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# The relationship between community diversity and exotic plants: cause or consequence of invasion?

Scott J. Meiners & Mary L. Cadenasso

## Introduction

Biological diversity is the modern unifying metric by which the health and status of communities and ecosystems are assessed throughout the world. Diversity is used to identify areas of special conservation concern while threats to biodiversity are the focus of remediation and legal action. Although the greatest threats to biodiversity are typically thought of as being the direct or indirect result of habitat loss and fragmentation, biological invasions follow closely behind. Despite this high priority position, our knowledge of the relationship between invasions and diversity remains relatively early in its development.

The invasion of terrestrial communities by exotic plant species is a major concern for ecologists and natural resource managers. With the increased speed of planned and unplanned movement of species throughout the world and greater rates of disturbance, exotic plants are becoming a larger component of regional floras [1–4]. Furthermore, exotic species already cover vast areas of many community types and sometimes dominate local plant communities. Invasions affect both natural and agricultural systems and cause financial, as well as biological problems in areas of heavy invasion. While there has been an increase in awareness of the problem of exotic invasive plant species, their community-level impacts remain relatively unknown [5–8]. A frequently observed pattern within plant communities is a negative relationship between diversity, typically expressed as species richness, and the cover of exotic plants (Fig. 1A). This simple pattern has been explained by two community-level mechanisms that differ in the cause/consequence relationship between diversity and invasion. In the first mechanism, diversity regulates the invasibility of the local plant community, causing the diversity/invasion relationship.

This view comes from theoretical and experimental community ecologists over the past several decades starting with Elton [9] and continues with empirical work (e.g., [10–12]). In the second mechanism, plant invasion results in the reduction of community diversity by driving other species from the local community. Changes in diversity in this context are a consequence of invasion. Conservationists largely present this view as justification for the control and regulation of exotic plant species [13, 14].

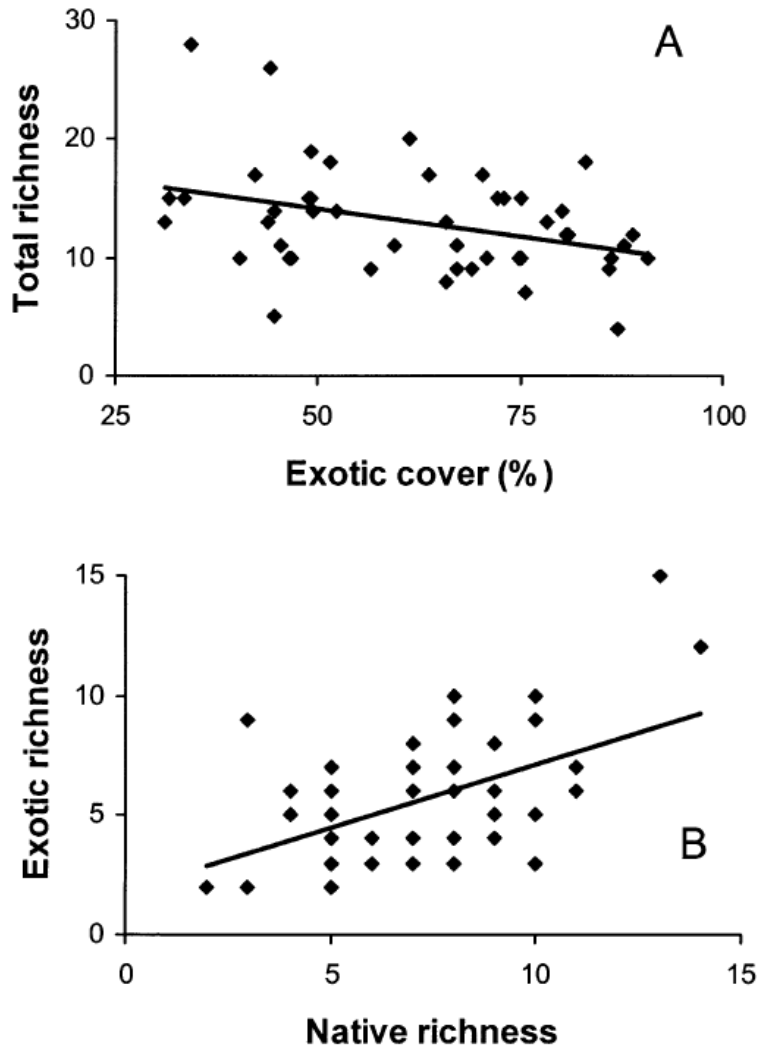


Figure 1. The relationship between invasion and species richness. (A) Total species richness as a function of the proportion exotic plant cover (Spearman rank-sum correlation  $R = -0.42$ ;  $P = 0.003$ ) (B) Exotic species richness as a function of native species richness (Spearman rank-sum correlation  $R = 0.40$ ;  $P = 0.005$ ). Data were collected as percent cover in 1 m<sup>2</sup> plots as part of the BSS.

Unfortunately, most studies have only addressed invasions from the cause or consequence perspective, leaving the true nature of the relationship unresolved. Currently, it is unknown whether the relationship between exotic plant invasion and diversity is caused by the local displacement of species by plant invaders, differential invasibilities of areas of varying diversity, or some combination of both. In this chapter, we specifically identify limitations of the current perspective on invasion and propose a conceptual framework from which to address the nature of the relationship between diversity and invasion. The framework aims to abstract the components of this relationship to allow generalization across systems and invaders, thereby enhancing ecological understanding of the causes and consequences of invasion. Several case studies are provided to illustrate

the necessity of separating these two disparate perspectives of plant invasions.

### **Scale and the invasion of plant communities**

Before directly addressing the relationship between diversity and invasion, it is first necessary to deal with the issue of scale. A hierarchical perspective of biological invasions reveals three nested scales which interact to determine invasions and their impacts in communities [15]. The coarsest scale, the regional scale, determines the species pool of invaders and residents, setting the potential range of species interactions. The intermediate scale, that of the landscape, determines which species within that larger regional pool will be able to colonize a given habitat based on their presence within the landscape, their vagility and physiological tolerances. The finest scale of interest is that of the neighborhood; the scale at which species interacts. Interactions lead to differential performance of the species, resulting in the realized composition of the neighborhood. At this fine scale, individuals may interact to influence invasion success or to generate the impacts of an invasion. Therefore, the most appropriate scale for studying the diversity/invasion relationship should match the scale at which organisms interact within a system.

The scale of interaction varies widely with the type of system being studied and with the specific interaction involved. Within experimental microcosms or modeling studies of community invasibility, all species within the community interact, or at least have the potential to interact [16, 17]. This is in marked contrast to the condition in terrestrial plant communities, where interactions occur at neighborhood scales [18, 19]. Typically, only plants with canopy or root overlap have the potential to interact. For example, two herbaceous plant species may compete strongly when in close proximity, but would have no effect on each other when separated by even a few meters. For this reason, the total number of plant species in an entire community should have no bearing on the overall invasibility of that community. Rather, fine-scale, within-community patterns of diversity may determine neighborhood invasibility. What constitutes a neighborhood in a particular system should parallel the scale at which organisms interact, probably from 10 cm<sup>2</sup> or less for small plants and emerging seedlings to 50 m<sup>2</sup> or more for large canopy trees.

Plants in terrestrial ecosystems are immobile and compete locally for largely immobile resources such as light and soil nutrients. This leads to the development of heterogeneity in local competitive environments, even within sites heavily invaded by an aggressive exotic species. This interaction heterogeneity explains why plant invasions rarely, if ever, directly lead to the loss of a species from an entire community. Species may be lost from areas directly impacted by an invasion, but will persist in spatial refugia not dominated by the invader (e.g., [20–22]).

While competitive interactions dominate the ecological literature on invasions

[23], there are several other direct and indirect mechanisms through which plant invaders could interact with the resident community. These include allelopathic interactions [24–26], associational defenses [27], influences on nutrient dynamics [28, 29] and alterations of soil biotas [30]. Similar to competitive interactions, all of these interactions function at relatively fine scales.

Scale emerges as a critical variable when assessing apparent conflicting relationships of diversity and invasion published in the literature. At regional scales, the relationship between exotic and native species richness is often a positive one [4, 31–34], while at fine scales within sites, the same communities may show a negative correlation between exotics plants and native species richness [32, 33, 35]. Diversity at regional scales is less determined by species interactions and more the result of changes in abiotic factors such as disturbance rate or productivity [36, 37] or variation in historical, evolutionary and biogeographical influences [38]. Native and exotic species appear to respond to this regional variation in abiotic conditions in a similar manner [4, 19, 34, 39, 40], resulting in the positive spatial associations at coarser scales. Overall, community-level controls on invasion must function through local processes of interaction with the resident community. Likewise, the majority of impacts on the community would be expected to be manifested at fine scales that match the scale of species interactions. These local dynamics are nested within the regional context that determines the pool of native and exotic species and the availability of species to colonize a particular site (i.e., propagule pressure). Throughout the remainder of this paper, we will focus only on finescale causes and consequences of plant invasion.

### **Cause: diversity and the regulation of community invisibility**

Interactions between invading species, the existing plant community and microhabitat conditions influence the ability of an exotic plant species to invade a site. Within plant communities, areas with lower diversity are often thought to be more susceptible to invasion than relatively species-rich areas [9, 39, 41–44]. This is because species-poor microsites may have more available resources, or vacant niches, allowing a specific exotic plant species to become established [9, 10, 45]. Experimental evidence suggests that higher diversity areas use resources more completely, leaving few colonizable niches [10, 12, 19, 45]. Local resource availability has been found to be critical in determining neighborhood invasibility in many studies [12, 46–49], and may represent a general explanation for fine-scale invasibility patterns [48, 50]. Alternatively, it may not be the diversity, but the composition of the neighborhood that regulates invasibility [11, 22, 51, 52]. Higher diversity areas would be more likely to contain competitively dominant species through sampling from a limited species pool [10, 11, 53] and are thus more likely to resist invasion. This is commonly referred to as an ecological sampling effect [53].

The diversity-invasibility hypothesis has been tested in herbaceous communities with contrasting results. Neighborhoods of higher diversity were more resistant to invasion in some studies [10–12, 19, 52] while other studies found higher diversity plots to have equal or greater invasibilities [4, 32, 33, 51, 54–56]. Positive associations between diversity and invasion suggest that the same basic factors which make a microsite able to support many native species also make them able to support a diverse group of exotic species [4].

The quantity of evidence currently available on the diversity–invasibility hypothesis shows that diversity can regulate neighborhood invasibility in some systems, but that the directionality of this relationship appears to vary. The more important research themes now become the determination of the conditions under which diversity regulates community invasibility and the development of conceptual models that explain the variation in the direction of this relationship. Neighborhood diversity appears to limit the establishment of invading plant species in communities dominated by equilibrium dynamics, particularly in those communities strongly structured by competitive interactions such as in the nutrient limited sites studied by Tilman and colleagues [10, 45, 57–59]. Sites dominated by non-equilibrium dynamics, such as successional sites or those with otherwise high species turnover, appear to have a positive association between invasion and fine-scale diversity [19, 32, 35, 55]. However, this dichotomy may be artificial, as invasibility has been predicted to respond unimodally along diversity gradients when both facilitative and competitive interactions structure the community [23, 55]. The directional responses seen in many systems may therefore represent the extremes of the gradient, or situations where either positive or negative interactions dominate.

The variation in the diversity–invasibility relationship across systems may also reflect the short-term nature of the majority of studies. Our ability to make reliable predictions about ecological systems is often limited by the temporal extent of available data [60]. The lack of predictive models in invasion biology may therefore be linked with the lack of sufficient long-term data.

### **Consequence: invasion impacts on diversity**

While exotic plant invasions alter plant community composition and structure, the direct effects on diversity patterns are largely unquantified. Unfortunately, the vast majority of studies are observational, with little ability to assess the direct impacts of plant invasion on diversity [8]. It appears that exotic plant invasions are associated with a decrease in the number of species in natural communities [6, 61–64]. However, this pattern is clearly not ubiquitous across all plant communities [65–68].

Differences among studies in the measure of invasion complicate attempts at generalization. Studies that relate richness of exotics to native diversity often find a positive correlation [66] while studies that assess invasion by cover

or dominance tend to find negative associations [61, 69, 70]. Within a single community, it is possible to have both a positive association between native and exotic species richness and a negative association between total richness and exotic plant cover (Figs 1A and 1B).

Negative associations between exotic plant cover and community diversity have been used to suggest that invading exotic species do not merely fill vacant niches in natural communities [10], or replace native species one-for-one, but that they displace species disproportionately from the community, lowering diversity. Field studies of invasive exotic plants often cite this hypothesis, either as a correlation or as anecdotal information. However, this direct interaction has rarely been experimentally tested.

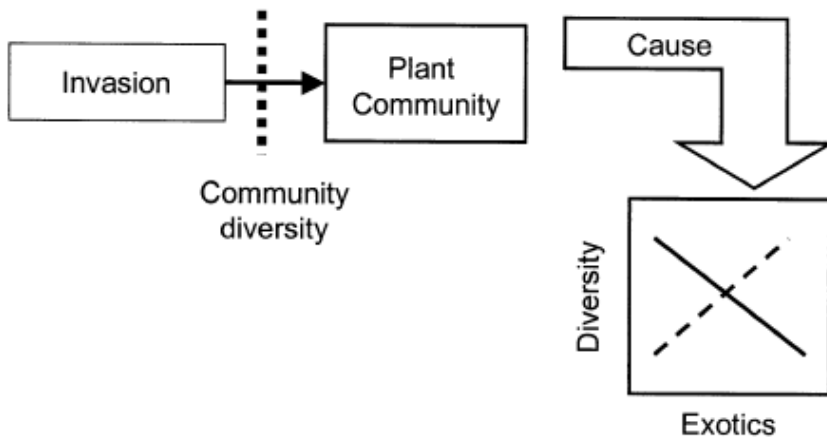
The competitive displacement of native plant species is often used as justification for the eradication of individual exotic species, although the perceived relationship with diversity may not exist [13, 67, 68, 71]. Many, if not most exotic species have only trivial impacts on community structure, becoming minor components of the plant community that increase regional species diversity [5, 72]. Problematic exotic species, those which become widespread and locally dominant, are generally found to be competitively superior to native species in two-species competition experiments [73–75]. However, it is not known whether exotic species are, on average, competitively superior to native plant species, which would be necessary to result in lowered diversity across a community. Increases in richness or species performance following invasive species removal suggest that competitive displacement may result from some invasions [76–83].

An excellent example of exotic plant invasion impacts is that of *Lonicera maackii*. This species, a bird-dispersed shrub native to Asia, has become widespread throughout the eastern United States [84]. It has become a problematic invader of deciduous forests, particularly second growth and disturbed forests [85–87] and often dominates the forest understory in heavily invaded sites. Observational data show that this invader is associated with declines in tree seedling abundance and in the abundance and diversity of the herbaceous understory [63, 83, 87]. The mechanisms behind this association have been tested experimentally, showing that *L. maackii* directly reduces the growth and fecundity of herbaceous annual and perennial understory plants [77, 78, 83] and competes with tree seedlings [88, 89]. Indirect impacts of *L. maackii* include protection of tree seedlings from deer browse [88] and increased tree seed predation by rodents (S. J. Meiners, unpublished data). Taken together, this suite of studies documents both patterns indicative of invasion impacts and documents direct and indirect interactions that generate these patterns. This is one of the few species invasions whose community-level impacts have been characterized mechanistically. However, beyond this species' connection to relatively open forest stands and gaps [85, 87], community-level controls on invasion success are unknown.

## Cause versus consequence: invasibility versus impacts

Clearly, the mechanism(s) that result in the often-observed relationships between exotic plant invasion and community diversity are unclear in current ecological literature. Associations between diversity and exotic plant cover have been used as evidence for both the regulation of neighborhood invasibility by diversity and the impacts of exotic plants on resident species. These two pathways of interaction must be separated conceptually to assess the relationship between exotic plant invasion and community diversity. These contrasting mechanisms can be formalized into two hypotheses, the invasibility hypothesis and the impact hypothesis (Fig. 2). The hypotheses differ in the role of diversity – as a regulator of exotic plant invasion or as a response to invasion. These two mechanisms also function at significantly different ecological stages, one at the establishment phase of the invader, the other once an invasion has successfully occurred and the species begins to spread within a site. In the invasibility hypothesis, the diversity of the neighborhood serves as an ecological filter that determines the invasion success of an exotic species. While there is no a priori reason to expect a single direction for the outcome of this interaction, most studies have focused on the inhibition of invasion by diversity. This reflects the overwhelming focus on competitive or other negative interactions in the exotic species literature [23]. Under this hypothesis, early seedling establishment and performance of the exotic species would be expected to vary with neighborhood diversity.

### Invasibility Hypothesis



### Impacts Hypothesis

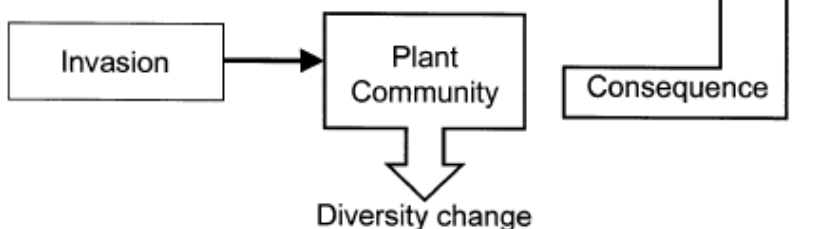




Figure 2. Schematic model of the two major hypotheses explaining the relationship between community diversity and exotic plant invasion. The invasibility hypothesis states that community diversity regulates the invasion of exotic species into a community, generating a relationship between diversity and exotic plant invasion. The impact hypothesis states that following invasion by exotic species, interaction between the resident community and the invader lead to changes in community diversity. As there is no a priori assumption of directionality for this relationship, both positive and negative diversity/invasion relationships are shown.

In the impact hypothesis, exotic species invade a neighborhood and subsequently interact with species residing within the community, resulting in altered diversity. This is typically thought to occur via the invader competitively displacing species currently in the area [8, 64, 77], or by preventing the establishment of other species [11, 22]. Species displacement would result in a reduction in neighborhood diversity if individual exotic species, on average, displaced more than one resident species. While positive interactions between invaders and other species have rarely been documented, the invasion of a species that facilitates the growth or establishment of other species may directly increase neighborhood species richness.

Both invasibility and impacts processes may generate similar changes in neighborhood diversity in association with exotic plant species, but would differ mechanistically. The diversity/invasion relationship of different exotic species may be explained by different mechanisms, or both may simultaneously operate to determine the relationship of an invader to community structure. The diversity/invasion pattern exhibited by the plant community will be the net effect of these two independent processes. It is also possible that species that exhibit no associations with neighborhood diversity may actually have counteracting invasibility and impact relationships.

Finally, as null a hypothesis, there may be no mechanistic relationship between exotic species and diversity. Diversity and invasion may both respond to similar extrinsic factors that generate associations without direct interaction. For example, microsite conditions that generate spatial patterning in diversity may also favor the establishment of an exotic plant species. However, this would probably lead to fine-scale variation in dominance of individual exotic species with variation in microsite conditions. Since many exotic species tend to be problematic across many community types and at regional scales, this alternative seems unlikely. Variation in local seed input may also generate positive associations between exotic and native species, even when higher diversity results in lower invasibility [19]. Because most plant communities are seed-limited [10, 90, 91], and exotic plant species tend to be extremely vagile [44, 92, 93], exotic species may be the first plants to invade a disturbed area, resulting in low diversity with high invasion. In this situation, the relationship between invasion and diversity would disappear as the less vagile native species invade [94].

The variation in the direction and strength of the relationship between exotic plant invasion and diversity in the ecological literature may partly result from the lack of a useful conceptual framework that separates out the invasion process from subsequent species interactions. Most observational and experimental studies artificially integrate both mechanisms into a single assessment of invasion, therefore obscuring the species interactions underlying the community dynamics associated with the invasion.

### **Case-studies: *Lonicera japonica* and *Rosa multiflora***

The limited temporal duration of most studies constrains our understanding of the causes and consequences of exotic plant invasions [5, 8, 66, 95–97]. While most plant invasions occur over time periods of decades or longer, most experimental studies of invasions are brief, lasting only 1–2 years. Similarly, observational sampling studies frequently only capture a single snapshot of community associations, yielding little information on how these associations developed. Even studies that have incorporated time spans matching the scale of invasions frequently have only a few sample periods, typically only before and after invasion [65, 97–99] and do not capture the complex dynamics during the intervening period.

To explore the utility of our conceptual framework for understanding the community dynamics that shape the relationship between exotic species and diversity, we use long-term data of species invasions in abandoned agricultural land from the Buell-Small Succession Study (BSS). This study has recorded the presence and percent cover of all species occurring within permanent plots in 10 abandoned agricultural fields since 1958 [100]. The fields vary in crop prior to abandonment (hay versus row crops) and in the year of abandonment (1958–1966). Each field contains 48, 0.5 × 2.0 m plots that were sampled annually from 1958–1976 and in alternate years since 1976. This longterm data has provided a unique opportunity to study the function of exotic plant species within dynamic communities [22, 72, 94]. Individual plots can be followed over the course of an invasion to simultaneously determine the factors that regulate community invasibility and the community impacts of the invasion [72].

The two most common and abundant exotic species within the study are *Lonicera japonica* and *Rosa multiflora*. We use these two species to examine patterns of invasion and impacts on species richness over the course of the invasions. Both of these species are problematic at a regional scale and are typical of the plant species that are the focus of diversity/invasion studies in that they are widely believed to be detrimental to native ecosystems [14]. *Lonicera japonica* is a bird-dispersed liana that is native to Asia and has become widespread throughout the eastern United States [101]. This species has been shown to compete strongly with native tree species [74]. *Rosa multiflora*, a

bird-dispersed shrub, also native to Asia, was purposefully introduced as a living fence and as erosion control [102].

We analyzed data from years 5–15 and 10–20 post-abandonment for *L. japonica* and *R. multiflora*, respectively. These periods represent the beginning and midpoint of the species invasions within the study (Fig. 3). We documented three basic patterns for each species to assess the relationship between invasion and diversity: 1) the relationship between invader cover and species richness as a general pattern at a single point in time, 2) the relationship between species richness and invasibility, and 3) the relationship between invasion and subsequent species loss.

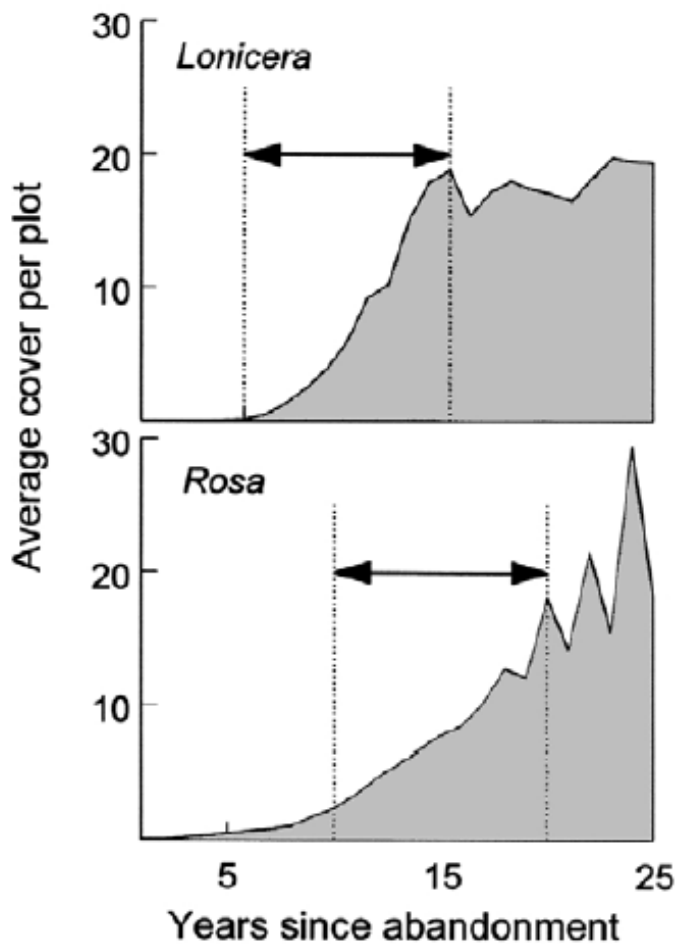


Figure 3. Temporal patterns of cover for *Lonicera japonica* and *Rosa multiflora* during succession within the BSS data. Arrows indicate the time span over which community dynamics in association with each invasion were assessed.

We determined the associations between total species richness and *R. multiflora* and *L. japonica* cover within plots at the midpoint of each invasion. This analysis is analogous to the one-time community sampling studies frequently

conducted to assess the impacts of exotic plant invasion. For both species, there was a significant, negative relationship between the cover of the invading species and the total species richness of each plot (Fig. 4). This relationship by itself does not elucidate any mechanisms that generate the observed pattern, but suggests interaction between the community and the invader.

For all plots that were uninvaded at the beginning of the observation period, we determined the relationship between initial species richness and the probability of subsequent invasion during the observation period for each species. This determines whether the invasibility of plots changes with species richness. For both species, plots with higher initial species richness were more likely to become invaded over the observation period than were plots with lower species richness (Fig. 5). The dynamics demonstrated by these species are in the opposite direction of most theoretical and experimental results, which show negative associations between invasibility and diversity. The selective invasion of high richness plots by these two species would tend to generate a positive association between invasion and diversity. Patterns of diversity are transient within the BSS, suggesting that there are no inherent differences between high and low richness plots that may influence invasibility. Invasibility at the neighborhood scale appears to be influenced primarily by stochastic events that generate opportunities for establishment [103], neighborhood species richness, and positive and negative interactions with resident species [55]. Once invasion had occurred, initial species richness did not influence the increase in cover of either species.

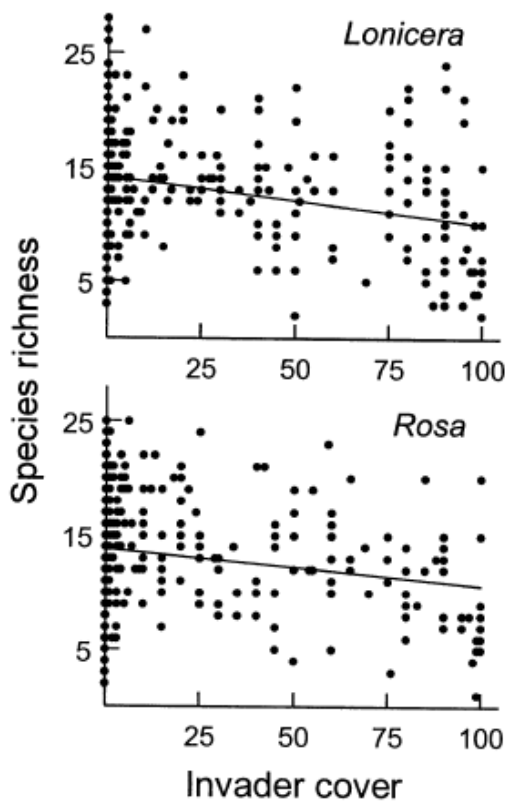


Figure 4. General association between invader cover and species richness for *Lonicera japonica* and *Rosa multiflora*. Regression analysis: *Lonicera* –  $F_{1,478} = 40.84$ ;  $P = 0.0001$ ;  $R^2 = 0.08$ ; *Rosa* –  $F_{1,478} = 16.86$ ;  $P = 0.0001$ ;  $R^2 = 0.03$ .

Finally, we determined the association between the increase in cover of the invading species and the change in species richness for those plots that were invaded during the observation periods. Change in cover for these two invaders represents increased cover of established individuals and, to a lesser extent, the recruitment of new individuals. This analysis assesses the ability of the invading plant to influence other species within the neighborhood [72]. As the cover of both invaders increased, the change in total species richness of the plot changed from a slight increase in richness over time to a net loss of species (Fig. 6). This shows that species were disproportionately lost from plots that were heavily invaded, strongly suggesting that both invaders were displacing resident species.

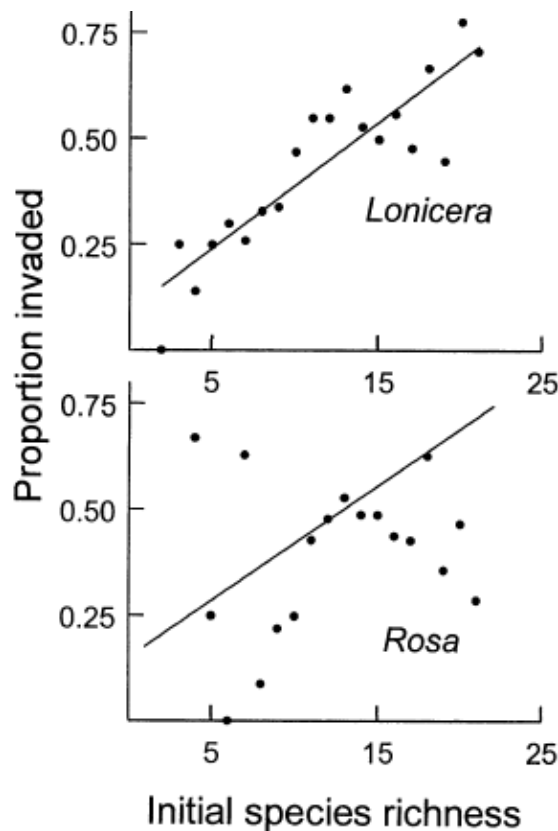


Figure 5. Influence of initial species richness on plot invasibility for *Lonicera japonica* and *Rosa multiflora*. Line represents logistic model predictions, points represent actual proportion of plots invaded where  $N = 3$ . Logistic regression analysis: *Lonicera* –  $\chi^2 = 7.51$ ,  $df = 1$ ;  $P < 0.01$ ; *Rosa* –  $\chi^2 = 4.62$ ,  $df = 1$ ;  $P < 0.05$

Both invasibility and impact processes interact to generate community structure and dynamics associated with the invasion of these two species. The

overall negative association seen in the single-sample data is the net combination of both of these factors. Interestingly, these two processes are antagonistic to each other, as selective invasibility would generate a positive association while invader impacts would generate a negative association. Invader impacts are clearly stronger in both of these cases, leading to the overall negative association even though invasibility partially obscures the impacts of invasion at the community level.

### Extensions of separating cause from consequence

There are some interesting extensions of our conceptual framework that suggest invasion may alter community structure at a broader scale under certain circumstances. In cases where invasibility and impacts of an invader are both in the same direction (e.g., low diversity areas are more invaded and invasion leads to species displacement), we would expect to see increased variance in neighborhood diversity across the site. Similarly, in cases where these two processes function antagonistically towards each other (e.g., high diversity areas are more likely to be invaded and there is subsequent species displacement), we would predict an overall decrease in the variance of neighborhood diversity as invasion intensity increases.

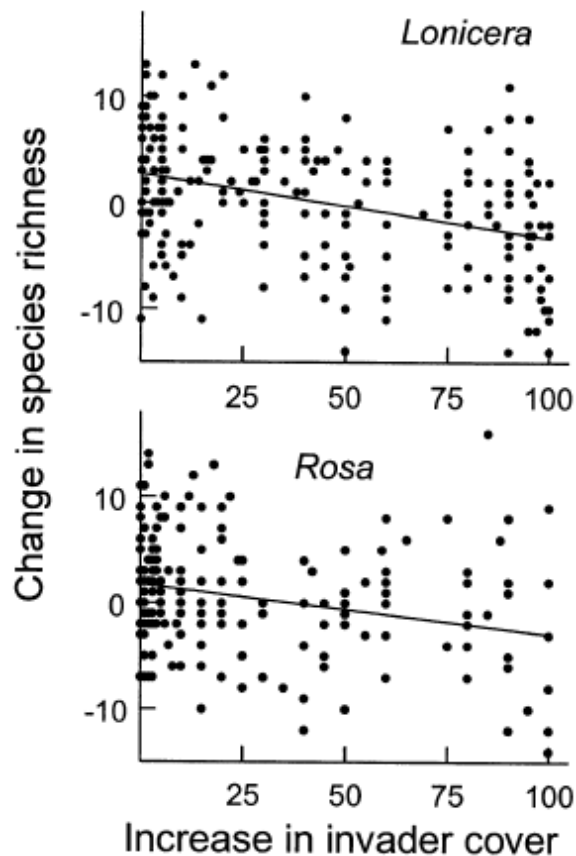


Figure 6. Impacts of invasion on species richness for *Lonicera japonica* and *Rosa multiflora*. Regression analysis: *Lonicera* –  $F_{1,218} = 34.88$ ;  $P = 0.0001$ ;  $R^2 = 0.14$ ;

Rosa –  $F_{1,186} = 13.53$ ;  $P = 0.0001$ ;  $R^2 = 0.07$ . Analyses were conducted only on invaded plots only to avoid confounding effects of richness on invasibility.

Of the three species within the BSS data that show significant species displacement and a positive association between invasion and species richness (*Elytrigia repens*, *Lonicera japonica* and *Rosa multiflora*), only *E. repens* (a grass) had decreased variance with invasion intensity as predicted. Thus, invaded systems may become more homogeneous during the course of invasion. The variation seen among invaders may represent the intensity of interaction between the invader and resident community and the time scale over which these interactions occur. The two species that did not exhibit a relationship dominate systems for much longer and may generate a response as the invasion proceeds. This relationship should be explored in other systems to see whether it is a common consequence of plant invasions.

The value of long-term monitoring of natural plant communities is clearly evident in the above case studies. The non-experimental nature of this and similar studies actually increases the range and breadth of questions that can be addressed with the resulting data, although direct experimental control has been sacrificed. In unmanipulated systems, the types of relationships and interactions that can be addressed are not limited by experimental protocols designed to separate out a small suite of effects. For this simple reason, a study began to document successional dynamics has been very useful in addressing plant invasions and their impacts.

## **Conclusions**

Invasion ecology has suffered from the artificial separation of invasibility and impact processes in understanding the relationship between diversity and plant invasion. By studying these independently functioning stages of invasion in concert, we can gain great insight into the biological causes and consequences of invasions, and develop crucial information for the generation of adequate management strategies. Our conceptual framework provides a structure to synthesize the current body of research, suggests research needed to fill the gaps in understanding and to organize results from future research. The framework is a powerful tool to guide ecological understanding of the relationship between invasion and diversity across systems, species, and scales.

The case studies discussed here clearly show how both the cause and consequence of diversity may operate simultaneously within an invasion to generate the community associations often noted in static studies. Currently, it is not possible to make generalizations about which mechanism is the most important because of the extreme lack of information for most plant invasions. To understand the nature of the relationship between diversity and invasion, both of these processes must be assessed to determine their relative contribution.

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