CHAPTER 1

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 ecologist's 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 km^2 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 hervivory has not prompted invasion (e.g. Stohlgreen et al. 1999b), however, most studies have shown that invasive species are favored by heavy hervibory (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 (*Elaegnus 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 INVADED 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 (1m^2 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 cm^2 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 cm^2 where he manipulated diversity and added seed of three invasive plants. Stohlgren et al (1999), looking at natural communities in a 1 m^2 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 m^2), 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 CO_2 concentration is also a potential factor for community invasibility, especially in the certainty that atmospheric CO_2 concentrations have continuously risen during the last century. Increases in CO_2 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 CO_2 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 CO_2 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 hervibory 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 CO_2 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

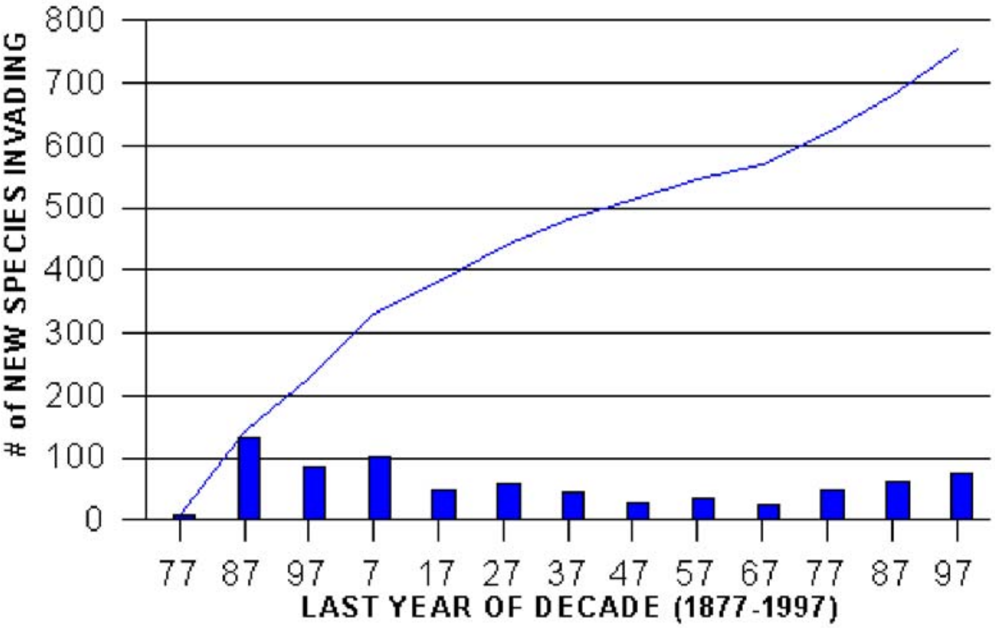

Fig. 1. New introductions of alien species by decades in five Northwest States in the United States. Bars indicate numbers per decade and the line indicate cumulative numbers. Taken with permission from Rice (2002).