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Models of Experimental Competitive Intensities Predict Home and Away Differences in Invasive Impact and the Effects of an Endophytic Mutualist

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ABSTRACT: Understanding the role of competition in the organization of communities is limited in part by the difficulty of extrapolating the outcomes of small-scale experiments to how such outcomes might affect the distribution and abundance of species. We modeled the community-level outcomes of competition, using experimentally derived competitive effects and responses between an exotic invasive plant, *Centaurea stoebe*, and species from both its native and nonnative ranges and using changes in these effects and responses elicited by experimentally establishing symbioses between *C. stoebe* and fungal endophytes. Using relative interaction intensities (RIIs) and holding other life-history factors constant, individual-based and spatially explicit models predicted competitive exclusion of all but one North American species but none of the European species, regardless of the endophyte status of *C. stoebe*. Concomitantly, *C. stoebe* was eliminated from the models with European natives but was codominant in models with North American natives. Endophyte symbiosis predicted increased dominance of *C. stoebe* in North American communities but not in European communities. However, when experimental variation was included, some of the model outcomes changed slightly. Our results are consistent with the idea that the effects of competitive intensity and mutualisms measured at small scales have the potential to play important roles in determining the larger-scale outcomes of invasion and that the stabilizing indirect effects of competition may promote species coexistence.

Keywords: endophyte, diversity, indirect facilitation, individual-based model, invasion.

Introduction

Exotic invasive species can suppress the abundances of native species and strongly reduce community diversity at

local and landscape scales (Parker et al. 1999; Mack et al. 2000). Despite these effects in their nonnative ranges, invasive species often do not express such dominance in their native ranges (Hierro et al. 2005; Callaway and Maron 2006; Lamarque et al. 2012). A few studies have linked this biogeographic difference in dominance to stronger competitive or allelopathic effects of invaders on species in newly invaded ranges than on species in their native range (Callaway and Aschehoug 2000; He et al. 2009; Thorpe et al. 2009; Ni et al. 2010; Callaway et al. 2011). This superior competitive ability of invasive species may be due to release from host-specific enemies (Elton 1958; Keane and Crawley 2002) or to particular traits (Callaway and Aschehoug 2000; Callaway and Ridenour 2004; Kim and Lee 2011).

Invasion success can be enhanced by niche opportunities created by mutualisms that facilitate the access of exotic species into native communities (Richardson et al. 2000; Shea and Chesson 2002) and improve the competitive ability of invaders (Reinhart and Callaway 2004, 2006; Aschehoug et al. 2012). Among these mutualisms, those involving fungal endophytes have the potential to have unusual effects on invasive species because of the range of ecological roles endophytes play, including increased herbivore and pathogen defense (Braun et al. 2003; Clay et al. 2005; Koh and Hik 2007; Musetti et al. 2007), altering rhizosphere microbial communities in ways that improve plant performance (Rudgers and Orr 2009), and enhancing the physiological capability to cope with water stress and high temperatures (Elmi and West 1995; McLellan et al. 2007). Fungal endophytes in grasses may also increase the competitive ability of infected plants (Marks et al. 1991; Rudgers and Orr 2009; Saari and Faeth 2012), but we know very little about how fungal endophytes affect competition in general and even less about how the symbiosis might affect the way exotic invaders interact with other species.

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Shipunov et al. (2008) and Newcombe et al. (2009) found that the seeds of *Centaurea stoebe*, an aggressive invader of western North American grasslands, are infected with a large diversity of nonclavicipitaceous endophytes in its native and nonnative ranges. Some of these endophytes have the potential to enhance the competitive and allelopathic effects of *C. stoebe*, while others may have strong negative effects (Newcombe et al. 2009).

Aschehoug et al. (2012) found that the presence of two root-associated phylotypes of *Alternaria* endophytes in *C. stoebe* increased both the competitive effect on and the competitive response to a suite of North American native grass species. Endophytes did not appear to affect interactions between *C. stoebe* and grass species native to Europe. Whether or not differences in strengths or intensities of competitive interactions translate into important drivers of community organization is poorly understood (Callaway et al. 1996; Brooker et al. 2005, 2008). Predictions can be made from the strengths of interactions among pairs of species (Besaw et al. 2011), but a major limitation on linking interaction strengths to their importance in communities is the logistical difficulty of extrapolating from mechanistic experiments to landscape processes and simultaneously integrating interactions among groups of species (see Miller 1994; Aschehoug 2011). Pairwise interactions between species may not be good estimators of the strength of interactions between species at the community level (Herben and Krahulec 1990; Perkins et al. 2007; Engel and Weltzin 2008; Aschehoug 2011); however, *C. stoebe* maintains strong suppressive effects on North American grass species in interactions in both pairwise and multispecies experiments (Aschehoug 2011). Modeling has been effective for predicting theoretical outcomes of multispecies interactions at larger scales (Laird and Schamp 2006; Allesina and Levine 2011; Michalet et al. 2011), but so far these models have not been parameterized with interaction strengths derived from experiments. Here we use experimentally derived specific values of the relative interaction intensity index (RII; Armas et al. 2004) in an individual-based model to estimate *Centaurea's* effects on and responses to four different North American native grass species and four different European native grassland species.

Individual-based models provide a powerful tool for analyzing the causal links between individual-level interactions and ecological patterns at the population or community level (Grimm and Railsback 2005) and are especially suitable for investigating the characteristics and dynamics of complex systems in community ecology (Xiao et al. 2009, 2010; Michalet et al. 2011). We focused on the following questions: (1) Can RIIs measured in empirical experiments be used in individual-based models to predict patterns of species abundances and diversity generally ob-

served in nature? (2) Do differences between the intensity of the *Centaurea*–North American native competition and that of the *Centaurea*–European native competition predict differences in abundances in model outcomes that are consistent with natural patterns? (3) Do the effects of fungal endophytes on the competitive interactions between *Centaurea* and native grasses from North America and Europe predict differences in the abundances of *Centaurea* in its native and nonnative ranges?

Material and Methods

We used relative interaction intensity indices (RIIs; Armas et al. 2004) from previous experiments (Aschehoug et al. 2012) to build individual-based, spatially explicit models. The RII is calculated by dividing the difference between the biomasses of the treatment and the control by the sum of those biomasses ($(B_T - B_C)/(B_T + B_C)$; Armas et al. 2004). The standard error was calculated with the formula provided by Armas et al. (2004, their app. A). Aschehoug et al. (2012) used individual plants grown alone as the control variable and plants grown in competition either with or without endophytes as the treatment variable when calculating the RII. 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 interaction strength across taxa and treatments. Experiments are presented in more detail in Aschehoug et al. (2012), but briefly, to obtain RIIs, *Centaurea* was grown from seed collected from an endophyte-free population in Idaho in three experimentally determined treatments: (1) endophyte-free, (2) inoculated with *Alternaria* phylotype “alt2f” (isolate CID120), and (3) inoculated with *Alternaria* phylotype “alt2b” (isolate CID73). The endophyte phylotypes used in experiments by Aschehoug et al. (2012) and in our models are found in the seeds of *Centaurea stoebe*. The CID73 isolate is found at low frequency in both the native and invaded ranges of its host (approximately 6% and 2%, respectively), while isolate CID120 is the most abundant phylotype in *C. stoebe* seeds from its native range ($\approx 44\%$) and is also among the most common in the invaded range ($\approx 10\%$; Shipunov et al. 2008). These endophytes are vertically transmitted within the host plant (Shipunov et al. 2008); however, the rates of transmission for these endophytes are unknown and may contribute to the differences in seed infection frequency observed in the wild. In addition, the native and nonnative ranges of these endophytes are unknown. Recently, it has been found that more than 90% of all *C. stoebe* seeds infected with endophytes contain just a single endophyte, suggesting that seedlings are also most com-

monly colonized by a single endophyte (A. K. H. Raghavendra and G. Newcombe, unpublished data). *Centaurea* plants were grown either alone ($n = 10$ per endophyte treatment) or in pairwise competition ($n = 10$ per endophyte treatment per competitor) with each of four North American and four European grass species in a greenhouse at the University of Montana, Missoula. Grass species were selected for being common species in their respective native ranges and were grown from collected wild seed. North American grasses were *Festuca idahoensis*, *Koeleria macrantha*, *Pseudoroegneria spicata*, and *Stipa comata*. European grasses were *Agropyron repens*, *Lolium rigidum*, *Melica ciliata*, and *Poa annua*. Fungal endophytes were cultured on potato dextrose agar and applied exogenously to *Centaurea* roots in the seedling stage before planting to infect the host plants (Newcombe et al. 2009). All plants were grown for 70 days in sterile soil before harvest. Total biomass of each plant was harvested, dried at 60°C, and weighed.

We used the RIIs derived from the experiment described above (app. A, available online) in an individual-based, spatially explicit, dual-lattice model (Travis et al. 2005, 2006; Michalet et al. 2011). In our model, three *Centaurea*-endophyte syndromes—*Centaurea* without endophytes, *Centaurea* experimentally infected with the endophyte phylotype CID120, and *Centaurea* infected with the endophyte phylotype CID73—occupied one two-dimensional lattice, while grass species occupied an overlapping two-dimensional lattice of the same size. We assumed that the competitive effects of the grass species decreased *C. stoebe* survival rate linearly with the increase of the RII value of grass species on *Centaurea*. The competitive effects of *Centaurea* on grass species also decreased their survival rates linearly with the increase of the RII value of *Centaurea* on grass species. The measured experimental variation (SE) for the mean RII value for each species interaction was included in the model. We present a complete description of the model in appendix B, available online.

Results

Centaurea stoebe Abundance and Native Diversity

In all models involving a single *Centaurea stoebe* syndrome, *Centaurea* was far more abundant in models with North American native species than in models with European species (fig. 1a), consistent with the natural patterns of the invader in the two ranges. Endophyte symbiosis affected the modeled dynamics of *Centaurea* abundance and final abundance. With North American species, *Centaurea* infected with the CID120 endophyte exhibited the largest increase in abundance at the beginning of the time sequence, and *Centaurea* infected with the CID73 endophyte

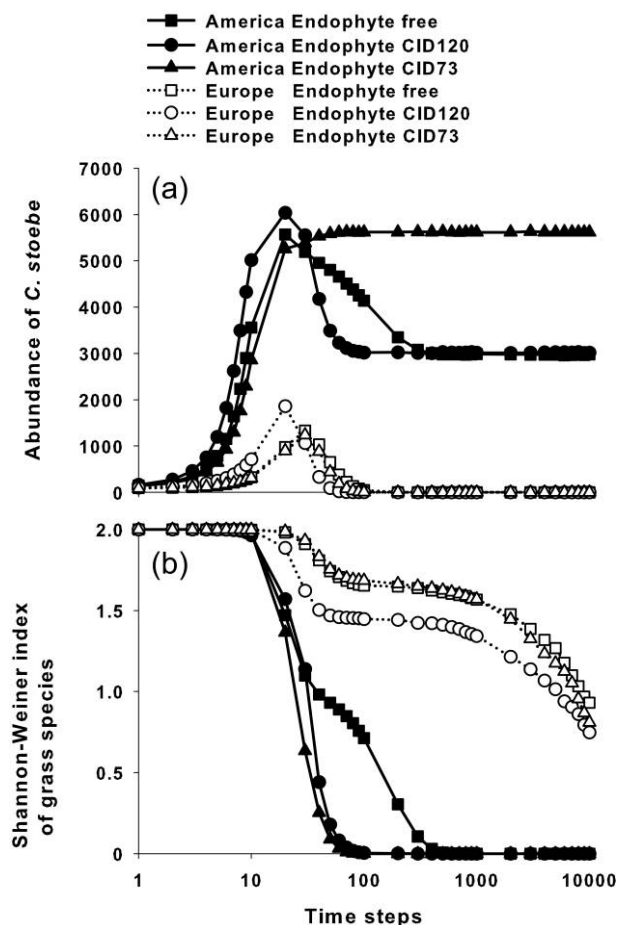


Figure 1: Model outcome of the dynamics of abundance for different *Centaurea stoebe* endophyte types (a) and corresponding grass species' diversity (b) in North America and Europe through time.

increased the least. In the middle of the time sequence, there was an abrupt decrease in abundance for *Centaurea*-CID120 and *Centaurea*-endophyte-free individuals. This abrupt decrease in abundance did not occur for *Centaurea*-CID73, which gradually achieved a stable maximum abundance. Ultimately, and based on individual RIIs in a somewhat counterintuitive way, *Centaurea*-CID73 became the most abundant treatment type and *Centaurea*-CID120 the least abundant. At the end of the time sequence, all *Centaurea*-endophyte syndromes maintained stable abundances in North American scenarios, with *Centaurea*-CID120 and *Centaurea*-endophyte-free at similar levels and *Centaurea*-CID73 at almost 90% greater abundances. Regardless of fungal-endophyte treatment, the abundance of *Centaurea* with European species followed similar, unimodal trajectories of early increases and then decreases before disappearing.

Solely on the basis of interaction strengths from exper-

iments, our models predicted that *Centaurea* would decrease the diversity of native North American communities far more than that of European communities (fig. 1*b*). However, the diversity of North American natives decreased more rapidly when modeled with *Centaurea* infected with either phylotype of endophytic fungus. At the beginning of the time sequence, when the abundance of *Centaurea* was low, there was little change in diversity for either North American or European natives. At the middle of the time sequence, the abundance of *Centaurea* increased and North American native diversity decreased concomitantly. With European natives, *Centaurea* infected with the CID120 endophytes decreased in diversity more than those in the other two treatment groups.

Dynamics of different Centaurea Types and Grass Species

On the basis of experimentally obtained RIIs, different endophyte treatments resulted in substantial species specificity in the way *Centaurea* interacted with North American natives, but not in the way *Centaurea* interacted with European natives (fig. 2). In all endophyte treatments with North American species, *Koeleria* and *Stipa* were inhibited more by *Centaurea* than were *Festuca* and *Pseudoroegneria*. However, *Pseudoroegneria* was the only species remaining in the model when *Centaurea* was without endophytes or was infected with the CID120 endophyte. *Festuca* was the only species remaining when *Centaurea* was infected with CID73. Not surprisingly, for each scenario the surviving North American species was the one for which *Centaurea* had the lowest competitive effects. In Europe, *Centaurea* was eliminated from all models, and no native species was eliminated from any scenario (fig. 2*d–2f*). *Lolium* and *Poa* increased to dominate the model, while *Melica* and *Agropyron* decreased in all scenarios. As would be expected, the abundant European grass species had lower competitive responses to *Centaurea* and stronger competitive effects on *Centaurea* than the two subdominant species.

Average Competitive Effects and Responses of Centaurea on Grass Species

Over time, the mean competitive effect of different *Centaurea* endophyte syndromes decreased against species from both North America and Europe (fig. 3*a*). Concomitantly, the mean competitive effects of all European grasses increased in the model, and the mean competitive effects of North American natives increased in the *Centaurea*-endophyte-free and *Centaurea*-CID120 models but not in the *Centaurea*-CID73 models.

Competition between Centaurea and Different Endophyte Treatments

When competition among the three *Centaurea* endophyte syndromes and the four native North American grass species was modeled without variation in interaction strengths in the same scenario, complex dynamics emerged (fig. 4*a*). When all three *Centaurea* types were in the same model, unlike the previous models, both *Pseudoroegneria* and *Festuca* remained in the model for more than 10,000 iterations. Interestingly, endophyte-free *Centaurea* was eliminated from the model, whereas *Centaurea* with either endophyte remained in the model. In fact *Centaurea*-CID120 coexisted with *Centaurea*-CID73 for almost 40,000 time steps, well beyond the time frame presented (data not shown). Ultimately, the model using interaction strengths without variation predicted long-term dominance of *Centaurea*-CID73 and *Pseudoroegneria*. An interesting characteristic of the North American model was very large population oscillations for endophyte-infected *Centaurea*, *Pseudoroegneria*, and *Festuca*. It is worth noting that *Pseudoroegneria spicata* was eliminated by *Centaurea*-CID73 in the single-invader treatment model but not in this model, where all *Centaurea* types competed together. In the European model with all *Centaurea* types considered together, *Centaurea* remained at low abundances and eventually was eliminated from the system, but there was no exclusion of any native species, and *Lolium* and *Poa* became dominant (fig. 4*b*).

Alternate Models with Variation

When we included experimental variation (SE) in the strength of interactions in the model, some aspects of our models changed. Qualitatively, the model results of the individual *Centaurea* syndromes competing with North American or European grass species with variation showed the same strong biogeographic patterns (fig. 5) as models that did not contain any variation (fig. 2). *Centaurea* remained in high abundance when in competition with North American grass species and was either in very low abundance or lost from the system when competing with European species.

In individual models of *Centaurea* competition that included experimental variation, *Centaurea*-endophyte-free persisted in higher abundances when competing against North American grasses than in models with no variation. In addition, both *P. spicata* and *Festuca idahoensis* remained in the system as codominant native species, a result not found in the model when no variation was included. Individual models of *Centaurea*-CID120 and *Centaurea*-CID73 competing against North American grasses were qualitatively the same with and without variation.

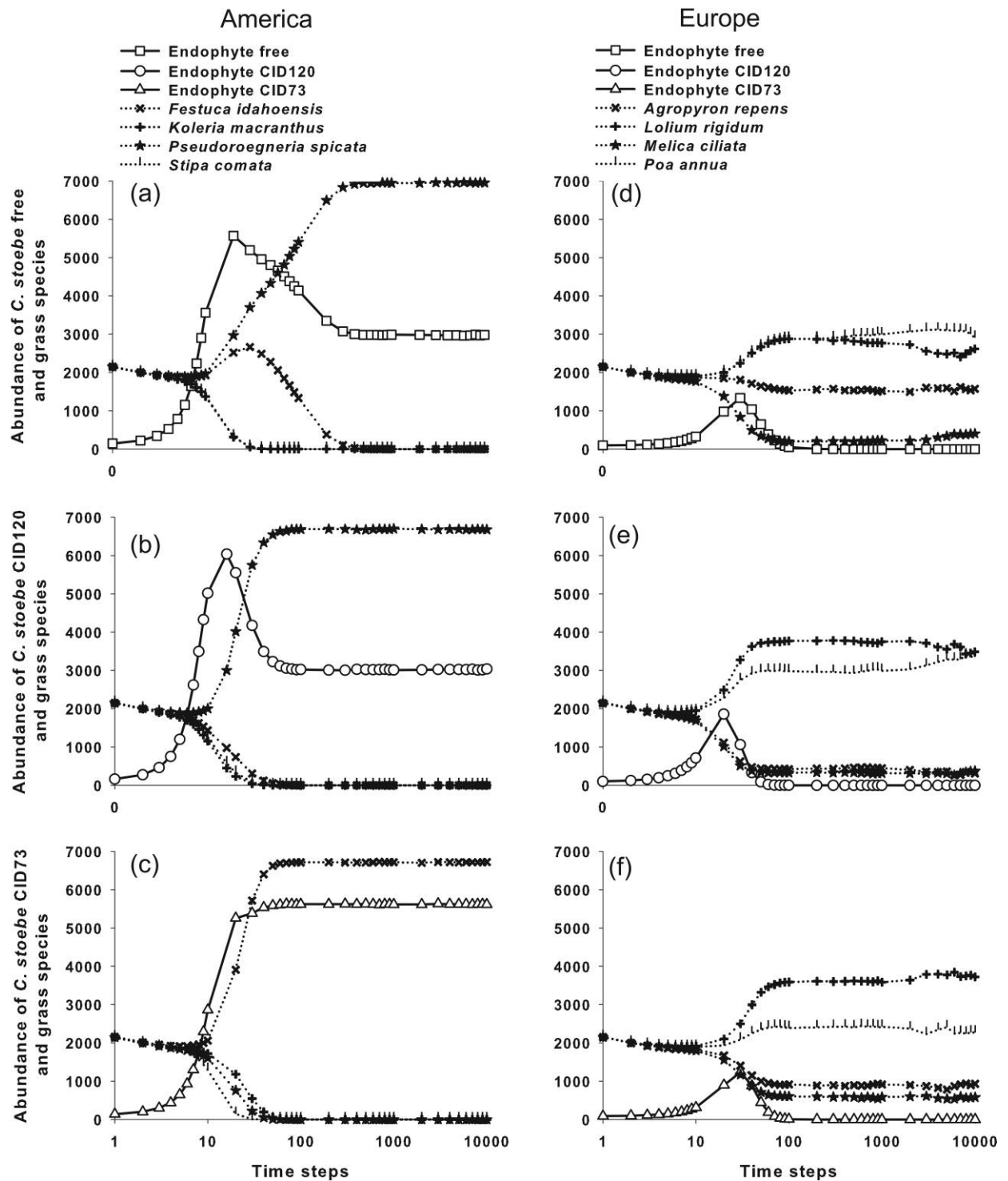


Figure 2: Model outcome of the dynamics of abundance for *Centaurea stoebe* and grass species through time for different endophyte types (rows: *C. stoebe*–endophyte-free, *C. stoebe*-CID120, *C. stoebe*-CID73) in different places (columns: North America, Europe) without variation in modeled interaction strengths. Open symbols represent *C. stoebe* syndromes, and filled symbols represent grass species. Note the logarithmic scale on the X-axis.

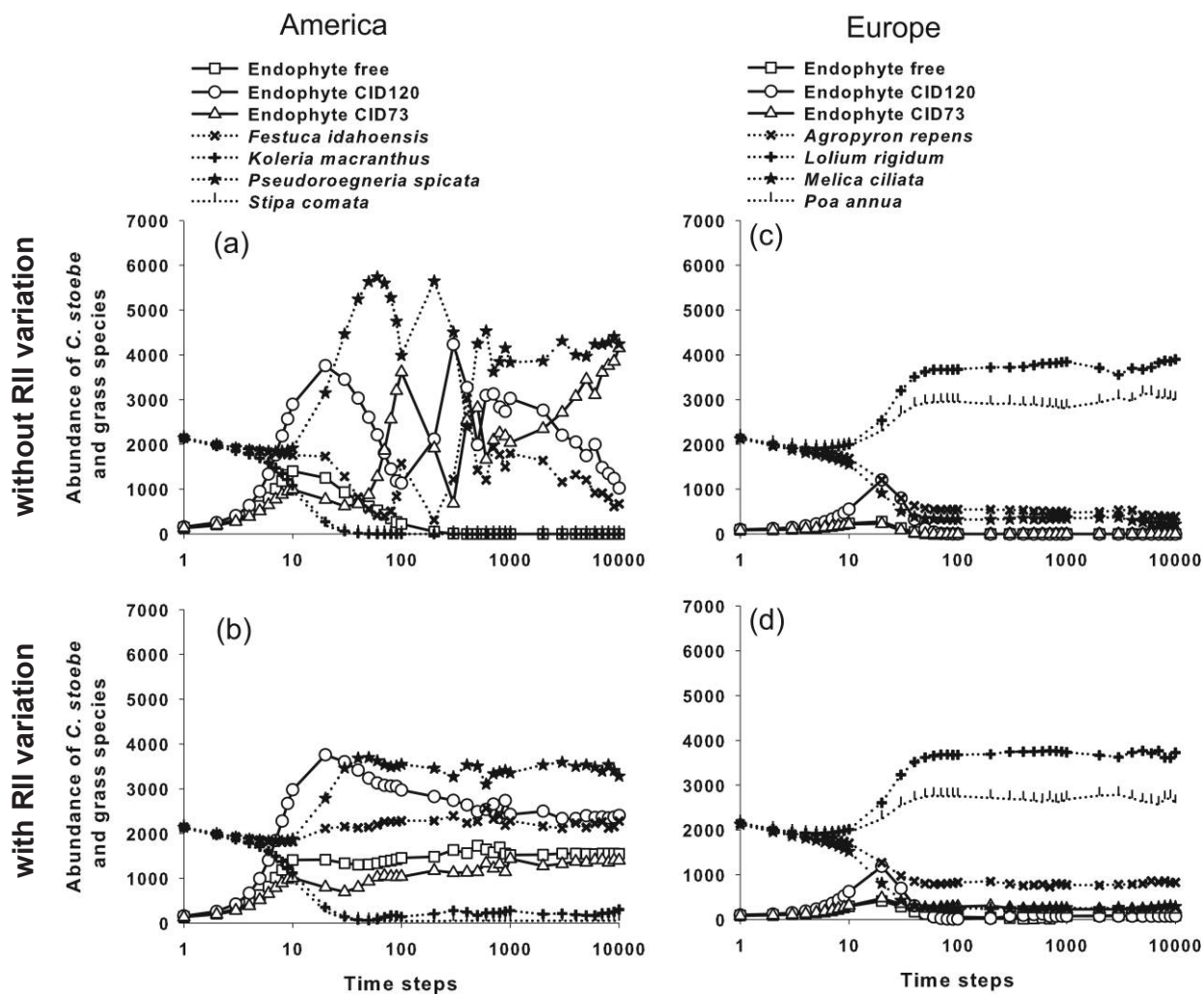


Figure 3: Model outcome of the dynamics of abundance for different *Centaurea stoebe* endophyte types when they compete with each other in North America (a, b) and in Europe (c, d) through time with and without variation. Note the logarithmic scale on the X-axis.

In models without variation, no *Centaurea* syndrome remained when in competition with European grasses. However, when variation was included, both *Centaurea*-endophyte-free and *Centaurea*-CID73 remained in the system at very low abundances (fig. 5).

In the model of competing *Centaurea* syndrome types and all North American grasses, the addition of experimental variation resulted in abundances of *Centaurea*-CID120 higher than those of *Centaurea*-CID73 and *Centaurea*-endophyte-free, although all three endophyte syndromes remained in the system (fig. 4). *Pseudoroegneria spicata* and *F. idahoensis* emerged as codominant natives in the system.

In contrast, when all three *Centaurea* syndromes competed against each other and the European grasses, the model outcomes were qualitatively the same whether var-

iation was included or not. In these models, all *Centaurea* syndromes were driven from the system in the first 100 time steps, while *Lolium rigidum* and *Poa annua* emerged as codominant native species.

Discussion

Biogeographic Differences in Communities

The results of models built from experimentally derived competitive responses and effects of *Centaurea* competing with species from its newly invaded range were diametrically different from those for *Centaurea* competing with species from its native range but consistent with the very high abundances of the invader in parts of western North America and its less common status in its native range

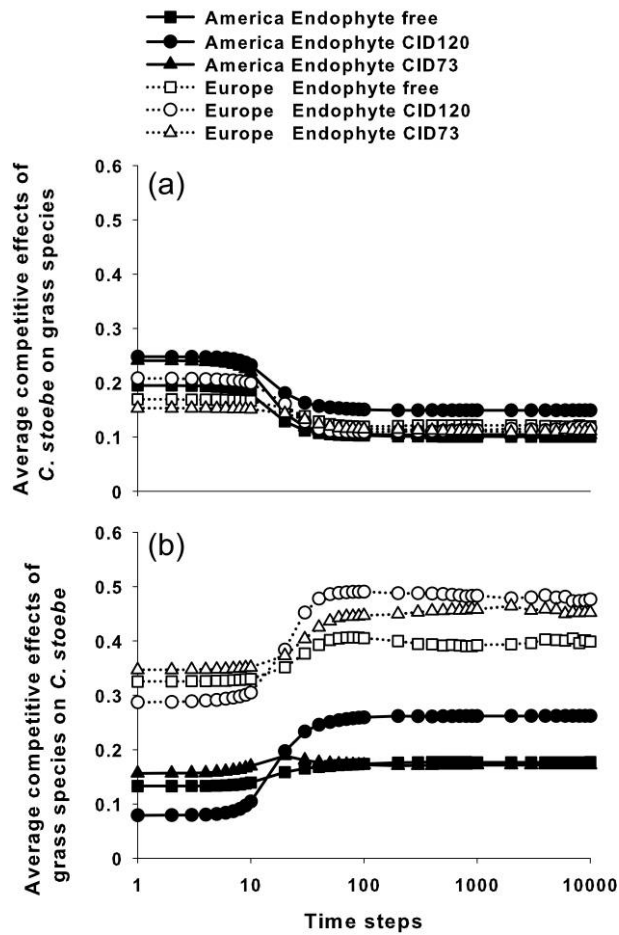


Figure 4: Model-predicted variation in the average competitive effects (relative interaction intensities) of different *Centaurea stoebe* endophyte types on grass species (a) and the average competitive effects of grass species on different *C. stoebe* endophyte types (b) through time. Note the logarithmic scale on the X-axis.

(Callaway et al. 2011). When models were constructed with North American natives, three of the four natives were competitively excluded, and *Centaurea stoebe* codominated the models with one other native. When models were constructed with European natives, no native grasses were competitively excluded, but *C. stoebe* was eliminated from all models. Thus, in North America, the *C. stoebe*-endophyte symbiosis appears to operate as a destabilizing mechanism for coexistence by increasing the strength of interspecific competition (Chesson 2000). Over the past few decades, *C. stoebe* has moved rapidly into western-US intermountain grasslands, where native species appear to have been displaced over large areas (Sheley et al. 2000; Kedzie-Webb et al. 2001; Ortega and Pearson 2005; Story et al. 2006). In some local cases, *C. stoebe* has established near monocultures (Tyser 1992; Lejeune and Seastedt

2001; Ridenour and Callaway 2001), and other research indicates that *C. stoebe* can alter the distribution and abundance of species within invaded-range communities (May and Baldwin 2011). However, *C. stoebe* does not reach such high relative abundances in its native range, and widespread observations indicate that the species appears to rarely reach high densities and is far less of a consistent landscape component (Müller 1989; R. M. Callaway, H. Müller-Schärer, and A. Diaconu, personal observations). Furthermore, in a recent field experiment conducted at many sites in the native and nonnative ranges of *C. stoebe*, the natural matrix of native vegetation in Europe had very strong competitive effects on *C. stoebe* growth and reproduction in Europe (Callaway et al. 2011). In contrast, identical experiments in Montana demonstrated very weak competitive effects.

Mechanistically, it is not clear why the competitive effects of *C. stoebe* on European species are weaker than those on North American species and why European species have stronger competitive effects on *C. stoebe*. However, the strong biogeographic differences in interaction strengths reported by Aschehoug et al. (2012) and modeled here correspond to other evidence suggesting that *C. stoebe* competes in inherently different ways with species from its native and nonnative ranges. In an experiment testing the effects and responses of many different *C. stoebe* populations, He et al. (2009) found that *C. stoebe* was a stronger competitor against a suite of North America plants than against congeners native to Romania. These results corresponded well to differences in the effects of experimentally applied (\pm)-catechin, a chemical in the root exudates of *C. stoebe* (Tharayil and Triebwasser 2010). However, recent studies suggest that *C. stoebe* may not produce enough (\pm)-catechin to be allelopathic, and thus whether this chemical may be a key novel competitive trait remains uncertain (Stermitz et al. 2009). It is important to note that Aschehoug et al. (2012) used *C. stoebe* seeds that originated from a population in Idaho, because plants from North American populations are often larger and have stronger competitive effects and responses than plants from European populations (Ridenour et al. 2008; Henery et al. 2010).

Interestingly, in models with and without variation in interaction strengths, the North American native *Pseudoroegneria spicata* coexisted with *C. stoebe* and appears to be one of the more resistant native species to *C. stoebe* invasion in the field. Ridenour and Callaway (2001) found that two of the weaker competitors modeled, *Festuca idahoensis* and *Koeleria macrantha*, dropped completely out of communities as *C. stoebe* increased in abundance but that *P. spicata* remained in the system at low abundances. Callaway et al. (2005) found that *P. spicata* was less affected

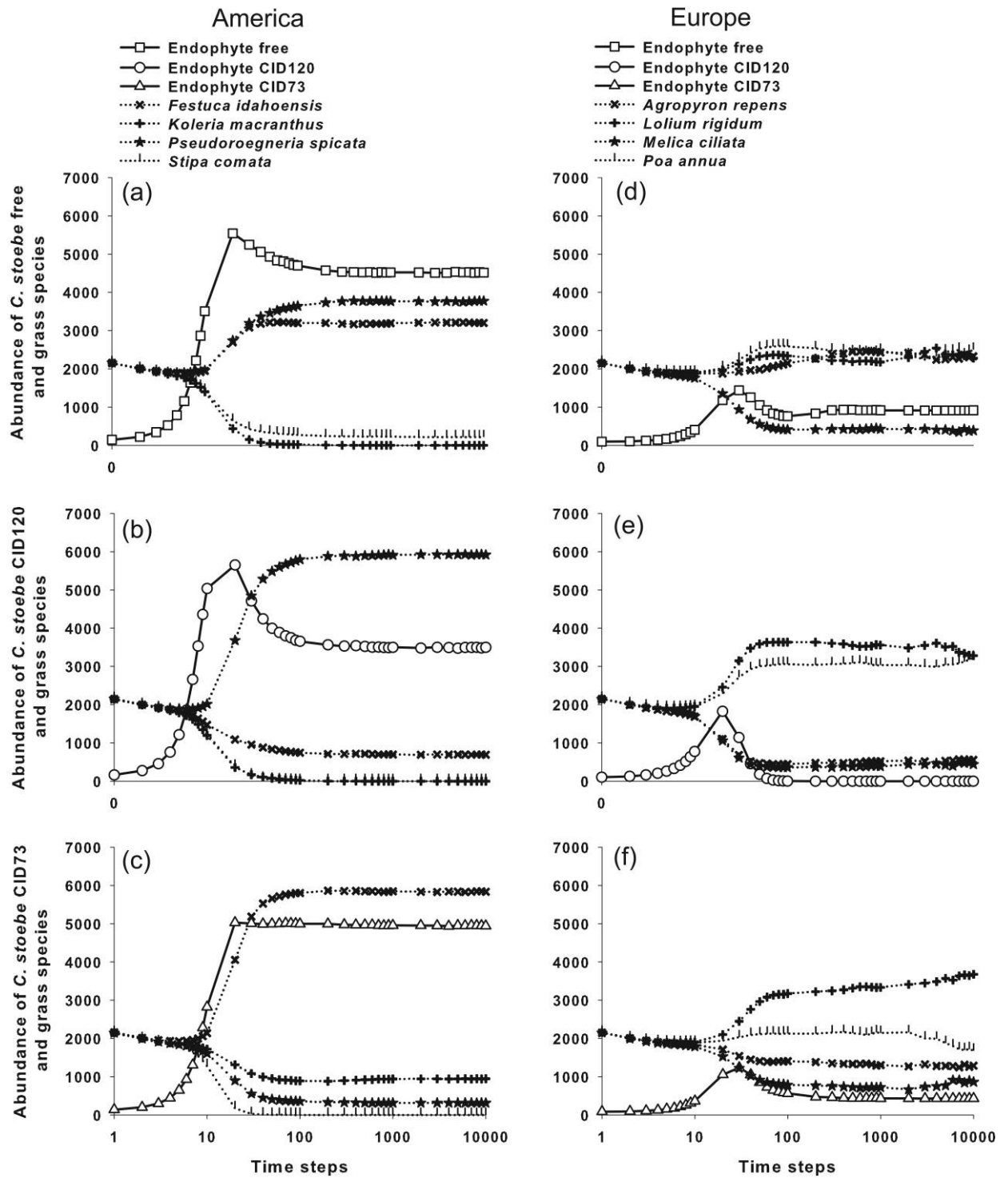


Figure 5: Model outcome of the dynamics of abundance for *Centaurea stoebe* and grass species through time for different endophyte types (rows: *C. stoebe*-endophyte-free, *C. stoebe*-CID120, *C. stoebe*-CID73) in different place (columns: North America, Europe) with observed variation in modeled interaction strengths. Open symbols represent *C. stoebe* syndromes, and filled symbols represent grass species. Note the logarithmic scale on the X-axis.

by competition with *C. stoebe* in controlled experiments than any of the other species modeled here.

Effects of Endophytes

Symbiotic fungal endophytes can provide indirect benefits via herbivore defense (Braun et al. 2003; Clay et al. 2005; Koh and Hik 2007; but see Faeth 2002; Faeth and Fagan 2002) and improve plant performance by altering rhizosphere microbial communities (Rudgers and Orr 2009). Fungal endophytes have also been shown to help plants cope with water stress (Elmi and West 1995), increase thermotolerance (McLellan et al. 2007), and protect against downy mildew (Musetti et al. 2007). There are examples of grass fungal endophytes directly increasing the competitive effects of infected plants on other species (Marks et al. 1991; Rudgers and Orr 2009, Saari and Faeth 2012), but these effects are far less understood than herbivore-mediated interactions. What is known about endophyte-increased competitive effects so far is limited to a relatively small group of endophytes in grasses: those belonging to the family Clavicipitaceae (e.g., *Neotyphodium*; Clay et al. 1993; Clay and Holah 1999). Nonclavicipitaceous fungal endophytes have been found in *C. stoebe* over a large part of its native and nonnative ranges (Shipunov et al. 2008).

One of the more interesting findings not evident in the empirical results but revealed in our models, both with and without variation in competitive strengths, is that when endophyte types were modeled together, they predicted greater abundance of *Centaurea* infected with CID73 than of *Centaurea* infected with CID120, despite the indication from experimentally derived RIIs that *Centaurea*-CID120's net competitive-effect response on North American species was stronger than that of any other *Centaurea* treatment. In other words, on the basis of the RIIs between North American natives and *Centaurea*-CID120, we expected this endophyte to be dominant, because it had the greatest mean RIIs on natives and is more widely distributed in nature than *Centaurea*-CID73. Instead, when *Centaurea* with different endophyte syndromes were allowed to compete with each other, CID73 excluded the other two and became dominant. We believe that this occurred because of the formation of a complex suite of indirect facilitative interactions that had important effects on final outcomes and population size. These indirect facilitative interactions had additive effects that caused oscillations in the abundances of the three *Centaurea* types as well as of North American natives (see fig. 4a), suggesting a mechanism for species coexistence similar to "stable limit cycles" (Holling 1966; Tanner 1975). The "keystone effect," a similar stabilizing mechanism based

on indirect interactions, has also been reported in food webs (Paine 1966, 1974; Power et al. 1996).

Variation in Competitive Strength

To our knowledge, this is the first time experimental variation in competitive interaction strengths has been incorporated into individual-based models such as ours. However, it is important to note that this experimental variation does not estimate the realistic natural variation that we might expect to find across the ranges of *C. stoebe*. It is not clear why models that incorporated standard error differed slightly from those that did not. However, high variation around some means permitted some model runs to produce facilitative effects of *C. stoebe* on natives and vice versa that are probably unrealistic. It is likely that including facilitative model runs affected the total model outcome.

Conclusions

Our model provides a novel integration of empirical experimental results with predictions of community-scale abundances and the potential effects of fungal symbionts on plant invasions and native species diversity. However, our models are limited in several ways. First, all intraspecific competition and interspecific competition among grasses were assumed to be equal in ability to occupy empty cells, because we had no empirical RII results for these species. Second, our model assumed equal reproductive rates, and species-specific differences in reproductive rates can have powerful effects on the abundance of species in communities. Third, our models did not take into account dispersal limitation, since all species had equal access to empty cells, and species-specific variation in dispersal distance and colonization rates can have important effects on the abundances of species in natural communities. Fourth, our RIIs are derived from highly controlled pairwise-interaction experiments, and as such are simply estimates of competitive abilities and intensities in nature. Fifth, our models assume that *Centaurea*-endophyte syndromes reproduce only endophyte-inoculated *Centaurea*; however, we do not know the vertical transmission rates of these endophytes in *Centaurea*. Despite these limitations, our model provides insight into whether competition with and without symbionts can produce outcomes that are similar to those observed in nature.

Finally, including variation in the strength of interactions between species affected the model outcomes in ways and for reasons that were not clear. When the measured levels of variation (SE) in the experiments were added to the models, there were slight differences in the dominant species and the numbers of species remaining in some

scenarios. Variation appeared to create instability by allowing some replications of the model runs to oscillate between negative and positive interaction outcomes, and this may be unrealistic for our particular species. We suspect that the development of new model formats may be required to integrate variation with confidence.

With these limitations in mind, the most important aspect of our study is that it provides a unique link between experimentally derived competitive intensities and a theoretical framework for how competition might drive biogeographic patterns of abundance and impact in invaded and native ranges. By integrating the effects of fungal-endophyte symbionts on these competitive scenarios, we demonstrate both stronger evidence for the potential organizational force of competition and the potential effects of mutualists on community outcomes. Of course, many other factors are involved in exotic invasions (Hierro et al. 2005), and these may determine competitive outcomes or far outweigh the importance of direct competition or the indirect effects derived from competition. However, our results provide a strong rationale for empirical and experimental exploration into biogeographic differences in the role of symbionts and the direct and indirect effects of competition in exotic invasions.

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Literature Cited

- Allesina, S., and J. M. Levine. 2011. A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences of the USA* 108:5638–5642.
- Armas, C., R. Ordiales, and F. I. Pugnaire. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85:2682–2686.
- Aschehoug, E. T. 2011. Indirect interactions and plant community structure. PhD diss. University of Montana, Missoula.
- Aschehoug, E. T., K. L. Metlen, R. M. Callaway, and G. Newcombe. 2012. Fungal endophytes directly increase the competitive effects of an invasive forb. *Ecology* 93:3–8.
- Besaw, L. M., G. C. Thelen, S. Sutherland, K. Metlen, and R. M. Callaway. 2011. Disturbance, resource pulses, and invasion: short-term shifts in competitive effects, not growth responses, favor exotic annuals. *Journal of Applied Ecology* 48:998–1006.
- Braun, K., J. Romero, C. Liddell, and R. Creamer. 2003. Production of swainsonine by fungal endophytes of locoweed. *Mycological Research* 107:980–988.
- Brooker, R. W., Z. Kikvidze, F. I. Pugnaire, R. M. Callaway, P. Choler, C. J. Lortie, and R. Michalet. 2005. The importance of importance. *Oikos* 109:63–70.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96:18–34.
- Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523.
- Callaway, R. M., E. H. DeLucia, D. Moore, R. Nowak, and W. H. Schlesinger. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. *Ecology* 77: 2130–2141.
- Callaway, R. M., and J. L. Maron. 2006. What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology & Evolution* 21:369–374.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2:436–443.
- Callaway, R. M., W. M. Ridenour, T. Laboski, T. Weir, and J. M. Vivanco. 2005. Natural selection for resistance to the allelopathic effects of invasive plants. *Journal of Ecology* 93:576–583.
- Callaway, R. M., L. P. Waller, A. Diaconu, R. Pal, A. R. Collins, H. Mueller-Schaerer, and J. L. Maron. 2011. Escape from competition: neighbors reduce *Centaurea stoebe* performance at home but not away. *Ecology* 92:2208–2213.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Clay, K., and J. Holah. 1999. Fungal endophyte symbiosis and plant diversity in successional fields. *Science* 285:1742–1744.
- Clay, K., J. Holah, and J. A. Rudgers. 2005. Herbivores cause a rapid increase in hereditary symbiosis and alter plant community composition. *Proceedings of the National Academy of Sciences of the USA* 102:12465–12470.
- Clay, K., S. Marks, and G. P. Cheplick. 1993. Effects of insect herbivory and fungal endophyte infection on competitive interactions among grasses. *Ecology* 74:1767–1777.
- Elmi, A. A., and C. P. West. 1995. Endophyte infection effects on stomatal conductance, osmotic adjustment and drought recovery of tall fescue. *New Phytologist* 131:61–67.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.
- Engel, E. C., and J. F. Weltzin. 2008. Can community composition be predicted from pairwise species interactions? *Plant Ecology* 195: 77–85.
- Faeth, S. H. 2002. Are endophytic fungi defensive plant mutualists? *Oikos* 98:25–36.
- Faeth, S. H., and W. F. Fagan. 2002. Fungal endophytes: common host plant symbionts but uncommon mutualists. *Integrative and Comparative Biology* 42:360–368.
- Grimm, V., and S. F. Railsback. 2005. *Individual-based modeling and ecology*. Princeton University Press, Princeton, NJ.
- He, W. M., Y. L. Feng, W. M. Ridenour, G. C. Thelen, J. L. Pollock, A. Diaconu, and R. M. Callaway. 2009. Novel weapons and invasion: biogeographic differences in the competitive effects of *Cen-*

- taurea maculosa* and its root exudate (\pm)-catechin. *Oecologia* (Berlin) 159:803–815.
- Henery, M. L., G. Bowman, P. Mrázl, U. A. Treier, E. Gex-Fabry, U. Schaffner, and H. Müller-Schärer. 2010. Evidence for a combination of pre-adapted traits and rapid adaptive change in the invasive plant *Centaurea stoebe*. *Journal of Ecology* 98:800–813.
- Herben, T., and F. Krahulec. 1990. Competitive hierarchies, reversals of rank order and the de Wit approach: are they compatible? *Oikos* 58:254–256.
- Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93:5–15.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* 98(S48):5–86.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17: 164–170.
- Kedzie-Webb, S. A., R. L. Sheley, J. J. Borkowski, and J. S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist* 61:43–49.
- Kim, Y., and E. Lee. 2011. Comparison of phenolic compounds and the effects of invasive and native species in East Asia: support for the novel weapons hypothesis. *Ecological Research* 26:87–94.
- Koh, S., and D. S. Hik. 2007. Herbivory mediates grass-endophyte relationships. *Ecology* 88:2752–2757.
- Laird, R. A., and B. S. Schamp. 2006. Competitive intransitivity promotes species coexistence. *American Naturalist* 168:182–193.
- Lamarque, L. J., S. Delzon, M. H. Sloan, and C. J. Lortie. 2012. Biogeographical contrasts to assess local and regional patterns of invasion: a case study with two reciprocally introduced exotic maple trees. *Ecography* 35:803–810.
- LeJeune, K. D., and T. R. Seastedt. 2001. *Centaurea* species: the forb that won the West. *Conservation Biology* 15:1568–1574.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- Marks, S., K. Clay, and G. P. Cheplick. 1991. Effects of fungal endophytes on interspecific and intraspecific competition in the grasses *Festuca arundinacea* and *Lolium perenne*. *Journal of Applied Ecology* 28:194–204.
- May, L., and L. K. Baldwin. 2011. Linking field based studies with greenhouse experiments: the impact of *Centaurea stoebe* (= *C. maculosa*) in British Columbia grasslands. *Biological Invasions* 13: 919–931.
- McLellan, C. A., T. J. Turbyville, E. M. K. Wijeratne, A. Kerschen, E. Vierling, C. Queitsch, L. Whitesell, and A. A. L. Gunatilaka. 2007. A rhizosphere fungus enhances *Arabidopsis* thermotolerance through production of an HSP90 inhibitor. *Plant Physiology* 145: 174–182.
- Michalet, R., S. Xiao, B. Touzard, D. S. Smith, L. A. Cavieres, R. M. Callaway, and T. G. Whitham. 2011. Phenotypic variation in nurse traits and community feedbacks define an alpine community. *Ecology Letters* 14:433–443.
- Miller, T. E. 1994. Direct and indirect species interactions in an early old-field plant community. *American Naturalist* 143:1007–1025.
- Müller, H. 1989. Growth pattern of diploid and tetraploid spotted knapweed, *Centaurea maculosa* Lam. (Compositae), and effects of the root-mining moth *Agapeta zoegana* (L.) (Lep.: Cochyliidae). *Weed Research* 29:103–111.
- Musetti, R., R. Polizzotto, A. Vecchione, S. Borselli, L. Zulini, M. D'Ambrosio, L. Sanità di Toppi, and I. Pertot. 2007. Antifungal activity of diketopiperazines extracted from *Alternaria alternata* against *Plasmopara viticola*: an ultrastructural study. *Micron* 38: 643–650.
- Newcombe, G., A. Shipunov, S. Eigenbrode, A. K. H. Raghavendra, H. Ding, C. L. Anderson, R. Menjivar, M. Crawford, and M. Schwarzländer. 2009. Endophytes influence protection and growth of an invasive plant. *Communicative and Integrative Biology* 2: 29–31.
- Ni, G. Y., U. Schaffner, S. L. Peng, and R. M. Callaway. 2010. *Acroptilon repens*, an Asian invader, has stronger competitive effects on species from America than species from its native range. *Biological Invasions* 12:3653–3663.
- Ortega, Y. K., and D. E. Pearson. 2005. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications* 15:651–661.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- . 1974. Intertidal community structure: experimental studies on relationships between a dominant competitor and its principal predator. *Oecologia* (Berlin) 15:93–120.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3–19.
- Perkins, T. A., W. R. Holmes, and J. F. Weltzin. 2007. Multi-species interactions in competitive hierarchies: new methods and empirical test. *Journal of Vegetation Science* 18:685–692.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Reinhart, K. O., and R. M. Callaway. 2004. Soil biota facilitate exotic *Acer* invasions in Europe and North America. *Ecological Applications* 14:1737–1745.
- . 2006. Soil biota and invasive plants. *New Phytologist* 170: 445–457.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmánek. 2000. Plant invasions: the role of mutualisms. *Biological Reviews* 75:65–93.
- Ridenour, W. M., and R. M. Callaway. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* (Berlin) 126:444–450.
- Ridenour, W. M., J. M. Vivanco, Y. Feng, J. Horiuchi, and R. M. Callaway. 2008. No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecological Monographs* 78:369–386.
- Rudgers, J. A., and S. Orr. 2009. Non-native grass alters growth of native tree species via leaf and soil microbes. *Journal of Ecology* 97:247–255.
- Saari, S., and S. H. Faeth. 2012. Hybridization of *Neotyphodium* endophytes enhances competitive ability of the host grass. *New Phytologist* 195:231–236.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17:170–176.
- Sheley, R. L., C. A. Duncan, M. B. Halstvedt, and J. S. Jacobs. 2000.

- Spotted knapweed and grass response to herbicide treatments. *Journal of Range Management* 53:176–182.
- Shipunov, A., G. Newcombe, A. K. H. Raghavendra, and C. L. Anderson. 2008. Hidden diversity of endophytic fungi in an invasive plant. *American Journal of Botany* 95:1096–1108.
- Stermitz, F. R., R. A. Hufbauer, and J. M. Vivanco. 2009. Retraction. Enantiomeric-dependent phytotoxic and antimicrobial activity of (\pm)-catechin: a rhizosecreted racemic mixture from spotted knapweed. *Plant Physiology* 151:967.
- Story, J. M., N. W. Callan, J. G. Corn, and L. J. White. 2006. Decline of spotted knapweed density at two sites in western Montana with large populations of the introduced root weevil, *Cyphocleonus achates* (Fahraeus). *Biological Control* 38:227–232.
- Tanner, J. T. 1975. The stability and intrinsic growth rates of prey and predator populations. *Ecology* 56:855–867.
- Tharayil, N., and D. J. Triebwasser. 2010. Elucidation of a diurnal pattern of catechin exudation by *Centaurea stoebe*. *Journal of Chemical Ecology* 36:200–204.
- Thorpe, A. S., G. C. Thelen, A. Diaconu, and R. M. Callaway. 2009. Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis. *Journal of Ecology* 97:641–645.
- Travis, J. M. J., R. W. Brooker, E. J. Clark, and C. Dytham. 2006. The distribution of positive and negative species interactions across environmental gradients on a dual-lattice model. *Journal of Theoretical Biology* 241:896–902.
- Travis, J. M. J., R. W. Brooker, and C. Dytham. 2005. The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model. *Biology Letters* 1:5–8.
- Tyser, R. W. 1992. Vegetation associated with two alien plant species in a fescue grassland in Glacier National Park, Montana. *Great Basin Naturalist* 52:189–193.
- Xiao, S., R. Michalet, G. Wang, and S. Y. Chen. 2009. The interplay between species' positive and negative interactions shapes the community biomass-species richness relationship. *Oikos* 118:1343–1348.
- Xiao, S., M. Zobel, R. Szava-Kovats, and M. Partel. 2010. The effects of species pool, dispersal and competition on the diversity-productivity relationship. *Global Ecology and Biogeography* 19: 343–351.

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