

Integrating the study of non-native plant invasions across spatial scales

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Abstract

Non-native (alien, exotic) plant invasions are affecting ecological processes and threatening biodiversity worldwide. Patterns of plant invasions, and the ecological processes which generate these patterns, vary across spatial scales. Thus, consideration of spatial scale may help to illuminate the mechanisms driving biological invasions, and offer insight into potential management strategies. We review the processes driving movement of non-native plants to new locations, and the patterns and processes at the new locations, as they are variously affected by spatial scale. Dispersal is greatly influenced by scale, with different mechanisms controlling global, regional and local dispersal. Patterns of invasion are rarely documented across multiple spatial scales, but research using multi-scale approaches has generated interesting new insights into the invasion process. The ecological effects of plant invasions are also scale-dependent, ranging from altered local community diversity and homogenization of the global flora, to modified biogeochemical cycles and disturbance regimes at regional or global scales. Therefore, the study and control of invasions would benefit from documenting invasion processes at multiple scales.

Introduction

One of the great challenges facing ecology is to understand the interaction of scale and ecological processes, explicitly recognizing the spatiotemporal context of natural phenomena (Allen and Starr 1982; Levin 1992; O'Neill and King 1998; Thompson et al. 2001; Willis and Whittaker 2001). Scale not only influences the patterns that we observe; ecological processes and mechanisms also differ at different spatial scales. The underlying cause of these scale-dependent relationships is that environmental heterogeneity changes across scales (Milne 1991), defining which processes dominate as the scale of observation changes (Levin 1992).

Non-native plant invasion patterns and processes show scale-dependent properties (Table 1).

Several sequential stages occur in plant invasions: movement to the new location and establishment at the new location are essential for an invasion to occur; spread and impact follow in many cases (Williamson 1999; Richardson et al. 2000). At any of these stages, from seed dispersal to production of new propagules, non-native plants face diverse ecological constraints that are scale-dependent.

A comprehensive approach to capturing the dynamic process of non-native invasion across multiple spatial scales may contribute to our understanding of its ecological causes and effects, and help us to identify more efficient and effective control strategies (Mack 2000; Pauchard et al. 2003). However, most studies of invasions have focused on only one spatial setting.

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

Element/scale	Global	Regional-landscape	Local
Dispersal	Intercontinental introductions	Range expansion, source-sink flows	Infilling of infected areas, patch expansion
Pattern: e.g. relation to diversity	Decrease in global diversity (homogenization)	Increases in regional species richness	Decreases or increases in diversity, depending on local extinction
Study and monitoring	Species lists, voucher specimens, first records. Search for "expected" non-natives	Georeference new invaded areas and monitor shifts (e.g. counties, other political boundaries). Determine infection centers, corridors and new patches, investigate changes in biochemical and disturbance cycles	Determine changes in plant communities, conduct population studies, including control, disease and insect interactions
Impacts	Homogenization of the 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
Control	Limit new introductions, international trade oversight. Early detection and rapid response	Concentrate efforts on rapid expansion fronts, watch lists. Adapt human uses to diminish the expansion of invaders	Direct control over non-native populations. Control new foci and local dispersal mechanisms

Recently, with the increasing interest in landscape ecology and long-term studies, researchers are trying to better describe and explain the process and implications of plant invasion across a range of scales. The studies that have addressed the importance of scale in biological invasions (e.g. DeFerrari and Naiman 1994; Levine and D'Antonio 1999; Stohlgren et al. 1999; Pauchard et al. 2003; Sax and Gaines 2003; Allen and Shea, this issue) have generated exciting and initially unexpected results that corroborate the existence of emergent properties of invasions.

In this paper, we discuss how spatial issues affect movement of organisms to a new location, and how they affect patterns and processes at the new location. In the case of dispersal, we can focus almost exclusively on the mechanisms involved, as that is what is most easily observed and traceable. When we consider the invader in its new environment, however, we usually have more information on patterns rather than mechanisms, and must delve more deeply to infer the underlying processes. As observed patterns of invasion in an environment depend both on dispersal to that location and on processes specific to the location itself, untangling the underlying processes is a significant challenge.

We then discuss how the type and relative importance of invasion impacts change across scales. The emergent properties of invasion impacts makes it necessary to adopt a multi-scale approach when assessing the risk posed by plant invasions to local and global biodiversity. In addition, we discuss how management of these invasions may be more efficient and successful if we can target key processes at different scales using a holistic approach rather than single-scaled and localized initiatives. Finally, we discuss some suggestions for future research, in order to take advantage of multi-scale approaches both for theoretical and practical purposes.

Dispersal mechanisms of non-native plants at different spatial scales

Dispersal is the process of movement of organisms between locations, and plant species exhibit a stunning array of adaptations for dispersal (Ridley 1930; van der Pijl 1982). Dispersal is now recognized as one of the most important processes determining invasion success, mainly because evidence suggests that limited propagule pressure may be one of the most significant

bottlenecks in the invasion process (D'Antonio et al. 2001).

Non-native plant species move into new environments with a wide set of scale-dependent dispersal mechanisms, from global dispersal, often human-mediated, to local short distance dispersal, by mostly natural mechanisms such as wind or animals (Nathan and Muller-Landau 2000). However, the ultimate result of dispersal at any scale is basically the same; propagules arrive in a new environment where a new population may establish. The success of a non-native plant is greatly constrained by dispersal at each of the scales at which this phenomenon occurs, from the local to the global scale. Recent definitions suggest that the major difference between non-natives and their native counterparts resides in the requirement for at least one human-caused (accidental or intentional) long distance dispersal event that goes beyond the natural range of their distribution (Hodkinson and Thompson 1997; Richardson et al. 2000; McNeely et al. 2001; Pyšek et al. 2004).

Global long distance dispersal

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 caught ecologists' attention as a quantifiable natural process of long distance dispersal, and a natural experiment to improve the understanding of dispersal. For example, the successful dispersal and establishment of one plant every 7900 years would explain the accumulation of species in the Galapagos Islands flora; and for the Hawaiian Islands one successful event every 20,000–30,000 years would be required (see review in Fenner 1985). Under natural conditions, most long distance dispersal is mediated by birds (internal and external transport), as well as ocean drift and wind dispersal. Transoceanic and continental global dispersal are highly constrained by physical and biological barriers, which have contributed to an increase in overall global biodiversity by allowing the evolution of unique floras and faunas in isolated regions of the world.

Natural and human global non-native plant dispersal processes differ in rate, intensity, mech-

anisms and scale. Human dispersal mechanisms of non-native species at a global scale are much more frequent, efficient and effective than natural mechanisms (Mack et al. 2000). Though humans have served as dispersal vectors for non-native plants since the first human migrations and the beginning of agriculture and livestock domestication, the rate and distances of long-distance dispersal have increased greatly with the intervention of modern humans (Hodkinson and Thompson 1997; Mack et al. 2000; Mack and Lonsdale 2001; Rossman 2001).

The arrival of Europeans in the Americas created a new scenario for both deliberate and accidental non-native plant invasion. Along with crop seed, came a number of non-native species capable of colonizing this geologically isolated continent. In the last 200–500 years, a significant number of species have been introduced, deliberately or accidentally, to the Americas. Species from the Americas have also become naturalized in Europe, Africa and Asia (Williamson and Fitter 1996). However, Eurasia is recognized as the main source of non-native species for all other continents. With only 4.4% of the total flora of the world, Eurasia contributes with 58.9% of naturalized non-native species (Pyšek 1998). This is partly attributable to human efforts, as Europeans transported domesticated plants and their associated weeds all over the globe, but also may indicate a competitive advantage of European species in disturbed environments (Sax and Brown 2000).

The continuous propagule flow of vascular plants across countries and continents has no parallel in evolutionary history and contributes greatly to the homogenization of the global flora (McKinney and Lockwood 1999; Mack et al. 2000). The number of propagules of new species that are introduced (both how often and how many) drives non-native success; the larger the number of propagules, the higher the probability a species will establish (Veltman et al. 1996; Memmott et al. 1998; Shea and Possingham 2000; D'Antonio et al. 2001; Kolar and Lodge 2001).

Regional long distance dispersal

Once a population of a non-native plant species is established in a new continent or region, regional

dispersal mechanisms come into play, allowing the species to expand its 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 recorded in the United States in 1859 in Pennsylvania (Novak and Mack 2001). Additionally, it had presumably entered through multiple ports on the West Coast by 1875. By 1930, *B. tectorum* had already reached its limits in the western United States. Using genetic markers, Novak and Mack (2001) found that *B. tectorum* populations are the result of various introductions and consequent complex pattern of terrestrial transport of seeds, from both the east and the west coasts across the continent.

The invasion of *B. tectorum* shows how regional long distance non-native plant dispersal is driven by different mechanisms than global dispersal. In regional dispersal, humans continue to be a main dispersal agent, but the complexity of dispersal pathways increases with landscape heterogeneity and the interaction of natural processes and the new invader. At the regional scale, propagule movement tends to follow landscape corridors such as roads and rivers, a process that is intensified by human mobility (Hodkinson and Thompson 1997; Parendes and Jones 2000; Trombulak and Frissell 2000; Pauchard and Alaback 2004). In addition, other natural factors such as wind and wild animals may differentially enhance dispersal success (e.g. Parendes and Jones 2000).

Another well-studied example of regional dispersal 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 (Zavaleta 2000). Once established, *Tamarix* can disperse downstream and, in disturbed flood regimes such as reservoirs and dams, may even disperse upstream, affecting the integrity of riparian habitats (Lesica and Miles 2001).

Local dispersal mechanisms

For a new population to establish, at least one individual must succeed in completing its life

cycle (Richardson et al. 2000). Short distance dispersal of this individuals' propagules is the initial stage in the development of a new population. At the local scale, dispersal mechanisms are highly influenced by the interaction with the new environment. In most cases, humans are not the primary agent of short distance dispersal, but they can modify the abiotic and biotic conditions enhancing invaders dispersal and the environmental conditions for survival. The intensity and frequency of propagules reaching new habitat is higher primarily because the propagule source is closer to the invadable habitat (Nathan and Muller-Landau 2000). This is the case for most non-native plant infestations, which after an initial introduction increase their density and extent by short distance dispersal of the propagules generated in the nucleus population (Sakai et al. 2001).

Non-native plant species, as their native counterparts, 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). Wind dispersal tends to dominate invasive dispersal mechanisms because most invasive plants have evolved in early successional habitats, where animals are scarce and a large amount of seed is required to rapidly colonize the disturbed environments (Sax and Brown 2000).

Asexual reproduction is another common and successful mechanism of local dispersal for invasive plants (Bazzaz 1996; Kolar and Lodge 2001). A large proportion of noxious invaders have asexual reproduction, a strategy that increases the chance of long-term survival for the new population even under harsh conditions (e.g. *Linaria vulgaris* in Pauchard et al. 2003).

Each of the scales at which invasion occurs is crucial for invasion success (Table 1). The failure of a dispersal mechanism at short, long or global scales may prevent a species from becoming invasive in a given environment. However, the three spatial scales of dispersal discussed above clearly do not have well-defined boundaries. In fact, any given dispersal event may comprise a series of different processes, and movement over different scales. This idea is well encapsulated by the concept of stratified dispersal (Shigesada et al. 1995; Shigesada and Kawasaki 1997). Where smaller

scale processes dominate, an invader will spread out from the source like a wave. Such movement can be modeled using diffusion models (e.g. Skellam 1951; Okubo 1980) and may be measured using relatively straightforward techniques (Greene and Calogeropoulos 2002). However, the same invader may also undergo occasional long distance dispersal events, which start new sources. Successful long-distance dispersal events are much harder to quantify (Nathan et al. 2003). The main infestation spreads like a wave across space, but later infestations coalesce with each other and the main wave front, so that the spread is less smooth than the simple spatial spread models would predict.

*Dispersal processes across spatial scales:
non-native plants in protected areas*

Invasions into protected areas illustrate the importance of multiple scales in the dispersal process. For a non-native 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 non-native species usually are naturalized in adjacent heavily disturbed areas under human land use types (DeFerrari and Naiman 1994; Pauchard et al. 2003; Pauchard and Alaback 2004). For example, many species in the northwest of the United States were introduced into agricultural or urban landscapes in the late 1800s and early 1900s (Toney et al. 1998). However, these species have taken longer to establish in parks and reserves due to their relative isolation at the regional scale.

An interesting example of how multi-scale processes drive the invasion of a natural area is the case of *Linaria vulgaris* (yellow toadflax), a perennial noxious weed, that was first recorded in the Pacific Northwest of the US in 1880 (Saner et al. 1995; Rice 2003). After its introduction, the species quickly advanced into inland counties (Figure 1). By 1950, the species had already reached the Rocky Mountains. In the present day, *Linaria* has expanded its distribution to most counties in the Pacific Northwest and it appears that there is no physical or biological constraint to limit its expansion. In the area of

West Yellowstone, near Yellowstone National Park, the species invades mostly disturbed soils and areas adjacent to roads (Pauchard et al. 2003). Its aggregated pattern, at the landscape scale, indicates that limited propagule dispersal influences its spread into less disturbed or less accessible areas. However, at the stand scale, *L. vulgaris* patches in clearcuts tend to be randomly distributed in advanced infestations, while in recent infestations it shows a cluster distribution (Pauchard et al. 2003). At finer scales, it is possible to detect that the cover of *L. vulgaris* increases significantly towards the center of the patch, while the cover of other plants significantly decreases (Pauchard et al. 2003).

In the case of *L. vulgaris* there is a clear relationship between spatial scale and temporal scale of invasion processes. Broad scale processes such as regional dispersal have occurred over more than a century, while landscape and stand scale changes are visible only after decades. At fine scales, such as the clonal patch, these changes occur over years. Looking at this broad range of scales helps our understanding of the invasion and its causal factors much better than would a single scale approach. Impact assessment and control of the species can, using this multi-scale approach, be much improved.

A similar phenomenon occurs in reserves of southern Chile, where non-native species inside reserves are a sub-sample of those located in the surrounding matrix (Pauchard and Alaback 2004). In rare cases, where a large number of long distance visitors enter a reserve, they also may act as vectors of intercontinental dispersal. This new wave of invasions may bring species that are absent from the disturbed matrix around the reserve.

The invasion of reserves is also constrained by relatively lower human transportation and disturbance, diminishing the chances of successful establishment. However, the presence of other dispersal agents such as large herbivores (domestic or wild) may increase the rate of successful introductions, by acting as major seed vectors that move freely across the landscape. Lesica and Ahlenslager (1993) found a significant correlation, for the period of 1910–1990, between the increase in the number of visitors and the

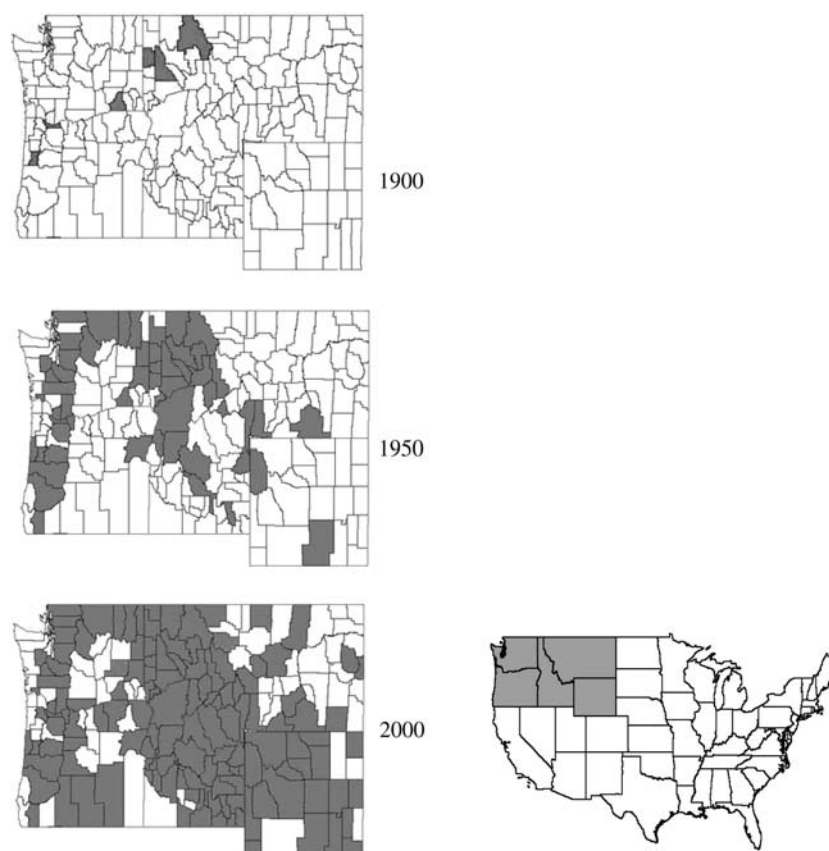


Figure 1. Presence of *Linaria vulgaris* by county (in gray) in the states of Washington, Oregon, Idaho, Montana and Wyoming. Series shows years 1900, 1950 and 2000. (Reproduced with permission from Rice 2003, <http://www.invader.dbs.umt.edu>.)

number of non-native species recorded 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 non-native species and the number of visitors, even after correcting for park size. This relationship does not necessarily imply causality. Increasing visitor numbers are also related to increased development of surrounding areas and increasing overall human activities inside the reserve (Liu et al. 2001). On the other hand, for 77 protected areas in the United States, McKinney (2002) found that visitation was not a significant variable in explaining non-native species richness; instead, native species richness and historical use were significant predictors. Similarly, in New Zealand the number of non-native weeds in reserves is related to proximity to propagule sources such as towns, road and railroads, human

use, reserve shape and habitat diversity (Timmins and Williams 1991).

A species established in a reserve does not necessarily become a major problem; local scale dispersal barriers and biotic and abiotic conditions may limit the invasion. For example, in Yellowstone National Park, most non-native species that invade adjacent lands are able to cross the park boundary and establish on roadsides and other disturbed areas. However, only a few become abundant or invade more pristine environments, at least in the short term (Olliff et al. 2001; Pauchard et al. 2003). Long-term invasion success in natural environments is difficult to predict and may depend heavily upon propagule production, genetic adaptations to the new environment and how the species is able to use niche opportunities in the new environment (Sakai et al. 2001; Lee 2002; Shea and Chesson 2002).

Invaders in their new environment: spatial scale

Once an invader has reached a new environment, its success will depend on how it responds to the niche opportunities available (Shea and Chesson 2002). That is, invasion success depends on how the invader, with its specific characteristics, responds to the resource opportunities, natural enemy escape opportunities and the physical environment in the new community (Shea and Chesson 2002).

All of these components vary in space and, indeed, may vary differently at different spatial scales. For example, resource competition between plants tends to occur at local spatial scales, while apparent competition (competition for enemy free space) may occur at larger spatial scales, relevant to the movement of the natural enemies in question. In such situations, both processes could contribute to observed patterns of non-natives. Furthermore, the resolution at which patterns are documented will affect the conclusions that can be drawn. For example, *Carduus* thistles are present in Pennsylvania and all surrounding states, yet studies at finer resolution show distinct within-species aggregation patterns at smaller scales that are completely obscured by larger scale records (Allen and Shea this issue; see also Table 1).

In this section, we consider the importance of spatial scale in determining the outcome of a non-native plant invasion in relation to niche opportunities in the invaded community.

The relationship between native and exotic diversity at different spatial scales

The pattern of native and exotic species richness is currently an exciting and rapidly moving area of research (Shea and Chesson 2002; Espinosa-García et al. 2004). 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), and has been supported by models and small-scale experiments (Knops et al. 1999; Stachowicz et al. 1999; Naeem et al. 2000). For example, Tilman (1997),

using experimental manipulations in grasslands, found that communities with higher species richness were more resistant to invasion (1 m² 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).

In contrast, larger scale studies have shown that more exotic species occur in more diverse communities (Lonsdale 1999; Stohlgren et al. 1999, 2003; Stadler et al. 2000; Sax 2002; Deutschewitz et al. 2003; Espinosa-García et al. 2004). 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. Similar results have been found by Brown and Peet (2003). At a larger regional scale, Stohlgren et al. (2003) found that the most diverse sites in terms of vascular plants, in the United States, contain the richest sets of non-native species, contradicting the common notion that hotspots of diversity are less susceptible to invasion. Deutschewitz et al. (2003) found that both non-native and native species richness increase with temporal and spatial heterogeneity at the regional scale in Germany.

Shea and Chesson (2002) discuss a possible explanation for the changes in responses of non-native diversity to native diversity across scales. A negative pattern of non-native richness as a function of native diversity may be 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 non-native and native diversity. At these larger scales, extrinsic factors vary and those factors that favor native diversity also favor non-native diversity (e.g. latitudinal and elevation climate variation).

This hypothesis has recently been supported by a study of competition models in which differences in resources (niche opportunities) between communities generates such a pattern of negative correlations at small scales and positive correlations at larger scales (Byers and Noonburg 2003). In the same vein, 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. Thus, if an area receives more invader propagules per unit area, it may be more invaded just because invaders have had more opportunity to invade. Such patterns may explain higher exotic diversity in popular protected areas, where visitors bring in a higher pressure of invaders (Lonsdale 1999).

An important component of this idea relates to the role played by spatial and/or temporal variation in resource (Davis et al. 2000; Shea and Chesson 2002) and natural enemy escape opportunities (Shea and Chesson 2002). Davies et al. (in press) studying a grassland data set in California, found the same pattern of a negative relationship between exotic and native diversity at small spatial scales with a positive relationship at larger spatial scales. However, a detailed analysis of the data suggests that, rather than extrinsic conditions per se driving the pattern, it is in fact heterogeneity or variation in extrinsic conditions that is responsible for the outcome. In this system at least, resource heterogeneity drives this pattern. Such ideas again come back to the role of niche differentiation, as in the case of the empty niche hypothesis (Simberloff 1995) or with limiting similarity (MacArthur and Levins 1967). In communities with high heterogeneity, there may be more unused niche opportunities for a given resident species richness. Thus, both average factors and the variance in those factors may play a role in determining observed covariance patterns between native and non-native diversity, with one or other aspect dominating under different circumstances (Davies et al. 2005). This is certainly an exciting avenue for future research.

Disturbance and scale

Given the importance of both mean extrinsic conditions and variation in extrinsic conditions at different spatial scales to patterns of invaders in native communities, processes which suddenly release nutrients or remove competitors or natural enemies are an important component of invasion ecology. Such events are usually studied under the general heading of “disturbance”.

Disturbances can be characterized by their type, intensity, extent, frequency and duration (Shea et al. 2004). Several of these characteristics have scale-dependent properties. The most obvious is the extent of a disturbance. Certain disturbances only modify conditions on a very local scale (e.g. rodent burrows), while others have effects on the stand scale (e.g. windthrows, clearcuts) and yet others over large landscape or regions (e.g. fire, volcanic eruptions, hurricanes). Large-scale disturbances modify niche opportunities over a wider area and generally have a greater effect on ecosystem processes than small-scale disturbances (Foster et al. 1998). With limited dispersal, new organisms may not reach portions of the large disturbed areas for some time, and the slower recovery rate of the ecosystem also opens a wider temporal window for non-native plants (e.g. Foster et al. 1998). As species are increasingly moved around (for example by humans) long distance dispersal is effectively increased. Thus, recolonization following a fire comes not only from the regional species pool, but also from further afield (Hobbs and Huenneke 1992). The extent of disturbances also influences the array of non-native species that are able to colonize an area. Pioneer species, which account for most non-native invaders, perform best in areas without competition and with high resource availability (Sax and Brown 2000). However, late successional species can invade areas via small-scale disturbances like forest openings (e.g. *Hedera helix*; Reichard 2000).

Despite the non-spatial nature of disturbance frequency, if there is an interaction between frequency and extent, spatial scale issues may arise. Larger scale disturbances tend to be more intense and less frequent than smaller scale disturbances. Ultimately, disturbance attributes interact with each other, modifying the biotic and abiotic

conditions for non-native plant invasions. The specific spatial and temporal scale of each disturbance creates a unique set of conditions that may favor a particular set of non-native species.

Impacts of invasions: from local to global scales

Biological invasions are considered a major threat to biodiversity (Sala et al. 2000), affecting ecological processes from the local-scale to the global-scale (Table 1). The impact of a non-native plant depends on its range, abundance and effect, all of which will change with the scale at which they are measured (Parker et al. 1999). For plant invasions, changes in species richness can be summarized across scales as increases in local diversity due to the arrival of new species, and decreases at the global scale by homogenization of the biota (Sax and Gaines 2003). However, at the local scale, over-dominance of a non-native species may produce local extinctions and the subsequent reduction in species richness.

Small-scale impacts are related to changes in native plant population dynamics, community structure and diversity (Parker et al. 1999; Mack et al. 2000). Changes in the diversity of invaded communities have been widely reported. However, in most field ecology studies where manipulation and prior monitoring are absent, it is difficult to isolate whether lower diversity is an invasion effect or a factor promoting invasion. 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 non-native species. Similar results were found for Californian serpentine grassland, where invasive annual grasses displace native forbs in fertilized plots (Huenneke et al. 1990).

At local scales, the demand for resources by non-native plants limits the resources available for the native species, reducing the growth, reproductive outcome and population size of native species (Davis 2003). For instance, *Centaurea maculosa*, an aggressive weed of the northwestern United States, reduces *Festuca idahoensis* seed production and root and shoot growth (Callaway et al. 1999).

The ecological effects of invasions may include the restriction of native populations to small areas of undisturbed environments, where their ecological function will be badly affected (McKinney and Lockwood 1999). However, differences in the set of non-native plants that invade a region may have a differentiating effect on their community composition, especially for areas with few non-native plants (McKinney 2004). This may reflect an early stage of the process where most invasive plants have not yet arrived at all localities, so that non-native species occurrence is a differentiating factor rather than a homogenizing factor. This may reverse rapidly with increased anthropogenic transport and disturbance.

Large-scale changes in ecosystem processes are induced by non-native species that become invasive (defined by Pyšek et al. 2004). Initial changes in vegetation diversity and structure produced by invaders may directly or indirectly alter ecosystem structure, disturbance regimes and biogeochemical cycles (Mack and D'Antonio 1998; Parker et al. 1999; Mack et al. 2000). 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 non-native tree has replaced cypress, sawgrass and other native species, degrading habitat for native animals, using higher amounts of water and intensifying the fire regime. Other similar cases include *Mimosa pigra* in Australia, *Chromolaena odorata* in Asia and Africa, and *Lantana camara* in East Africa (Mack et al. 2000). Impacts of invasive species on 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 has increased fire frequency and intensity, and eventually may cause the conversion of tropical forest into a savanna-like ecosystem (D'Antonio and Vitousek 1992). Non-natives may even impact processes outside the area they invade, for example if invaders change riparian habitat dynamics by increasing runoff erosion or stabilizing disturbed substrates, thus modifying geomorphological disturbances (D'Antonio et al. 1999).

At the global scale, species area curves have been used to model the effects of cross continental dispersal by humans and the homogenization of the global biota. Vitousek et al. (1997) projected that reduction in dispersal barriers would significantly reduce world species richness. However, it may be difficult to accurately predict such changes using existing data collected at the smaller scales of modern continents (Collins et al. 2002).

The economic cost of non-native plant invasions is hard to estimate as most studies tend to focus on a single species at very localized scales. However, Pimentel et al. (2000) estimated that, for the United States, non-native plants are responsible for \$26.5 billion in damage and control of crops weeds and \$6 billion more in weeds in pastures. Additionally, \$100 million of costs are estimated for aquatic weed control (Pimentel et al. 2000). Nonetheless, in estimating the cost of plant invasions, precautions should be taking to avoid scaling up the results of local studies without considering the heterogeneity at multiple scales. A focus on areas with high concentrations of invaders may lead to over-estimation of the economic impacts of non-native invaders, particularly if native weeds are not explicitly excluded.

The challenge for ecologists and managers is to determine the variation in ecological and economic impacts over space and time and to predict, based on that variation, the overall effects of non-native invasions (Parker et al. 1999). Small scale studies may miss spatio-temporal variation; therefore, more large-scale studies are needed. However, large scale studies alone may be confounded by spatial or temporal gradients. Integrated multi-scale studies may reduce this uncertainty by providing a more complete picture of the invasion. Ultimately, the effects of an invader should be judged by the degree to which it 'changes the rules of the game' (Vitousek 1990). Defining which species are affecting ecological functions, and how they are doing it, will be critical to prioritizing control efforts (Byers et al. 2002). As society increasingly values biodiversity and realizes the impacts of non-native species, 'more sophisticated and science based information on the ecological impacts of invaders should play a

greater and greater role in practical decision-making' (Parker et al. 1999).

Implications for management of invasives at different spatial scales

Controlling invasive species requires an understanding of the mechanisms underlying invasion. A multi-scale approach may improve the effectiveness and efficiency of the management of non-native plant invaders by, for example, identifying and targeting the driving processes that contribute to the success of the invader. Single scale approaches may provide only a limited set of management actions, where a multi-scale approach may more closely tailor a management response to the scale that dominates. Thus, a multi-scale approach may help to identify and target the limiting processes or the "Achilles heel" for a given invasion.

Most strategies for controlling invaders in natural or semi-natural areas have been developed at the stand scale (e.g. herbicides, hand pulling) to limit the impacts of the invaders on native communities and to diminish the potential propagule sources. However, increasing awareness of the complexity of invasion processes has resulted in the development of initiatives at larger scales such as the landscape (e.g. weed free hay, clean boots, clean wheels) and global scales (e.g. limitations on the imports of the horticulture industry, a focus on local rather than non-native natural enemies for biological control, voluntary limitation to new introductions). For example, the implementation and use of a global database on invasiveness of non-native species would improve both the risk assessment for new inter-continental introductions and the management strategies at the local scale for already existing populations (White and Schwarz 1998; Ricciardi et al. 2000). Comprehensive multi-scale schemes for controlling invasive species are especially useful when dealing with new species. In such cases, global scale efforts are as important as local control initiatives in the process of early detection and confinement of new populations (see White and Schwarz 1998).

Looking at broader scales may help to identify the factors responsible for a specific invasion

scenario. For example, two national parks may have similar patterns of invasion. In this hypothetical example, in one of the parks invasion has occurred because of intense propagule pressure from nearby nurseries (a dispersal problem) while in the other, large fires have disturbed and opened areas up to the invasion of non-native species better adapted to fire than native species (creation of niche opportunities). The outcome in both situations is similar. However, looking at the phenomena beyond the local scale (park boundaries), it is possible to determine that the two invasion processes differ in the causal mechanism. Effective control will require unique solutions for each case.

The goal should be to implement management strategies based on the integration of the multiple scales or to identify and target the most appropriate scale for a specific problem. An illuminating example of such tailored management strategies is the work by Moore and Possingham (lamentably unpublished, but discussed in Shea et al. 2002) which asks whether it is better to use limited resources to either (i) reduce the number of new propagules issuing from a major infestation of a new weed or (ii) to stamp out new small infestations of the weed. The optimal management strategy depends on the life history of the species in question. Species with high, longer distance dispersal are more likely to be controlled with a focus on the source of propagules than on new outbreaks. Destruction of new, isolated populations is more likely to be effective for species that spread more slowly. Further exploration of such rules of thumb for the appropriate spatial scale of control would be incredibly useful.

The magnitude of non-native plant invasions in natural ecosystems is not only related to the processes occurring in the specific area, but is also greatly influenced by the broader scale processes of propagule flow and human-induced changes in the adjacent landscape. Therefore, acting only by controlling the populations of non-native plants will not have a sustainable effect in diminishing the threat posed by plant invasions. On the other hand, holistic approaches that intend to understand the invasion process in a multi-scale setting may be more efficient and have a more lasting effect on the protection of native diversity.

The next step: understanding invasions across scales

To enhance our understanding of the mechanisms of non-native 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 integrating our understanding of invasion processes over a range of scales. This is not a simple matter of scaling up, because most processes controlling invasion are scale-dependent (Levin 1992). Processes at one scale tend to generate patterns at another; to explain large scale patterns may require studies at smaller scales, or small scale patterns may be constrained by larger scale factors (Levin 1992). Therefore, spatial ecology may provide the tools to capture patterns and processes over multiple scales and the conceptual framework within which to analyze the results. Without sufficient knowledge of invasion-driven processes at different scales it is difficult to understand, and therefore manage, plant invasions. Assessing invasion at multiple scales may help to better understand the dynamics of invasion and its implications for ecosystem processes.

Ideally, researchers could study a range of scales, which should be broad enough to generate insight about underlying mechanisms. This multi-scale approach would require scale-specific research methods and techniques (Bullock et al. 2002; see, for example, Pauchard et al 2003; Allen and Shea 2006), which can be awkward to implement. However, methodological complications may be resolved by cooperation among researchers with expertise in such a range of scales. Techniques for working at larger scales are rapidly being developed (for example, Geographic Information Systems (GIS)), and an increasing number of databases are available to explore larger spatial contexts. Herbarium databases, county records and floristic lists may provide a useful source of information about large scale patterns of non-native species (e.g. Stohlgren et al. 2006; Pyšek 1998; Toney et al. 1998; McKinney 2002; Pyšek et al. 2004; Pauchard et al. 2004).

Probably the most difficult task will be to integrate and properly interpret the combined multi-scale results. For that purpose, it is necessary to remember that most commonly we will find multiple patterns and mechanisms at the different scales and that generalities may be constrained to a specific scale. As Thompson et al. (2001) recommend, we should look for the driving mechanisms in an explicit spatial context, because as we move over multiple scales emergent mechanisms arise.

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 non-native species invasion, and the characteristics of disturbance that favor this process. Additionally, interactions among the driving factors behind invasion should be addressed explicitly. For example, this has been proven to be particularly important for determining the specific role of propagule pressure, or community aspects in community invasibility (e.g. Levine 2000).

Temporal context should also be more fully incorporated into invasion research. 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 (Kowarik 1995), as shown in the historical reconstruction of invasive species detection (e.g. 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 classical approach to temporal variation in vegetation, are necessary to understand long-term changes in plant communities (Mack 2000). 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.

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 an integrated multi-scale approach.

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References

- Allen EB and Knight DH (1984) The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. *The Southwest Nature* 29: 407–421
- Allen MR and Shea K. (2006) Spatial segregation of congeneric invaders in central Pennsylvania, USA. *Biological Invasions* 18: 525–537
- Allen EB and Starr TB (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago
- Bazzaz FA (1996) *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge, UK, 320 pp.
- Brown RL and Peet RK (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology* 84: 32–39
- Bullock JM, Kenward RE and Hails R. (2002) *Dispersal Ecology*. Blackwell Science, Oxford
- Byers JE and Noonburg E (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84(6), 1428–1433
- Byers JE, Reichard S, Randall J, Parker I, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky

- E and Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16: 630–640
- Callaway R, DeLuca TH and Belliveau WM (1999) Control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. *Ecology* 80: 1196–1201
- Collins ME, Vázquez DP and Sanders NJ (2002) Species-area curves, homogenization and the loss of global diversity. *Evolutionary Ecology Research* 4: 457–464
- D'Antonio C, Meyerson LA and Denslow J (2001) Exotic species and conservation: research needs. In: Soulé ME and Orians GH (ed) *Conservation Biology: Research Priorities for the Next Decade*, pp 59–80. Island Press, Washington, DC
- D'Antonio CM and Vitousek PM (1992) Biological invasions by alien grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87
- D'Antonio CM, Dudley TL and Mack M (1999) Disturbance and biological invasions: direct effects and feedbacks. In: Walker LR (ed) *Ecosystems of Disturbed Ground*, pp 413–452. Elsevier, Amsterdam
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA and Rice KJ (2005). Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86: 1602–1610
- Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *Bioscience* 53: 481–489
- Davis MA, Grime JP and Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534
- DeFerrari CM and Naiman RJ (1994) A multi-scale assessment of the occurrence of alien plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science* 5: 247–258
- Deutschewitz K, Lausch A, Kühn I and Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography* 12: 299–311
- Dukes JS (2001) Biodiversity and invasibility in a grassland microcosm. *Oecologia* 126: 563–568
- Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. Methuen and Co, London
- Espinosa-García F, Villaseñor JL and Vibrans H (2004) The rich generally get richer, but there are exceptions: correlations between species richness of native plant species and alien weeds in Mexico. *Diversity and Distributions* 10: 399–407
- Fenner M (1985) *Seed Ecology*. Chapman and Hall, New York
- Foster DR, Knight DH and Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystem* 1: 497–510
- Greene DF and Calogeropoulos C (2002) Measuring and modelling seed dispersal of terrestrial plants. In: Bullock JM, Kenward RE and Hails R (ed) *Dispersal Ecology*, pp 3–23. Blackwell, Oxford
- Hobbs RJ and Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6: 324–337
- Hodkinson DJ and Thompson K (1997) Plant dispersal: the role of man. *Journal of Applied Ecology* 34: 1484–1496
- Huenneke LF, Hamburg SP, Koide R, Mooney HA and Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71: 478–491
- Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E and Groth J (1999) Effects of plant species richness on invasions dynamics, disease outbreaks, insect abundances, and diversity. *Ecology Letters* 2: 286–293
- Kolar C and Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199–204
- Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species. In: Pyšek P (ed) *Plant Invasions: General Aspects and Special Problems*, pp 15–38. SPB Academic Publishing, Amsterdam
- Lee CE (2002) Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* 17: 386–391
- Lesica P and Ahlenslager K (1993) New vascular plant records and the increase of alien plants in Glacier National Park, Montana. *Madroño* 40: 126–131
- Lesica P and Miles S (2001) Tamarisk growth at the northern margin of its naturalized range in Montana, USA. *Wetlands* 21: 240–246
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967
- Levine JM (2000) Species diversity and biological invasions: relating local processes to community patterns. *Science* 288: 852–854
- Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15–26
- Liu J, Linderman Z, Ouyang LA, Yang J and Zhang H (2001) Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science* 292: 98–101
- Lonsdale WM (1999) Concepts and synthesis: global patterns of plant invasions, and the concept of invasibility. *Ecology* 80: 1522–1536
- MacArthur RH and Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101: 377–385
- Mack MC and D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13: 195–198
- Mack RN (2000) Assessing the extent, status and dynamics of plant invasions: current and emerging approaches. In: Mooney HA and Hobbs RJ (ed) *Invasive Species in a Changing World*, pp 141–168. Island Press, Washington, DC
- Mack RN and Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. *Bioscience* 51: 95–102
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710
- McKinney ML (2002) Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. *Diversity and Distributions* 8: 311–318

- McKinney ML (2004) Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions* 6: 495–504
- McKinney ML and Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450–453
- McNeely JA, Mooney HA, Neville LE, Schei P and Waage JK (2001) Strategy on Invasive Alien Species. IUCN in collaboration with the Global Invasive Species Programme, Gland, Switzerland, and Cambridge, UK
- Memmott J, Fowler SV and Hill RL (1998) The effect of release size on the probability of establishment of biological control agents: gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand. *Biocontrol Science and Technology* 8: 103–115
- Milne BT (1991) Heterogeneity as a multiscale characteristic of landscapes. In: Kolasa J and Pickett STA (ed) *Ecological Heterogeneity*, pp 70–84. Springer-Verlag
- Naeem S, Knops JMH, Tilman D, Howe KM, Kennedy T and Gale S (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91: 97–108
- Nathan R and Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285
- Nathan R, Perry G, Cronin JT, Strand AE and Cain ML (2003) Methods for estimating long-distance dispersal. *Oikos* 103: 261–273
- Novak SJ and Mack RN (2001) Tracing Plant Introduction and Spread: Genetic Evidence from *Bromus tectorum* Cheatgrass. *Bioscience* 51: 114–122
- Okubo A (1980) *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, New York
- Olliff TR, McClure RC, Miller P, Price D, Reinhart D and Whipple J (2001) Managing a complex alien vegetation program in Yellowstone National Park. *Western North American Naturalist* 61: 347–358
- O'Neill RV and King AW (1998) Homage to St. Michael; or why are there so many books on scale? In: Peterson DL and Parker VT (ed) *Ecological Scale: Theory and Applications*, pp 3–16. Columbia University Press, New York
- Parendes LA and Jones JA (2000) Role of light availability and dispersal in alien plant invasion along roads and streams in the HJ Andrews Experimental Forest Oregon. *Conservation Biology* 14: 64–75
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE and Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 11: 3–19
- Pauchard A and Alaback P (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology* 18: 238–248
- Pauchard A, Alaback P and Edlund E (2003) Plant invasions in protected areas at multiple scales: *Linaria vulgaris* (Scrophulariaceae) in the West Yellowstone area. *Western North American Naturalist* 63: 416–428
- Pauchard A, Cavieres L and Bustamante R (2004) Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions* 10: 371–375
- Pimentel D, Lach DL, Zuniga R and Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50: 53–65
- Pyšek P (1998) Is there a taxonomic pattern to plant invasions? *Oikos* 82: 282–294
- Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M and Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143
- Reichard S (2000) *Hedera helix* L. English Ivy. In: Bossard CC, Randall JM and Hoshovsky MC (ed) *Invasive Plants of California's Wildlands*, pp 212–216. University of California Press, Berkeley, California
- Rice P (2003) INVADERS database. <http://invader.dbs.umt.edu/>. Viewed May, 2002
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD and West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107
- Ridley HN (1930) *The Dispersal of Plants Throughout the World*. L. Reeve & Co., Ltd., Ashford, Kent
- Ricciardi A, Steiner WM, Mack RN and Simberloff D (2000) Toward a global information system for invasive species. *BioScience* 50: 239–244
- Rossman AY (2001) A special issue on global movement of invasive plants and fungi. *BioScience* 51: 93–94
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN and Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–333
- Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA and Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774
- Saner MA, Clements DR, Hall MR, Doohan DJ and Crompton CW (1995) The biology of Canadian weeds. 105. *Linaria vulgaris* Mill. *Canadian Journal of Plant Science* 75: 525–537
- Sax DF (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* 8: 193–210
- Sax DF and Brown JH (2000) The paradox of invasion. *Global Ecology and Biogeography* 9: 363–371
- Sax DF and Gaines SD (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* 18: 561–566
- Shea K and Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17: 170–176
- Shea K and Possingham H (2000) Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied Ecology* 37: 77–86

- Shea K, Roxburgh SH and Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7: 491–508
- Shea K, Possingham H, Murdoch WW and Roush R (2002) Active adaptive management in insect pest and weed control: Intervention with a plan for learning. *Ecological Applications* 12: 927–936
- Shigesada N and Kawasaki K (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, UK
- Shigesada N, Kawasaki K and Takeda Y (1995) Modeling stratified diffusion in biological invasions. *American Naturalist* 146: 229–251
- Simberloff D (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49: 87–97
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38: 196–218
- Stachowicz JJ, Whitlatch RB and Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286: 1577–1579
- Stadler J, Trefflich A, Klotz S and Brandl R (2000) Exotic plant species invade diversity hot spots: the alien flora of north-western Kenya. *Ecography* 23: 169–176
- Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M and Son Y (1999) Alien plant species invade hot spots of native plant diversity. *Ecological Monograph* 69: 25–46
- Stohlgren TJ, Bennett DT and Kartese JT (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology of the Environment* 1: 11–14
- Thompson JN, Reichman OJ, Morin PJ, Polis GA, Power ME, Sterner RW, Couch CA, Gough L, Holt R, Hooper DU, Keesing F, Lovell CR, Milne BT, Molles MC, Roberts DW and Strauss SY (2001) *Frontiers of Ecology*. *Bioscience* 51: 15–24
- Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81–92
- Timmins SM and Williams PA (1991) Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology* 15: 153–162
- Toney JC, Rice PM and Forcella F (1998) Alien plant records in the northwest United States 1950–1996: an ecological assessment. *Northwest Science* 72: 198–213
- Trombulak SC and Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30
- Pijl L van der (1982) *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin
- Veltman CJ, Nee S and Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. *American Naturalist* 147: 542–557
- Vitousek PM (1990) Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57: 7–13
- Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M and Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1–16
- White PS and Schwarz A (1998) Where do we go from here? The challenges of risk assessment for invasive plants. *Weed Technology* 12: 744–751
- Williamson M (1999) Invasions. *Ecography* 22: 5–12
- Williamson M and Fitter A (1996) The varying success of invaders. *Ecology* 77: 1661–1666
- Willis KJ and Whittaker RJ (2001) Species diversity. Scale matters. *Science* 295: 1245–1248
- Zavaleta E (2000) Valuing ecosystem services lost to *Tamarix* invasion in the United States. In: Mooney HA and Hobbs RJ (ed) *Invasive Species in a Changing World*, pp 261–300. Island Press, Washington, DC