REVIEW

A meta-analysis of biotic resistance to exotic plant invasions

Jonathan M. Levine,*
Peter B. Adler and
Stephanie G. Yelenik
*Department of Ecology,
Evolution, and Marine Biology,
University of California, Santa
Barbara, CA 93106, USA*
**Correspondence: E-mail:
levine@lifesci.ucsb.edu*

Abstract

Biotic resistance describes the ability of resident species in a community to reduce the success of exotic invasions. Although resistance is a well-accepted phenomenon, less clear are the processes that contribute most to it, and whether those processes are strong enough to completely repel invaders. Current perceptions of strong, competition-driven biotic resistance stem from classic ecological theory, Elton's formulation of ecological resistance, and the general acceptance of the enemies-release hypothesis. We conducted a meta-analysis of the plant invasions literature to quantify the contribution of resident competitors, diversity, herbivores and soil fungal communities to biotic resistance. Results indicated large negative effects of all factors except fungal communities on invader establishment and performance. Contrary to predictions derived from the natural enemies hypothesis, resident herbivores reduced invasion success as effectively as resident competitors. Although biotic resistance significantly reduced the establishment of individual invaders, we found little evidence that species interactions completely repelled invasions. We conclude that ecological interactions rarely enable communities to resist invasion, but instead constrain the abundance of invasive species once they have successfully established.

Keywords

Competition, fungal community, herbivory, invasion, species diversity.

Ecology Letters (2004) **7**: 975–989

INTRODUCTION

Concern over the ecological and economic impacts of biological invasions has generated tremendous interest in the factors controlling invasion success (Crawley 1987; Drake *et al.* 1989). Numerous studies have examined the traits of successful invaders (Baker 1965; Rejmánek & Richardson 1996; Rejmánek 1996) and the types of communities most susceptible to invasion (Rejmánek 1989; Levine & D'Antonio 1999; Lonsdale 1999; Davis *et al.* 2000). A dominant paradigm in this literature is that successful invaders must overcome *biotic resistance*, the reduction in invasion success caused by the resident community. Although investigated in a wide range of systems, biotic resistance is particularly well studied in the invasive plant literature, where competition from resident plants is commonly assumed to regulate invasion success (Levine 2000; Seabloom *et al.* 2003). Still, biotic resistance can arise from any effect of resident species on colonizing invaders, including predation, herbivory and disease.

Interest in biotic resistance arises from its potentially important conservation applications and links with classic ecological theory. An understanding of biotic resistance might be used to predict which communities are most susceptible to invasions or where invasions are most likely to occur (Levine & D'Antonio 1999). Similarly, restoration ecologists need to design communities that will best resist invasion (Seabloom *et al.* 2003; Corbin & D'Antonio 2004). Meanwhile, basic researchers are interested in biotic resistance questions because they have parallels in mainstream ecology. For example, biotic resistance is implicit within questions of whether plant populations are seed or safe-site limited (Harper 1977; Parker 2001), or whether systems become more difficult to colonize as community assembly proceeds (Moulton & Pimm 1983; Drake *et al.* 1996; Fargione *et al.* 2003).

How effective is biotic resistance?

Although biotic resistance is a well-accepted property of communities, three fundamental questions remained

unresolved. First, how effective is biotic resistance? Is it capable of completely repelling exotic invasions? Second, when in the invasion process does it operate most strongly? Third, which ecological interactions contribute most to resistance? Here we evaluate conventional wisdom concerning each of these questions by taking a meta-analytical approach to the plant invasions literature.

Although opinions vary, many ecologists expect that biotic resistance is a strong process, capable of repelling exotic invasions (Moulton & Pimm 1983; Case 1990; Kennedy *et al.* 2002). This is not to say that resistant communities repel all potential invaders, but rather that some invaders are absent because of interactions with resident species. This perspective was most influentially laid out by Charles Elton who in his 1958 classic book, *The Ecology of Invasions by Animals and Plants* noted that in addition to the many invasions that are successful, there are 'enormously more invasions that never happen, … they meet with resistance' (p.109). Classic theoretical ecology through the 1960s and 1970s also frequently described systems where ecological interactions excluded potential invaders (May & MacArthur 1972). The strong biotic resistance perspective has persisted as a dominant paradigm in many papers (Moulton & Pimm 1983; Case 1990; Kennedy *et al.* 2002). For example, Kennedy *et al.*, in a 2002 paper entitled *Biodiversity as a barrier to ecological invasion*, advocate restoring communities with a diversity of plants because 'diverse communities will probably require minimal maintenance and monitoring because they are generally effective at excluding undesirable invaders.' Our review challenges this paradigm, showing that although biotic resistance significantly reduces the seedling performance and establishment fraction for individual invaders, it is unlikely to completely repel them.

Addressing our first question about the effectiveness of biotic resistance also addresses our second, concerning where in the invasion process resistance is most important. Whether species interactions categorically exclude invaders from communities or simply reduce their populations involves processes that operate at different stages of the invasion process. For biotic resistance to act as a barrier to invasion (Fig. 1, stage A), as it is often conceived (Case 1990; Erneberg 1999; Kennedy *et al.* 2002), it must prevent establishment by driving invader growth rates when rare to less than zero. If, alternatively, biotic resistance simply reduces the establishment and performance of individual populations, invaders successfully establish, but ecological interactions regulate the subsequent growth and spread of invader populations (Fig. 1, stage B).

Which processes contribute most to biotic resistance?

Communities may resist invasion through a diversity of biotic processes, including predation, competition, herbivory or disease. In addition, abiotic factors, such as high temperature or salinity can also make an ecosystem difficult to colonize. Because many mechanisms can underlie the phenomenon, Elton (1958) noted that '(resistance) describes ignorance and not knowledge' (p. 117). Still, most ecologists focus on competition as the primary source of resistance. In defining ecological resistance, Elton (1958) explained that introduced animals 'search for breeding sites and find them occupied, for food that other species are already eating, for cover that other animals are sheltering in, and they will bump into them and be bumped into- and often be bumped off' (p. 116–117). An emphasis on competition in the current literature is borne out in the disproportionate number of studies in our review which examine the process (see section Competition from resident plants).

The importance of competition in biotic resistance also follows from another classic idea in invasion ecology, the enemies release hypothesis (Maron & Vilà 2001). This hypothesis poses that exotic species escape the specialist herbivores and pathogens present in their native range. Herbivory and disease, especially by specialists, should therefore have a relatively minor influence on invasive species performance in their exotic range. This is in contrast
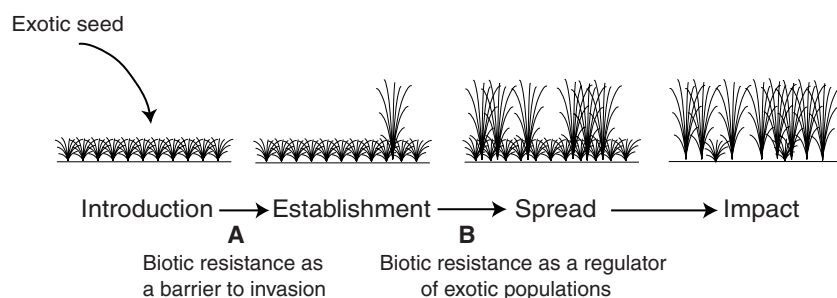

Figure 1 Conception of the invasion process and where in that process biotic resistance is most effective at influencing invasions. It is often assumed that biotic resistance acts to repel invaders prior to establishment (Location A). We argue, however, that it may be more effective at regulating the spread and impacts of invaders once they have successfully established (Location B).

to competition, a processes invaders do not escape (Thebaud *et al.* 1996).

We organize our review around four different sources of biotic resistance: competitors, species diversity, herbivores and soil fungal communities. After evaluating the effect of each source of resistance, we examine which are most effective at inhibiting invasions, testing the common assumption that biotic resistance arises most strongly through competition. Although previous reviews have examined individual components of biotic resistance, such as herbivory (Maron & Vilà 2001) and species diversity (Levine & D'Antonio 1999; Levine *et al.* 2002), no comprehensive synthesis has compared the relative strength of different sources of resistance or attempted to identify the stages of invasion when they are most effective.

METHODS

Our meta-analysis included studies which examined the effects of biotic resistance on invader establishment and individual performance measures. All papers were located by searching keywords in BIOSIS, and examining references within. Because of differences in methodological approaches, the specific criteria for inclusion varied amongst the competition, herbivory, diversity and soil fungal community sections of the review, but all sections used the following general criteria.

The focus of each study needed to be an invader exotic to the habitat in question. In nearly all cases this was a species from a different biogeographic region altogether, but in a few cases it was a native species expanding its range. A second criteria was that the study examine the effects of biotic resistance on early life stages of the invader, meaning the invader was added as seed or transplanted seedlings or small cuttings. The resident community could not be assembled in a greenhouse, except for studies of soil fungal effects. The community was typically entirely native, and in some cases a mix of native and previously colonized exotic species. However, we did not include studies of invasions into cropland systems or forestry plantations, nor did we consider released biocontrol agents as sources of biotic resistance.

Each study needed to experimentally manipulate the putative source of biotic resistance and have appropriate controls. In addition, we included several mensurative experiments (Hurlbert 1984), where the investigator compared invader establishment in locations with and without resident resistance. We only included studies that measured at least one of the following response variables: invader colonization such as germination, survival or establishment (the aggregate of the other two) or individual performance measures such as biomass, growth or

fecundity. Note that even though invaders were added as seedlings, performance and establishment were measured at later life stages.

For each study we calculated an effect size *d* (Gurevitch & Hedges 1993).

$$d = \frac{\overline{X}_E - \overline{X}_C}{SD_{pooled}} J$$

where $\overline{X}_C$ is the mean of the control group (resistance present) and $\overline{X}_E$ is the mean of the experimental group (resistance removed). The pooled standard deviation is calculated:

$$SD_{pooled} = \sqrt{\frac{(n_E - 1)(SD_E)^2 + (n_C - 1)(SD_C)^2}{n_E + n_C - 2}}$$

where SD is the standard deviation of the experimental (E) or control (C) group and *n* is the sample size. Studies that did not report data with estimates of variability could not be included in the analysis. Most often, the standard error was reported, allowing us to calculate the standard deviation. In the expression for *d*, *J* corrects for bias because of different sample sizes by differentially weighting studies as follows:

$$J = 1 - \frac{3}{4(n_C + n_E - 2) - 1}$$

One can think of the effect size *d* as the difference between invader performance in the presence and absence of resident species, measured in units of standard deviations (analogous to a *t* statistic). Thus large differences and low variability generate the largest effect sizes. We measured effect size with *d* rather than the response ratio (Osenberg *et al.* 1997) because some of our studies found zero invader establishment with resident species, making the response ratio difficult to interpret.

We treated experiments where investigators subjected different invader species to the same experimental treatments, or the same invader to different communities, as separate experiments (Gurevitch & Hedges 1993). Different measures on the same experiment were never included in the same analysis. In such cases, we chose the response variable most directly linked to the establishment of a viable invader population. For each source of biotic resistance, we report results of separate analyses of invader establishment and individual performance variables, because they may respond differently to resistance. When identical studies were repeated in multiple years, the average *d* and sample size from the different years were analysed to prevent undo weighting of those studies. To test for significant differences between classes of studies, we used the *Q* statistic in a mixed effects model. For details regarding the calculation of *Q*, the average effect size and 95% confidence intervals, see Gurevitch & Hedges (1993).

Limitations

Although our meta-analysis can test the effect of biotic resistance on invader establishment and performance, the available literature prevents us from testing whether exotic species invasions fail because of biotic resistance. This would require experiments where investigators added propagules of invaders not already present in the recipient community. By contrast, almost all published studies in the literature examine the effects of residents on exotic species that have already invaded the system to some extent. Thus, to explore the effectiveness of biotic resistance, we relied on studies in addition to those in the meta-analysis.

Another limitation of our meta-analysis is that sample sizes were small for tests of whether resistance differed across community and invader type. Although we report these results, we do not discuss them at length.

COMPETITION FROM RESIDENT PLANTS

Of the different processes that can contribute to biotic resistance, competition is the most commonly invoked. This is confirmed in the relative number of studies which examined competition as a source of biotic resistance. Of the 52 biotic resistance studies which fit our criteria for inclusion in the meta-analysis, 24 examined competition. If we add to this the seven diversity studies as they too examine competition, and remove the eight soil biota studies conducted in controlled environments, this makes 70% of field studies competition-focused. This emphasis on competition parallels its attention in the plant ecology literature in general (Elton 1958; Goldberg & Barton 1992).

Meta-analysis of resident plant effects on invasion success

Our meta-analysis of competition effects on invader establishment incorporated 65 experiments from 24 different studies that compared invader establishment and performance in intact communities to treatments in which resident competitors were removed (Table 1, competition studies). The method of removal differed across studies and included hand weeding, aboveground clipping, shoot pull-back, herbicide, disturbance that turned over the soil and the use of natural openings in the vegetation (mensurative experiments sensu Hurlbert 1984). If a single experiment involved multiple removal treatments, we used data from the most severe treatment for $\overline{X^E}$. In addition, when studies crossed their manipulation of resident species competition with resource addition, herbivory, or other factors, we used the results from only those treatments with ambient levels of resource availability, herbivory, etc.

The meta-analysis revealed strong and significant effects of resident competitors on both the establishment and individual performance of exotic invaders (Fig. 2). d's of 0.94 and 1.12 for establishment and performance are both considered 'strong' effect sizes (Cohen 1969). A typical result with respect to direction (but stronger in magnitude) was found by Peart (1989a,b) who examined the colonization of the exotic perennial grass *Anthoxanthum odoratum* into a patch of California grassland dominated by the native perennial *Deschempsia holciformis*. With an expected 9718 *Anthoxanthum* seeds arriving into the plot, an average of 5.9 seedlings successfully colonized with the resident vegetation intact, while 455 colonized plots where the resident vegetation had been killed with herbicide. When the sample size and variance were incorporated, the d for this study was 3.00. Five studies of the 65 reported positive effects of the surrounding vegetation on invaders, but in contrast to general reviews of competition (Connell 1983; Goldberg & Barton 1992), the fraction of facilitation studies was rather small.

Within the competition studies, our meta-analysis identified several interesting patterns. For invader performance, but not establishment, grasses, forbs and woody plants differed significantly in their susceptibility to biotic resistance from competition (establishment $Q = 2.18$, d.f. = 2, $P > 0.25$; performance $Q = 5.19$, d.f. = 2, $P < 0.05$), with grasses and forbs showing greater sensitivity than woody species. Differences among community types, however, were not significant.

Can resident plant competition repel exotic invaders?

Although our meta-analysis showed that competition from resident plants reduced invader establishment and performance, it is not clear whether competition is capable of completely repelling invaders. In all competition studies in our meta-analysis, the target invaders were already present in the community, demonstrating that inhibition by residents was ultimately overcome. Moreover, several authors were struck by how easily intact vegetation was invaded. Scherber *et al.* (2003) observed that '… it is not surprising that (exotic *Senecio*) survival in our experiment was highest on disturbed, ungrazed ground. It is much more remarkable that plants were also able to survive under high competition in mature grassland vegetation.'

Although resident plants may have repelled invaders not observed in the various communities of Table 1 (competition studies), we believe this unlikely for several reasons. First, even when intense, competition is inherently a local interaction (Pacala & Silander 1985), and microsites with reduced competition are pervasive features of ecological communities (D'Antonio *et al.* 2001). For example, in northern California, Hobbs & Mooney (1991) found consistent exotic grass invasion of gopher mounds by *Bromus*, a species rare in more vegetated parts of the

Table 1 Studies examined in our meta-analysis of biotic resistance achieved through (a) competition, (b) species diversity, (c) herbivory and (d) soil fungal communities

Citation	Exotic invader	Growth form	Habitat	Manipulation type	Response variable
(a) Competition studies					
Amsberry *et al.* 2000	*Phragmites australis*	Perennial grass	Salt marsh – *S. alterniflora* Salt marsh – *Juncus* Salt marsh – *S. patens* Salt marsh – *Typha*	Clipping	Ramet density
Bakker & Wilson 2001	*Agropyron cristatum*	Perennial grass	Grassland	Vegetation removal	Growth rate
Barger *et al.* 2003	*Melinus menutiflora*	Perennial grass	Grassland	Disturbance	Biomass
Bellingham & Coomes 2003	*Cytisis scoparius*	Shrub	Shrubland	Clipping	Survivorship, biomass
Bossard 1991	*Cytisis scoparius*	Shrub	Grassland	Disturbance	Establishment fraction
D'Antonio 1993	*Carpobrotus edulis*	Perennial forb	Backdune Coastal scrub Grassland	Disturbance	Emergence fraction, biomass
D'Antonio & Mack 2001	*Myrica faya*	Shrub	Grassland	Vegetation removal	Number establishing
Erneberg 1999	*Anthemis cotula*	Annual forb	Grassland	Vegetation removal	Biomass
Grieshop & Nowierski 2002	*Linaria genistifolia* ssp. *dalmatica*	Perennial forb	Grassland	Vegetation removal	Number of seedlings
Hamilton *et al.* 1999	Multiple annual grasses	Annual grass	Grassland	Clipped	Number establishing
Jesson *et al.* 2000	*Cerastium fontanum* *Heiracium pilosella* *Anthoxanthum odoratum* *Holcos lanatus*	Perennial forb Perennial forb Perennial grass Perennial grass	Forest clearings	Disturbance	Establishment fraction
Lambrinos 2002	*Cortaderia jubata*	Perennial grass	Dunescrub Grassland Maritime chaparral Seasonal wetland	Disturbance	Germination
	Cortaderia selloana	Perennial grass	Dunescrub Grassland Maritime chaparral Seasonal wetland	Disturbance	Germination
Lenz & Facelli 2003	*Orbea variegata*	Perennial forb	Shrubland	Natural opening	Floral bud number
Levine 2001	*Plantago major* *Cirsium arvense* *Agrostis stolonifera*	Perennial forb Perennial forb Perennial grass	Riparian vegetation	Vegetation removal	Establishment fraction
Mazia *et al.* 2001	*Gleditsia triacanthos* *Prosopis caldenia*	Tree Tree	Grassland	Disturbance	Establishment fraction
Meekins & McCarthy 2001	*Alliaria petiolata*	Biennial forb	Forest	Edge vs. interior habitats	Establishment fraction
			Forest	Litter removal	Establishment fraction
Parker 2001	*Cytisis scoparius*	Shrub	Grassland	Cryptogam removal	Establishment fraction
Peart 1989a,b	*Anthoxanthum odoratum*	Perennial grass	Annual grassland *Deschempsia* grassland *Holcos* grassland	Herbicide	Number establishing
	Rytidosperma pilosum	Perennial grass	Annual grassland	Herbicide	Number establishing
	Holcos lanatus	Perennial grass	Annual grassland *Anthoxanthum* grassland	Herbicide	Number establishing
	Vulpia bromoides	Annual grass	*Anthoxanthum* grassland	Herbicide	Number establishing
Pierson & Mack 1990	*Bromus tectorum*	Annual grass	Forest understory	Clipping	Survivorship, biomass
			Forest canopy	Forest clear cut	Survivorship, biomass

Table 1 Continued

Citation	Exotic invader	Growth form	Habitat	Manipulation type	Response variable
Scherber *et al.* 2003	*Senecio inequidens*	Perennial forb	Grassland	Disturbance	Number of flower heads
Seabloom *et al.* 2003	*Bromus hordeaceus*	Annual grass	Grassland	Assembled communities	Fecundity
	Bromus madritensis	Annual grass			
	Hordeum murinum	Annual grass			
Siemann & Rogers 2003	*Sapium sebiferum*	Tree	Grassland	Aboveground pull-back	Biomass
Thebaud *et al.* 1996	*Conyza canadensis*	Annual forb	Old field	Vegetation removal	Stem diameter (mm)
	Conyza sumatrensis	Annual forb			
(b) Species diversity studies					
Dukes 2002	*Centaurea solstitialis*	Annual forb	Grassland mesocosm	Assembled communities	Biomass
Kennedy *et al.* 2002	*Multiple herbaceous*	Multiple	Grassland	Assembled communities	Number establishing, size
Knops *et al.* 1999	*Digitaria ischaemum*	Annual grass	Grassland	Assembled communities	Biomass
	Crepis tectorum	Annual forb			
Levine 2001	*Plantago major*	Perennial forb	Riparian vegetation	Assembled communities	Establishment fraction, biomass
	Cirsium arvense	Perennial forb			
	Agrostis stolonifera	Perennial grass			
Lindig-Cisneros & Zedler 2002	*Phalaris arundinacea*	Perennial grass	Wetland mesocosm	Assembled communities	Establishment fraction
Lyons & Schwartz 2001	*Lollium multiflorum*	Annual grass	Grassland	Diversity reduction experiment	Establishment fraction
Prieur-Richard *et al.* 2000	*Conyza bonariensis*	Annual forb	Grassland	Assembled communities	Fecundity
	Conyza canadensis	Annual forb			
(c) Herbivory studies					
Bossard 1991	*Cytisus scoparius*	Shrub	Grassland Woodland	Cage (mammals)	Fecundity
Case & Crawley 2000	*Conyza sumatrensis*	Annual forb	Grassland	Cage (mammals)	Number establishing
D'Antonio 1993	*Carpobrotus edulis*	Perennial forb	Backdune Grassland Coastal scrub	Cage (mammals)	Survivorship
Erneberg 1999	*Anthemis cotula*	Annual forb	Grassland	Spray (insects)	Biomass
Lambrinos 2002	*Cortaderia jubata*	Perennial grass	Backdune Grassland Coastal scrub	Cage (mammals)	Survivorship
	Cortaderia selloana	Perennial grass	Backdune Grassland Coastal scrub	Cage (mammals)	Survivorship
Peart 1989b	*Anthaxanthum odoratum*	Perennial grass	Grassland	Cage (mammals)	Number establishing, plant size
Pierson & Mack 1990	*Bromus tectorum*	Annual grass	Forest	Cage (mammals)	Survivorship
Rachich & Reader 1999	*Lythrum salicaria*	Perennial forb	Riparian wetland	Cage and spray (mammals and insects)	Inflorescence mass
Rice 1987	*Erodium botrys*	Annual forb	Grassland	Cage (mammals)	Survivorship
	Erodium brachycarpum	Annual forb	Grassland	Cage (mammals)	Survivorship
Scherber *et al.* 2003	*Senecio inaequidens*	Perennial forb	Grassland	Cage (mammals)	Fecundity
Schierenbeck *et al.* 1994	*Lonicera japonica*	Shrub	Forest	Cage and spray (mammals and insects)	Net assimilation
Vilà & D'Antonio 1998	*Carpobrotus edulis*	Perennial forb	Backdune Coastal scrub	Cage (mammals)	Survivorship, biomass
(d) Soil fungal community studies					
Beckstead & Parker 2003	*Ammophila arenaria*	Perennial grass	Coastal dune	Soil sterilization in greenhouse experiment	Shoot biomass
Bray *et al.* 2003	*Ardisia crenata*	Shrub	Forest	Field inoculum in greenhouse experiment	Growth rate

Table 1 Continued

| Citation	Exotic invader	Growth form	Habitat	Manipulation type	Response variable
Callaway et al. 2001	Centaurea melitensis	Annual forb	Grassland	Field inoculum in greenhouse experiments, grown with various neighbours	Biomass
Callaway et al. 2003	Centaurea melitensis Avena barbata	Annual forb Annual grass	Grassland	Field inoculum in greenhouse experiments, grown with various neighbours	Biomass
Callaway et al. 2004a	Centaurea maculosa	Perennial forb	Grassland	Field inoculum in greenhouse experiments	Biomass
Callaway et al. 2004b	Centaurea maculosa	Perennial forb	Grassland	Fungicide in common garden, grown with various neighbours	Biomass
Marler et al. 1999	Centaurea maculosa	Perennial forb	Grassland	Field inoculum in greenhouse experiments, grown with various neighbours	Biomass
Reinhart et al. 2003	Prunus serotina	Tree	Forest	Field inoculum in greenhouse experiments, grown with various neighbours	Biomass
Yoshida & Allen 2001	Bromus madrisensis	Annual grass	Coastal scrub	Field inoculum in greenhouse experiments	Number of leaves
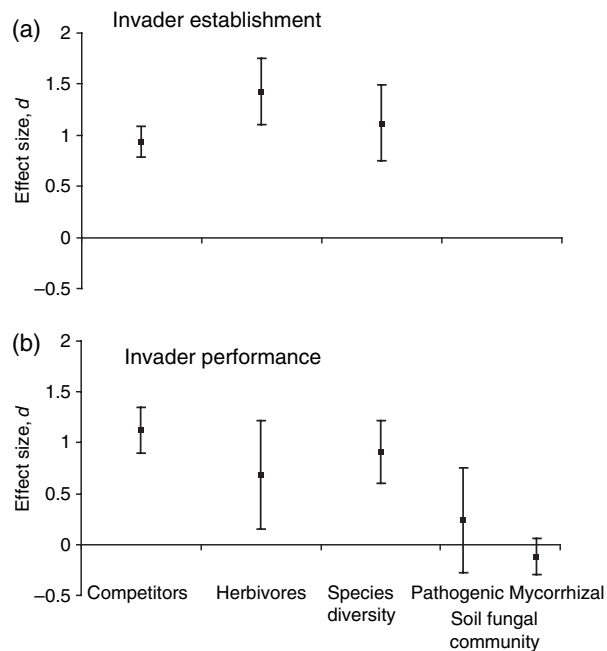
Figure 2 Effects of resident competitors, herbivores, species diversity and soil fungal communities on invader (a) establishment and (b) individual performance variables. Points show means bracketed by 95% confidence intervals. Effects of the soil fungal community are presented for individual performance variables only because too few studies examined establishment.

grassland. Second, the persistence of native species also requires seedling recruitment into intact communities. Thus, as long as invaders have enough arriving seed to overcome demographic stochasticity, and are equal if not better than resident species as seedling competitors, they will successfully invade. Indeed, a recent review of competition experiments between exotic and native species confirms that exotic species are often better competitors than natives (Vilà & Weiner 2004).

Finally, in our meta-analysis, the invaders suppressed by intact vegetation to zero establishment were often those barely establishing when the resident vegetation was removed. These invaders are thus primarily constrained by demographic or physiological limitations. For example, Jesson et al. (2000) found that when 40 seeds of four different exotic grasses were added to plots in forest clearings, none established, suggesting strong biotic resistance. However, when the surrounding vegetation was removed, establishment only increased to an average of 0.2 to 0.6 seedlings of the forty added. Amsberry et al. (2000) also showed biotic resistance excluding an invader at the edge of its physiological capacities. In the absence of resident plant competition, Phragmites australis invaded high marsh elevations more readily than the more saline and flooded low marsh elevations. Although the absolute effect of competition was greatest at the high marsh locations, only at the low marsh elevations, where Phragmites was barely surviving in the absence of competition, was it completely excluded by surrounding vegetation.

In sum, our review supports the commonly held notion that competition is a major contributor to biotic resistance. However, we found little evidence that it provides a complete barrier against invasion.

RESIDENT SPECIES DIVERSITY

The effect of species diversity on the invasion of exotic species is one of the classic problems in ecology, and has consequently received considerable attention (Levine *et al.* 2002). The most common mechanism involves more diverse communities better using available resources, leaving less resources for potential invaders. This mechanism could involve a diverse guild of herbivores or soil pathogens more effectively suppressing invaders, but nearly all of the research examines effects of competitor diversity on invasion success (Levine *et al.* 2002).

The studies examining biotic resistance achieved through a diversity of competitors (Table 1, species diversity studies) were qualitatively different than those we review regarding the effects of competition or herbivory. While nearly all of the latter studies examined the effects of experimentally removing competitors or herbivores, the diversity studies experimentally created a gradient in diversity in an otherwise homogeneous setting. The protocol differed slightly among studies but generally began by establishing a pool of residents from the local habitat. For each replicate plot within a given diversity level, the investigator randomly assigned species from the pool, so that there was no correlation between species composition and diversity. After some period of community establishment, the investigator added invader propagules, or invaders from the surrounding community were allowed to naturally colonize the plots. This was the basic methodology employed by all studies in our review except Lyons & Schwartz (2001), who created their diversity gradient by removing different numbers of resident species from plots. Because their study experimentally removed biotic resistance achieved through high diversity, it is more similar in approach to the competition and herbivory studies.

Meta-analysis of species diversity effects on invasion

Nearly all studies in our meta-analysis examined invader performance as a continuous response to experimentally imposed variation in diversity. Nonetheless, in order to use the same effect size as used in other sections of our review, we calculated d for each study from the mean and standard deviation of invader success in the maximum and minimum diversity levels. Although studies differed in the range of diversity imposed, the range had no influence on the effect size ($R^2 = 0.001$, $P > 0.95$). Overall, we found only seven citations containing 13 experiments that matched our general criteria (Table 1, species diversity studies). Many of the studies in this general research area were not included in our meta-analysis because they examined the colonization of native species or were not conducted in field settings. Although we do not review studies of functional group

diversity, they tend to show similar results (Dukes 2002; Fargione *et al.* 2003).

Our meta-analysis showed that resident species diversity had a significant negative effect on both invader establishment and individual performance (Fig. 2). For example, Knops *et al.* (1999) found that the biomass of *Crepis tectorum* was four times greater in communities that had been planted with just one resident species vs. those planted with 24. Even though the d values in Figure 2 show similar effects of diversity as competition and herbivory, these numbers are not comparable because of methodological differences. The competition and herbivory studies contained sources of natural variation largely absent in the more controlled diversity studies, meaning larger differences between control and experimental groups were required to produce the same d. This was borne out in an analysis of the effect sizes. Looking specifically at the subset of studies measuring the fractional establishment of invader propagules (all response variables are on the same scale), the difference between control and experimental treatments was 74% greater in competition studies than diversity studies. However, the pooled standard deviation was 18% greater in the competition studies, reducing the difference in d's between the two sources of resistance.

Can high diversity cause invasions to fail?

Because only one study, Lyons & Schwartz (2001), added an invader not present in the surrounding habitat, our meta-analysis was inappropriate for testing whether diversity ever repels invaders. Still, Lyons & Schwartz (2001) found that *Lolium multiflorum* invaded the most diverse plots in their experiment to a significant extent. Other evidence also supports the assertion that diversity does not categorically prevent invasions. First, the most diverse natural communities contain the greatest number of exotic species (Stohlgren *et al.* 1999; Levine *et al.* 2002), showing that diverse communities are clearly susceptible to the invasion. However, it is still possible that in the absence of the diversity effect, many more invaders would be found in these communities. We can bolster this evidence by examining correlative studies that measure the abundance of individual invader species in relation to resident species diversity. Species completely repelled by a diversity of residents would be absent in species-rich areas while present in species-poor locations. By contrast, existing evidence suggests that species-rich locations are not only invaded, but contain the greatest number of invader individuals (Robinson *et al.* 1995; Wiser *et al.* 1998; Levine 2000). The latter result is most likely related to ecological factors spatially covarying with diversity across the landscape. Nonetheless, for such processes to override any negative effect of diversity, that diversity effect cannot be strong, let alone absolute. Thus resident species

diversity, even if it reduces invasion success, is not strong enough to categorically prevent invasion.

HERBIVORY BY RESIDENT ANIMALS

The extent to which herbivores control the abundance of plant populations is a long-standing problem in ecology (Hairston *et al.* 1960). In the plant invasions literature, the role of herbivory is often tested within the framework of the enemies release hypothesis (Keane & Crawley 2002). If invaders escape specialist predators, herbivory by resident species in their new habitat might be a weak source of biotic resistance. To quantify the role of herbivory in constraining invasions, we searched for studies testing the impact of native herbivores in natural ecosystems on the establishment and performance of exotic invaders (Table 1, herbivory studies). These strict criteria naturally excluded most of the vast literature on plant-herbivore interactions, leaving us with 12 studies comprising 27 individual experiments. The most common approach involved transplanting invader seedlings into field plots, half of which were open to herbivores and the other half protected by cages and/or insecticide (Table 1, herbivory studies). Most studies involved mammalian herbivores, or the combined effects of mammalian and insect herbivores; two studies examined the effects of insect herbivores only, and one study focused on birds as seed predators.

Our meta-analysis (Fig. 2) showed that herbivory has a significant and strong negative effect on invader establishment ($d = 1.42$) and individual performance ($d = 0.68$). For example, D'Antonio (1993) found that caging out mammals increased exotic iceplant seedling survivorship from 8 to 40% in open backdune habitats, yielding a d of 1.59 after incorporating the variability. Only three of the 27 experiments found higher invader performance with herbivory. There was no difference between the herbivory effects of mammals compared to insects or birds on plant performance, but the response differed significantly by invader life form ($Q = 1.93$, d.f. $= 2$, $P < 0.001$): herbaceous plants were more negatively affected ($d = 2.48$) than woody plants ($d = 0.02$). This comparison could be not be made for establishment variables because of an absence of woody plant studies.

Although herbivory had a strong negative effect on survivorship and individual plant performance, as pointed out by Maron & Vilà (2001), whether this was strong enough to reverse the course of an invasion is difficult to infer. In addition, even when herbivory negatively affects an invader population, its relative abundance increases if herbivory impacts other species to a greater extent, an outcome discussed by Scherber *et al.* (2003).

Of the 27 experiments included in our meta-analyses, eight showed that herbivory could reduce invader establishment or fecundity to zero. Six of these (D'Antonio 1993; Lambrinos 2002), however, came from the same coastal California habitat. Although a small group of studies, all of them examined the effects of mammalian herbivores on perennial herbaceous invaders. This is consistent with experimental work showing that vertebrate herbivores have stronger negative effects on plant performance than arthropods, probably because of the ability of vertebrate herbivores to consume whole plants and plant parts (Hulme 1994, 1996). It also consistent with the observation that herbivory is more destructive to perennials than annuals (Vesk *et al.* 2004) because perennials have a longer period of vulnerability prior to reproduction. Despite the categorical failure of invaders observed in these experiments, in every one, the invader had already invaded the recipient community to some extent and thus resistance was overcome.

Do resident herbivores cause invasions to fail?

As with competition and species diversity, we find it unlikely that herbivory enables communities to completely resist exotic invasions. First, herbivory has very rarely caused the extinction of native species, even under intense grazing by introduced livestock. In a review of grazing refuges, Milchunas & Noy-Meir (2002) found only two cases where the introduction of an exotic vertebrate herbivore resulted in the restriction of rare plant species to grazer-free locations. O'Connor (1991) showed that severe grazing in conjunction with drought could cause local elimination of perennial grasses, but this was transient in most cases. Although the lack of grazer-induced extinctions may reflect a paucity of long-term data, the nature of herbivory may prevent the process from completely excluding species. As Maron & Vilà (2001) argue, to repel invader establishment or cause extinction, herbivores must consume a high proportion of a species occurring at very low abundance. This behaviour is only likely to occur with the most specialized herbivores, yet exotic species are often argued to escape these species. This reasoning suggests an important contrast between competition and herbivory as sources of biotic resistance in the establishment phase: competition is likely to be more severe for seedlings than adult plants, because of size asymmetry. The effects of herbivory, in contrast, may be less severe for small plants, especially those at low density.

SOIL FUNGAL COMMUNITIES

Recent work suggests that soil fungal communities, including both pathogenic and mycorrhizal groups, may play a crucial role in determining patterns of plant abundance and invasion success (Klironomos 2002; Callaway *et al.* 2004b). Following the enemies release

hypothesis, we might expect invasive plants to possess an advantage in their exotic range because they have escaped from specialist fungal pathogens, yet benefit from generalist mycorrhizal mutualists (van der Putten 2002). However, recent work has shown that mycorrhizal fungi may exert a range of effects from mutualistic to parasitic in nature (Klironomos 2003) that could either benefit or harm exotic species.

A growing number of experiments have quantified the performance of exotic plants grown with and without soil fungal communities. The most common methodology involved soil sterilization through either autoclaving or gamma radiation. In some cases it was the entire soil that was sterilized, while in others it was soil inoculum, but all approaches incorporated a control for the nutrient flush that occurs with sterilization. Still, because of limitations associated with sterilization, authors often noted that the identity of the soil community components being manipulated was unclear. Other studies in the meta-analysis used fungicide to reduce or eliminate the fungal community around target seedlings in common garden experiments (Callaway et al. 2004a). Because the experimental manipulations often required careful controls, eight of nine studies in our fungal community meta-analysis were performed in greenhouses (Table 1, soil fungal community studies). We did not compare the effects of the fungal community to that of competition or herbivory because of this methodological difference. Almost all studies we found examined performance measures (biomass, number of leaves and growth) rather than establishment, and thus our meta-analysis was conducted on the former response variables only.

An initial meta-analysis showed no significant effect of soil biota on invasive plant seedlings [$d = -0.06 \pm 0.17$ (95% CI)]. However, this analysis ignored the fact that different groups of soil fungi would be expected a priori to have opposite effects on colonizing invaders. Soil pathogens should be expected to harm recruiting invasive plants, while mycorrhizal fungi should have a continuum of effects ranging between beneficial mutualism to harmful parasitism (Klironomos 2003). For this reason, we divided the meta-analysis of soil fungal communities into two separate analyses.

Effects of mycorrhizal fungi

In a meta-analysis of 18 experiments from seven studies, mycorrhizal fungi did not significantly effect invasive seedling performance (Fig. 2b). However, rather than reflecting a generally weak effect, this result emerged because native soil fungal communities sometimes increased and sometimes decreased invader biomass. This is evidenced by a $d > 1$ if we averaged the absolute value of the individual effects. For example, a series of studies on

Centaurea spp. found that intact soil fungal communities decreased Centaurea biomass when it was grown alone or with a conspecific, yet increased Centaurea biomass when grown with a native heterospecific (Marler et al. 1999; Callaway et al. 2001; Callaway et al. 2003; Callaway et al. 2004a,b). In the other studies of the analysis, where invaders were grown alone in pot experiments, native fungal communities increased plant biomass (Yoshida & Allen 2001; Bray et al. 2003).

Because the work is conducted in controlled environments, our results concerning mycorrhizal fungi are challenging to interpret with respect to biotic resistance in the field. For example, in the case of the Centaurea studies, it was difficult to determine which greenhouse treatment would best apply to the natural conditions Centaurea invaders experience. Although not the intention of these studies, growing Centaurea alone or near a conspecific could be used to predict fungal effects on an invasion into disturbed locations. Growing Centaurea near a native heterospecific could apply to invasions of already occupied habitats. More generally, it remains unclear whether the differences in biomass reported in the studies of Table 1 (soil fungal community studies) would still be significant under the influence of other community level factors, such as competition.

Fungal pathogens

Soil fungal pathogens also failed to significantly affect invasive plant seedlings (Fig. 2b), although we found only two studies with three experiments for this meta-analysis. When we included studies of foliar fungal pathogens (Siemann & Rogers 2003; DeWalt et al. 2004), raising the total number of experiments to seven, the result was the same [$d = 0.11 \pm 0.26$ (95% CI)]. As with mycorrhizal fungi, the effect of fungal pathogens in individual cases is strong, but on average, positive and negative effects cancel out. For an example of negative effects, Beckstead & Parker (2003) found in a greenhouse study that the germination, survival, and biomass of the exotic dune grass, Ammophila increased with soil sterilization. Soil fungal pathogens were identified with DNA markers in non-sterilized controls but were not found in sterilized soil, implying a role for pathogens in driving Ammophila performance. Still, they noted that the invader germinated and grew well with the intact pathogen community, so pathogens are not precluding species invasion. Reinhart et al. (2003) found that Prunus serotina attained higher biomass on control soil than sterilized soil, implying that the soil pathogen effect was so weak that it was overrode by mutualists.

In sum, unlike the other sources of biotic resistance we have reviewed, pathogenic or mycorrhizal soil fungal communities had no significant effect on invader performance.

This reflects the strong but contrasting effects that these species can have on invader performance, the species-specific nature of the effects, and the relatively few studies in this research area. An important next step is to examine the importance of these interactions in controlling invasions in natural communities.

DISCUSSION

Our meta-analysis confirms that across the broad plant invasions literature, resident competitors, competitor diversity and herbivores significantly reduce the establishment and performance of colonizing invaders. More surprisingly, however, our review raises important questions about which ecological interactions contribute most to biotic resistance, the overall effectiveness of resistance, and where in the invasion process it is most important.

Which factors contribute most to biotic resistance?

Our review questions the overriding emphasis on competition as the primary source of biotic resistance. We found no significant difference between the reduction in invader establishment and individual performance caused by competition vs. herbivory (Fig. 2) (for establishment, $Q = 0.212$, d.f. $= 1$, $P > 0.10$; for individual performance, $Q = 0.244$, d.f. $= 1$, $P > 0.50$). In fact, of the six studies in our meta-analysis which examined the individual and combined effects of competition and herbivory on colonizing invaders, four found strong effects of herbivores and weaker effects of competition (Bossard 1991; D'Antonio 1993; Lambrinos 2002; Scherber *et al.* 2003), one found both to be strong (Erneberg 1999) and one found stronger effects of competition (Thebaud *et al.* 1996). Even though competition may be no stronger than herbivory when experimentally evaluated, this must be tempered with the greater number of studies examining competition (23) vs. herbivory (13). Considering that investigators are unlikely to manipulate a factor unless motivated by observation, this disparity may reflect the prevalence of these interactions in nature.

Another important finding, though preliminary, was that the soil fungal community, and the mycorrhizal community specifically, did not in general facilitate invasions. This conflicts with hypotheses that exotic invaders benefit from reduced loads of specialist fungal pathogens, while benefiting from generalist mycorrhizal mutualists (van der Putten 2002). Our results better support the emerging view that depending on the identity of the plant and fungal species, mycorrhizal fungi can be either mutualistic or parasitic (Klironomos 2003).

The intimate relationship between the enemies release hypothesis and our understanding of community resistance to biological invasion is underappreciated. Nonetheless, the unsupported expectations of weak herbivory and beneficial soil fungal communities in our review are both predictions of the enemies release hypothesis. Our results are thus consistent with the equivocal evidence for this hypothesis in recent research (Maron & Vilà 2001; Agrawal & Kotanen 2003; Beckstead & Parker 2003; Colautti *et al.* 2004), and call into question the use of this hypothesis to infer resident species controls over invasion success.

Can biotic resistance repel invasions?

As discussed at several points in our review, the available literature does not permit a meta-analytical test of whether species interactions cause plant invasions to fail. Still, we found no studies demonstrating that specific invaders were absent from communities because of biotic resistance. In addition, we presented considerable evidence that biotic resistance was unlikely to completely prevent invasions. The invader species most effectively repelled by plant competition were barely able to physiologically survive the habitat, suggesting a more important role for abiotic factors in regulating invasions. The most diverse communities tended to have the greatest density of individual invader plants. Herbivory seemed unlikely to drive exotic species to negative growth rates when rare, if even severe grazing by livestock was unlikely to do so for rare native species. In the soil fungal community manipulations, positive and negative effects cancelled out across studies, even when conducted with the same invader species.

Although much of the current evidence is indirect, whether biotic resistance repels invasions could be tested experimentally. Introducing exotic invaders to habitats that do not contain them is unethical, though such experiments can be conducted at a very local scale (10s of meters) where adjacent habitats differ in their exotic flora. The question then becomes what processes are responsible for the restricted distribution of exotic plants. Where seed exchange between habitats is known to occur, the investigator could use the experimental protocols outlined in our review to ask whether biotic resistance is responsible for invader distribution patterns. Similar experiments could be conducted just ahead of an expanding invader population.

If we suspect that biotic resistance is unlikely to explain the absence of invaders from a particular habitat, then what is? Clearly, adjacent communities differ markedly in the number of exotic species they contain (Knops *et al.* 1995). We hypothesize that the absence of most invaders in communities, even when present in surrounding systems, results from a physiological inability to tolerate the habitat. At broad scales, we know this to be true. Within the habitats of California, coastal and foothill grasslands contain the greatest number of invaders, while the harsher desert,

chaparral, and alpine environments contain the least (Knops *et al.* 1995; Randall *et al.* 1998).

If biotic resistance does not deterministically drive colonizing invaders to extinction, it may still cause invasions to fail if the invaders have a limited number of arriving seeds (D'Antonio *et al.* 2001, Tilman, 2004). For example, if resident plant competition can reduce the probability of establishment for a given invader to 0.001, then upwards of 1000 seeds will likely be required to establish an individual. Moreover, those first individuals must also overcome demographic and environmental stochasticity to establish a population. Thus, if a community is isolated from invader sources, and only a few seeds arrive per year, biotic resistance may effectively repel invasion for many decades or centuries. Although in theory the invader would eventually colonize, limited seed arrival coupled with biotic resistance could dramatically alter the course of an invasion. More generally, interactions between different sources of biotic resistance and between biotic and abiotic factors have the potential to more strongly inhibit invasions than each ecological process in isolation.

When in the invasion process is biotic resistance most effective?

The invasion process can be envisioned as proceeding through a series of stages (Fig. 1): introduction, where propagules first enter a system; establishment, where those propagules become a reproducing population; spread, where that population moves across the landscape, and impact, where the invader alters the ecosystem. For biotic resistance to act as a barrier to invasion, as suggested by Elton, it must operate most strongly at the establishment phase (Location A in Fig. 1). Our review, however, suggests that ecological interactions are unlikely to repel invasions. The 'resistance' evaluated in our meta-analysis acts later in the invasion process, constraining spread and impact (Location B in Fig. 1). For example, although reducing invader establishment from 30 to 10% of arriving seed (as in Levine 2001) is unlikely to prevent invader establishment, it should affect population growth. More generally, we hypothesize that the consistent negative effects of competitors and herbivores on invader establishment and the occasionally strong effects of soil fungal communities are critical processes regulating invader population abundance, but not their initial colonization.

Recognizing that species interactions constrain the spread and impact of invaders rather than repel them from communities represents a different paradigm of biotic resistance. From a theoretical standpoint, resistance is not driving colonizing invaders to negative population growth rates. Rather, it is reducing their equilibrium abundance or slowing their rise to dominance. Even Elton (1958)

understood that when the species interactions failed to repel exotic species, they could still cause invaders to 'find a place for themselves without very much disturbance of other populations' (p. 148). In this context (and consistent with the militaristic terms in this research area), 'biotic containment' is a more appropriate than 'biotic resistance.'

What factors enable the coexistence of native species with exotic invaders?

If species interactions do not completely repel invaders, but rather, constrain their abundance within communities, new questions gain prominence. Among the most interesting is what factors allow native species to persist with invaders once the latter have established. This question is no different than what allows species to coexist more generally, yet it has received almost no attention in the invasions literature. Perhaps this reflects an assumption that spread and impact are inevitable outcomes once invaders establish, yet only a small fraction of invaders ever reach high abundance or exert large impacts (Simberloff 1981; Williamson & Fitter 1996). Moreover, many communities, such as grasslands in California (Levine & Rees 2004), have been exotic-dominated for over a 100 years, but still contain numerous native species. Understanding the ecological dynamics enabling native species to persist in these communities is critical to preserving their diversity.

ACKNOWLEDGEMENTS

REFERENCES

Agrawal, A.A. & Kotanen, P.M. (2003). Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecol. Lett.*, 6, 712–715.

Amsberry, L., Baker, M.A., Ewanchuk, P.J. & Bertness, M.D. (2000). Clonal integration and the expansion of *Phragmites australis*. *Ecol. Appl.*, 10, 1110–1118.

Baker, H.G. (1965). Characteristics and modes of origin of weeds. In: *The Genetics of Colonizing Species* (eds Baker, H. G. & Stebbins, G. L.). Academic Press, London, UK, pp. 147–172.

Bakker, J. & Wilson S. (2001). Competitive abilities of introduced and native grasses. *Plant Ecol.*, 157, 117–125.

Barger, N.N., D'Antonio, C.M., Ghneim, T. & Cuevas, E. (2003). Constraints to colonization and growth of the African grass, *Melinus minutiflora*, in a Venezuelan savanna. *Plant Ecol.*, 167, 31–43.

Beckstead, J. & Parker, I.M. (2003). Invasiveness of *Ammophila arenaria*: release from soil-borne pathogens?. *Ecology*, 84, 2824–2831.

Bellingham, P.J., Coomes, D.A. (2003). Grazing and community structure as determinants of invasion success by Scotch broom in a New Zealand montane shrubland. *Div. Distrib.*, 9, 19–28.

Bossard C.C. (1991). The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. *Am. Midland Nat.*, 126, 1–13.

Bray, S.R., Kitajima, K. & Sylvia, D.M. (2003). Mycorrhizae differentially alter growth, physiology, and competitive ability of an invasive shrub. *Ecol. Appl.*, 13, 565–574.

Callaway, R.M., Newingham, B., Zabinski, C.A. & Mahall, B.E. (2001). Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbours. *Ecol. Lett.*, 4, 429–433.

Callaway, R.M., Mahall, B.E., Wicks, C., Pankey, J. & Zabinski, C. (2003). Soil fungi and the effects of an invasive forb on grasses: neighbor identity matters. *Ecology*, 84, 129–135.

Callaway, R.M., Thelen, G.C., Barth, S., Ramsey, P.W. & Gannon, J.E. (2004a). Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. *Ecology*, 85, 1062–1071.

Callaway, R.M., Thelen, G.C., Rodriguez, A. & Holben, W.E. (2004b). Soil biota and exotic plant invasion. *Nature*, 427, 731–733.

Case, T.J. (1990). Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl Acad. Sci.*, 87, 9610–9614.

Case, C. & Crawley M. (2000). Effect of interspecific competition and herbivory on the recruitment of an invasive alien plant: *Conyza sumatrensis*. *Biol. Invasions*, 2, 103–110.

Cohen, J. (1969). *Statistical Power Analysis for the Behavioral Sciences*. Academic Press, New York, NY.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & Mac Isaac, H.J. (2004). Is invasion success explained by the enemies release hypothesis? *Ecol. Lett.*, 7, 721–733.

Connell, J.H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.*, 111, 1119–1144.

Corbin J.D. & D'Antonio C.M. (2004). Can carbon addition increase competitiveness of native grasses? A case study from California. *Restoration Ecol.*, 12, 36–43.

Crawley, M.J. (1987). What makes a community invasible? In: *Colonization, Succession, and Stability* (eds Crawley, M.J. & Edwards, P.J.). Blackwell Scientific Publications, Oxford, UK, pp. 429–451.

D'Antonio, C.M. (1993). Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology*, 74, 83–95.

D'Antonio, C.M. & Mack, M. (2001). Exotic grasses potentially slow invasion of an N-fixing tree into a Hawaiian woodland. *Biol. Invasions*, 3, 69–73.

D'Antonio, C.M., Levine, J.M. & Thomson, M. (2001). Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *J. Mediterr. Ecol.*, 27, 233–245.

Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.

DeWalt, S.J., Denslow, J.S., & Ickes, K. (2004). Natural-enemy release facilitates habitat expansion of an invasive shrub, *Clidemia hirta*. *Ecology*, 85, 471–483.

Drake, J.A., Mooney, H.A., DiCastri, F., Groves, R.H, Kruger, F.J., Rejmanek, M. & Williamson, M. (1989). *Biological Invasions: A Global Perspective*. John Wiley, Chichester, UK.

Drake, J.A., Huxel, G.R. & Hewitt, C.L. (1996). Microcosms as models for generating and testing community theory. *Ecology*, 77, 670–677.

Dukes, J.S. (2002). Species composition and diversity affect grassland susceptibility and response to invasion. *Ecol. Appl.*, 12, 602–617.

Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.

Erneberg M. (1999). Effects of Herbivory and Competition on an Introduced Plant in Decline. *Oecologia*, 118, 203–209.

Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl Acad. Sci.*, 100, 8916–8920.

Goldberg, D.E. & Barton, A.M. (1992). Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.*, 139, 771–801.

Grieshop, M.J. & Nowierski, R.M. (2002). Selected factors affecting seedling recruitment of dalmation toadflax. *J. Range Manage.*, 55, 612–619.

Gurevitch, J. & Hedges, L.V. (1993). Meta-analysis: combining the results of independent experiments. In *Design and Analysis of Ecological Experiments* (eds Scheiner, S.M. & Gurevitch, J.). Chapman and Hall, New York, NY, pp. 378–398.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *Am. Nat.*, 94, 421–425.

Hamilton, J.G., Holzapfel, C., Mahall, B.E. (1999). Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia*, 121, 518–526.

Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London, UK.

Hobbs, R.J. & Mooney, H.A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology*, 72, 59–68.

Hulme, P.E. (1994). Seedling herbivory in grassland: relative impact of vertebrate and invertebrate herbivores. *J. Ecol.*, 82, 873–880.

Hulme, P.E. (1996). Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc, and rodent herbivory. *J. Ecol.*, 84, 43–51.

Hurlbert S.H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.*, 54, 187–211.

Jesson, L., Kelly, D. & Sparrow, A. (2000). The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. *N. Z. J. Bot.*, 38, 451–468.

Keane, R.M. & Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.*, 17, 164–170.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638.

Klironomos J.N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, 417, 67–71.

Klironomos, J.N. (2003). Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, 84, 2292–2301.

Knops, J.M.H., Griffin, J.R. & Royalty, A.C. (1995). Introduced and native plants of the Hastings reservation, central coastal California: a comparison. *Biol. Conser.*, 71, 115–123.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarsted, J. *et al.* (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.*, 2, 286–293.

Lambrinos, J.G. (2002). The variable invasive success of cortaderia species in a complex landscape. *Ecology*, 83, 518–529.

Lenz, T.I., Facelli, J.M. (2003). Shade facilitates and invasive stem succulent in a chenopod shrubland in South Australia. *Aust. Ecol.*, 28, 480–490.

Levine, J.M. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852–854.

Levine, J.M. (2001). Local interactions, dispersal, and native and exotic plant diversity along a California stream. *Oikos*, 95, 397–408.

Levine, J.M. & D'Antonio, C.M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.

Levine, J.M. & Rees, M. (2004). Effects of temporal variability on rare plant persistence in annual systems. *Am. Nat.*, 164, 350–363.

Levine, J.M., Kennedy, T. & Naeem, S. (2002). Neighborhood scale effects of species diversity on biological invasions and their relationship to community patterns. In: *Biodiversity and Ecosystem Functioning* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, UK, pp. 114–124.

Lindig-Cisneros, R. & Zedler, J.B. (2002). *Phalaris arundinacea* seedling establishment: effects of canopy complexity in fen, mesocosm, and restoration experiments. *Can. J. Bot.*, 80, 617–624.

Lonsdale, W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.

Lyons, K.G. & Schwartz, M.W. (2001). Rare species loss alters ecosystem function – invasion resistance. *Ecol. Lett.*, 4, 358–365.

Marler, M.J., Zabinski, C.A. & Callaway, R.M. (1999). Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology*, 80, 1180–1186.

Maron, J.L. & Vilà, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, 95, 361–373.

May R.M. & MacArthur, R.H. (1972). Niche overlap as a function of environmental variability. *Proc. Natl Acad. Sci.*, 69, 1109–1113.

Mazia, C.N., Chaneton, E.J., Ghersa, C.M. & Leon, R.J.C. (2001). Limits to tree species invasion in pampean grassland and forest plant communities. *Oecologia*, 128, 594–602.

Meekins, J.F. & McCarthy, B.C. (2001). Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecol. Appl.*, 11, 1136–1348.

Milchunas, D.G. & Noy-Meir, I. (2002). Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, 99, 113–130.

Moulton, M.P. & Pimm, S.L. (1983). The introduced Hawaiian avifauna: biogeographic evidence for competition. *Am. Nat.*, 121, 669–690.

O'Connor, T.G. (1991). Local extinction in perennial grasslands: a life-history approach. *Am. Nat.*, 137, 753–773.

Osenberg, C.W., Sarnelle, O. & Cooper, S.D. (1997). Effect size in ecological experiments: the application of biological models in meta-analysis. *Am. Nat.*, 150, 798–812.

Pacala, S.W. & Silander, J.A. (1985). Neighborhood models of plant population dynamics 1. Single-species models of annuals. *Am. Nat.*, 125, 385–411.

Parker, I.M. (2001). Safe site and seed limitation of *Cytisus scoparius* (Scotch broom): invasibility, disturbance, and the role of cryptogams in a glacial outwash prairie. *Biol. Invasions*, 3, 323–332.

Peart, D.R. (1989a). Species interactions in a successional grassland. II. Colonization of vegetated sites. *J. Ecol.*, 77, 252–266.

Peart, D.R. (1989b). Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds, and grazing on colonization. *J. Ecol.*, 77, 267–289.

Pierson, E.A. & Mack, R.N. (1990). The population biology of *Bromus tectorum* in forests: effect of disturbance, grazing, and litter on seedling establishment and reproduction. *Oecologia*, 84, 526–533.

Prieur-Richard, A. H., Lavorel, S., Grigulis, K. & DosSantos, A. (2000). Plant community diversity and invasibility by exotics: the example of *Conyza bonariensis* and *C. canadensis* invasion in Mediterranean annual old fields. *Ecol. Lett.*, 3, 412–422.

van der Putten, W.W. (2002). How to be invasive. *Nature*, 417, 32–33.

Rachich, J. & Reader, R.J. (1999). An experimental study of wetland invasibility by Purple Loosestrife (*Lythrum salicaria*). *Can. J. Bot. Revue Canadienne De Botanique*, 77, 1499–1503

Randall, J.M., Rejmanek, M. & Hunter, J.C. (1998). Characteristics of the exotic flora of California. *Fremontia* 26, 3–12.

Reinhart, K.O., Packer, A., van der Putten, W.H. & Clay, K. (2003). Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecol. Lett.*, 6, 1046–1050.

Rejmánek, M. (1989). Invasibility of plant communities. In: *Biological Invasions: A Global Perspective* (eds Drake, J.A., Mooney, H., DiCastri, F., Groves, R.H., Kruger, F.J., Rejmanek, M. & Williamson, M.). John Wiley, Chichester, UK, pp. 369–388.

Rejmánek, M. (1996). A theory of seed plant invasiveness: the first sketch. *Biol. Conser.* 78, 171–181.

Rejmánek, M. & Richardson, D.M. (1996). What attributes make some plant species more invasive? *Ecology* 77, 1655–1661.

Rice, K.J. (1987). Interaction of disturbance patch size and herbivory in *Erodium* colonization. *Ecology*, 68, 1113–1115.

Robinson, G.R., Quinn, J.F. & Stanton, M.L. (1995). Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology*, 76, 786–794.

Scherber, C., Crawley, M.J. & Porembski, S. (2003). The effects of herbivory and competition on the invasive annual plant *Senecio inaequidens* (Asteraceae). *Div. Distrib.*, 9, 415–426.

Schierenbeck, K.A., Mack, R.N. & Sharitz, R.R. (1994). Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, 75, 1661–1672.

Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl Acad. Sci.*, 100, 13384–13389.

Siemann, E. & Rogers, W.E. (2003). Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *J. Ecol.*, 91, 923–931.

Simberloff, D. (1981). Community effects of introduced species. In: *Biotic Crises in Ecological and Evolutionary Time* (ed. Nitecki, T.H.). Academic Press, New York, NY, pp. 53–81.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A. *et al.* (1999). Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.*, 69, 25–46.

Thebaud, C., Finzi, A., Affre, L., Debussche, M. & Escarre, J. (1996). Assessing why two introduced Conyza differ in their ability to invade Mediterranean old fields. *Ecology*, 77, 791–804.

Tilman, D. (2004). A stochastic theory of resource competition, community assembly and invasions. *PNAS*, in press.

Vesk, P.A., Leishman, M.R. & Westoby, M. (2004). Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *J. Appl. Ecol.*, 41, 22–31.

Vilà, M. & D'Antonio, C.M. (1998). Fitness of invasive *Carpobrotus* (Aizoaceae) hybrids in coastal California. *Ecoscience*, 5, 191–199.

Vilà, M. & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. *Oikos*, 105, 229–238.

Williamson, M. & Fitter, A. (1996). The varying success of invaders. *Ecology*, 77, 1661–1666.

Wiser, S.K., Allen, R.B., Clinton, P.W. & Platt, K.H. (1998). Community structure and forest invasion by an exotic herb over 23 years. *Ecology*, 79, 2071–2081.

Yoshida, L.C. & Allen, E.B. (2001). Response to ammonium and nitrate by a mycorrhizal annual invasive grass and native shrub in Southern California. *Am. J. Bot.*, 88, 1430–1436.