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Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion

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Contents

Summary	256	IV. Conclusion	268
I. Introduction	257	Acknowledgements	269
II. Stages of invasion	260	References	269
III. A case for the four-stage framework: forecasting the response of nonindigenous plant species to climate change	268		

Summary

Key words: biotic resistance, climate change, disturbance corridors, exotic plants, global change, invasive spread, landscape pattern, nonindigenous plants.

Invasive nonindigenous plant species (NIPS) threaten native diversity, alter ecosystem processes, and may interact with other components of global environmental change. Here, a general framework is outlined that attempts to connect patterns of plant invasion to processes underlying these patterns at four well-established spatio-temporal stages of the invasion process: transport, colonization, establishment, and landscape spread. At each stage we organize findings and ideas about the filters that limit NIPS success and the interaction of these filters with historical aspects of introduction events, NIPS traits, and ecosystem properties. While it remains difficult to draw conclusions about the risk of invasion across ecosystems, to delineate universal 'invader traits', or to predict large-scale extinctions following invasions, this review highlights the growing body of research that suggests that the success of invasive NIPS is controlled by a series of key processes or filters. These filters are common to all invasion events, and will interact throughout the stages of plant invasion, although the relative importance of a filter may be stage, species or location specific. It is suggested that both research and management programs may benefit from employing multiscale and stage approaches to studying and controlling invasion. We further use the framework to briefly examine potential interactions between climate change and filters that limit NIPS invasion.

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I. Introduction

The invasion of nonindigenous plant species (NIPS) is an important component of global environmental change. Invasive NIPS disrupt ecosystems, compete with native species and cause economic losses (Hobbs & Humphries, 1995; Vitousek *et al.*, 1996; DiTomaso, 2000; Levine *et al.*, 2003; Dukes & Mooney, 2004; D'Antonio & Hobbie, 2005). In the USA alone, the estimated economic impact of invasive NIPS is \$34 billion per year (Pimentel *et al.*, 2005). Invasive NIPS can act synergistically with other elements of global change, including land-use change (Vitousek *et al.*, 1996; Hobbs, 2000), climate change (Dukes & Mooney, 1999; Simberloff, 2000; Kriticos *et al.*, 2003), increased concentrations of atmospheric carbon dioxide and nitrogen deposition (Dukes & Mooney, 1999; Dukes, 2002; Weltzin *et al.*, 2003).

Studies of traits that make NIPS invasive (Baker, 1965; Rejmanek & Richardson, 1996), characteristics of invulnerable communities (Elton, 1958; Lonsdale, 1999; Davis *et al.*, 2000), and ecosystem or community responses to invasion (Levine *et al.*, 2003; D'Antonio & Hobbie, 2005) have increased our understanding of the invasion process. However, patterns of invasion observed in the field at one site may be difficult to extrapolate to other sites because those observations are specific to a time, place and spatial scale (Table 1). Studies may employ different methods or measures of invasion success

and there is often no standardized method for evaluating the generality of these conclusions (Cadotte *et al.*, 2006). Recognition of this problem led to field studies and synthesis papers that examined invasion across spatio-temporal scales, often exploring the role of one or two factors (e.g. propagule pressure) in the invasion process (e.g. Kolar & Lodge, 2001; Hamilton *et al.*, 2005; Colautti *et al.*, 2006; Dietz & Edwards, 2006; Pauchard & Shea, 2006; Melbourne *et al.*, 2007). These papers suggest that the failure to identify a general suite of factors underlying invasion success may have resulted from attempts to extract generalities from diverse studies that do not address invasion at the same spatio-temporal stage (e.g. Kolar & Lodge, 2001).

In this review, we examine the broad categorical filters that NIPS pass through at four well-established (e.g. Vermeij, 1996) spatio-temporal stages of invasion: transport, colonization, establishment, and landscape spread (Figs 1, 2). These stages are not discrete and filters will likely affect more than one stage. However, separating invasion into stages allows us to compare patterns of NIPS success from disparate studies and to discuss the relative importance of filters to invasion at each stage. Further, identifying the stage at which an invasion fails may allow us to understand the interaction of invasion filters with invasion character (e.g. number of introduction events), species traits, and ecosystem characteristics (Table 2, Fig. 3). Generalities arising from this type of synthesis can then be used to predict the outcome of invasion events, or to

Table 1 Different approaches to invasion research that may complicate comparisons among studies

Potential difference	Example	Explanation of critical differences	Solutions
Scale	Landscape-scale observational study vs experimental neighborhood-scale study	Landscape patterns are generally observational and correlative Experimental factors at a small scale are easy to manipulate It is easier to isolate invasion mechanisms in small-scale studies	Conduct studies at more than one scale Relate local-scale studies to large-scale spatial pattern studies
Stage	Mature forest study vs microcosm assembled community study	NIPS may respond to different factors at different stages Initial success may not predict landscape spread	Conduct studies at multiple stages
Definition of invader	Native species not in original plot vs NIPS	Different factors may be responsible for success of this new species Cannot test the same questions on native and NIPS invaders	Only compare studies that use all NIPS or all native invaders Compare similar traits between natives and NIPS
Definition of invader success or invasibility	Biomass of one specific invader vs diversity of exotic species within the entire community	Diversity of NIPS does not necessarily correlate with NIPS success or potential impact Biomass may correlate more strongly with impact and success	Use biomass and other abundance or cover-related measures to get at invader success
Ecosystem studied	Forest vs grassland	Forests have more complex canopy structure with more diffuse competition Forest succession is longer, and forest plants are longer lived	Direct comparisons between studies in different ecosystems should focus on general concepts, not specific results

NIPS, nonindigenous plant species.

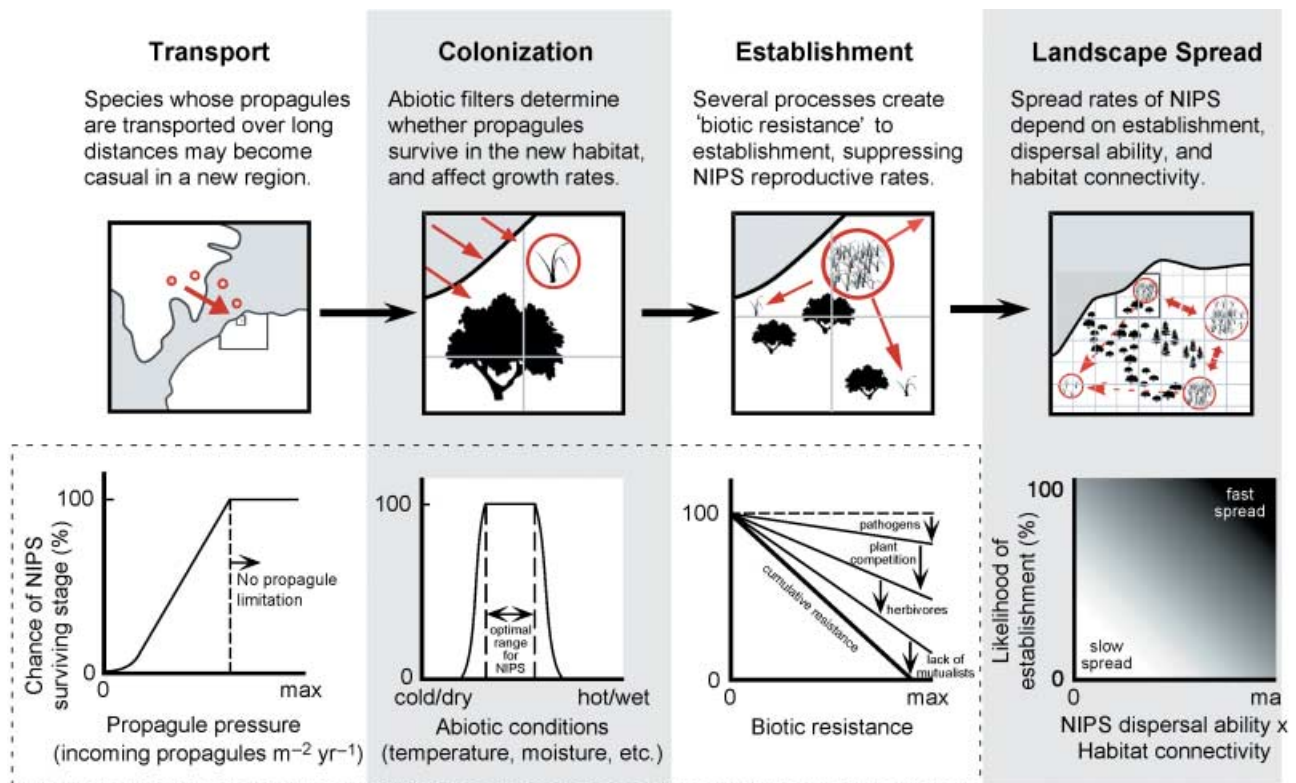


Fig. 1 Four stages of invasion, and the factors affecting nonindigenous plant species (NIPS) success at each stage. Graphics at the top of the figure depict the dominant process occurring at a stage, and conceptual diagrams below identify dominant mechanisms determining the success of NIPS at the relevant stage. The three conceptual figures on the left share the same vertical axis. The conceptual figure for spread shows the dependence of spread rates on success of a species at passing through the previous stages, in addition to its typical propagule dispersal characteristics and the characteristics of the landscape. Conceptual figures are hypothetical, although many featured mechanisms are widely supported by experimental results (see text). Figures are meant to be illustrative, but not comprehensive.

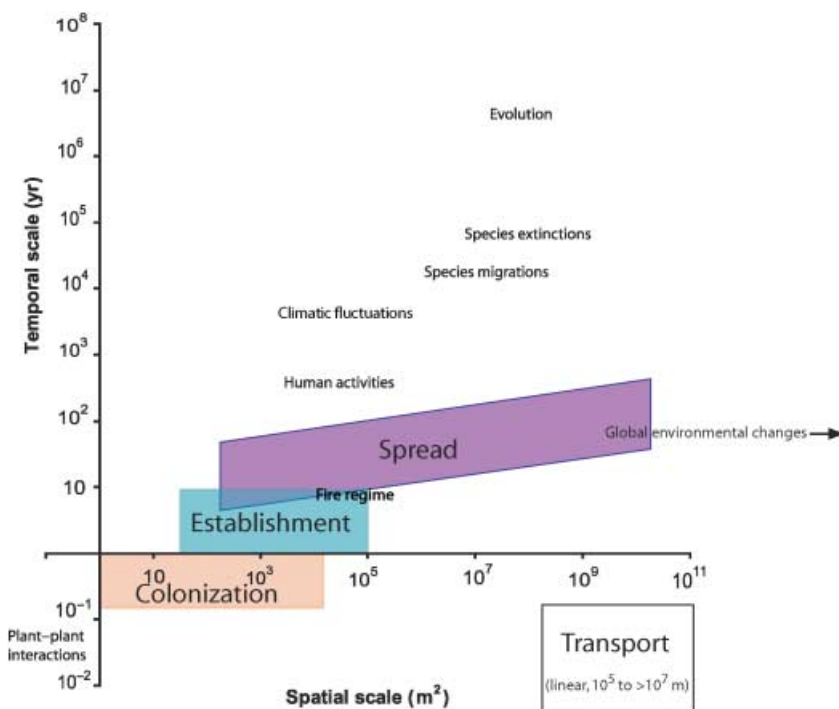


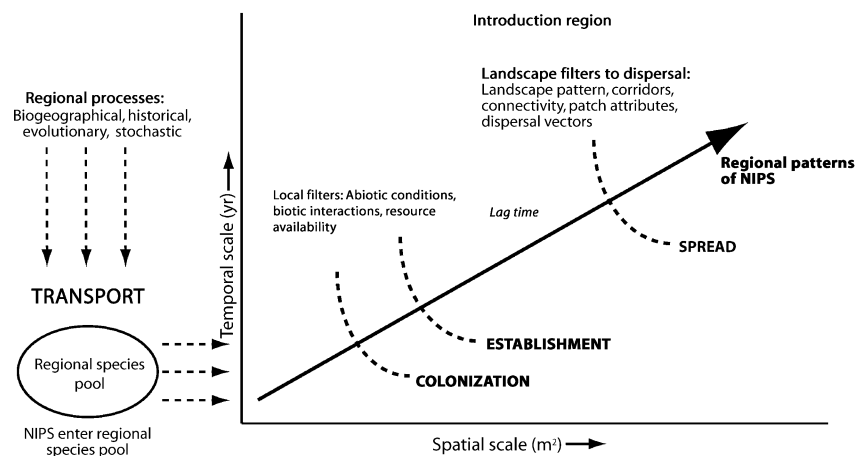
Fig. 2 The spatial and temporal scale of the four stages of invasion relative to other key biological processes. Adapted from Chapin *et al.* (2002).

Table 2 The major filters, character of the invasion, nonindigenous plant species (NIPS) traits and physical factors in the recipient ecosystem that interact to affect NIPS success at each stage of invasion

Invasion stage	Major filters	Character of the invasion event	NIPS traits	Physical factors in recipient ecosystem
Transport	Geographic distance and barriers to long-distance dispersal (waterbodies, intervening deserts, etc.)	Type of introduction (accidental vs deliberate, etc.) Propagule pressure Cause of species transport	Wide native range Seed longevity Association with humans Human desirability	NA
Colonization	Abiotic barriers to colonization	Propagule pressure Genetic variation contained in introductions Reason a species is introduced Spatial distribution of introductions	Phenotypic plasticity Wide abiotic tolerances Fast growth/short juvenile period Self-compatibility Germination without pretreatment	Climate Soil Resource availability Disturbance regime
Establishment	Biotic filters to population growth and establishment	Propagule pressure Reason a species is introduced Genetic variation	Competitive ability Fast growth Efficient resource use	Climate Soil Resource availability Disturbance regime
Spread	Landscape filters to dispersal and establishment in new areas	Propagule pressure Number of invasive foci Distribution of invasive foci	Effective long- and short-distance dispersal High fecundity Phenotypic plasticity Dispersal by seed Generalist Fast generation time	Disturbance regime Patch attributes Presence of suitable patches for colonization and establishment Dispersal corridors Heterogeneity of landscape

NA, not applicable.

Fig. 3 The assembly of local communities is influenced by filters at local, landscape and regional scales. The regional species pool is assembled through speciation, migration, biotic exchange and geological events. Transport into this regional pool occurs on a much faster time-scale than most natural movements of species. Here transport is shown outside the axis of spatial and temporal scales. Following transport, colonizing nonindigenous plant species (NIPS) move through local abiotic filters to colonization success, biotic filters to establishment success, and dispersal barriers to success in landscape spread. As the NIPS moves from colonization to landscape spread, the temporal and spatial scales of processes underlying the invasion increase.



explore mechanisms responsible for deviations from these generalizations (Cadotte *et al.*, 2006).

Integration of processes occurring at different spatial and temporal scales (Figs 2, 3) will allow us to connect local and regional invasion filters with the factors affecting NIPS success (Table 2, Fig. 3). The importance of local and regional

processes has been widely debated, but it is clear that communities are shaped by both (Ricklefs, 1987, 2004; Schluter & Ricklefs, 1993). Studies of local filters focus on species interactions and niche-based processes, as well as environmental constraints. Local communities assemble from the larger regional species pool (Fig. 3), which is shaped by history, biogeography, range

expansions, evolution, and extinction (Ricklefs, 1987). The success of NIPS likewise reflects the interaction of local filters that reduce diversity and regional processes that enhance it (Fig. 3; Davis *et al.*, 2005; Smith & Shurin, 2006). To enter a new regional species pool, a NIPS must first be transported over long distances. Upon arrival, local environmental conditions, biotic interactions, and demographic processes limit its entrance into the new community. Following local establishment, the NIPS may spread across the landscape, navigating across or around dispersal barriers (Fig. 3). Successful landscape spread can entrench the NIPS in the species pool of a new region. The invasion process therefore reflects a series of regional, local, and landscape filters that limit NIPS success during four stages of invasion.

II. Stages of invasion

1. Long-distance transport

Transport involves the intercontinental movement of a species into a new region. Although such species movements have always occurred, current species movements are happening faster than before and from more distant regions, primarily as a result of global commerce and travel (Huenneke, 1997; Mack *et al.*, 2000; Reichard & White, 2001; Le Maitre *et al.*, 2004). However, many species are unlikely to be purposefully or accidentally transported by humans or may not survive such transport (Perrings *et al.*, 2005). The factors that allow NIPS to pass through geographic filters are sometimes elusive because most transport events are studied long after they have occurred. We can gain insight from studies examining past transport events or studies addressing general patterns of human-mediated transport at global scales.

i. Invasion character and species traits The character of the invasion (Table 2) will affect NIPS transport success. In general, higher numbers of propagules increase the likelihood that species survive transport (Kolar & Lodge, 2001; Lockwood *et al.*, 2005). NIPS originating from large native ranges that are introduced across a wide swath of the nonnative range may be particularly successful. The invasion of *Phalaris arundinacea* (reed canary grass) was facilitated by multiple introduction events from a variety of sources within the native European range (Lavergne & Molofsky, 2007). Multiple introductions resulted in the transport of continental-scale genetic variation from the native range of *P. arundinacea* and subsequent reshuffling within North American populations. High genetic variation alleviated bottlenecks at expanding invasion fronts and increased genetic diversity. New genotypes coding for advantageous traits such as vegetative reproduction have also evolved in North American populations through genetic recombination (Lavergne & Molofsky, 2007).

Species traits may also influence transport. It is important to distinguish between traits that allow NIPS to survive

transport and traits preferentially selected by humans before transport. Humans may preferentially transport plants with qualities that make them strong horticultural or agricultural species such as cold hardiness, disease resistance and showy flowers. Human-selected traits may not confer invasiveness to NIPS, although many human-selected traits may be advantageous. Traits that correlate with successful transport and introduction relate mainly to geographic origin, native range extent and dispersal ability. Widespread species may have a higher overall chance of transport as they are more likely to come into human contact (Goodwin *et al.*, 1999; Cadotte *et al.*, 2006).

ii. Human activities and NIPS transport Humans are the primary dispersers of NIPS during the transport stage (Vermeij, 2005; Pauchard & Shea, 2006), so understanding patterns of trade, travel, and human desires may allow predictions of the types of NIPS that will be transported, common origin and destination regions of NIPS, and the potential success of different types of introduction events.

Today there are higher numbers of NIPS in the Americas and Africa than in Eurasia (Vermeij, 2005). Pysek (1998) reports that Eurasia, with 4.4% of the world's total floral diversity, contributes 58.9% of nonnative species to other regions. This asymmetrical pattern closely parallels historical trends in human colonization, agriculture, horticulture, and trade (Delcourt, 1987; Lonsdale, 1999; Williamson, 1999). Large-scale movements of plant species began with the establishment of European colonies (1500 AD) and trade routes running to the New World from Europe (Mack & Lonsdale, 2001; Le Maitre *et al.*, 2004).

Intercontinental plant transport has occurred accidentally, for utilitarian reasons, and for aesthetic purposes (Huenneke, 1997; Mack & Lonsdale, 2001). Accidental introductions occurred (more frequently in the past than today) in ships' cargo, in seed stock, or with livestock and travelers from other regions (Gerlach, 1997; Mack & Lonsdale, 2001; Perrings *et al.*, 2005). These NIPS tended to be ruderal species, capable of fast growth and high resource uptake (Mack & Lonsdale, 2001). NIPS were also deliberately introduced for food, fuel, forage, lumber and medicinal purposes in many European colonies. The introduction of European food crops in the Americas reflects an ingrained human avoidance of novel food sources (Mack, 1999), while forage and fuel crops were often introduced in areas with 'insufficient' native species. Utilitarian plant introductions continue today as developed and developing nations struggle to keep pace in a global economy (Huenneke, 1997; Le Maitre *et al.*, 2004). Some countries have adopted high-yield NIPS to increase agricultural production despite knowledge that these plants are invasive elsewhere (Le Maitre *et al.*, 2004).

The human desire for both familiar and exotic species resulted in the introduction of NIPS for aesthetic purposes during the 19th century and continues today (Mack &

Lonsdale, 2001). Species introduced ornamentally may have a significant advantage over species introduced accidentally. Because species introduced for human use are intentionally cultivated, they may suffer less as a result of environmental stochasticity and low population size (Mack, 1995, 2000). Species growing under human care can form stable source populations that may eventually spread into natural areas. Additionally, NIPS introduced for horticulture typically pass through a climate-matching process to determine where they will best grow. Climate matching, combined with intentional cultivation, greatly increases the likelihood that the species will escape cultivation (Huenneke, 1997; Mack & Lonsdale, 2001). Invasive species introduced for ornamental purposes in the USA include *Cortaderia jubata* (pampas grass), *Fallopia japonica* (Japanese knotweed) and *Lonicera japonica* (Japanese honeysuckle).

2. Colonization

Species that pass through the transport phase do not necessarily colonize their destination area. Survival depends on environmental conditions (e.g. soil type and climate) and biotic processes at the neighborhood scale. Arriving populations must survive and achieve positive growth rates at low densities (Chesson, 2000; Sakai *et al.*, 2001). Founder populations of NIPS are also strongly regulated by incoming propagule pressure. Because of small population sizes, colonizing NIPS must overcome environmental and demographic stochasticity, lack of genetic variability and allee effects (Mack, 1995; Sakai *et al.*, 2001). As a very approximate rule, Williamson & Fitter (1996) suggest only 10% of imported species give rise to naturalized populations.

i. Propagule pressure Propagule pressure strongly influences NIPS colonization success (Williamson, 1999; Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Pauchard & Shea, 2006). Propagule pressure is the combined measure of the number of individuals reaching a new area in any one release event and the number of discrete release events. Propagule pressure may range widely. For example, forage species have sometimes been introduced in large numbers by airplane, while populations of *Salix babylonica* (weeping willow) in New Zealand may have invaded from a single cutting (Mack, 1995). NIPS introduced across a wide area of the new region may have a better chance of landing in suitable locations for colonization (Lockwood *et al.*, 2005). Repeated introductions from the source region may save a population at the brink of extinction (Mack, 1995), and greater genetic variation may allow NIPS to adapt to novel conditions (Sakai *et al.*, 2001; Lavergne & Molofsky, 2007). The importance of propagule pressure can vary based on local conditions (Foster *et al.*, 2004; Lockwood *et al.*, 2005). Very little propagule pressure may be necessary for colonization to occur in benign environments where disturbance has eliminated native

competitors. However, in locations with intense competition or harsh abiotic conditions, high propagule pressure may be necessary (D'Antonio *et al.*, 2001; Foster *et al.*, 2004; Lockwood *et al.*, 2005).

ii. Abiotic filters and species traits Climate sets the broad limits to plant distribution and productivity and may cause NIPS to fail immediately during colonization (Sakai *et al.*, 2001). While many NIPS become naturalized in new ranges with similar climates to their native range, there are examples of species moving to areas with very different climates (e.g. *Coryza canadensis*), as well as NIPS failing to establish under similar climates (e.g. *Lantana trifoliata*) (Mack, 1995). Plants with wide geographic ranges in their native region may be more likely to survive in a new region, as a result of broader climatic tolerances (Goodwin *et al.*, 1999). Additionally, phenotypic plasticity and high levels of genetic variability may allow NIPS to adapt to less favorable conditions or environmental variability (Sakai *et al.*, 2001; Lavergne & Molofsky, 2007). Fast growth, self-compatibility, a short juvenile period, and seeds that germinate without pretreatment may also be advantageous (Goodwin *et al.*, 1999; Sakai *et al.*, 2001).

Many successful NIPS invasions occur in areas of high resource availability or under fluctuating resource conditions where temporal heterogeneity in resource availability opens a window for colonizing NIPS (e.g. Burke & Grime, 1996; Davis *et al.*, 2000; Tilman, 2004; Leishman & Thomson, 2005; but see Funk & Vitousek, 2007). Increased light, moisture, and soil nutrients have been shown to increase NIPS success and alter community dynamics (Huenneke *et al.*, 1990; Burke & Grime, 1996; Parendes & Jones, 2000; Davis & Pelsor, 2001). In California's nutrient-poor serpentine grassland, Huenneke *et al.* (1990) found that macronutrient additions increased the overall productivity of the community, decreased species richness, and increased NIPS biomass with or without soil disturbance. Results from this and other studies, as well as theoretical findings, indicate that some NIPS respond more strongly to increased resource availability than native species. Others capitalize on resource opportunities following disturbance events that remove native vegetation or directly add resources to a community (Huenneke *et al.*, 1990; Burke & Grime, 1996; Davis *et al.*, 2000; Davis & Pelsor, 2001; Leishman & Thomson, 2005). However, in order for a plant to establish it must continue to increase from low density over the long term. While short windows of resource availability may allow colonization success, periods of low resource availability may not allow NIPS to establish. Alternately, NIPS could retain gains made during high resource availability or in high-resource locations through the storage effect (e.g. storing temporal gains in storage organs) (Melbourne *et al.*, 2007). We will discuss resource availability and plant invasion further in the context of establishment.

3. Establishment

To establish, a NIPS must colonize a site and develop self-sustaining, expanding populations. Establishment may last longer than colonization and occurs on a slightly larger spatial scale (Fig. 2). At this stage, small subpopulations of individuals may be tightly linked through dispersal (Melbourne *et al.*, 2007). During establishment, biotic filters that constrain the population size of NIPS may be most important, although they will interact with environmental conditions, species traits, and continued propagule pressure from source regions (Table 2). Biotic filters are barriers to invasion created by the actions or presence of living organisms. While biotic filters will not necessarily prevent the germination of seeds or the spread of NIPS, these filters can affect survival, growth, and reproduction.

Traits that enhance competitive performance, reduce niche overlap between NIPS and natives or increase enemy resistance may be most important during establishment (Lloret *et al.*, 2005; Dietz & Edwards, 2006). Species that share similar resource acquisition traits are likely to compete strongly. Conversely, NIPS representing functional groups not present or in low abundance within a new community may encounter less competition with native species, especially in regions with a number of different resources or heterogeneous resource conditions (Lloret *et al.*, 2005; Turnbull *et al.*, 2005; Melbourne *et al.*, 2007). Other advantageous traits include secondary chemical compounds that deter herbivores, 'novel weapons', such as root exudates that negatively impact other plants, fast growth, and high fecundity (Rejmanek, 1996; Callaway & Ridenour, 2004; Richardson & Rejmanek, 2004; Dietz & Edwards, 2006). Although specific traits conferring these abilities may vary among habitats, examples of traits that correlate with competitive ability include vegetative reproduction, leaf size, stem height and flowering phenology (Goodwin *et al.*, 1999; Lloret *et al.*, 2005).

i. Plant–plant interactions: competition (–), novel weapons (–), and facilitation (+) Competition is likely the best studied of the biotic filters of invasion, although this filter alone appears unlikely to fully exclude invasive plant species (Levine *et al.*, 2004). Competition or, more specifically, exploitation competition occurs at local scales when plants reduce the growth of their neighbors by consuming resources. Because invasive NIPS are generally most successful in areas with high resource availability (Dukes & Mooney, 1999; Davis *et al.*, 2000; but see Funk & Vitousek, 2007), competition undoubtedly reduces the size, density, and impact of many NIPS. In some instances a single, strongly competitive species may slow the growth of an NIPS by reducing availability of a limiting resource. In other cases a suite of species may collectively reduce the availability of critical resources to levels that suppress growth of the NIPS. This latter scenario, along with growing recognition of the pace of global biodiversity

loss, has given rise to dozens of studies examining the role of plant community diversity in determining invasibility (e.g. Knops *et al.*, 1999; Levine, 2000; Naeem *et al.*, 2000; Dukes, 2001; Hector *et al.*, 2001; Kennedy *et al.*, 2002; Fargione *et al.*, 2003; van Ruijven *et al.*, 2003; Fargione & Tilman, 2005).

Taken together, results of these neighborhood-scale diversity–invasibility studies suggest that diverse plant communities often (but not always) provide greater competitive resistance to NIPS (Hooper *et al.*, 2005). So, does resistance result from niche complementarity or reduced resource overlap (i.e. many species with different resource requirements collectively reducing the perceived availability of resources for the invader)? Or are diverse communities resistant to invasion simply because they are more likely to include the species that most strongly compete with a suite of NIPS (i.e. the much-discussed 'sampling effect' of the biodiversity literature) (Hooper *et al.*, 2005)? While many early studies were unable to address this question (Wardle, 2001), it now seems that the answer may be: both.

Recent studies suggest three nonexclusive patterns of competition. (1) In some systems, growth of invasive species can be suppressed by species that are morphologically, phenologically, and physiologically similar, that is, species of the same functional type (e.g. Dukes, 2001; Fargione *et al.*, 2003; van Ruijven *et al.*, 2003). (2) In other cases (and even in some of the same systems), a single dominant species or functional group can most strongly suppress all or most invaders (Symstad, 2000; Fargione *et al.*, 2003). (3) Finally, in some systems, an assemblage of species with different traits can compete more strongly with an invader than any one species alone (Fargione & Tilman, 2005; Milbau *et al.*, 2005; Losure *et al.*, 2007). Thus, niche complementarity among residents can contribute to a community's biotic resistance to invasion in cases where a single resident species is unlikely to out-compete the invader. The degree to which complementarity (and thus species diversity) plays a role in determining invasibility may be influenced by resource availability of a site, with more fertile sites being more prone to the influence of dominant species. In some cases, losses of even the least abundant native species can markedly increase the invasibility of resident communities (Lyons & Schwartz, 2001; Zavaleta & Hulvey, 2004). The critical variable in the diversity–invasibility relationship is likely to be whether the species that are lost contribute to lowering the availability of a limiting resource below some threshold level at a sensitive time for the invasive species (Davis & Pelsor, 2001). For example, in systems with a strong temporal component to resource availability (e.g. water in Mediterranean-climate systems), there may be greater opportunity for rare species to affect resource availability at these sensitive times (e.g. Dukes, 2001; Zavaleta & Hulvey, 2004).

Negative interactions between NIPS and native plants may also result from NIPS with novel weapons. Some NIPS have biochemical root exudates that act as allelopathic agents or

alter plant–soil microbial interactions in the introduced range (Callaway & Ridenour, 2004). One mechanism through which NIPS root exudates can negatively impact native plants is through the disruption of beneficial relationships between native plants and soil biota. In forests of the northeastern USA, *Allaria petiolata*, an herbaceous mustard species, contains a type of phytotoxic glucosinolate that appears to disrupt the mutualism between arbuscular mycorrhizal fungi and hardwood canopy trees. Because the success of these juvenile hardwoods depends on the association with arbuscular mycorrhizal fungi, the invasion of *A. petiolata* results in tree mortality that favors further success of this invader because of reduced competition with tree species (Stinson *et al.*, 2006).

Resident species do not always suppress growth of NIPS, and sometimes contribute to their success. Facilitation is less studied in invasion biology and perhaps generally in ecology, although recent studies suggest that it may be an important local regulator of community assembly (but see Prieur-Richard *et al.*, 2000; Bruno *et al.*, 2003). Facilitative relationships are most commonly observed in harsher abiotic environments where neighboring plants ameliorate microclimatic stressors (Bruno *et al.*, 2005; Brooker, 2006), but facilitation is not limited to these environments. Smith *et al.* (2004) found that native dominants increased seedling establishment of the invasive *Melilotus officinalis* in a relatively productive North American grassland. Additionally, certain invasive species may facilitate the success of other invaders, leading to invasional meltdown (Simberloff & Von Holle, 1999). For example, invasions of nitrogen fixers into communities without native nitrogen fixers can increase the pool of soil nitrogen (Vitousek & Walker, 1989; Hughes & Denslow, 2005), facilitating the invasion of other NIPS previously limited by nitrogen availability (Yelenik *et al.*, 2004).

ii. Interactions with other trophic levels Herbivores, parasites, pathogens, mutualistic soil biota, pollinators, and dispersal agents also influence NIPS establishment. Escape from herbivory or disease may increase growth rates, and the chance of establishment in a new region. The enemy release hypothesis (ERH) suggests that NIPS benefit from transport outside the range of their natural enemies (Elton, 1958; Maron & Vila, 2001; Keane & Crawley, 2002; Carpenter & Cappuccino, 2005). Building on the ERH, the evolution of increased competitive ability (EICA) hypothesis (Blossey & Notzold, 1995) may also explain disproportionate success of invasive plants in new ranges. The EICA hypothesis suggests that, under reduced enemy pressure, selection may shift the resource allocation of NIPS from enemy defense to faster growth (Blossey & Notzold, 1995). Greater enemy pressure on native species should shift the competitive balance to favor NIPS (Keane & Crawley, 2002; Blumenthal, 2006).

There are mixed results for both the ERH and the EICA hypothesis (Keane & Crawley, 2002; Daehler, 2003). Studies show that some NIPS have longer life-spans, grow larger, and

achieve higher reproduction in invaded ranges than in native ranges (Daehler, 2003; Leger & Rice, 2003). However, these studies have not always found mechanistic explanations linking increased NIPS growth to herbivory (Keane & Crawley, 2002). Covarying factors such as competition (Leger & Rice, 2003) and resource availability (Blumenthal, 2006) may also complicate predictions of the relative importance of herbivory. The Resource–ERH (Blumenthal, 2006) suggests that enemy release in combination with areas of high resource availability increases the success of fast-growing, ‘high resource use’ NIPS in novel environments (Fig. 4).

Herbivores also influence interactions between NIPS and the native plant community. For instance, intense grazing by introduced ungulates can increase the invasibility of native plant communities (D’Antonio *et al.*, 2000). In a meta-analysis of 63 studies, Parker *et al.* (2006) found that native generalist herbivores suppressed introduced plants more than they suppressed natives, while native specialist herbivores did not suppress NIPS. Introduced generalist herbivores facilitated NIPS through their negative impact on natives. These results suggest that novel pressure from generalist herbivores may be an important line of defense against NIPS, but, in ecosystems heavily invaded by nonnative herbivores, native plants may also suffer from novel herbivore damage. Specialist enemies that switch from native hosts to NIPS, or that accompany NIPS from other regions, can limit the degree of enemy release. Although rare, host-switching has been observed among native and NIPS congeners (Creed & Sheldon, 1995).

Plant–soil feedbacks can strongly regulate the diversity and productivity of plant communities and affect NIPS success. Plant–soil interactions may be positive or negative, although negative feedbacks are most common (Reinhart & Callaway, 2006). Negative feedback is driven by soil pathogens, herbivores and parasites. These organisms reduce plant growth, provide density regulation and maintain higher degrees of diversity within plant communities. Positive feedback results from the presence of mycorrhizal fungi, nitrogen-fixing bacteria and other beneficial soil biota. Positive feedback may disproportionately facilitate the success of some species over others (Reinhart & Callaway, 2006). In general, interactions between native plants and soil communities tend to be negative, while positive feedbacks often occur between NIPS and soil biota in their introduced range (Klironomos, 2002).

Altered relationships and feedback with soil biota in the introduced vs native range may partially explain why some NIPS are so successful. Several studies have demonstrated that soil communities favor NIPS over native species (Reinhart *et al.*, 2003, 2005; Callaway *et al.*, 2004; Wolfe & Klironomos, 2005). In a California grassland, Klironomos (2002) found that four out of five nonnative species experienced positive soil feedbacks, while all five rare native plants experienced negative feedback. Reinhart *et al.* (2003) found that invasion of *Prunus serotina* (black cherry) was facilitated by soil communities of north-western Europe, while soil communities in

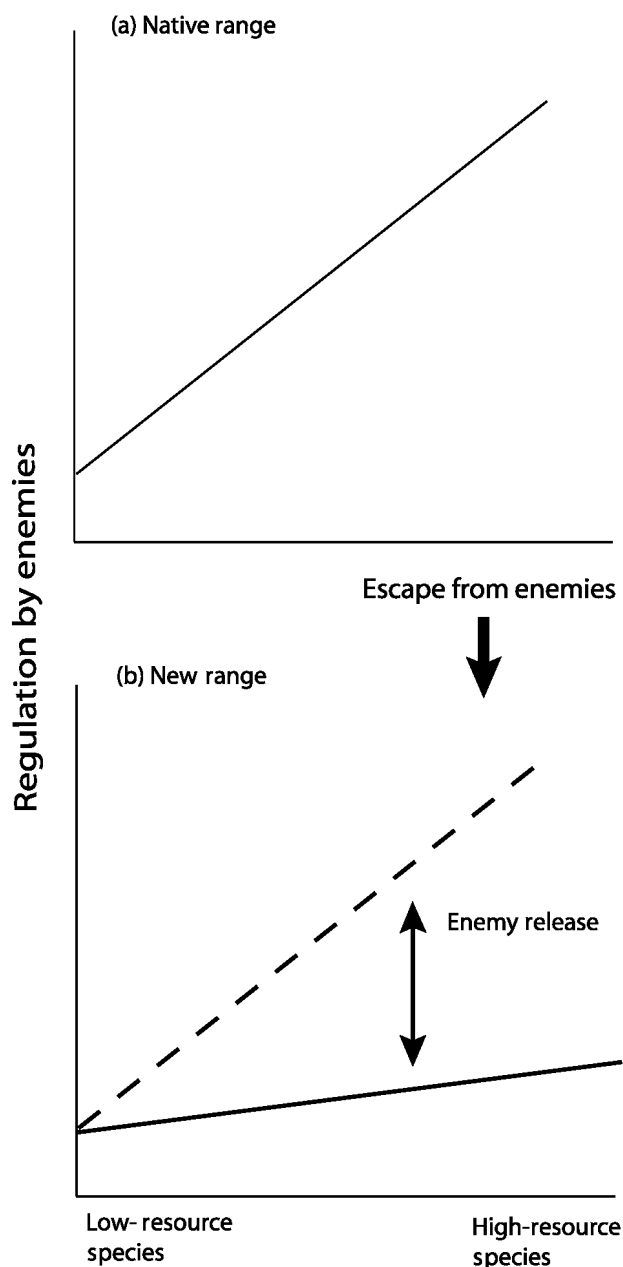


Fig. 4 The resource–enemy release hypothesis (Blumenthal, 2006) suggests that nonindigenous plant species (NIPS) that require the most resources for growth will benefit most from enemy release in their introduced range. (a) Enemy regulation may be highest for high-resource-use species in their native range. (b) In an introduced range, high-resource-use species may have greater potential to increase growth in response to enemy release (solid line) relative to native competition (dashed line). Low-resource-use NIPS will be less influenced overall. Figure redrawn from Blumenthal (2006).

the native range of the species inhibited its survival and growth. Reinhart & Callaway (2006) recently reviewed available biogeographical comparison studies investigating the effect of soil biota on NIPS in native and nonnative ranges. In all six studies the direction of soil–plant feedback was

strongly negative in the native ranges of the NIPS. In the introduced ranges, feedback was strongly negative in only one case.

NIPS can directly affect the structure and function of soil biota (Wolfe & Klironomos, 2005), with a variety of consequences. In some cases, NIPS form novel mutualisms, increasing establishment success and changing the availability of soil nutrients (Richardson *et al.*, 2000a; Callaway *et al.*, 2004). For example, many NIPS increase soil nitrogen by forming associations with native nitrogen-fixing bacteria (Richardson *et al.*, 2000a; Callaway *et al.*, 2004). Increases in soil nitrogen resulting from these mutualisms may change native community structure and increase the success of future NIPS invasions (Vitousek *et al.*, 1987; Vitousek & Walker, 1989; Yelenik *et al.*, 2004). In other cases, NIPS may alter the prevalence of disease in a community. In a model with field-estimated parameters, Borer *et al.* (2007) showed that invasive annual grasses in California may increase the presence of generalist viral pathogens in native perennial communities. Annual grasses are inferior competitors in this system, but they may be able to successfully invade in part because of the negative effect of increased viral pathogens on native perennial grasses. Finally, as already discussed, NIPS may have biochemical exudates that act as ‘novel weapons’ and may disrupt beneficial mutualisms between native plants and soil fungi (Stinson *et al.*, 2006).

Mutualisms with pollinators and seed dispersal agents in the introduced region are also necessary to ensure establishment of some NIPS (Richardson *et al.*, 2000a), although seed dispersal agents are most important during spread. It is unlikely that plants with very tightly coevolved pollinator or disperser mutualisms will find replacements in their introduced range. Plants that are pollinated by generalists, display vegetative reproduction or are self-compatible may have significant advantages (Richardson *et al.*, 2000a). Competition for pollination, similar to competition for resources, may occur between natives and NIPS (Brown & Mitchell, 2001). Showy NIPS may draw pollinators away from native species, reducing pollen quantity and seed set. Alternatively, these NIPS may attract more pollinators to natives, facilitating increased pollination (Brown *et al.*, 2002).

iii. Lag phase A lag phase often takes place between establishment and spread, when small populations of established NIPS adapt to their new community. This phase may correspond to a lack of genetic variation, which prevents rapid adaptation to novel conditions, or the time necessary for the population to reach a threshold size that allows it to spread (Sakai *et al.*, 2001; Barney, 2006). Lag time may also reflect a lack of suitable local habitat, inclement environmental conditions, or a statistical artifact (Pysek & Hulme, 2005). During this period, multiple introductions, range expansion and migration of NIPS, and gene flow between populations of establishing NIPS may decrease the time spent in the lag

phase (Sakai *et al.*, 2001; Lavergne & Molofsky, 2007). Rapid evolution can sometimes produce new genotypes capable of surviving in different climates, competing more successfully with native species, or deterring enemies (Lee, 2002). For example, *Abutilon theophrasti* (velvetleaf) was originally introduced before 1700 in the USA. This species has only recently become an aggressive invader as a result of the evolution of different life-history strategies based on the nature of competition in its new environment (Weinig, 2000; cited in Lee, 2002).

4. Landscape spread

NIPS spread occurs at the scale of the regional metacommunity: a region containing groups of populations connected through long-distance dispersal (Melbourne *et al.*, 2007). While transport occurs at an interregional scale, 'spread' refers to dispersal within a region over significantly longer time periods (Fig. 2). At the metacommunity scale the landscape is heterogeneous, and NIPS populations exist as interacting groups of species at different stages of colonization and establishment. In this regard, spread incorporates all three of the previous stages: regional spread rates of NIPS are influenced by landscape heterogeneity, the size and distribution of suitable habitat patches for colonization and establishment, the distance between suitable patches, and the population characteristics, growth rates, invasion history and dispersal ability of NIPS (Fig. 1, Table 2). The mosaic of local conditions or heterogeneity across the region will determine the interaction of local-scale population dynamics with local and long-distance spread. Heterogeneity includes both environmental (geomorphology, resource availability and soil types) and biotic (often measured as beta diversity) heterogeneity. In general, larger landscapes contain a greater heterogeneity of habitat patches and thus may maintain higher degrees of diversity of both natives and NIPS (Huston, 1994; Davies *et al.*, 2005; Melbourne *et al.*, 2007).

i. Invasion character, species traits, and dispersal The spread rates of NIPS are primarily determined by landscape pattern and barriers to dispersal. However, many other factors will influence spread. For instance, at this scale, range expansion is faster if it stems from many small foci with the same aggregate area as a single large focus (Pysek & Hulme, 2005). Regional spread results from slow and steady local spread and rare long-distance dispersal (LDD) events. While local dispersal may result in linear rates of expansion moving out radially from the initial invasion foci, LDD tends to make spread rates nonlinear (Lewis & Kareiva, 1993; Kot *et al.*, 1996; Neubert & Caswell, 2000; Hastings *et al.*, 2005). Rates of local spread vary among species depending on the dispersal mechanism. Pysek & Hulme (2005) reported average local dispersal rates ranging from 2 to 370 m yr⁻¹. Intraspecific variation can also be significant, suggesting that population

dynamics and rare LDD can strongly influence dispersal. In Australia, *Opuntia stricta* invasions spread up to 18.5 km from their origin with an average rate of 370 m yr⁻¹. However, in the first 2 yr, outlying populations were established up to 14 km away as a result of LDD early in the invasion. LDD may lead to aerial expansion of 3–500 km² yr⁻¹, allowing plants to spread significantly more rapidly than average local dispersal rates suggest (Pysek & Hulme, 2005). LDD is also largely decoupled from landscape pattern (With, 2004).

Traits promoting dispersal are most important during the spread stage of invasion (Lloret *et al.*, 2005). Timing of flowering, length of juvenile period, mode of dispersal, phenotypic plasticity, and seed size may also affect spread (Kolar & Lodge, 2001; Garcia-Ramos & Rodriguez, 2002; Hamilton *et al.*, 2005; Lloret *et al.*, 2005; Pysek & Hulme, 2005; Cadotte *et al.*, 2006; Dietz & Edwards, 2006). Pysek & Hulme (2005) argued that the available literature does not support close correlations between invasive traits and spread rates at the landscape scale. Wind, water and animal-mediated dispersal may be equally effective, although nonclonal species may spread marginally more rapidly than clonal species. The lack of correlation between dispersal-related traits may be a result of variations in the local success of NIPS.

Dispersal vectors also influence spread. NIPS dispersed by animals depend on the presence of these vectors (Richardson *et al.*, 2000a), which may also be affected by landscape pattern. Dispersal agents and pollinators are unlikely to respond to the same features of landscape pattern as plants. In a German study conducted at landscape scales, the spread of invasive *P. serotina* depended on the presence of roosting trees across the landscape – locations where birds perch and defecate seeds (Deckers *et al.*, 2005). NIPS may also come into contact with dispersal vectors more frequently in disturbance corridors (see section 4. iv.; D'Antonio *et al.*, 2000) or at the interface of suburban and natural landscapes (Williams & Ward, 2006). For instance, where suburbs abut forest in the eastern USA, long-distance dispersal of NIPS by white-tailed deer (*Odocoileus virginianus*) may promote NIPS success (Williams & Ward, 2006). Deer range throughout both habitats, often defecating in areas of heavily browsed native vegetation. NIPS benefit both from transport and from competitive advantages as a result of reduced densities of native species. Humans also play a large role in intraregional dispersal. For example, Macdonald *et al.* (1989) and Lonsdale (1999) showed that the number of visitors to national parks in North America and South Africa is positively correlated with the number of exotic species in the park. However, it is not clear whether this finding results from higher propagule pressure or increased disturbances caused by heavy foot traffic (Pysek & Hulme, 2005).

ii. Landscape pattern and the disturbance regime Landscape pattern – or the spatial arrangement of different landscape elements – affects the spread rate of NIPS (Neubert & Caswell, 2000; Richardson *et al.*, 2000b; With, 2002;

Hastings *et al.*, 2005). Landscape pattern arises from a variety of geological and biological phenomena, and the disturbance regime in a region. The disturbance regime describes the frequency, spatial extent, severity, and intensity of killing events over time. Natural disturbance regimes are often linked to physical site characteristics, extrinsic factors (e.g. weather), and the biotic community. Geomorphology, vegetation patterns, and edge effects can influence the spread of disturbances such as fire. Anthropogenic disturbance tends to differ from natural disturbance, and may alter the regional disturbance regime (D'Antonio *et al.*, 2000). Variable spread and timing of disturbance events create a mosaic of patches in various stages of succession. This pattern strongly influences the presence and persistence of different species across the landscape (Mouquet *et al.*, 2003). Changes to the natural disturbance regime may dramatically alter landscape pattern, facilitating invasive spread.

Both anthropogenic activities and plant invasions can disrupt, intensify, or suppress the natural disturbance regime (Hobbs & Hueneke, 1992; D'Antonio *et al.*, 2000; Hobbs, 2000; D'Antonio & Hobbie, 2005). Alterations of the disturbance regime that increase resource availability or change landscape pattern can promote NIPS spread by creating favorable patches for colonization and establishment (e.g. Hobbs & Hueneke, 1992; Burke & Grime, 1996; D'Antonio *et al.*, 2000; Davis *et al.*, 2000; Hobbs, 2000). Disturbances alter resource availability in a local site by killing resident individuals or by directly increasing resource supply (D'Antonio *et al.*, 2000; Davis *et al.*, 2000). Disturbance can also interact with other factors that influence NIPS success during colonization and establishment. In a study comparing the response of *Centaurea solstitialis* (starthistle) to uniform disturbance treatments in two invaded ranges and its home range, response to disturbance was found to be significantly higher in both invaded ranges than in its native range (Hiero *et al.*, 2006). The authors suggested that soil microbes may suppress the response of *C. solstitialis* to disturbance in its home range. In the invaded range, escape from these microbes may allow the weed to capitalize on disturbance events that eliminate competitors (Hiero *et al.*, 2006).

Alterations of natural landscapes may favor weedy NIPS that have coevolved with human land use and disturbances (Delcourt, 1987; Pyle, 1995; D'Antonio *et al.*, 2000; Parendes & Jones, 2000; Stohlgren *et al.*, 2001; Teo *et al.*, 2003; Kim, 2005; Vermeij, 2005). For example, native perennial grasses in Australia and North America may suffer more damage from introduced ungulate grazing than from introduced annual species, resulting in a shift to higher NIPS abundance (D'Antonio *et al.*, 2000). Both Kim (2005) and Pyle (1995) found that human disturbance regimes promoted NIPS invasion success, while natural disturbance regimes either had no relationship with NIPS success (Kim, 2005) or actually prevented invasion (Pyle, 1995). Similarly, in riparian systems, natives tend to respond positively to the natural

disturbance regime, while disruptions to natural cycles favor NIPS (D'Antonio *et al.*, 2000). In some cases NIPS invasions may lead to further land transformation, altering the natural disturbance regime, landscape pattern, and ecosystem function (Hobbs, 2000).

iii. Patch attributes and edge effects Increasingly, humans have fragmented landscapes into habitat patches within a matrix of human land use. Patch attributes, patch connectivity, and dispersal corridors influence NIPS spread (Huston, 1994; With, 2002; Davies *et al.*, 2005; Knight & Reich, 2005; Ohlemuller *et al.*, 2006). The size, shape, and edge-to-interior ratio of a patch may affect NIPS success. While large patches often favor natives, smaller patches may promote NIPS (Timmens & Williams, 1991; Harrison *et al.*, 2001; Ohlemuller *et al.*, 2006). Edge effects are more pronounced in small patches, and increased light, space, and soil moisture may favor NIPS (Timmens & Williams, 1991; Parendes & Jones, 2000). Small patches may also experience a greater influx of propagules from the surrounding landscape (Saunders *et al.*, 1991; Brothers & Spingarn, 1992; Trombulak & Frissell, 2000; Bartuszevige *et al.*, 2006; Ohlemuller *et al.*, 2006). Similarly, the shape of patches can influence the rate of NIPS introduction. Nature reserves with high edge-to-interior ratios may experience a higher rate of NIPS invasions than those of similar size that are more circular in shape (Timmens & Williams, 1991).

Habitat patches near developed edges may contain more NIPS than patches in interior habitat. In some cases, patches near edge experience increased resource availability or altered microclimate conditions. For example, forest sites abutting agricultural fields may have more light and soil nutrients (as a consequence of nearby fertilization), and less soil moisture (as a consequence of higher evapotranspiration) (Brothers & Spingarn, 1992; Trombulak & Frissell, 2000). Edge areas may also experience higher propagule pressure. In human-dominated systems, NIPS may be cultivated in gardens, or weedy NIPS may grow in areas of frequent disturbance, providing a source of propagules to neighboring natural areas (Esler, 1987; Timmens & Williams, 1991; Brothers & Spingarn, 1992; Rose, 1997; Searcy *et al.*, 2006). For this reason, sites closest to development are often most heavily invaded (Gelbard & Harrison, 2003; Deckers *et al.*, 2005; Knight & Reich, 2005; Bartuszevige *et al.*, 2006; Ohlemuller *et al.*, 2006) or differ significantly in composition from interior sites (Brothers & Spingarn, 1992; Rose, 1997; McDonald & Urban, 2006).

iv. Corridors, connectivity and metapopulation dynamics Connectivity of suitable patches influences dispersal of NIPS, movements of other species, and metapopulation dynamics of NIPS populations. Metapopulation theory suggests that the balance between local extinction and migration determines the regional persistence of a species. Therefore, connectivity

between NIPS populations may promote spread and persistence across the landscape (Murphy *et al.*, 2006). Corridors between suitable patches provide transport for natives and NIPS across unfavorable landscape matrix, encouraging spread and facilitating interactions between local populations (With, 2002), although natives and NIPS may require different types of corridors to disperse (Harrison *et al.*, 2001; With, 2002; Damschen *et al.*, 2006).

Native plants often require wide undisturbed corridors of intact habitat, while NIPS may disperse best through strips of human-disturbed habitat or 'disturbance corridors' (D'Antonio *et al.*, 2000; Parendes & Jones, 2000; Rubino *et al.*, 2002; Searcy *et al.*, 2006). Disturbance corridors include roads, trails and power-line rights of way. These habitats can facilitate rapid NIPS dispersal for two reasons. First, removal of native vegetation from disturbance corridors leads to disturbed soil, high light, altered hydrology, and destruction of the native seed bank (D'Antonio *et al.*, 2000; Trombulak & Frissell, 2000). Thus, disturbance corridors often provide favorable conditions for NIPS colonization and establishment. Secondly, disturbance corridors may increase physical transport of NIPS by providing pathways for dispersal vectors. Humans and horses have been blamed for carrying NIPS propagules along trails (MacDonald *et al.*, 1988; Timmens & Williams, 1991; Campbell & Gibson, 2001), and vehicles transport weedy species along Australian roadsides (Lonsdale & Lane, 1994). Deer and other small mammals may transport large numbers of NIPS between disturbance corridors and from suburban landscapes into forest interiors (Vellend, 2002; Meyers *et al.*, 2004; Williams & Ward, 2006). It is not clear that disturbance corridors always facilitate invasion into the adjacent habitat matrix; corridors may act solely as habitat refugia for NIPS not able to establish in intact natural habitat (Rubino *et al.*, 2002). However, studies conducted at landscape scales often reveal correlations between the distance to disturbance corridors and NIPS presence or abundance (Timmens & Williams, 1991; D'Antonio *et al.*, 2000; Parendes & Jones, 2000; Rubino *et al.*, 2002; Gelbard & Harrison, 2003; Watkins *et al.*, 2003; Searcy *et al.*, 2006). D'Antonio *et al.* (2000) reviewed 14 studies of disturbance corridors and found that half reported NIPS movement into adjacent undisturbed habitat, while the other half found that NIPS remained only in corridors. NIPS spread from corridors into adjacent natural systems likely depends on the nature of the ecosystem, the traits of the invader and the time since invasion (D'Antonio *et al.*, 2000; Rubino *et al.*, 2002).

Landscape structure and connectivity also affect gene flow, influencing the ability of NIPS to adapt to novel conditions (With, 2004; Taylor & Hastings, 2005). Isolation may be particularly detrimental at the expanding edge of a population where allee effects are most common as a result of patchy dispersal and pollen limitation (Lewis & Kareiva, 1993; Kot *et al.*, 1996; Keitt *et al.*, 2001; With, 2002; Davis *et al.*,

2004). Small population size and landscape boundaries that limit connectivity among satellite populations may ultimately prevent NIPS spread or increase the lag time between local establishment and further spread (Lewis & Kareiva, 1993). Reproductive isolation in spreading populations may also lead to speciation events as a result of the interaction of a NIPS genotype with the environment and subsequent adaptation, or as a result of genetic drift (Lee, 2002).

v. Coexistence at landscape scales Positive correlations between native and NIPS diversity at landscape scales have sometimes been used to suggest that native diversity is not an important barrier to invasion (e.g. Stohlgren *et al.*, 1999). While native diversity is only a small component of a complex 'defense system' limiting invasion (Fig. 1), the importance of native diversity can be underestimated at larger scales (Davies *et al.*, 2005; Smith & Shurin, 2006). Theory predicts that increasing heterogeneity in resource availability and site conditions should allow native species and NIPS with different functional traits, competitive abilities and resource optima to coexist at the regional metacommunity scale, resulting in high diversity of both (Grime, 1974; Davies *et al.*, 2005; Smith & Shurin, 2006; Melbourne *et al.*, 2007). Because resource levels vary among local sites, one patch may have greater resistance to invasion while another provides a niche opportunity to the NIPS (Shea & Chesson, 2002). While native diversity provides 'biotic resistance' at neighborhood scales, at the landscape or regional scale the correlation between native and NIPS diversity is merely indicative of high heterogeneity which promotes diversity of both (Smith & Shurin, 2006).

For these reasons, the potential impact of NIPS on native species is more difficult to predict at regional scales (Stachowicz & Tilman, 2005; Smith & Shurin, 2006). Evidence from historic biotic exchange events, as well as ongoing NIPS invasions, suggests that diversity almost always increases following species introductions (Vermeij, 2005; Smith & Shurin, 2006), especially in island ecosystems (Sax *et al.*, 2002). However, Smith & Shurin (2006) noted that patterns of species diversity at regional scales may not reflect the impact of local biotic interactions between natives and NIPS. Invasions initially result in reduced local abundance, reproduction or range size of natives and small changes may not be readily observed (Levine *et al.*, 2003; Miller & Gorchoy, 2004). Melbourne *et al.* (2007) suggested that heterogeneity at the scale of the metacommunity reduces the impact of invasive NIPS on natives by providing coexistence opportunities not present in homogeneous environments. However, while native species may maintain viable populations at regional scales, escape from extinction may only be temporary (Tilman, 1994; Harding *et al.*, 2006). Studies documenting declines in beta diversity (distinctness of species composition between local sites) suggest that homogenization may be occurring regionally (Smith & Shurin, 2006).

Table 3 The framework can help categorize consequences of climate change that may affect success of invasive plant species (see text for details)

Stage	Possible consequences of climate change that affect nonindigenous plant species (NIPS)
Transport	Horticultural species imported to new areas Crops imported to new areas (with associated weeds?) New NIPS cultivated as biofuel? Shifting commercial activities and shipping pathways
Colonization	Climatic range restrictions will shift Potential ranges may increase or decrease Some ornamental species may become weedy Some invasives may spread from disturbance corridors into natural areas Many invasive species share advantageous traits? Broad environmental tolerances Rapid evolution High phenotypic plasticity
Establishment	Shifting resource availability alters competition Reduced competition from natives? Range shifts for herbivores, pathogens, mutualists
Spread	Invasive NIPS propagules spread to newly suitable climatic zones more rapidly than many natives?

III. A case for the four-stage framework: forecasting the response of nonindigenous plant species to climate change

Addressing invasion in four stages helps to identify the different processes that affect NIPS success at each stage of invasion, and provides a conceptual 'map' with which to predict and test the effects of environmental changes on these filters. Changes in climate and atmospheric CO₂ are already affecting plant communities at local and regional scales (Dukes, 2000; Weltzin *et al.*, 2003). NIPS have the potential to benefit if climate change affects the filters that limit invasion success (Table 3).

Climate change and increasing CO₂ are unlikely to directly alter transport of most NIPS, but may affect patterns of trade and introduction success. Warming is likely to increase horticultural imports into regions with cold winters. Similarly, patterns of transport of agricultural species are likely to change, and agricultural weeds may 'hitchhike' into new environments. Concerns over climate change may also lead to the intentional introduction of nonnative crops for biofuel production. Many potential biofuel species possess similar traits to established NIPS, suggesting that they could become invasive (Raghu *et al.*, 2006).

Colonization and survival of NIPS may also change with changing climate. For many species, decreasing frequencies of lethal cold temperatures will allow poleward range expansions (Simberloff, 2000; Kriticos *et al.*, 2003). Conversely, warming

may cause drying and desiccation at warmer range margins, decreasing colonization success (Kriticos *et al.*, 2003; Brooker, 2006). In other cases, increased precipitation and/or increased plant water-use efficiency (WUE) as a result of higher concentrations of atmospheric CO₂ may expand the warmer range boundaries of some species. Kriticos *et al.* (2003) modeled the range of an invasive *Acacia nilotica* under climate change scenarios and found that warming temperature increased the range poleward, while higher precipitation and enhanced WUE expanded the range inland.

Changes in resource availability resulting from climate change and CO₂ enrichment are likely to alter competitive interactions during NIPS establishment. Potential effects of elevated CO₂ on NIPS establishment are discussed elsewhere (Dukes, 2000; Weltzin *et al.*, 2003). Increased moisture resulting from precipitation changes or greater WUE may favor some NIPS (Dukes & Mooney, 1999), especially in arid communities and regions with strong seasonal patterns of precipitation. For example, in years with high rainfall, exotic annual grasses successfully invaded resource-limited California serpentine grasslands that had previously repelled NIPS (Hobbs & Mooney, 1991). Warming would reduce physiological stress on some introduced NIPS. These NIPS might then compete more effectively with native plants (Dukes & Mooney, 1999; Shea & Chesson, 2002). Phenological shifts in the timing of spring leaf-out may also allow certain NIPS to compete more strongly (Brooker, 2006). Pathogen, mutualist and herbivore ranges may also shift with unpredicted consequences for NIPS and native plants.

Landscape spread may be influenced by shifts in the ranges of species. NIPS that could once only survive in gardens or disturbance corridors may be able to spread into natural areas if the climate becomes more favorable for their survival and growth. Plants that cannot shift ranges quickly enough to maintain populations in suitable climates may decline, while species that can may expand (Dukes & Mooney, 1999; Higgins & Richardson, 1999; Simberloff, 2000). Thus, rapid warming may disproportionately benefit NIPS with traits such as rapid dispersal, short juvenile periods, high fecundity and small seed mass (Rejmanek, 1996; Dukes & Mooney, 1999; Simberloff, 2000). Invasive NIPS with fast reproduction, short life cycles, and high phenotypic plasticity may also respond to change with rapid genetic or phenotypic adaptation (Dukes & Mooney, 1999; Schweitzer & Larson, 1999).

IV. Conclusion

The four-stage framework acknowledges the multiscale nature of the NIPS invasion process and attempts to integrate invasion patterns and the mechanisms underlying these patterns at the different stages. Future studies that approach at least two different stages of invasion (e.g. Levine, 2000; Davies *et al.*, 2005; Knight & Reich, 2005) can provide excellent insights into invasions. Where possible, we recommend

Table 4 Potential management strategies to reduce nonindigenous plant species (NIPS) success at each stage of the invasion process

Stage	Management strategies
Transport	Regulate nursery trade more strictly Promote native species in landscape design Screen seed stock more effectively Educate the public about the consequences of NIPS and how to prevent their introduction (not buying nonnative ornamentals, not planting house plants outdoors, etc.)
Colonization	Use climate envelope techniques to predict range of potential NIPS Reduce habitat fragmentation and edge effects Start cutting, mowing, and herbicide treatments immediately
Establishment	Increase health and seed recruitment of native plants Promote intact native communities and trophic structure Study the effects of native generalist herbivores on NIPS for potential control (make sure these species do not prefer natives) Investigate other (native) biocontrols Reduce human disturbances, promote natural disturbance regime Continue cutting, mowing, and herbicide application
Spread	Minimize disturbance corridors through natural landscapes Promote native species that can compete with NIPS at the edges of disturbance corridors (e.g. early successional natives) Isolate source populations of NIPS Eliminate or reduce transport vectors (such as deer) in natural areas during reproductive stage of NIPS growth Prioritize use of local techniques to manage colonization and establishment in sites that are most susceptible to invasion (e.g. sites with high numbers of reproducing individuals, and adjacent sites, sites on the edge of landscapes).

adopting this approach. We also recommend that management approaches explicitly consider the targeted stage, and enhance natural filters in order to prevent invasion success (Table 4). It is likely that managing multiple stages of the invasion process simultaneously will be most effective.

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