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**A SYNTHESIS OF PLANT INVASION EFFECTS ON BIODIVERSITY  
 ACROSS SPATIAL SCALES<sup>1</sup>**

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- *Premise of the study:* Invasive plant species are typically thought to pose a large threat to native biodiversity, and local-scale studies typically confirm this view. However, plant invaders rarely cause regional extirpations or global extinctions, causing some to suggest that invasive species' influence on native biodiversity may not be so dire. We aim to synthesize the seemingly conflicting literature in plant invasion biology by evaluating the effects of invasive plant species across spatial scales.
- *Methods:* We first conducted a meta-analysis on the effects of invasive plants on the species richness of invaded communities across a range of spatial extents. We then discuss studies that consider the role of invasive plants on regional spatial scales for which such meta-analyses are not possible. Finally, we develop a conceptual framework to synthesize the influence of invasive species across spatial scales by explicitly recognizing how invasive species alter species-occupancy distributions.
- *Key results:* We found a negative relationship between the spatial extent of the study and the effect size of invasive plants on species richness. Our simulation models suggest that this result can occur if invaders, either proportionately or disproportionately, reduce the occupancy of common species to a greater degree than rare species.
- *Conclusions:* Future studies should consider the influence of invaders on the abundance and occupancy-level changes in native species to inform how invasive plants will influence native species richness relationships across spatial scales. This approach will allow greater predictive ability for forecasting changes in biodiversity in the face of anthropogenic biological invasions and will inform invasive species management and restoration.

**Key words:** biodiversity; biological invasions; common; effect size; invasive plants; meta-analysis; occupancy; rare; spatial scale; species richness.

Among the many threats to global biodiversity, the transport of species across historically distinct biogeographic boundaries remains one of the most enigmatic (Facon et al., 2006; Barney and Whitlow, 2008; Moles et al., 2008). Some introductions have led to dramatic declines in biodiversity of native species and the functioning of ecosystems, such as the extinctions that have resulted from predation of nonnative animal species on previously enemy-free oceanic islands (e.g., Savidge, 1987; Fritts and Rodda, 1998; Courchamp et al., 2003). However, the effects of introduced plant species on patterns of biodiversity are more equivocal (Davis, 2009). Some studies have shown large declines in biodiversity in areas that are heavily invaded by introduced plants, leading some to conclude that such invasive species are one of the most important threats to biodiversity (next to habitat destruction) across the planet (Wilcove et al., 1998; Pimentel et al., 2001; Pauchard and Shea, 2006). Others have noted that plant invasions are rarely implicated as the cause of species extinctions either regionally or globally (Sax et al., 2002; Gurevitch and Padilla, 2004; Maskell et al., 2006; Stohlgren et al., 2008). Davis (2003) pointed out that the majority of extinctions caused by introduced species are caused

by intertrophic interactions rather than competition within trophic levels (e.g., by invasive plants) and suggested that overall, most introduced plant species are rather innocuous. These disparate views have percolated into the public realm and, along with a variety of other piecemeal evidence, have incited a number of popular articles to ask if invasive species are really that bad (Burdick, 2005; Zimmer, 2008).

A variety of contentious terms are used to describe species that are introduced outside of their historical biogeographic range (Richardson et al., 2000; Colautti and MacIsaac, 2004), but for the purposes of this paper, we will categorize them into two broad classes: (1) exotic species, a subset of which may be naturalized and reproduce self-sustainably, which generally represent a small fraction of the community in which they are introduced and typically have negligible influence on the communities in which they inhabit, and (2) invasive species, which have high rates of population growth and spread, can often become dominant members of the community, have a negative influence on native species, and often alter the functioning of ecosystems. In this article, we focus on invasive species, which more often have negative consequences on local communities (Mack et al., 2000); exotic species are often relegated to marginal or novel habitats (e.g., urban areas) and can in actuality increase the biodiversity of a given region.

The mechanisms by which introduced plant species can become invasive are varied and are the subject of many reviews and syntheses (e.g., Facon et al., 2006; Richardson and Pyšek, 2006). Thus, we only very briefly overview those mechanisms here, as they relate to the primary subject of our review—the influence of invasives on patterns of biodiversity. Invasive species can either be “passengers” or “drivers” of environmental change (Didham et al., 2005; MacDougall and Turkington, 2005).

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If passengers, invasive species become dominant as a result of human-mediated habitat degradations (e.g., frequent disturbance), disfavoring native species and either directly favoring nonnative species' traits, or indirectly favoring them due to the reduction of native biodiversity (Byers, 2002). If drivers, invasive species dominate as a result of a variety of related mechanisms generally having to do with their traits. For example, invasive species may possess traits that make them relatively unique among species in the native community, such as having novel weapons (Callaway and Ridenour, 2004) or novel resource use (Funk and Vitousek, 2007). Regardless of whether they are drivers or passengers, the presence of an invasive species in a community is generally associated with a concomitant lower diversity of species than that observed in uninvaded communities (e.g., Holmes and Cowling, 1997; Alvarez and Cushman, 2002; Adams and Engelhardt, 2009; Hejda et al., 2009, but see Fischer et al., 2009). However, there is discrepancy among ecologists on how they perceive the negative influence of invasive species on biodiversity, with some suggesting they are a great threat to biodiversity in the short- and long-term (Wilcove et al., 1998), whereas others more recently have suggested their overall influence on global biodiversity patterns will be negligible (Rosenzweig, 2001; Davis, 2003; Sax and Gaines, 2008).

In this article, we synthesize the disparate perspectives of the influence of invasive species on patterns of biodiversity. Our overarching thesis is that the influence of invasive species on biodiversity is generally scale-dependent. That is, at small spatial scales (e.g., samples taken from plots less than  $\sim 100$  m<sup>2</sup>), the influence of invasive species on biodiversity is large, whereas at broader spatial scales, even in the same system, the influence of invasive species on biodiversity is lower. We first use a meta-analysis of observational and experimental studies to explicitly show that invasive species typically reduce native species richness, but that the strength of this effect weakens as the spatial scale of the study increases. Next, we use a simple patch-occupancy model to show that this result is expected under most realistic scenarios of native species' evenness patterns and invasive species' effects on the occupancies of rare vs. more common native species in the region. Invasive species potentially change the overall structure of species' relative abundances and occupancies in a spatial context and thus change the slope of the species-area relationship (contra Rosenzweig's [2001] fundamental assumption). While this synthetic view reconciles the influence of invasive species on biodiversity at small and broad spatial scales, there remains much to be understood about the overall influence of invasive species on biodiversity, and we conclude with some possible avenues for future research directions.

#### EFFECTS OF INVASIVE PLANTS ACROSS SPATIAL SCALES

**A meta-analysis of invasive species' effects**—We conducted a meta-analysis on the effects of invasive plants on biodiversity by examining total plant species richness (i.e., all native and exotic species) as well as native plant species richness. We compared their influence across studies that varied in their spatial extent to test the hypothesis that the negative influence of invasive plants should decrease with increasing spatial scale. We used the reduction in species richness caused by the presence of a dominant invasive species as our measure of effect size.

Although studies on the community-level effects of invasive plants are sometimes considered scarce (Alvarez and Cushman, 2002; Hejda and Pyšek, 2006), we found 76 such studies. We began with ISI Web of Science and Google Scholar searches, using a combination of the following keywords or phrases: community, diversity, impact, invasi\*, plant, and species richness. We also examined the citations from those papers, which allowed us to find several more studies.

We included both experimental (removal or addition of invasive plants) and observational studies that compared species richness among invaded and uninvaded habitats in close proximity. We also included observational studies that used distance from invader or gradients of percent cover of the invader. In such cases, we used plots at the extremes (i.e., nearest and farthest from invader; lowest and highest percent cover). For studies conducted across multiple years, we used the final year of data; for studies in multiple seasons, we used the season in which the majority of the plant community was present. We excluded studies that focused on invader effects on only small subsets of the species present in the community (e.g., only woody seedlings).

We collected information from each study on average species richness with and without invaders (data extracted from text, tables, and figures using the software ImageJ [Rasband 1997–2009]). We used these data to obtain a log response ratio effect size ( $I_r$ ) between uninvaded and invaded plots [ $I_r = \ln(\text{uninvaded species richness}) - \ln(\text{invaded species richness})$ ], which provides information on the proportional difference in richness with and without invaders and has minimal sample bias compared to other metrics (Hedges et al., 1999). We also calculated another popular effect size metric, Hedges'  $d$ , and found similar (but weaker) relationships (Appendix S1; see online file at <http://www.amjbot.org/cgi/content/full/ajb.1000402/DC1>) and so only report  $I_r$  here for brevity.

After excluding studies that did not provide measures of variance, we incorporated 57 studies into our meta-analysis, which led to 125 data points because some studies included multiple invasive species, multiple sites, and/or multiple habitats. Of the 125 data points, 110 were observational, and 15 were experimental. Of the 110 observational data points, only six from three studies compared species richness before and after invasions; the rest compared invaded areas relative to spatially controlled uninvaded areas. Although unlikely, this could have served as a comparative limitation if invaded and uninvaded habitats differed in environmental characteristics other than the presence of the focal invasive species. Appendix S2 (see online) contains the data obtained for the meta-analysis, including the focal invasive plant(s), focal invasive plant growth form, location of the study, type of study (i.e., observational vs. experimental), sample size, spatial scale at which the data were collected, and the mean and variance of the effect sizes.

The majority of studies only presented species richness at a single spatial scale, and thus we were not able to do within-study comparisons of invaders' effects across spatial scales. However, we can test the hypothesis of scale-dependent effects of invaders across studies by regressing the effect size of invasive species relative to the spatial scale on which the data were collected. We conducted linear mixed models, with log (spatial scale [m<sup>2</sup>]) as the independent variable and effect size as the dependent variable weighted by the inverse of the variance of each study,  $v_j$  (Gurevitch and Hedges, 2001). We also conducted an unweighted version of the model to evaluate whether the incorporation of all 76 studies qualitatively changed our results.

We calculated  $r^2$  of the regression models by dividing  $Q_{\text{regression}}$  (heterogeneity explained by the model) by  $Q_T$  (total heterogeneity). Analyses were conducted in the program MetaWin version 2.1 (Rosenberg et al., 2000).

As predicted, we found a negative relationship between  $\ln$  and spatial scale ( $Q_{\text{regression}} = 20.01$ ,  $r^2 = 0.10$ , slope =  $-0.20$ ,  $P < 0.001$ , Fig. 1), suggesting scale-dependent effects of invasive plants on species richness. Using only native species richness did not qualitatively change our results. Incorporating all 72 studies on the effects of invasive plants also revealed a negative relationship between  $\ln$  and spatial scale ( $Q_{\text{regression}} = 6.08$ ,  $r^2 = 0.08$ , slope =  $-0.20$ ,  $P = 0.014$ ).

The majority of case studies (99/125) were conducted at relatively small spatial scales ( $\leq 25 \text{ m}^2$ ), where there was a large amount of variation in the  $\ln$  effect size (ranging from  $-0.26$  to  $2.98$ ) that was not well explained by spatial extent. This variation was also not explained by other independent variables that we examined, including the average species richness in the uninvaded plots and the growth form of the focal invader. In addition, we found no evidence of publication bias using two separate approaches: (1) we found a funnel-shaped distribution of sample sizes, as expected with no publication bias (Palmer, 1999), and (2) we found no relationship between the magnitude of the effect size and the impact factor for the journal where the study was published based on the 2009 or 5-yr average ISI Journal Citation impact factor (See Appendix S1 for graphical and statistical results). However, some of this variation was explained by the magnitude of dominance of the invasive species, which was highly variable among studies (ranging from 8–100% cover). To examine the effect of invasive species' dominance, we investigated the subsample of studies from which we could discern the relative dominance (i.e., percent cover) of the focal invasive species. When a range of percent cover was given, we used the midpoint, whereas when a minimum percent cover was

reported, we used that minimum value. We found a positive relationship between  $\ln$  and the percent cover of the invasive species ( $Q_{\text{regression}} = 9.02$ ,  $r^2 = 0.08$ ,  $P = 0.003$ , Fig. 2).

Despite the influence of the degree of dominance of the invasive species on its effect size, there remains a large amount of unexplained variation in effect sizes. This variation could be due to several factors, such as ecosystem-level effects of the focal invader (Vitousek and Walker, 1989; D'Antonio and Vitousek, 1992) and time since invasion. Further, other site- and landscape-level factors unique to each case study may interact with, exacerbate, or dilute the effects of the focal invasive species at the plot-level, including historical factors, spatial extent of the invasion, and the size of the regional species pool in uninvaded areas.

**Invasive species' effects at broader spatial scales**—Although our meta-analysis was able to discern scale-dependent effects of invasive species on native species richness, all of these experimental and observational studies were conducted at relatively small scales, whereas the processes of extinction takes place at much broader scales. At broader biogeographic scales, the effects of an invader are difficult to evaluate since these studies typically use presence/absence data for both the invader and the native species from large, national or global databases such as the IUCN Red List (Atkinson and Cameron, 1993; Lonsdale, 1999; Vié et al., 2008; but see, Maskell et al., 2006; Vilà et al., 2010). From such data, studies often conclude that many naturalized invaders are present, but no native species have gone extinct from the introduction of plant competitors (Sax et al., 2002; Davis, 2003; Maskell et al., 2006; Sax and Gaines, 2008; Tsai et al., 2010), even in locations that are infamous for being devastated by species invasions, such as remote oceanic islands (e.g., Hawai'i; Denslow et al., 2009). However, the presence and effects of the invader are likely to only occur in a subset of the spatial scales under consideration.

A number of authors have recognized the difficulty in linking broad-scale extinctions of native plants to effects of invasive plants because species invasions typically correlate with concomitant anthropogenic factors including habitat destruction, changes in fire regimes, climate change, pollution, and infectious diseases (Davis, 2003; Didham et al., 2005, 2007; Gurevitch and Padilla, 2004; Smith et al., 2006). However, the lack of evidence of plant invaders causing extinctions is still surprising given the levels of dominance invasive plants can reach, as well as the population-level declines and local extinctions that they cause (see meta-analysis section). It is possible that these declines could eventually lead to plant extinctions in the future (Sax and Gaines, 2008; Corlett, 2010), but that it takes many decades, centuries, or longer for regional or global extinction to occur for these plant species. For example, a federally endangered endemic plant, Tidestrom's lupine (*Lupinus tidestromii*), is restricted to less than 15 populations in coastal northern California (United States) and is declining toward extinction due to indirect effects caused by the presence of invasive beachgrass, *Ammophila arenaria* (Dangremond et al., 2010). However, even in this extreme case, extinction caused by the invasive species is not projected to occur for several decades. Until it does go extinct, this species will be considered present in California and in the United States and thus not contribute to a reduction in species richness at these broad spatial scales, even though it is greatly imperiled and locally extirpated from many sites from which it once occurred. However, as we show in the next section, invasive species might be expected to have greater

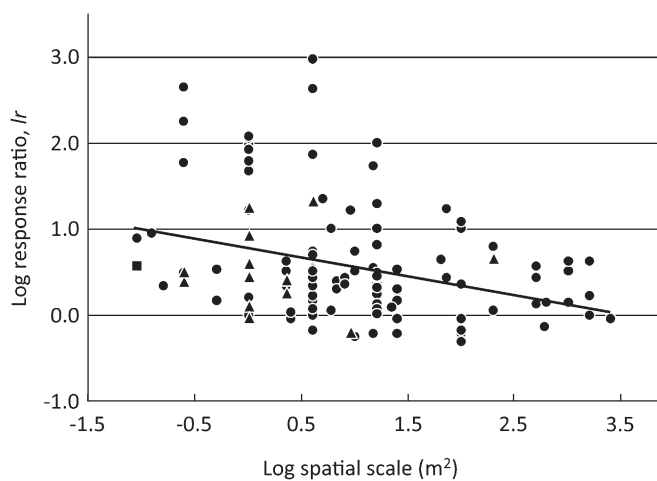


Fig. 1. Significant negative relationship between log spatial scale ( $\text{m}^2$ ) and the log response ratio effect size,  $\ln$ , between uninvaded and invaded plots [ $\ln = \ln(\text{uninvaded species richness}) - \ln(\text{invaded species richness})$ ] using a weighted, mixed-model regression. Each point represents a case study of invasive species' effects at the plot level. The fitted regression line includes all study types, including observational (i.e., comparing plots with and without invaders) and experimental (i.e., removal and addition) studies ( $N = 125$ ,  $Q_{\text{regression}} = 20.01$ ,  $r^2 = 0.10$ , slope =  $-0.20$ ,  $P < 0.001$ ). Circles represent observational studies, triangles represent removal studies, and squares represent addition studies.

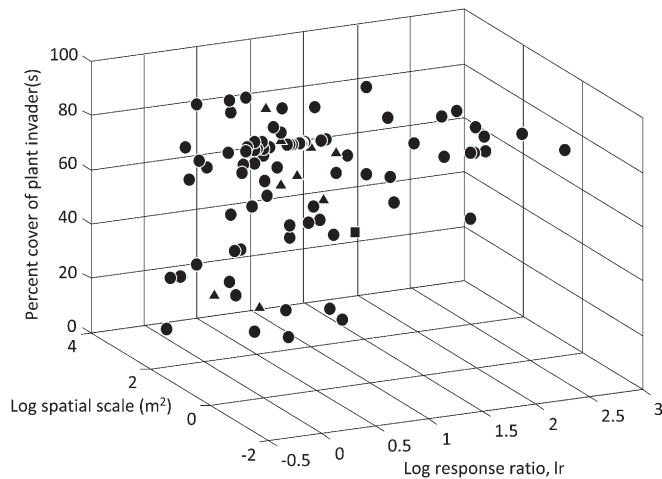


Fig. 2. Three-dimensional visualization of the negative relationship between the log response ratio,  $lr$ , of the effect of a focal invader on species richness and spatial scale ( $m^2$ ), and the positive relationship between  $lr$  and percent cover of the invasive species in invaded plots. Each point represents a case study that included a measure of invader percentage cover at the plot level ( $N = 92$ ). Circles represent observational studies, triangles represent removal studies, and squares represent addition studies.

effects on local compared to regional extinctions under a variety of simple but realistic scenarios of community structure (i.e., species evenness) and invasive species' effects on rare vs. common species in a community.

#### A CONCEPTUAL FRAMEWORK FOR INVASIVE PLANT EFFECTS ACROSS SPATIAL SCALES

Here, we develop a synthetic conceptual framework that incorporates two observations that have been made with regards to the influence of invasive species on native communities across spatial scales. We incorporate these observations into a simple modeling framework to illustrate how invasive species may cause local but not regional extirpations and thus reduce local but not regional biodiversity.

(1) Invasive species are often more widespread and abundant than native species in nearby, uninvaded habitats (e.g., Allen and Knight, 1984; Chmura and Sierka, 2006; Petsikos et al., 2007; Hejda et al., 2009; Jäger et al., 2009).

(2) Invasive species reduce the local richness of native species (e.g., Christian and Wilson, 1999; Frappier et al., 2003; Reinhart et al., 2005); our meta-analysis makes it apparent that invasive species generally have a strong, albeit variable, influence on patterns of biodiversity at relatively small spatial scales (Fig. 1).

We use a patch-occupancy model that considers a diverse native community of species that vary in their relative commonness and rarity (e.g., Preston, 1962; He and Legendre, 2002), and incorporate the influence of invasive plant species on the occupancy distributions of these species. We specifically explored three scenarios:

(1) Neutral effects of invasive species. Here, we assume that the invasive plant has similar negative effects on all native species at the local level regardless of the identity or relative occupancy of each native species (i.e., all native species have similar competitive abilities against the invader). In this sce-

nario, each species is affected equally and is thus equally likely to go extinct from the presence of the invader.

(2) Invasive species influence common species more than rare species. Here, the invasive plant has a larger proportional effect on native species with higher patch occupancies. In this scenario, common species are worse competitors than rare species when in competition with the invader. This scenario could occur, for example, due to overlapping niche space, in which the invader and common species share common resources accompanied by higher invader fitness (MacDougall et al., 2009), leading to larger declines in common species that rely more heavily on the shared resource than rare species. It is also possible that species with low patch occupancies exist in more specialized (or less common) habitat refuges that are less invadable (Huenneke et al., 1990; Marvier et al., 2004; Harrison et al., 2006) or that rare species that occupy these specialized refuges are better competitors than more generalized common species in these locations (Marvier et al., 2004).

(3) Invasive species influence rare species more than common species. Here, the invasive plant has a larger proportional effect on native species with lower patch occupancies. In this scenario, rarer species are worse competitors than dominant, native species when in competition with the invader. This scenario could occur due to sharing common resources or if the distribution of rare species were restricted to habitats or microhabitats that are *more* heavily invaded by an invasive plant, for example, when invaders can invade low-nutrient sites or sites with high endemism (Funk and Vitousek, 2007; Miller et al., 2010). Rare species are sometimes poor competitors compared to more common species, leading to lower site occupancies (Griggs, 1940; Kunin and Gaston, 1993; Runk et al., 2004).

To model each of these scenarios, we assigned species randomly to patches based on a regional patch-occupancy distribution ( $N = 150$  native species before invasion). Regional occupancy distributions were established by drawing each of the species (with replacement) from a log-normal distribution,

$$\Phi_j = \frac{M}{j} \exp \left\{ -\frac{1}{2} \left[ \frac{\log_2(j/j_0)}{\sigma} \right]^2 \right\},$$

where  $\Phi_j$  is the expected frequency of species occupying  $j$  patches, and  $M$ ,  $j_0$ , and  $\sigma$  are fitted parameters (Volkov et al., 2003; Chisholm, 2007). With the exception of  $\sigma$ , which represents the proportional evenness of the occupancy distribution, other fitted parameters were held constant with  $M = 40$ ,  $j_0 = 300$ , and  $j = 1$  to 100 patches (e.g., the most common native species can at most occupy 100 patches and the rarest species can occupy a single patch). We simulated the invasion of a dominant invader, invading 90% of the patches, based on observation 1 above, and causing dramatic (~40%) of native species to decline to extinction in each patch, based on observation 2 above. Species were driven locally extinct by the invasive species according to each one of the three scenarios described above (neutral effects, greater effects on common species, or greater effects on rare species). Each species was assigned a probability of local extinction (1) equivalent among all species, (2) proportional to their relative site-occupancy to simulate a gradient of decreasing effects of invasive plant from common to rare species, or (3) inversely proportional to their relative site occupancy to simulate a gradient of increasing effects from common to rare species. Before invasion, we obtained

$\alpha$ -diversity (average number of native species present in a single patch) and  $\gamma$ -diversity (the sum of species richness across all patches); we simulated each patch-occupancy model 1000 times and obtained 95 percentile confidence intervals for  $\gamma$ -diversity values to distinguish among the three different invasion scenarios. All simulations were performed in MATLAB version 7.4 (MATLAB, 2007).

We first examined the expected outcomes when the region had high evenness, summarized here as Pielou's  $J$ , but specifically referring to more equivalent occupancies across species, with fewer extremely common or extremely rare species. Higher evenness was based on the lognormal patch-occupancy distribution with  $\sigma = 2.4$ ,  $J = 0.9636$ , mode  $\approx 19$  patches occupied, where the mode is

$$j = j_M = j_0 2^{-\sigma^2 / \log_2 e}$$

(Chisholm, 2007). In each scenario, invasive species had large effects on local but not on regional richness (Fig. 3), despite high occupancy by the invading species. This result is explained by the presence of few rare (low occupancy) species, which were thus unlikely to be lost from all patches in the presence of the invasive species. This result is consistent with the trends we see in the literature, whereby dramatic local-scale effects of invasive species do not scale up to regional-level effects on species richness or extinctions (see meta-analysis section).

Importantly, the steeper slope of the relationship between local ( $\alpha$ -diversity) and regional ( $\gamma$ -diversity) scales in the presence of invasive species implies higher  $\beta$ -diversity in the presence of invasive species. That is, because  $\gamma = \alpha\beta$ , if  $\alpha$  is affected more than  $\gamma$  with invasive species, then  $\beta$  is higher. On the surface, this seems to conflict with the common observation that invasive species commonly homogenize species composi-

tion among localities (because homogenization is often equated with low  $\beta$ -diversity) (McKinney and Lockwood, 1999). However, these seemingly opposing observations can be consistent by recognizing that  $\beta$ -diversity is calculated among all localities, whereas species compositional differences are generally calculated as pairwise differences among communities, and thus cumulative vs. pairwise  $\beta$ -diversity patterns can have opposing signs (Anderson et al., 2011).

When we allowed the initial evenness of species to be lower (i.e., more rare species), the scaling of the effects of invaders on regional-level extinctions and  $\gamma$ -diversity differed across the three scenarios. Specifically, with lower evenness ( $\sigma = 10.0$ ,  $J = 0.8761$ ), the relative influence of the invasive species on common vs. rare species determines the overall outcome of invasive species' effects on  $\gamma$ -diversity. If common species are affected proportionately more than rare species,  $\gamma$ -diversity was unaffected by the invader (or can even be higher in some cases when the invader is included in calculations of species richness) (Fig. 4A). Alternatively, when the effects of the invader were neutral, or when rare species are more affected than common species, extinction was more prevalent at the regional level, leading to overall reductions in  $\gamma$ -diversity (Fig. 4B, C). When the effects were neutral, there was approximately an equal loss of species at both the local and regional scale (Fig. 4B), whereas when rare species were proportionately more affected than common species, there was a much greater absolute loss of species richness at the regional scale (Fig. 4C) as a result of homogenization of species across patches.

An important implication of our results is that the differential effects of invaders on common and rare native species (or even neutral effects) can strongly alter the slope of the species–area relationship (Figs. 3, 4A, 4C). This is in contrast to Rosenzweig's (2001) fundamental assumption that invasive species do not alter the slope of the provincial species–area relationships and thus would not be expected to alter patterns of species diversity across scales. If instead, abundance and occupancy distributions are shifted in the presence of invasive species, we should expect concurrent increases or decreases in the slope of the species–area relationship (Tjørve et al., 2008) and thus a potentially strong influence of the presence of invasive species on biodiversity scaling.

Overall, we can generalize the effects of invaders along a spectrum of proportional influence on common vs. rare species (Fig. 4D). As the effect of the invader changes from proportionately greater effects on common to neutral to proportionately greater effects on rare species, the potential for extinctions at the regional level increases, so long as the overall patch occupancy is relatively uneven (i.e., a large number of low occupancy species). However, it is clear from this simple analysis that for invasive species to be able to drive species regionally extinct, and thus significantly reduce  $\gamma$ -diversity, a very specific and potentially rather unlikely set of conditions must be met. In particular, the system must have a large number of low-occupancy (rare) species, and those rare species must be strongly and disproportionately influenced by invasive species relative to the more widespread, common species. In all other combinations of conditions, we would instead expect a larger observed effect of invasive species at local relative to regional spatial scales, as we observed in our meta-analysis and literature review above.

A wide range of parameters could be altered in this model, including changes in the number of overall patches, pre-invasion native species richness, maximum occupancy levels of native

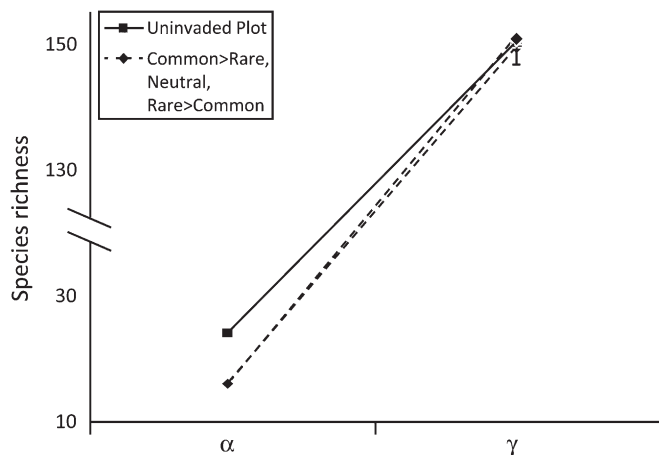


Fig. 3. Invader effect on the loss of native species richness at local ( $\alpha$ -diversity) and regional ( $\gamma$ -diversity) scales. Results were based on a patch-occupancy model, in which species' occupancies were drawn from a highly even log-normal distribution with Pielou's  $J = 0.9636$ . Each species was assigned to patches randomly based on the regional patch-occupancy distribution, and their location remained fixed. We simulated a loss of native species at the local scale due to the colonization of a dominant invader. We observed no significant differences in  $\gamma$ -diversity among neutral losses of native species, a greater local loss of common species, or a greater local loss of rare species (see conceptual framework section for more details).

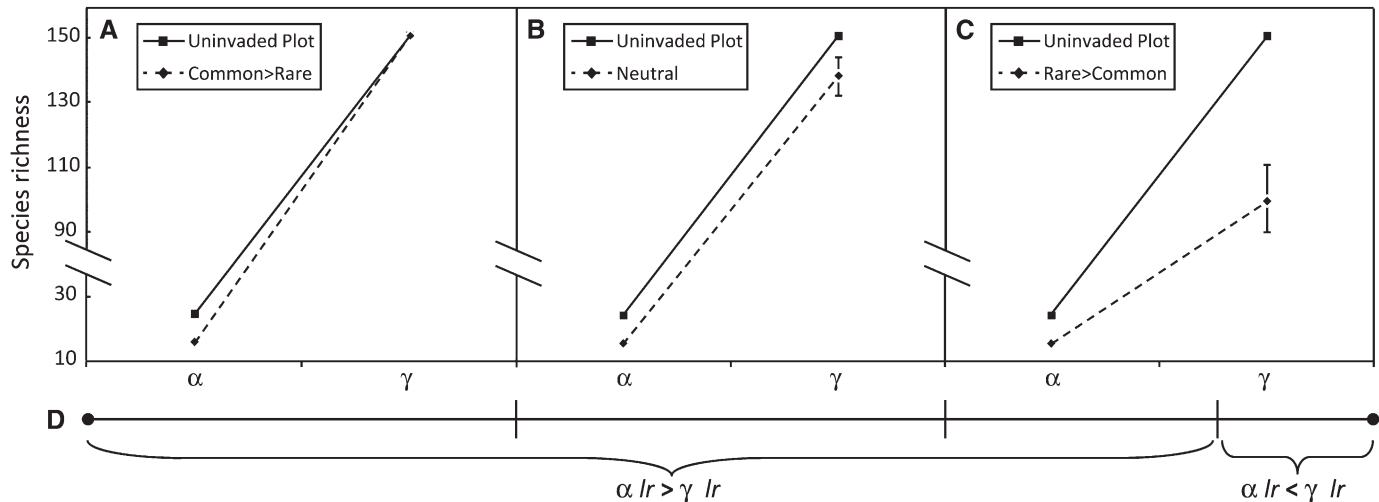


Fig. 4. Invader effect on the loss of native, resident species at local ( $\alpha$ -diversity) and regional ( $\gamma$ -diversity) scales. Results were based on a patch-occupancy model, in which species' occupancies were drawn from a relatively uneven log-normal distribution with Pielou's  $J = 0.8761$ . With lower evenness,  $\gamma$ -diversity is determined by the relative influence of the invader on common vs. rare species. (A) When common species are proportionately more affected than rare species,  $\gamma$ -diversity is equal to or greater than  $\alpha$ -diversity before invasion. (B) When all species are equally affected by an invasion, the effect on  $\gamma$ -diversity is approximately equal to the effect on  $\alpha$ -diversity. (C) Only in the very specific case of rare species being greatly more affected than common species in conjunction with a highly uneven regional occupancy-distribution, will the log response ratio effect size,  $lr$ , of  $\gamma$ -diversity be greater than  $\alpha$ -diversity. (D) The effect of an invader along a spectrum ranging from greater effects on common species to greater effects on rare species. Again, only at the far right end of the spectrum (i.e., greater log response ratio,  $lr$ ) of plant invaders at broad spatial scales compared to local spatial scales (see conceptual framework section for more details).

species, and the identity of the invading plant species that could create differences in their level of dominance and competitive ability (Ortega and Pearson, 2005). We chose parameters we considered to be realistic for species occupancy distributions and highly invasive species. If we alter these parameters, some of the qualitative results seen in Fig. 4A–C will change, but will in general follow similar principles. For example, as we show in contrasting Fig. 3 vs. Fig. 4, high evenness (i.e., few endemic and highly cosmopolitan species) in the system will result in qualitatively different results than from systems with low evenness (i.e., high endemism) (Fig. 4). This difference is expected because higher species' occupancies buffer against regional extinctions.

Overall, our conceptual framework and model is intended to be a very simple depiction of how different invasive species' effects on native communities could lead to differential patterns of species richness and extinctions at local and regional spatial scales. As a result, it is lacking in several potentially quite important aspects of the way invasive species might influence native communities in more realistic scenarios. These include the elements of time, stochastic extinction, local abundance vs. regional occupancy relationships, environmental heterogeneity, and multiple anthropogenic forces that may synergistically affect the extinction of species.

However, our intention is to emphasize, in the simplest way possible, that the influence of invasive species can greatly depend on the proportional effects of invaders on rare and common native species, regardless of other covarying factors. For example, within patches, some species are much more locally abundant than others. If locally rare species also have low patch occupancy or if locally common species have low patch occupancy, invasive species should cause higher extinctions, moving the system to the right end of the extinction spectrum (Fig. 4D). On the other hand, if locally rare species have high patch

occupancy or locally common species are also the most widespread, invasive species should cause fewer regional extinctions, moving the system to the left end of the spectrum (Fig. 4D). Similarly, environmental heterogeneity could either provide refuges for rare species through patches of less-invasible habitat or conversely, increase the influence on rare species if they occupy more invulnerable habitat. In addition, environmental heterogeneity could influence the regional occupancy of the invader based on habitat preferences. Though not explicitly modeled, these factors are implicitly incorporated into the model through the influence of invaders on rare vs. common species. Last, if extinctions caused by plant invaders are exacerbated by other anthropogenic forces such as habitat destruction (Didham et al., 2007), there could be an overall decrease in the patch occupancy of a majority of the species, creating more uneven communities that are more vulnerable to regional extinctions.

Variation in the invaders' effects across spatial scales requires explicit recognition of how shifts in the dominance of invaders should influence the abundance and/or occupancy of native species at local scales and how local-scale extinctions will scale up to broader scales. Using species-abundance and species-occupancy distributions, we can determine the expectation for species losses under a null/neutral model and the likelihood of observing large effects of invaders on species richness at broad spatial scales. In the following section, we provide some suggestions for incorporating these population-level changes in native species' abundance and/or occupancy into future research.

#### A PROSPECTUS FOR FUTURE STUDIES

We found a negative relationship between the effect of invasive plant species and spatial scale, synthesizing disparate views in the literature about the effect of plant invaders on biodiversity.

This result parallels a recent study by Gaertner et al. (2009), who conducted similar analyses for 11 studies in Mediterranean ecosystems, finding a negative relationship between the loss of species richness and spatial scale. We use a conceptual model to illustrate that these patterns might be expected under a variety of assumptions of species occupancy patterns and invasive species' effects. An important line of future research lies in examining species occupancy patterns and invasive species' effects on rare vs. common species in the field to determine if these patterns are consistent with those in our model. If so, then we would suggest that our conceptual framework provides a general explanation for the larger effects of invasive species on biodiversity at local compared to regional spatial scales.

We suggest that a thorough investigation of the effects of invasive species across spatial scales will provide important insights into the causes and consequences of invasive species' effects on native biodiversity. The effects of a single plant invasion on biodiversity across spatial scales (e.g., measuring the species–area relationship) is rarely used as a tool for understanding whether focal invasive plant species cause changes in the rate of species accumulation with increasing area (i.e., the slope of the species–area relationship). For example, Jackson (2005) evaluated the effects of an invasive grass, *Cenchrus ciliaris*, across relatively small spatial scales (from 1 to 64 m<sup>2</sup>) and found an increase in the slope of the species area curve in *Cenchrus*-invaded habitat, revealing faster rates of increasing species with increasing area in invaded relative to uninvaded habitats, leading to smaller losses of species richness with increasing spatial scale, as we observed in our meta-analysis. However, whether this is a generalizable pattern is unknown, as relatively few other studies have taken the same approach (Rejmánek and Rosén, 1992; Michelan et al., 2010; K. I. Powell, J. M. Chase, and T. M. Knight, unpublished data). To evaluate whether focal invading plants cause consistent patterns of scale-dependence in the loss of biodiversity, we suggest evaluating how scaling of richness is influenced by plant invaders across varying habitats and growth forms.

Evaluating species abundance and occupancy distributions across a continuous spatial extent in the presence and absence of invasions allows one to investigate how these patterns change due to the presence of a dominant invasive plant species at different spatial scales of investigation. For example, Farnsworth (2004) investigated occupancy distributions of invasive plants in habitats occupied by rare species to evaluate the direct and indirect threat of invasion on rare plant populations. Invasion-driven shifts in the relative abundance and occupancies of common and rare species could help to explain scale-dependent effects of invasions on biodiversity, changes in the slope of the species–area relationship in invaded habitats, and they could help forecast invasion-induced extinctions (Sax and Gaines, 2008). For example, as illustrated by our conceptual model, a larger decline in abundance and occupancy of common species will result in a faster accumulation of species with increasing spatial scale, leading to relatively small losses of diversity at broad spatial scales (Fig. 4A). On the other hand, a larger decline in the abundance and occupancy of rare species can lead to a homogenization of the community, a slower accumulation of species with increasing spatial scale, and larger declines of species richness at broader spatial scales (Fig. 4C). If naturally occurring rare species are generally less affected by the presence of plant invaders, we should expect less dramatic declines in species richness than if rare species are a target for local extinction, but have yet to manifest these extinctions at broader

spatial scales. We also emphasize the importance in comparing these proportional losses in common vs. rare species to null models that account for sampling effects caused simply from the large declines in the numbers (and biomass) of native species in invaded habitats (e.g., Linneman and Palmer, 2006; Schutzenhofer and Valone, 2006). Sampling effects alone can lead to scale-dependent effects of invasive species without any selective effects on common or rare species by increasing the slope of the species–area relationship (Preston, 1962).

If declines in native species abundance and occupancy distributions differ from null-expected sampling effects, understanding the mechanisms behind differential species effects will be essential for a general understanding of how invasive species alter the patterns of native species diversity and for the management of native species and restoration of habitats. For example, it is possible that some native species possess life history traits that allow them to cope with environmental changes associated with dominant plant invaders (Chabrierie et al., 2010), such as shade tolerance (Myers and Kitajima, 2007) and growth under low-resource conditions (Daehler, 2003). Investigating whether these traits are associated with patterns of abundance and occupancy relationships of native species can help pinpoint conservation strategies for groups of species.

Summary statistics of native communities in response to the presence of invasive species, such as evenness and diversity, provide some information about community-level changes to native species (e.g., Brown et al., 2006; Hejda and Pyšek, 2006). However, these summary statistics lack the population-level insight needed to gain a more complete understanding of invasive species influences on the native flora. Communities are typically less even when heavily invaded compared to uninvaded habitats (Olden, 2006; Hejda et al., 2009) due to the presence of an invader with a much higher abundance than the most common native species. However, exactly how the evenness of the community changes with the invader is less clear. It is possible to observe increased evenness when common species are more affected by invasive species or when rare species are driven extinct by invasive species, leaving extant common species with more even abundances. Thus, understanding the influence of invasions from a population perspective on species that vary in their relative abundances is of utmost importance (Ricciardi, 2004; Comita et al., 2010).

To gain a more general understanding of the effects of invasive plant species on biodiversity, meta-analyses on (meta-) population-level studies evaluating the relative influence of invaders on common and rare plants are needed. Such meta-analyses could include reductions in the abundance of rare and common species, as well as changes to their life-history traits (e.g., growth, fecundity) and consequent changes in their population growth. Meta-analyses could reveal which species are facing unsustainable increases in extinction probability due to deterministic and stochastic processes from lower local population sizes (abundance) and/or altered meta-population dynamics (occupancy). The trajectory of plant extinctions due to invasive species can be better understood with knowledge of (meta-) population-level shifts of common and rare species as a supplement to what we currently understand from information on species richness alone.

## CONCLUSIONS

Changes in the relative abundances and occupancies of common and rare species due to the influence of invasive species will likely be a more telling measure of their influence on both



local- and broad-scale biodiversity patterns. Though we will likely not be able to predict time frames for species loss, changes in the abundance and/or occupancy of native species will enable us to target species of concern in invaded communities as well as evaluate how to restore invaded communities. For example, if common species are more negatively affected by plant species invasions, restoration may be a more straightforward process since common species tend to be easily obtained for restoration as well as more easily established than rarer species. Common species are sometimes overlooked in restoration goals, but in the case of the effect of invasive plant species, may actually be facing equal or greater threats than rare species and cannot go unnoticed (Gaston, 2010). With a solid conceptual framework and set of expectations for the current and future consequences we face from plant invasions, we will be better able to address the needs of preservation of native biodiversity at the intersection of an overwhelming number of anthropogenic forces.

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