

Species Invasions and the Relationships between Species Diversity, Community Saturation, and Ecosystem Functioning

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In this chapter, we examine how the ecology of invasions helps clarify the relationships among community saturation, diversity, and ecosystem functioning. We begin with a theoretical approach that suggests a common underlying mechanism for the negative effect of diversity on community invasibility and other ecosystem functions, such as productivity. This stochastic model of community assembly predicts that, within a given habitat, increasing species richness should reduce resource availability and decrease invasion success. A brief review of evidence from the fossil record of biotic interchanges reveals that the less diverse region is typically more invaded by species than the more species-rich region. The reason for this could be either that species-poor regions have greater resource availability (there are empty niches), or that species from more diverse regions are competitively superior. Experimental studies with recent invaders suggest that, all else being equal, increasing diversity decreases invasion success by decreasing resource availability. More complete or efficient utilization of resources at higher diversity extends beyond invasion resistance in its contribution to other ecosystem processes, such as productivity, nutrient recycling, and stability/consistency. In accord with theory, data from both grassland plants and marine invertebrates suggest that successful invaders are those with niche requirements most different from those of species in the existing community, providing a degree of determinism to an otherwise

stochastic community assembly process. We also suggest some other ways in which the study of introduced species could increase our understanding of diversity and its impacts on ecosystem processes.

Introduction

The geologic history of life on earth has been one of long periods of isolation of biogeographic realms interrupted by periods of immigration when continents collided or land bridges were exposed by lowered sea levels (e.g., Flannery 2001). More recently, human transport has caused a massive increase in introductions of nonindigenous species. For instance, about half of the plant species of Hawaii are exotics, as are about 20% of those of California (Sax et al. 2002; Sax and Gaines 2003). Similarly, San Francisco Bay contains at least several hundred exotic invertebrates, which constitute up to 99% of the biomass at some sites (Cohen and Carlton 1998; Ruiz et al. 2000). Because the same processes that influence invasion by exotic species should also influence the assembly, composition, structure, and diversity of natural communities, the study of invasions—whether human-driven or natural—should provide insight into fundamental ecological processes. In this regard, invasions can be viewed as inadvertent and often unreplicated, but large-scale and long-term, “experiments” that, in total across a wide variety of situations, may provide ecological insights that small-scale, short-term deliberate experiments might never provide.

From a societal perspective, species invasions can pose serious threats to human economic interests or to native species. Introduced agricultural pests such as the Mediterranean fruit fly and various agricultural weeds and diseases impose significant costs on agriculture. Introductions of rats, snakes, and other predators led to a massive wave of bird extinctions in the Pacific islands (Pimm 1987). Invasions of the North American Great Lakes by zebra mussels and sea lampreys have dramatically altered the biota of those lakes via both alteration of the standing stock of phytoplankton and effects on commercially important fish species. Similarly, on land, Argentine ants have displaced native ant fauna in the western United States and imposed significant pest control costs. Regardless of the potential consequences of invasions, it is undeniable that new species are being added to regional biotas by human-mediated transport and that increased understanding of the causes and consequences of these invasions would be valuable.

In this chapter, we discuss the application of the study of invasions in both geologic and recent times to understanding the relationship between community saturation, diversity, and ecosystem functioning. Theoretical discussions of the relationship between the number of species in a system and the productivity or stability of the system have a long history (see Tilman and Lehman 2001 for review). With growing threats to global species diversity from human activities such as habitat modification, concern has mounted as to the

consequences of species losses for the functioning of ecosystems. This concern has renewed interest within ecology in the relationship between the number or diversity of species in a community and the extent to which that community maintains its functioning. Indeed, experimental tests of relationships between diversity and ecosystem processes such as productivity, stability, and invasibility have increased rapidly in the last 10 years (e.g., see chapters in Kinzig et al. 2001 and in Loreau et al. 2002).

One of the older hypotheses about the relationship between diversity and ecosystem processes is that more diverse communities should be more resistant to invasion (Elton 1958). The most commonly cited mechanism behind this phenomenon is that as species accumulate, competition intensifies and fewer resources remain available for new colonists (Elton 1958; Case 1990). Experimental and observational approaches to this problem have sometimes yielded conflicting results (see the excellent review by Levine and D'Antonio 1999; Fargione et al. 2003; Taylor and Irwin 2004). Studies that employ both approaches simultaneously show that, all else being equal, diversity does reduce invasion success, although this mechanism is sometimes overwhelmed by other forces, such as propagule supply or disturbance (Levine 2000; Stachowicz et al. 2002a). But the issue of more complete or efficient utilization of resources extends beyond invasion resistance in its contribution to ecosystem functioning, with links to other ecosystem processes such as productivity, nutrient recycling, and stability/consistency. Our aim in this chapter is to assess how studies of invasions inform us about the relationship between the number of species and the utilization of resources in a community and to apply this knowledge to enhance our understanding of the relationship between diversity and ecosystem functioning.

We begin by considering some simple theory, based on trade-offs in resource use, that outlines how increasing species diversity is expected to decrease the amount of available resources and thus decrease invasion success. We then proceed to assess the mechanistic experimental evidence in support of the theory and how this evidence has already contributed to our broader understanding of diversity-saturation-ecosystem functioning relationships. We then evaluate experimental and theoretical predictions in light of evidence from invasions across spatial and temporal scales. To do this, we begin by briefly reviewing evidence from natural biotic interchanges that occur among biogeographic regions on geologic time scales and evaluate possible hypotheses for the highly asymmetrical exchange among biotas that typically occurs. We then compare these findings with those from more recent, human-mediated, biotic exchanges. Next, we compare observational and experimental approaches to studying the diversity-invasibility relationship within a single biogeographic region, reconciling the often disparate results obtained by the two approaches. These sections paint a picture of how changing species richness affects resource use across spatial and temporal scales. Because total resource use is coupled to so many other ecosystem functions, such as productivity and nutrient cycling, we then assess what diversity-invasibility studies can tell us more gen-

erally about the relationship between diversity and ecosystem functioning. We end with suggestions for additional ways in which invasions may be exploited to learn about these relationships.

Theory

Insight into the factors controlling the success or failure of invasive species is provided by considering the mechanisms of interaction among established and invading species. Because there are many such mechanisms, including competition for resources, interference competition, mutualism, and top-down forces such as herbivory, predation, and disease, there is no simple, general theory of invasion. Here we will focus on the role that competitive interactions can play as controllers of invasion dynamics (e.g., Case 1990; Tilman 1999a, 2004), but we stress that top-down forces are likely to be of at least equal importance, as witnessed by the major effects that invasive diseases and predators have had on their host and prey species (e.g., Lafferty et al. and Bruno et al., this volume).

Resource competition theory predicts that numerous species can coexist if species have trade-offs in their traits and if the habitat is spatially or temporally heterogeneous (Tilman 1982, 1988). Consider a case in which plant species compete for two limiting resources and in which the habitat has spatial heterogeneity in these two resources (Tilman 1982). The trade-off needed for species to coexist is that species that are better at competing for one of the resources are necessarily poorer at competing for the other resource. This causes each species to have a particular ratio of resource 1 (R_1) and resource 2 (R_2) at which it is the superior competitor. These ratios all fall on a curve, the interspecific trade-off curve (Figure 2.1A). Every point on this curve represents the traits of a potential species that would be able to stably coexist with any and all other potential species if the habitat had a continuous gradient in the supply rates of these resources.

How, then, might established species influence the success or failure of potential invaders? Insight might be provided by stochastic niche assembly theory, which explores the effects of resource competition and stochastic birth-death processes on the probability of establishment of rare invaders (Tilman 2004). Let us start by considering cases in which the invaders have traits that are drawn from the same trade-off curve as the established species. A new invader has to survive, grow, and reproduce using the resources left unconsumed by established species. Consider the pattern of unconsumed resources left by the three-species community in Figure 2.1B. These species create four distinct “patches” of usable resources (shaded areas). The probability that an invader could survive and grow to maturity and then reproduce would be highly dependent on its traits relative to the traits of the established species. These probabilities (calculated as in Tilman 2004) are shown in Figure 2.2B as a function of the optimum $R_1:R_2$ ratios of potential invaders. Invaders that are

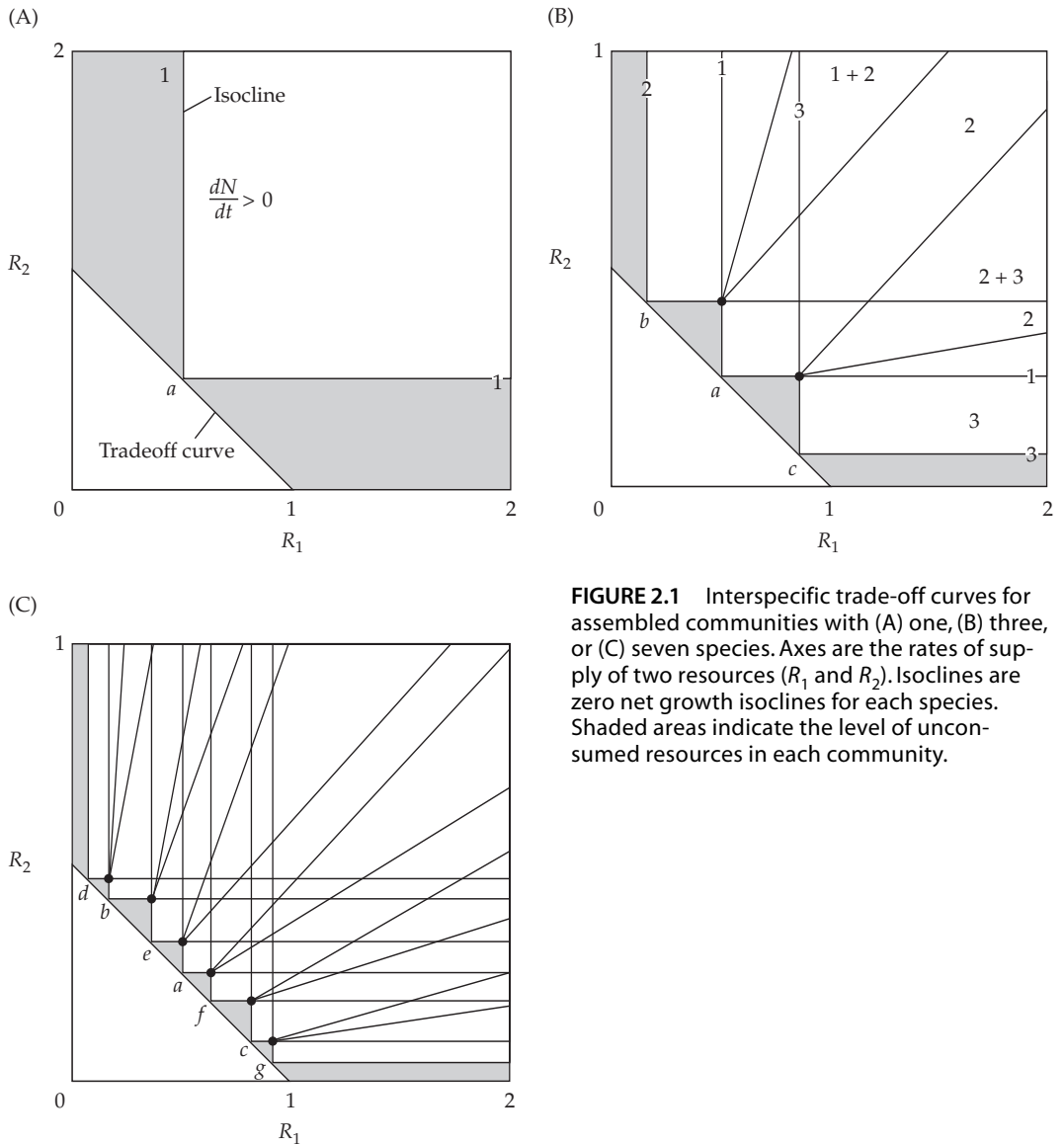


FIGURE 2.1 Interspecific trade-off curves for assembled communities with (A) one, (B) three, or (C) seven species. Axes are the rates of supply of two resources (R_1 and R_2). Isoclines are zero net growth isoclines for each species. Shaded areas indicate the level of un-consumed resources in each community.

similar to the three established species would have very low chances of successful establishment because of their extremely low growth rates. Their low growth rates would cause such invaders to require a long period to become reproductive adults, and thus expose them to mortality for a long time. This greatly decreases the probability of establishment by an invader that is similar to the established species. In contrast, potential invaders would have much higher growth rates, reach maturity more quickly, and have a higher proba-

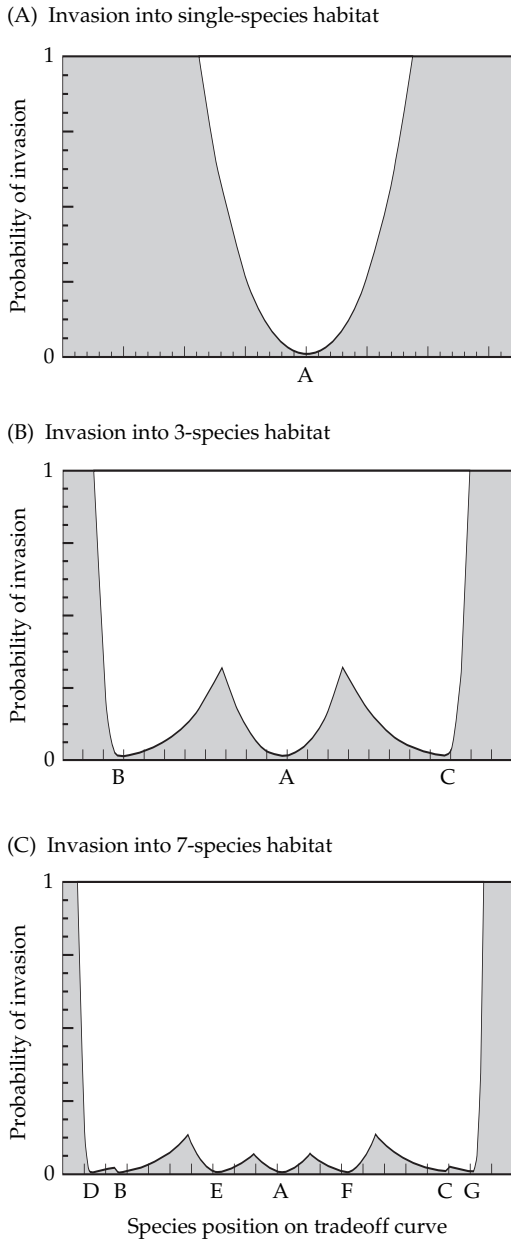


FIGURE 2.2 Probability of invasion as a function of the invader's position on the interspecific trade-off curve for each of the communities in Figure 2.1. Species with a position on the trade-off curve most distant from those of the species in the existing community have the highest probability of successful invasion. Thus, while there is no absolute limit to the number of species in a community, the probability of successful invasion becomes smaller with increasing numbers of species in the community.

bility that they and their progeny would become established if they had resource requirements that better matched the peaks of resources left unconsumed by the established species (Tilman 2004).

The probabilities of invasion into the three-species community can be compared with those of invasion into the seven-species community in Figure 2.1C. In this more diverse community, there is more complete utilization of the limiting resources, creating much smaller peaks of unconsumed resources. Compared with the less diverse community, this greatly reduces the probabilities of invasion (Figure 2.2C) by species drawn from the same trade-off curve. Note, though, that there would still be a strong patterning to any invasion, with potential invaders that are maximally different from existing species having the greatest chance of establishment.

This brief summary of stochastic niche theory (Tilman 2004), which combines the effects of competition and demographic stochasticity on rare invaders, shows that the chance of successful invasion should decrease markedly as the diversity of the established community increases (Figure

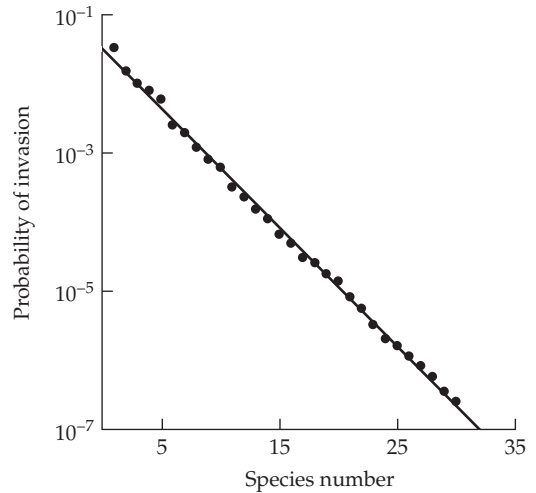
2.3; see also Tilman 2004). Indeed, the log of the probability of further invasion is an approximately linearly decreasing function of the number of established species. In the example of Figure 2.3, each additional species that becomes established in a community decreases by about 30% the chance that another invader

FIGURE 2.3 Results of simulations showing that the probability of invasion decreases with increasing numbers of species in the community. See text and Tilman 2004 for details.

will become established. Once the habitat of Figure 2.3 had accumulated 32 species, for instance, only 1 propagule out of every 10^7 would tend to be successful at becoming established. This extremely low probability of establishment is a result of the low and relatively uniform levels of resources left unconsumed by communities assembled by stochastic niche processes.

This theory (Tilman 2004), as summarized above, assumes that established and invading species have competitive trade-offs that are drawn from the same underlying trade-off surface. With this assumption (which we will later relax), the theory predicts that (1) high-diversity naturally assembled communities should be highly resistant to invasion, (2) successful invaders should decrease the abundances mainly of species that are competitively similar to themselves (that are close to them on the trade-off surface), and (3) successful invading species should rarely, if ever, drive established competitors extinct. From these three predictions, it also should follow that (4) invasions by exotic species should lead to a net increase in regional diversity (e.g., as shown experimentally by Tilman 1997 and via survey by Sax et al. 2002) and (5) exotic species should be much more common and abundant in disturbed habitats because of higher resource levels or lower diversity due to recent extinctions.

Some of these predictions may seem, on their surface, to be contradicted by the many examples of high abundances reached by exotic invasive species in contemporary communities. For example, exotic annuals reach high abundances in California grasslands, and the exotic grass *Bromus tectorum* forms abundant stands in the Intermountain West of the United States, as does (or did) the *Opuntia* cactus in Australia and *Hypericum* (St. John's wort) in Oregon and northern California. However, in each of these cases, exotic species were invading and spreading across habitats that had already been disturbed by cattle grazing. Similarly, the Asian clam *Potamocorbula* in San Francisco Bay and the ascidian *Didemnum lahellei* in the Gulf of Maine have reached high abundances in environments disturbed by mechanized fishing and other human activities. These examples demonstrate that resident species richness is by no means the only factor affecting resource availability and that the combined and interactive effects of resident species richness, disturbance regimes, and site fertility on resource levels and invasions must be considered (e.g., Davis et al. 2000). For example, disturbance, by freeing up resources, could facilitate inva-



sion simply by increasing the probability that a non-native will become established if introduced or by favoring invaders with life histories that are better adapted to disturbance than those of residents.

Now that we have laid out some basic theory and predictions, let us begin by examining the experimental evidence for the proposed linkages between diversity, resource use, and invasibility and what it can contribute to our understanding of diversity-ecosystem function relationships.

Invasions and the Mechanistic Underpinnings of Diversity-Ecosystem Functioning Relationships

Investigations of the role of diversity in invasion success have already contributed significantly to our understanding of the relationship between diversity and ecosystem processes in the broader sense by pushing for more rigorous examination of the mechanism(s) underlying the potential effect of diversity on invasibility. The studies that have examined this issue have supported the idea that, all else being equal, higher species richness leads to a reduction in the availability of resources (Stachowicz et al. 1999, 2002a; Tilman 1999a; Fargione et al. 2003), in agreement with the theory presented above. We discuss below specifically what these findings contribute to our understanding of the consequences of changing diversity for ecosystem structure and functioning.

By what mechanisms might increasing diversity enhance resource use and thus lead to increased ecosystem functioning? First, diversity may lead to enhanced ecosystem functioning simply because more species-rich communities have a higher probability of containing a “strong interactor”; that is, a species with a dominant effect on resource levels. This effect, termed the “sampling effect” (Aarssen 1997; Huston 1997; Tilman et al. 1997), would seem to be a plausible explanation for observed diversity-invasibility and diversity-ecosystem functioning relationships. However, a variety of tests have rejected the sampling hypothesis as a significant explanation for the observed diversity-productivity relations, suggesting instead that complementary use of resources by species with different niche requirements, such that more diverse communities more completely use available resources, may best explain the effect of diversity on productivity (e.g., Loreau and Hector 2001; Tilman et al. 2001, 2002; Hille Ris Lambers et al. 2004). Although sampling effects may overwhelm complementarity in some studies, this appears likely to occur only in the short term (e.g., Tilman et al. 2002). Similarly, sampling rarely seems to be the major explanation underlying diversity-invasibility relationships (e.g., Knops et al. 1999; Stachowicz et al. 1999, 2002; Naeem et al. 2000; Fargione et al. 2003). Rather, these studies suggest that niche differences and resulting complementary interactions better explain the observed effects of diversity on productivity and invasibility.

In addition to complementary use of resources at any one time, species might differ in their seasonal phenologies such that they occupy different “temporal” niches. As Davis et al. (2000) pointed out, fluctuations in resource availability

can have a major effect on the susceptibility of the local community to invasion. Resident species and their temporal patterns of resource use (e.g., seasonal phenologies) are one possible cause of predictable variation in resource availability. For example, in sessile marine invertebrate communities, invasion resistance increases with diversity because individual species are complementary in their temporal patterns of space occupation (Stachowicz et al. 1999, 2002a). Established communities with many species maintain relatively high cover and low resource availability over time, despite high variation in the temporal abundance of individual species (Stachowicz et al. 2002a). In contrast, species-poor communities undergo large fluctuations in resource availability as a result of the seasonal boom-and-bust cycles of their dominant species (Figure 2.4A). Thus, as suggested by Davis et al. (2000), invasion is more likely in areas of fluctuating resource availability (species-poor communities) than in areas of predictably low resource availability (species-rich communities) (Stachowicz et al. 2002a).

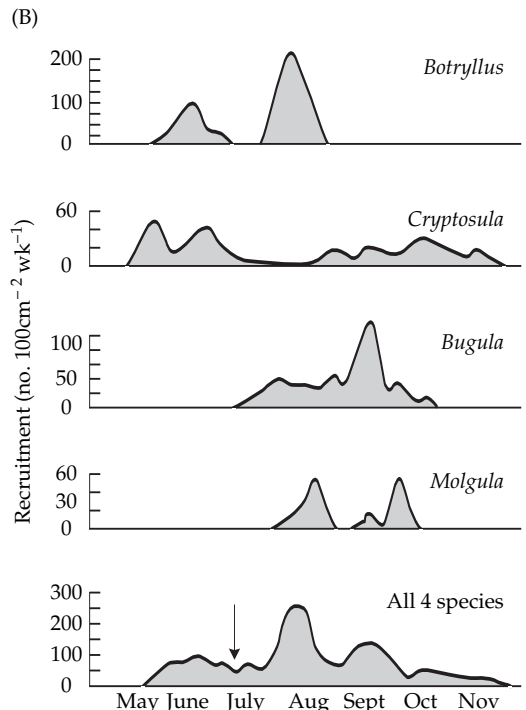
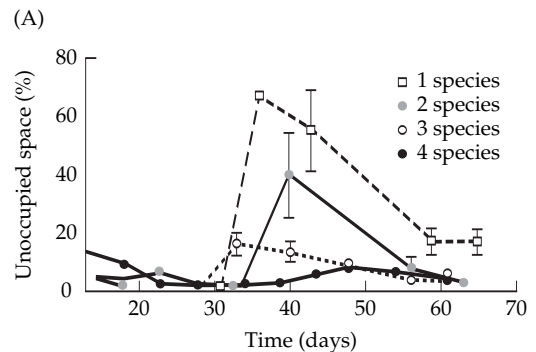


FIGURE 2.4 (A) Results of experimental manipulations of diversity, showing large peaks in the availability of a limiting resource (available space) in low-diversity communities and consistently low resource availability (i.e., high space occupation) in more diverse communities. This pattern resulted in a negative relationship between native diversity and invader survival and abundance. (B) Temporal variation in the recruitment patterns of sessile marine invertebrates, showing temporal complementarity in seasonal patterns of abundance among native species. Total recruitment is consistently high over the course of the entire season when multiple native species are added to the system, and there are few periods of low recruitment. The arrow indicates the peak in the timing of recruitment for one of the most successful introduced species in this community, *Botrylloides violaceous*. Note that the peak in seasonal abundance of this invader corresponds to a period of low recruitment by natives. (A after Stachowicz et al. 1999, 2002a; B after J. Stachowicz, unpublished data.)

Observational studies across multiple years show similar correlations between local species richness and occupation of space in rocky subtidal habitats (Osman 1977). Despite differences in growth forms, species seem to compete primarily for space, the likely limiting resource in this system. Because species differ in growth rates, in the timing, duration, and magnitude of reproductive output, in the degree to which they are capable of local recruitment, and in their response to biotic and physical stresses, the seasonal fluctuations in abundance of each species tend to be out of phase with one another. In Figure 2.4B we provide one example from records of settlement of marine invertebrates onto 10×10 cm bare substrates placed within an established community (detailed methods are given in Stachowicz et al. 2002b). Such substrates reach 100% cover within a few months after deployment, with the dominant species being those that recruited in the first few weeks of deployment. Thus, one can view these settlement records as a proxy for which species would be likely to become established in gaps within established communities throughout the course of the season. As a result of seasonal complementarity in settlement patterns, communities with more species will have residents recruiting to gaps for a greater percentage of the season, resulting in fewer resources (less space) available for new species to exploit. Additionally, those invaders that are successful (see the legend of Figure 2.4B) are often those that have seasonal recruitment periods that coincide with temporal minima in the recruitment of natives.

This temporal niche partitioning is completely analogous to the sorts of resource partitioning presented above, and a more complete theory of invasion and community assembly would account for both. The temporal dimension may be incorporated into models of resource competition like that presented above by adding a third axis, time, to the trade-off plot. In the simplest case, even if all species were at a similar point on the $R_1:R_2$ trade-off surface, they might coexist if each were distinct on the temporal axis. As a corollary, invasions can occur into communities in which temporal use of resources is not complete (e.g., Figure 2.4).

A similar pattern of temporal variation in the use of resources may occur among grassland plants (McKane et al. 1990; Tilman and Wedin 1991; Wedin and Tilman 1993). For example, C_4 grasses are the best competitors for nitrogen during the hottest time of year (summer), whereas C_3 grasses use nitrogen during cooler parts of the year (spring and autumn). Different groups also appear to use different spatial pools of N, with forbs using primarily deeper soils for N, C_4 grasses using N from shallower soils, and legumes utilizing atmospheric N via nitrogen-fixing symbionts in their roots. Thus, total N utilization is greater in communities with a greater diversity of these functional groups (Fargione et al. 2003). A prediction that follows from these sorts of functional group arguments (and the theory outlined above) is that invading species most different from those in the established community will have the highest probability of establishment. In other words, communities will be most susceptible to invasion by species with functional traits that are currently rare or

absent. In the temporal niche framework, this would suggest that invaders with seasonal phenologies most unlike those of any of the natives would be the most successful. Fargione et al. (2003) did find, in an experiment in which seeds of 27 different plant species were added to plots that differed in diversity and functional guild composition, that the strongest inhibitory effects of resident plants were on introduced plants of the same functional guild.

These patterns suggest a degree of determinism to the community assembly process that may apply broadly to the processes of colonization and establishment: established species should most strongly inhibit invaders that are most similar in resource requirements to them (Tilman 2004). Although which species become part of a new community depends on the composition of the propagule pool and on chance events (e.g., who arrives first, which seed happens to fall in a more favorable spot), this phenomenon could cause communities to assemble toward specific relative abundances of different functional guilds (Tilman 2004). Whether communities are assembled randomly or via a repeatable process has important implications for ecological theory and application, and these few studies from invasion biology suggest that niche-based models may more adequately describe community assembly processes than neutral models (e.g., Fargione et al. 2003). They also suggest that there is some hope for developing predictive models of community assembly.

These insights also have implications for the ways in which we study and manage invasive species. Two major questions of invasion biology are what makes a community more or less invulnerable than others, and what makes some species better invaders than others. If resident species do more strongly inhibit invading species that are functionally similar to them, then these two questions would be best studied interdependently rather than separately. That is, the invulnerability of a community may depend not only on community properties, but also on the characteristics of the invader under consideration. Similarly, the invasive potential of a species may depend not only on its intrinsic properties, but also on the diversity and composition of the community into which it is being introduced.

Having presented theory and experimental evidence suggesting that increasing community diversity can decrease invasion by decreasing resource availability, we now examine the degree to which these mechanisms and theoretical predictions actually correlate with patterns in both natural and human-mediated invasions.

Biotic Interchange

Natural invasions occur when biogeographically isolated biotas are brought into contact via major geologic events. This can occur when, for example, long-separated continents are connected via land bridges, such as happened when the Isthmus of Panama formed during the Pliocene, joining the terrestrial floras and faunas of North and South America. Similarly, the opening of new

ocean passages, as occurred with the opening of the Trans-Arctic seaway 3 million years ago, can connect formerly separate marine floras and faunas. What happens when these large groups of independently evolved species come into secondary contact can be quite informative for the study of current ecological and evolutionary scenarios. The study of these interchanges and their contribution to our more general understanding of community assembly is complementary to the study of more recent, human-mediated introductions, because only for the former do we know the ultimate outcome with respect to which species were successful invaders and which, if any, went extinct—as opposed to current invasions, in which consequent species extinctions may not be realized for a long time (Tilman et al. 1996a).

Paleontological data suggest that the flow of species within these interchanges was often unidirectional, or at least highly asymmetrical, from areas of higher species richness to areas of lower species richness. In addition, as predicted from theory, and in agreement with data from recent invasions (Sax et al. 2002), these invasions led to only modest extinction in the recipient biota and generally caused a net increase in diversity over time (e.g., Vermeij 1991a). For example, when the Isthmus of Panama joined North America to South America, mammals were more diverse in North America (where grassland and savanna habitats dominated), and these mammals were very successful in invading South America, where such animals were far less diverse (e.g., Marshall 1981; Marshall et al. 1982; Webb 1991). Conversely, South America, being more tropical and wet and thus having a greater area of rainforest, was more diverse than North America with respect to rainforest plants and associated species, which were very successful invaders into tropical habitats in North America (Gentry 1982). Similarly, movement of marine organisms (particularly mollusks) was predominantly from the Pacific to the Atlantic in the Trans-Arctic interchange, with the species-rich North Pacific contributing far more species to the species-poor North Atlantic than vice versa (Vermeij 1991a). Vermeij (this volume) discusses these and other examples in greater detail and concludes that, although there are exceptions, the pattern of invasion from areas of high diversity to areas of low diversity is robust across a range of taxa, latitudes, and biomes.

The simplest possible explanation for these patterns is that they reflect the statistical expectation: species-rich systems have more species, and thus would be expected to contribute more invaders, than species-poor systems. One way of phrasing this is that if the native diversity of region A outnumbered that of region B by 5:1, then one should expect 5 times more invaders from region A to region B than from region B to region A. Because pre-exchange diversity can be difficult to estimate, relatively few studies have explicitly tested this null hypothesis. However, Vermeij (1991b) found that the exchange of marine organisms across the Trans-Arctic seaway during the Pliocene was more asymmetrical than expected based on the ratios of either the current or the pre-exchange faunal diversities of the North Pacific and North Atlantic. Similarly, prior to the Great American interchange, terrestrial mammal genera in North America

outnumbered those in South America by 125:71 (1.76:1), whereas the number of recent genera of northern origin in the south outnumbered southern invaders in the north by 80:24 (3.33:1) (data from Figure 1 in Marshall et al. 1982). A more formal test of the null model for the Great American interchange that differentiated patterns of "invasion" from subsequent patterns of "diversification" would be more complex, particularly as this invasion occurred in stages, but this casual look at the data suggests that an explanation beyond the null may be required. Vermeij (in press) also reports that marine invasions from the Caribbean to Florida are more asymmetrical than predicted by a null hypothesis. These examples do not discount the possibility that some uneven biogeographic exchanges may have a simple null explanation; however, they suggest that in at least some cases, the exchange among regions is even more uneven than expected based on pre-exchange diversity levels.

Multiple ecological and evolutionary mechanisms could underlie this asymmetry in biotic exchanges. First, as first suggested by Darwin in *The Origin of Species* (see McNaughton 1993), biotas with fewer species might utilize available resources less completely or consistently, leaving more opportunities for speciation and subsequent increases in productivity. Such "empty niches" in low-diversity realms could also be readily occupied by invaders from other realms. In this situation, it is possible that successful invaders have traits that fall on the same trade-off curve as those of established species, and are successful merely because their traits allow them to exploit resources left unconsumed by the more species-poor resident community. This is a plausible explanation, for example, for the Trans-Arctic marine interchange, in which the invaded Atlantic biota had recently suffered a series of extinctions, whereas the more diverse source biota of the Pacific had not (Vermeij 1991b). Thus, at least one ancient invasion is in agreement with predictions from theory and mechanistic experiments that decreasing resident diversity should increase susceptibility to invasion.

Alternatively, species from more diverse biotas might possess superior competitive abilities as a result of evolutionary innovation. Areas with more diverse floras or faunas tend to have a greater area of available suitable habitat. Larger regions might also lead to larger total population sizes and thus higher genetic variation. With greater variation, there is greater potential for natural selection to act to maximize resource use efficiency and thus lower the resource levels required for persistence (i.e., lowering the overall trade-off surface). Overall, then, all else being equal, individual species found in regions with a larger physical area and greater diversity might thus be able to subsist on lower levels of resources. With a superior trade-off curve, invaders would have positive growth rates even if they had a $R_1:R_2$ ratio identical to that of an established species. This would increase their chance of establishment, and would mean that, once established, they would competitively displace the original species that were similar to them. On the other hand, if invaders came from a biogeographic realm that had an inferior trade-off curve, they would be highly unlikely to invade new habitats unless those habitats had low diversity and

lacked species with $R_1:R_2$ requirements similar to their own. Additionally, trade-off surfaces can be more complex than the simple two-dimensional approach of the model above: adding a third (or greater) axis could allow one to specify the rates of resource supply required in different habitats or seasons. Regions with a greater range of available habitat types might then have more species specialized for each habitat type and be more resistant to invasion by species from biogeographic realms with less habitat differentiation and specialization. While it would be unreasonable to expect that all species from one continent would be superior to all others from another, it might prove informative and a useful test of the theory outlined above to compare, in a common garden approach, the competitive abilities of a broad range of taxa from biogeographic provinces of differing species richness and/or invasibility.

There are, of course, other ways for invading species to have evolved superior competitive abilities. In particular, key innovations or “novel weapons,” such as allelopathic chemicals (see Callaway et al., this volume), may allow invading species to circumvent the normal competition for resources, effectively allowing them, once established, to persist with or exclude competitors with lower resource requirements in the biogeographic realm into which they are being introduced. Root exudates from the European weeds *Centaurea maculosa* and *C. diffusa* strongly inhibit potential competitors in North America, allowing these weeds to become competitive dominants, despite the minimal effect their root exudates have on similar European species with which these species share a long coevolutionary history (Callaway and Aschehoug 2000; Callaway et al., this volume). More generally, superior interference competitive abilities of animals, via aggressive or territorial behavior, might allow them to invade areas even if they require higher resource supply rates than native species to persist.

Alternatively, an invader could be temporarily competitively superior to established species if the invader entered a new habitat that lacked natural enemies (diseases, pathogens, predators, herbivores, etc.) like those that kept it in check in its native habitat (e.g., Torchin et al. 2003; Lafferty et al., this volume, and Ricklefs, this volume). Lower loss rates could allow a species to maintain itself on lower levels of resources and thus increase its competitive ability. Such an increase could allow the invader to become readily established, and possibly dominant, even in a highly diverse community. The successful biological control of species such as *Opuntia* and *Hypericum* suggests that the absence of natural enemies probably contributed at least to their initial success as exotic invasive species. Missing parasites might, however, be a less plausible explanation for invasions following the formation of land bridges or the opening of seaways between once-separated realms because diseases or predators would seem likely to spread with, or soon after, their hosts or prey. Additionally, given enough time, diseases and parasites are likely to either be acquired from the new fauna (e.g., Strong et al. 1977) or arrive in subsequent invasion events, reducing the abundance of the invader to levels more similar to those in its native habitat.

Regardless of the underlying mechanisms, these patterns from large-scale natural invasions are consistent with the hypothesis that habitats with greater

species diversity are less readily invaded than habitats with lower diversity. The reported patterns of major biotic interchanges thus seem, at least on first inspection, to be consistent with the hypothesis that communities with a greater diversity of competing species may have lower resource levels and/or fewer “unfilled niches” and thus inhibit invasion. If lower resource levels lead to more intense competition, and thence to evolution of greater competitive ability, it seems plausible that a region with more species would be both harder to invade and more likely to produce successful invaders. Invasions thus present an opportunity to examine biogeographic patterns in competitive ability and resource depletion that have been largely unaddressed.

Does this pattern of asymmetrical exchange hold for more recent, human-mediated interchanges between biogeographic regions? We know of no direct tests in recent invasions that explicitly address the null hypothesis that the number of invasions between two regions is a simple function of the ratios of the pre-contact diversities of the two regions. Of course, unlike ancient natural interchanges, recent invasions involve more than two previously separated regions, complicating any such test. Nevertheless, it is useful here to review a few commonly cited examples of asymmetrical biotic exchange in contemporary invasions.

Elton’s original treatise formalizing the idea of asymmetrical biotic exchange drew on comparisons of islands and continental environments, pointing out that islands, with smaller areas and more depauperate biotas, are more frequently invaded than mainlands, which are typically much more diverse. However, the number of attempted introductions of mainland species to islands is often far greater than the number of island species introduced to mainlands; thus, in many analyses, propagule supply appears more likely to be the cause of high rates of island invasion (e.g., Blackburn and Duncan 2001a). Alternatively, it might be that island floras and faunas are inherently different from those of the mainland because only a small proportion of species were capable of being dispersed to islands before humans began transporting species freely. If, for instance, there is a general trade-off between dispersal ability and competitive ability, then the flora and fauna of islands would be biased toward being poor competitors. This could mean that islands are readily invaded not because of their low diversity, but because they are populated with poor competitors relative to the species being introduced to them. Humans often preferentially introduce species that are abundant in their native range; to the extent that abundance correlates with competitive ability, human-introduced species may represent a nonrandom sample of the species from the native range that have high competitive ability but low dispersal ability (e.g., Blackburn and Duncan 2001b).

Because a large fraction of introductions to novel marine ecosystems are the accidental result of transoceanic shipping, these might allow a less biased assessment of the relative invasibility of regions of differing resident diversities. For example, estuaries along the Pacific coast of North America are few in number, small in area, and spaced relatively widely on this geologically active continental margin. These estuaries are geologically quite young and

relatively species-poor and are among the most invaded in the world (Cohen and Carlton 1998; Ruiz et al. 2000). Many of the invaders in these regions come from the western North Atlantic—a region with a far greater area of estuarine habitat and a greater diversity of estuarine biota. Of course, there are alternative explanations for why Pacific coast estuaries are so highly invaded, including the volume of ship traffic that passes through those estuaries (Ruiz et al. 2000) and the relatively benign climate of the region.

The available data from human-mediated biotic interchanges appear to be unsuitable, then, for testing theories regarding diversity effects on resource use and invasibility, although they do remind us that diversity and its effect on resource use represent just one of many possible factors that may interact to determine invasibility.

Reconciling Pattern and Processes in Community Invasibility

We now turn to the question of whether diversity, and its effects on resource use, are useful predictors of the relative invasibility of a particular community *within* a given biotic province. A review of the literature highlights the lack of consensus on the strength and direction of the effects of diversity on community resistance to invasion (Levine and D'Antonio 1999). A major characteristic of this debate is the discordant results of studies employing observational versus experimental approaches. Many observational studies find that more diverse native communities support more invaders (Knops et al. 1995; Planty-Tabacchi et al. 1996; Rejmanek 1996; Wisser et al. 1998; Lonsdale 1999; Stohlgren et al. 1999). These studies are often conducted at large scales (e.g., 10–1000 km² or more; but see Sax 2002), involve many species, and are favored by some because they involve “natural” communities. But many other factors correlated with diversity can affect the establishment and spread of invaders, confounding such studies and urging caution in their interpretation (e.g., Rejmanek 2003). In particular, a recent reanalysis of the data used by Stohlgren et al. (1999) found that a high level of real estate development was a much better predictor of high rates of invasion by exotic species across the United States than was high regional diversity (Taylor and Irwin 2004).

In contrast to most of the simpler analyses of broad-scale invasion patterns, most experimental manipulations (necessarily conducted at smaller scales) support the idea that species richness decreases invasion success (McGrady-Steed et al. 1997; Knops et al. 1999; Lavorel et al. 1999; Stachowicz et al. 1999, 2002; Levine 2000; Naeem et al. 2000; Symstad 2000; Kennedy et al. 2002; Fargione et al. 2003). Such experiments reveal the potential of diversity to reduce invasion success, but rarely assess whether diversity is important relative to other factors, such as propagule supply, disturbance, or predation, for generating patterns of invasion in the field. Two studies have employed a combination of field experiments and observational approaches: both find that when all other things are equal (experimentally controlled), diversity has a nega-

tive effect on invasion success, but one shows a positive (Levine 2000) and one a negative (Stachowicz et al. 2002) relationship between native and invader diversity in field surveys. Thus, these results suggest that diversity *can* reduce invasion success in the field, but that it should be visualized as one of several potentially correlated factors (including disturbance and propagule supply) that may affect the invasibility of a community (Tilman 1999a).

Once it is recognized that diversity (through its effects on resource use) is one of many factors, including human-driven habitat disturbance (Taylor and Irwin 2004), that may affect invasion success, a resolution of the apparent contradiction between observational and experimental results emerges. Positive native-invader diversity relationships may often be driven by inherent spatial variation in biotic and abiotic conditions that overwhelms the effects of competition between species for resources. Thus, the positive correlation between native and exotic richness is not causal, but rather results from both natives and exotics responding similarly to some extrinsic factor, such as propagule supply, predation, degree of disturbance, or temperature. Thus, a positive native-exotic relationship will result if the area sampled includes sufficient spatial heterogeneity in these extrinsic factors. But when samples are taken from locations that vary little in these factors (and thus have a smaller range of native diversity), a negative native-exotic relationship is more likely, but not guaranteed. Note that the scale of partitioning of spatial heterogeneity can lead to situations in which negative native-exotic relationships exist at particular spatial scales while a positive relationship exists across spatial scales (Figure 2.5; see also Shea and Chesson 2002). Experimental approaches explicitly control for and attempt to minimize such sources of variability, so they should be viewed as asking what the causal effect of diversity on invasion is “when all else is equal.” Thus, even when a positive correlation between native and exotic diversity exists, losses of native species should still lead to an increase in invasion success.

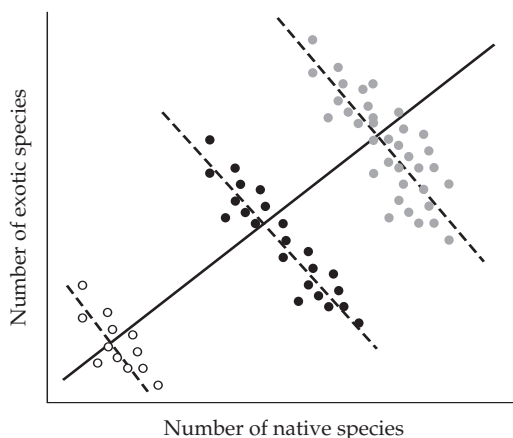


FIGURE 2.5 Hypothetical relationship between native and exotic richness across spatial scales. Clusters of points from a particular location across which extrinsic (abiotic) factors vary little form negative correlations, but when data are lumped across sites that vary considerably in extrinsic factors, an overall positive relationship results, because these factors affect the diversity of native and exotic species in similar ways and overwhelm any effects of diversity on biotic resistance. (After Shea and Chesson 2002.)

So why, then, do observational studies of biotic exchange over geologic time at the largest spatial and temporal scales support theoretical ideas about the negative effects of diversity on invasibility while the evidence from more recent surveys suggests, if anything, that a positive relationship between the number of natives and the number of invaders may be more common? We present three possible explanations. One possibility is that differences between biotic interchanges and current patterns of change may be due to differences in the number of sources for species invasions. In biotic interchanges historically, there were generally just two pools of species involved, whereas in modern invasions, species are often invading from many different regions of the world. This may allow many more species, with a much greater range of traits, to get to species-rich regions than would have been possible historically. Such biotic homogenization should increase the probability of arrival of invaders that occupy novel niche spaces or possess superior trade-off surfaces, as it is unlikely that any single regional biota will be superior in all respects to all other biotas on the planet, even if it is relatively resistant to one particular biota. A second difference between recent and geologic invasions is that recent interchanges are associated with a major source of disturbance—human activities—that can increase the patchiness and spatial heterogeneity of habitat types, potentially allowing more species to coexist (especially species adapted to disturbed habitats, as many invaders are). It may thus be that under the current disturbance regime, the niche space available for opportunist species is unsaturated by native biota. A final possibility is that there has not been enough time since these most recent invasions for exclusion to occur on a global or even a regional scale, and that communities currently carry an extinction debt (Tilman et al. 1996a) that will eventually be paid. Competitive exclusion over large spatial scales may often be a slow process, and it could be that the current patterns are transient and reflect other, faster-acting forces (see discussion in Bruno et al., this volume). Each of these possibilities suggests interesting lines of future research—more in-depth comparisons between natural biotic interchange and our current situation should prove illuminating.

Synthetic approaches that compare experimental results and field surveys in the same system have provided insight into the diversity-invasibility debate, but are generally rare in the diversity-ecosystem functioning literature. This approach was used for native grasslands and for a related biodiversity experiment, which both showed higher productivity and more complete nitrogen use at higher plant diversities (Tilman et al. 1996b). In marine systems, in which experiments are still relatively rare, there have been some promising attempts to assess the relationship between diversity and ecosystem functioning using a correlational approach (Emmerson and Huxham 2002). Pairing these approaches with simultaneous manipulative experiments (as in Levine 2000 or Stachowicz et al. 2002) would allow for significant advances in our understanding of the conditions under which diversity plays a major role in controlling ecosystem functioning and of how their relationship might change across spatial scales.

Broader Implications and Future Directions

The theme of this chapter has been how the study of invasions has contributed to the understanding of the relationship between species diversity, resource utilization, and the functioning of ecosystems. Resource use itself can be considered an important measure of ecosystem functioning, and it can be linked to other processes. For example, if more diverse communities have higher resource utilization, then they are also likely to have greater biomass or productivity and lower losses of resources, such as to leaching, than less diverse communities. The suggestion that diversity enhances the consistency of resource use and space occupancy (e.g., Figure 2.4) lends further evidence to the idea that diversity is related to community stability. For instance, in terrestrial studies and in theoretical work, as diversity increases, the stability of individual species' populations tends to decrease slightly (May 1974), whereas the stability of aggregate community properties, such as biomass or percentage of cover, tends to increase (Tilman 1996; Tilman and Lehman 2002). Here we discuss a few additional ways in which the study of invasions may contribute significantly to the diversity and ecosystem functioning debate.

Multivariate complementarity

The effect of diversity on ecosystem functioning is often measured with a single response variable. For example, the influence of diversity on productivity may be measured in one study, while its influence on nutrient cycling is measured in another. However, while the influence of any species or suite of species may be critical to the performance of any single ecosystem process (e.g., productivity), other species may exert a dominant influence on other ecosystem variables. In many communities, then, any suite of species might seem unlikely to simultaneously control all ecosystem processes. Therefore, an incorporation of multiple ecosystem processes into a multivariate index of ecosystem functioning might prove useful to the study of diversity and ecosystem functioning. For instance, a common critique of the application of the results of diversity-ecosystem functioning experiments to conservation is that the ecosystem process examined often saturates at low levels of diversity, such that, for example, only some small fraction of diversity is required to obtain maximum productivity (e.g., Schwartz et al. 2000; but see Tilman 1999b). However, if a different fraction of that diversity is required to maintain some other function (e.g., nutrient cycling), a larger amount of the diversity may be required to saturate the multivariate index of ecosystem functioning. Alternatively, in spatially or temporally heterogeneous habitats, different species may maximize productivity in different locations in space or time (e.g., Hector et al. 1999; Tilman 1999b; Stachowicz et al. 2002a).

Intriguing results in this vein have been reported for a community of mobile invertebrate grazers in coastal seagrass meadows (Duffy et al. 2003). Different grazer species maximized values of grazer production, grazing impact, and

sediment organic carbon, such that the high value of each of these processes at maximum diversity levels is explained by the fact that diverse communities contain individual species with a dominant effect on a particular ecosystem process (a.k.a. the sampling effect, *sensu* Tilman et al. 1997). However, the multispecies mixture was the only combination to achieve high values for all three of these response variables simultaneously. Although this “multivariate complementarity” has been relatively unrecognized explicitly, the work on the relationship between diversity and invasions (in which no single species seems able to exclude all potentially invading species) suggests that it may in fact be quite common. This insight, combined with the joining of experimental and observational approaches, may help broaden our understanding of the role of diversity in ecosystem functioning.

Does increasing diversity enhance ecosystem functioning?

At least in the short term, many invasions have resulted in a net gain in the number of species present at the local or regional level (Sax and Gaines 2003). This is not surprising, and it is similar to what is seen in invasions at the geologic scale: most regions gain in the total number of species, though some resident species eventually go extinct (e.g., Marshall et al. 1982). The diversity-ecosystem functioning debate has mostly been framed in the context of what will happen to ecosystem functioning as species richness declines due to extinctions. But in cases in which invasions cause a net increase in diversity at the scale at which ecosystem processes are measured, it is worth considering what effects this might have on ecosystem functioning. There are virtually no data to address this question, although it is clear that invasive species can affect ecosystem structure and function. For example, aquatic ecosystems lacking dominant filter-feeding organisms (either because natives have been driven ecologically extinct or because there were none to begin with) are dramatically altered when such species are introduced (e.g., Alpine and Cloern 1992). The introduction of a rapidly growing N-fixing legume into a low-nutrient ecosystem lacking such species can also have dramatic effects (Vitousek and Walker 1989; see also D’Antonio and Hobbie, this volume). Assessing the role of increasing diversity in other ecosystem processes might contribute to a fuller understanding of the degree to which ecosystem functioning saturates at high levels of diversity, particularly across multidimensional measures of ecosystem functioning.

Can communities ever be saturated?

If invasions lead to increased local diversity, then, all else being equal, communities might be expected to become less invasible over time as more species accumulate. However, there are many instances in which invasion rates appear to hold constant or even increase after the addition of new species (e.g., Cohen and Carlton 1998). One confounding factor is that many invasive species enter habitats that are highly disturbed. Because increased disturbance can allow

more species to coexist, the net effect of disturbance and invasion may be communities that are proportionately less saturated with species than the original undisturbed habitats. Additionally, when species at multiple trophic levels are considered, it is possible that the addition of new species adds some resources while consuming others. Basal species, for example, might consume nutrients but provide food and habitat for many species at higher trophic levels. Adding a species takes away resources for species similar to that one (i.e., in the same functional group), but may add food or shelter resources for other species or modify habitat in a way favorable to some species. For example, while the invasion of a new C_3 grass undoubtedly decreases the resources available to other C_3 grasses (Fargione et al. 2003), it may add a new host plant that can be exploited by different species of herbivorous insects. While it is broadly appreciated that invaders can have cascading effects on species at the same trophic level via competition or at lower trophic levels via predation, the potential importance of cascading effects from the bottom up via facilitation or resource provision is less appreciated, although such effects may be common (Simberloff and Von Holle 1999; Richardson et al. 2000; Bruno et al., this volume). Recognition of these effects would lead to the prediction that as invasion within a functional group occurs, further invasion within that group should decline, while the potential for invasion within other functional groups might stay the same or even increase.

Whether overall invasion rates increase or decrease with the addition of exotics is hard to say, and the influence of propagule supply, disturbance, and other factors may play a larger role in determining the net change in invasion rates. This problem was recognized by Davis et al. (2000), who argued that a more predictive approach to invasions may come from focusing more explicitly on resource availability rather than on the specific factors that affect resource availability. Resource availability does appear to be the proximate determinant of the success of establishment of many invaders, but it is still of interest to understand the ultimate chain of causation that has led to recent changes in resource availability and hence to greater invasion.

Concluding Thoughts

For decades, ecological research has focused on how various ecosystem-level properties (such as productivity and stability) affect the maintenance of diversity on local scales. The emerging research agenda of the past decade has turned this around and has begun to rigorously examine the effects of diversity on these very same ecosystem processes. The data thus far support both directions of causation, revealing that diversity and ecosystem variables mutually influence one another. A serious challenge for ecology lies in assessing the potential for positive and negative feedbacks among diversity and various ecosystem processes to understand more broadly how these two critical ecosystem properties interact. In this chapter, we have outlined some ways in which

the study of introduced species has provided significant insights into this area and other ways in which it may contribute further. There is significant potential for such research on introduced species to contribute to the synthesis of traditionally isolated fields ranging from evolution to ecosystem ecology.

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