

# No consistent small-scale native–exotic relationships

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**Abstract** The perception that native and exotic species are negatively related to each other at small scales has proliferated in the ecological literature. Although mounting evidence shows that such a perception is not always reality, the degree to which the mismatch occurs and the causes are not clear. Here, I compile and synthesize data based on the smallest scales used in 75 case studies in plant communities around the world, and analyze detailed data from a study in early successional California chaparral. I show that (1) different metrics (community variables) yielded different results, (2) native biomass and cover had much stronger negative effects on exotic richness than native richness and density, (3) there is no consistent correlation between native and exotic richness, especially in natural and immature communities, and (4) proportionally more experimental studies revealed negative relations than field observations. Collectively, these results reveal and confirm a high degree of mismatch between perceptions and

reality in small-scale patterns of biotic invasions which have management implications.

**Keywords** Community variables · Degree of invasion (DI) · Invasibility · Niche theory · Richness · Space

## Background

The role of biodiversity in habitat invasibility has long been a central focus in studying biotic invasions and ecosystem functions (Lonsdale 1999; Alpert et al. 2000; Richardson and Pyšek 2006). It has frequently been claimed that native and exotic richness are (1) positively related to each other at large scales (Brooks et al. 2013) and (2) negatively related at small scales (Lonsdale 1999; Shea and Chesson 2002; Fridley et al. 2007; Knight and Reich 2005; Chen et al. 2010). Theoretical and experimental studies to date seem to support either Elton's (1958) theory that diversity generally resists invasion or Shea and Chesson's model (2002) that the native–exotic richness relationships change with scale (Levine and D'Antonio 1999; Herben et al. 2004; Davies et al. 2005; Pauchard and Shea 2006).

Previous studies also show that different measures used to determine the degree of invasion (DI) or invasibility for the same community could yield different results (e.g., MacDougall et al. 2014). The

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majority of studies to date on habitat invasibility have used the number of exotic species present as the measure of DI (Lonsdale 1999; Byers and Noonburg 2003). However, depending on the specific invaders, species identity may often contribute at least equally as species richness (Crawley et al. 1999; Davies et al. 2011). For example, some monocultural stands appear difficult to invade, either due to high biomass already built up or because the ‘right’ (more competitive) species have not yet been introduced. Partly for this reason, some studies have used measures such as survivorship, fecundity, establishment, density, size, and biomass or cover of individual exotic species or all exotics in the community (Robinson et al. 1995; Kennedy et al. 2002; Smith et al. 2004; Von Holle and Simberloff 2005). For species diversity to be effective in resisting invasion, the resident species must have sufficient abundance (or biomass). Thus, it is the combination of complementary use of various resources and resident species’ relative abundance that represents a habitat’s resources use that resists biotic invasions (e.g., Guo et al. 2015).

Understandably, small-scale studies on biotic invasions are far more common than those on large scales; yet the conclusions on small-scale patterns remain controversial. In particular, how frequent negative correlations exist and what causes the inconsistency in observed results are not clear. Here, I review recent literature and reexamine small-scale native–exotic relationships. I hypothesize that (1) native–exotic relationships at small scales are not consistent when different measures of DI are used, (2) theoretical/experimental studies are more likely to yield negative relationships than field observations in natural communities, and (3) the same community may show various invasion patterns and resistance forces when different variables (metrics) are used. I test these hypotheses with a compilation of published data from around the world, and a dataset from Santa Monica Mountains in California.

## Data and literature

To examine the patterns on smallest scales possible, rather than across sites and/or spatial scales (e.g., Herben et al. 2004; Symonds and Pither 2012), I focus on the smallest scales only (0.01–10 m<sup>2</sup>) used in each individual study from the 75 cases around the world that use native (or resident) richness as the

independent variable. Data from these case studies were compiled by searching Google scholar with key words such as exotic, non-native, alien, native, correlation, relationship, and scale (up to June 29, 2014; see Supplementary Table S1, Appendix S1).

The dataset included 36 observational field studies (i.e., non-manipulated), 30 field/lab experiments, 6 theoretical studies, and three studies with combined field observation and experiments. Among these case studies, 43 used native richness as the independent and exotic richness as the dependent variables. Of these, 30 were field observations and 13 were based on field experiments. In addition, many of these 75 studies use multiple responsive variables such as species richness, germination rate, survivorship, plant size (or height), cover, or biomass of either individual invaders or all exotic species (or planted native species as invaders in experimental communities; Supplementary Table S1, Appendix 1).

To examine the invasion patterns and relative effects of different community variables on exotic plant richness, I used data from an early post-fire successional chaparral community on Santa Monica Mountains in southern California, USA. The community was dominated by herbaceous species and seedlings of shrubs. The richness, density, and cover data were simultaneously collected from the same permanent quadrats (1 m × 1 m), and biomass data were collected at the end of growing season from neighboring quadrats (also 1 m × 1 m) to minimize disturbance on permanent quadrats. All aboveground plants parts falling into the quadrats vertically were included in measurements (Williamson 2003; for more details about the sampling and data collection, see Guo 2001).

I used simple and Poisson regression analyses to examine the invasion patterns involving multiple community variables (e.g., richness, biomass, cover, and density) on Santa Monica Mountains). When regression analysis failed to detect any correlation between natives and exotics, I performed randomization tests using SAS (SAS Institute 2011) to see if there was a constraint effect between the two species groups (for details about the test, see Guo et al. 2000).

## Inconsistent small-scale relationships

In contrast with frequent claims, the synthetic results show that there was no consistent negative relationship

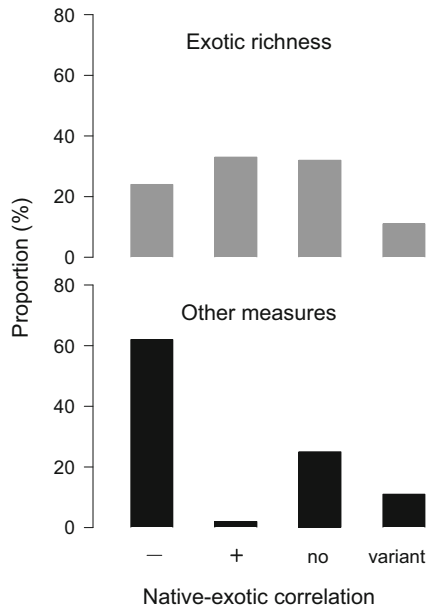
between native and exotic richness at small scales, and negative native–exotic richness relationships were not predominantly common, especially in natural and mature communities. This synthetic study reveals remarkable difference among the three settings: field (more heterogeneous), experiment (more homogeneous), and simulation/modeling (most likely assume equilibrium status and homogeneous habitats and all species with maximum abundance).

Most strong negative relationships have been found in small-scale, experimental studies, not field observations. Overall, of the 43 cases based on richness, only 19 % (8/43) of the field studies observed negative correlations between native and exotic richness, and the remainder found either no or multiple or variant ( $\geq 2$ ) forms of correlations (Figs. 1, S1). Out of 30 observational field studies, only four (13 %) reported negative correlations. In contrast, among the 13 field experimental studies, four (31 %) reported negative correlations.

Understandably, little experimental work exists over large scales; but even on the small scale, “natural” microhabitats usually have greater heterogeneity than “experimental” plots of the same size

(van Ruijven et al. 2003). In natural settings, ‘harsh’ microhabitats not favorable to many native and even exotic species thus having low biomass or cover are located at the left-lower corners of Figs. 2, 3; and using regression analyses may not detect any relationships between natives and exotics. Also, time is critical as when community has not had enough time (e.g., after major disturbances such as fires) to reach its full capacities in terms of richness and biomass, the relationships between native and exotic species could be lacking or even positive (Guo et al. 1998, 2015). Thus, heterogeneity and time-lags may be most responsible for the lack of relationships between native and exotic species, even at small scales.

It is equally important to note the differences between field and lab (greenhouse) experimental communities, which are under different levels of control or manipulation. For example, field experiments still allow some natural variation/fluctuation in physical environments (climate, soil, water, or topography), while tightly controlled lab (tubes, microcosm) experiments do not. Therefore, simply pooling data from all types of experimental studies could still yield inconsistent results.



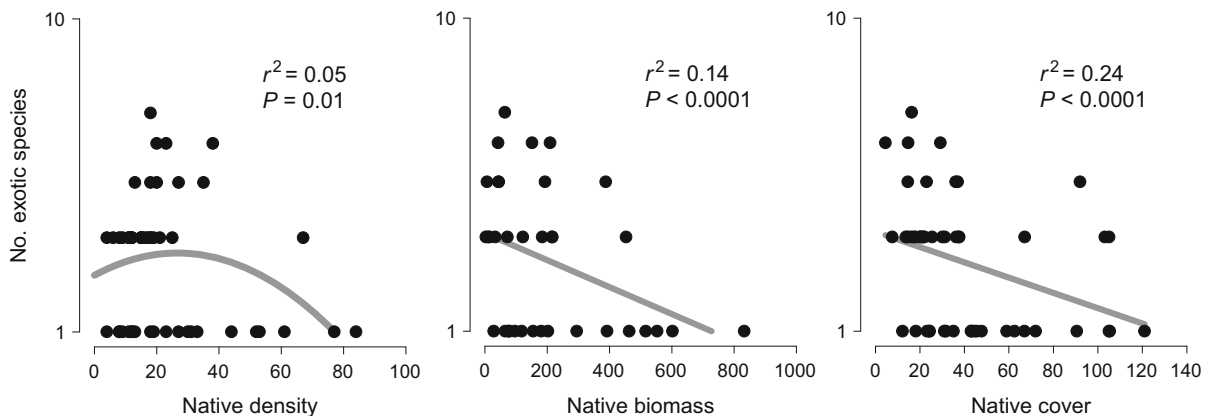
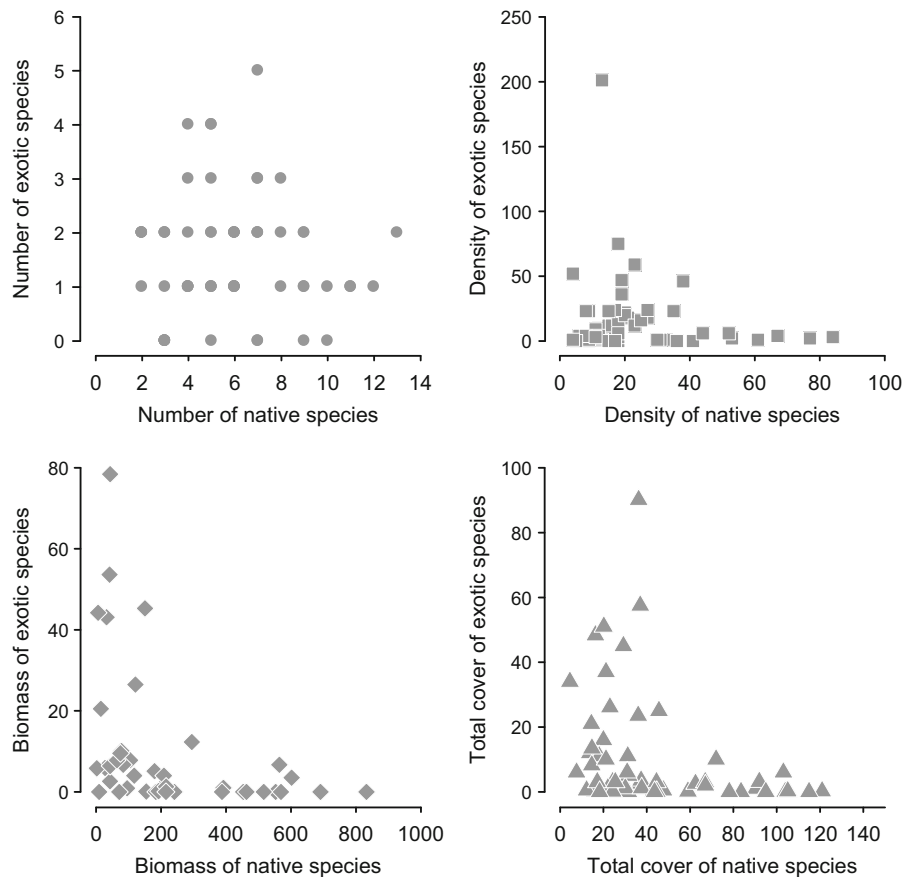
**Fig. 1** The proportion of correlations using native richness versus exotic richness (*top*) and using native richness versus other measures for exotics such as biomass, cover, survivorship, density based on the 75 case studies. The signs of correlations were classified into four categories, i.e., -, +, no (non-significant), and variant ( $\geq 2$  correlations) (see also Fig. S1)

### Different variables reveal different patterns

Due to technical challenges, large-scale studies almost universally use native and exotic richness as the independent and dependent variables, respectively; they generally show positive relations between natives and exotics. In contrast, small-scale studies often also measure diverse variables such as biomass, cover, plant size (height) and survivorship, among others, especially in experimental studies. For the same community, different variables or measures at a given time can yield different results, mostly due to the non-linear or allometric relationships among each other (e.g., Wardle 2001; Williamson 2010; Hill and Fischer 2014), which contributes to the inconsistency in results especially when a particular variable is not specified in drawing the conclusions regarding DI. Data from a chaparral community on Santa Monica Mountains show clearly that, even in the same community, different variables reveal different relationships between native and exotic species (Fig. 2).

More than half of the studies that measured DI as biomass, cover, or size of invaders found negative

**Fig. 2** An example of discrepancy in assessing degrees of invasion (DI) or invasibility in the same community when different variables (richness, density, biomass, and cover) are used. Data from Santa Monica Mountains, Southern California, USA (Guo 2001). Randomization test revealed negative relationships between native and exotic species (in all cases,  $P < 0.05$ ) for density, biomass, and cover but not richness ( $r^2 = 0.05$ ,  $P = 0.19$ )



**Fig. 3** The effects of native plant density, biomass, and cover on the number of exotic plants (exotic richness) in a chaparral community on Santa Monica Mountains, Southern California

(data from Guo 2001). Results are based on Poisson (or log-linear) regressions

correlations (22/36 = 61 %) and almost all the rest found no correlation ( $n = 11$ ) or mixed correlations (–, +, no;  $n = 3$ ). Of the 36 studies, 69 % (25/36) were field experiments. Only six studies used density of

exotics as the dependent variable (three field experiments and three simulations) and they all found negative correlations with native richness. Among the nine studies using survivorship, fecundity, or

germination rate as dependent variables, six field experiments observed negative correlation, and one field observation plus one experiment observed two forms of correlation (– and no) and one simulation reported variant correlations (–, +, and no). Interestingly, among the 13 studies that examined both richness and other measures of DI such biomass or cover, only six reported similar correlations for both variables.

In the chaparral community on Santa Monica Mountains, native plant biomass and cover had much stronger resistant effects on the number of exotic plants (exotic richness) than native plant richness; and native density showed a hump-shaped relationship with exotic richness (Fig. 3). Such results further strengthen the argument that richness should be used in combination with biomass to measure biotic resistance and degree of invasion (DI) as the two variables together better represent resource availability and usage (Alpert et al. 2000; Guo et al. 2015; but see Delmas et al. 2011). As mentioned above, because of the vast difference in body size among species, plant density often shows a non-linear relationship with biomass thus could not be a good indicator for resource uptake. Furthermore, the identity of both resident and invading species may also play a major role (Crawley et al. 1999; Davies et al. 2011).

### “Small scale” as a relative term

The term of “small” (vs. “large”) scale is highly relative and is usually defined artificially in research design. Although both field and experimental studies that used plot size of 0.01–1 m<sup>2</sup> had higher proportion of negative correlations (4/15 = 27 %) than those used plots of  $\geq 1$ –10 m<sup>2</sup> (4/26 = 15 %), the difference was not significant (*G*-test, *G* = 0.50, *df* = 1, *P* = 0.48). Within each site and at the plot-level ( $\leq 10 \times 10$  m), there was no close relationship between exotic richness and biomass (or cover) on plot-level whether total value or proportion is used (not shown).

Thus, identifying the critical scales where the native–exotic relationships switch (or shift) for a particular community or community type is important for understanding the ecological causes and informing management policies and practice. This is mostly because the sizes (or heights) of component species vary drastically among different communities and

even within the same community/ecosystem types (e.g., many types of grasslands). For some of the 75 cases examined here, it is possible that the plot size could still not be “small” enough for the negative native–exotic relations to be detectable. To test this hypothesis, further reduction of the plot sizes for these communities in future field research design would be useful as the findings from such investigation could have direct implications for management. Therefore, it would be useful to test for each community type the ideal plot size within which individual interactions among species at the same trophic level are mostly detectable (which is needed for biotic resistance to take place; Sandel and Corbin 2010; but see Knight et al. 2008).

In short, while the positive native–exotic correlations over large scales seem more consistent, mounting evidence shows that there is no consistent relationship between native and exotic richness on small scales. Small-scale native–exotic relationships depend on the community variables or metrics used, community type (theoretical, experimental, vs. natural), and whether correlation or causal relation is used in assessing invasibility. It should be pointed out that lack of strong negative correlation between native and exotic species at small scales does not mean that species saturation cannot occur at certain times, especially when disturbance is absent and community biomass is high (late succession). As many other factors such as disturbance interactively determine species invasions (e.g., Larson et al. 2001; Larson 2002; MacDougall et al. 2014), further comparative studies across different ecosystems are needed to better understand the role of biodiversity in habitat invasibility.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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