CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

THE INVASION PARADOX: RECONCILING PATTERN AND PROCESS IN SPECIES INVASIONS

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Abstract. The invasion paradox describes the co-occurrence of independent lines of support for both a negative and a positive relationship between native biodiversity and the invasions of exotic species. The paradox leaves the implications of native–exotic species richness relationships open to debate: Are rich native communities more or less susceptible to invasion by exotic species? We reviewed the considerable observational, experimental, and theoretical evidence describing the paradox and sought generalizations concerning where and why the paradox occurs, its implications for community ecology and assembly processes, and its relevance for restoration, management, and policy associated with species invasions. The crux of the paradox concerns positive associations between native and exotic species richness at broad spatial scales, and negative associations at fine scales, especially in experiments in which diversity was directly manipulated. We identified eight processes that can generate either negative or positive native–exotic richness relationships, but none can generate both. As all eight processes have been shown to be important in some systems, a simple general theory of the paradox, and thus of the relationship between diversity and invasibility, is probably unrealistic. Nonetheless, we outline several key issues that help resolve the paradox, discuss the difficult juxtaposition of experimental and observational data (which often ask subtly different questions), and identify important themes for additional study. We conclude that natively rich ecosystems are likely to be hotspots for exotic species, but that reduction of local species richness can further accelerate the invasion of these and other vulnerable habitats.

Key words: biodiversity; exotic; invasibility; native; nonindigenous; scale; species diversity.

INTRODUCTION

The recent history of ecology has been an unfolding story of the sensitivity of patterns and processes to scale (Levin 1992). One such example of considerable cultural and economic importance is the relationship between the number of native or resident species ("natives") in an ecosystem and how many exotic or introduced species ("exotics") have invaded it. In general, a variety of observational, experimental, and theoretical studies have often documented negative relationships between the number of native species and the number of species or relative success of exotics at fine scales (often a resolution of 10 m^2 or less). In contrast, broad-scale studies (typically a resolution of 1 km^2 or more) yield roughly the opposite pattern of positive correlation of native and exotic species richness. These seemingly conflicting results (Levine and D'Antonio 1999, Shea and Chesson 2002, Byers and Noonburg 2003, Fridley et al. 2004, Herben et al. 2004, Davies et al. 2005) constitute what we refer to as the "invasion paradox."

Although fine-scale patterns have been taken as evidence that native richness protects ecosystems against invasions (Case 1990, Knops et al. 1999, Levine 2000, Kennedy et al. 2002), broad-scale patterns have led researchers to suggest the opposite (Stohlgren et al. 1999, 2003, Davis et al. 2000, Huston 2004). How can these patterns be reconciled, and what are the implications for the conservation and management of natural ecosystems?

Our use of the term "paradox" to describe the interaction of scale and native–exotic richness patterns is convenient shorthand for a complex situation that reflects both contradictory relationships reported in the literature on invasion and the varying import attributed to different methodological approaches by individual scientists. A paradox is "something with seemingly contradictory qualities or phases" (Webster's Third New International Dictionary; Grove 1993), and there are at least three apparent contradictions we refer to in our usage of "invasion paradox." First, there is an apparent conflict between the findings of experimental and observational studies. Second, there is a conflict between some findings of fine-scale and broad-scale observational studies. Unfortunately, the experimental literature concerning this issue consists entirely of studies that are (unavoidably) of fine scale, thus conflating scale and methodology. Third, individual views vary on the relative merits of findings from observational vs. experimental studies. We acknowledge that different methodological views among scientists play a role in motivating the debate surrounding the invasion paradox, but these are well known (Naeem 2001). Our emphasis in this review is therefore on differences in invasion patterns across scales (see Plate 1) and a corresponding synthesis of the underlying processes responsible for these shifting patterns.

Although the invasion paradox has been the subject of several recent studies, perspectives of different authors are highly divergent (Stohlgren et al. 1999, 2006b, Tilman 1999, 2004, Shea and Chesson 2002, Byers and Noonburg 2003, Herben et al. 2004, Davies et al. 2005). The reporting of native–exotic richness patterns from a variety of ecosystems is growing (e.g., Stohlgren et al. 1999, 2003, 2006a, Brown and Peet 2003, Cleland et al. 2004, Gilbert and Lechowicz 2005), but is also controversial (Rejmanek 2003, Taylor and Irwin 2004). Observational evidence still lags behind advances in theory (Shea and Chesson 2002, Byers and Noonburg 2003, Bruno et al. 2004, Fridley et al. 2004, Herben et al. 2004, Tilman 2004, Davies et al. 2005). Experimental approaches to the paradox are of limited duration, spatial grain, and spatial extent (Stachowicz et al. 1999, 2002, Levine 2000, Naeem et al. 2000, Fargione et al. 2003, Smith et al. 2004, Fargione and Tilman 2005). Several pertinent reviews have focused on the role of biotic resistance, and thus fine-scale native–exotic richness processes (Levine and D'Antonio 1999, Hector et al. 2001, Levine et al. 2004), while relatively few have

focused exclusively on large-scale processes driving the positive half of the paradox (Davies et al. 2005, Stohlgren et al. 2005, 2006a, b). Herben et al. (2004) reviewed the paradox by summarizing a range of studies with both negative and positive native–exotic richness relationships, and focused on a particular mechanism of neutral community assembly. However, there remains no general treatment of how the paradox in pattern can be resolved by variation in process with scale, through an examination of the intersection of experimental, observational, and theoretical approaches to this topic.

Here, we synthesize the range of perspectives offered to explain the invasion paradox. We first built on the work of Herben et al. (2004) and others by adding much recent additional information on the general pattern of the native–exotic species richness relationship at different spatial scales. In summarizing this growing picture of the pattern, we asked: (1) whether certain habitats or environments are associated with negative or positive native–exotic richness relationships (NERRs); and (2) subsequently, whether the invasion paradox is a real phenomenon across many systems. We then review processes that may underlie NERR patterns at both fine- and broad-spatial scales. Fine-scale processes focus on species interactions but include both niche-related and species-neutral models. Broad-scale processes are typically less precisely specified than those described by fine-scale models, and focus on abiotic conditions rather than species interactions, particularly heterogeneity in the environment. By combining the key processes from each model that could produce the invasion paradox, we asked how a general model might be obtained and whether it would be useful. We conclude with a list of unresolved questions related to the paradox, and briefly explore the implications for the management of exotic species invasions.

Throughout, we define fine scales as spatial grains in which all or most individuals have the potential to interact directly with one another, and often those in which spatial heterogeneity in environmental and dispersal processes are minimized. Broad scales include spatial grains that are inhabited by many individuals, the large majority of which do not directly interact with more than a few individuals within their neighborhoods, and where within-grain spatial heterogeneity is considerable enough such that no one species is able to inhabit the entire area. Because organisms differ by many orders of magnitude in body size and the spatial grain at which they respond to underlying heterogeneity, absolute scaling of fine vs. broad scales will depend on focal taxa.

PATTERNS OF NATIVE AND EXOTIC SPECIES RICHNESS

Fine spatial scales

Patterns of native and exotic species richness at fine scales have only recently been widely reported (see Table 1 in Herben et al. 2004). Observational studies in plant communities have documented negative native–exotic richness relationships at scales below 1 m^2 in riparian

Plate 1.   Invasion of scotch broom (*Cytisus scoparius*; lighter color on slope) on the western coast of the South Island of New Zealand in 2004. Patterns of invasion and dominance within small patches may be unrelated to such patterns at the scale of the hillside. Photo credit: S. Naeem.

corridors of the southern Appalachians (North Carolina and Tennessee, USA; Brown and Peet 2003), agricultural borders in North Carolina, USA (J. D. Fridley and R. K. Peet, *unpublished data*), tallgrass prairie in Iowa and sagebrush in Colorado, USA (Stohlgren et al. 2006*b*), Australian grassland (McIntyre and Lavorel 1994, Morgan 1998), and coastal grassland in California, USA (Kolb et al. 2002). Stachowicz et al. (2002) found negative NERRs in subtidal marine invertebrate communities. Many experimental studies of NERRs suggest a negative relationship at fine scales; we refer the reader to several recent reviews of these studies (Levine and D'Antonio 1999, Hector et al. 2001, Herben et al. 2004, Levine et al. 2004). There is a bias of these studies toward temperate grasslands (Hector et al. 2001; see also Fargione and Tilman 2005). Many experimental studies report the performance of specific invaders rather than focus on exotic species richness, and so only indirectly involve NERRs. Furthermore, experimental studies, while often of similar spatial grain to observational studies, are almost always of smaller spatial extent, thereby comprising a smaller range of spatial heterogeneity. That experimental and observational studies often ask different questions and employ different methods suggests that their synthesis may increase our understanding of invasions rather than leading to a paradox; we comment further on this below in *Synthesis: One theory fits all or a plea for pluralism?*

Positive NERRs, however, have also been widely reported at scales as small as 1 m² in systems as diverse as California chaparral, savannas, and conifer forests (Keeley et al. 2003), Chilean scrub communities (Sax 2002), desert grasslands (Cleland et al. 2004), many arid upland and riparian systems in the U.S. Great Basin and Rocky Mountain regions (Stohlgren et al. 2006*b*), old fields in Michigan and Minnesota, USA (Cleland et al. 2004), and marine invertebrate communities (Dunstan and Johnson 2004, Stachowicz and Byrnes 2006). Positive NERRs also occur in 10 m² plots in old-growth temperate forest (Gilbert and Lechowicz 2005) and tallgrass prairie (Smith and Knapp 1999, Cleland et al. 2004), at several scales below 1000 m² in riparian corridors (Brown and Peet 2003), and in 500-m² plots in Rhode Island, USA, coastal strandline communities (Bruno et al. 2004).

Overall, we conclude that fine-scale NERRs exhibit high variance and do not appear to be predictable based on habitat type or geographic region. The observation that fine-scale NERRs are negative cannot be said to be a simple, accurate generalization based on current evidence. Many of these patterns have only recently been brought to light, however, and many more surveys (especially from tropical systems) are needed. Experimental studies appear to report much more consistent NERRs than natural surveys. Moreover, measures of exotic success in experimental studies generally extend beyond those of observational studies to include the growth, survival, or reproduction of particular exotic species, in addition to the abundance or richness of all exotics.

Broad spatial scales

With few exceptions, empirical studies of the NERR at scales of landscapes and larger indicate that biotically
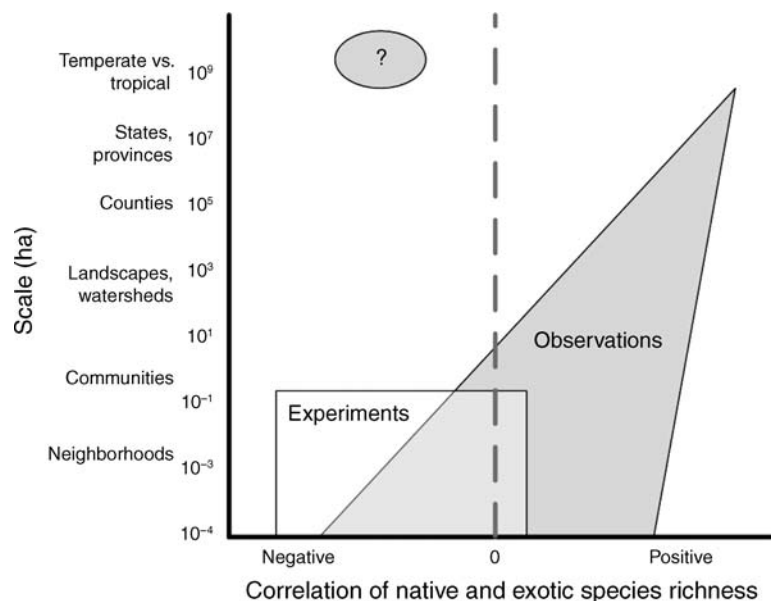
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FIG. 1. Conceptualized diagram of the invasion paradox. Fine-grained studies, many of which are experimental, often suggest negative correlations between native and exotic species richness but are highly variable. Nearly all broader-grain observational studies indicate positive native–exotic richness correlations. Likely exceptions are comparisons between temperate and tropical biomes, where preliminary data suggest that biodiversity hotspots have very few exotic species.

rich native areas support many more species of exotics than areas with relatively few native species. Herben et al. (2004) list nearly 50 instances of published observations of NERRs at a variety of different scales; none of the negative relationships are for areas >30 m^2. Most of the larger scale plant communities examined to date, whether continental (Planty-Tabacchi et al. 1996, Stohlgren et al. 1998, 1999, 2001, 2003, 2005, 2006a, Lonsdale 1999, Dark 2004, Davies et al. 2005, Seabloom et al. 2006) or island floras (Sax et al. 2002), exhibit highly significant positive NERRs. All known exceptions to the broad-scale positive NERR within temperate zones occur for certain faunal assemblages, such as freshwater fishes on a watershed scale (Brown 1995: Fig. 12.2) and some marine invertebrates at landscape scales (Stachowicz et al. 2002). Furthermore, for many vegetation types it has been reported that the slope and correlation coefficient of the NERR increase with scale (Brown and Peet 2003, Fridley et al. 2004, Stohlgren et al. 2006b), although work on insular floras suggests that the NERR is scale invariant across a certain range of spatial scales (D. F. Sax and J. P. Price, unpublished manuscript). At a global scale, however, both marine and terrestrial tropical communities (generally the most diverse on earth) appear to support relatively few exotic species (Rejmanek 1996, Sax 2001), and thus, the largest scale NERRs are probably negative. There is a relative paucity of exotic survey data from the tropics, however, leaving a significant gap in our understanding of broad-scale NERRs.

Taken at face value, current evidence suggests that the NERR is scale dependent, but in complex ways (Fig. 1). For most groups of organisms (and especially plants),

large-scale NERRs are universally positive, but the extent to which this relationship decays to nonsignificance or a negative NERR as spatial grain or extent decreases appears system specific. It is plausible that experimental manipulation in systems that exhibit positive broad-scale NERRs could result in negative fine-scale NERRs. Moreover, although univariate analyses of many systems do not exhibit any empirical "invasion paradox" because negative relationships are not found at any scale, it is unclear what patterns might be revealed by including additional factors in multivariate analyses. For example, both Rejmanek (2003) and Taylor and Irwin (2004) reanalyzed the data that Stohlgren et al. (2003) used to show a strongly positive NERR for the 50 U.S. states, within the context of covariates representing human-caused habitat disturbance and propagule pressure. Rejmanek (2003) showed that the positive NERR became significantly negative once state population density and latitude were included in a model predicting exotic plant richness. Similarly, Taylor and Irwin (2004) found no effect of native plant richness on exotic richness after controlling for the effects of latitude and real estate gross state product (a measure of economic activity), and concluded that there was no support for the hypothesis that native and exotic species richness are causally related at the state level. The lack of support for positive NERRs once additional covariates are considered also extends to finer scale studies. For example, M. Smith (unpublished manuscript) showed that the positive NERR for 10-m^2 plots in tallgrass prairie reported in Smith and Knapp (1999) disappeared when disturbance factors such as fire frequency and grazing intensity, as well as temporal

shifts in species composition, were included in a structural equation modeling framework. Thus, as is true with all correlative studies, broad-scale NERRs in no way demonstrate causation, and these examples suggest that they are likely to be the combined result of human-caused disturbances and the similar responses of native and exotic richness to broad-scale environmental variation.

FINE-SCALE PROCESSES:
BIOTIC RESISTANCE OR ACCEPTANCE?

Elton (1958) has been credited with constructing the first theoretical framework of community invasibility (Levine and D'Antonio 1999), which was subsequently developed in lock-step with theoretical models of species diversity, niche partitioning, and community saturation and stability (see MacArthur 1970, 1972). Although much has been added to niche partitioning models (Tilman 1982, 2004, Case 1990, Chesson 2000), the basic prediction remains the same as Elton advocated: Communities of more resident species should be more resistant to invasion by new species, and thus, all else equal, areas of high native richness should contain fewer exotic species (the "balance of nature" hypothesis; Cronk and Fuller 1995). A more modern perspective that includes stochastic mortality and spatially explicit resource competition (Tilman 2004) suggests a more complicated set of predictions. For example, extrinsic factors including disturbance rates, resource pulses, and nonresident immigration rates all increase the incidence of local invasion. Nonetheless, if control of composition by niche partitioning remains high compared to these extraneous factors, NERRs should be negative.

Experimental support for niche-based theory in the context of species invasions is well established (Knops et al. 1999, Hector et al. 2001, Levine et al. 2004, Fargione and Tilman 2005), but questions remain as to whether the mechanism of niche partitioning per se has been proven for a wide range of communities (Cronk and Fuller 1995, Davis et al. 2000, Wardle 2001). Sampling effects, where more diverse communities are more likely to include particularly invasion-resistant species, are thought to be an important component of experimental invasion studies (McGrady-Steed et al. 1997, Wardle 2001, Smith et al. 2004, Fargione and Tilman 2005). It is clear that single-species populations strongly differ in their ability to resist invasion (Davis et al. 2000). However, it is also clear that certain types of niche partitioning are highly relevant for invasion patterns in natural systems. For example, open space and unutilized resources enhance invasion rates (Davis et al. 2000), and there is much evidence that single species cannot continually usurp all available space or resources in seasonal or yearly fluctuating environments (Stachowicz et al. 1999, 2002, Dukes 2002, Fargione and Tilman 2005). Although it is unlikely that very high levels of local native richness are necessary to effectively eliminate all open patches of resources, the importance of seasonal partitioning of resources suggests that native species mixtures should be generally better at resisting invasion than most monocultures.

Niche-based models of species invasion frequently ignore the importance of facilitation in many systems (Bruno et al. 2003), and facilitative interactions between natives and exotics may lead to positive NERRs at fine scales (Richardson et al. 2000, Stachowicz 2001, Bruno et al. 2003). Communities of very different growth forms often exhibit a complex web of interactions that include positive and negative species interactions; marine invertebrate and plant communities, in particular, include "foundation" species that have been shown to be important facilitators of marine exotic invasions worldwide (Bruno et al. 2005). Theory from plant communities along environmental stress gradients (e.g., Callaway and Walker 1997) predicts increasing importance of facilitative interactions as stress increases; if so, then native species, not necessarily resident richness, may facilitate the establishment of exotics in stressful situations (Smith et al. 2004; B. Von Holle, *unpublished manuscript*). Palmer and Maurer (1997) have also suggested that diversity may beget diversity, in the sense that a structurally complex community may provide a greater array of microenvironments for potential invaders. Indeed, Stachowicz and Byrnes (2006) found that the NERR shifted from positive in the presence of a structurally complex exotic species to negative in the absence of structural complexity. Stohlgren and colleagues (2006b) have proposed a theory of "biotic acceptance" that also builds on positive or negative NERRs at fine scales, but consistently positive NERRs at broad scales; we leave discussion of this theory to the next section on broad-scale processes.

The recent emergence of neutral theory (Hubbell 2001) has invited researchers to envision what NERRs would look like in communities that are not structured by niche-related processes. Both Fridley et al. (2004) and Herben et al. (2004) have shown that the invasion paradox can be produced in communities populated by species with identical ecological properties. Fridley et al. (2004) demonstrated that NERRs at the finest spatial scales are constrained to produce negative NERRs due to the impossibility of accommodating high numbers of both natives and exotics in a small sample of individuals. At larger spatial scales, any process creating variance in total richness among communities will also lead to a positive NERR, even in lieu of species differences (Fridley et al. 2004, Herben et al. 2004, Seabloom et al. 2006). The inevitability of such statistical artifacts at both fine and large scales demands that researchers carefully consider null-modeling approaches when evaluating observational data. Moreover, comparison of observed fine-scale NERRs to a species-neutral null model for several plant communities revealed essentially no difference in observed patterns and null predictions for scales containing tens to hundreds of individuals ($0.1–100$ m^2; Fridley et al. 2004), suggesting that many

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reported fine-scale negative relationships are, in fact, the result of statistical artifacts rather than niche-based processes. At the very least, the existence of statistical constraints at fine scales contributes to the large variance in fine-scale NERRs described in the literature.

The panoply of processes that may be relevant to local coexistence, resident species richness, and the ability of residents to resist invasion surely contributes to the inconsistent pattern of NERRs in natural ecosystems. Ideally, a synthesis of the relative importance of these processes (niche partitioning and local competitive exclusion; neutral processes of stochastic mortality and immigration; top-down control; disturbance and non-equilibrium conditions; climate tolerances and physiological trade-offs) in different habitats would allow predictions of which areas are under greatest threat from species invasions. Such a synthesis does not appear to be forthcoming.

BROAD-SCALE PROCESSES: GENERAL THEORY FOR RICH GETTING RICHER?

In contrast to coexistence theories that are thought to govern NERRs at fine scales where individuals interact with one another, theories proposed for broad-scale NERRs are vague and rarely expressed mathematically (but see Davies et al. 2005). As a result, it is difficult to find a theory that makes precise, falsifiable predictions of species invasions at large scales. At such scales where within-unit environmental variation is an obvious driver of coexistence, it is no surprise that some aspect of environmental heterogeneity is universally advocated as the underlying cause of positive NERRs, although dispersal processes have also been implicated (Levine 2000, Byers and Noonburg 2003). Here, we focus on theoretical contributions that are particularly relevant for broader scales where positive NERRs are common, or those that are flexible enough to accommodate the shift from fine-scale negative to broad-scale positive NERRs.

The theory of biotic acceptance (Stohlgren et al. 2006b; see also Huston 2004) suggests that patterns of native species richness are largely the result of good or bad environmental conditions: "Good" habitats are universally desirable for most species and others require costly (and thus rare) adaptations to stress and disturbance. Sites that are good for native species are also generally good for exotic species, and thus, the "rich get richer" (Stohlgren et al. 2003, see also Huenneke et al. 1990, Burke and Grime 1996, Naeem et al. 2000, Sax 2002). The theory suggests that positive NERRs should be found across a broad range of spatial scales (Stohlgren et al. 2006b).

Outside of the context of species invasions, biotic acceptance theory has much older precedents in plant community ecology, such as the discussion of plant strategy trade-offs in stressful or "extreme" vs. competitive or "favorable" environments (Whittaker 1972, Grime 2001), the centrifugal organization of plant

communities along stress gradients (Keddy 1990), expected niche distributions along resource and regulator gradients (Ellenberg 1974, Austin and Smith 1989), and much of the contemporary discussion of species pools and local plant coexistence (e.g., Taylor et al. 1990, Pärtel et al. 1996, Pärtel 2002, Peet et al. 2003). Inherent in all of this work is the assumption that most species thrive given abundant resources and benign conditions (water, sunlight, soil nutrients; non-extreme cold or salt or pH), and yet few are tolerant of chronic resource shortages or extreme environmental conditions. Interestingly, there appears to be no consensus that this is true in any absolute sense (Grubb 1998, Pärtel 2002), and indeed there has been strong debate among plant ecologists concerning plant adaptations for gross resource shortage vs. net resource shortage, i.e., the tolerance of plants to environmental stress vs. competition-induced stress (see, e.g., Grace 1990, Davis et al. 1998). Moreover, as Davies et al. (2005) have noted, there is virtually no theory to suggest that mean resource enrichment enhances species richness; rather, the bulk of theoretical and experimental studies suggests the opposite (Tilman 1982, Tilman and Pacala 1993, Chesson 2000, Gough et al. 2000), at least beyond a certain threshold of available resource (Grime 1973, Huston 1979). Thus, the theory of biotic acceptance can only work with a process that prevents local competitive exclusion. Such "equalizing" processes could come in many forms (Chesson 2000), but without them, a "good" site for many should be reduced to a great site for one. In addition, biotic acceptance theory does not explain why the rich tropics appear generally less invaded.

Two recent theories have been proposed specifically to account for the shift from fine-scale negative to large-scale positive NERRs. Both presume local communities are structured by competition for resources, and that the strength of local competitive interactions as a control on community invasibility diminishes as the variance of environmental conditions increases with scale. Byers and Noonburg (2003) presented a Lotka-Volterra competition model in which the number of unique resources available could increase with spatial scale. At fine scales with presumably few resources, invasion probability was relatively low; with fixed or only slightly increasing native richness at larger, more resource-rich spatial scales, the probability of invasion increased. Such a process of covarying scale and unique resources could thus drive a shift in negative to positive NERRs with increasing scale. However, as Byers and Noonburg note, (1) such a shift is predicted to be relatively small, (2) the shift requires native richness to be insensitive to the increase in unique resources with scale, and (3) other factors such as propagule pressure and disturbance are likely to be key contributors to the NERR shift.

Davies et al. (2005), building on the premise of Shea and Chesson (2002), presented a conceptual model of "niche opportunity" explaining the invasion paradox founded on the framework of spatial environmental

heterogeneity. Noting that few models predict increased invasion success with increases in mean resource levels (but see Tilman 1999), Davies et al. showed that positive NERRs at large scales (in this case >2500 m^2 in California grassland) are more tightly associated with the beta diversity of smaller (1 m^2) units within larger patches, rather than increases in mean alpha diversity as scale increases. Native and exotic richness were influenced by variance in soil resources (such as soil depth) rather than mean resource levels, suggesting that shifts in competitive dominance of different species over a range of resource levels favors the coexistence of natives and exotics on scales where such heterogeneity emerges (see also Huston and DeAngelis 1994, Tilman 2004). This theory is a spatial analogue to a temporal theory of fluctuating resources put forth by Davis et al. (2000).

A variation on these ideas also provides a potential solution to the invasion paradox (D. Tilman, *unpublished manuscript*). It also assumes that the number of coexisting species in a region is dependent on magnitude of the spatial habitat heterogeneity within that region. Within a biogeographic realm, the species pool of the realm would be able to saturate regions with low heterogeneity, making them difficult to invade because all combinations of conditions would be occupied by species with those niche requirements. In contrast, the fixed species pool of the realm would be progressively less able to saturate those regions with progressively greater heterogeneity. Such regions would have greater native richness and be more susceptible to invasion by exotics because the niche diversity of species could not fully exploit the greater heterogeneity of conditions in these regions. Thus, the niche saturation effect that is so consistently observed when novel species are added to biodiversity experiments could explain the greater number of exotic species in regions with greater native diversity, but only if the most diverse regions do have greater heterogeneity and it is less fully exploited.

Most would agree that the diversity of habitats (however defined) is an important contributor to large-scale native species richness (Preston 1960, Shmida and Wilson 1985, Rosenzweig 1995); areas containing more habitats will, all else equal, contain more native and exotic species. Missing from this general assessment are the particulars: If competitive processes dominate at fine scales, at what area thresholds should the shift from biotic- to abiotic-control of richness (and thus the NERR) occur (Shmida and Wilson 1985)? Which resources or environmental conditions underlie the shift to abiotic control? Theories of invasion are silent on these issues. There is thus a great need to incorporate studies that explicitly address the scaling of the underlying environmental template (e.g., Urban 2005) into invasion studies. Furthermore, heterogeneity can change without changing spatial scale: In particular, the variance in heterogeneity among small plots may be very large depending on underlying edaphic conditions or the presence of key habitat modifying species. Because fine-

scale NERRs can shift from positive to negative as heterogeneity decreases (Stachowicz and Byrnes 2006), this variability in the heterogeneity of fine-scale plots may also contribute to the lack of a consistent NERR at this scale.

SYNTHESIS: ONE THEORY FITS ALL OR A PLEA FOR PLURALISM?

Taken as a whole, the body of theory underlying patterns of native and exotic species richness offers as many as eight separate processes, which we summarize in Table 1. Given so many processes, a framework for invasion research that incorporates each mechanism would be complex and riddled with contingencies, and there is no reason to expect one simple solution will give adequate predictive ability of species invasion in all cases. However, we suggest the core of a framework for invasion is clear, built on the shift from biotic to environmental drivers with increases in scale. At fine scales where environmental and disturbance-based drivers of community composition are relatively homogenous, biotic interactions should have predictable impacts on the relative abundance of native and exotic invasive species. Such interactions could come in several forms, including (1) "neutral" competitive interactions at the level of individuals that place fundamental constraints on the total number of natives and exotic species that can coexist in a small area (thereby creating rarefaction-based statistical artifacts; process 1 in Table 1); (2) competitive interactions at the species level whereby ecologically similar species cannot coexist, thus making richer native communities more difficult to invade (process 2); and (3) facilitative interactions between exotic species that promote the invasion of additional exotics at the expense of native species, a process termed "invasional meltdown" (process 3; Simberloff and Von Holle 1999). The importance of each of these processes is particularly acute at scales where variation in other exogenous factors (disturbance, resource levels) is minimized, and each predicts a negative NERR (Table 1).

As spatial grain increases, the probability of significant spatial heterogeneity in environment or management regime increases; the more heterogeneous the area under consideration, the more likely biogeographic principles apply and the less likely biotic interactions will correctly predict the NERR. Processes 4 through 7 in Table 1 stem from the positive association between area and spatial heterogeneity. The dominant mechanism of biologically relevant heterogeneity could be that some communities are closer to propagule sources than others, and thus, may have more exotics or more total species overall regardless of the role of endogenous biotic interactions (process 4). Some communities may be subject to higher rates of disturbance, which, in turn, facilitate immigration-driven assembly and higher levels of native and exotic richness (process 5). At spatial grains large enough to incorporate significant environ-

TABLE 1. Summary of processes related to native–exotic richness relationship (NERR) patterns, listed with examples from theory, experiments, and observational data, and presumed relevance at fine and broad spatial scales.

Process	Examples from theory	Empirical or experimental demonstration
Negative NERR		
1) Statistical artifact	Fridley et al. (2004), Herben et al. (2004)	Fridley et al. (2004)
2) Eltonian biotic resistance	MacArthur (1970), Case (1990), Tilman (2004)	Levine et al. (2004), Fargione and Tilman (2005)
3) Invasional meltdown	Simberloff and Von Holle (1999)	Ricciardi and MacIssac (2000), O'Dowd (2003)
Positive NERR		
4) Neutral processes + spatial variance in community immigration rates	Fridley et al. (2004), Herben et al. (2004)	Tilman (1997), Levine (2000), Brown and Fridley (2002)
5) Neutral processes + spatial variance in disturbance rates	Tilman (2004)	none
6) Niche processes: spatial environmental heterogeneity	Shea and Chesson (2002), Byers and Noonburg (2003), Tilman (2004), Davies et al. (2005)	Naeem et al. (2000), Davies et al. (2005)
7) Niche processes: biotic acceptance + non-equilibrium conditions	Stohlgren et al. (2006b), Huston (2004)	Huenneke et al. (1990)
8) Facilitation (generalist)	Richardson et al. (2000), Bruno et al. (2003)	Von Holle (2005)

Notes: Neutral processes describe species with identical behaviors where properties of the habitat determine NERRs, while niche processes mandate that species respond differently to the environment.

mental heterogeneity, more heterogeneous sites should contain more natives and exotics (process 6), or those sites of higher quality on average should contain more natives and exotics if species in general prefer resource-rich conditions ("biotic acceptance"; process 7). The importance of these processes should be relevant to both spatial grain and spatial extent, given that NERRs are sensitive to the variance in environmental conditions both within and between survey units (Davies et al. 2005). In each case, the NERR prediction is positive, thus fitting the NERR pattern reported from nearly all broad-scale observational studies (Fig. 1).

In those circumstances where resident individuals facilitate the colonization and establishment of new species, a mechanism is established for positive relationships between native and exotic species richness at fine scales (process 8; Table 1). As for processes 1–3 related to biotic interactions, the significance of this mechanism should diminish as survey area increases. Because the processes of facilitation and niche-based competitive exclusion can act antagonistically in their effects on the NERR (cf. processes 2 and 8), where each is of equal strength, the net result may be no NERR, despite both processes being in operation (Stachowicz and Byrnes 2006).

To our knowledge, no single process of the eight identified in Table 1 can by itself generate the invasion paradox. Several general theories of invasion, however, couple at least two of the processes, including Byers and

Noonburg (2003), Tilman (2004), and Davies et al. (2005; see also Shea and Chesson 2002). The most common coupling of processes is that of biotic resistance (process 2) and spatial heterogeneity in environmental resources (process 6), immigration rates (process 4), or disturbance (process 5); any of which can produce the invasion paradox. But what of the other processes? At small enough scales, statistical artifacts (process 1) must occur (Preston 1960, Fridley et al. 2004); moreover, there is some evidence (at least for plant communities) that some environments are "good sites" (process 7) that can potentially support many more species than others (MacArthur 1972, Brown 1995, Grime 2001, Peet et al. 2003). Facilitation of exotics (process 8) is of clear importance in some systems, especially marine invertebrate systems (Stachowicz 2001, Stachowicz and Byrnes 2006), and the invasional meltdown hypothesis (process 3) has received some empirical support, especially in aquatic systems (Ricciardi and MacIsaac 2000, Ricciardi 2001, Adams et al. 2003, O'Dowd et al. 2003, Floerl et al. 2004, Grosholz 2005). Any general theory of invasion must, therefore, be able to accommodate each process. But must one theory fit all? Theorists are all too familiar with the necessary trade-offs of model accuracy and efficiency for making general predictions of ecological phenomena; we leave the epistemological issues of seeking laws to explain biodiversity across scales and systems to others (Lawton 1999, Gaston 2000). Within the specific context of the invasion paradox, however,

Table 1. Extended.

Consistent observational data	Fine-scale importance	Broad-scale importance
Brown and Peet (2003), Bruno et al. (2004), Fridley et al. (2004), Herben et al. (2004)	high	low
Morgan 1998, Stachowicz et al. 2002	high	low
Crosby (1986)	high	high
Levine (2000), Brown and Peet (2003), Stohlgren et al. (1999, 2006b), Seabloom et al. (2006)	low	high
Stohlgren et al. (1999, 2006b), Brown and Peet (2003)	low	high
Stohlgren et al. (1999), MacDonald et al. (1989)	low	high
Stohlgren et al. (1999, 2006a), Brown and Peet (2003), Gilbert and Lechowicz (2005), Seabloom et al. (2006)	high	high
Stachowicz and Byrnes (2006), B. Von Holle (unpublished manuscript)	high	low

we make the following observations that may aid in unifying processes across systems.

First, we observe that the invasion paradox may not exist for many types of habitats, in that (1) NERRs are positive at both fine- and broad-spatial scales, or (2) broad-scale NERRs are explicable once additional causative factors, such as temporal or spatial variability in environmental factors or disturbances rates, are considered. In the first case, a model of such systems may not require processes that lead to negative NERRs, although at a small enough scale, negative NERRs are inevitable due to statistical artifacts (Fridley et al. 2004, Herben et al. 2004). In the second case, explicit consideration of the covarying factors that control both native and exotic richness and how they are distributed at multiple spatial scales, while often logistically difficult, could allow fine-scale experimental results to be scaled up to whole landscapes (Shea and Chesson 2002, Davies et al. 2005).

Second, simple positive NERRs do not preclude the existence of negative resident neighborhood effects on species invasion. It may be that neighborhood effects decrease the slope of NERRs without actually producing a negative NERR; the actual slope is determined by the net outcome of numerous interacting processes that operate on local and regional scales (Davis et al. 2000, Levine 2000, Naeem et al. 2000, Seabloom et al. 2003, Tilman 2004, Stachowicz and Byrnes 2006). Phenomenological models that include the effects of both local and regional processes have been shown to provide the best fit to multi-scale invasion data (Huston 2004; M.

Smith, *unpublished manuscript*). Null-modeling approaches that examine community assembly by statistically removing a particular process of interest (such as niche-based competitive sorting) should help identify how particular processes influence the shape of NERRs at different scales (Fridley et al. 2004).

Third, community theory may be better able to explain the behavior of particular exotic species in relation to biotic (neighborhood) and abiotic (regional) influences, rather than exotic richness per se. Although focus on exotic richness is understandable, given the current popularity of biodiversity in community and ecosystem ecology (Naeem 2002), exotic richness is a coarse measure of invasion and may not be related to the threat imposed by exotics on native extinctions. Still, it is interesting from a theoretical standpoint to document whether there is any nontrivial limit to how many species a given area can hold; that is, whether communities are becoming truly species saturated (Sax et al. 2002, 2005, Sax and Gaines 2005).

Finally, we conclude that a principal cause of the invasion paradox is the necessary but analytically difficult juxtaposition of experimental and observational data (Fig. 1). Although we suspect most researchers of species invasions would agree that truth lies at the confluence of observation, theory, and experiment, we acknowledge that some researchers remain strongly divided over whether either fine-scale experimentation by itself, or broad-scale univariate or multivariate correlation by itself, can address the causes and management of species invasions. Well-conceived experiments are essential tools by which we arrive at ecological truth (and thus construct tools for managing ecosystems), but they are highly constrained, imperfect instruments that must be continually evaluated and framed by correlative observations (Naeem 2001). Correlational studies are similarly imperfect and always subject to the possibility that some unmeasured or otherwise ignored process is the true cause of whatever pattern has been observed. Appropriate application of experiments to broader scales and different systems requires some knowledge of how experimental processes scale up to heterogeneous landscapes; such rules are potentially complex (Levin 1992). Managers of species invasions face the difficult task of seeking insight from the currently conflicting results that are the basis of the invasion paradox. Broad-scale inventory and monitoring data (i.e., correlations) provide preliminary models of how invasive species are distributed in relation to native biota, the environmental template of the landscape, and various natural and human-caused disturbances. There would appear to be considerable management utility in the development of scaling rules that allow application of fine-scale experimental results, or in developing techniques that must be implemented locally, such as plant community restoration. Indeed, experimental results offer much guidance for restorations, for example, by

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suggesting which native species may offer greatest resistance to recruitment of invasive species.

We also note that theory and experiments often ask subtly different questions than observational studies, and thus, negative NERRs from experiments and theory need not have to "fit" within observational patterns at either fine or broad scales. Within an invasion context, experiments (and most theory) tend to address the consequences of species loss (or addition) on community invasibility. Thus, for a given community, experiments isolate the influence of composition and resident richness on invasibility (Levine 2000, Shea and Chesson 2002), while using replication and randomization to "hold all else constant." In nature, though, all else is rarely, if ever, constant. Suites of factors are likely to be correlated, negatively and positively, and thus, to exert influence in nature that would not be observable in experiments that did not manipulate these factors, or at best are only able to examine a limited extent of spatial heterogeneity. Observational surveys, if they are thorough and measure such additional variables, can help identify which processes and factors can best explain, in a statistical sense, the propensity of sites to be subject to invasions. Such analyses should then lead to experimental tests of these added factors, and so on.

We advocate an approach to species invasions that is inherently pluralistic and reflects the strong likelihood that: (1) Broad-scale patterns of native and exotic species richness are strongly influenced by abiotic factors such as disturbance rates, environmental favorableness and heterogeneity, and landscape configuration and history as a determinant of immigration rates; (2) the imprint of species interactions on native–exotic richness patterns is most apparent at the fine scales at which individual organisms interact with each other; (3) experimental approaches, when designed for a particular broader scale context, can provide strong inference for specific mechanisms underlying native–exotic richness relationships but are often difficult to scale up to large areas; (4) observational approaches are an essential piece of the research strategy on species invasions and are often the only predictive tool available for managing invasive species within landscapes. A solution to the invasion paradox will likely emerge when more ecologists from both sides of the experimental–observational spectrum explicitly engage in the process of uncovering scaling rules for coupling fine and broad-scale patterns for a diverse array of ecosystems.

Remaining Questions

We have suggested that the library of NERRs for natural systems is far from complete as a general representation of ecosystems: Few such data are available for tropical systems, while terrestrial grasslands and forests are well represented, and most analyses, to date, have been univariate. As patterns accumulate, new questions will emerge and theory will be refined. Our survey of the current body of evidence

for the invasion paradox suggests several currently unresolved issues, which include the following.

Where should negative vs. positive fine-scale NERRs be expected?

Brown and Peet (2003; see also Davis et al. 2000, Levine 2000) suggest that positive NERRs should be expected in dispersal- or immigration-driven communities, such as riparian corridors, or highly disturbed systems such as roadsides or agrarian landscapes. Systems where niche-driven assembly is important should yield negative NERRs (Tilman 2004); it is likely that these will be in areas where disturbance rates are low, such as shaded, non-successional uplands or nutrient-poor ecosystems. Systems with generalist facilitators (foundation species) might produce positive NERRs (Stachowicz 2001, Bruno et al. 2004, Stachowicz and Byrnes 2006). Additionally, facilitation between nonnative invaders and native species (Richardson et al. 2000) may occur in stressful (Smith et al. 2004; B. Von Holle, *unpublished manuscript*) or highly disturbed areas, whereas competition-based processes may occur more commonly in more benign areas, as has been found for native–native interactions across a range of ecosystems (Callaway and Walker 1997). Additional accumulation of patterns from different systems may bring about emergence of a general context-dependent theory of species invasions built upon the relative importance of immigration vs. extinction processes.

If many rich areas are getting richer, is there a limit to how many species an area can contain?

Although many areas are seeing net increases in species, with few exceptions (such as the addition of annual exotic grasses to shrublands in the western United States), there is little evidence that areas are increasing in how many individuals they contain. If true, then a trivial limit to species richness is the total number of individuals in an area. For large areas where populations are not influenced by outside immigration, there is an additional consideration of minimum population size, which will place still lower limits on total species richness, suggesting a "species capacity concept" (Sax et al. 2005). Even for smaller areas, the necessary decrease of population size as total richness increases could lead to eventual local extinction of species that are increasingly rare (Parker et al. 1999). Over evolutionary time scales, communities more saturated with species are expected to exhibit lower speciation rates (Rosenzweig 2001). Given the obvious net rise in species richness from species introductions in many plant communities (Sax et al. 2002, Sax and Gaines 2003), this is an important area for future research. A key consideration will be whether the current net increases are stable, or whether significant time lags to native extinctions will ultimately reveal few changes in richness. The clear difference between plant

and animal communities in the frequency of exotic-caused native extinctions (Gurevitch and Padilla 2004) may be an indication of the greater time lag associated with species interactions in sessile organisms, thus creating the possibility that the increasing net richness of plant communities is ephemeral. However, the historical importance of isolation in reducing the importance of colonization suggests that many taxonomic groups may instead be expected to see continuing increases in net richness at regional scales (Whittaker 1972, Sax et al. 2005, Sax and Gaines 2005).

How do patterns of invasion differ in the tropics?

Very few patterns of species invasion for the New or Old World tropics have been published, but preliminary examinations suggest that species rich tropical ecosystems (particularly continental ones) are substantially less invaded than temperate ecosystems (Sax and Gaines 2005), as evinced for vascular plants (Rejmanek 1996), as well as birds and mammals (Sax 2001). This disconnect between patterns of invasion in temperate and tropical areas means that examinations of NERRs that span temperate and tropical latitudes (i.e., a larger spatial extent) may show negative relationships, i.e. the opposite of the positive relationships typically seen when examining NERRs at large spatial scales within temperate areas. An example of this can be seen with plants in U.S. and Mexican states (Fig. 2). In this case, despite a positive trend between native and exotic richness within the U.S. states and despite a significantly positive relationship within Mexican states, the overall trend is flat (Fig. 2). Although the pattern illustrated here for vascular plants within Mexican states shows a positive NERR, we stress that so little work has been done on NERRs in the tropics (particularly across taxonomic groups or spatial scales) that it is not possible to conclude yet whether there are general relationships between native and exotic richness in tropical areas. What is clear at this point is that overall tropical mainland areas are invaded by many fewer exotic species than temperate mainland areas. We note, however, that patterns of invasion on islands are often comparable between tropical and temperate islands (Sax et al. 2002).

Several factors could explain the apparent shortage of exotic species in the tropics. Tropical mainland areas may be relatively more difficult to invade. Although the tropical weed flora associated with human-dominated ecosystems is extensive and well dispersed globally (Holm et al. 1991), there appear to be very few species able to invade intact tropical forests (Fine 2002), in contrast to some of the most widespread invaders of temperate biomes. Reasons for this remain unclear. Tropical systems are generally highly weathered and have nutrient-poor, acidic soils (Sanchez et al. 1982), conditions that are associated with lower invasion rates in temperate ecosystems (Stohlgren et al. 2006b). It has also long been suggested that biotic interactions are more intense in the tropics (Dobzhansky 1950, Mac-
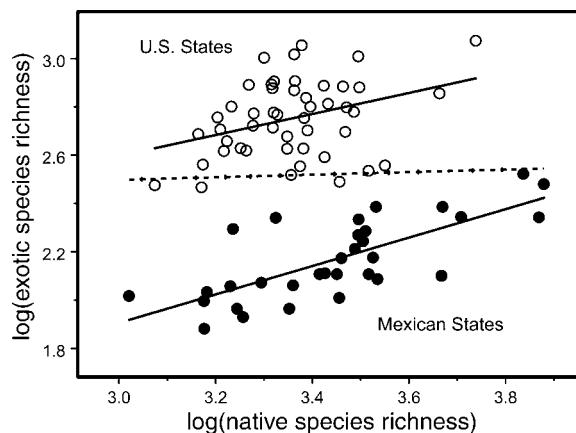

FIG. 2.   State-level richness of native and exotic plants in the continental United States and Mexico. The dashed line is a linear regression on both data sets; solid lines are regressions within data sets. Data from the United States are for all vascular plants (Kartesz 1999), and data from Mexico are for angiosperms (Villaseñor and Espinosa-Garcia 2004).

Arthur 1972, Brown 1995), which, if true, suggests that biotic interactions are a more important component to invasion resistance in tropical systems. However, tropical systems may also experience limited propagule supply, i.e., a limited number of introduction attempts (both intentional and unintentional) relative to mainland temperate areas. This seems unlikely to be the entire explanation, as, for example, mainland areas of tropical Mexico should have been subject to many species introductions due to their historical patterns of occupation by humans (Sax 2001). Nevertheless, the relative importance of propagule pressure remains largely unknown for most groups (Lockwood et al. 2005), and it would be premature to rule out this explanation with out additional data. Finally, in passing, we note that human cultures have also generally resisted invasion in the tropics (Crosby 1986, Diamond 1999); whether this bears significance to ecological systems remains unknown. There is an urgent need for additional study of species invasion patterns in the tropics, particularly within the context of their apparent invasion resistance and its relevance to other ecosystems.

How important is competition as a contributor to species invasion patterns?

Global species extinctions attributed to invasive species have been from invasions by predators, parasites, or diseases and susceptible native prey; few if any known examples have been directly linked to competitive exclusion (Davis 2003, Gurevitch and Padilla 2004). Furthermore, recent reviews of species interactions (Bruno et al. 2003, 2005) have suggested that the relative importance of positive interactions in structuring communities may be far more important than previously thought. If true, then reliance on competition as the major foundation for theoretical predictions of relation-

ships between native and exotic species richness may be misleading. Instead, theory that also incorporates facilitative interactions (Bruno et al. 2003), environmental tolerances of natives and exotics (Davies et al. 2005, Stohlgren et al. 2006b), or examinations of the role predation, parasitism, and disease play in limiting species invasions may ultimately be more predictive. As some form of biomass disturbance within the lifespan of many organisms is a common component to most ecosystems (Pickett and White 1985), the absence of disturbance from many experimental studies may partially explain the divide between experiments and observations of NERRs (Tilman 2004, Stohlgren et al. 2006b; M. Smith, *unpublished manuscript*). Furthermore, the processes of competition and local species interactions in general may not contribute much to broad-scale biodiversity patterns, or at least aid in their prediction, even though they are strongly manifest in fine-scale studies.

What essential features of natural systems are missing from invasion experiments?

Multifactorial experiments that either manipulate extraneous factors (Seabloom et al. 2003) or perform in situ manipulations amid natural ecosystem variation (Levine 2000) have added important information on the relative controls of local and regional processes in promoting species invasions. However, there have been relatively few attempts to construct experimental manipulations that simulate natural patterns of environmental heterogeneity, disturbances regimes, or realistic community assembly processes (Stohlgren 2002), for obvious reasons of practicality. Species in natural communities occur at various levels of spatial aggregation at different scales and do not represent one simultaneous cohort. Researchers rarely exploit natural patterns of environmental heterogeneity within which to perform experiments. Exotic species are also a highly nonrandom selection of the world's biota; it is thus likely that "invasion" experiments that use a native invader will differ qualitatively from those using exotic invaders (Von Holle and Simberloff 2005). There are other considerations that may be outside the limits of experimentation, such as processes occurring at large spatial and temporal scales (such as disease effects on long-lived organisms) and the relative importance of large natural disturbance events (such as hurricanes) that are extremely difficult to simulate. Use of observational data and careful monitoring (such as pre- and post-disturbance) are necessary to derive a complete picture of the processes underlying invasions across scales.

CONCLUSION: WHAT DOES THE PARADOX IMPLY FOR INVASION MANAGEMENT?

Whether a true invasion paradox exists or not for a particular system, the separation of negative vs. positive native–exotic richness relationships for different scales and research methods gives two complementary recommendations for the management of exotic species invasions. We conclude that these observations are substantively supported by current evidence.

1) *For the purposes of conservation of native plant communities and resisting the undesirable ecological and economic effects of invasive species, managers should be aware that diverse native communities are often readily invaded by exotic species.* Where such information is available, managers should focus invasive resistance efforts in (1) riparian corridors, locations near shipping ports, and other habitats of high propagule supply; (2) sites of high resource availability and heterogeneity; for plants, sites might include those of fertile, mesic soils and high light availability; and (3) frequently disturbed habitats. These conditions often produce high native species richness, and yet are heavily invaded by exotic species (Stohlgren et al. 1999, 2003, Huston 2004).

2) *Given a particular location that is susceptible to recurrent exotic invasion, native species richness can contribute to invasion resistance by means of neighborhood interactions and should be maintained or restored.* It may be cost prohibitive for resource stewards to manage species at highly local scales across whole landscapes. However, maintaining local biodiversity should be particularly important in highly seasonal or annually fluctuating environments where single or few species cannot exploit all available resources through time (e.g., Stachowicz et al. 2002). Exceptions might include systems where resident diversity facilitates invasion (Von Holle 2005) and where facilitators benefit both natives and exotics (Stachowicz and Byrnes 2006). Nonetheless, continual saturation of habitats by native individuals should often be an effective deterrent to exotic invasion, particularly in favorable environments where environmental resistance to exotic colonization is low.

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CONCEPTS & SYNTHESIS