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Source: *Oikos,* Vol. 87, No. 1 (Oct., 1999), pp. 15-26
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3546992
Accessed: 10-04-2015 19:45 UTC

MINI-REVIEW

Elton revisited: a review of evidence linking diversity and invasibility

Jonathan M. Levine and Carla M. D'Antonio

It is commonly believed that diverse communities better resist invasion by exotic species than do simple communities. We examined the history of this notion, and evaluated theoretical and empirical work linking diversity and invasions. We found that much of the historical work that has contributed to the perception that diverse communities are less invasible, including Elton's observations and MacArthur's species-packing and diversity-stability models, is based on controversial premises. Nevertheless, more recent theoretical studies consistently supported the predicted negative relationship between diversity and invasibility. The results of empirical studies, however, were decidedly mixed. Constructed community studies directly manipulating diversity found both positive and negative effects of diversity on invasibility in both field and microcosm settings. Other empirical studies tracking the assembly of ecological communities generally suggested that communities decline in invasibility as species accumulate over time, though the role of diversity itself was often ambiguous. Studies of the spatial correlation between diversity and invasion and studies experimentally adding invaders to natural systems indicated that diverse communities tend to be more invasible. We argue that these results most likely reflect environmental factors spatially covarying with diversity in natural communities (e.g. resources, disturbance), and not the effects of diversity itself as uncovered by constructed community studies. Nevertheless, the consistent positive relationship between exotic species abundance and resident species diversity found in spatial pattern studies suggests that invaders and resident species are more similar than often believed, and the implications of this for theories of invasion are discussed.

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Concern over the impacts of biodiversity loss on the functioning of ecosystems has stimulated renewed interest in the importance of species diversity to community stability. Stability has several components; among these is "resistance" – the ability of a community to resist change in the face of a potentially perturbing force (Connell and Sousa 1984, Pimm 1991). These forces are often abiotic, such as storms, fires, and droughts,

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though increasingly, the major perturbations experienced by natural communities are biological in origin (Drake et al. 1989). Extremely common is the human-mediated introduction of plant, animal, or pathogen species into communities where they did not previously exist. The ease with which these newcomers become established members of communities defines the "invasibility" of a system. Neither the general controls over community invasibility nor the role of species diversity in influencing susceptibility to invasion are well understood. Yet, the widespread occurrence of invasive introduced species, their documented impact on native biological diversity (e.g. Mooney and Drake 1986, Drake et al. 1989, Vitousek et al. 1997) and the developing interest in restoration of native diversity mandate a clear understanding of the community-level processes influencing invasions. Here, we review empirical and theoretical research linking diversity and invasibility in an attempt to provide a critical framework for approaching research in this area.

Historical considerations

It is widely believed that high native diversity decreases the invasibility of communities (Lodge 1993), an idea with perhaps three origins. The first lies in the natural history observations and writings of Elton (1958) and the second and third emerge from classic ecological theory exemplified by the work of MacArthur (1955, 1972) and colleagues.

In his book, *The ecology of invasions by animals and plants*, Elton (1958) argued that "the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones; that is more subject to destructive oscillations in populations . . . and more vulnerable to invasions". He supported this argument with observations that "oceanic islands and crop monocultures are simple ecosystems that show high vulnerability to invasions . . . and frequent outbreaks of population subsequently". Elton's notion that diverse systems are less invasible (also see Allee et al. 1949) has been echoed many times by authors such as Moyle (1986) examining fish invasions in North America and Moulton and Pimm (1983) examining bird invasions of Hawai'i. It is important, however, to clarify what Elton (1958) was proposing.

As evidenced by the above quotations, Elton was interested in community stability, and focused on invaders with particularly large impacts. He did not clearly distinguish between the ability of non-resident species to establish in depauperate communities versus the susceptibility of organisms in those communities to the effects of invaders. Only the former is strictly a question of invasibility. This confusion between invasibility and the vulnerability of communities to impact permeates much of the literature linking diversity and invasion, and has fueled recent challenges to Elton's observation that species poor, oceanic islands are particularly vulnerable to invasion. Simberloff (1986, 1995) and D'Antonio and Dudley (1995) have concluded that while island species are often more susceptible to the impacts of invaders than their continental counterparts, there are insufficient data to evaluate the inherent invasibility of intact island communities.

Classic ecological theory has also strongly contributed to the belief that more diverse systems are less invasible. Much of the research conducted in the 1960's and 1970's was based on assumptions that niche space in natural communities is limiting and that communities are strongly structured by competition (May and MacArthur 1972). Several authors, but most notably MacArthur (1970, 1972) explored the conditions under which an assemblage arrayed along a resource axis could be invaded by a new species. In general, this work suggested that the more species occupying a resource axis, the more fully resources were monopolized, and the more difficult it was to insert new species (but see Case 1991). These models, however, have been challenged on several grounds, including the point that competitors along a niche axis may indirectly facilitate one another via competing with shared competitors. When such indirect interactions are included, the same types of models suggest that for some combinations of species, diverse communities might be more invasible (Levine 1976, Lawlor 1979, Stone and Roberts 1991, Levine 1999). In spite of the now widespread acceptance that indirect interactions are common and more generally, that many systems are loosely structured and not at equilibrium (Wiens 1977), conclusions from classic niche theory continue to strongly influence the study of biological invasions.

The third origin of the belief that more diverse systems are less invasible lies in MacArthur's (1955) classic work on the relationship between diversity and stability. He suggested that systems with fewer linkages were more subject to population fluctuations if one linkage was disrupted than were systems with more linkages, work which spurred an enormous debate over the diversity–stability relationship (May 1973, Pimm 1991). Though MacArthur (1955) did not evaluate invasibility, this work has contributed to the perception that diverse systems are more stable and possibly less invasible as resistance to invasion is a common measure of stability (Elton 1958). It is also important to note that MacArthur and May's models were based on linkages among as well as within trophic levels. Yet very few empirical studies have examined multi-trophic level interactions when invoking the diversity-resistance linkage.

In this manuscript we examine evidence for a link between diversity and invasibility with the goal of clarifying some of the strengths and weaknesses of current approaches. Overall, we believe that the search for

generality in this area will be improved by careful definition of the important questions, attention to mechanism, consideration of relevant spatial scales, and recognition that factors controlling native biological diversity also control invasions.

Why should diversity affect invasibility?

The most commonly cited and often implicit mechanism by which diversity confers resistance to invasion is that more diverse assemblages more fully utilize available resources, thus leaving little resource space for individuals of new species. This mechanism follows from the "species-packing" or "diffuse competition" models of MacArthur (1970) described above, and is an extension of the "empty niche" concept in invasion biology (Herbold and Moyle 1986, Crawley 1987). More diverse communities are also more likely to have a diverse guild of consumers, and this may limit the number of prey species that can potentially invade (Pimm 1991, Naeem and Li 1998). By contrast, Palmer and Maurer (1997) point out that due to differences among plants in canopy height, rooting depth, rhizosphere microbial communities, etc., diverse communities contain more microheterogeneity than monocultures (Aarssen 1983), and might therefore be more invasible.

More diverse communities are also more likely to contain species with particularly strong impacts on invasibility. Whether or not this mechanism is considered an effect of diversity per se has been considered elsewhere (Huston 1997, Tilman 1997a). Regardless, if a key species that is more often found in more diverse assemblages strongly deters invasion, diverse communities will show enhanced resistance. Alternatively, key species that are strong facilitators can cause diverse systems to be more invasible. These facilitators have been termed "diversity promoters" by Palmer and Maurer (1997) and may be common in communities where facilitation is an important structuring force (Bertness and Callaway 1994, Callaway 1995). In sum, while it is commonly believed that diversity should enhance resistance to invasion, arguments can be made that diversity may promote invasion.

Understanding how invasibility varies with diversity in natural systems is complicated by the fact that variation in diversity is controlled by, and thus covaries with disturbance, resource availability, physical stress, competitors, consumers, etc., the same factors known to influence invasibility (Rejmanek 1989, Huston 1994, Robinson et al. 1995, Wiser et al. 1998). These covarying factors are not intrinsic effects of diversity, though most of the studies we review do not make this important distinction. Thus, recognizing that correlations between diversity and invasibility in natural communities reflect both the effect of diversity on invasibility, and

the direct effects of ecological factors that influence diversity is critical to properly interpreting these studies.

Review of the evidence

We located the following studies by conducting a BIOSIS search of articles dating back to 1985, and examining references therein.

Models

All of the mathematical models relating diversity and invasibility indicate that increasing diversity decreases invasibility (Robinson and Valentine 1979, Post and Pimm 1983, Shigesada et al. 1984, Drake 1988, 1990, Case 1990, 1991, Law and Morton 1996). This general result was independent of whether the communities were composed of species competing via interference (Shigesada et al. 1984) or exploitation (Case 1990, 1991), or if these species were members of a single or multiple trophic levels (Post and Pimm 1983, Drake 1988, 1990).

Robinson and Valentine (1979) and Case (1990, 1991) examined the invasibility of stable model communities varying in diversity. The interactions and dynamics of these systems were described by Lotka-Voltera equations with interaction strength most often drawn from a uniform distribution. All inter- and intraspecific pairwise interactions were compiled as the elements of a community matrix, with matrices of varying size representing communities of varying diversity. Each community matrix was analyzed for local stability, and unstable communities were discarded. The locally stable communities were then "invaded" by a new species, which expanded the matrix by one row and one column, the elements of which were the interactions of the invader with each of the resident species. Communities were invasible if the new species persisted in the expanded community at equilibrium.

While the models of Case (1990, 1991) and Robinson and Valentine (1979) differed in how the elements of the community matrix were assigned, both found that the proportion of invaded communities declined with diversity. Case found that even invaders that were equivalent competitors to the resident species were often unsuccessful in more diverse communities, a result attributed to the increased frequency of multiple domains of attraction in more diverse systems (Gilpin and Case 1976). These multiple domains of attraction or equilibria are more familiar in the context of the simple Lotka-Voltera two species competition model with unstable coexistence where the initially more abundant species dominates. Case suggested that the importance of these "priority effects" increases with species diver-

sity, and thereby decreases community vulnerability to competitors entering in low numbers, such as invaders.

The assembly models of Post and Pimm (1983), Drake (1988, 1990), and Law and Morton (1996) are also based on Lotka-Voltera equations, but they differed from those of Case (1990) and Robinson and Valentine (1979) in how the communities were "assembled". These models began with a finite species pool with all pairwise interactions drawn from a specified range of values. Species were then randomly drawn to invade initially depauperate communities. Invasion was successful if the invader increased when rare, and maintained positive equilibrial abundance as inferred from the community matrix expanded to include that species (for a mathematical critique, see Case 1991, Law and Morton 1996). This process was iterated hundreds of times, with each successful invasion yielding a new locally stable equilibrium. Law and Morton (1996) provided an alternative "permanence" criteria for successful invasion that allows for coexistence or invader success even when species do not tend to an equilibrium point.

Regardless of the invasion criteria, all of these models indicated that the rate of successful invasions declined with time, a result that has been inferred by some to mean that diversity enhances resistance. Case (1991), however, notes that due to the finite species pool, the degree to which this result reflects the effects of diversity versus the exhaustion of good invaders early in the assembly process is unclear. Furthermore, Law and Morton (1996) showed that certain combinations of species better resist invasion than others of equal diversity. These invasion resistant and presumably more connected communities develop as the requisite members are introduced, and thus invasion resistance may develop over time independent of community diversity.

Law and Morton (1996) also explored how the diversity of the species pool influences community invasibility and found that communities assembled from richer pools were more resistant to invasion. This result was not an effect of local diversity since all communities, regardless of the pool size, tended towards five species. Rather, Law and Morton argued that communities derived from richer pools have been tested by more kinds of species and are thus less likely to be invaded by a new species than are communities of the same diversity but assembled from a smaller pool.

There are several features of all of these models that we believe qualify their generality. First, the predictions may be most appropriate for relatively small spatial scales. Lotka-Voltera models assume well-mixed populations, such that all species interact with a potential invader. This does not invalidate Lotka-Voltera predictions, but rather restricts their applicability to scales at which all constituent species do interact – the neighborhood scale (Tilman 1994, Naeem et al. 1998). Yet, as we will show, empirical work at this scale is rare.

In each of the models of diversity and invasion, the interactions of the invader were similar to those of the resident species. In the assembly models, the invaders were drawn from the same species pool as the residents, while Robinson and Valentine (1979) and Case (1991) drew invader and resident species interactions from the same distribution. Though Case (1991) showed that increasing the invader's growth rate had little effect on model results, what happens when invaders are better competitors or predators than all of the native species? Several investigators have observed that some successful invaders, particularly ones with large impacts, tend to have qualitatively different traits than the resident species (Vitousek 1990, Chapin et al. 1994). We hypothesize that when invaders are superior competitors or use different resources than the native species, the effects of diversity on invasibility are likely to be weak.

Another important assumption of most of these models is that a community is invasible if the invader persists at equilibrium. Crawley (1987) points out that understanding what factors allow the equilibrium persistence of invaders, does not in itself explain why communities are invasible in the first place (see also Rejmanek 1989, Law and Morton 1996). Furthermore, invaders that fail to persist in communities at equilibrium may still strongly impact these systems. One of the outcomes of Case's (1990, 1991) models are what he terms "indirect failures" – situations where the invader population initially grows, but in the process influences other species such that its own population goes extinct. Case (1991) notes that though the frequency of these indirect failures is relatively small, their frequency increases with diversity. Further exploring non-equilibrium outcomes of invasion is an interesting area for future work.

Lastly, in all of the models, prior to invasion, the communities have reached equilibrium, a state rarely reached by natural systems (Connell and Sousa 1984). This mismatch between the models and field systems is further complicated by the fact that community diversity is often dynamic and the outcome of non-equilibrium processes. How diversity relates to invasibility in successional or unsaturated systems is an interesting question ripe for exploration in models.

Spatial pattern studies

Spatial pattern studies correlate the abundance of a single or multiple invaders with the diversity of the surrounding assemblage. These studies are not mechanistic in that correlations between diversity and invasion reflect both the independent effects of diversity as well as the effects of processes covarying with diversity. As we describe below, it is these latter factors which tend to drive broad scale field patterns. Nevertheless, these studies address the question, "Are naturally di-

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verse assemblages more or less invaded than their species-poor counterparts?". Interestingly, most of the studies we found suggest that more diverse assemblages are more invaded, contrary to Elton's (1958) observations.

Note from the question above that spatial pattern studies do not explicitly measure invasibility, but instead use invader abundance or diversity as a proxy for susceptibility to invasion. These measures not only reflect invasibility and features intrinsic to the community, but also external factors, such as variation in propagule supply. In systems such as rivers, where propagule supply covaries with resident species diversity (Nilsson et al. 1993), correlations between invader abundance and diversity may be driven entirely by invader input. A second caveat about spatial pattern studies is that they correlate invasion with current diversity, which is not diversity at the time of invasion (but see Wiser et al. 1998). Given sufficient time, exotic species may reduce the diversity of invaded assemblages, so the results of some of these studies may better reflect the impact of invaders on native diversity rather than vice versa.

Species lists from well defined areas, such as reserves, provide interesting data sets to explore patterns of diversity and invasion. Fox and Fox (1986) showed that the percentage of alien plant species is negatively correlated with native plant diversity in Australian heathland and shrubland reserves. In contrast, Knops et al. (1995) showed that the percentage of alien plant species was greater in more diverse communities of coastal, central California. However, Rejmanek (1989), Brown (1989), and others have pointed out that the percentage of species that are alien is a biased measure of invasibility because even if invasibility is independent of diversity, diverse systems will contain a lower percentage of invaders simply because of the high number of native species in the denominator (similar problems emerge in a study by Bridgewater and Backshall 1981). For the study by Knops et al., this means that the strength of the positive correlation was under-estimated. For the study by Fox and Fox (1986), we recalculated the relationships. Using the number of invaders rather than the percentage as the dependent variable, we found a positive correlation between native richness and exotic richness for shrubland sites (Fig. 1) and a non-significant relationship for the heathland sites ($R^2 = 0.002$, $p = 0.80$). Similarly, Kruger et al. (1989) showed that for Mediterranean plant systems in California, more diverse native communities also contained more non-native species.

Area can often be a confounding variable in these correlational studies between diversity and invasion because larger areas are likely to contain both more exotics and more natives (Case and Bolger 1991), leading to positive correlations unrelated to invasibil

ity. For example, Timmins and Williams (1991) found that area could explain the positive correlation between native plant and weed diversity among forest and scrub reserves in New Zealand. By contrast, MacDonald et al. (1986, 1989) analyzed invasion patterns among nature reserves in South Africa, and found that while more diverse reserves were more invaded ($R^2 = 0.44$, $p < 0.001$), reserve size was not correlated with the number of exotic species. The positive correlation between native and exotic diversity was attributed to the greater environmental heterogeneity in diverse reserves (also see Higgins et al. 1999).

Many studies have used equal size areas to explore patterns of diversity and invasion, and most indicated positive correlations between these factors. Examining invasion patterns in multiple plant communities of the central United States, Stohlgren et al. (1998, 1999), showed that more diverse communities contained greater numbers of exotic species than their species-poor counterparts, though within communities, at the scale of 1 m^2, results were mixed (see below). Focusing on riparian systems, Planty-Tabacchi et al. (1996) showed that sites with high native plant diversity along the McKenzie River in Washington and the Adour River in France contained more exotic species than sites with lower native diversity. They attributed this result to riverine factors covarying with diversity. Pickard (1984) found that floristically diverse sites in the Lord Howe Islands had more exotic species than did species-poor sites, a result he attributed to the soil nutrient status of diverse sites.

In a rigorous analysis of invasion patterns Wiser et al. (1998) found that the occurrence of the exotic forb
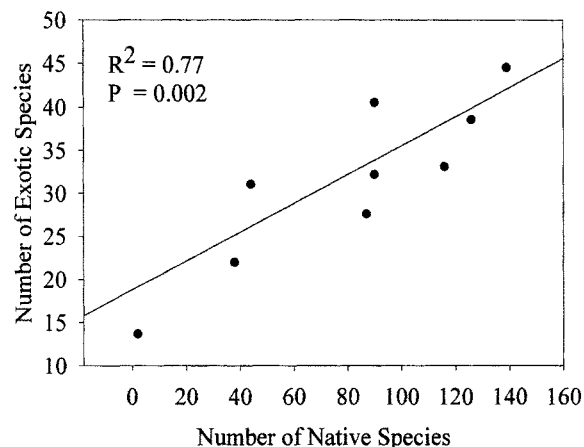

Fig. 1. Reanalysis of the relationship between diversity and invasion for shrubland sites presented by Fox and Fox (1986). See text for biases in the original presentation of these data. Data were obtained by digitizing Fig. 5 in Fox and Fox (1986). We back-calculated the number of exotic species per site from the number of native species and the percentage of species that were exotic.

Hieracium lepidulum in New Zealand was positively correlated with species richness across 250 permanent plots. Their data included three time points over 23 years and measures of a wide variety of other site conditions that might influence invasion. Using multiple logistic regression, they partitioned out the factors covarying with species diversity, and still found a positive correlation between diversity and invasion. In another investigation tracking an invasion through time, Holway (1998) found that the spread of 20 Argentine ant populations in California was not correlated with native ant richness.

Several studies have found that invaded communities are less diverse than their uninvaded counterparts. In each case, however, the invaders were so abundant that the results most likely reflected the impact of the invader on native diversity. Woods (1993) used the negative correlation between exotic honeysuckle cover and native richness in Eastern US forests to argue that honeysuckle negatively impacted native diversity. Similarly, Morgan (1998) found a weak negative correlation between native richness and exotic richness ($R^2 = 0.16$, $p < 0.001$) in an Australian grassland. By comparing plots with low and high exotic cover, he argued that this correlation reflected the impact of the exotic species on native richness. Similarly, Stohlgren et al. (1999) reported that 1 m^2 plots placed in more heavily invaded communities of the Central US showed negative correlations between native and exotic diversity, while those in less invaded areas showed positive relationships. Pysek and Pysek (1995) reported that habitats in the Czech Republic invaded by the tall forb *Heracleum mantegazzianum* had lower diversity and richness than uninvaded plots. They reported that *H. mantegazzianum* occupied between 50% and 100% cover in the study area and replaces native vegetation, providing the simplest explanation for the lower diversity of invaded areas.

Several investigators have explored biogeographic scale patterns of diversity and invasion. Case and Bolger (1991) found a weak negative correlation between native and exotic reptile diversity on islands throughout the world. They noted, though, that the degree to which this reflects the number of native species per se versus the evolutionary isolation of species poor islands remains difficult to untangle. Weaker trends for birds and mammals are presented by Brown (1989) and Case (1996). Rejmanek (1996) found that for vascular plants, the tropics are less invaded than the temperate zone, though he concluded that this correlation was unrelated to diversity. In another analysis, Rejmanek (1996) reported a positive correlation between the number of native and exotic plants per log area on islands between 50°S and 50°N. He argued that native diversity seemed to be an indicator of favorable conditions. These results are supported by Lonsdale's (1997) study of global patterns plant invasions, which showed that worldwide, communities richer in native plant species are also more invaded.

Invader addition studies

Invader addition studies differ from the studies above only in that invasibility is measured by adding a fixed number of propagules to assemblages varying naturally in diversity. Thus, the investigator knows the diversity of the assemblage at the time of invasion. This eliminates the possibility that the invader has somehow influenced patterns of native diversity. In addition, by controlling the number of propagules added, invasibility reflects features intrinsic to the community, and not differential propagule supply. Nevertheless, like spatial pattern studies, diversity is not manipulated, so the results are still driven by both diversity and factors covarying with diversity. Nonetheless, invasibility is actually measured, though how this is done can influence the conclusions.

Invasion is a probabilistic process (Crawley 1987, 1989). Diversity does not deterministically render a community completely resistant or vulnerable to invasion, but rather, influences the probability that a given propagule will be successful. One approach for assessing invasibility is to score communities as invaded or not invaded after adding a given number of propagules (e.g. Robinson and Dickerson 1984, McGrady-Steed et al. 1997, Tilman 1997b). However, with this approach, the magnitude of any effects on invasibility depend on the number of propagules added. Even if diversity influences the probability of successful invasion, if enough propagules are added, all communities may be invasible. The sensitivity of invader success to propagule input is well known from the purposeful introduction of biocontrol agents (e.g. Crawley 1987, Hopper and Roush 1993) and birds (Duncan 1997). Alternatively, by examining the proportion of successful propagules as a function of diversity (e.g. Robinson et al. 1995), studies can estimate the per capita probability of success. This probability is independent of the number of added propagules as long as propagule density is low enough to prevent interactions among the colonists.

A second problem with assessing invasibility is determining the point at which an invader is considered "successful". We find the definition of Crawley (1987) useful: an invader is successful if it increases when rare. Using this definition, invader addition studies evaluating sexual or asexual population growth make the most convincing case for examining invasibility.

Robinson et al. (1995) added seeds of California poppy (*Eschscholzia californica*) to grassland plots that varied naturally in diversity and found that more diverse plots were more invasible by this poppy than species-poor plots. Specifically, they found that more poppies germinated, flowered, and produced fruit in the more diverse plots. This result can be partly attributed to the fact that *Bromus diandrus*, a strong suppressor of poppies and other plants was more abundant in low

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diversity plots. In a similar study, Peart and Foin (1985) examined the invasibility of patches within a coastal California grassland by adding the seeds of five grasses to plots varying in composition. Though their study did not focus on diversity, Peart and Foin found that plots dominated (near 100% cover) by a single productive perennial grass were more difficult to invade than were mixed species plots of annual grasses and forbs. More generally, low diversity patches may often be the least invasible when the low diversity results from competitive dominance by one or a few species.

Tilman (1997b) added seeds of 54 native species to Minnesota grassland plots varying naturally in diversity. In contrast to Robinson et al. (1995) and Peart and Foin (1985), he found that more diverse plots were less invasible. The mechanism, however, remained unclear. The effects of diversity on invasibility were not mediated by effects on nitrogen, since as Tilman pointed out, plots with the less nutrients were more invaded.

Assembly studies

Assembly studies assess patterns of diversity and invasion over time, asking, "Do communities become more difficult to invade as time progresses with the accumulation of species?". Invasibility is measured as the number of new species establishing over a given time interval. If diverse communities better resist invasion, the number of new species in a community should level off with time. However, as with the assembly models, a declining number of invasions over time may also reflect the formation of more connected communities (Law and Morton 1996) or the exhaustion of good invaders early in the assembly process, selectively leaving poorer invaders to establish later on (Case 1991).

Due to the difficulty of obtaining frequent censuses of a developing community and the long-term data sets required, most assembly studies are conducted in microcosms. These have been reviewed elsewhere by Drake et al. (1996), the general result being that communities decline in invasibility over time. The degree to which this depends on diversity is less clear. Moulton and Pimm (1983) took advantage of historical bird counts to examine the success of avian introductions to Hawai'i. They found that on certain islands, the success rate of introductions decreased over time as the communities accumulated more introduced species. They argued that this resulted from increased competition in the more diverse communities. Simberloff and Boecklen (1991), however, showed that nearly all of the successful invaders in Moulton and Pimm's study were successful when introduced throughout the Hawaiian islands, regardless of island diversity and unsuccessful species tended to be unsuccessful everywhere, a result

which calls to question the diversity effect (but see Moulton 1993). In a similar analysis of bird invasions into New Zealand, Duncan (1997) was unable to isolate an effect of diversity.

Constructed community studies

Studies that experimentally construct communities, directly manipulating diversity are the only ones that experimentally isolate the independent effects of diversity on invasibility. In this light, they are the most comparable to the modeling work. In addition, they have the potential to isolate the mechanisms underlying the effects of diversity, though this has not yet been done.

Knops et al. (1997) examined the number of invasions into Minnesota grassland plots where plant diversity had been experimentally manipulated (see Tilman et al. 1996). Their results indicated that invasibility was a negative but asymptotic function of diversity, providing some of the first empirical evidence that diversity may deter invasion in a natural system (Naeem et al. 1998). Palmer and Maurer (1997) examined weed invasion into plots planted with one or five crop plants. As in Tilman et al. (1996), the one-species treatment included monocultures of all species in the pool. They found that more diverse plots were significantly more invaded, though the mechanisms remained unclear.

Due to the relative ease of manipulating communities of microorganisms, these systems have proven useful for examining the relationship between diversity and invasibility. Much like the models, these studies create communities of varying diversity and then subject them to invasion. In the studies we describe below, the identity of the species in each replicate community was not randomly assigned, and prior to invasion, the communities were given time to equilibrate, during which species were lost. Thus it is difficult to determine the extent to which these studies reflect just the independent effects of diversity. Nevertheless, since the initial number of species in each replicate was determined by the investigator, diversity is still unlikely to be highly correlated with other environmental factors. In Mc-Grady-Steed et al. (1997), roughly 17 microorganism communities containing up to 17 species, and three trophic levels were invaded with a facultative heterotroph. Of the five successfully invaded communities, all contained fewer than six species. Thus, their work generally supports the hypothesis that diversity enhances resistance to invasion, though they argued that rather than a species-packing mechanism, the effect of diversity was attributable to particular key species that were more abundant in the diverse communities.

In a similar type of experiment, Robinson and Dickerson (1984) used three different invaders to examine if diversity enhanced ecological resistance. The first in-
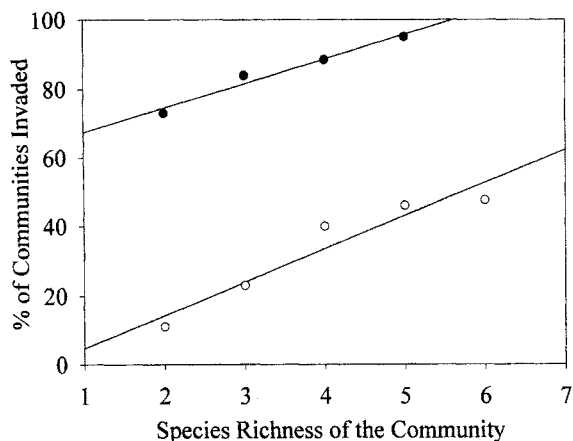
Fig. 2. Reanalysis of microcosm results from Robinson and Dickerson (1984). We used simple linear regression to examine the relationship between community diversity and the percentage of communities successfully invaded three weeks after introduction of (○) *Staurastrum* ($R^2 = 0.91$, $p < 0.05$) and (●) *Dictyosphaerium*. ($R^2 = 0.97$, $p < 0.05$). In order for these results to be comparable to those of McGrady-Steed et al. (1997), we selected week 3 data from Robinson and Dickerson (1984) since week 2 data were not available for both invaders (McGrady-Steed et al. presented week 2 data). Nevertheless, a positive relationship between diversity and invasibility emerged regardless of when invasion was assessed. Diversity levels with four or fewer replicates were excluded due to the inherent inaccuracy of percentages calculated from small numbers (all percents in the figure were based on at least nine replicates).

vader, though capable of growing in isolation, failed to invade any community, regardless of diversity. For the other two invaders, Robinson and Dickerson (1984) concluded that persistence time was independent of diversity. This conclusion was based on a contingency table analysis where the rows were progressively increasing levels of diversity, and the columns were progressively increasing invader persistence times. The simple G-test used by the authors treated each cell as independent, and was inappropriately weak considering that both the rows and columns were ordered (Feinberg 1980). We reanalyzed their data using doubly ordered contingency table analysis, and found that diversity significantly influenced invader persistence time for both species (linear by linear association tests, $p < 0.05$), but in contrast to their expectations, invaders persisted longer in more diverse communities. We also used simple linear regression to examine the relationship between community diversity and the percentage of communities successfully invaded three weeks after introduction (Fig. 2). These results also indicated a significant positive relationship between diversity and invasibility.

In spite of the possibilities provided by studies that directly manipulate diversity, very little of such work is currently published. We believe that particularly in light of the large number of habitat restoration projects currently taking place and management concerns over

exotic invaders, there is considerable opportunity to explore the diversity/invasibility relationship with an experimental approach. Some revegetation studies have explored the effects of using various native seed mixes on weed invasion (e.g. Tyser et al. 1998) but have not specifically addressed the importance of species diversity.

Discussion

Current models evaluating the effects of diversity on invasibility unilaterally support the common belief that species diversity enhances resistance to invasion. Those empirical studies most similar to the models, the constructed community studies, only sometimes supported this notion, suggesting that diversity does not consistently enhance resistance in natural communities. The most striking finding of this review was that the majority of the spatial pattern and invader addition studies indicated that naturally diverse assemblages tended to be more invasible than their species-poor counterparts, contrary to Elton's (1958) observations. This finding is particularly important from a conservation standpoint since it suggests that our most diverse habitats are the most prone to invasion (Stohlgren et al. 1999).

Why might diverse assemblages be the most invaded? Nearly all of the spatial pattern studies cited favorable biotic or abiotic factors covarying with diversity that were presumed to underlie the positive correlations between diversity and invasibility, including moisture, nutrients, habitat heterogeneity, physical factors, and competitors (e.g. Pickard 1984, MacDonald et al. 1989, Robinson et al. 1995, Rejmanek 1996, Stohlgren et al. 1999). In general, unless native and exotic species differ markedly, the factors controlling native diversity should similarly control invaders, and thus the number of native species simply becomes an indicator of biotic or abiotic conditions favorable to invasion (Rejmanek 1989; but see McIntyre and Lavorel 1994).

Because of the importance of factors consistently covarying with diversity, the observation that naturally diverse communities are more invasible cannot be translated to mean that diversity promotes invasion (e.g. Stohlgren et al. 1999). While we believe that positive effects of diversity on invasibility are very much under-appreciated, the small scale at which the mechanisms underlying the effects of diversity operate precludes them from driving community or landscape-level patterns. Each of the proposed mechanisms, such as species-packing or the effects of key species, operate on the scale of species interactions, or the neighborhood (Naeem et al. 1998; but see Law and Morton 1996). Yet, the scale of nearly all of the spatial pattern and invader addition studies was significantly greater than the neighborhood, with most examining entire

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communities or landscapes. We believe that independent of whether the neighborhood effects of diversity on invasion are positive or negative these effects are likely to be swamped by factors covarying with diversity at broader spatial scales. This hypothesis is analogous to the observation that competitors which are negatively associated at small scales are often positively associated at broader scales due to similar habitat requirements (Wiens 1986).

Positive correlations between native and exotic diversity suggest that if local scale diversity enhances resistance to invasion, this effect is weak relative to other factors influencing invasions in these systems. Quantitatively evaluating the importance of diversity relative to disturbance, nutrients, consumers, and other factors limiting invasions has rarely been accomplished, though is an important goal for future work in this area. Such information is essential to accurately predicting the consequences of species loss for community invasibility.

Are native and exotic species all that different?

A common perception in the study of biological invasions is that exotic species somehow differ from the residents of the communities they invade. However, the results of spatial pattern and invader addition studies suggest that exotic and native species respond to the same factors. The notion that major differences separate invader and resident species is based largely on classic theories of what makes a good invader (Baker 1965) and the invader impact literature. While it does seem true that invaders with large impacts differ considerably from native species (Vitousek 1990, Chapin et al. 1994), the traits behind large impacts need not be the same as those allowing the invader to enter in the first place. Moreover, while the exact percentage is debated, most invaders do not have major impacts (Simberloff 1981, Herbold and Moyle 1986, Moyle and Light 1996).

That invaders and resident species must be somewhat similar is also an implicit assumption of arguments regarding species-packing: the resource requirements of the invader and the resident species must overlap for the species-packing mechanism to operate. If an invader requires a portion of the resource space outside that of the resident species, then resident species diversity may be inconsequential to its invasion. Thus, if invaders with large impacts are truly different from the residents of the communities they invade, an interesting problem arises: the factors controlling invasion may differ for species with large and small impacts. We note that few diversity-invasibility investigations have focused on high-impact species.

The biotic resistance paradigm

Much of the research and hypotheses concerning the effects of diversity on invasion have been strongly driven by the focus on "biotic resistance", a focus that is evident in the seminal work of Elton (1958). Based on the results of this review, we believe that resolving the diversity-invasibility relationship and more generally, enhancing the predictability of invasions requires that we not only uncover the community members that repel invaders, but also those that facilitate invasion. A new focus on species that promote invasions is beginning to emerge. Richardson et al. (1999) suggest that mutualisms between introduced plants and native organisms (pollinators, dispersers, fungi, N-fixing bacteria) are quite common and are possibly very important in promoting invasion. Palmer and Maurer (1997) and Wiser et al. (1998) discuss "invasion promoters", whose increased abundance in areas of greater diversity make these areas particularly susceptible to invasion. Indeed, a surprising fraction of the empirical studies suggest that in some systems diversity might promote invasion (Robinson and Dickerson 1984 (reanalyzed), Robinson et al. 1995, Palmer and Maurer 1997, Wiser et al. 1998). Even more generally, facilitations, both direct and indirect (Bertness and Callaway 1994, Callaway 1995, Levine 1999) are increasingly recognized as important structuring forces in communities, and the implications of this for the diversity-invasibility relationship should not be ignored.

Conclusions

Ecologists have long been searching for a general theory of the factors controlling invasions. Based on the results of this review, and more specifically, the suggestion that exotic and resident species show similar responses to the environment, we believe that our understanding of the ecological controls over native species diversity may provide our best theory of the controls over invasibility. It is no coincidence that the dominant factors known to influence diversity such as competition, disturbance, resource availability, and propagule supply (see Huston 1994 for review) are the same factors known to influence invasions.

Considering the controversial foundations and weak empirical support for a negative relationship between diversity and invasibility, we believe that there is much room for innovative models and careful empirical studies that go beyond current approaches. More specifically, we urge investigators to explore the mechanisms underlying the effects of diversity on invasibility. Empirical studies rigorously evaluating mechanisms are conspicuously absent from the literature, yet a mechanistic understanding of the diversity-invasibility relationship is essential for accurately predicting the

assemblages or circumstances where diversity matters most. Furthermore, what mechanistic evidence we do have provides little support for the often-cited species packing mechanism and biotic resistance paradigm. Moving beyond this paradigm is critical to better understanding the diversity-invasibility relationship and more generally, enhancing the predictability of biological invasions.

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