of snow in the winter (Finckh 1996; CONAF 2002). Soils have formed from andesitic volcanic ejecta, tuffs, and scoria over basaltic deposits (von Buch 1970). Soil development is less at higher elevations and areas closer to volcanic cones. In lower valleys, deep andisols or “trumaos” with high water retention and drainage represent a rich substrate for plant growth (Frank and Finckh 1997). However, low levels of plant available phosphates may be a constraint for growth in these volcanic soils (Frank and Finckh 1997).

Villarrica National Park and adjacent areas contain a strong elevational gradient of vegetation (Finckh 1996). In lower valleys natural vegetation consists of *Nothofagus dombeyi* - *Nothofagus obliqua* forests that have been extensively replaced by grazing pastures dominated by alien grasses and forbs. *Nothofagus dombeyi* forests, *Nothofagus alpina* forests, and isolated patches of evergreen rainforests occupy middle elevations (600-1200m). At higher elevations, *Nothofagus pumilio* and *Araucaria araucana* form forest and shrubland. The alpine zone starts around 1200 - 1500 m, and is frequently associated with volcanic deposits. Natural disturbances include frequent and catastrophic volcanic activity, from the Villarrica Volcano, mudflows and small-scale windthrows (Finckh 1996).

European settlers in the 1800s converted much of the forests in low elevation valleys to grazing pastures. However, less productive and inaccessible land was not harvested and was set aside for protection in 1940 when Villarrica National Park was created (Finckh 1996). Secondary forests and low elevation pastures are the result of more recent fires (ca. 50 years) and continuous cattle grazing (Finckh and Thomas 1997). Currently, land clearing, firewood cutting, tourism and real estate development are affecting adjacent areas. However, aside from a popular ski development, the park maintains a relatively pristine status crossed only by a few dirt-gravel roads. Huerquehue National Park also covers an isolated area with rugged topography surrounded by private non-industrial agricultural land. There are no roads to the interior of the park, however intense recreation occurs on the park boundary and interior trails.

METHODS

Road Transects

Roadside transects were used to evaluate the influence of elevation, landuse and landscape context on alien species distribution and abundance. We sampled 43 km of road habitat on 3 roads from Villarrica National Park and 1 road from Huerquehue National Park. Elevation of transects ranged from 280 m to 1290 m. All roads were approximately 10 m wide and consist of gravel and natural volcanic substrate. We located roadside transects (500 m in length) starting at each kilometer of road from the park core to the adjacent matrix. Twenty one transects were located inside parks and 22 in their surrounding matrices. Seventeen transects were located in the Pucón entrance of Villarrica National Park (Rucapillán); 14 in the main access road of Villarrica National Park (Chinay); 4 on the international road that crosses Villarrica National Park (Puesco); and 8 in the access road of Huerquehue National Park (Huerquehue). Transects were 5 m wide at each side of the road. In each transect, we recorded all alien species and their abundance on a qualitative scale: A: abundant (>25% of the transect length), C: common (10-25%), I: intermittent when more than one group of individuals was present (<10%), and R: rare when only one group

of individuals was found. Alien plant species were considered as those non-native to Chile (*sensu* Richardson et al. 2000) and confirmed using Matthei (1995) for their taxonomic classification. We recorded for each transect the elevation and landuse in the surrounding matrix using four categories: pastures, secondary forests, primary forests and volcanic deposits. Elevation was recorded using an aneroid altimeter and a topographic map.

Edge transects

Forest-road edges in Villarrica National Park were studied to assess the degree to which alien plant species are percolating into interior habitat and explore the relationship between plant community attributes and the presence and abundance of alien species. A total of 15 edge-transects was established; 10 in Chinay and 5 in Puesco. Transects were distributed in four forest types: *A. araucana* - *N. pumilio* (n=4), *N. dombeyi*, *A. araucana* (n=2), *N. alpina* (n=6), *N. dombeyi*- *N. obliqua* (n=3). Edge transects were composed of 4 plots of 2 x 20 m and were randomly established in representative forest-road edges. Plots were located at 0, 10, 20 and 40 m from the end of the road surface. Each plot was divided into 2 subplots of 2 x 10 m to increase cover estimation accuracy. In each subplot cover for native and alien species in the understory was recorded, using the Braun-Blanquet cover classes (Mueller-Dombois and Ellemberg 1974). Native taxonomy followed Marticorena and Quezada (1985). In each subplot, as indicators of forest structure, we visually estimated total canopy cover, recorded dominant tree height using a clinometer and counted total tree seedlings by species. Canopy cover was estimated by recording the percentage of the central plot axis that was intercepted by the canopy vertical projection.

Distributional patterns of alien species

To understand the general taxonomic and biogeographical patterns of alien species, a list of all alien species found in the 43 transects was compiled. Species biogeographic origin and life form group (annual, biennial, perennial herb or woody perennial) based on Matthei (1995) was

established. Linear regression analysis was used to evaluate the correlation between alien species richness and elevation. The relative significance of elevation, landuse, and their interaction in explaining variation in alien species richness, was evaluated using multiple regression analysis (Ott and Longnecker 2001). The landuse and the interaction landuse-elevation factors were treated as sets of dummy variables (Ott and Longnecker 2001). To test for differences in the mean number of species by landuse type, the Kruskal-Wallis non-parametric test ($p \leq 0.01$) was used, for both the complete model and pairwise comparisons.

The elevational range for species present in at least two transects was determined. For each species, elevation of the lowest and highest transects where the species occurred was plotted. The influence of landscape context (location inside or outside the protected area) on alien species establishment was evaluated by calculating mean species richness for each transect inside and outside parks and testing for differences in abundance categories using the Kruskal-Wallis test ($p \leq 0.01$). To detect gradients in alien species assemblages we ran Detrended Correspondence Analysis (DCA) on transect species-abundance data using PC-ORD 4.0 (Hill and Gauch 1980). The ordination matrix contained 42 of the 43 transects, (one lacked alien species), and all species present in more than one transect ($n=45$). A subjective % cover value was assigned to each of the qualitative abundance classes: R=1, I=10, C=25 and A=50. Finally, to evaluate the role of physical variables in the compositional gradient, the relationship of transect scores in DCA axis 1 with elevation and landuse was analyzed. We evaluated elevation with a simple linear regression analysis and included landuse categories as a set of dummy variables (Ott and Longnecker 2001).

Evaluation of alien species percolation into forest habitats

Percolation of alien species into forest interiors was studied by comparing mean native species richness and mean alien species richness at the four distances from the edge, using the non-parametric Kruskal-Wallis test ($p \leq 0.01$). Analyses were run for each of the four forest types. We

averaged species abundance and canopy cover from the two subplots of 200 m² located at specific distances from the edge into one plot of 400 m² for all our edge transect data. Multiple regression models were used to determine which factors were most closely associated with native and alien species richness at the plot scale. Quantitative variables studied were distance from the edge, canopy cover (sum of all tree canopy cover), elevation, dominant forest height (the highest from the two subplots). Additionally, orientation (N, S, W, E) and forest type were included as set of dummy variables. Final models were selected using manual entry (all factors) and removing factors with $p > 0.1$. The correlation between native and alien species richness at 200 and 400 m² plots was evaluated, considering both the complete set of sampling units and also stratified by distance from the edge. To determine gradients in community composition and their relationship with distance from the edge and forest type, we ran a DCA ordination of all plots (n=60) and all species present in more than one plot (n=60). One outlier plot was removed in the final DCA model (n=59) because it was located in a forest gap and therefore its composition was affected by higher light availability. DCA diagrams with plots classified by distance from the edge and forest types were plotted to visualize any relationship of these variables with axis 1 and axis 2. Using linear regression models, we tested for correlations between DCA axis 1 and axis 2 and elevation and distance from the edge.

The effects of distance from the edge, elevation, canopy cover, forest dominant height, orientation and forest types in tree seedlings density were evaluated using multiple regression. We ran these models for total seedling density, and for *A. araucana*, *N. dombeyi*, and *N. alpina* seedling densities. All regression models and non-parametric statistics were performed using SPSS 10.0.

RESULTS

Roadside transects

A total of 66 alien species was found in roadsides, 39 in park transects and 61 outside parks (Table 1). Only five species were restricted to roadsides inside parks. The other 34 alien species present in the park were a subset of the species found in adjacent areas. The 66 species belonged to 26 families. The most represented families were Poaceae (14), Asteraceae (10), Fabaceae (7) and Scrophulariaceae (4). The most common species, measured by constancy in road transects, were *Hypochaeris radicata*, *Agrostis capillaris*, *Rumex acetosella* and *Lotus uliginosus* (Table 1). Only five species were classified as abundant in 10 or more transects: *Agrostis capillaris* (19), *Lotus uliginosus* (14), *Hypochaeris radicata* (11), *Holcus lanatus* (11), and *Rubus constrictus* (10). Of the 66 species, 57 (86%) were native from Eurasia, 4 from North America and 2 from Australia (Table 1). Perennial herbs were the most abundant life form with 23 species (34.8%). Annuals and woody perennials follow with 18 species each (27.2%) and 4 biennials account for only 6.0%.

Alien species richness was negatively correlated to elevation along roadsides ($p < 0.001$, $R^2 = 0.552$) (Fig. 1). Two roads in Villarrica National Park (Chinay and Rucapillán) showed a highly significant negative relationship between elevation and alien species richness ($p < 0.001$), the other two roads studied showed no significant trend ($p > 0.1$). Multiple regression showed that elevation, landuse and their interaction are significantly correlated to alien species richness for all transects, explaining 71% of the variation (Table 2). Mean alien species richness for road transects differed significantly with landuse. Pastures and secondary forests had the most diverse alien flora (Fig. 2). Roads inside parks had a significant lower mean number of alien species per transect (ca. 9) than roads in the adjacent matrix (ca. 18) (Fig. 3). This trend also applied to the number of alien species by abundance classes (abundant, common and intermediate) (Fig. 2). The only abundance class that did not show a significant difference based on landscape context was “rare”.

Elevational ranges of 45 alien species indicated that the upper limit was restricted to low elevations (<700 m) for only 3 species; for 35 species it occurred between 700 and 1000; and for 8 species it occurred over 1000m (Table 1; Fig. 4). Agricultural weeds such as *Lotus uliginosus* and *Dactylis glomerata* tended to colonize low to mid elevations. However, species associated with grazing reached higher elevations (e.g. *Hypochaeris radicata*, and *Rumex acetosella*). The principal gradient for alien species assemblages, DCA axis 1 (EIG=0.268), was closely correlated with elevation ($R^2=0.64$, $p<0.001$). DCA axis 2 was not significantly correlated with either elevation or landuse. In the ordination diagram, transects appear weakly clumped by landuse (Fig. 5)

Forest-road edge transects

Mean native species richness was not significantly different at the four distances from the forest-road edge in any of the forest types. However, for all plots, elevation and distance were negatively correlated with native species richness. The final model including type, elevation and distance only explained 36% of the variation (Table 3). All other factors were not significant in explaining residual variation. All 17 alien species found in edge transects were already recorded in roadsides transects (Table 1). Alien species did not appear in forest interiors in both subalpine forest types (*A. araucaria* - *N. pumilio* and *N. dombeyi* - *A. araucaria* forests) and only one species occurred in their edges. In the case of *N. alpina* forests, a significantly higher number of alien species occurred in edges than in interiors ($p<0.005$). However, there was no significant difference between edges and interiors of *N. dombeyi* - *N. obliqua* forests ($p>0.1$). Elevation, canopy cover and forest type explained 47% of the variation in alien species richness (Table 2) and all variables were negatively correlated. No significant correlation was found between alien and native species richness in the 200 or 400m² plots.

The most significant compositional gradient (DCA axis 1, EIG=0.884) in forest-road edges was associated with elevation ($R^2=0.815$, $p<0.001$) and forest type (Fig 6a), while DCA axis 2 (EIG=0.384) was weakly associated with distance from the edge ($R^2=0.05$, $p<0.1$) (Fig.

6b). *Araucaria araucaria* - *N. pumilio* forests appeared clustered showing little variation in composition. On the other hand, low elevation forest dominated by *N. dombeyi* or *N. alpina* showed a higher level of variation in their composition. Overall, plots closer to the edge had a higher axis 2 value, especially those located at the edge (Fig. 6b).

No significant effect of distance from the edge in total tree seedling density was detected ($p>0.1$). *Araucaria araucana* seedling density was positively correlated with elevation (Table 3). *Nothofagus dombeyi* seedling density was correlated with type and positively correlated with height (Table 3). *Nothofagus alpina* seedling density was correlated with forest type and orientation (Table 3). Overall, total seedling density was weakly correlated with type (Table 3).

DISCUSSION

Elevation as a constraint for alien species

Elevation is assumed to be a key factor influencing invasion success worldwide, yet few studies have documented this relationship or tested its generality. Elevation is an important indicator of microclimatic variations, which may physiologically constrain alien plant invasion (Forcella and Harvey 1983; Wilson et al. 1992). For example, Chong et al. (2001) found that elevation is the second most important variable, after location, to explain variability in the number of alien species in Rocky Mountain National Park. Similarly, Stohlgren et al. (2002) found that low elevation areas were more invaded than higher ones in North-central United States.

In Southern Chile, most alien species have originally evolved in agricultural systems in Eurasia (Arroyo et al. 2000); therefore, they are adapted to moderate climatic conditions and may lose their competitive advantage at high elevations (Sax and Brown 2000). High elevation environments also present unpredictable and stressful conditions that may constrain R-strategy species (Grime 1977). These factors may explain, at least partially, the reduction of species richness and abundance with increase in elevation in our study site. However, elevation may also

be acting as a physical barrier for alien species dispersal, restraining propagule flow to higher elevations. In our study site, the few alien species found over 1,000 m were “rare”. This suggests that even when climatic conditions are sufficient for the establishment of alien plants, few propagules get dispersed to these higher roadsides or only a small portion of the propagules are successful.

The negative correlation between elevation and alien species richness in our study site supports the hypothesis that elevation is an important constraint to invasion and that alien species tend to concentrate in milder, low elevation environments (Forcella and Harvey 1983). However, the correlation ($R^2=0.492$, $p<0.001$) between elevation and landuse complicates the independent role of each variable. In our study sites, anthropogenic landuses of the matrix tend to be clumped at low elevations. Thus, elevation not only is an indicator of microclimate, but also indirectly represents the gradient of landuse from intense pasture use at low elevations to pristine forests at high elevations. This relationship between elevation and landuse occurs worldwide, especially around protected areas, making it difficult to isolate the effect of elevation as a climatic constraint.

Landuse and landscape processes

Landuse is one of the most influential variables in determining the distribution of alien species worldwide (Hobbs 2000; Sax and Brown 2000). Landuse directly affects the invasion processes by modifying disturbance regimes and environmental conditions. However, it can also influence the invasion process by indirectly creating sources of propagules in the landscape. Areas with higher human intervention, such as agricultural or urban landscapes, serve as sources for invasions into more pristine environments (Hobbs 2000; Parendes and Jones 2000; Tyser and Worley 1992). Propagule pressure from these sources appears as the most influential mechanism by which landuse affects abundance and distribution of alien species in roadsides of our study sites. Consequently, alien species invasions may be responding to the spatial arrangement of

landuse. Landscape context explains why park interiors, are less invaded than those located in the human disturbed matrix (Fig. 3).

In southern Chile, pastures are dominated by alien plant species because few native species tolerate grazing by cattle, serving as the main source for invasions (Scherer and Deil 1997; Finckh and Thomas 1997). We found that the species that are more frequent and more abundant in roadsides were reported as dominant in pastures of Villarrica National Park and its surroundings (Finckh and Thomas 1997). This included *Trifolium repens*, *Plantago lanceolata*, *Dactylis glomerata*, *Taraxacum officinale*, *Holcus lanatus*, *Rumex acetosella*, *Hypochaeris radicata*, *Agrostis capillaris* and *Poa pratensis*. Finckh and Thomas (1997) found these species in most pastures in the area of Villarrica National Park, but their abundance was proportional to the degree of grazing. In our study sites, cows and horses are probably the main vectors for seed dispersal, bringing alien species propagules from pastured lands in adjacent matrices to park interiors (Personal observation; Arroyo et al. 2000). Dispersal via cattle dung is predominant for many grasses and herbs with small seeds (e.g. *Agrostis* spp. *Bromus* spp., *Rumex acetosella*, *Trifolium* spp.) including exozoochorous species like *Lotus uliginosus*, and anemochorous species like *Cirsium vulgare*, *Hypochaeris radicata* and *Taraxacum officinale* (Malo and Suarez 1995, Matthei 1995, Finckh and Thommas 1997).

Our results suggest that roadsides in secondary forests and agricultural areas have higher alien species due to the higher propagule flow from surrounding areas, frequent grazing, milder climate associated with lower elevations, and higher sunlight due to open canopies (Milton and Dean 1998, Finckh and Thommas 1997, Wilson et al. 1992, Parendes and Jones 2000). In addition, secondary forests occur in areas that previously have been clearcut and used as pastures. Thus, some species may still remain in the seedbank and are establishing themselves given the adequate soil disturbance and light levels (Finckh and Thomas 1997, Holmes et al. 1997). These low elevation areas are heavily grazed, incorporating new alien species brought in livestock food

supplies (Park rangers personal communication; Tyser and Worley 1992). Low levels of alien species on roadsides in primary forests may be caused by lower light availability due to a closer canopy and because these forest are now restricted only to higher elevations (Parendes and Jones 2000; Finckh 1996). Soils in primary forests have a low nitrogen mineralization rate due to shady-cool conditions, which may be an additional constraint for the establishment of agricultural weeds adapted to high nutrient levels (Scherer-Lorenzen et al. 2000). Finally, a thick litter layer and a low proportion of bare soil may limit the establishment of invasive species (Mazia et al. 2001, Myster 1994). Low soil development and nutrient content may explain the extremely low susceptibility to invasion of roadsides in volcanic deposits, which are barely colonized even at low elevation and close to pastures. Our results indicate that landuse may overcompensate for the effects of elevation gradients in alien species richness. For example, Huerquehue National Park is located in a lower elevation site surrounded by agricultural fields, which translates into an increasing number of alien species in higher elevations outside the park.

Edge effects

The inconsistency of edge effects on native plant diversity and seedling density in the four forest types studied is similar to other edge studies reported in the literature (Murcia 1995). Our results may be explained by the high structural diversity of the forests studied. *Araucaria araucana* - *N. pumilio* forest are usually open with narrow roads, which may explain the lack of an edge-effect (Finckh 1996). *Nothofagus dombeyi* - *A. araucana* are closed forests (over 80% canopy cover) and secondary roads only partially disrupt the canopy; therefore, edge effects are due to changes in soil disturbance but not in light availability. In lower elevations, *N. alpina* forms closed forests that are affected by wider and more “heavily used” roads, showing significant edge effects. Finally, *N. dombeyi*- *N. obliqua* forests are open communities under intense pressure for grazing and firewood, which makes it difficult to isolate the causal variable of species richness spatial patterns.

While roadsides represent a continuously disturbed environment ideal for alien plant colonization, the conditions in interior forested habitats represent a much higher challenge (Cadenasso and Pickett 2001; Honnay et al. 2002). Nonetheless, our results for Villarrica National Park showed that elevation, type and canopy cover explain the distribution of alien species more precisely than distance from the edge. As found for roadsides, the strong elevational and landuse gradients appeared as the driving factors for alien species richness in forest-road edges (Table 2). The presence of alien species in the interior of secondary forests may be explained as a combination of the following factors: 1) these forest have reclaimed open areas affected by fire and clearcuts, therefore while most alien species quickly disappear as the canopy closed, some still remain mainly in sterile forms (Finckh and Thomas 1997), 2) dispersion by cattle still occurs in these areas, bringing propagules from outside sources, and 3) higher light and bare soil in these younger and more disturbed forests favors alien plant establishment (Parendes and Jones 2000).

General taxonomic and biogeographical patterns of invasion

Even though Villarrica National Park is a moderate to high-elevation temperate park and has low levels of human disturbance, the number of alien species documented in this study suggest a significant alien flora for the park. Villarrica National Park has approximately 310 species of native plants (Finckh 1996). Our results suggest an alien/total species ratio of 11.2%, considering both alien species in roadsides of Villarrica and Huerquehue National Parks. The estimation is conservative because even though most alien species tend to appear first in roadsides, additional alien species could be established in grasslands or forests in boundary areas of the park. For Villarrica National Park and surrounding pastures, Finckh and Thomas (1997) estimated an alien/total species proportion that varied from 75% in low elevation pastures in the matrix, around 30% in regenerating shrublands to 7% in forests outside the park and 0% in forests in the park. Pauchard et al. (2000) found an alien/total species ratio of 18% in the main

recreational area of Conguillio National Park, located 100 km north from Villarrica. Muñoz-Schick (1980 in Arroyo et al. 2000) found 12 percent of alien species for Puyehue National Park, which is 200 km south of our study area. However in the highly urban and agricultural central valley, 150 km northwest from Villarrica National Park, alien species account for 45% of the total flora of an small 60 ha reserve (Hauenstein et al. 1988). Arroyo et al. (2000) predicted a growth in the ratio of alien species in Chilean protected areas with increasing visitors and horse trekking.

The families Poaceae (21%), Asteraceae (15%), Fabaceae (11%) accounted for 47% of the alien species. Pysek (1998) found that these families are the most represented in alien floras worldwide. Surprisingly, Brassicaceae, the fourth most abundant family in global alien floras (Pysek 1998) was not represented. The percentage of Eurasian species in our study sites (85%) is higher but consistent with the ratio for Chile (71.2%) and for the central region (74.4%) (Arroyo et al. 2000). However, this is much higher than the worldwide average of 59% (Pysek 1998). Most species in our sites are natives to European grasslands and probably were introduced to Chile before the 1900s (Finckh and Thomas 1997). For example, 11 Eurasian species are common both in our study sites and in roads and streams of the Cascade Range in Oregon, USA (Parendes and Jones 2000). Certainly this trend toward a high proportion of Eurasian species may change with increasing global dispersion and new “exotic” introductions of ornamentals (Swenson et al. 1998). We also found a higher proportion of woody perennials compared to the 14.1% for the Chilean alien flora (Arroyo et al. 2000). The high rainfall of the area may favor woody species over annuals. Additionally, the shorter growing season may also provide an advantage for those perennial alien species (34.8%) over annuals (27.2%), differing from the overall Chilean pattern where annuals account for 50.9% and perennial for 37.5% (Grime 1977; Arroyo et al. 2000).

Management recommendations

Our results confirm the importance of roads as corridors of plant invasions from disturbed landscape matrices into protected areas in temperate forest regions (Spellerberg 1998; Trombulak and Frissell 2000; Parendes and Jones 2000). Although elevational gradients produce climatic constraints for alien species, sufficient propagule availability allows some species to establish in harsh environmental conditions. Our results also support evidence that roadsides are the first landscape elements to be colonized by alien species and therefore may indicate their potential ranges of invasion (Spellerberg 1998; Trombulak and Frissell 2000; Parendes and Jones 2000, Tyser and Worley 1992, Forman and Alexander 1998).

Because propagules disperse from source populations abundant in specific landuse conditions, invasive species management in protected areas should include both reserve corridors and adjacent matrixes to limit the rate of invasion and new introductions (Parendes and Jones 2000, Tyser and Worley 1992, Pauchard et al. unpublished data). The increasing development of matrixes adjacent to protected areas make early detection and control of invasive species a priority for conservation both inside and outside of parks (Pauchard et al. accepted).

If regional patterns applied to a smaller scale, the increasing changes in landuse and increasing road density may increase the number and the impact of alien species in reserves of Southern Chile (Arroyo et al. 2000). At present, few species are aggressively invading. However, the increasing rate of introductions and genetic adaptation could change this scenario (Arroyo et al. 2000, Mack et al. 2000). Two groups of concern are conifers and Fabaceae shrubs. *Pseudotsuga mensiezii* and *Pinus contorta* has been reported as invading native forest understory in protected areas of the region (Peña and Pauchard 2002). *Citrus scoparius* and *Ulex europaeus*, both recognized invaders of temperate climates (Matthei 1995, Bossard et al. 2000), are abundant in low elevation areas and populations are establishing around Villarrica National Park. Specific management recommendations for protected areas in southern Chile should include 1) the

complete elimination of cattle grazing in park interiors and boundaries (Finckh and Thomas 1997), 2) impact assessment of road construction and increasing traffic in the dispersion of alien species propagules (Spellerberg 1998, Tyser and Worley 1992), 3) control of invasive species in the surroundings of the parks before their dispersion (Chapters 4 and 6) and 4) establishing monitoring plans for alien species to prioritize the control of species with negative effects over those that have no significant impact (Byers et al. 2002, Tyser and Worley 1992).

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Table 1. Alien species for the study areas. LF: life form (W: woody, P: perennial herb, B: Biannual, A: annual). * Species occurring in roadside transects inside parks (P) or forest-road edge transects (E). Constancy indicates the number of roadside transects were the species was found. Habitat: 1) low elevation, 2) low-middle elevation, 3) high elevation. Continental origin, AU: Australia, E: Eurasia, NA: North America.

Species	Family	LF	P	E	Constancy	Habitat	Origin
<i>Acacia dealbata</i>	Fabaceae	W	*		4	2	AU
<i>Acer platanoides</i>	Aceraceae	W			1		E
<i>Achillea millefolium</i>	Asteraceae	P	*		5	3	E
<i>Agrostis capillaris</i>	Poaceae	P	*	*	38	3	E
<i>Anagallis arvensis</i>	Primulaceae	A			1		E
<i>Arrhenatherum elatius ssp. bulbosus</i>	Poaceae	P			5	2	E
<i>Asteracea</i>	Asteraceae		*		1		-
<i>Asteracea</i>	Asteraceae				1		-
<i>Asteracea</i>	Asteraceae				1		-
<i>Briza minor</i>	Poaceae	A			4	1	E
<i>Bromus hordeaceus</i>	Poaceae	A	*	*	20	2	E
<i>Bromus rigida</i>	Poaceae	A			7	2	E
<i>Castanea sativa</i>	Castanaceae	W			1		E
<i>Cerastium arvensis</i>	Cerastaceae	P	*		5	3	E
<i>Cirsium vulgare</i>	Asteraceae	A	*	*	22	2	E
<i>Crepis capillaris</i>	Asteraceae	A	*		8	2	E
<i>Cupressus macrocarpa</i>	Cupressaceae	W			1		E
<i>Cynosorus echinatus</i>	Poaceae	A			6	2	E
<i>Cytisus striatus</i>	Fabaceae	W			3	1	E
<i>Dactylis glomerata</i>	Poaceae	P	*	*	18	2	E
<i>Daucus carota</i>	Apiaceae	A			1		E
<i>Dichondra sericea</i>	Convolvulaceae	P	*		6	2	E
<i>Digitalis purpurea</i>	Scrophulariaceae	B	*		10	2	E
<i>Echinochloa crus-galli</i>	Poaceae	A	*		8	2	E
<i>Echium vulgare</i>	Boraginaceae	B	*		10	2	E
<i>Eucalyptus nitens</i>	Myrtaceae	W			1		AU
<i>Festuca arundinacea</i>	Poaceae	P		*	1		E
<i>Foeniculum vulgare</i>	Apiaceae	P			1		E
<i>Geranium core-core</i>	Geraniaceae	P	*	*	11	2	E
<i>Hedera helix</i>	Araliaceae	W			1		E
<i>Holcus lanatus</i>	Poaceae	A	*	*	24	2	E
<i>Hypericum perforatum</i>	Hypericaceae	W	*	*	10	2	E
<i>Hypochaeris radicata</i>	Asteraceae	P	*		39	3	E
<i>Leucanthemum vulgare</i>	Asteraceae	P	*		1		E
<i>Lolium perenne</i>	Poaceae	P	*		3	3	E
<i>Lotus uliginosus</i>	Fabaceae	A	*	*	33	2	E
<i>Melissa officinalis</i>	Lamiaceae	P	*		2	2	E
<i>Mentha pulegium</i>	Lamiaceae	P			1		E
<i>Myosotis arvensis</i>	Boraginaceae	B			1		E
<i>Panicum capillare</i>	Poaceae	A	*		3	2	NA
<i>Parentucellia viscosa</i>	Scrophulariaceae	A	*		1		E
<i>Pinus radiata</i>	Pinaceae	W			1		NA
<i>Plantago lanceolata</i>	Plantaginaceae	P	*		26	2	E
<i>Plantago major</i>	Plantaginaceae	P			2	2	E
<i>Polygonum persicaria</i>	Polygonaceae	A	*		2	2	E
<i>Polypogon monspeliensis</i>	Poaceae	A	*		5	2	E

Continues next page...

Species	Family	LF	P	E	Constancy	Habitat	Origin
<i>Populus alba</i>	Populaceae	W			1		E
<i>Prunus avium</i>	Prumnaceae	W	*	*	4	2	E
<i>Prunella vulgaris</i>	Lamiaceae	P	*	*	28	2	E
<i>Pseudotsuga menziesii</i>	Pinaceae	W	*		5	2	NA
<i>Rosa moschata</i>	Rosaceae	W	*	*	23	2	E
<i>Rosa vulgaris</i>	Rosaceae	W			1		E
<i>Rubus constrictus</i>	Rubiaceae	W	*	*	25	2	E
<i>Rubus radicans</i>	Rubiaceae	W			2	2	E
<i>Rumex acetosella</i>	Rumeaceae	P	*	*	34	3	E
<i>Rumex crispus</i>	Rumeaceae	P			2	2	E
<i>Sonchus asper</i>	Asteraceae	A	*		5	2	E
<i>Symphoricarpos albus</i>	Caprifoliaceae	W			1		NA
<i>Taraxacum officinale</i>	Asteraceae	P	*	*	20	2	E
<i>Trifolium pratensis</i>	Fabaceae	P	*		15	2	E
<i>Trifolium repens</i>	Fabaceae	P	*	*	18	2	E
<i>Triticum aestivum</i>	Poaceae	A	*	*	2	2	E
<i>Ulex europaeus</i>	Fabaceae	W			2	2	E
<i>Verbascum thapsus</i>	Scrophulariaceae	B	*		8	2	E
<i>Veronica cf. anagallis-aquatica</i>	Scrophulariaceae	P	*		1		E
<i>Vicia sativa</i>	Fabaceae	A			2	1	E

Table 2. Regression models for native and alien diversity in plots along roadside and road-forest edge transects in Villarrica National Park. Relation for a set of dummy variables is non-applicable (NA).

Dependent variables/ Factors of variation	R ²	Relation +/-	df/ (variables)	p for the factor	p
a) Alien spp. richness in roadside transects(n=43)	0.714		35		0.0000
Elevation		+		0.1269	
Land-use		NA	(3)	0.0099	
Interaction		NA	(3)	0.0058	
Intercept			(1)	<0.0001	
b) Native spp richness in edge plots (n=60)	0.360		54		0.0002
Elevation		-		0.0002	
Type		NA	(3)	0.0196	
Distance		-	(1)	0.0244	
Intercept			(1)	<0.0001	
c) Alien spp. richness in edge plots (n=60)	0.477		54		0.0000
Type		NA	(3)	0.0159	
% Canopy cover		-	(1)	0.0025	
Elevation		-	(1)	0.0247	
Intercept			(1)	0.0032	

Table 3. Regression models for seedling density in edge-transect plots. Relation for a set of dummy variables is non-applicable (NA).

Dependent variables/ Factors of variation	R ²	Relation +/-	df/ variables	P for the factor	P for the model
a) Total seedling density in edge transects (n=60)	0.132		56		0.0462
Type		NA	(3)	0.0452	
Intercept			(1)	0.2606	
b) <i>Araucaria araucana</i> seedling density in edge transects (n=60)	0.403		56		<0.0001
Type		NA	(3)	<0.0001	
Intercept			(1)	1.0000	
c) <i>Nothofagus dombeyi</i> seedling density in edge transects (n=60)	0.435		55		<0.0001
Type		NA	(3)	<0.0001	
Dominant height		+	(1)	0.0189	
Intercept			(1)	0.0104	
d) <i>Nothofagus alpina</i> seedling density in edge transects (n=60)	0.372		53		0.0040
Type		NA	(3)	0.1000	
Orientation		NA	(3)	0.0221	
Intercept			(1)	<0.0001	

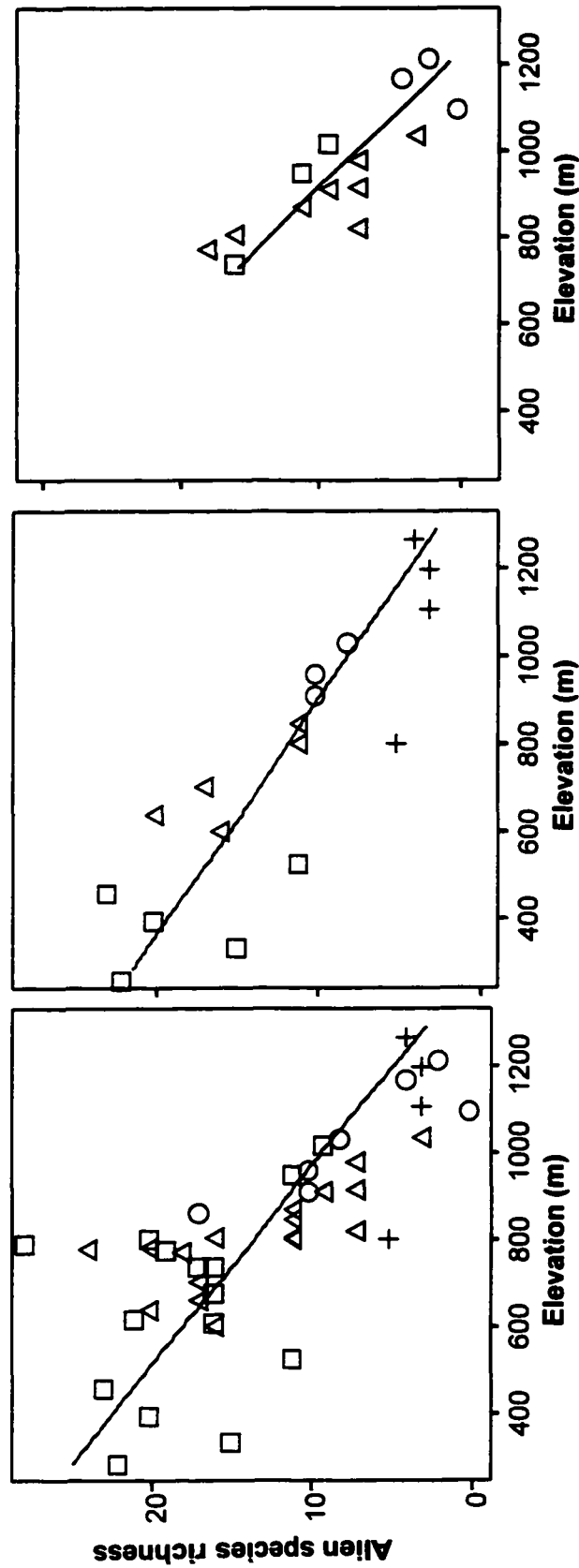


Fig. 1. Linear regression of number of alien species per roadside transect on elevation. A) All transects sampled ($n=43$, $r^2=0.539$, $p<0.001$, constant=31.46, slope=0.716, $p<0.001$, constant=26.88, slope=0.0187), B) Rucapillan road ($n=17$, $r^2=0.0221$, $p<0.001$, constant=38.76, slope=-0.0320). Symbols indicate land-use of the surrounding matrix. Land-use: + = Volcanic deposits, o = primary forests, Δ = secondary forests and □ = pastures.

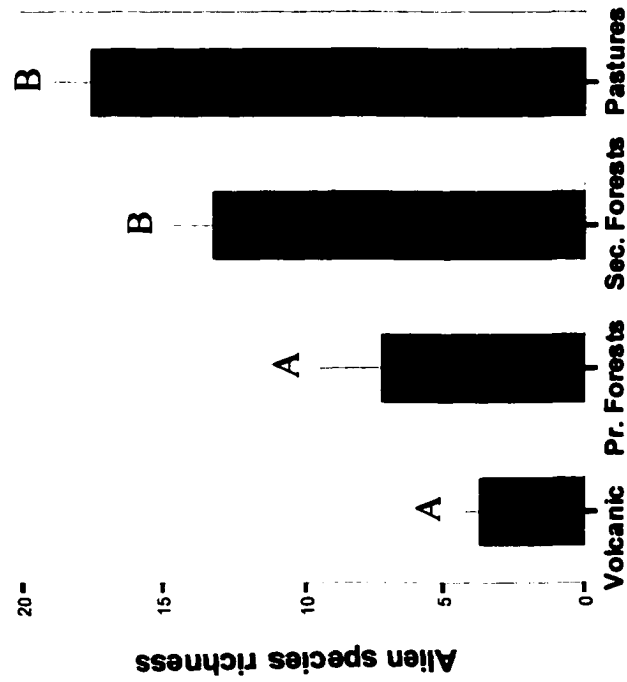


Fig. 2. Mean (+SE) of alien species in transects classified by land use and ordered by mean number of species. Groups with different letters are significantly different using Kruskal-Wallis ($p < 0.05$). Overall model has a $p < 0.001$.

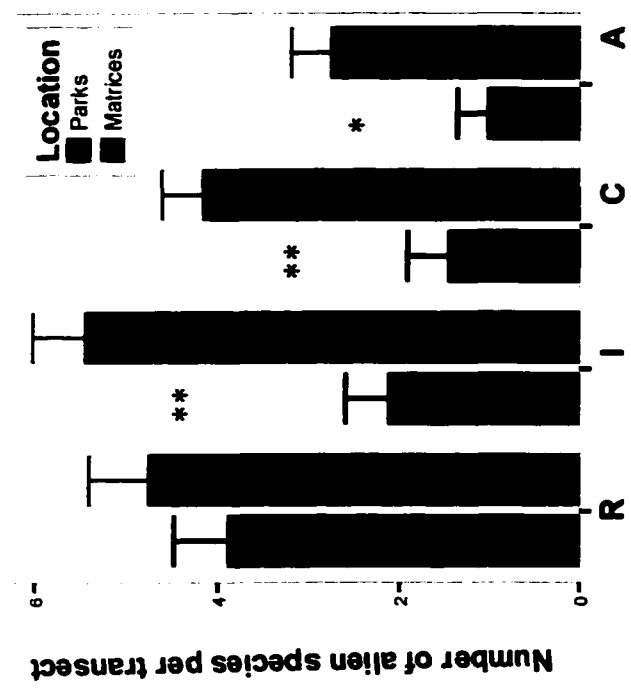


Fig. 3. Mean (+SE) number of alien species in transects classified by abundance classes (A: Abundant, C: Common, I: Intermediate, R: Rare) and by location (inside parks or matrixes). Levels of significant differences using Kruskal-Wallis: *= $p<0.05$, **= $p<0.001$, #= $p<0.001$. Symbols indicate differences due to location for each abundance class. Totals are 8.52 for parks and 17.09 for matrixes ($p<0.001$). Mean elevation for parks is 996 m and for matrixes 690 m.

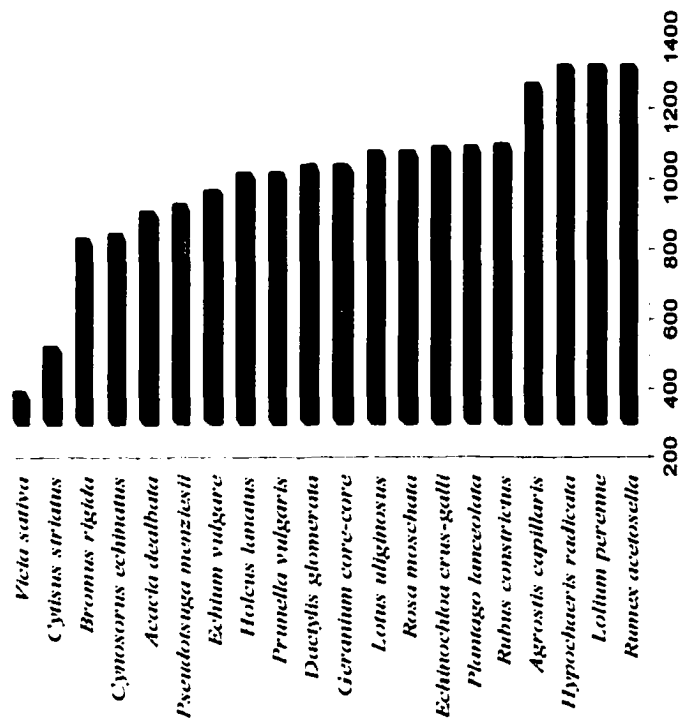


Fig. 4. Range of elevation for some common alien species on roadsides. Sampling ranges from 284 m to 1290 m.

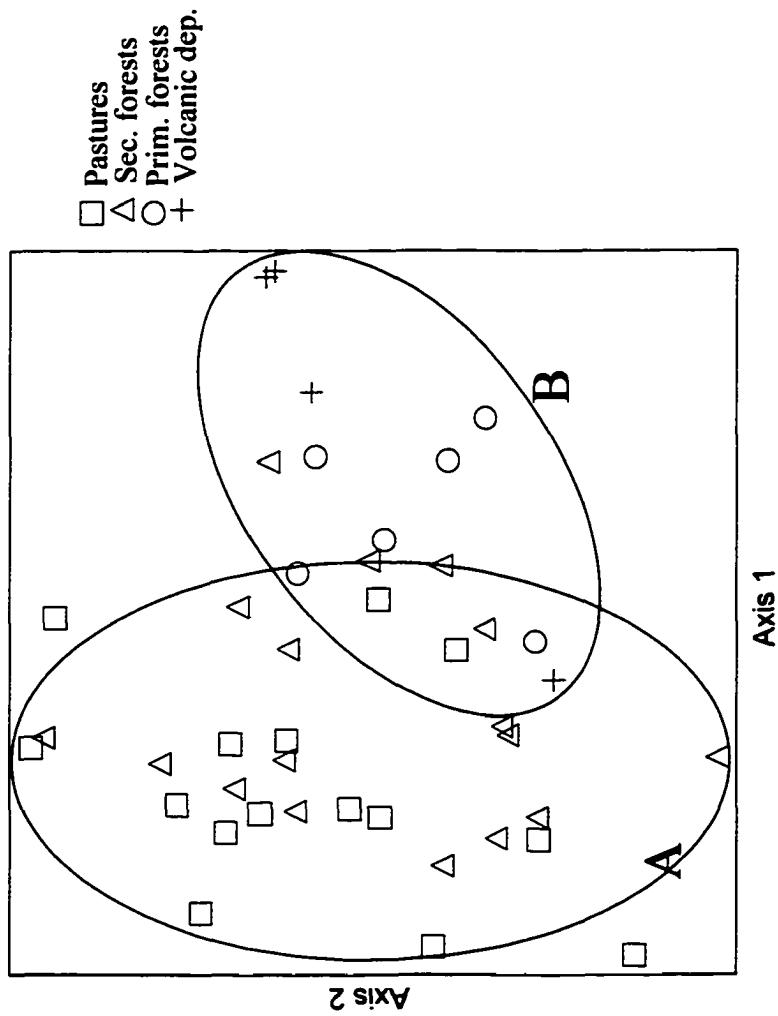


Fig. 5. DCA diagram for roadside transects. Transects are classified by landuse. Ellipses show two groups A: pastures and secondary forests, and B: primary forests and volcanic deposits.

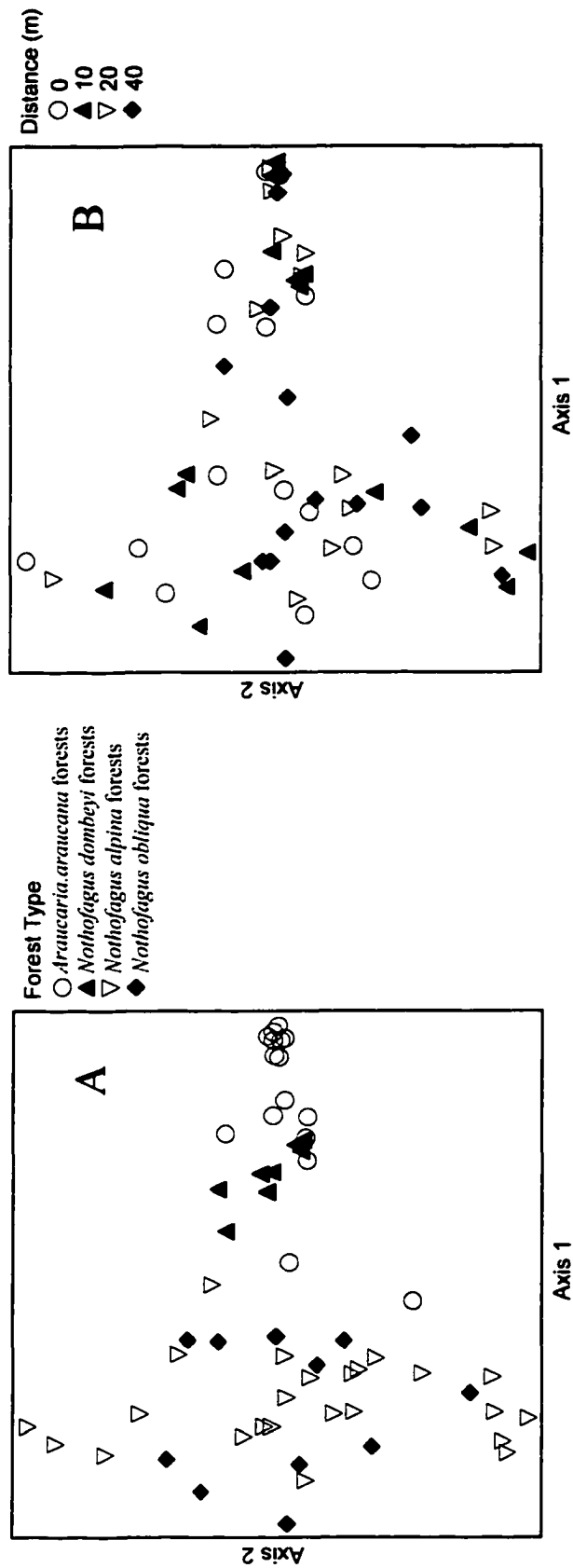


Fig. 6. DCA diagram of forest-road edge plots. Plots classified by A) forest type and B) distance from the edge. Axis 1 represents a gradient from low (left) to high (right) elevation (A). Plots near edges tend to occur in the upper section of the diagram (B).

CHAPTER 3

EDGE EFFECTS FOR ALIEN AND NATIVE PLANT SPECIES ARE RELATED TO EDGE TYPE:

A COMPARISON OF FIRE, ROAD AND CLEARCUT EDGES IN *Pinus contorta* FORESTS IN WEST YELLOWSTONE, MONTANA.

ABSTRACT

Forest edges are key elements in the percolation of alien plant species into forest interiors. However, little research has been conducted to understand the role of forest edge type in controlling edge effects on invasive species. In the Northern Rocky Mountains of the United States, forest edges are a common feature in the landscape with anthropogenic (roads, clearcuts) and natural (burns) edge types. High elevation *Pinus contorta* (lodgepole pine) forests are no exception. In this paper we aim to test for differences in patterns of alien species invasion and native communities among three forest edge types in the *P. contorta* forests around West Yellowstone, Montana. We also explore the role of forest structure, edge type and distance from the edge in these patterns. Six transects were located in each of five edge types: 1) highway in Gallatin National Forest, 2) highway in Yellowstone National Park, 3) a burn forest of the 1988 fires in Yellowstone National Park, 4) a burned forest in Gallatin National Forest and 5) clearcuts of Gallatin National Forest. Edge-transects consisted of 5 plots of 2 by 20 m, distributed from the adjacent matrix to 40 m inside the forests. We found a significant effect of edge type and the interaction of edge type and distance on native species richness and native species cover ($p < 0.05$, ANOVA). Alien species richness was significantly related to edge type, distance and interaction between both variables ($p < 0.01$, ANOVA), with higher values in highway matrices and edge plots. Burn and clearcut edges had, on average, less than one alien species per plot. Overall, alien species richness was negatively correlated with native species richness in plots with at least one alien species ($R^2 = 0.30$, $p < 0.001$). Patterns in the distribution of native and alien species in forest edges appear to be not only affected by physical changes in relation to proximity to the edge, but also by the pool of propagules that is able to reach them. Our study suggests that patterns of native and alien plants are related to both the physical effects of creating a forest edge and also to the landscape context in which these edges occur. These results should help to prioritize management efforts to control invasive alien species into edges adjacent to human corridors.

INTRODUCTION

Increasing evidence suggest that landscape structure and land-use are key elements in influencing alien species invasion processes (Hobbs 2000). At the landscape scale, forest edges are recognized as a potential starting point for invasions, acting as facilitators of the percolation of alien species into less disturbed environments (Saunders et al. 1991, Brother and Spingarn 1992, Cadenasso and Pickett 2001, Honnay et al. 2002). However, little research has been conducted to understand the role of forest edge type in controlling edge effects on invasive species and their implications for landscape invasions.

Most of the evidence of edge effects in forests on native and alien species comes from road and clearcut edges (Chen et al. 1992, Murcia 1995, Euskirchen et al 2001). Other natural and anthropogenic forest edges, which have been less studied, may show distinct responses due to their unique characteristics including landscape context and causal agent. This may prove particularly critical in the case of alien species invasion where landscape processes influence smaller scale phenomena. For example, clearcut edges may appear physically similar to road edges, but the dispersion of alien species may be significantly lower than in road-forest edges that are continuously receiving propagules carried by vehicles from other distant areas that act as sources (Spellerberg 1998, Parendes and Jones 2000).

While changes in physical environment along edges have been intensively studied (Cadenasso et al. 1997, Matlack et al. 1993, Young and Mitchell 1994), these physical factors may actually play a secondary role in alien plant invasion, whereas propagule availability may represent the main constraint for invasion (Cadenasso and Pickett 2001, Honnay et al. 2002, D'Antonio et al 2001).

Edge types (e.g road, cleacuts, burned forests) provide natural experiments to compare invasion processes in relation not only to distance from the edge, but to other variables including the nature of the matrix (landuse adjacent to the forest edge sensu Lindermayer and Franklin 2002). By comparing edge effects through several types of edges, it may be possible to examine

the relative importance of propagule flow as compared to physical factors in invasions of forest edges.

In the Northern Rocky Mountains of the United States, forest edges are a common feature in the landscape. Road and clearcut forest edges are the dominant anthropogenic edge types (Reed et al. 1996), while edges in burned forests are a naturally abundant edge type (Turner et al. 1994). Even though edges are important landscape elements in high elevation *Pinus contorta* (lodgepole pine) forests, edge effects have been scarcely studied and most of the emphasis has been in the effects of fire on overall forest dynamics (Turner et al. 1994; Turner et al. 1997). Studying these forests may provide important information about invasion processes in high elevation forest edges and their relation to edge type. The results may further help to identify generalities in edge-effects and alien invasions.

Pinus contorta forests around West Yellowstone, Montana provide a unique opportunity to study the influence of edge type in invasion processes. In a relatively small and homogeneous forested area it is possible to find highways, burned forests, and clearcut forest edges. In addition, these edges occur both in the managed areas of Gallatin National Forest and in undeveloped areas of Yellowstone National Park. All these edge types can be found in the Madison Plateau area on one habitat type with similar soil, elevation, and topographic conditions.

In this paper we aim to test for differences in patterns of alien species invasion and native communities among three forest edge types (burned forests, clearcuts and highways). We also explore which variables may be related to these patterns including forest structure, edge type and distance from the edge. We hypothesize that alien species invasion will be related to edge type as a function of propagule availability. We expect that edges located closer to dispersal corridors or in a matrix with high presence of alien species will show higher levels of infestation. We also hypothesized that distance from the edge will influence the presence of alien by modifying available resources and competition. However, we expect that alien species will only colonize an

area given sufficient propagule pressure. We expect that changes in native communities will be more related to physical conditions modified by proximity to the edge.

Study Site

The study area (Fig. 1) is located in the West Side of Yellowstone National Park and adjacent Gallatin National Forest (44°48'N, 111°12'W and 44°37'N, 111°00'W). The area represents a strong contrast between landuse outside and inside the park, but the entire study area has an almost constant elevation, soil type and habitat type (Despain 1990).

The geomorphology of the study area is primarily a product of glacial erosion and deposition. These factors determined the formation of the Madison valley (slopes less than 5%), which extends along the Madison River from Mount Jackson to the Hebgen Lake. The majority of soils are Typic Cryochrepts with obsidian sand alluvial parent material (Gallatin NF, soil survey). These soils are coarse textured, well drained and have low organic matter content.

Climate in the study area is strongly influenced by its high elevation (2000 m) and protected valley topography. Precipitation in the area averages 550 mm/year, with peaks in the months of December, January, and June. During the winter, snow accumulation averages 100 cm for March. The snow cover may last from November to April. Mean temperature ranges from a low of -11.1 °C during January to a high of 15.2 °C in July (Climate data from Western Regional Climate Center, 2001).

Pinus contorta forests and *Artemisia tridentata* shrublands are the dominant vegetation types. Forests are classified as lodgepole pine / bitterbrush habitat type for most of the area (Pfister et al. 1977). These forests have a low productivity, with heights around 20 m (Pfister et al. 1977; Despain 1990). Understory species include *Purshia tridentata*, *Lupinus* spp, *Antennaria rosea*, *Oryzopsis exigua* and *Sixtry histranion*. Forests are open and tree seedlings occur only in more protected areas, drought being the most limiting factor (Despain 1990). This habitat type

(PICO/PUTR) has been found only for West Yellowstone and it is associated with this alluvial soil type (Pfister et al. 1977).

Disturbances in the area include fire, logging, and road development. Fire is the main natural disturbance, but low rates of fuel accumulation in these low productivity forests limits their intensity and thereby the frequency of catastrophic fires. Fire average return intervals range from 400 to 600 years, but frequency may increase in more productive sites (Despain 1990). Gallatin NF has been subjected to great logging pressure, with clear-cutting and selective cutting as the major extractive techniques (Susan LaMont, Personal communication 2000). Road development for both local transportation and regional transportation has fragmented the area, especially in Gallatin National Forest.

Grazing, logging and transportation have facilitated the introduction of aggressive weeds. Among the most invasive are *Centaurea maculosa*, *Linaria vulgaris*, *Linaria dalmatica*, *Melolitus officinalis*, *Cirsium vulgare* and *Verbascum thapsus* (Ollif et al. 2001, Whipple 2001). The harsh, high elevation climate restricts the intensity of weed invasion, especially those adapted to more temperate agricultural conditions (Forcella and Harvey 1983; Sax and Brown 2000). Nevertheless, human disturbed areas (e.g. roads, clearcuts) have been already modified by plant invaders. Furthermore, weeds are progressively colonizing riparian habitats and other pristine environments (See Chapter 4 and 5).

METHODS

We established a total of 30 edge-transects in south facing forest edges. Six transects were located randomly in each of five edge types: 1) highway 93 in Gallatin NF (GNF-hwy), the west entrance park highway (YNP-hwy), burned forests of 1988 in YNP (YNP-burns), a burned forest in Gallatin NF (GNF-burns) and clearcuts of Gallatin NF (CC). GNF-hwy is a high traffic highway with wide roadsides (15 to 20 m) cleared of forest or shrubs. YNP-hwy has lower traffic than GNF-hwy and forest edges occur around 5 m from the road surface. The YNP-burns were

caused by high intensity fire and no machinery was used to limit the fire perimeter. Instead, the GNF burn also occur in 1988, but have a perimeter built by heavy machinery and salvage logging was conducted after the fire. Finally, clearcuts were logged between 1978-1982 and edges were sharply delimited.

Edge-transects were composed of 5 plots of 2 by 20 meters. Plots were located at -10, 0, 10, 20 and 40 m from the end of the road surface (plots E1, E2, E3, E4, and E5 respectively). YNP-hwy transects lacked of plot E1 due to the <5m distance from the edge to the road. Each 40 m² plot was divided in two 10 m by 2 m subplots to make cover estimation more accurate. In each subplot cover class for every species (native and alien) present in the subplot was recorded using Braun-Blanquet cover classes (Mueller-Dombois and Ellenberg 1974). Nomenclature followed Hitchcock and Cronquist (1973). For each subplot, we visually estimated canopy cover for all strata, dominant height and DBH for all trees inside the plot. In each subplot, we also recorded seedlings by tree and height class (<0.5m, 0.5-1.0 m, 1.0-1.5m, 1.5-2.0m, >2.0m).

Analyses

For analytical purposes, we averaged the data from the two adjacent subplots of 200m² into one plot of 400m². We characterized vegetation structure in each edge type by calculating mean canopy cover, mean dominant height and mean basal area at each plot. We used ANOVA to test for the effects of distance and edge type on seedling density.

Using ANOVA, we tested for the effects of 1) distance from the edge and 2) edge type on the following plot variables: a) alien species richness, b) alien species cover, c) native species richness, b) native species cover, d) total species richness and e) total species cover. Normality was tested in the model studentized residuals using Wilcox index ($p < 0.05$).

Linear regression models were used to test the relationship between native species and alien species richness for all plots (20x2 m). The relationship was also tested for plots stratified by distance from the edge and for plots stratified by edge type.

For all understory species, we recorded a relative decrease or increase in cover of each species from the matrix to forest interiors. For this purpose, a ratio between the mean cover of each species in the matrix (E0) to that in the interior (E4) was calculated. Similarly, we recorded increase or decrease to the interior in mean cover of species grouped in life form types (annuals grasses, annual herbs, perennial grasses, perennial herbs, shrubs and trees; based on Grime 1977). For all statistical analyses we used SPSS 10.0.

Using PC-ORD 4.0, we ran a Detrended Correspondance Analysis (DCA, Hill and Gauch 1980) of all plots (n=144) with all species present in more than one plot (n=65). We plotted DCA diagrams to visually assess variations in community composition in relation to distance from the edge and edge types. Differences among groups were tested using MRPP ($p < 0.05$) (McCune and Mefford 1999).

RESULTS

Patterns of native species

We found a significant effect of edge type and the interaction of edge type and distance on native species richness and native species cover ($p < 0.05$, ANOVA), however distance by itself was not a significant factor (Table 1). When edge types were contrasted, plots in GNF-hwy had the lowest mean native species richness ($p < 0.01$, t-test; Fig. 2), the other edge types were not significantly different.

Within each edge type, native species richness varied by distance from the edge, but it was significantly different only in YNP-hwy, where E1 plots had the highest mean number of native species for that type ($p < 0.01$, t-test). When comparing plots located right in the edge (E1)

among types, YNP-hwy had the higher native species richness ($p < 0.01$, ANOVA). For all other distances, we found no significant differences among edge types.

Native cover, when analyzed within each edge type, was lower in E0 for GNF-hwy ($p < 0.05$, t-test). Within all other edge types, no significant differences were found among distances (Fig. 2).

Patterns of alien species

Alien species richness was significantly related to edge type, distance and interaction between both variables ($p < 0.01$, ANOVA, Table 1). When contrasting edge types, the highest mean alien species richness by plot occurred at GNF-hwy and the lowest at YNP-burns (Fig. 2). Within edge types, alien species richness responded to distance from the edge, with significantly higher values for plots E0 and E1 in the GNF-hwy and E1 in the YNP-hwy ($p < 0.001$, t-test). In clearcuts, a slight difference was found in mean alien species richness between E0 and E4 ($p < 0.05$, t-test). For burned edges, both in Gallatin and Yellowstone, no consistent difference was found.

When comparing positions between edge types, GNF-hwy had the higher alien species richness for E0, and burns had the lowest ($p < 0.001$, t-test). For position E1, YNP-hwy and GNF-hwy, both had significantly more alien species than the other edge types ($p < 0.001$, t-test). For all other distances, no significant differences were found among edge types. The mean alien species richness for E2, E3 and E4 was less than 1 species per plot for all edge types (Fig. 2).

Alien species richness was negatively correlated with native species richness for all plots with at least one alien species ($R^2 = 0.30$, $p < 0.001$) (Fig. 3). When plots were classified by edge type, the relationship was significant only for GNF-hwy ($R^2 = 0.69$, $p < 0.001$) and YNP-hwy ($R^2 = 0.33$, $p < 0.01$) (Fig. 3). However, slope was negative in GNF-hwy and positive in YNP-hwy. No correlation was significant when plots of all edge types combined were classified by distance from the edge.

Alien species total cover followed a similar trend to alien species richness (Fig. 2). However, differences among cover values were stronger than for richness. Highest alien species cover was found in GNF-hwy (plots E0 and E1) and YNP-hwy (E1) ($p < 0.001$, t-test). All other edge types and distances showed mean alien cover lower than 5% with no significant differences (Fig. 2).

Total species pattern

Total species richness was significantly related to edge-type and distance from the edge, while total species cover was only related to distance from the edge ($p < 0.05$, ANOVA, Table 1). Most of the variation in total richness occurred in YNP-hwy where E1 showed a significantly higher number of species compared to interior plots ($p < 0.001$, t-test, Fig. 2).

As expected in all edge types, height of the upper stratum was lower in the matrix (E0, test, $p < 0.01$), but showing no significant variation within interiors (Fig. 1). Canopy cover was lower in the matrix for all edge types (t-test, $p < 0.01$), but considerable variation occurred over the transect depending on the edge type with peak values on E1 and E2 (Fig. 1). Basal area followed a similar distribution to canopy cover (Fig. 1). Seedlings of *Pinus contorta* showed a complex pattern with higher mean densities in plots E2 and E3 in all edge types (Fig. 1).

Distance and edge type were significant factors determining *Pinus contorta* seedling densities ($p < 0.001$ and $p < 0.05$ respectively, ANOVA). However, the interaction between both variables was not significant in explaining *P. contorta* seedling density. Considering all edge types, density in E2 and E3 was significantly higher than in other distances ($p < 0.05$, t-test). We found no significant correlation between *P. contorta* seedling density and canopy cover.

Species-specific responses

Species showed individualistic responses to distance from the edge (Table 2). Most native species increased in abundance in forest interiors in GNF-hwy (Table 3). However, no

clear trend was observed in YNP-hwy, mainly because this edge type lacked E0 plots and therefore the contrast was less intense. In all other edge types, the majority of native species decrease their cover in forest interiors. The vast majority of alien species in all edge types decreased in the interior (Table 2, Table 3). Only *Taraxacum officinale* was found from E0 to E4, and *Lactuca serriola* and *Agropyron repens* were found in from E0 to E3 plots.

The cover of understory species, grouped in life form types, showed group-specific trends from edges to interiors (Table 2). The cover of annual grasses and annual herbs decreased, in most cases, into forest interiors. Perennial grasses increased to the interiors in highways and YNP-hwy. Shrubs showed a mixed response, increasing in YNP-burn, clearcuts and GNF-hwy. Finally, trees increased to the interiors with the exception of GNF-fire.

Ordination gradients

Axis 1 of the DCA ordination (Eig=0.717) discriminated those plots located in E0 and E1 of the two highways edge types from the rest of plots (Fig. 4). All other plots appeared similar in Axis 1 with variation in Axis 2 (Eig=0.288). MRPP tests showed a significantly lower than expected variation within groups compared to overall variation for both edge types and distance from the edge ($p < 0.0001$, Euclidean distance).

DISCUSSION

Alien and native species patterns in relation to edge type

Patterns in the distribution of native and alien species in forest edges are not only affected by physical changes in relation to proximity to the edge but also by the pool of propagules that is able to reach them (Cadenasso and Pickett 2001). Therefore, both distance from the edge and edge type should determine variation in plant community, especially for the distribution of alien species. In our study that included three anthropogenic (highways and clearcut) and two natural (forest burns) edge types, we expected to find a relationship between alien species distribution

and edge type, in addition to the well-documented relationship to distance from the edge. We found that both edge type and distance from the edge significantly influenced alien species patterns and native community composition.

Edges located along highways show the highest number of alien species, while the other edge types show only traces of alien species. Interestingly, high cover of alien species coincided with low cover of native species in the E0 and E1 plots of highway edges. This inverse relationship may be the product of long history of disturbance in the matrix (roadside) and continuous propagule introduction due to high vehicular traffic (Trombulak and Frissell. 2000, Spellerberg 1998).

In highway matrices of our forest edges, the complete destruction of the native community due to road construction allows the dominance of a combination of alien annual grasses and annual herbs (as reviewed by Trombulak and Frissell 2000). These edges are also the oldest in our study, thus alien plants have had more time to colonize the edge (E1) and displace native species. In addition, roadsides are mowed annually in the middle of the summer to decrease fire risk, which has been shown to increase the chances for alien species (Spellerberg 1998).

Contrary to the results for GNF-hwy that show high richness of alien species but low levels of native species richness, the E1 plots in YNP-hwy show both a high richness of alien species and a high richness of native species. This may indicate that highways act as corridors for both native and alien plant propagules, increasing overall diversity, at least in areas less developed like Yellowstone National Park.

In interior plots of highway edges, only *Taraxacum officinale* has established, suggesting that most alien species cannot survive in less disturbed and more shaded *P. contorta* forests (Table 2). Brother and Singarn (1992) reported a similar exponential decline in abundance and richness of alien species for old growth forests in Indiana, United States. Interior plots may be less susceptible to invasion because of a combination of factors including less soil disturbance,

less light availability and less propagule arrival (Brother and Singam 1992, Parendes and Jones 2000).

The DCA analysis supports the trend found in our previous analyses, that most changes in native and alien species abundance occur in the matrix and edges (E0, E1) of highways and that all other plots show a similar community composition independent of edge type and distance from the edge.

The low number of alien species in clearcuts compared to highways may be associated with both lower disturbance frequency and lower propagule availability. Edges in clearcuts have also suffered intense disturbance in the matrix, but less constant over time. Additionally, these areas have not been under heavy propagule pressure by alien species, because most clearcuts have not been heavily invaded (See Chapter 4), which has allowed for the recovery of the native perennial herb and perennial grass community.

The presence of only one alien species (*Taraxacum officinalis*) in forest burns edges suggests that disturbance by itself does not trigger invasion process in *Pinus contorta* forest edges. Turner et al. (1997) only found two alien species in 1988 burn areas of Yellowstone NP. In our case, the YNP-burn edges are located more than 2 km away from roads and other corridors, limiting the possibility of alien propagules dispersal. However, the GNF-burn edges are less than 0.5 km away from secondary roads and heavy machinery was used to control the fire, but they still show little invasion by alien species. These results suggest that for alien species to get established in matrices and edges it is necessary for a propagule source sufficiently close to the area to generate a frequent and intense seed shadow.

Structural differences

Structural attributes in the forest edges studied follow the trends observed in previous edge research (Murcia 1995). Height, canopy cover and basal area, in general, increase toward forest interiors as has been shown for other forest types (Chen et al. 1992). However, we

observed considerable variation in canopy cover and basal area, variability that may be related to the intrinsic heterogeneity in the spatial distribution of *Pinus contorta* forests. Overall, tree canopies appeared highly sparse with mean cover around 20%.

Most studies that have found a linear negative or positive relationship between distance from the edge and seedling density, which depends mainly on the species light requirements (e.g. Chen et al. 1991). These studies have usually been conducted in closed forests where light availability is a constraint for regeneration of shade intolerant species. However, our results, which suggest a non-linear response of seedling density to distance from the edge, denote the complexity of edge effects and the difficulty in making generalizations (Murcia 1995). *Pinus contorta*, in these sites, is probably achieving a higher recruitment in environments that are more protected from drought than forest edges, but that are not overly shaded as interiors.

Implications for edge ecology and management

Much emphasis has been put into understanding and measuring forest edge effects and trying to find generalities among forest ecosystems. However, the interaction of physical edge effects with other landscape processes such as dispersal is often overlooked. Studying patterns of distribution of native and alien plants across several edge types can increase our understanding of the importance of landscape factors in determining the magnitude and nature of edge effects.

Our study suggests that patterns of native and alien plants are related to both the physical effects of creating a forest edge and also to the landscape context within which the edge occurs. Highway or road edges should have a much higher chance of being invaded by alien species, due to the frequent propagule introduction by human and animal vectors (Forman and Alexander 1998), than edges occurring in areas which are isolated from propagule sources. This principle of propagule pressure as a limiting factor should hold both for natural created edges, such as burn forest edges, and for anthropogenic edges, such as clearcuts. Our results contribute to understand the interactions between landscape context and edge effects, but generalizations

from these results are limited by the uniqueness of the area studied and the lack of the replicates in other ecosystems. Further, studies should try to capture these processes over larger scales to increase the inference power.

Management efforts to diminish the impact of edge-effects in native forest communities should emphasize the control of alien species along human corridors. Also, the dispersal of alien species into edges should be avoid by limiting the extent and amount of source populations in heavy disturbed areas such as clearcuts or other logged areas. These preventive actions may limit the percolation of alien species into interior forests and reduce their negative effects on native communities.

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Table 1. ANOVA for species richness and cover percentage variables for all edge plots (n=144). Variables were recorded for each plot. Edge type includes 5 categories (GNF-highway, YNP-highway, GNF-burns, YNP-burns and clearcuts). Distance represents distance from the edge (-10, 0, 10, 20 and 40 m).

Dependent Variable	Source	df	SS	F	p
Alien species richness	Edge Type	4	125	73.02	0.000
	Distance	4	115	67.13	0.000
	Type*distance	15	212	32.93	0.000
	Error	120	52		
Alien species cover %	Edge Type	4	5995	27.92	0.000
	Distance	4	6010	27.99	0.000
	Type*distance	15	17075	21.21	0.000
	Error	120	6441		
Native species richness	Edge Type	4	335	8.69	0.000
	Distance	4	84	2.18	0.075
	Type*distance	15	360	2.49	0.003
	Error	120	1159		
Native species cover %	Edge Type	4	21270	7.51	0.000
	Distance	4	667	0.24	0.918
	Type*distance	15	22322	2.10	0.014
	Error	120	84919		
Total species richness	Edge Type	4	134	2.97	0.022
	Distance	4	311	6.90	0.000
	Type*distance	15	248	1.47	0.128
	Error	120	1351		
Total species cover %	Edge Type	4	6467	2.13	0.081
	Distance	4	7606	2.51	0.045
	Type*distance	15	14151	1.25	0.249
	Error	120	90950		

Table 2. Variation in the distribution of species and life form groups from E0 to E4 in relation to edge type (for YNP-Hwy comparison is between E1 and E4). Native species include only those present in more than 10 plots. Alien species include only those present in more than 3 plots. Life form=1) annual grasses, 2) annual herbs, 3) perennial grasses, 4) perennial herbs, 5) shrubs, 6) trees. Signs indicate: += an increase in cover, - = a decrease in abundance and () indicates that the species was present in both plots E0 and E4. Nomenclature followed Hitchcock and Cronquist (1973).

Species \ Type	Life form	T. Count	GNF-Hwy	YNP-Hwy	YNP-Burns	GNF-Burns	Clearcuts
Natives							
<i>Collomia linearis</i>	2	15	(-)	-	a	-	-
<i>Crepis acuminata</i>	2	15	+	a	a	(-)	+
<i>Arabis holboellii</i>	2	33	-	-	-	(-)	-
<i>Gayophytum diffusum</i>	2	34	(-)	-	-	-	-
<i>Agoseris glauca</i>	2	94	(+)	()	(+)	(-)	(-)
<i>Danthonia sp.</i>	3	11	a	a	a	(-)	a
<i>Danthonia intermedia</i>	3	13	a	-	(-)	a	a
<i>Stipa nelsonii</i>	3	28	a	(-)	(-)	-	(-)
<i>Oryzopsis exigua</i>	3	71	+	a	(+)	(+)	(-)
<i>Poa nervosa</i>	3	73	+	+	(-)	(+)	(-)
<i>Festuca idahoensis</i>	3	79	+	(+)	(-)	-	(-)
<i>Sitanion hystrix</i>	3	85	(-)	(+)	(-)	(-)	(+)
<i>Agropyron spicatum</i>	3	105	(+)	(+)	(+)	(-)	(+)
<i>Phacelia hastata</i>	4	13	-	-	a	a	-
<i>Lupinus sericeus</i>	4	15	a	(+)	-	a	a
<i>Castilleja occidentalis</i>	4	16	a	()	(+)	a	a
<i>Erigeron speciosus</i>	4	16	+	-	(-)	-	a
<i>Erigeron compositus</i>	4	19	-	-	-	a	-
<i>Eriogonum ovalifolium</i>	4	20	a	-	(-)	-	(-)
<i>Ivesia gordonii</i>	4	25	a	a	a	(+)	a
<i>Hieracium albiflorum</i>	4	29	+	+	-	+	+
<i>Senecio canus</i>	4	32	-	-	()	(-)	-
<i>Achillea millefolium</i>	4	39	(-)	-	(-)	-	(-)
<i>Penstemon procerus</i>	4	45	+	(+)	(-)	(+)	+
<i>Epilobium angustifolium</i>	4	48	+	+	(-)	(-)	+
<i>Geum triflorum</i>	4	59	+	(+)	(+)	(-)	(+)
<i>Arenaria capillaris</i>	4	84	+	(+)	(+)	(-)	(+)
<i>Eriogonum umbellatum</i>	4	88	+	(-)	(+)	(-)	(-)
<i>Phlox multiflora</i>	4	106	+	(-)	(+)	(-)	(-)
<i>Lupinus argenteus</i>	4	112	+	(+)	(+)	(-)	(+)
<i>Carex rossii</i>	4	129	+	(+)	(+)	(-)	(+)
<i>Antennaria rosea</i>	4	132	(+)	(+)	(-)	(-)	(-)
<i>Artemisia tridentata</i>	5	15	a	-	a	+	(-)
<i>Arctostaphylos uva-ursi</i>	5	38	+	+	(+)	+	a
<i>Purshia tridentata</i>	5	85	+	a	(-)	(+)	(+)
<i>Pinus albicaulis</i>	6	11	+	a	+	a	a
<i>Pinus contorta</i>	6	128	+	(+)	(-)	(+)	(+)
Aliens							
<i>Poa pratensis</i>	1	7	-	-	a	a	a
<i>Lactuca serriola</i>	2	7	-	-	a	a	a
<i>Melilotus officinalis</i>	2	10	-	a	a	a	a
<i>Berteroa incana</i>	2	15	-	-	a	a	a
<i>Tragopogon dubius</i>	2	16	-	-	a	a	-
<i>Taraxacum officinale</i>	2	66	()	(+)	()	(-)	(-)
<i>Bromus inermis</i>	3	13	-	-	a	a	a
<i>Centaurea maculosa</i>	4	4	-	-	a	a	a
<i>Mentha arvensis</i>	4	7	-	-	a	a	a
Life form groups							
Annual Grasses			-	-	a	a	a
Annual Herbs			182.50	4.00	0.19	4.11	2.54
Perennial Grasses			2.15	1.88	1.54	2.22	1.61
Perennial Herbs			0.60	0.85	0.74	1.47	1.16
Shrubs			0.00	2.25	4.36	0.83	0.34
Trees			0.00	0.08	1.51	0.92	0.95

Table 2. Total number of species that decreased or increased their percentage cover, by edge type, when comparing their cover in E0 to E4 (YNP-hwy considers E1 to E4). Hwy= highway and burns= forest burns. ()= number of alien species. YNP= Yellowstone National Park and GNF= Gallatin National Forest.

Edge type	Increase	Decrease	No-change
GNF-hwy	24	12 (11)	(1)
YNP-hwy	15(1)	18 (8)	4
YNP-burns	14	22	2
GNF-burns	10	24	-
GNF-Clearcuts	13	18 (1)	-

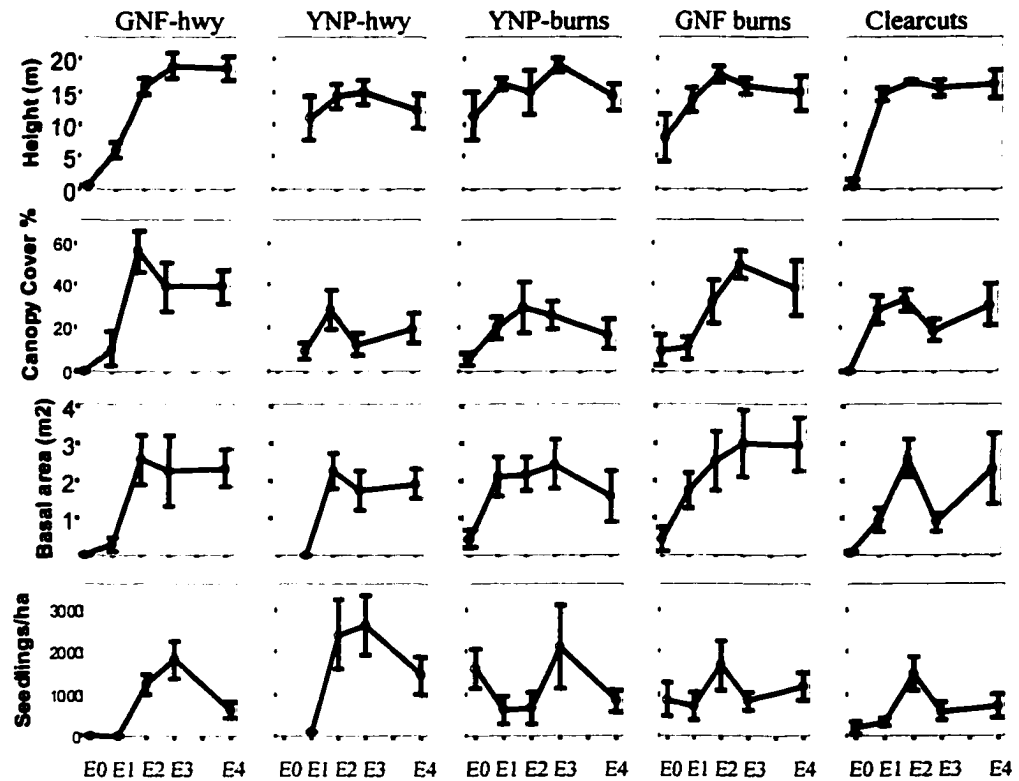


Fig. 1. Structural attributes by edge type: height of the higher stratum, canopy cover percentage, basal area, and *Pinus contorta* seedling density per ha. E0, E1, E2, E3 and E4 represent distance from the edge (-10, 0, 10, 20, 30 and 50m respectively). YNP-hwy does not have an E0 location. Means \pm SE are for 6 plots for each location and each edge type (total n=144).

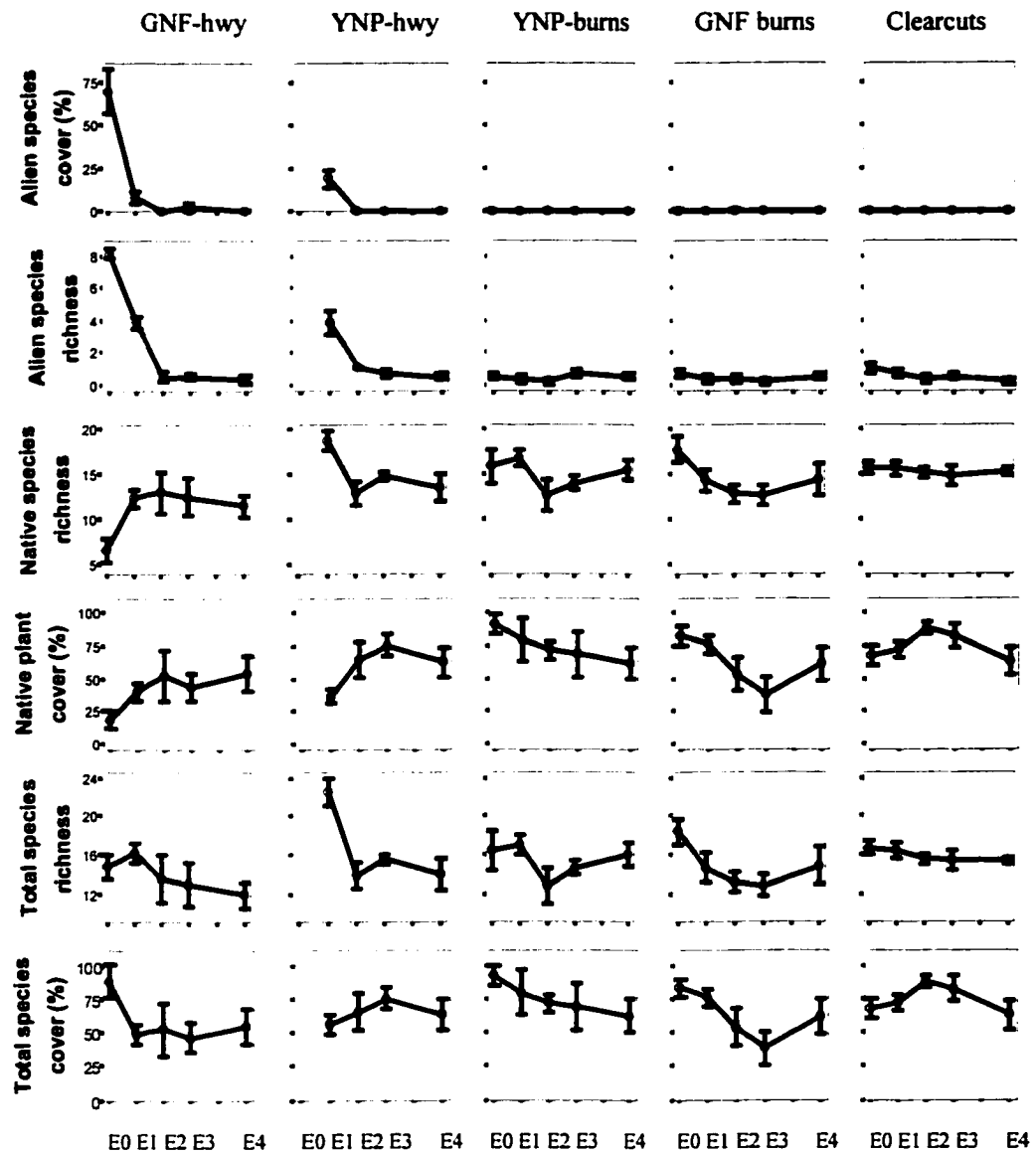


Fig. 2. Species richness and cover percentage by edge type, for alien species, native species and all species. E0, E1, E2, E3 and E4 represent distance from the edge (-10, 0, 10, 20, 30 and 50m respectively). YNP-hwy does not have an E0 location. Means \pm SE are for 6 plots for each location and each edge type (total n=154).

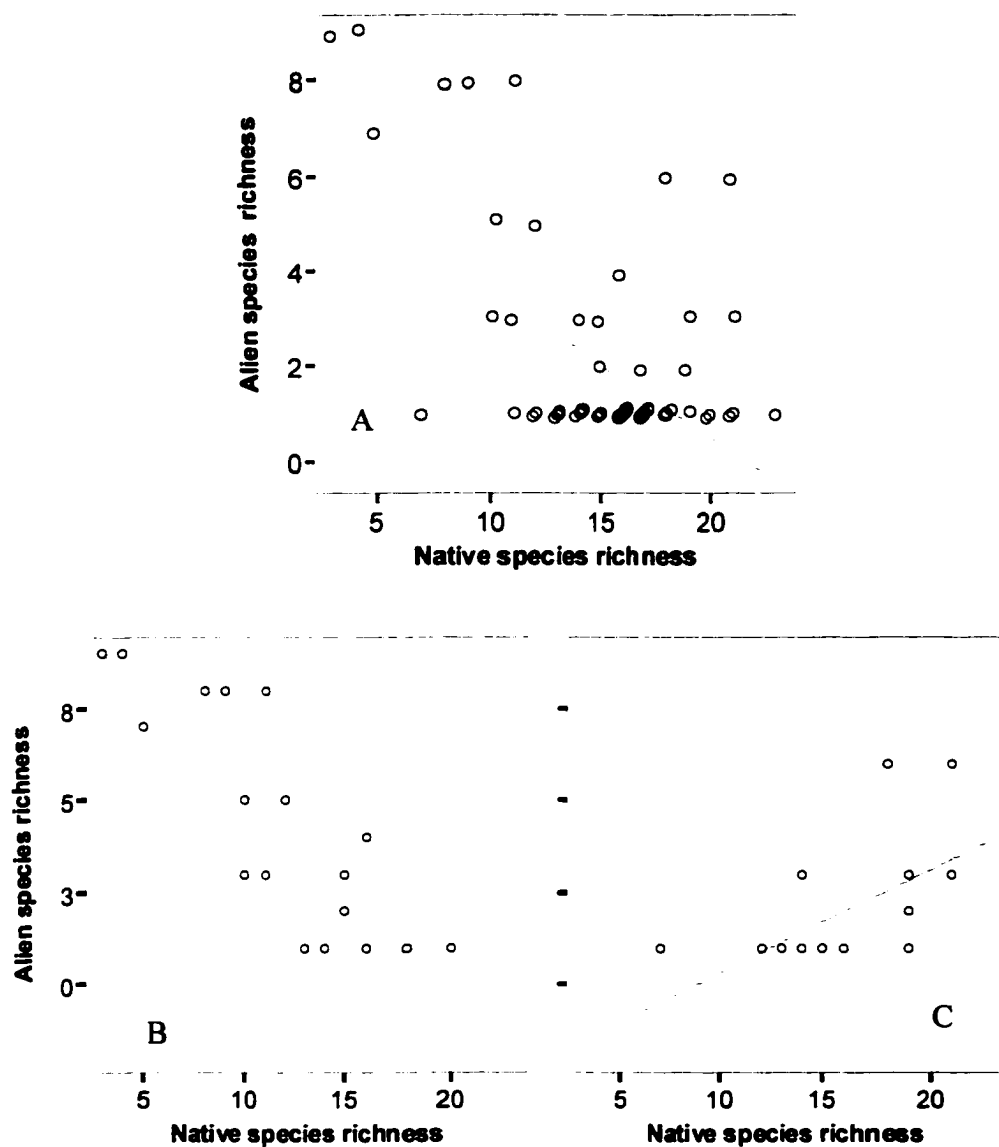


Fig. 3. Alien vs. native species richness for plots, in edge transects, with at least one exotic species. A) all plots ($R^2=0.30$, $p<0.001$), B) Gallatin National Forest highway ($R^2=0.69$, $p<0.001$), C) Yellowstone National Park highway ($R^2=0.33$, $p<0.01$). Notice that Yellowstone NP highway has a positive slope. All other edge types show no significant correlation.

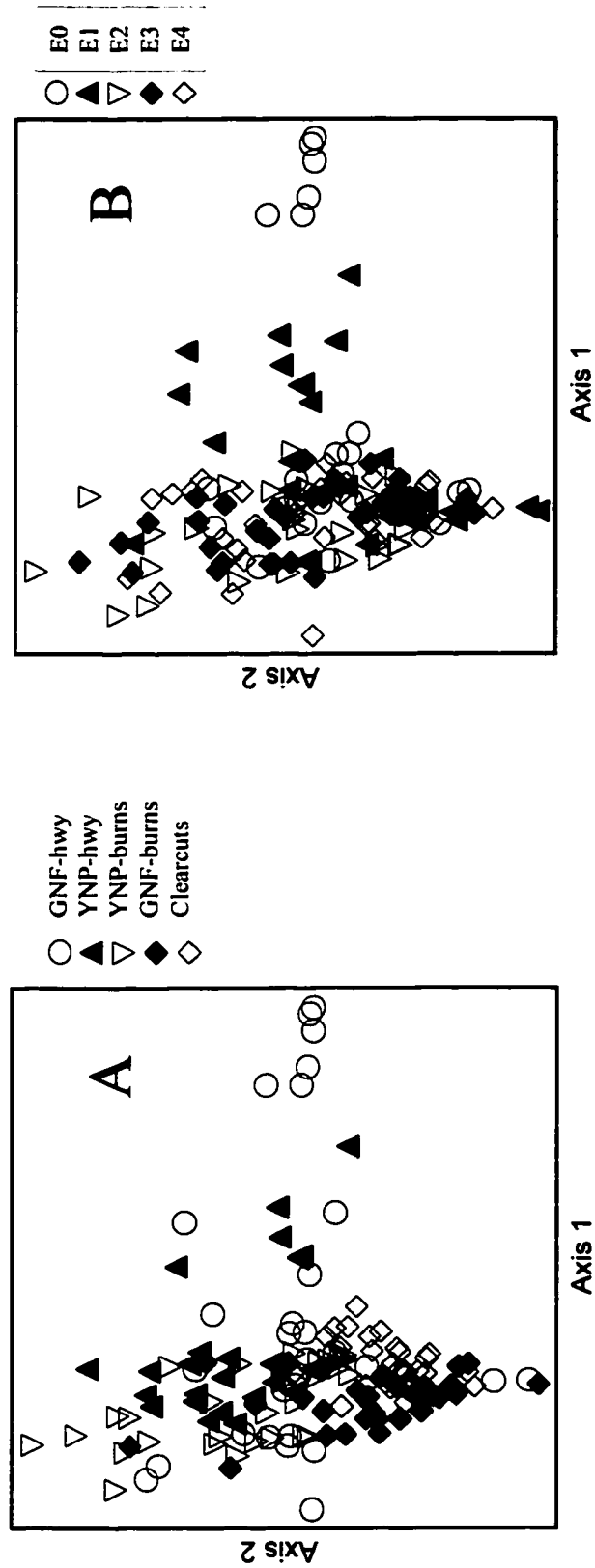


Fig. 4. DCA diagram of edge plots (Total $n=144$). Plots classified by A. Forest type and B. distance from the edge. E0, E1, E2, E3 and E4 represent distance from the edge (-10, 0, 10, 20, 30 and 50m respectively). YNP-hwy does not have an E0 location.

CHAPTER 4

**STUDYING PLANT INVASIONS IN PROTECTED AREAS
AT MULTIPLE SCALES: *Linaria vulgaris* (SCROPHULARIACEAE)
IN THE WEST YELLOWSTONE AREA**

ABSTRACT

Invasive alien plants have long been recognized as a threat to low elevation, disturbed environments, but the case of *Linaria vulgaris* Mill. in Yellowstone National Park and Gallatin National Forest shows that invasions can also spread to high elevation natural reserves. Because invasions in protected areas are a product of complex processes occurring over a broad range of scales, we argue that a multi-scale research approach is needed to capture both patterns and potential mechanisms of the invasion process. Mapping *L. vulgaris* at the landscape scale, we found the species occupying a broad range of sites, apparently originating from just two historical sources. Analyzed at the stand scale, patches tend to be aggregated in newly invaded areas and become dispersed in heavily-infested areas. The data suggest that patches grow in size by clonal advance and in number by creation of new satellite patches. Radial patch growth rates are related to site characteristics. Clonal patch scale analysis shows that ramet densities and *Linaria's* effects on native plants are highest in the patch centers. Both mean ramet height and reproductive vs. vegetative ramet height ratio are higher in patch cores. These results suggest that *L. vulgaris* may displace natural vegetation by maintaining vigor even in large and old clonal patches. Our results confirm that *L. vulgaris* is a significant threat to native biodiversity in open, human- or naturally-disturbed environments in protected areas of the Rocky Mountains. A multi-scale method can allow managers to better understand patterns of invasion and prioritize management activities to control invasive alien plants, especially in heterogeneous protected area landscapes.

INTRODUCTION

Invasive alien plant species threaten biodiversity worldwide (Mack et al. 2000, Sala et al. 2000, McNeely et al. 2001). Invasive alien plants not only change the composition of invaded communities, but also affect ecosystem processes such as disturbance regimes, wildlife interactions, evolutionary processes and biogeochemical cycles (Mack et al. 2000). Most invasive alien species are adapted to highly disturbed, nutrient rich, low elevation agricultural or urban environments (Hobbs 2000, Sax and Brown 2000, D'Antonio and Naiman 1994). In contrast, many protected areas or natural reserves, at least in temperate zones, occur at high elevations and relatively undisturbed environments (Noss and Cooperrider 1994, Scott et al. 2001). Consequently, the number and abundance of invasive alien plants is much lower in protected areas than in surrounding human dominated landscapes (Forcella and Harvey 1983, Lonsdale 1999, Pauchard and Alaback in review). However, these invasive species can still become a significant threat to ecosystems conserved in protected areas (MacDonald et al. 1989, Lesica and Ahlenshalager 1993, DeFerrari and Naiman 1994, Stohlgren et al. 1999, Ollif et al. 2001).

The high ecological value of protected areas and often low abundance of alien invasive plants pose unique challenges for monitoring and studying invasion processes. Most commonly used methods for monitoring weed populations are designed for highly disturbed and homogenous landscape elements where invasive plants are abundant (Cousens and Mortimer 1995). A conceptual framework for sampling invasive plant populations and their effects is needed for protected areas and their adjacent matrixes (*sensu* Lindemayer and Franklin 2002), recognizing both the complex and heterogeneous landscapes and the invaders' low numbers of initial populations.

To capture the underlying mechanisms of plant invasions in protected areas landscapes, it is necessary to consider the broad range of scales and processes involved (Stohlgren et al. 1999, Mack 2000, Chong et al. 2001). According to hierarchy theory, each scale involves a unique set of processes and mechanisms (Allen 1998). The description of any ecological phenomenon may be incomplete or misleading without assessment of related patterns at coarser scales. A fine-scale

approach (for example, monitoring an invasive plant using a 1-m² quadrat commonly used in agricultural weed studies) may illuminate specific elements of that species' population biology and effects on local biodiversity; however, that approach would likely overlook processes occurring outside the infested area, such as long distance dispersal. Conversely, landscape studies often fail to integrate fine-scale phenomena that may ultimately control landscape patterns. For managers, an assessment strategy that integrates methodologies across multiple scales may identify the dominant mechanisms governing the invasion process and thereby inform an effective control strategy (Table 1).

In the West Yellowstone area, *Linaria vulgaris* Mill. (common or yellow toadflax, “butter and eggs”) is one of the most invasive alien plants, occupying heavily disturbed areas of the Gallatin National Forest and threatening to expand into more pristine areas in the adjacent Yellowstone National Park (Whipple 2001, Ollif et al. 2002). *Linaria vulgaris*, a member of the Scrophulariaceae family native to disturbed sites in Eurasia, was introduced in North America as an ornamental as much as 300 yr ago (Saner et al. 1995), but it has only recently become an important problem in natural areas of the Rocky Mountains. It is an aggressive perennial weed in agricultural and rangeland environments, reproducing by both sexual and asexual mechanisms (Saner et al. 1995, Nadeau et al. 1992). It invades from sea level to over 3000 m and up to 60 degrees latitude. It prefers open, wet environments, and usually grows on gravelly or sandy soils after heavy natural or human soil disturbance, creating discrete patches due to its clonal growth and predominantly short distance dispersal (Saner et al. 1995, Nadeau et al. 1991). A small proportion of its winged seed disperses long distances both by wind and animal vectors (Saner et al. 1995). Biocontrol insects may attack *L. vulgaris* from roots to seeds and have been extensively used with variable success (Saner et al. 1995).

Linaria vulgaris invasion in the West Yellowstone area serves as an ideal case study to demonstrate the utility and feasibility of the multi-scale approach framework to study invasions in protected areas. In this paper we report on our ongoing investigation into *Linaria vulgaris* invasion of Yellowstone National Park and Gallatin National Forest. *L. vulgaris* has the potential to invade new

high elevation environments in the Rocky Mountains, and we hypothesize that its ability to invade depends on several mechanisms occurring at the landscape, stand and patch scale. We relate spatial patterns and characteristics at these scales to factors of land use and site history. We discuss the advantages and disadvantages of our method and the conservation implications of studying plant invasions in protected areas using a multi-scale approach.

Study Area

The study area (Fig. 1) is located in the Madison Valley around the western entrance of Yellowstone National Park and the adjacent Gallatin National Forest (44°48'N, 111°12'W and 44°37'N, 111°00'W). The National Park boundary reflects a strong contrast in land use, while the two sides of the study area are similar in elevation, soil type and habitat type (Despain 1990, Hansen and Rotella 1999). Soils, formed on glaciofluvial outwash plains derived from rhyolite (Rodman et al. 1996), are sandy, well-drained, low in nutrients and highly susceptible to drought during the summer months. Climate is strongly influenced by high elevation (2000 m) with annual precipitation around 550 mm, mostly as snow. Mean temperature ranges from a low of -11.1 °C during January to a high of 15.2 °C in July (Western Regional Climate Center, 2001).

Pinus contorta forests and *Artemisia tridentata* semi-arid shrublands are the dominant vegetation types (Despain 1990). Fire is the main natural disturbance with catastrophic fires occurring every 400 to 600 years (Despain 1990). The 1988 Yellowstone fires burned an important portion of the study site inside the park but little on the Gallatin NF. Gallatin NF has been highly disturbed by logging during the past three decades, declining in the 90s (Susan LaMont personal communication). At present, an increasing number of tourists are visiting the area year round.

Beginning in the late 1800s, grazing, logging and transportation have facilitated the introduction of aggressive weeds like *Centaurea maculosa*, *Linaria vulgaris*, *Linaria dalmatica*, *Melilotus officinalis*, *Cirsium arvense* and *Verbascum thapsus* (Ollif et al. 2001). The harsh high

elevation climate restricts the intensity of weed invasion (Forcella and Harvey 1983). Nevertheless, plant invaders have colonized human-disturbed areas such as roads and campgrounds (Allen and Hansen 1999) and are progressively invading riparian habitats and other pristine environments. Both the Park Service and the Forest Service have developed management plans for controlling weed invasion, but *L. vulgaris* has only been targeted along major corridors (Ollif et al. 2001).

METHODS

Linaria vulgaris invasion and its effects were studied at three scales: landscape, stand and clonal patch (Table 1). Each scale was defined arbitrarily to capture a unique set of processes, and the specific methods used varied with scale (Table 1). The landscape scale was defined to understand dispersal processes and habitat invasibility in the portion of the Madison Plateau where *L. vulgaris* was abundant in both the Gallatin NF and Yellowstone NP (ca. 20 by 10 km, Fig. 1, Fig. 2). Short distance dispersal processes, infilling of infestations and interactions with local site characteristics were studied using the stand scale. The sampling size unit was defined as a macroplot of 50 m by 100 m, sufficient to evaluate the structure and dynamics of groups of clonal patches. At the finest scale, the clonal patch varies from 50 cm to 25 m in diameter. A 20 by 50 cm sample unit was used at this scale to evaluate processes including population structure of *L. vulgaris* and the species interaction with native vegetation.

Landscape Scale

In the summer of 2001, a census was completed of the locations and attributes of 300 clusters of *L. vulgaris* clonal patches. Regions of patch clusters were searched systematically in an effort to capture the majority of existing patches. Differential GPS positions were recorded with a Trimble GeoExplorer 2. Patch clusters were considered separate units when the distance to the nearest *L. vulgaris* plant was more than 5 m. Large areas with solid infestations (clusters larger than 50m) were recorded as polygons instead of as individual clusters. Attributes collected for each

cluster were (Table 2): land use class; longest diameter and longest perpendicular axis length; azimuth of the longest diameter; ramet density in a randomly located 50 x 20 cm microplot; average dominant height; visually estimated percent of reproductive ramets; soil disturbance; fire intensity; tree height; and visually estimated canopy cover %, shrub cover %, and plant cover %, excluding *L. vulgaris*, both inside and outside the cluster. Location and cluster attributes were plotted in ArcView 3.2. SPSS 10.0 was used to characterize diameter, land use, soil disturbance and fire intensity variables.

Stand Scale

In August of 2000, we recorded spatial attributes of *L. vulgaris* patches in five 50 x 100 m macroplots. In the Gallatin NF, three macroplots were located in old clearcuts (logged between 1978 and 1982), and one in a newer clearcut (logged in 1992). In Yellowstone NP one macroplot was located on a riverbank of the Madison River. The three old clearcut macroplots were randomly selected from areas with high levels of *L. vulgaris* infestation. The newer clearcut and riverbank macroplots, on the other hand, represented unique characteristics of early invasion that were impossible to replicate and were therefore considered study cases. We recorded the longest length, perpendicular longest width and azimuth for each patch in each macroplot. Plants separated more than 50 cm were considered as different patches. Patch corners and centers were permanently marked with metal stakes. Polygons were built in ArcInfo 8.0 and plotted in ArcView 3.2. In August of 2001, we returned to each patch and recorded its positive or negative radial (horizontal) growth along the previously-measured axes. New patches in the macroplots were added to the spatial data. We also recorded the substrate condition in 4 categories: *Pinus contorta* litter (>50%), herbaceous plant cover (>25%), bare soil (>75%), and coarse woody debris (>50%).

We assessed spatial patterns in the 2000 data using two macroplots, one in an old clearcut under severe invasion and one in a newer clearcut at early stages of invasion. We conducted point pattern analyses using patch centroids within macroplots. Patches were classified as clustered,

random, or dispersed using a nearest neighbor R-statistic (Fotheringham et al. 2000). For old clearcuts, differences in mean patch radial growth were tested using a Kruskal-Wallis nonparametric test for each factor (macroplot, land use, substrate) and a Mann-Whitney test for pairwise comparisons (significant when $p < 0.05$). A linear model tested correlation between radial growth and longest patch diameter (significant when $p < 0.01$).

Clonal Patch Scale

In August of 2000, patches were randomly selected in each macroplot to locate 20 x 50 cm microplots (Daubenmire 1968). Patches were stratified into small, medium and large classes. For medium (5-10 m long) and large patches (> 10 m long), seven one-meter microplots were located along the longest patch axis: two outside the edge, two within the patch along the edges, two in the interior and one in the middle (Fig. 3). In small patches (less than 5 m long), only 5 microplots were located (Fig. 3). Microplots were marked permanently using metal stakes. In each microplot, every ramet was recorded along with its height class (10 cm) and reproductive stage (vegetative, reproductive) based on the presence of reproductive structures. Cover for each plant species was assigned to the five cover classes of Braun-Blanquet (described in Mueller-Dombois and Ellemborg 1974). Microplots were remeasured in August of 2001.

Differences in microplot variables at the outside, edge, interior and middle of patches were tested in medium and large patches combined using only the data for old clearcuts ($N=12$ patches, $n=84$ microplots). Variables tested were ramet density, ramet density by reproductive stage, ramet height, *L. vulgaris* cover %, species richness and total cover % of other plants. In all cases, because the data were not normally distributed (Kolmogorov-Smirnov, $p < 0.01$), non-parametric tests were used (Kruskal-Wallis and Mann-Whitney for pairwise comparisons, significant when $p < 0.05$).

RESULTS

Landscape distribution

At the landscape scale, *Linaria vulgaris* occupies a wide variety of environments in the Gallatin NF, from clearcuts to sagebrush communities, while in Yellowstone NP it is constrained to roadsides, riverbanks and isolated areas in burned sites (1988 fires) and rocky hillsides (Fig. 2). Patch size distribution followed an inverted exponential curve, indicating a continuous recruitment of new patches (Fig. 4). In the study area, most patches occurred in logged areas (39.3%), roadsides (35.3%) and within 10 m of a road (20.3%), while just a fraction occurred in more pristine lake or river environments (3.2%) or in other natural vegetation (1.7%). The majority of recorded clusters were located in and around a heavily-infested area 6 km west of West Yellowstone around Highway 12 (Fig. 2). This area has been intensively logged in the last 20 years, favoring the establishment of *L. vulgaris*, and several infestations are dense enough to not have been recorded as separate patch clusters (Fig. 2). In addition, a small number of patches and a heavily-infested area were mapped along the sandy shores of Hebgen Lake (Fig. 2).

Linaria vulgaris is abundant in loose and bare soils with more than 52% of the recorded clusters in periodically disturbed sites such as roadsides (Fig. 4). *Linaria vulgaris* was also abundant in fire piles or areas that had been subject to intense fire, with almost 10% of the patches developing in areas with signs of severe burn, which are frequent in logging areas, but may also occur following natural fires (Fig. 4).

A total of 19 patch clusters (6.3%) were found in the interior of Yellowstone NP. In the park, clusters were found along the highway (58%), in riverbanks (21%), secondary roads (11%) and in natural vegetation, including a burn area and a hillside (Fig. 2).

Stand scale

The spatial distribution of *L. vulgaris* patches in the old clearcut and new clearcut macroplots suggested clear differences in patch patterns (Fig. 5). Patches covered 12.5% of the total area of the

old clearcut, but only 1.3% of the new clearcut. Patch density was also higher in the old clearcut (58/ha) compared to the new clearcut (20/ha). Mean patch size differed significantly between the old (26.3 m^2) and the new clearcut (6.7 m^2) (Mann-Whitney, $p < 0.01$).

Within the new clearcut, the centroids of the 10 mapped patches were significantly aggregated (nearest-neighbor $R = 0.53$, $p < 0.05$) (Fig. 5b). Clonal patches of *L. vulgaris* occurred in only three areas of the clearcut, and in two of those areas clusters of 3-4 small patches ($< 1 \text{ m}$ diameter) were found in close proximity to individual large patches (diameter $> 5 \text{ m}$). Within the old clearcut, on the other hand, patch centers inside the $50 \text{ m} \times 100 \text{ m}$ macroplot showed statistically significant dispersion (nearest-neighbor $R = 1.34$, $p < 0.005$) (Fig. 5a). Because most patches in the old clearcut measured at least 5-10 m in one or both diameters, the frequency of closely-neighboring patch centers was reduced below the rate that would be found in a random point distribution.

In the period 2000-2001, there were no significant differences in mean radial growth between the three old clearcut macroplots (Kruskal-Wallis, $p > 0.05$). Mean radial growth in the old clearcuts was $21.2 \pm 1.4 \text{ cm}$ (Fig. 6a), significantly higher than the growth rate in the new clearcut ($32.8 \pm 3.8 \text{ cm}$) (Mann-Whitney, $p < 0.01$). Meanwhile, mean radial growth in the riverbank macroplot ($28.5 \pm 4.6 \text{ cm}$) was not significantly different from either of the other land use types (Mann-Whitney, $p > 0.05$). In old clearcuts, substrate was a significant factor in determining radial growth (Kruskal-Wallis, $p < 0.01$) (Fig. 6). However, the only pairwise significant difference was between bare soil and *Pinus contorta* canopy ($p < 0.01$), which had the highest and lowest growth respectively.

Clonal Patch scale

In old clearcuts, *Linaria vulgaris* cover and ramet density were affected by position within the patch longest axis (Kruskal-Wallis, $p < 0.01$), and were higher in the interior and center than in the edges of clonal patches (Mann-Whitney $p < 0.01$) (Fig. 7a, c). The total cover of other species was also related to position (Kruskal-Wallis, $p < 0.01$), but tended to decrease in patch cores (Mann-

Whitney, $p < 0.05$) (Fig. 7b). Species richness was not related to position in the *L. vulgaris* patches (Kruskal-Wallis, $p > 0.05$).

In old clearcuts, the density of vegetative ramets in patch edges was significantly greater than the density of reproductive ramets (Mann-Whitney, $p < 0.05$) (Fig. 7d). At patch centers and interiors, reproductive and vegetative ramet densities were not significantly different (Mann-Whitney, $p > 0.05$). Overall, plants were taller in the patch centers (Fig. 8a). However, when ramets were classified by reproductive stage, average height for vegetative and reproductive ramets did not vary with position (Fig. 8b). Therefore, differences in average height corresponded mainly to differences in the proportion of reproductive vs. vegetative ramets.

DISCUSSION

Our method proved to be useful in understanding invasion processes at each of the three scales and evaluating the overall potential threat of the species over ecosystems of the West Yellowstone area. Long-distance dispersal and patterns of overall invasion at the landscape scale, rapid patch expansion at the stand scale and loss of native vegetation at the patch scale indicate that *Linaria vulgaris* can strongly impact ecosystems both through its rapid expansion and its competitive ability. These results suggest a strong potential of *L. vulgaris* to invade high-elevation protected areas in the Rocky Mountains. The species can follow road corridors and establish new patches in a wide range of disturbance regimes and habitats. Once established in a new environment it continues to grow, in term of number of patches, density of patches and regularity of patch distribution, ultimately causing the decline of native plant species.

Landscape Scale

Linaria vulgaris is widely dispersed across the landscape, but patch cluster density is highly variable. Management differences between Gallatin NF and Yellowstone NP appear to be key factors in *L. vulgaris* invasion. Patterns of cluster distribution are consistent with the presence of one major

source of propagules in the Gallatin NF. We hypothesize that an old ranch (late 1800s) located on the western edge of the study site has been the major source of propagules (Susan LaMont personal communication). There is also evidence that a small population was established in the park for aesthetic purposes and now is responsible for at least one wild population in the riverbank of Madison River (McClure personal communication). However, most clusters inside the park appear to have been initiated from propagules brought by vehicle flow along the entrance highway, which passes through the main infestations in the Gallatin NF (10 km apart). Long term monitoring and additional spatial analysis of cluster distribution is needed to understand the invasion dynamics at this scale. Since invaders show rapid genetic change, genetics techniques may also help to elucidate flow of propagules in the landscape (Lee 2002, Sakai et al. 2001).

Our landscape assessment supplemented previous reports that were qualitative and incomplete, missing *L. vulgaris* clusters in more pristine areas (Susan LaMont, Craig McClure personal communication). The landscape scale analysis also helped us to develop hypotheses as to where the initial infestation occurred and which were at present the major sources of propagules for long-distance dispersal. One of the major constraints of our method at the landscape scale is the lack of true replicates, which reduces the feasibility of using statistical tools. While we were able to document general landscape patterns with our intensive census technique, for future studies we recommend a broader coarse-scale assessment of weed populations utilizing for example long transects, to provide statistically robust and complete information on the distribution of critical new populations. Simple qualitative measures of weed presence extended over extensive areas would provide more useful information on locations of rare and small new populations, compared to more detailed but less extensive surveys (Maxwell et al. 2001).

Stand Scale

At the stand scale, we hypothesize that a clumped distribution is indicative of an early stage of invasion, as shown in the case of the new clearcut. Aggregation caused by clonal growth and poor

dispersal (Saner et al. 1995, Nadeau et al. 1991) may be an ecological strategy to overcome interspecific competition and assure persistence (Murrel et al. 2001). After overcoming local dispersal barriers by sufficient propagule production and colonization of the majority of suitable sites, the invasion process leads to a more random, and in some cases, dispersed distribution, as is the case in old clearcuts. These areas generally show dense and sometimes continuous *L. vulgaris* patches that are controlled mainly by environmental conditions rather than by the propagule availability. Our monitoring data suggests that new patches tend to be established as satellite patches and in some cases are absorbed into the parental patch. Even in heavily-infested areas, new patches can become established in the remaining non-invaded sites. These findings suggest that given sufficient time *L. vulgaris* will be able to dominate all areas with suitable conditions.

The higher radial growth of *L. vulgaris* in the new clearcut confirms its aggressive vegetative growth in recently disturbed soils. The relatively low overall average rate of growth (ca. 20-30 cm) reflects the harsh natural environment (cf. up to 2 m/yr growth of *L. vulgaris* in recently disturbed barley crops [Nadeau et al. 1991b]). The lower radial growth in *Pinus contorta* litter suggests that *Linaria* is not a good competitor in tree-shaded environments. The lack of relationship between patch diameter and radial growth shows that the potential for patch expansion does not diminish in older patches, confirming that a patch could persist indefinitely as long as the overall environmental conditions do not change (Lajeunesse 1999). Negative radial growth in a few patches could indicate a temporal dynamic in spatial distribution related to climate variations (e.g. intense summer drought), competition with native plants, the presence of herbivory or a combination of these factors (Saner et al. 1995, Pauchard and Alaback, unpublished data). We expect that our monitoring data will eventually help to answer those questions. The presence of both native and introduced insect predators may be the major factor controlling the expansion of these populations, but data are not yet available to confirm assess this factor (Bruce Maxwell personal communication, Saner et al. 1995).

Our method was efficient in evaluating the spatial distribution of *L. vulgaris* patches, determining overall characteristics of patch populations, and showing how stand structure converged from clumps to random distribution over time. However, our methods at the stand scale presented difficulties in assessing patch shape, because of irregular shapes that are more difficult to characterize than an ideal ellipse. Also, as we have observed in the monitoring process, patches tend to grow unevenly, changing their shape and orientation year by year so that re-mapping may be needed (Lajeunesse 1999). Replication of macroplots in early stages of invasion is needed because these areas probably have the most rapidly changing populations.

Clonal Patch Scale

At the patch scale, higher ramet density in patch cores compared to edges indicates that patches are expanding and maintaining a high ramet density. We found mean densities of almost 200 ramets/m², slightly higher than those found by Clements and Cover (1990 in Saner et al. 1995) in Ontario natural grasslands, but lower than the 300-700 plants/m² found in agricultural crops (Nadeau et al. 1991). The high ramet density in patch centers suggests that this species does not experience significant die-off after reaching maximum densities. *L. vulgaris* thereby presents a more difficult control problem than *Linaria dalmatica*, which has shown die-off or ring growth (Vujanovic and Wein 1997).

As it appears in old clearcuts, *L. vulgaris* is diminishing the cover of native plants in the core of the patches but not reducing species richness. We do not know if this pattern is due to rapid colonization of bare soils or if it really implies a displacement of the native species. The higher ramet density and mean height in the interior of the patches shows a trend of increasing biomass as the patches expand. This may reduce the available resources and lead to impoverishment of the native plant community. However, preliminary soil tests on patch centers and exteriors show no significant trend in nutrient availability. Even at higher densities, *L. vulgaris* height is not affected by intraspecific competition in patch cores; the tallest ramets grow in the densest areas of the patches.

Similarly, the height of reproductive ramets does not decrease with intraspecific competition. Therefore, we could expect a proportional relationship between patch area and propagule output.

Data from the clonal patch scale suggest a negative effect of *L. vulgaris* on native vegetation and confirm that the species maintains high densities, even years after patch establishment. This scale is crucial to understand the behavior of the invader and its interaction with native vegetation (Table 1). Our ability to determine population structure is limited due to the dominant vegetative reproduction of *L. vulgaris*. The proportion of ramets and genets is impossible to calculate with our method, and thereby it is difficult to assess the importance of sexual reproduction in the dynamics of patch expansion. Overall, the clonal patch scale provides the most information on the dynamics of interaction between the invasive plant and native species. From a monitoring perspective, this type of data may reveal how the invader diminishes the cover of other plants to the point of reducing local species richness.

Conservation Implications: Integrating Scales

Linaria vulgaris invasion in the West Yellowstone area illustrates that invasive plant species are becoming a threat not only to low-elevation disturbed environments, but also to remote, high-elevation protected areas. Ecological phenomena such as invasions do not distinguish political boundaries (Landres et al. 1998, Lindenmayer and Franklin 2002), and thus land use practices that favor invasive species in adjacent land may be the starting point of invasion processes in protected areas. The distribution, abundance and growth trends of *L. vulgaris* in the Yellowstone area, as deduced from our multi-scale approach, suggest that this species has the potential to invade both pristine and human-disturbed areas in high elevation environments in the Rocky Mountains. Furthermore, the increase in visitation and development around protected areas is facilitating the spread of alien invasive species invaders into natural communities even under harsh climatic conditions. Anecdotal data from other areas confirm this trend. *L. vulgaris* is an important problem in Rocky Mountain National Park, Colorado, where it occurs up to 3,600 m elevation in naturally

disturbed ground (Jeff Connor personal communication). In the Northern Rockies, Forest Service weed specialists have observed *L. vulgaris* populations between 1,000 and 2,000 m in a number of National Forests (Pauchard unpublished data).

The overall effect of *L. vulgaris* invasion on native communities is difficult to assess. However, our findings suggest high *L. vulgaris* densities reduce plant cover of other species. Other effects such as impacts on wildlife may be expected as *L. vulgaris* displaces native plants. Global warming may also enhance weeds' invasiveness (Dukes and Mooney 1999). We have also found what appear to be natural hybrids of *L. vulgaris* and *L. dalmatica* in our study area (Saner et al. 1995, Vujnovi and Wein 1997; genetic analyses are in progress). These hybrids may pose a new threat due to plasticity and rapid genetic change (Sakai et al. 2001).

In Yellowstone NP, *L. vulgaris* could easily expand into other open areas such as riverbanks, burned areas, meadows or sagebrush shrublands. We have already found patches far from human corridors in naturally disturbed grounds. Activity of both gophers and large herbivores seems to favor *L. vulgaris* establishment (Bruce Maxwell personal communication). Increased recreation and visitation could promote further dispersal into remote areas. Identifying correlations of *L. vulgaris* invasion with habitat characteristics (e.g. disturbance regime) and dispersal constraints (e.g. distance from nearest seed source) would help to predict future infestations.

Our multi-scale results suggest that *L. vulgaris* control would be most efficient by emphasizing control on new populations and dispersal corridors. Disturbed environments close to major dispersal corridors should be emphasized in monitoring activities. At present, Yellowstone NP applies herbicides to all *L. vulgaris* patches that are sources of seeds that may be dispersed by vehicles or pedestrians (Ollif et al. 2001, Craig McClure personal communication). A similar control approach is used by the Gallatin NF and Gallatin County. Biocontrol agents have been released in Gallatin NF during the last two decades (Susan LaMont personal communication) and some have dispersed into *L. vulgaris* patches inside Yellowstone NP (Ollif et al. 2001). Even so, *L. vulgaris*

expansion continues, especially in isolated areas of the southern corner of Yellowstone National Park (Whipple 2001).

Conclusion

Protected areas and their contiguous matrixes represent a unique setting for studying the interactions between major causes of invasion such as disturbance, environmental factors and dispersal strategies, all of which tend influence the invasion process at specific scales. A multi-scale method may help to promote integration in our understanding of invasion processes in complex natural landscapes since it allows consideration of coarse scale phenomena such as patterns of spread along dispersal corridors and effects of land use or disturbance regimes on invisibility, along with fine-scale phenomena such as population dynamics and native species decline as related to more site specific factors. A multi-scale method may lead to more successful invasion management in these particularly sensitive and critical natural areas. To allocate limited resources, a multi-scale method should be used to determine which mechanisms exert the greatest influence in the invasion process.

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Table 1. Theoretical multi-scale framework for assessing alien plant invasions. At each scale, a different set of processes can be evaluated and unique management strategies can be designed.

<i>Element/Scale</i>	<i>Landscape</i>	<i>Stand</i>	<i>Invader Patch</i>
Spatial dimensions	- Defined by geoeological system (Over 10 ⁶ m ²)	- Area of the stand and large plots (1,000-10,000 m ²)	- Patch size and microplots (0.1-500 m ²)
Temporal scale	- Events that occur over hundreds of years	- Events occur in decades	- Events occur yearly
Key processes & structures affecting invasion	-Topography, winds -Land-use and history -Macroclimate	-Soil series -Disturbance regimes -Microclimate -Plant community types	-Microsite variation (e.g. soil disturbance, coarse woody debris) -Plant interactions -Plant-animal interactions
Spatial pattern detection	-Identify infection loci and sinks, and dispersal corridors.	- Identify patches' spatial arrangement. - Patterns of short distance dispersal.	- Individual ramets' distribution - Density patterns
Processes studied	- Long term dispersal and interactions with landscape structure (e.g. long-term patterns of spread along corridors)	- Interaction between invasion and disturbance and site characteristics.	-Population dynamics -Interaction with native plants
Monitoring	- Identify key loci of infection and detect new isolated patches.	- Monitor infilling of colonized stands - Monitor successional changes	-Monitor population characteristics -Monitor effects on native species
Conservation and management applications	- Detection and prioritization of infested areas.	- Test efficacy of control methods and their interactions with site factors - Determine invasion effects on overall native plant community	-Quantify control effects on population dynamics -Determine the effects of control in native plants

Table 2. Scale definition for three attributes of the landscape scale assessment of *Linaria vulgaris* patch clusters.

Attribute	Classes			
Land use	Roads: areas located 10 m from a road or highway	Logged areas: areas that have been clearcutted or intensively logged during the last 30 years	Riversides: areas that are near a river, lake or in riverbanks	Natural vegetation: Areas that do not show signs of heavy human disturbance
Fire Intensity	1: Areas with no historical record or physical sign of fire	2: Areas with historical record of fire but no physical signs	3: Areas with scattered physical signs of fire such as coarse woody debris charcoal	4: Areas with high density of coarse woody debris charcoal (burn piles in logging operations)
Soil Disturbance	1: Present of bare soil, but no signs of soil turn over	2: Presence of bare soil, signs of turnover disturbance but more than 25% herbaceous cover	3: High levels of soil turnover (e.g. gophers mounds), less than 25% herbaceous cover.	4: Areas where soil is disturbed periodically with less than 5% of plant cover (e.g. roads, trails).

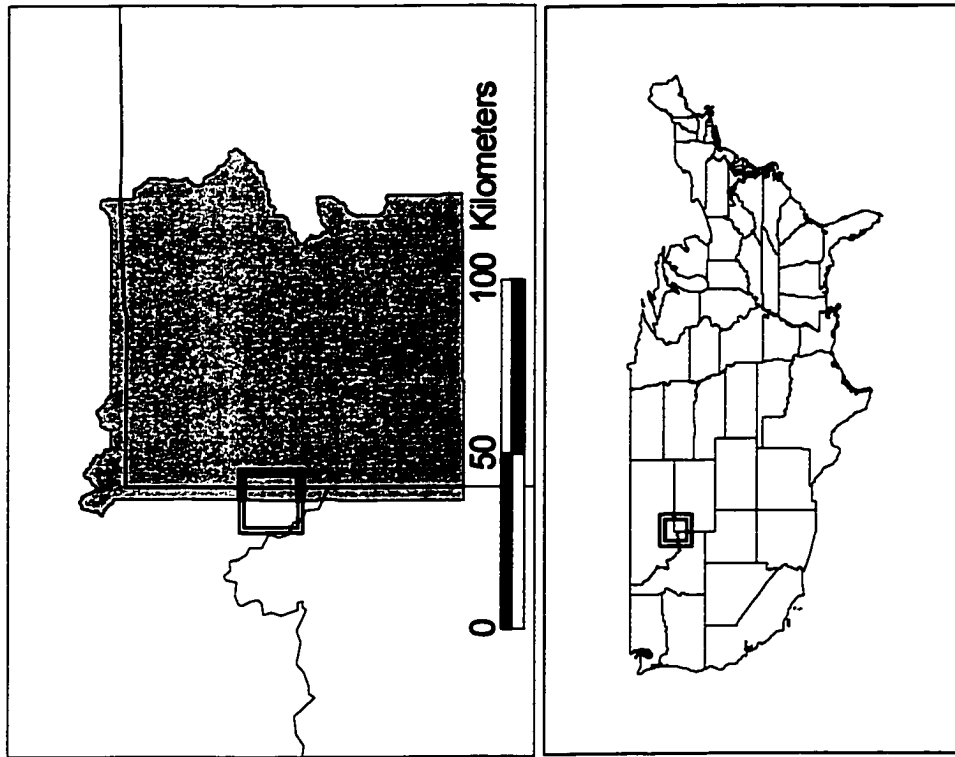


Fig. 1. Map of the study area in West Yellowstone, Montana. The square indicates the location of the study area. A detailed map of the study area is presented in Fig. 2.

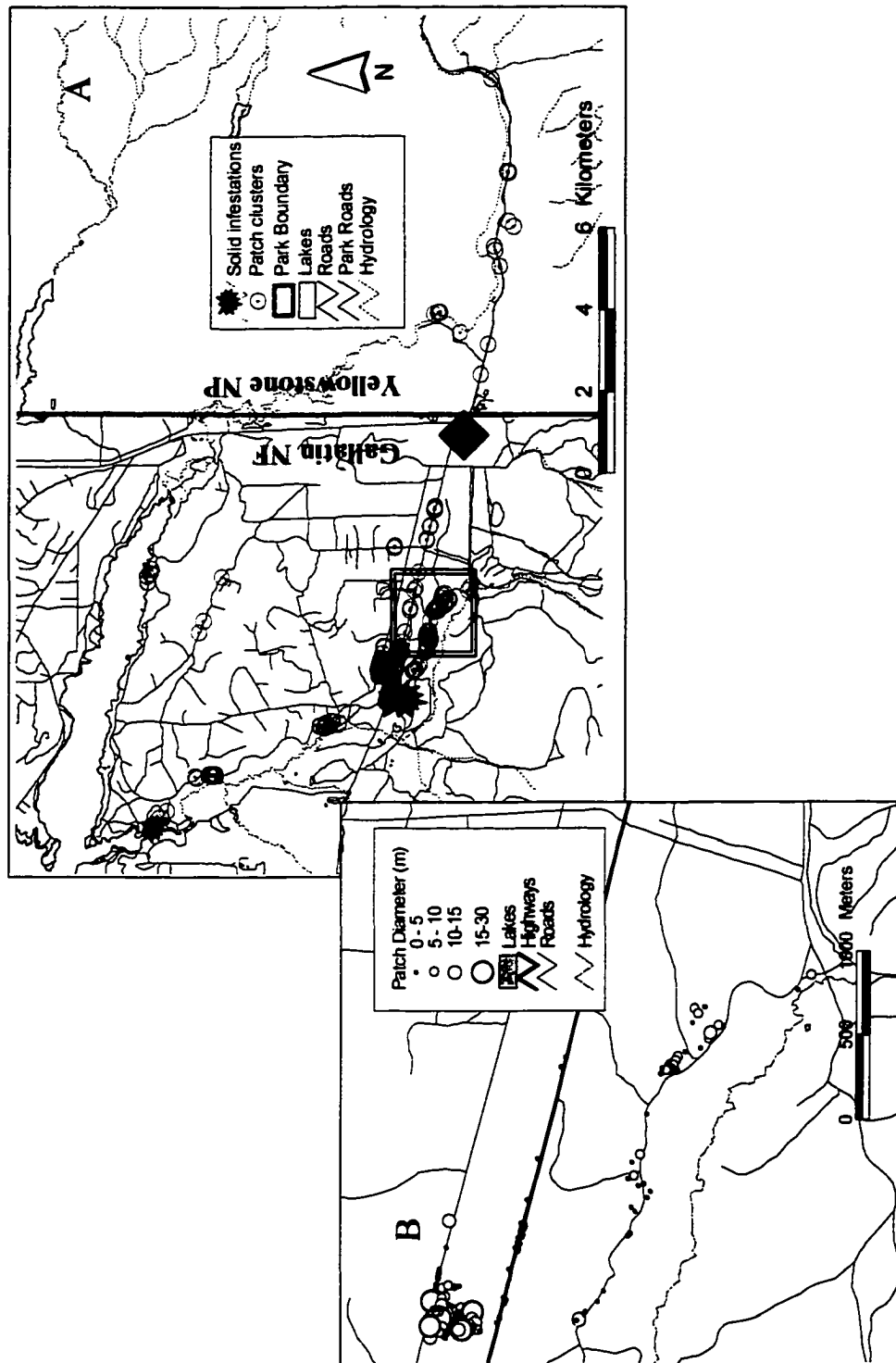


Fig. 2. Landscape distribution of *Linaria vulgaris* patch clusters in the study site. A. West Yellowstone Study site (the rhomboid indicates the town of West Yellowstone; the square is enlarged in part B). B. An example of spatial cluster distribution at the landscape scale, with clusters classified by size.

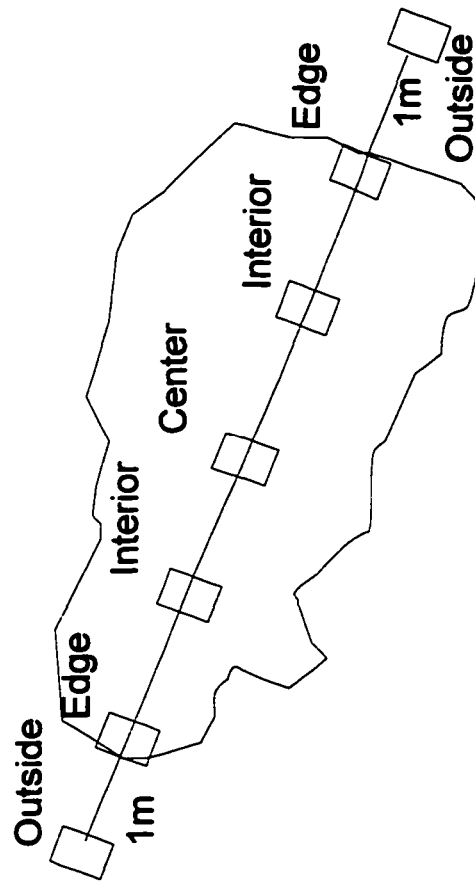


Fig. 3. Schematic diagram showing the location of 7 microplots (50 by 20 cm) used in large and medium-sized patches of *Linaria vulgaris*. Spacing between plots is 1/4 of patch length. In small patches (<5m) only 5 microplots were located (2 outside, 2 along the edges and one in the center).

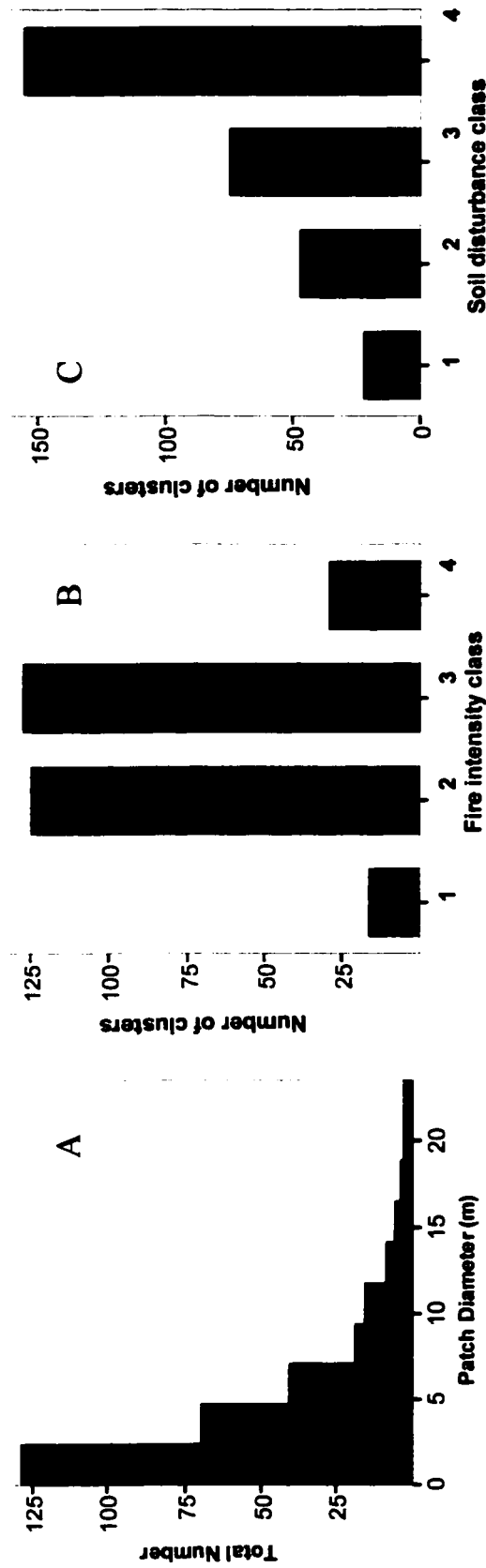


Fig. 4. Attributes histograms for 300 *Linaria vulgaris* clusters in the West Yellowstone area. A. Patch diameter, B. Fire history class (1: minimal signs of historical fire, to 4: signs of severe fire; see Table 2 for details). C. Soil disturbance class (1: no disturbance, to 4: periodically disturbed soil; see Table 2 for details).

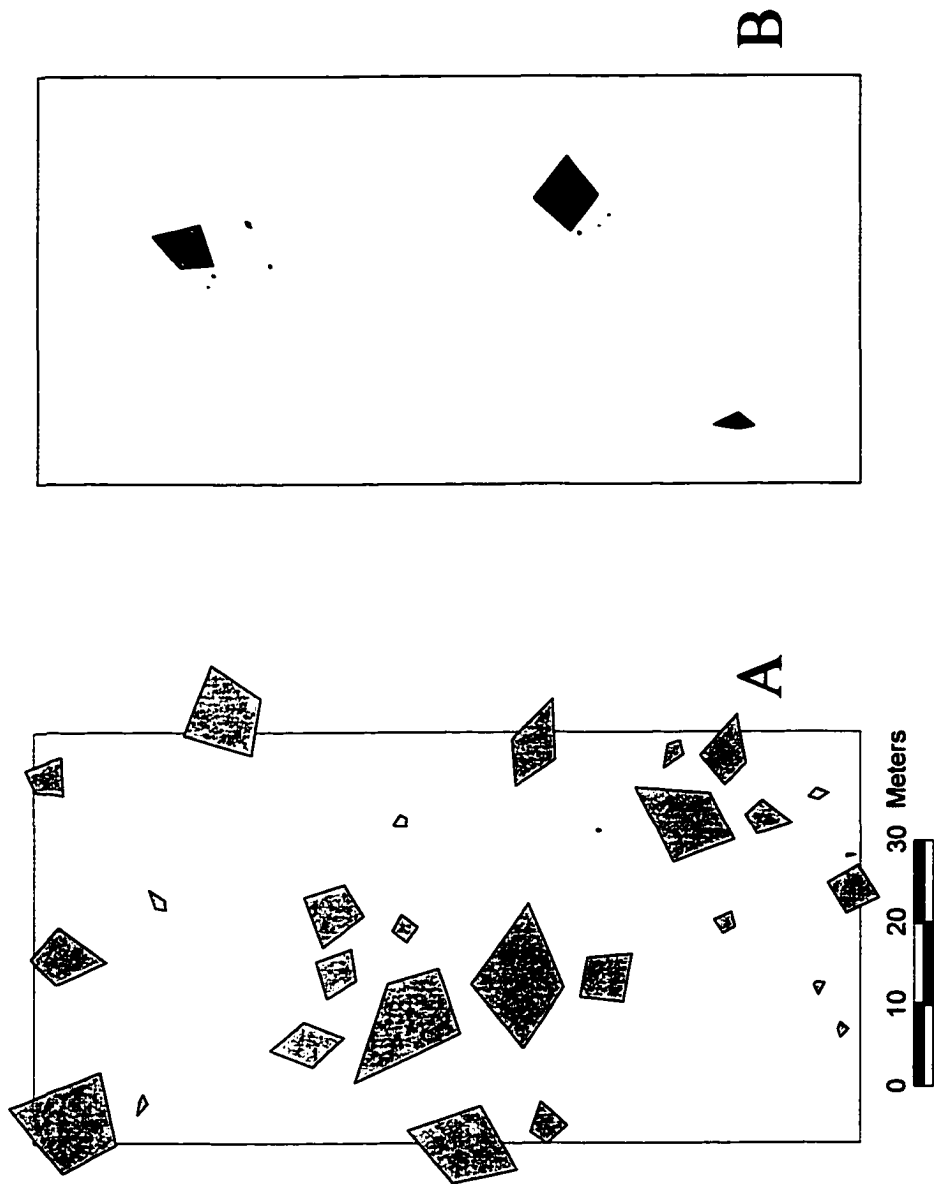


Fig. 5. Clonal patch spatial arrangement in A) an old clearcut, B) a new clearcut, both in the Gallatin National Forest. The macroplot is 50 by 100 m and the total number of patches is 27 for A and 10 for B.

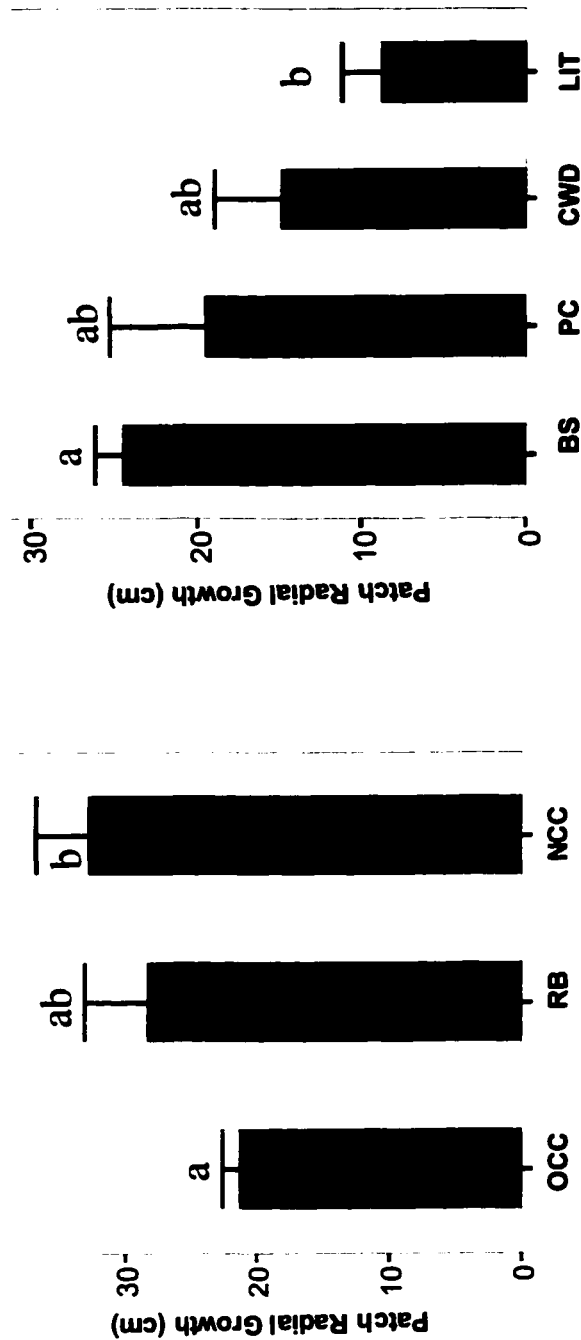


Fig. 6. Radial growth (+SE) of *Linaria vulgaris* clonal patches from 2000-2001. A. Patch growth in new clearcuts (NCC, number of patches n=10, corners=36) was significantly greater than in old clearcut patches (OCC, n=70, corners=271) (Mann-Whitney, $p<0.01$). The growth in the riverbank macroplot (RB, n=8, corners=28) was not significantly different from either of the other land use types. Because some patches had merged in 2001, the number of corners is less than 4x the total number of patches. B. Patch growth (2000-2001) in old clearcuts by substrate (BS: bare soil, PC: more than 25% plant cover, CWD: more than 50% coarse woody debris, LIT: 50% or more cover of *Pinus contorta* litter). Only Canopy and bare soil were significantly different (Mann-Whitney, $p<0.05$).

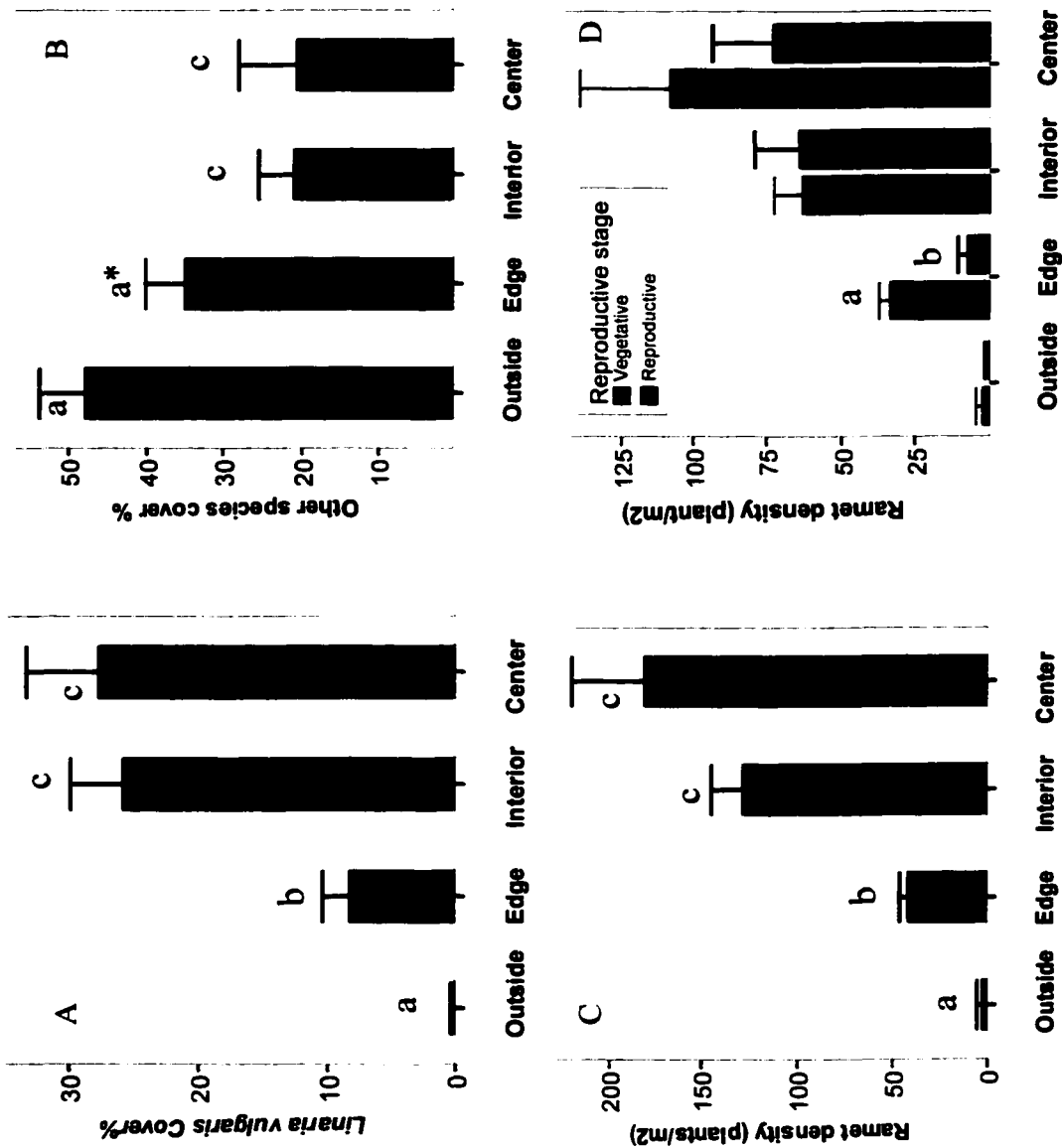


Fig. 7. Microplot variables (mean \pm SE) from outside (1m) to the center in large and medium *Linaria vulgaris* clonal patches from clearcuts and riverbanks (N=18; center plots=N, all others=2N). A. *L. vulgaris* cover %. B. Other species cover %. C. *L. vulgaris* ramet density. D. *L. vulgaris* ramet density separate by reproductive stage. *L. vulgaris* cover %, other species cover and ramet density were significantly correlated with location in the patch (Kruskal-Wallis, $p<0.01$). Lowercase letters indicate significant pairwise differences (Mann-Whitney, $p<0.01$, * indicates $p<0.05$). Mean vegetative and reproductive ramet densities were only significantly different in the patch edges.

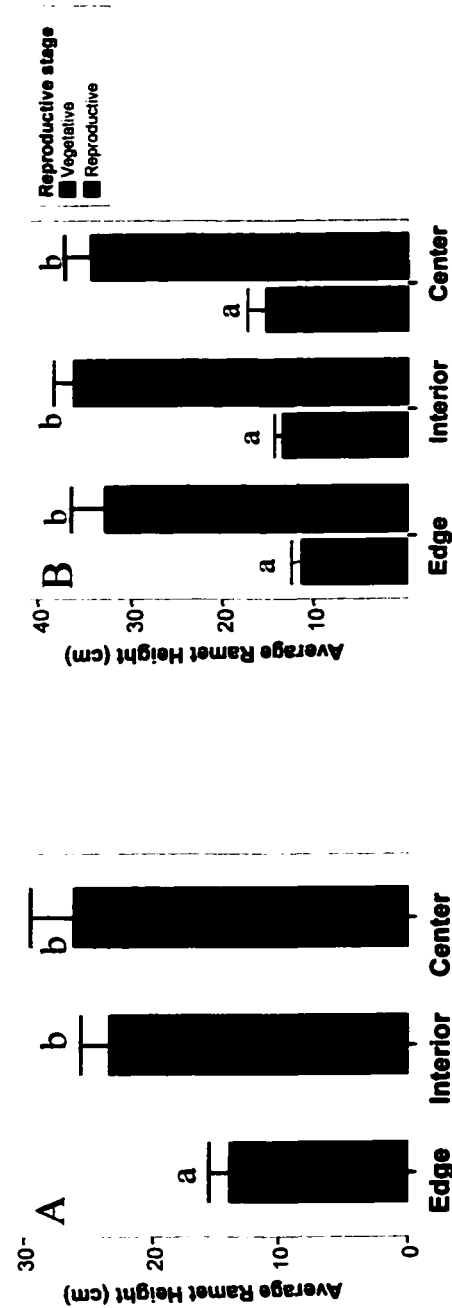


Fig. 8. Microplot mean average height (\pm SE) in the edge, interior and center in large and medium *Linaria vulgaris* clonal patches (n=24 for edge, interior; n=12 for center). A. Average height considering both vegetative and reproductive ramets is significantly different from the edge to the center (Kruskal-Wallis, $p < 0.01$). Lowercase letters indicate significant differences (Mann-Whitney, $p < 0.01$). B. Average height by reproductive stage. Height differences are not significant for either vegetative and reproductive stages across the three positions (Kruskal-Wallis, $p > 0.05$). However, mean height of vegetative ramets is always significantly different from the mean of reproductive ramets (Mann-Whitney, $p < 0.01$). Lowercase letters indicate significant differences (Mann-Whitney, $p < 0.01$).

CHAPTER 5

EFFECTS OF CLIMATE VARIABILITY ON *Linaria vulgaris* INVASION IN THE WEST YELLOWSTONE AREA.

ABSTRACT

Alien plant invasions are dynamic processes affected by climatic variability. Anomalies in precipitation and temperature regime can modify the overall environmental conditions, triggering the expansion or retraction of invasive populations. In the West Yellowstone area, expansion in the landscape distribution and infilling of populations of *Linaria vulgaris* has been observed during the last decade, but no data has been collected systematically to report changes over time. This paper aims to describe the variation over a three year period of *Linaria vulgaris* invasion and its effects on plant community at two scales: clonal patch scale and stand scale. *Linaria vulgaris* invasion and its effects were monitored in a three-year period at two spatial scales: stand and clonal patch. At the stand scale, short distance dispersal processes, infilling of infestations and interactions with local site characteristics were studied using a macroplot of 50 by 100. At the clonal patch scale a 20 by 50 cm sample unit was used to evaluate population structure inside the patches, development of clonal patches, and the interaction of *L. vulgaris* with native vegetation. Spatial patterns of *L. vulgaris* patches at the stand scale appear related to stages of invasion. However, it appears that our 3 year effort was not sufficient in detecting temporal changes in spatial patch distribution with the exception of a new clearcut site. Analyses of radial growth by period suggest that there was a lower growth rate of *L. vulgaris* patches in the 2001-2002 period. that was correlated with drier more difficult growing conditions. Annual variation appears as a significant factor for most of the variables studied at the microplot scale (MANOVA repeated measures, $p < 0.01$). Climate variation appears to be closely associated with changes the density of reproductive ramets; in drier springs less reproductive ramets are produced. This study illustrates the importance of monitoring invasive species in order to understand the ecological implications of invasions. This interannual variation may have more ecological importance in areas with harsh climatic conditions that are limiting to plant growth, as in high elevation protected areas.

INTRODUCTION

Alien plant invasions are dynamic processes affected by climatic variability (Cousens and Mortimer 1995, Bazzaz 1996). Temporal changes in climatic conditions can be a key factor in determining the extent and impact of invasions. Understanding the effect of climatic variability on invasion process may help to identify the environmental conditions which determine invasion success (Dukes and Mooney 1999). Climatic variability also affects invaded natural communities, influencing their susceptibility to invasion and its impacts (Dukes and Mooney 1999).

Climatic variability is usually related to the spatial scale at which processes are occurring. For example, at global scale, climate is relatively stable and they only fluctuate with major global climate changes as has been shown with global warming. However, at regional or local scales, fluctuations in climate patterns can be observed in decades or years. Climatic cycles as El Niño and la Niña modify local climate patterns. At these smaller scales, annual climatic variability may be one of the most important drivers of environmental change.

Anomalies in precipitation and temperature regime can modify the overall environmental conditions, triggering the expansion or retraction of invasive populations (Davis et al. 2000). Even though, environmental variability has been recognized as a driving factor of invasion, much of the research has focused in capturing invasions at a specific point in time (snapshot) with little attention to annual variation in climate (Mack 2000). Monitoring efforts are scarce and usually limited to the extent of grants or the duration of graduate studies (Mack 2000). At regional scales, some efforts utilized herbaria and historical information to trace the development of invasions in long term scenarios (Toney et al. 1999, Arroyo et al. 2000). However, at the local scale most studies are not continued through time. In cases where permanent plots have been located and remeasured, new insights often emerge. For example, in New Zealand, data from permanent plots was instrumental in confirming the consistent expansion of *Hieracium lepidulum* in the understory of *Nothofagus* forests (Wiser et al. 1998).

Linaria vulgaris, a noxious invader of high elevation and cool environments, has been observed increasing its distribution and density in the area around West Yellowstone, Montana (Chapter 4). The species already has invaded disturbed areas in the Gallatin National Forest and is threatening to invade natural ecosystems such as riverbanks, grasslands and shrublands where has already been able to establish, in both Gallatin NF and Yellowstone National Park.

In the West Yellowstone area, expansion in the landscape distribution and infilling of populations of *Linaria vulgaris* has been observed during the last decade, raising the awareness of managers in both conservation units (Chapter 4). However no data has been collected systematically to report changes over time. For these reasons, *Linaria vulgaris* in this area represents a unique opportunity to understand the responses of invasions to high elevation environments in relation to temporal variability.

This paper aims to describe the variation over a three year period of *Linaria vulgaris* invasion and its effects on plant community at two scales: clonal patch scale and stand scale. This chapter complements the findings of chapter 4 by considering changes over time in *L. vulgaris* invasion in the West Yellowstone area. I will describe *L. vulgaris* invasion at the stand and patch scales over three sampling seasons and correlate observed trends with climatic variability, focusing both in the spatial arrangement of patches and in population and community characteristics. I hypothesize that *Linaria vulgaris* and the invaded community presents a strong interannual variation that is associated with annual climatic variation. I expect that this study will help document the value of multi-year monitoring of invasive plants.

Study area

The study area is the same as in chapter 4, located in the Madison Valley around the western entrance of Yellowstone National Park and the adjacent Gallatin National Forest (44°48'N, 111°12'W and 44°37'N, 111°00'W). A complete analysis of the study area and the biology of *Linaria vulgaris* is presented in chapter 4.

METHODS

Linaria vulgaris invasion and its effects were monitored in a three-year period at two spatial scales: stand and clonal patch. Each scale was defined arbitrarily to capture a unique set of processes, and specific methods were developed for each scale (described in chapter 4). At the stand scale, short distance dispersal processes, infilling of infestations and interactions with local site characteristics were studied using. The sampling size unit was defined as a macroplot of 50 by 100 m, sufficient to evaluate the structure and dynamics of groups of clonal patches. The patch scale was defined by the size of clonal patch, which varies from 0.5 to 25 m, using a 20 by 50 cm sample unit. At this scale, processes evaluated included population structure inside the patches, development of clonal patches, and the interaction of *L. vulgaris* with native vegetation.

Data Collection

Stand scale

In August of 2000, we recorded spatial attributes of *L. vulgaris* patches in five macroplots of 100m by 50m (chapter 4). In the Gallatin NF, three macroplots were located in old clearcuts (ca. 20 yr old), and one in a newer clearcut (ca. 6 yr old). In Yellowstone NP one macroplot was located on a riverbank of the Madison River. The three macroplots in old clearcuts were randomly selected from areas logged between 1978 and 1982 with high levels of *L. vulgaris* infestation. In late August of 2001 and late August of 2002, positive or negative radial (horizontal) growth in previously-measured patch axes was recorded for all patches in macroplots. New patches in macroplots were added to the spatial data. Spatial datasets in ArcView were created using the monitoring data.

Clonal patch scale

In August of 2000, patches were randomly selected within each macroplot to locate a set of 50 by 20 cm microplots in randomly selected *L. vulgaris* patches (described in chapter 4, Daubenmire 1968). Microplots were marked permanently using metal stakes. In each microplot, every ramet was recorded along with its height class (10 cm) and reproductive stage (vegetative, reproductive) based on the presence of reproductive structures. In addition, we estimated cover class for each plant species using the five cover classes of Braun-Blanquet (described in Mueller-Dombois and Ellenberg 1974). Microplots were remeasured in August of 2001 and August of 2002.

Analyses

Stand scale

To assess changes in spatial patterns, we conducted point pattern analyses in the 2000 and 2002 macroplot data. Analyses were run for four macroplots, two in old clearcuts under severe invasion, one in a newer clearcut at early stages of invasion, and one in a riverbank of Yellowstone NP. Distribution patterns in patch centroids within macroplots were estimated using Ripley's K statistic and Duncan's (1990) statistical program. The Ripley's K method compares the number of points that fall in a circle as a function of diameter and compares the function with the 95% confidence interval of random runs using MonteCarlo simulation. Results for 2000 and 2002 were compared to explore the possibility of detecting changes in spatial patterns in the short-term (2 years). In addition, area covered by *L. vulgaris* patches, mean patch size and total number of patches were calculated for each macroplot by year.

The role of year and macroplot in determining patch radial growth was tested using ANOVA and t-test for pairwise comparisons among years (judged significant when $p < 0.05$). The effect of patch diameter in determining annual radial was tested using a linear model (significant when $p < 0.01$) for each of the two periods studied (2000-2001 and 2001-2002).

Clonal patch scale

MANOVA repeated measures was used to test for the effect of annual variation in *Linaria vulgaris* and the invaded community. In medium and large patch combined of old clearcuts (N=12 patches, n=84 microplots), we tested for the effects of year of measurement (2000, 2001, 2002) and its interaction with location in the patch (outside, edge, interior, center) and macroplot in microplots variables. Microplot variables (dependent variables) tested included *L. vulgaris* attributes (total ramet density, vegetative ramet density, reproductive ramet density, cover %, biomass, maximum height, average height), and community attributes (total cover % of other plants, species richness, and species richness without considering *L.vulgaris*). Density, biomass and cover variables were transformed using lognormal. In addition, for each year, MANOVA was used to determine the effect of position and macroplot in these microplot variables. Biomass was calculated using a regression curve with plant height obtained from 80 individual samples homogenously distributed from 0 to 80 cm and randomly chosen from old clearcuts in August of 2002 ($R^2=0.92$, $p<0.001$, $\text{Height}=b*\text{biomass}^{1/3}$).

To test for changes in the correlation between *L. vulgaris* attributes and the invaded community in old clearcuts, linear models were run for each of the three sampling period datasets. For all microplots in old clearcut patches (N=114), including small, medium and large patches (N=18), correlation between species richness and other plant cover vs. *L.vulgaris* density, cover and biomass were tested using single variable linear regression models.

To detect temporal changes in the new clearcut and the riverbank macroplots, microplot variables were graphically displayed using standard errors, but due to the lack of replicates, not statistical analyses were conducted.

Climatic variation

To find correlation patterns between annual climatic variation and *Linaria vulgaris* invasion, climate data was analyzed for the three years of data collection and compared with climate averages (normals) for the last 107 years (1895-2002). Data was obtained for the Yellowstone Drainage climate division (Western Regional Climate Center 2002). Weather data was not available for the study site due to discontinuity on the records of the West Yellowstone weather station. Variables were analyzed as monthly averages and included mean daily temperature (C) and precipitation (mm). Anomalies for the historical monthly average were compared among the three-year period. Data was interpreted by correlating anomalies with significant changes in *L. vulgaris* and the invaded community at the stand and patch scales.

RESULTS

Stand scale

Results from the Ripley's K tests indicated that in 2000, *Linaria vulgaris* patches showed a random distribution at all distances in old clearcuts, and in the riverbank site (Table 1, Fig. 1, Fig. 2). Patches in the new clearcut showed clumpiness between 0 to 15 m, being randomly distributed at longer distances (Fig. 2). The old clearcut and riverbank macroplots showed no change in spatial arrangement during the two year period, however the new clearcut tended to be more randomly distributed in 2002 than in 2000 (Fig. 2).

Year and macroplot were both significant in determining radial growth (ANOVA, $p < 0.001$). Radial growth was higher during the period 2000-2001 than the period 2001-2002 for all macroplots, but t-tests showed significant differences for only one old clearcut macroplot (Fig. 3). For old clearcuts, no significant relationship was found between patch diameter and radial growth at neither period (linear regression, $p > 0.05$).

Total area cover by *L. vulgaris* increased from 2000 to 2002 in all macroplots, however the number of patches was reduced in new clearcuts (Table 1, Fig. 4). A trend towards increased

patch size was observed, but was influenced by the formation of smaller new patches, which lowered the mean size. In old clearcuts the total coverage of *L. vulgaris* patches approaches 18%, while in new clearcuts and the riverbank is only ca. 2% (Table 1).

Clonal patch scale

In medium and large patches within old clearcuts, year was a significant factor in most of the microplot variables (Table 2, Fig. 5). For four variables, the interaction year*position (in the patch) was significant. However, for only biomass and height the interaction year*position*macroplot was significant, while the interaction year*macroplot was not significant for any variable. For the new clearcut and the riverbank, variables showed much higher variation when compared to old clearcuts (Fig. 6).

MANOVA analyses for each year showed that position was a significant factor in most microplot variables, while macroplot and the position*macroplot interaction was rarely significant (Table 3). Significant variation in the model and explanatory factors by year was observed in other species total cover and species richness without *L. vulgaris*.

Weak relationships were found among species richness and other plant total cover vs. *L. vulgaris* density, cover, height and biomass (Table 4, Fig. 7). However, *L. vulgaris* height was the best predictor for other species total cover and maximum height was the best predictor of species richness w/out *L. vulgaris*. No variable was significantly correlated to species richness when considering *L. vulgaris*. Minor changes, from year to year, were found in model precision (R^2), but no clear trend was evident.

Climatic effects

Spring of 2000 was wetter than normal, but summer was drier than normal (Fig. 8). However, 2001 had close to average precipitation for spring and summer drought with deficit of precipitation in previous winter months. Precipitation for the year 2002 was lower than normal

for winter, spring and summer. For the three years, winters and summers were dryer than normal and much of the inter-annual variation occurred in spring.

Mean temperatures were on average higher than normal for the three-year period in all seasons. Only 1999 and 2002 appear closer to normal records during spring, reporting cool temperatures between April and June.

The wetter than normal spring of 2000 is associated with the highest values for reproductive ramet density, species richness, and other species total cover (Fig. 5). All these variables decreased in 2001 and 2002. Most microplot variables show a similar response in 2001 and 2002, however reproductive ramets diminished abruptly in 2002. During 2002, few plants reached reproductive maturity and visual observations showed a low percentage of ramets producing floral structures and even fewer containing viable seeds. In microplots located in patches edges and outsides, the negative effects of climate variation were compensated by intrinsic patch growth (Fig. 5). Patch edges still show growth regardless of climatic variations. However, the drier than normal 2002 growing season was associated with a decrease in the rate of radial patch growth compared to previous growing season (Fig. 4). No clear pattern emerged between temperature and *L. vulgaris* and the invaded community variables, mainly because all years showed higher than normal temperatures.

DISCUSSION

Stand scale

Spatial patterns of *L. vulgaris* patches at the stand scale appear related to stages of invasion. Early stages of invasion show a clumped distribution that may be caused by insufficient propagule dispersal. However, as *L. vulgaris* increases its abundance, as in old clearcuts, its patches become randomly distributed. These results confirmed preliminary statistical analyses of this data (chapter 4). It appears that the 3-year effort was not long enough to detect temporal changes in spatial patch distribution with the exception of the new clearcut site. These results

suggest that processes of expansion and structuring of patch arrangement in *L. vulgaris* can take several years or decades, demanding a longer term monitoring effort.

However, I was able to detect changes in the overall coverage of patches by determining radial growth. As it appears, old clearcut infestations are still growing in abundance covering over 16% of the total area, adding ca. 1% annually (Table 1). In the case of riverbanks and the new clearcut, the coverage is much lower (ca. 2%) but increasing a proportionally higher rate (Table 1). Our method presented some limitations in addressing changes in patch shape and aggregation of adjacent patches (see field methods in chapter 4). These limitations probably did not have major implications in estimating patch structure in this short term monitoring, because most patches did not change drastically their shape. However, improvement in the field method is required for longer-term monitoring.

Analyses of radial growth by growing season suggest that there was a lower growth rate of *L. vulgaris* patches in 2002. These changes are consistent across landuses suggesting that climatic variations or other landscape phenomena are determining growing patterns. As mentioned before, the growing season of 2002 presented more difficult growing conditions for *L. vulgaris*, which could explain the decrease in radial growth, especially considering that *L. vulgaris* has been shown to have higher invasion success on wet and cool environments (Saner et al. 1995).

Clonal Patch scale

Annual variation appears as a highly significant factor for most of the variables studied at the microplot scale. Interestingly, total ramet density is not significantly affected by yearly variation. However, when analyzed separately, both reproductive and vegetative ramet densities are related to yearly variation. This suggests that intrinsic population growth and reproductive effort may be interacting. The relationship between spring precipitation and the number of reproductive ramets suggests that climate variation may be responsible for changes in

reproductive effort. On the other hand, vegetative ramets could be less sensitive to climatic variation, which would explain the continuous vegetative growth of patches (Fig 5).

Year does not significantly correlate with biomass changes, but the interaction of year and position and the interaction of year, position and macroplot are significant. This suggests that biomass is more sensitive than density to specific site conditions. In this case, it appears that the decrease in height and density during the last two years in the interior and center plots contrasted to the increasing trend for these variables at edge plots.

Changes in height, density and biomass also appear associated with macroplot, which was an indirect indicator of site differences between old clearcuts. When analyzed by year, position is consistently a significant factor in explaining biomass.

A significant annual variation in species richness ($p < 0.01$), with an overall decrease in 2001 and slight recovery in 2002 (Fig. 5), illustrates that the invaded community may also be influenced by climatic variation. In the three-year period, species richness was not related to position in the patch, indicating no effect of *L. vulgaris* in overall diversity. (Tables 2, 3). Similarly to *L. vulgaris* cover, other species total cover decreased consistently during the three-year period even in outside microplots not affected by the invasion, suggesting major effects of climatic variability. These results suggest that while *L. vulgaris* tends to diminish cover of other species, it has little effect on the overall species number.

The displacement of native species however, is not clearly expressed in the relationship between native species richness and other species total cover, versus *L. vulgaris* attributes. I interpret these results as evidence that there may not be direct competition for resources between native plants and *L. vulgaris* and therefore, their abundance and overall diversity is mainly constrained by other abiotic and biotic factors. For example, observed changes in reproductive effort may also be a product of the interactions between climate variability and herbivores, which in the case of *L. vulgaris* effect strongly reproductive structures (Saner et al. 1995).

Monitoring invasions

This study illustrates the importance of monitoring invasive species in order to understand the ecological implications of invasions (Mack 2000). A one time “snapshot” could provide partial and misleading information about the invasion process. For example, with one-year observation I could have concluded that *L. vulgaris* was an extremely vigorous invader with high seed production.

The multi-year effort allowed me to detect short-term annual variation, which could have profound effects in the overall invasion success. It appears that *L. vulgaris* is remarkably sensitive to climatic changes and that these could explain, at least partially, why it has not been shown to be a consistently aggressive species (Saner et al. 1995). Also, this annual variation seems not to only affect the invader, but also the native community (e.g. species richness, plant cover). The interaction between both invader and native species and annual cycles may be crucial to understand the elements that define years of high invader recruitment and population expansion or years of retraction. Climate may influence the potential of the invader but also the susceptibility to invasion of the native community. I found that for *Linaria vulgaris* sensitivity to annual climatic variation is primarily related to changes in precipitation patterns rather than changes in temperature regimes. This data are consistent with the widely held view that water availability is a key constraint to vegetation growth in this harsh environment (chapter 4).

Interannual variation may have greater ecological importance to areas with harsh climatic conditions that are limiting to plant growth, as in high elevation protected areas. Fluctuations in climatic factors could define the outcome for alien species populations in these extreme environments. This environmental variability may also stimulate cyclical behavior of invasive populations with wide implications in terms of their impacts and their management. In these sensitive environments, global warming can also worsen the effects of invaders by altering precipitation and temperature patterns (Dukes and Mooney 1999).

This study, by focusing on short term monitoring, alludes to the potential value of longer term monitoring efforts in plant invasions. The observed short-term trend of slower expansion of *L. vulgaris* in adverse conditions may be reversed in the long term if climatic conditions change. If the goal is to understand and manage invasions, monitoring efforts should follow a similar scheme to that of a multi-scale assessment (chapters 1, 4). Different temporal windows should be used to study invasion processes, which should allow us to capture a broader range of phenomena related to the invasion process.

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Table 1. Annual summary of stand scale attributes for four macroplots. Values correspond to 2000, 2001 and 2002 measurements. Spatial distribution based on Ripley's K function (R= random, C= clumped).

Macroplot	Patch number			Mean Patch Size (m ²)			Total Area (%)			Mean Radial Growth		Spatial Pattern 2000	Spatial Pattern 2002
Old clearcut 1	29	33	34	26.3	25.9	27.5	15.3	17.1	18.7	24.20	23.91	R	R
Old clearcut 2	17	19	19	45.8	46.0	44.2	15.6	16.6	16.8	16.08	5.65	R	R
New clearcut	10	9	6	6.7	9.7	16.9	2.8	3.4	3.7	32.78	19.79	R/C	R
Riverbank	8	8	8	17.7	21.0	23.3	1.3	1.7	2.0	28.50	16.29	R	R

Table 2. MANOVA repeated measures for microplot variables in large and medium patches of old clearcuts (N=18 patches, n=84 microplots). Factor are year (Y: 2000, 2001, 2002), macroplot (M) and position in the patch (P: outside, edge, interior, center). Values indicate significance of relationship.

Variable	Year Factor (p)	Y*P Interaction (p)	Y*M Interaction (p)	Y*P*M Interaction (p)	3Y average- Position (p)
<i>Linaria vulgaris</i> attributes					
Ramet density (log10)	0.091	n	n	n	0.000
Reproductive ramet density (log10)	0.000	0.006	n	n	0.000
Vegetative ramet density (log10)	0.000	n	n	n	0.000
<i>Linaria vulgaris</i> cover (log10)	0.029	n	n	n	0.000
<i>Linaria vulgaris</i> biomass (log10)	n	0.007	n	0.001	0.000
Average Height	0.000	0.008	n	0.019	0.000
Maximum Height	0.000	0.000	n	0.000	0.000
Community attributes					
Other species cover (log10)	0.000	n	n	n	0.021
Species richness	0.000	n	n	n	n
Species richness w/out <i>L.vulgaris</i>	0.000	n	n	n	0.026

Table 3. ANOVA, by year, for microplot variables in large and medium patches of old clearcuts (N=18 patches, n=84 microplots). Factor are year macroplot (M) and position in the patch (P: outside, edge, interior, center). Macroplot and Macroplot*Position interaction were never significant. SS: sum of squares, F: F value, p: probability of significance, R²: R squared for the model.

Variable	Year	Corrected SS	Model F	p	Position SS	Factor F	p	Error SS	R2
<i>Lnaria vulgaris</i> attributes									
Ramet density (log)	2000	38.80	15.0	0.000	37.52	53.2	0.000	16.92	0.70
	2001	43.07	13.5	0.000	41.66	48.0	0.000	20.84	0.67
	2002	37.02	14.8	0.000	36.51	53.7	0.000	16.33	0.69
Reproductive ramet density (log)	2000	39.10	10.2	0.000	35.33	33.8	0.000	25.10	0.61
	2001	25.92	5.2	0.000	24.71	18.2	0.000	32.54	0.44
	2002	13.59	2.7	0.006	11.89	8.7	0.000	32.82	0.29
Vegetative ramet density (log)	2000	55.49	37.7	0.000	54.02	134.5	0.000	9.64	0.85
	2001	53.45	20.9	0.000	52.39	75.1	0.000	16.75	0.76
	2002	42.67	17.6	0.000	42.42	64.2	0.000	15.87	0.73
Cover (log)	2000	23.11	14.8	0.000	22.38	52.5	0.000	10.23	0.69
	2001	20.28	10.8	0.000	19.86	38.7	0.000	12.32	0.62
	2002	16.99	11.3	0.000	16.42	40.1	0.000	9.82	0.63
Biomass (log)	2000	44.26	21.0	0.000	41.69	72.5	0.000	13.80	0.76
	2001	31.47	12.1	0.000	30.32	42.8	0.000	17.00	0.64
	2002	28.95	15.3	0.000	28.24	54.6	0.000	12.41	0.70
Average Height	2000	8568.68	11.8	0.000	7818.37	39.6	0.000	4739.19	0.64
	2001	4703.90	5.5	0.000	4230.12	18.1	0.000	5611.23	0.46
	2002	4169.80	9.8	0.000	4027.30	34.5	0.000	2798.80	0.60
Maximum Height	2000	25657.14	12.6	0.000	23640.48	42.5	0.000	13350.00	0.66
	2001	13985.42	7.6	0.000	12981.25	25.7	0.000	12106.25	0.54
	2002	10866.07	8.4	0.000	10207.74	28.9	0.000	8487.50	0.56
Community attributes									
Other species cover (log)	2000	7.07	2.3	0.020	3.46	4.1	0.010	20.41	0.26
	2001	5.56	1.6	0.130	2.36	2.4	0.073	23.35	0.19
	2002	5.55	1.9	0.049	2.69	3.4	0.022	18.82	0.22
Species richness	2000	35.66	1.0	0.441	12.24	1.3	0.288	229.63	0.13
	2001	27.56	1.0	0.450	8.73	1.2	0.328	179.25	0.13
	2002	30.81	1.2	0.312	4.73	0.7	0.575	170.00	0.15
Species richness w/out <i>L. vulgaris</i>	2000	32.19	0.9	0.514	9.10	1.0	0.413	225.63	0.13
	2001	49.81	1.9	0.048	32.73	4.7	0.005	168.00	0.23
	2002	49.24	2.0	0.039	23.16	3.5	0.020	160.00	0.24

Table 4. Changes in R^2 in regression for variables in all microplots of old clearcuts (n=14). Community attributes (a. other species total cover, b. species richness and c. species richness without *Linaria vulgaris*) vs. *L. vulgaris* attributes (ramet density, cover percentage, maximum height and biomass).

Variable\ <i>Linaria vulgaris</i>	Density (log)	Cover (log)	Max. height	Biomass (log)
a. Other species total cover	0.14 0.13 0.07	0.12 0.16 0.12	0.13 0.15 0.11	0.14 0.16 0.11
b. Species richness	* * *	* 0.04 *	* * *	* * *
c. Spp richness (w/out <i>L. vulgaris</i>)	* 0.10 0.06	* 0.17 0.10	0.05* 0.07 0.14	* 0.16 0.09

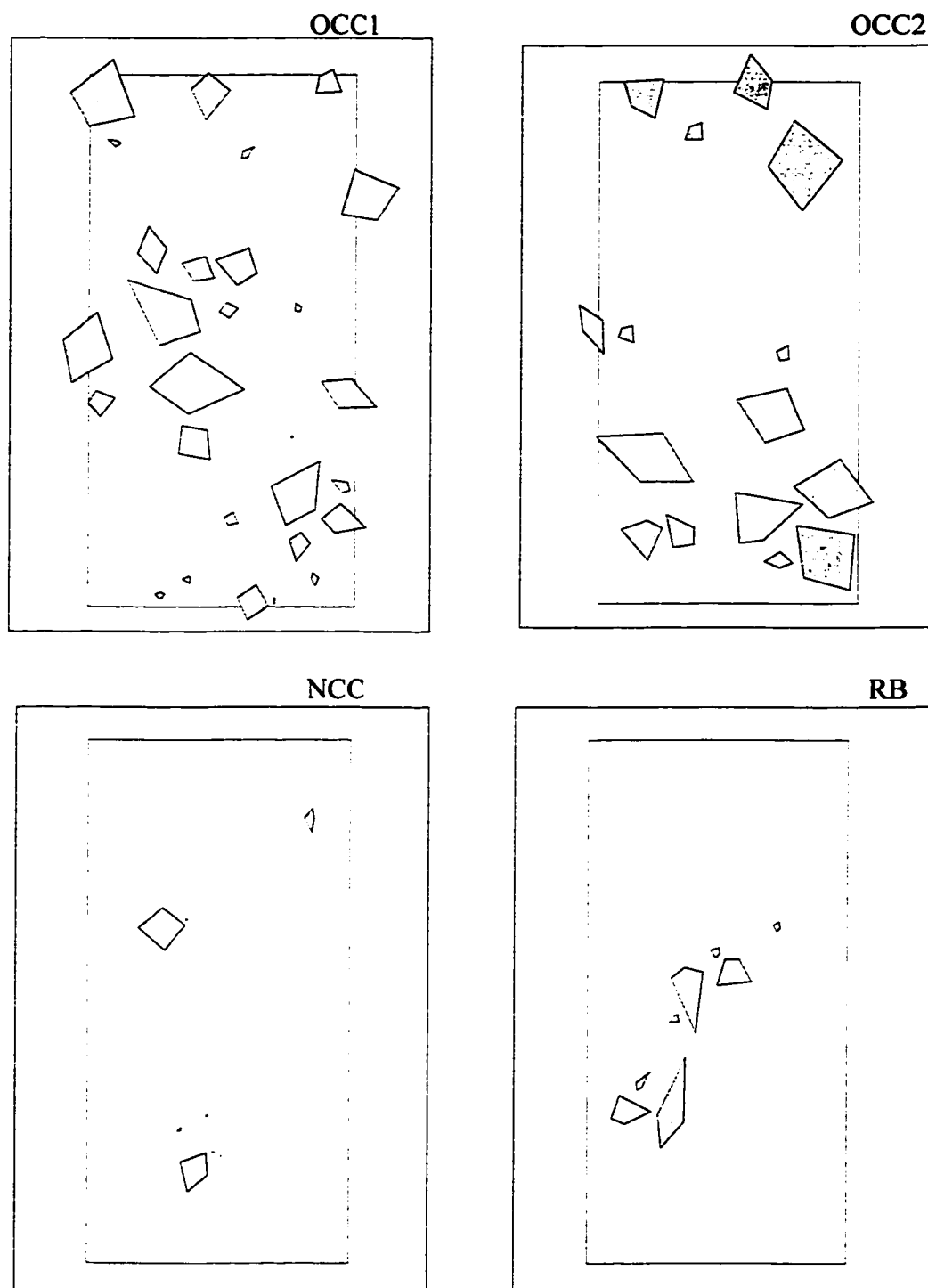


Fig. 1. *Linaria vulgaris* patch distribution at the stand scale for old clearcuts (OCC), a new clearcut (NCC) and a riverbank (RB). Macroplots are 50 by 100 m.

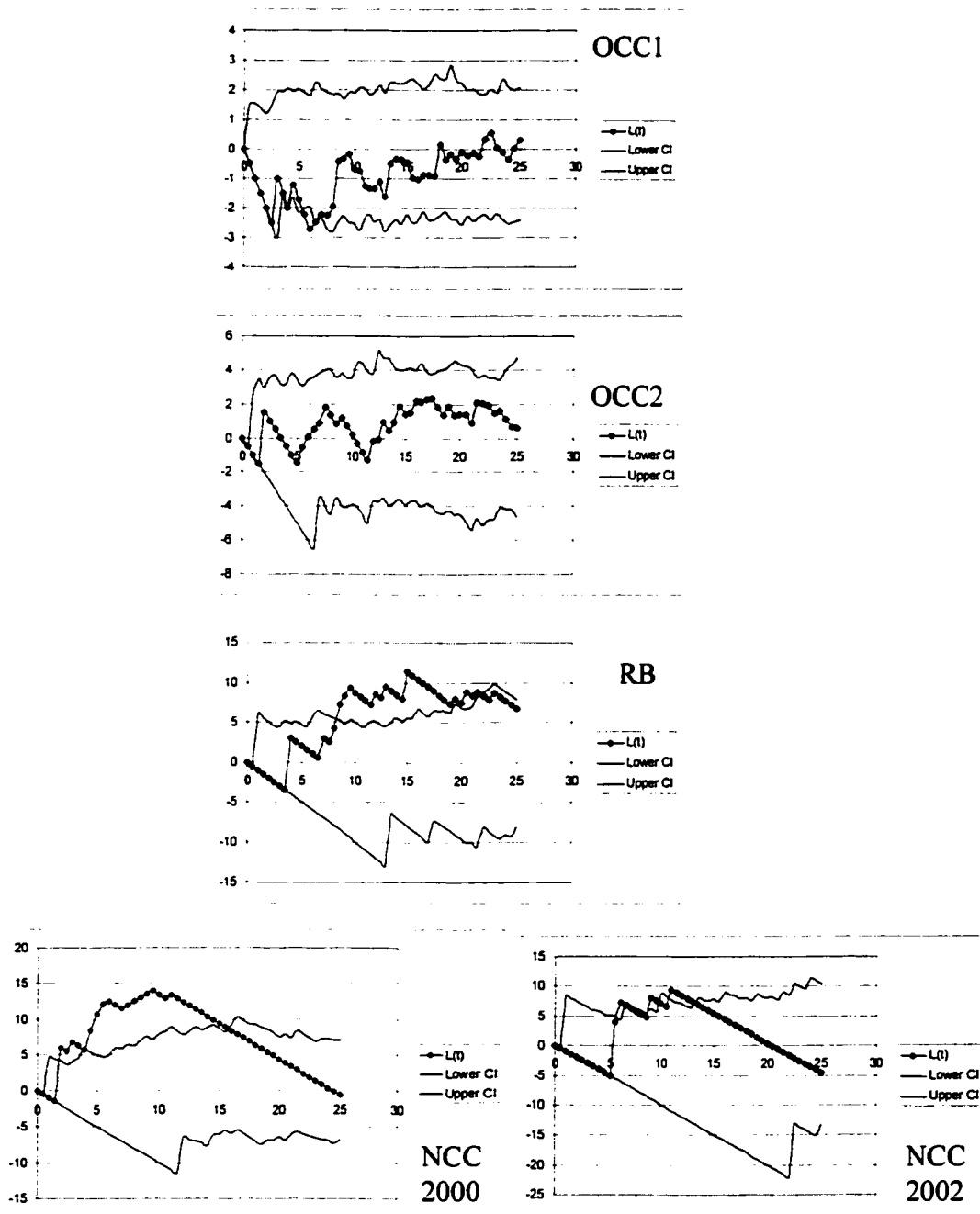


Fig. 2. *Ripley's K* simulation for four macroplots in 2000: two old clearcuts (OCC1, OCC2), one in riverbank (RB) and one in a new clearcut (NCC). A simulation for 2002 is shown for the NCC. L represents the K statistic for a determined distance (t) shown in axis X. Simple lines represent the lower and upper confidence limit at 95%.

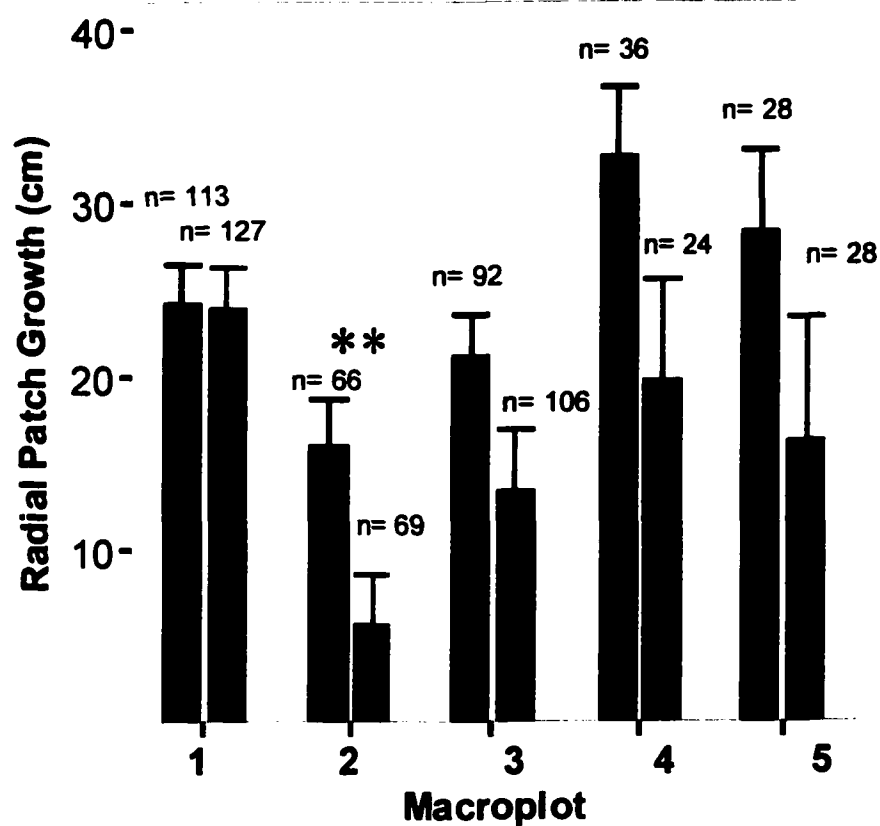


Fig. 3. Radial patch growth for *Linaria vulgaris* in periods 2000-2001 and 2001-2002 by landuse in old clearcuts (1,2,3), a new clearcut (4) and a riverbank (5). N indicates the number of corners used for measuring radial growth. ** indicates significance at $p < 0.01$.

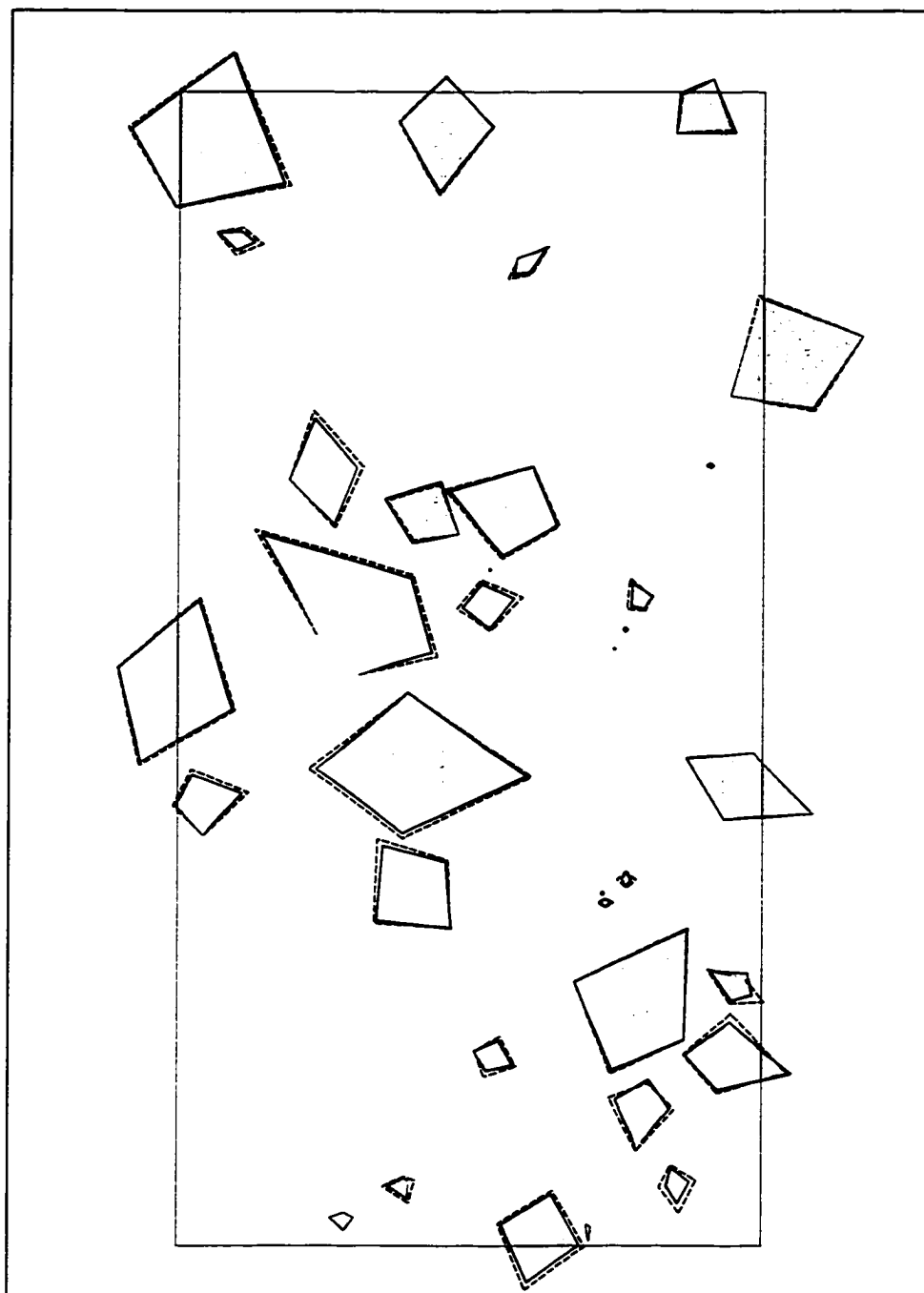


Fig. 4. Temporal changes in *Linaria vulgaris* patch distribution at the stand scale for an old clearcut (OCC1). Grey indicates the initial patch shape in 2000; continuous line indicates shape in 2001; and dashed line indicates shape in 2002. Changes in patch shape were determined using measures of annual radial growth.

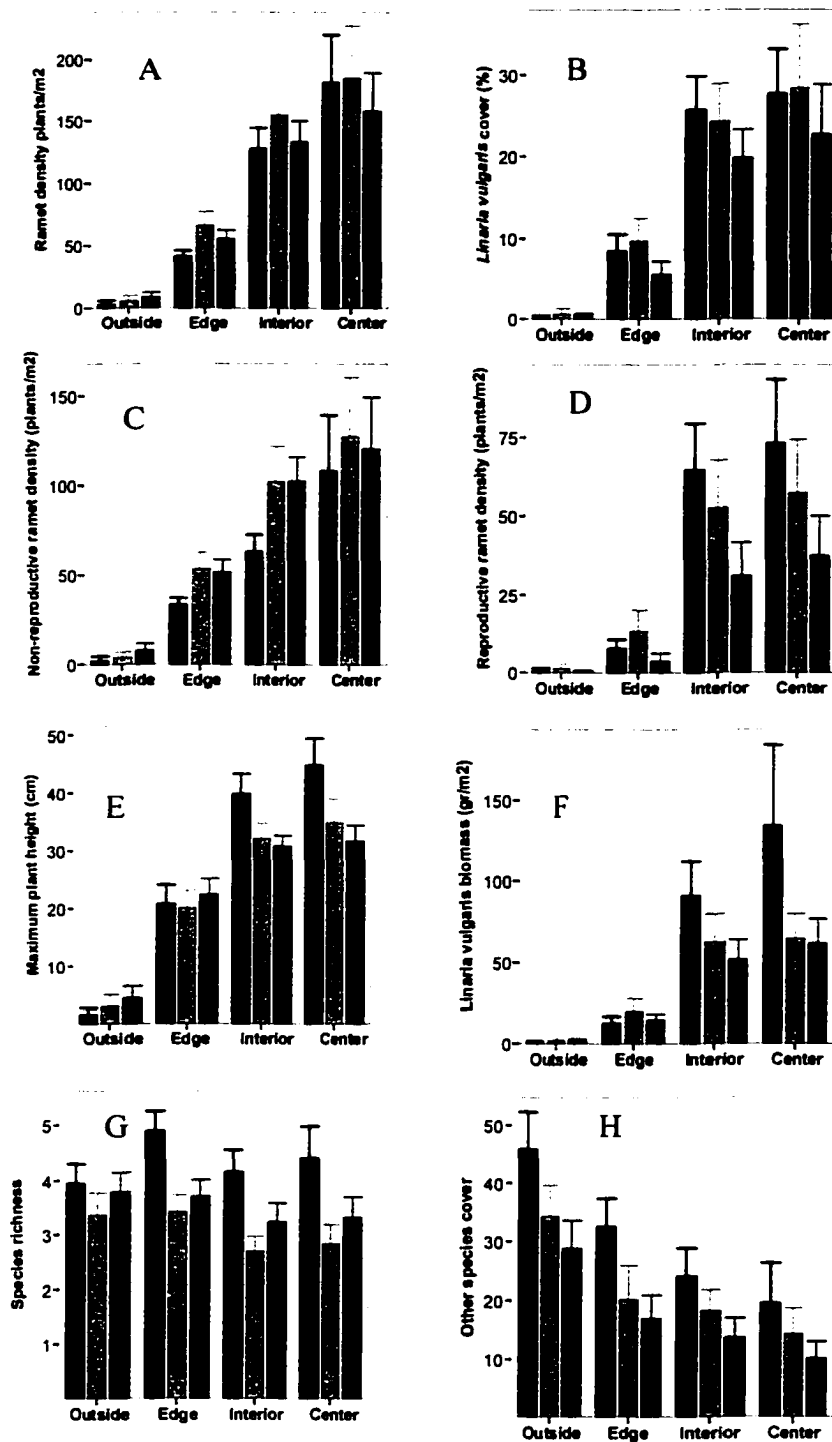


Fig. 5. Mean microplot variables \pm SE in old clearcuts by location and year. *Linaria vulgaris* attributes: a) ramet density, b) cover %, c) vegetative ramet density, d) reproductive ramet density, e) maximum height and f) biomass, and community attributes g) species richness and h) other species total cover.

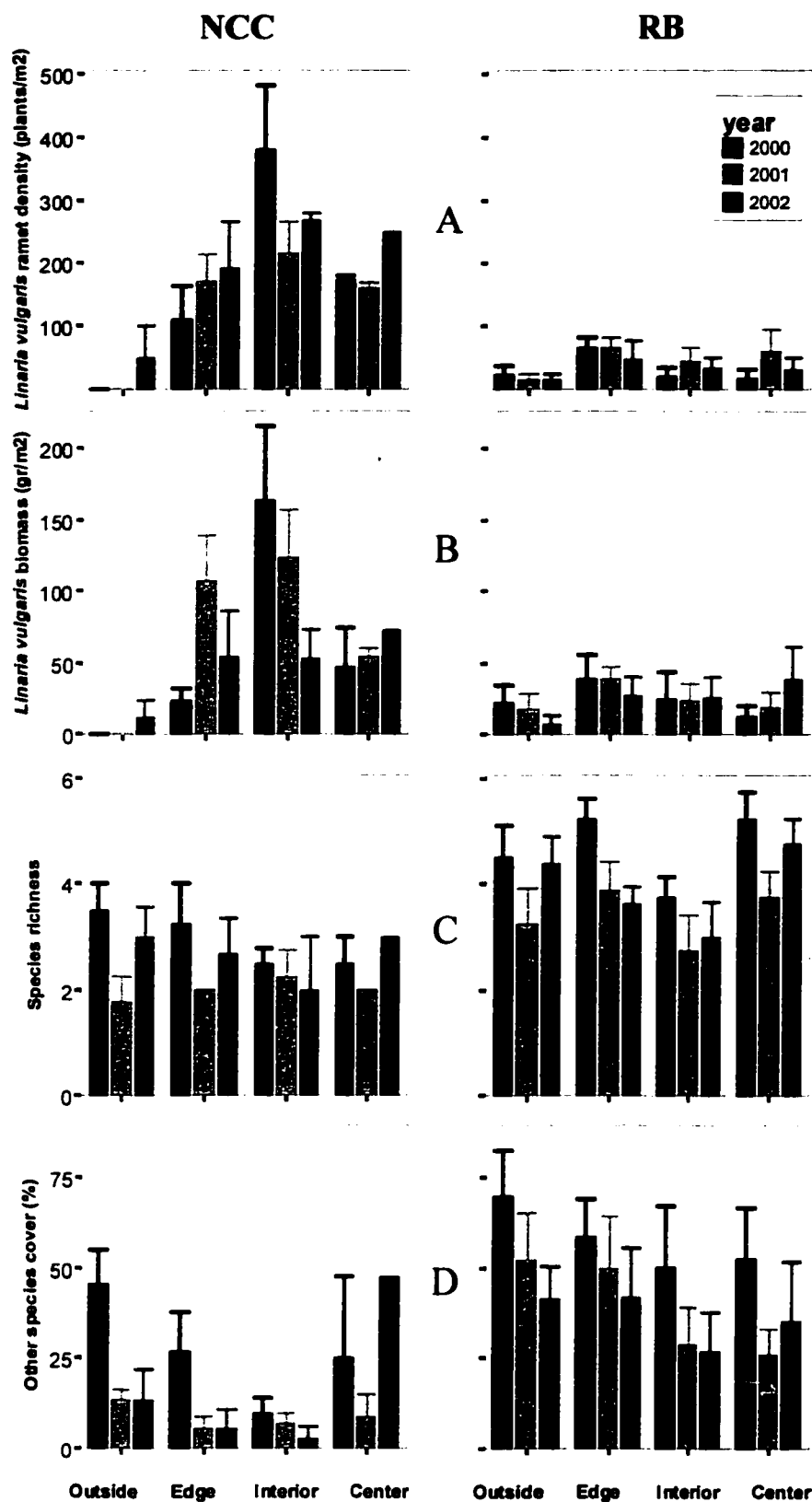


Fig. 6. Mean microplot variables \pm SE in new clearcut (NCC) and riverbank (RB) by location and year. *Linaria vulgaris* attributes: a) ramet density, b) biomass, and community attributes c) species richness and d) other species total cover.

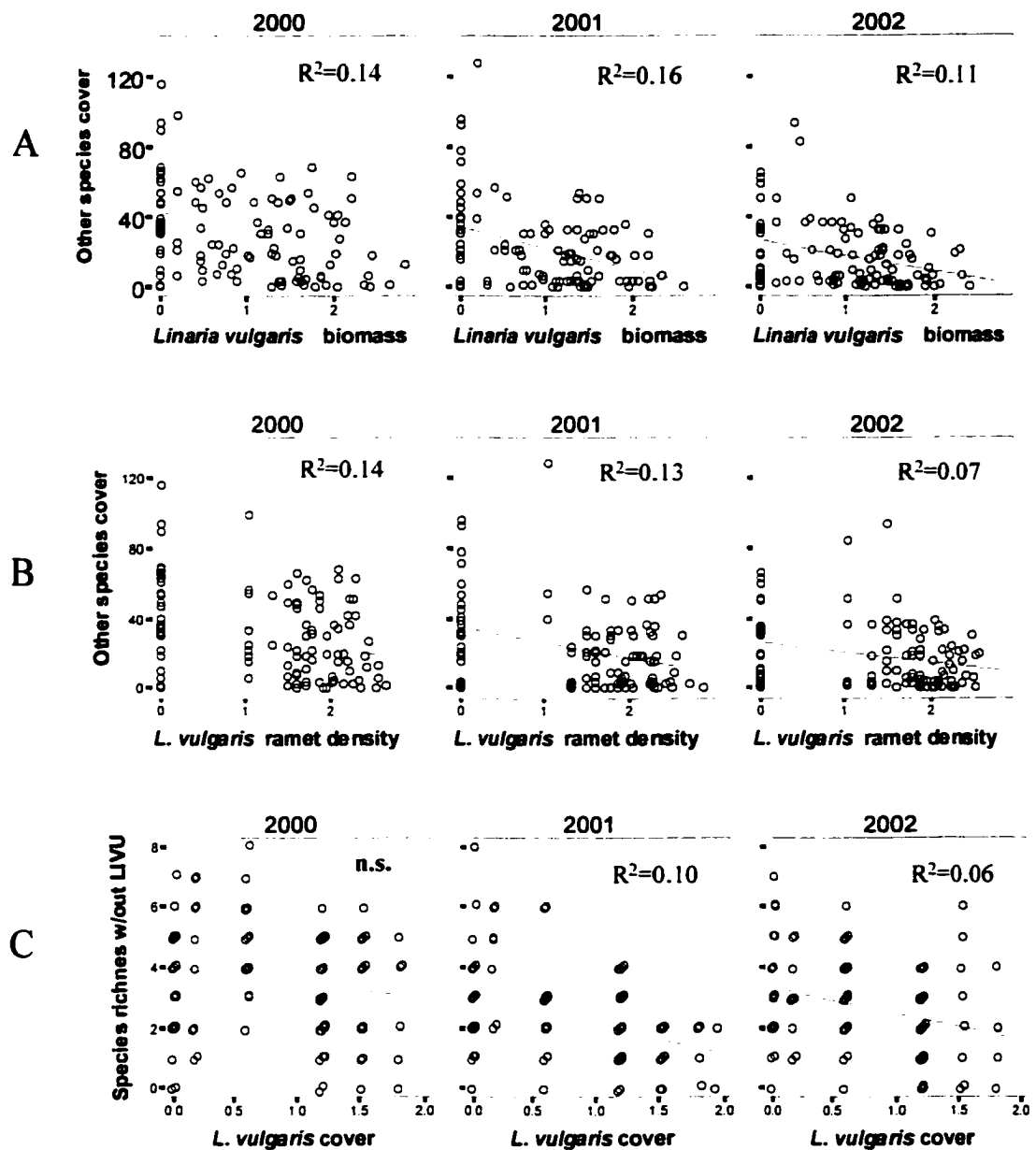


Fig. 7. Regression lines and scatterplots for variables in microplots of small, medium and large patches of old clearcuts combined (N=114). a) Other species cover vs. *L. vulgaris* biomass (log), b) Other species cover vs. *Linaria vulgaris* density (log), c) Richness without considering *L. vulgaris* vs. *L. vulgaris* cover (log). All relationships were significant ($p < 0.05$), except for one (n.s.).

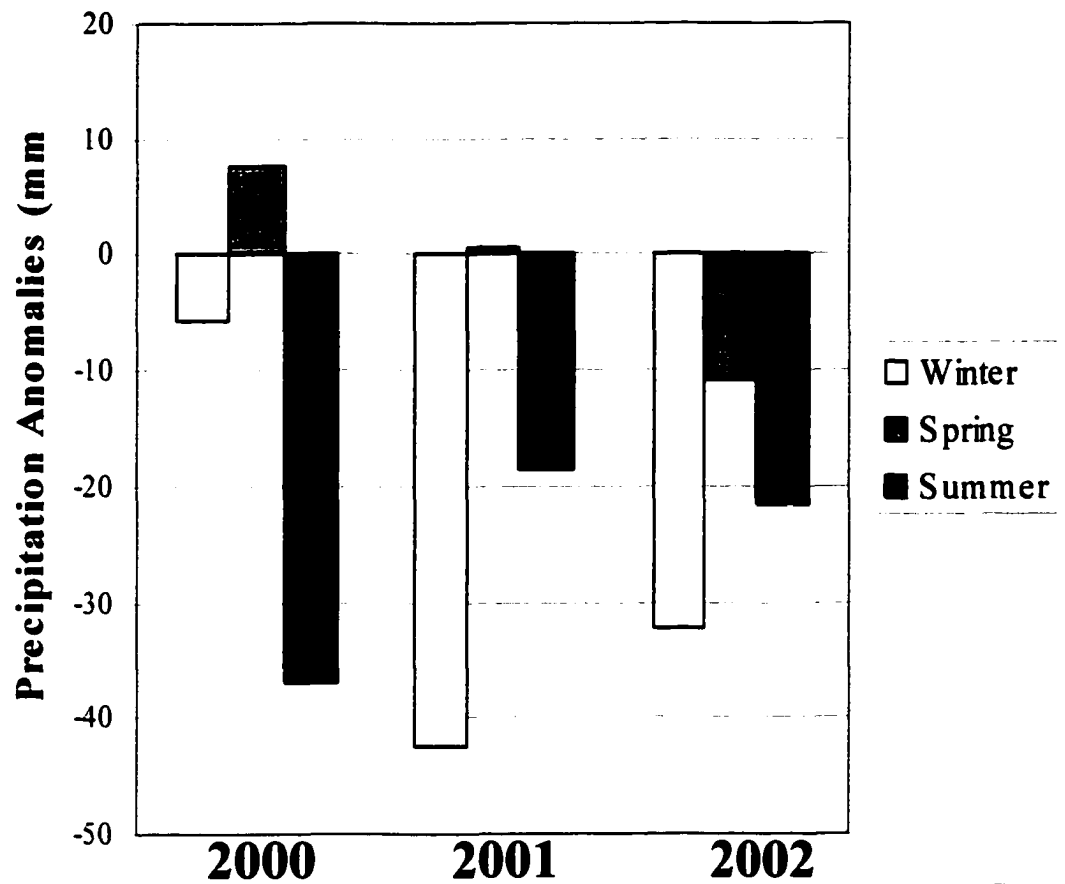


Fig. 8. .Precipitation anomalies from the normal (107 yrs record) for the Yellowstone Drainage climate division during the three years of data collection. Winter precipitation includes January, February, March; Spring includes: April, May, June; and Summer includes July and August.

CHAPTER 6

FINAL REMARKS: LOOKING FOR GENERALITIES IN CROSS BOUNDARY INVASIONS IN PROTECTED AREAS

ABSTRACT

This dissertation comprises work in two completely different ecological and cultural systems: West Yellowstone, Montana and Villarrica, Chile. However, some common trends in invasions in natural reserves and adjacent matrix were found. In this chapter I briefly summarize the major generalities observed in my dissertation research. First, in both study sites a higher density of alien species populations were found in adjacent matrix compared to park interiors. Second, in both cases landuse is a significant factor in determining the distribution of alien species, having higher susceptibility to invasion in areas with human disturbance. Third, roads or highways act as major corridors of alien species dispersal, but little percolation to interior forests is observed in road-forest edges. This dissertation delivers evidence of the increasing problem of alien species in protected areas, and illustrates the importance of adjacent matrices as sources of propagules for these invasions. The parallels observed for biogeographic regions with widely distinctive history, geology and biota suggest that these trends are general and not restricted to the unique characteristics of either study site. A multi-scale approach may provide a more powerful tool to understand these processes and their driving mechanisms than a single-scale approach. Research is needed to better understand and manage the complex invasion processes that occur in the interface of natural reserves and adjacent matrixes.

INTRODUCTION

A major priority in invasion biology is to develop ecological models to predict the dynamics of invasion processes (D'Antonio et al. 2001). This will require the evolution from a descriptive discipline to one which elucidates the mechanisms which drive invasions. Ultimately, ecologist should be able to forecast both alien species dynamics and the responses of the invaded ecosystems (Parker et al. 1999). For developing such an approach, descriptive data is fundamental to have a solid understanding of the array of factors that can affect these processes.

In this final chapter, I compare the two study sites, West Yellowstone and Villarrica, in both their general characteristics and the observed patterns of cross boundary park invasions. Using this broad comparison, I highlight the differences and generalities in alien species invasion of protected areas in these contrasting case studies.

ECOLOGICAL AND CULTURAL DIFFERENCES

In this dissertation I have collected data from invasions occurring in completely different ecosystem types. Yellowstone National Park and Villarrica National Park (and adjacent lands) differ greatly in ecological attributes and human landuse. The ecological differences can be recognized in climate, topography, geology, vegetation, biogeography and the pool of alien species (Table 1). As discussed in previous chapters, the West Yellowstone site is located in sedimentary soils, forming a flat plateau under a dry and cold climate, which allows *Pinus contorta* to dominate. On the other hand, the Chilean study site comprises areas with recent volcanic activity, abrupt topography in a wet temperate climate, dominated by closed forest of *Nothofagus* spp. Furthermore, biogeographically, West Yellowstone represents an area open to a much larger pool of species in geological time (Whitlock and Millspaugh 2001), while South Central Chile is an area with high endemism and a long history of isolation (Arroyo et al. 1995).

The type of human impact on the land varies between West Yellowstone and Villarrica both in quality and quantity. West Yellowstone has a recent history (ca. 80 years) of intense logging, grazing and transportation. Villarrica, has even a longer history of development (120 years), but no systematic activity of logging has been conducted around parks. Most logging is small scale and its related to land clearing for agricultural and wood fire production. Yet both regions are experiencing rapid expansion of human development due to tourist activities. This development have also increased commercial activities around park boundaries.

The pool and level of dispersal of alien species differs among sites. West Yellowstone has acquired most invaders from grazing pastures and dispersal through road corridors. Also the harsh climate of the area has limited alien species to grasses and herbs. Most invaders in the area are highly aggressive in grassland and open environments, but few are adapted to forest interior conditions (Ollif et al. 2001).

On the other hand, Villarrica has also have a large number of alien species originated in European introduced grasslands, but also an important number of alien species are ornamental and commercial shrubs and trees. These species are also invasive in coastal temperate regions of North America (Heckman 1999). In Villarrica, invaders can colonize from grasslands to forest interiors, and while most alien species are seral species, several species are aggressive under shaded and humid forest conditions (Chapter 2).

INVASION PATTERNS ACROSS SCALES

For practical reasons, I conducted different assessments of invasion patterns in the two study areas. (Table 2). While for West Yellowstone, I was able to conduct a multi-scale analysis and focus my research on one noxious weed as an indicator of invasion processes, for Villarrica I only conducted a landscape assessment of invasion patterns.

Species moving across the landscape

The landscape assessment in West Yellowstone was focused on the distribution of *Linaria vulgaris*, a perennial herb already invasive in Gallatin National Forest. Even though, detailed analyses have not yet been conducted with this data, I was able to show that *L. vulgaris* is abundant in disturbed and undisturbed areas of Gallatin NF and that it is being dispersed across the border of Yellowstone National Park (Chapter 4). This process is occurring both by highway corridors and by other long distance dispersal mechanisms (e.g. animal vectors), which allow the species to get into isolated pristine areas.

In Villarrica, using roadside transects I was able to show how species decrease in their richness and abundance from matrices to park interiors (Chapter 2). The most interesting result is the negative relationship between alien species richness and elevation. This relationship may imply both a causal factor (changes in microclimate) but also a combination with other factors such as landuse and distance from propagule sources.

In both cases, I was able to study alien species distribution along forest edges, however the West Yellowstone study included several edge types, while Villarrica only road-forest edges (Chapters 2 and 3). Overall, road edges in West Yellowstone appear more susceptible to invasion than Villarrica edges. This may be explained by the differences in road type: major highways for Yellowstone and gravel roads for Villarrica, and by the effect of open canopies (ca. 30% cover) in *Pinus contorta* compared to the closed canopies of *Nothofagus* forests (ca. 70% cover). A major result for West Yellowstone was the almost completely lack of alien species in forest edges in clearcuts and burned areas, which I hypothesize is related to the low propagule pressure due to the relative isolation of these areas. Interestingly, no significant relationship was found at either site between native species richness and alien species richness, relationship that has been widely discussed in the literature (Chapter 1, Shea and Chesson 2002).

Infilling of infested areas

For studying the infilling of areas already affected by an aggressive invader, I looked at several infestations of *Linaria vulgaris* in West Yellowstone. I was able to show differences in the rate of infilling due to differences in land use (riverbanks, old clearcuts and new clearcuts) (Chapter 5). Also, important annual variation was noticed during the three-year study. Overall, it appears for this species that once patches are established in a new area, local dispersal and vegetative reproduction allow it to increasingly dominate the area. However, climatic variation generates fluctuations in the rate of growth of clonal patches (Chapter 4).

Native and alien species dynamics at the clonal patch scale

By studying *Linaria vulgaris* at the clonal patch scale, I was able to corroborate the hypothesis that patches are actively expanding. Also, at this scale I could identify the reduction of overall cover of native species in patch centers and interiors. However, this effort was inconclusive in showing a decrease in species richness with *L. vulgaris* invasion. Similar to the stand scale, we found significant annual variation in both *L. vulgaris* and native species attributes. These changes appear more related to annual climate anomalies than to intrinsic population dynamics, and in some cases indicated a decrease in the species abundance and vigor. It appears that precipitation was the major factor responsible for these variations (chapter 4).

INTERPRETING RESULTS IN A LARGER CONTEXT

Given the differences between study sites I observed a few common trends in patterns of invasions in protected areas and adjacent matrixes. First, in both cases there was a greater density of alien species populations in matrices compared to park interiors. In Villarrica, this pattern was suggested by the number of species that decreased in interior roadsides. In West Yellowstone, a low density of *L. vulgaris* infestations and lower number of alien species in forest edges of Yellowstone NP compared with Gallatin NF suggested a similar pattern.

Second, roads appear as major corridors for invasions in both areas. In Villarrica, this can be seen in the results of roadsides and forest edges plots. While in Yellowstone that can be interpreted from *L. vulgaris* distribution and the high number of alien species in highway edges. Third, landuses related to human activities tend to be more susceptible to invasion, apparent in roadsides of Villarrica and the landscape distribution of *L. vulgaris* in West Yellowstone that was highly associated to clearcuts and other logged areas. Elevation, a major factor in Villarrica, was basically constant in West Yellowstone, thus limiting the possibility for comparisons using the same methodology. In the regional context, however, we know by previous research that the negative relationship between elevation and alien species richness can be found in the Northern Rockies (Forcella and Harvey 1983, Chong et al. 2001)

Trends observed at the stand and clonal patch scale were not studied in Villarrica, but they tend to confirm previous evidence in the dynamics of invasive species populations in natural areas (Cousens and Mortimer 1995). These results illustrate the local impacts and dynamics of weed populations and the effects of annual climatic variations in their dynamics. In the case study, drier years were related to lower reproductive activity and lower overall growth in clonal patches. These abnormal years also impacted the invaded community by decreasing its diversity and total cover.

FURTHER STUDIES

One of the major contributions of this research is to provide evidence of the movement of alien species into natural reserves from adjacent matrices and to do this with study sites in two contrasting continents. However, the methods applied in both areas were different, limiting the power to establish generalities. I recommend that the roadside method used in the Villarrica study be applied to other protected areas around the region and worldwide. This method is fairly simple and does not require intensive use of personnel. While, it has limitations by only studying

disturbed environments (roadsides), it provides a extensive understanding of the potential for invasion of natural reserves given climatic and dispersal constraints. Based on this simple method, comparisons could be made among protected areas and their surrounding matrixes even when other factors remain uncontrolled (e.g. topography, biome).

Individual species studies such as the one conducted for *Linaria vulgaris* remain a powerful tool to understand the dynamics of invasion, even though their scope is limited to specific species and systems (Mack 2000). These studies may help to understand specific mechanisms by which an alien species become an invader and is able to trespass boundaries of natural reserves. Mechanisms of dispersal may be easily understood by looking at individual species than by trying to capture the whole array of alien species. Also, individual species studies may help to understand the impacts of alien species over native species, by simplifying the study systems.

The use of multi-scale methods may also help to answer some of the questions addressed here. The critical importance of scale in determining the mechanism involved in ecological processes has been recently emphasized. Hierarchy theory offers new tools to understand complex ecological processes, and has already has been used to model biological diversity. However, studies on invasive species have only superficially explored the advantages of multiple scale approaches. Unique insights may be obtained regarding both the biology of the invader and the interaction with the invaded community.

My research opens new questions in the search for generalities about invasive species moving across the complex landscapes created by the interface of natural reserves and adjacent matrixes. Nonetheless, I was able to demonstrate the importance of studying invasions considering the larger landscape ecological units where they occur and capturing ecological processes that are not limited by administrative boundaries. Furthermore, invasion of alien species is only one of the multitude of processes that affect natural reserves, whose influence over the ecosystem can be better understood or managed when analyzed within the landscape context.

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Table 1. Summary table showing administrative, climatic and biological characteristics for both study sites: West Yellowstone and Villarrica.

Attributes	West Yellowstone	Villarrica
Location	44 th and 45 th North	39°18' and 39°38' S
(latitude and longitude)	110 th and 111 th West	71°27' and 72°01' W
Area under protection	898,349 ha (Yellowstone NP)	61.000 ha (Villarrica (NP)
Elevation	1895 – 3900 m	500-2800 m
Climate	Cold and dry temperate (500 mm precipitation)	Humid temperate (2000 mm precipitation)
Soils	Rhyolitic volcanic rocks and andesitic volcanic rocks	Andesitic volcanic soils
Vegetation	Evergreen coniferous forests (<i>Pinus contorta</i>), shrublands and grasslands	Evergreen and deciduous broadleaf forests (<i>Nothofagus spp- Araucaria araucana</i>) and alpine vegetation.
Disturbance regime	Fire, windthrows, landslides	Human induced fire, volcanic activity, windthrows, landslides
Exotic plant species	170 species	ca. 60 species
Number of visitors	ca. 4 Million /yr	Not available data
Year of designation as protected area	1872	1926
Social importance	Very high in the US and worldwide	High in Chile, some international value

Table 2. Comparison of results between the two study sites by scale.

Scale	West Yellowstone	Villarica
Landscape scale	<p>Distribution of <i>Linaria vulgaris</i> is related to land use, more abundant and invasive in the matrix but cross park boundaries</p> <p>Forest edges are barely susceptible to invasion, but overall only highway edges have a significant number and abundance of alien species</p>	<p>The number of alien species is related to elevation and land-use, more abundant in the matrices but still they get to park interiors</p> <p>Forest edges are not susceptible to percolation of alien, all species in all types tend to stay along roadsides</p>
Stand scale	Establish infestations of <i>L. vulgaris</i> ten to infill the areas, by growing vegetatively (patch growth) and by establishing new patches within the infestation.	
Clonal patch scale	<p>Density and other attributes of <i>L. vulgaris</i> increase toward patch centers, while native abundance and diversity tend to decrease.</p> <p><i>L. vulgaris</i> populations show high annual variation in their reproduction and growth.</p>	