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Diversity Increases Indirect Interactions, Attenuates the Intensity of Competition, and Promotes Coexistence

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ABSTRACT: A fundamental assumption of coexistence theory is that competition inevitably decreases species diversity. Consequently, in the quest to understand the ecological regulators of diversity, there has been a great deal of focus on processes with the potential to reduce competitive exclusion. However, the notion that competition must decrease diversity is largely based on the outcome of two-species interaction experiments and models, despite the fact that species rarely interact only in pairs in natural systems. In a field experiment, we found that competition among native perennial plants in multispecies assemblages was far weaker than competition between those same species in pairwise arrangements and that indirect interactions appeared to weaken direct competitive effects. These results suggest that community assembly theory based on pairwise approaches may overestimate the strength of competition and likelihood of competitive exclusion in species-rich communities. We also found that *Centaurea stoebe*, a North American invader, retained strong competitive effects when competing against North American natives in both pairwise and multispecies assemblages. Our experimental results support an emerging body of theory suggesting that complex networks of competing species may generate strong indirect interactions that can maintain diversity and that ecological differentiation may not be necessary to attenuate competition.

Keywords: coexistence, community assembly, competition, competitive exclusion, indirect interactions, invasion.

Introduction

The way in which diverse groups of species coexist in nature remains a largely unresolved question in ecology. The primary processes thought to maintain species coexistence can be organized into three general categories: (1) avoidance of competition through spatial or temporal niche partitioning (Hutchinson 1959; MacArthur and Levins 1967; Warner and Chesson 1985; Levine and HilleRisLambers 2009;

Adler et al. 2010; HilleRisLambers et al. 2012), (2) weakening of strong competitors through forces such as disturbance and herbivory (Connell 1978; McNaughton 1979; Pickett 1980), and (3) nontransitive competitive interactions (i.e., rock-paper-scissors; Buss and Jackson 1979), or some combination of these three (e.g., Chesson 2000). The common theme of these processes is that they are thought necessary to counteract the competitive exclusion principle, the assumption that strong unmitigated interspecific competition inevitably leads to the loss of species from communities (Hardin 1960; Huston 1979). This perspective is based to a large degree on the outcomes of classic two-species interaction experiments of Gause (1934; Schoener 1982), additive effects of competition models (Volterra 1926), and the subsequent development of community assembly theory derived from pairwise interactions (Diamond 1975), also known as hierarchical assembly rules (Keddy and Shipley 1989).

But competing species in nature almost never occur only in isolated pairs, particularly plant species. Thus, the highly complex and aggregate structure of natural plant communities includes large numbers of potentially important but poorly understood indirect interactions among competitors (Strauss 1991; Miller 1994; Wootton 1994; Levine 1999). Indirect interactions occur when the impact of one species on another is mediated by a third species (Wootton 1994) and are therefore only possible among groups of species. Indirect interactions can occur within or across trophic levels and can have positive or negative effects on species interactions. For a complete review of indirect interactions, see Wootton (1994).

Indirect interactions in the form of a series of pairwise nontransitive interactions, also known as competitive loops, have been shown to promote or maintain community diversity (Buss and Jackson 1979; Sinervo and Lively 1996). Nontransitive interactions require that at least one competitively subordinate species in a group outcompete at least one species higher in the competitive hierarchy (e.g., rock-

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paper-scissors; fig. 1*a*). In plants, nontransitive interactions have strong theoretical support. For example, models indicate that nontransitive interactions among groups of competitors are a form of indirect facilitation that can promote or sustain coexistence among competitors (Laird and Schamp 2006; Allesina and Levine 2011). Nontransitive interactions may also maintain genetic diversity within a plant species (Lankau et al. 2011), and there is empirical evidence for nontransitive interactions among multiple genotypes of a species and its competitors in invaded plant systems (Lankau and Strauss 2007). But clearly identifying nontransitive interactions among multiple species of plants in communities has proven elusive; there are no empirical examples of plant species interacting in nontransitive ways to drive coexistence.

Indirect interactions can also arise as a result of species interacting with a shared competitor but without the formation of nontransitive interactions (fig. 1*b*). In other words, interactions can be mediated by competition among groups of species where “an enemy of my enemy is a friend of mine.” There are many experimental studies that demonstrate such indirect facilitative interactions among plant species (Miller 1994; Levine 1999; Callaway and Pennings 2000; Metlen et al. 2013; Aschehoug and Callaway 2014). However, theory that incorporates indirect facilitative interactions such as these into how communities assemble is not well developed. This leaves an important knowledge gap in competition and community assembly theory: does competition among diverse groups of species promote coexistence through the emergence of indirect facilitative effects, but without nontransitive interactions?

Nonnative invasive species represent one of the few cases in nature where competitive exclusion of nearly entire com-

munities of species appears to occur (Ridenour and Callaway 2000; de Abreu and Durigan 2011). Also, invasive species can exhibit far stronger and more intense competitive effects in new ranges compared to their native range (Maron and Marler 2008; Shah et al. 2014). This biogeographic shift suggests that shared evolutionary histories among species in a community may be an important determinant of the competitive effect one species has on another (Callaway and Aschehoug 2000). Therefore, invaders may compete in ways that are somewhat different from those of native species. Thus, invasive species may present a unique context to ask questions about how competitive interactions among groups of native species may change in the presence of a new, highly competitive species—an aspect of biotic resistance that is poorly understood.

Here, we explore the importance of direct and indirect interactions among multiple plant species in an experimental test of competition in both natural and invaded communities. A primary motivation for this work was to understand whether classic pairwise experiments could predict competitive outcomes among species in diverse communities. Specifically, we conducted a 3-year field experiment in which we experimentally measured the competitive interactions among five native North American intermountain prairie grasses and forbs and one highly invasive European forb, *Centaurea stoebe*, in two-species pairwise and multispecies community plots. We hypothesized that competitive effects in multispecies plots would be lower than the competitive interactions among species in pairwise plots because of the presence of indirect facilitation. We also hypothesized that the invasive species *C. stoebe* would compete strongly with natives, forming a classic hierarchy in both pairwise and multispecies plots, leading to competitive exclusion.

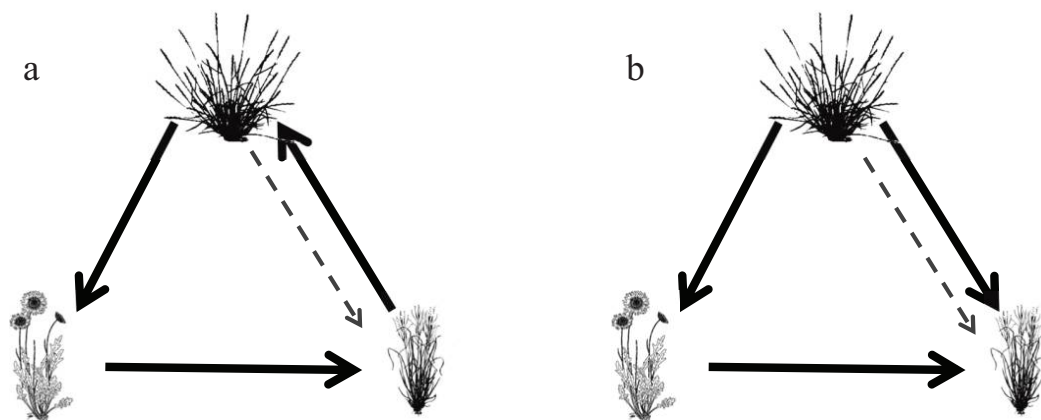


Figure 1: *a*, Nontransitive interaction. *b*, Indirect facilitative interaction. Solid arrows represent direct, negative, competitive interactions; and dashed arrows indicate indirect, positive, facilitative interactions.

Material and Methods

In the summer of 2007, we created 322 experimental plots varying in species composition and complexity. We chose three perennial bunchgrasses (*Pseudoroegneria spicata*, *Festuca idahoensis*, *Stipa comata*), two forbs (*Linum lewisii*, *Gaillardia aristata*), and one highly invasive species (*Centaurea stoebe*). We selected these species because they are common and widespread in intermountain prairies in the northern Rocky Mountains. Rocky Mountain intermountain prairies are characterized as semiarid, low-productivity grasslands dominated by perennial cool-season grass species. All plots were 0.25 m² (0.5 m × 0.5 m) in size and were in a controlled-access experimental site at the Fort Missoula Biological Field Station, Missoula, Montana (46°50'16.92"N, 114°3'24.58"W; 960 m). Growing seasons in western Montana are variable but tend to be 6 months long for native perennials such as those we used in this experiment. Plots were established in an area with homogeneous soil and solar exposure and were subjected to the same water regimes. The site was fenced and thus free from large herbivores and disturbance. Prior to planting, the site was sprayed with the herbicide glyphosate to remove all vegetation and tilled to ensure highly uniform conditions.

To quantify and compare interactions, all species were grown alone, pairwise, and in multispecies plots of four native species, five native species, invaded four native species, and invaded five native species compositions. All multispecies plots were planted using a Latin square plot design that allows for all possible combinations of contact among species (figs. A1–A3, available online). In multispecies plots, all species occupied all possible locations within the plot (e.g., edge vs. interior positions) to control for the possible effect of position within each plot type. Plants were first grown in 100-mL “cone-tainers” (2.5 cm × 16.5 cm; Stuewe and Sons, Corvallis, OR) from purchased (Wind River Seed, Manderson, WY) and locally collected (*C. stoebe* only) seed in a greenhouse. We planted seedlings in July 2007 and provided supplemental water during the first growing season to improve transplant success. Following planting and for three growing seasons, we weeded all plots and buffer zones by hand to minimize the effects of garden weeds on the interactions among target species. After three growing seasons, in June we harvested, dried in ovens for 72 h at 60°C, and weighed aboveground biomass for each individual.

Drought either killed or prevented the resprouting of large numbers of one native forb, *G. aristata*, and the invasive forb, *C. stoebe*, during the last 2 months of the experiment. Because we were unable to harvest these species, we were not able to quantify the effects of competition by other species on *C. stoebe* and *G. aristata* in our experimental treatments. But since these species had grown in the plots for the previous two seasons and a portion of the

third growing season, the competitive effects of *C. stoebe* and *G. aristata* on other species were still present. Thus, we quantified 16 of the 20 possible direct competitive effects among species in our experimental treatments. We excluded four plots that were damaged by underground herbivores (e.g., moles and pocket gophers). We also excluded all individuals that died from our analysis, because we could not reliably assess the cause of death (e.g., consumers, pathogen, or competition) in all cases across three growing seasons. Average mortality was consistent across all treatments (≈20%). In addition, mortality in the alone treatment where no competition occurs (≈22%) was similar to mortality in all multispecies plots where competition can occur (≈21%), suggesting that exclusion of mortalities from our analyses does not bias our results. We calculated direct competitive effects using the relative interaction intensity (RII; Armas et al. 2004) index. The RII is calculated by dividing the difference between the biomass of the treatment and control by the sum of the biomass of the treatment and control $((B_T - B_C)/(B_T + B_C))$. Standard error was calculated using the formula provided by Armas et al. (2004). The RII is a measure of the strength of interaction between species centered on 0, with negative interactions (competition) indicated by values between 0 and −1 and positive interactions (facilitation) indicated by values between 0 and +1. The RII allows for simple comparisons of the impact of species on each other across taxa and treatments.

For all species in pairwise plots, we calculated RIIs (table A1, available online) using the mean biomass of plants grown alone as controls and the mean biomass of plants in pairwise competition as the treatment (fig. A1). For all species grown in multispecies experimental plots (native and invaded treatments), RIIs for the net direct effect of a single species on another were calculated using the mean biomass of individuals grown in a four-native-species plot lacking the competitor of interest as controls and the mean biomass of individuals grown in complete five-native-species assemblages as the treatment (figs. A2, A3). In order to avoid pseudoreplication, we took the mean size of the surviving individuals of each species in each plot and used it to calculate overall treatment means and standard errors. Statistical tests were performed on RIIs using *t*-tests (Excel 2007) to determine whether interactions were significantly different from zero. All statistical comparisons of RIIs among different species or between treatments utilized either a one-way ANOVA with Tukey post hoc comparisons, two sample means *t*-tests, or Whitney-Mann sum rank tests (Sigmaplot 12; Systat, San Jose, CA). We built null models in R (R Development Core Team, Vienna, Austria) to statistically test the number of significant interactions within each treatment. Models were constructed by randomly reassigning the biomass results of an individual species within the type of plots being compared (e.g., four native species vs.

five native species) to either a control or a treatment position and recalculating the RII for all interactions. Each model run consisted of 1,000 replications, and the observed number of significant interactions was compared to the 95% confidence interval of the model output to determine statistical significance. We tested the effect of position in multispecies plots on biomass using a one-way ANOVA (SPSS Statistics for Windows, version 22.0; IBM, Armonk, NY).

Results

In pairwise competition, eight of 16 interspecific interactions were significantly competitive (fig. 2), with RIIs ranging from -0.20 ± 0.08 to -0.58 ± 0.11 (table A1). Data underlying figure 2 and table A1 are deposited in the Dryad Digital Repository: <https://datadryad.org/resource/doi:10.5061/dryad.4s94n> (Aschehoug and Callaway 2015). In addition, three other interactions tended toward competition but were not significant ($P < .10$). When tested against a null model,

the number of significant interactions was greater than expected by chance, indicating strong and frequent competition. In contrast, when the same native species competed in complex communities with other natives, only four of the 16 interactions were significantly negative, and a null model found that this number was not significantly different from the number expected by chance, indicating weak and infrequent competition.

In contrast to the relatively weak interactions among native species, we found that the invader *Centaurea stoebe* had very strong net effects in all experimental contexts, consistent with the competitive exclusion principle. The competitive effects of the *C. stoebe* on native species were far stronger than those measured among natives, ranging from RIIs of -0.20 ± 0.09 to -0.80 ± 0.08 in pairwise interactions and from -0.08 ± 0.11 to -0.34 ± 0.10 in multispecies communities (table A1). When grown in communities, the competitive effects of *C. stoebe* on natives were dampened for three of the four species, with the one exception being the strongest native competitor, *Pseudoroegneria*

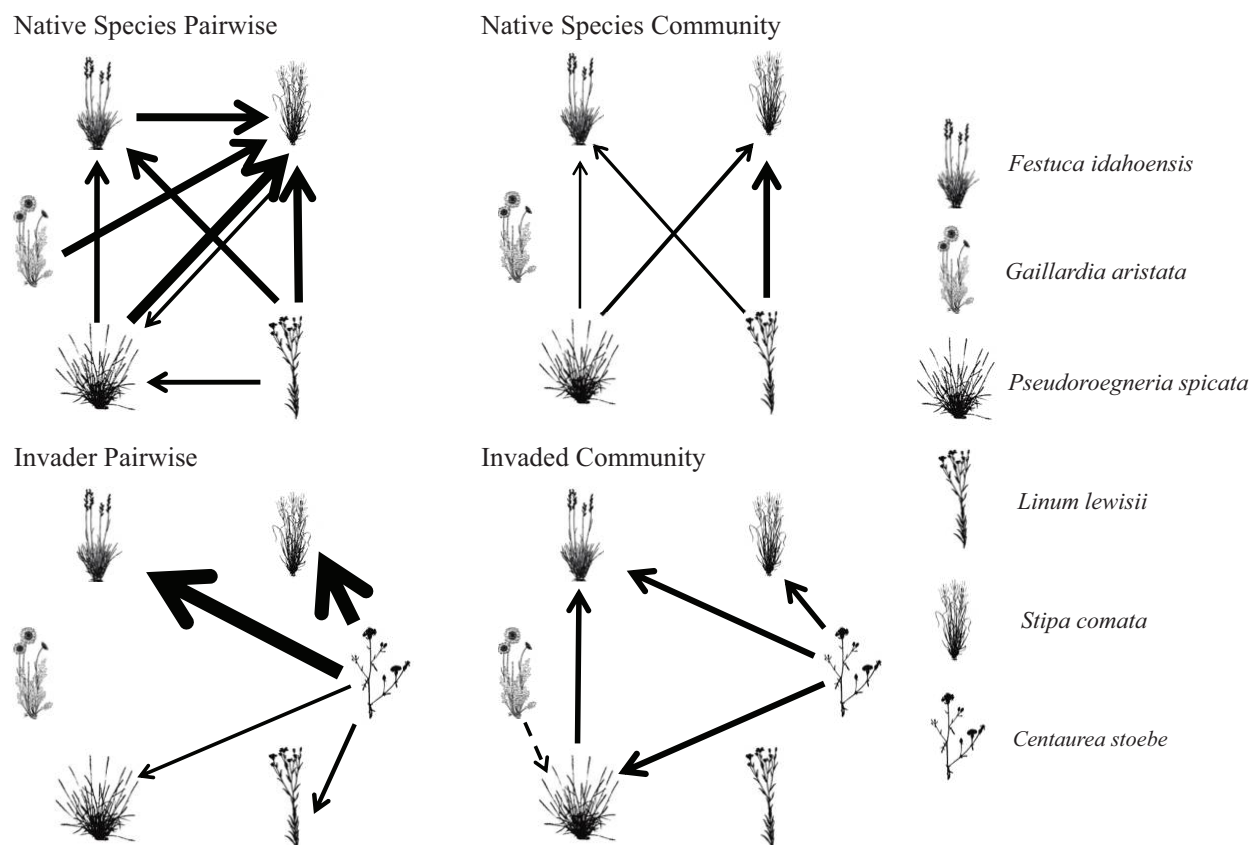


Figure 2: Net direct effects between species grown in pairwise, native multispecies groups and between species grown in multispecies groups that include the exotic invader *Centaurea stoebe*. Solid arrows are negative interactions and dashed lines are positive interactions. All arrows represent significant interactions ($P < .05$), and arrow thickness represents interaction strength. Mortality of two species at the end of the experiment precluded calculation of the net direct effect of species on *Gaillardia aristata* and *C. stoebe*.

spicata (fig. 2). The average net direct effect of *C. stoebe* on native species was an RII of -0.50 ± 0.16 in pairwise arrangements versus -0.26 ± 0.06 in multispecies arrangements, but these did not differ significantly ($P = .69$), suggesting that the competitive effects of very strong invaders on natives are not as highly attenuated by diverse assemblages as the competitive effects of natives on each other.

Competitive effects among groups of natives were further weakened after the introduction of the very strong non-native competitor *C. stoebe*. Only two of the 16 interactions, one competitive and one facilitative, among natives were significant. Native species had very weak effects on each other when competing in communities that included *C. stoebe*. In the presence of *C. stoebe*, *Gaillardia aristata*, a perennial forb, facilitated *P. spicata*, a dominant bunchgrass. *Gaillardia aristata* also tended to facilitate *Festuca idahoensis* in the community with *C. stoebe*, but this effect was not significant. The number of significant interactions within complex communities containing *C. stoebe* was not statistically different from the number predicted by the null model, suggesting that competition between native species in these communities was infrequent and weak.

The average biomass of individuals grown in edge positions of multispecies plots was approximately 50% greater than the average biomass of individuals grown in interior positions in all multispecies plot types ($P < .05$). However, the benefit of growing in an edge position was consistent across all plot types. The average biomass of individuals grown in edge positions in four-native-species plots was not significantly different from the average biomass of individuals grown in edge positions of five-native-species plots ($P = .613$). Similarly, the average biomass of individuals grown in edge positions in invaded four-native-species plots was not significantly different from the average biomass of individuals grown in edge positions of invaded five-native-species plots ($P = .726$).

Discussion

We found that the strong effect of interspecific competition between pairs of native species was highly attenuated and in one case was facilitative, when species competed simultaneously in groups. In addition, the number of significant competitive interactions we observed in pairwise arrays was greater than predicted from a random model, suggesting that competition when measured in pairs of species is strong, frequent, and likely to lead to hierarchical assembly of plant communities and competitive exclusion. However, the number of competitive interactions found in multispecies assemblages was not greater than predicted from a random model, suggesting that competition in diverse groups of species is weak, infrequent, and unlikely to lead to competitive exclusion. Importantly, the reduction in com-

petitive intensity we observed was not caused by nontransitive interactions. These results suggest that current theory on competition based on pairwise interactions may overestimate the general strength of competition in communities and, as a consequence, the likelihood of competitive exclusion.

The strong decrease in competitive intensities that we found in multispecies communities was likely due to indirect facilitative effects. Indirect effects among competitors have been demonstrated in field experiments (Miller 1994; Levine 1999; Callaway and Pennings 2000; Metlen et al. 2013; Aschehoug and Callaway 2014) but have proven difficult to separate fully from direct effects or the effects of disturbance. For example, Miller (1994) used removal experiments to build models that highlight the potential importance of indirect positive effects among five annual exotic old-field plant species. Our results strongly support the conclusions of Miller's models. However, the results reported here are derived from experimental communities in which the effect of a single native perennial species on another has been experimentally quantified, not modeled, both in pairwise interactions and in complex communities. Our experiment was also conducted without the effects of herbivory by ungulates, nutrient limitation, and the disturbance that occurs in removal experiments, all of which alter the competitive environment and subsequently confound the strength and direction of competition. Because we empirically measured competitive effects between species in a community context, our results have broad implications for understanding both how competition operates within communities and the ways that species coexist.

We estimated the effects of competition on plants during their growth and reproduction phases and did not include the effects of seed dispersal and establishment, which could have changed our results. Instead, we focused on the ways that established individuals of many species compete and what the implications of interspecific competition are for coexistence and community assembly.

An important caveat for our results is that the comparison of the average competitive effect one species has on another (RII) in pairwise versus multispecies plots may be confounded by the number of interactions that an individual experiences within each treatment. For instance, the number of interactions that individuals experience increases from zero when grown alone, to one in pairwise arrangements, to as many as eight in multispecies plots. As a result, pairwise plots are characterized by a change from no neighbors to one neighbor, while species in community plots effectively interact with the same number of neighbors regardless of species composition. In this way, our results may be more indicative of a numerical neighbor effect than a species-species competition effect. However, neighbor identity appeared to be important in our experiment because

competitive effects were variable both between and among species in our treatments (fig. 2). In addition, a major motivation for this study was to understand whether pairwise interactions can predict the outcomes of competition in diverse groups of assemblages, which necessitates comparison among treatments with different methodologies.

The difference in the number of competitive interactions an individual experiences is affected by the spatial position any single individual holds within an experimental plot (figs. A1–A3), and this may affect performance. We found that individuals growing on the perimeter of the experimental plots were $\approx 50\%$ larger than individuals growing in the interior, but this effect was consistent across all plot types. In other words, no multispecies experimental plot type had greater edge effects than another. To account for this in our design, we replicated the experiment such that all species occupied all positions equally. We also tested our experimental results against a randomized null model to see if the number and proportion of edge locations biased our results. Importantly, although edge effects improve individual performance, they did not skew the results of our multispecies plots.

It is also possible that the difference we found in competitive outcomes between pairwise and multispecies communities is the result of factors other than indirect interactions. For instance, we did not control for some trophic interactions. Our plots were accessible to insect herbivores, root herbivores, and soil pathogens, all of which may have affected our results, although we did not observe widespread evidence of this within our plots.

Despite these challenges, the complexity and diversity of our experimental assemblages represent the conditions of interspecific competition that plants experience in nature far more accurately than do pairwise plots. Thus, our results indicating that competitive outcomes derived from pairs of species do not predict the competitive outcome of species in diverse assemblages are an important contribution to our understanding of how interspecific competition functions within communities.

*Effects of the Invader *Centaurea stoebe* on Native Species*

Centaurea stoebe appears to be an exceptionally strong competitor in western North American grasslands, based on its ability to replace natives and form near monocultures and its very strong competitive effects in experiments (Ridenour and Callaway 2001). Contrary to our results for native species, *C. stoebe* had strong, significant negative effects on native species in both pairwise and multispecies assemblages. This suggests that powerful invaders may disrupt or overwhelm indirect interactions among natives and exclude species from the community—as predicted by hierarchical community assembly rules (de Abreu and Durigan 2011).

When native species competed with each other in multispecies communities containing *C. stoebe*, the individual effects of a single species on another either diminished in competitive strength or became facilitative (fig. 2). This provides an unusual perspective on the way that invaders might alter landscapes through their competitive effects (Maron and Marler 2007). Not only do they suppress natives but they may also alter the way natives interact with each other such that they compete more weakly with each other. This suggests a potential mechanism by which diversity might resist exotic invasion. For example, if increasing diversity consistently decreases the competitive effect that natives have on each other in invaded communities and increasing diversity reduces the mean competitive effect of invaders, this may provide a form of biotic resistance that is inherent to diverse communities. While competition from the recipient native community and species diversity are thought to promote biotic resistance, little is known about how they influence invader establishment and success (Levine et al. 2004). Even though the competitive effects of *C. stoebe* were not significantly reduced in our multispecies assemblages, our results hint that indirect interactions in species-rich assemblages may be an important component of resilient, stable plant communities in the face of invasion.

Implications for Models of Competition

Overestimation of the effect of competition within communities by models has the potential to cloud our understanding of how competition affects coexistence, diversity, and stability in natural communities. Commonly, population models that seek to link the effects of interspecific competition to the distribution and abundance of species are based on the additive direct effect of all competing species (Levins 1966, 1979; MacArthur and Levins 1967), derived from randomly constructed pairwise competitive interaction intensities (May 2001). In other words, most competition-effects models are based not on empirically derived outcomes of competition but instead on hypothetical interaction strengths added together to create multispecies interactions, despite the sensitivity of such models to input parameters and assumptions (Smale 1976). With this in mind, we found that the intensity of competition between species in complex assemblages was much lower than the intensity of competition between species in pairwise competition. Therefore, even models that are based on empirically derived pairwise interaction strengths are likely to overestimate the effect of competition among species in communities.

Our results support a developing body of theory highlighting the importance of indirect facilitative interactions among species (Stone and Roberts 1991; Levine 1999; Callaway and Pennings 2000; Pages and Michalet 2003; White

et al. 2006; Callaway and Howard 2007; Weigelt et al. 2007; Saccone et al. 2010; Metlen et al. 2013; Aschehoug and Callaway 2014). Explicit tests of the predictive power of pairwise interactions suggest that nonadditive or higher-order interactions greatly change the way that species compete in complex multispecies groups (Dormann and Roxburgh 2005; Dormann 2007; Perkins et al. 2007; Weigelt et al. 2007; Engel and Weltzin 2008). For example, Dormann and Roxburgh (2005) found that Lotka-Volterra-type models built from pairwise outcomes did not accurately predict biomass and coexistence for three species mixtures in five out of the six combinations grown, as well as an experimental seven-species mixture. However, when a nonadditive competition coefficient was added to the models, predictions more closely matched experimental outcomes. This suggests that models of competition that assume perfectly additive effects (i.e., do not include indirect interactions) may have poor predictive power and that indirect interactions promote emergent properties that are important for determining the outcomes of competition in communities of species.

Our results empirically demonstrate that classic theory based on two-species experiments and models derived from pairwise interactions may overestimate the likelihood of competitive exclusion in multispecies communities. Importantly, the attenuation of competitive effects in species-rich assemblages was not dependent on nontransitive interactions, or competitive loops, which have been the only competition-based mechanisms thought so far to promote coexistence among competitors (Stone and Roberts 1991; Laird and Schamp 2006; Allesina and Levine 2011). Instead, our results suggest that indirect facilitative interactions occur among groups of competitors, and this may help explain why some diverse communities in nature appear to be more inherently stable than predicted by models and two-species experiments. This supports a more recent and rapidly expanding body of theory on the effects of multispecies interactions on coexistence (Dormann and Roxburgh 2005; Dormann 2007; Perkins et al. 2007; Weigelt et al. 2007; Engel and Weltzin 2008).

An explicit understanding of how species on the same trophic level interact in diverse assemblages is crucial if we are to understand the mechanisms that drive the emergent properties of communities, such as the relationship between species diversity and ecosystem function. The highly attenuated competitive effects we report here may lead to a better understanding of how high species diversity drives coexistence in communities.

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