

The rich get richer – responses

Are species-rich communities inherently more susceptible to biological invasion than those that are species poor? While many small-scale experiments ($\sim 1 \text{ m}^2$) in controlled environments have found negative relationships between diversity and invasibility, these often become positive when viewed at larger spatial scales.

In the February issue of *Frontiers*, Stohlgren *et al.* (2003; 1: 11–14) report on datasets from the US that suggest native (S_{nat}) and non-native (S_{non}) plant species richness is positively correlated across many orders of spatial magnitude – in other words, species-rich communities get richer because non-native species accumulate. We argue that, although these findings are of great importance, a positive relationship is expected when various environmental factors are not controlled, and offer an explanation for the spatial scale paradox in diversity–invasibility relationships.

Stohlgren *et al.* suggest that small-scale, controlled experiments may explain little of the invasion patterns and processes at larger scales. Yet these studies effectively isolate the potential negative effects of S_{nat} from those of environmental factors that positively covary with S_{nat} and S_{non} , such as habitat heterogeneity, moderate disturbance, and climate (Levine and D'Antonio 1999; Naeem *et al.* 2000). In addition, the ability to manipulate both local neighborhood interactions and environmental factors can elucidate their relative contribution towards community invasibility. Without these estimates, we fail to explain the processes affecting invasion patterns, and thus cannot offer effective management strategies.

As we move from smaller plots ($1\text{--}672 \text{ m}^2$) to areas the size of counties and states, and the relative impacts of biotic interactions diminish and the forces affecting regional biodiversity become paramount (Levine 2000), it is not surprising that positive, albeit weak, correlations

appear as in Stohlgren *et al.*'s Table 1 and Figure 2. Imagine, for example, a large field subjected to high non-native propagule input, in which a dense assemblage of evenly distributed native species prevents invasion from occurring. We then remove vegetation patches in checkerboard fashion, which reduces the vegetation cover by 50%, but does not change S_{nat} . The likely establishment of non-native species in the bare patches and the subsequent increase of S_{non} within the field are consequences of including disturbance, and demonstrate how S_{non} can increase even though strongly negative local diversity effects exist.

Biodiversity “hotspots” may also harbor many non-native species if powerful anthropogenic disturbances weaken the competitive ability of native plants. Ubiquitous, multi-scale disturbances include global climate change, acid rain and other pollutants, eutrophication, disease, and disruption of the disturbance regimes under which native species have evolved (Byers 2002). These factors can contribute to community invasibility despite high local diversity (Davis *et al.* 2000).

As spatial scale increases, the negative effects of diversity decrease because of the inevitable inclusion of spatially covarying environmental factors (Levine 2000). This emergent property of scale may explain the disparity between small-scale experiments and large-scale observations. If anthropogenic stresses currently favor non-native species over residents, managers of native biodiversity could approximate the frequency, magnitude, and duration of historic disturbance regimes to limit the impacts of non-native species (Byers 2002). Finally, we echo the authors' plea that ecologists must better understand how processes beyond plant neighborhoods promote invasions, but also propose that studies explicitly incorporate spatially covarying factors at the level which ultimately dictates plant establishment – the neighborhood scale.

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Except on very small plots, ecologists often find a positive correlation between native and non-native plant species richness. The paper by Stohlgren *et al.* (*Frontiers* 2003; 1: 11–14) also reported positive correlations at the state and county scales in the US. Here I present the corrected regression for the state-scale relationship (Table 1, regression 1) based on the data in Kartesz and Meacham (1999), the only available source for comparison of all 50 US states. Only species introduced from outside the US are defined as non-native and no distinction is made between casual, naturalized, and invasive taxa (Richardson *et al.* 2000). The resulting relationship is positive and statistically significant. When the outlier represented by California is excluded, however, the relationship is weak ($p = 0.15$).

In several studies of non-native flora, the human population size (H) has been identified as the most important factor (Chown *et al.* 1998, Dalmazzone 2000, McKinney 2001). The regression of the number of non-native species on the square root of H in individual states explains 60% of the variance (Figure 1a). When H is included as an independent variable, together with native species richness, contribution of the last variable becomes non-significant and negative (Table 1, regression 2). When the mean latitude of individual states is also included, the contribution of native species richness becomes significant again, but remains negative (Table 1, regression 3).

Based on a stepwise regression analysis, the best available predictors of non-native species richness are $H^{1/2}$ and the time since the state was admitted to the Union (U) (this variable is used as a surrogate for the length of intensive disturbance/intro-

Table 1. Regression analyses relating number of non-native species in US states to selected independent variables.

Regression number	Independent variables	Standardised regression coeff	p	Adjusted r^2
1*	No. of native species	0.370 (= r)	0.008	0.137
2*	No. of native species	-0.176	0.134	0.598
	Human population ^{1/2}	0.881	<0.0001	
3*	No. of native species	-0.257	0.034	0.627
	Latitude	-0.204	0.037	
	Human population ^{1/2}	0.881	<0.0001	
4**	Human population ^{1/2}	0.693	<0.0001	0.774
	Years in the Union	0.365	<0.0001	
5**	Human population ^{1/2}	0.671	<0.0001	0.769
	Years in the Union	0.374	<0.0001	
	No. of native species	0.030	0.75	

*n = 50, **n = 49, Hawaii is not included (admitted to the US only in 1959, but intensive disturbance and plant species importation started much earlier).

duction history). These two variables explain 77% of the variance in non-native species richness of the US states (Table 1, regression 4).

Interestingly, the inclusion of U into the analyses helped to reveal one intriguing result. While a positive relationship between species number and area is one of the most robust gen-

eralizations in ecology, there is a marginally significant but negative correlation between the number of non-native species and $\log(\text{area})$ of individual US states ($r = -0.251$, $p = 0.079$). However, as there is a strong negative correlation between $\log(\text{area})$ and U ($r = -0.689$, $p < 0.0001$), this counterintuitive rela-

tionship is explained. In general, smaller states were admitted earlier, and their history of intensive disturbance and species introduction was therefore longer.

Admittedly, the whole question of major patterns of non-native species richness in the US is more complicated (data are not independent but spatially autocorrelated). One point, however, is clear: the human population size and the length of intensive disturbance/introduction history are the two primary factors in determining species richness of non-native flora.

Finally, as there is a strong positive correlation ($r = 0.66$, $n = 50$) between $H^{1/2}$ and the standardized species richness of native plants (species/ $\log(\text{area})$), it seems that the very conditions that favor native species richness are also preferred by people (McKinney 2001). As a consequence, it is probable that more non-native species will be introduced and established in states that are favorable for both native plants and humans. The fact that environmental conditions in these states are also favorable for many exotics, represents an important – but not the most important – factor (Figure 1b).

Just how much this effect of human population is an issue at smaller scales (ie counties) remains to be seen. Moreover, two additional confounding factors may be important at that scale: different areas of individual counties and uneven intensity of sampling. Each of these factors can produce a “positive correlation” between non-native and native species richness.

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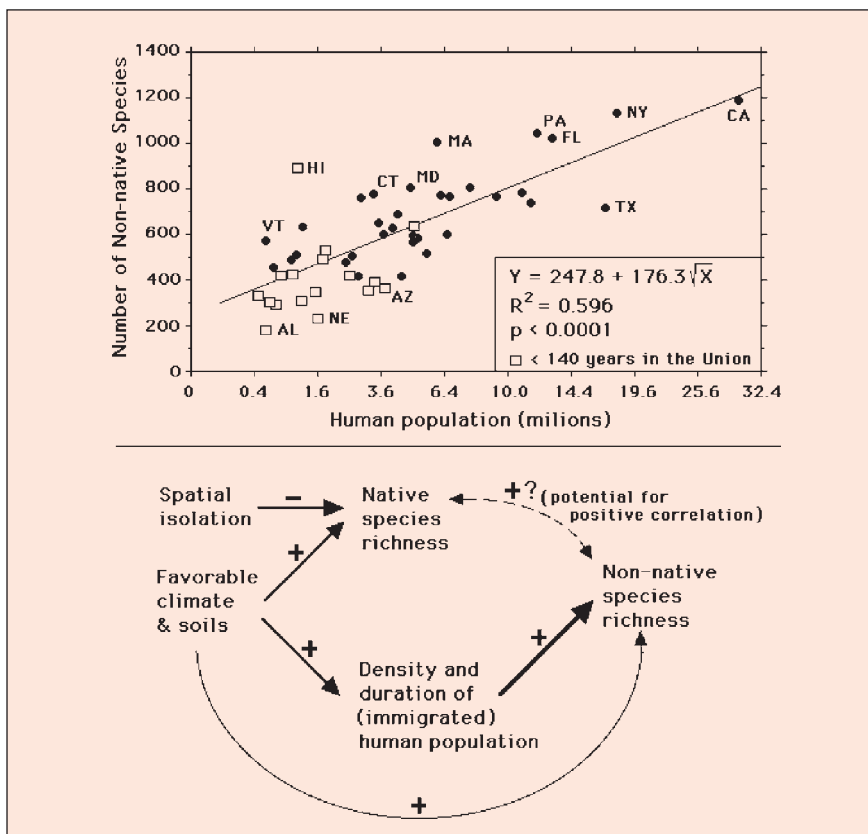


Figure 1. (top) Dependence of the number of non-native plant species on the size of human population in 1990 by state. (bottom) Relationships between environmental conditions, human populations, and non-native plant species richness. Thickness of the arrows indicates the magnitude of considered causal effects.

The authors reply

Renne and Tracy raise some interesting points in response to our paper 2003; 1: 11–14. We take this opportunity to reiterate that we did not try to explain the mechanisms that created this obvious and widespread pattern of species-rich areas successfully invaded by non-native species. We stated, and agree with Renne and Tracy, that there are various mechanisms and covarying factors that operate at many scales, but the mechanism they refer to as a “negative-diversity effect” may either be too weak or too rare to detect in natural systems.

There are few experiments that would predict the “rich get richer” pattern at large spatial scales (Levine 2000). Sax (2002) recently showed significant positive relationships for native and non-native plant species richness at multiple scales (1 m², 25 m², and 100 m²) in California and Chile, despite a 2:1 or a 1:1 ratio of native to non-native species. Renne and Tracy may have to “Imagine a large field that is subjected to high non-native propagule input but a dense assemblage of evenly distributed native species prevents invasion”, because many species-rich hotspots such as wetlands and riparian zones have already been heavily invaded with tamarisk, purple looses-trife, and many other non-native plant species. We agree that native species must be present for a negative-diversity affect. Unfortunately, nearly all our study sites from Utah to Minnesota (richness and cover; Stohlgren *et al.* 2001, 2002), and the 2958 plots and 2798 counties we reported on generally had >80% native species (richness), without a measurable negative-diversity effect.

The “paradox” they mention may have less to do with the differences in scale, than with the differences between highly controlled, artificial, small-scale experiments and the real world patterns (Stohlgren 2002). We agree that if vegetation in a meadow were removed in a checkerboard pattern that non-native species would

increase. We would add that if the experiment were repeated in a gradient from species-poor, infertile sites to species-rich, fertile sites, that non-native species would be greater in the latter sites.

We also agree that “powerful anthropogenic disturbances” may “weaken the competitive ability of native plants.” However, there are a large number of cases of successful invasion in protected habitats (Smith and Schmutz 1975, Lacey *et al.* 1990, Stohlgren *et al.* 1999), and natural mortality and disturbances from ground mammals, floods, and natural fire regimes can also facilitate invasions (Grace *et al.* 2002). It may be the case that many native plant species are just weak competitors under natural levels of mortality and disturbance. If experiments greatly increased the scope of covarying factors with replicated studies in many habitats and landscapes, the studies might reveal truer patterns of native and non-native species widely observed at local, regional, national, and global scales.

In response to the letter from Marcel Rejmánek, we commend his investigation of our results and his exploration of such patterns in greater detail, especially as they relate to the role of human populations in broad-scale patterns of non-native species richness. However, we find no biological reason for excluding California data in any analysis, since it represents about a quarter of the nation’s floral diversity.

Despite Rejmánek’s comments, our findings hold at multiple spatial scales and they should not be trivialized at plot-, landscape-, and county-scales, where strongly significant positive relationships between native and non-native species richness can’t be ignored (our original Figure 1). We know of no biases in data collection or in sampling intensity that would reverse these pronounced patterns.

More importantly, we are more concerned with the establishment and spread of non-native species *within* states, counties, and land-

scapes into species-rich habitats – an obvious pattern in our riparian zones, wetlands, and fertile soils throughout the nation. Since non-native species control efforts will be conducted at these local scales, our statistical models might be put to better use predicting sites of establishment and spread. We agree with Rejmánek that human populations may drive coarse-scale patterns better than finer-scale patterns that are of greater urgency in the battle of invasive species.

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