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 compromises 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 histoy (ca. 80 years) of intense logging, grazing and transportation. Villarrica, has even a longer history of development (120 years), but no systematically 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 11 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	Villarrica
Landscape scale	Distribution of <i>Linaria vulgaris</i> is related to land use, more abundant and invasive in the matrix but cross park boundaries	The number of alien species is related to elevation and land- use, more abundant in the matrices but still they get to park interiors
	Forest edges are barely susceptible to invasion, but overall only highway edges have a significant number and abundance of alien species	Forest edges are not susceptible to percolation of alien, all species in all types tend to stay along roadsides
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	Density and other attributes of <i>L. vulgaris</i> increase toward patch centers, while native abundance and diversity tend to decrease.	
	L. vulgaris populations show high annual variation in their reproduction and growth.	