ABBIOTIC CONSTRAINTS ECLIPSE BIOTIC RESISTANCE IN DETERMINING INVASIBILITY ALONG EXPERIMENTAL VERNAL POOL GRADIENTS

FRITZ GERHARDT1,3 AND SHARON K. COLLINGE1,2

1 Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA
2 Environmental Studies Program, University of Colorado, Boulder, Colorado 80309 USA

Abstract. Effective management of invasive species requires that we understand the mechanisms determining community invasibility. Successful invaders must tolerate abiotic conditions and overcome resistance from native species in invaded habitats. Biotic resistance to invasions may reflect the diversity, abundance, or identity of species in a community. Few studies, however, have examined the relative importance of abiotic and biotic factors determining community invasibility. In a greenhouse experiment, we simulated the abiotic and biotic gradients typically found in vernal pools to better understand their impacts on invasibility. Specifically, we invaded plant communities differing in richness, identity, and abundance of native plants (the “plant neighborhood”) and depth of inundation to measure their effects on growth, reproduction, and survival of five exotic plant species.

Inundation reduced growth, reproduction, and survival of the five exotic species more than did plant neighborhood. Inundation reduced survival of three species and growth and reproduction of all five species. Neighboring plants reduced growth and reproduction of three species but generally did not affect survival. Brassica rapa, Centaurea solstitialis, and Vicia villosa all suffered high mortality due to inundation but were generally unaffected by neighboring plants. In contrast, Hordeum marinum and Lolium multiflorum, whose survival was unaffected by inundation, were more impacted by neighboring plants. However, the four measures describing plant neighborhood differed in their effects. Neighbor abundance impacted growth and reproduction more than did neighbor richness or identity, with growth and reproduction generally decreasing with increasing density and mass of neighbors.

Collectively, these results suggest that abiotic constraints play the dominant role in determining invasibility along vernal pool and similar gradients. By reducing survival, abiotic constraints allow only species with the appropriate morphological and physiological traits to invade. In contrast, biotic resistance reduces invasibility only in more benign environments and is best predicted by the abundance, rather than diversity, of neighbors. These results suggest that stressful environments are not likely to be invaded by most exotic species. However, species, such as H. marinum, that are able to invade these habitats require careful management, especially since these environments often harbor rare species and communities.

Key words: abiotic constraints; biotic resistance; competition; diversity; environmental gradient; exotic species; inundation; invasibility; vernal pools.

INTRODUCTION

Successful management of biological invasions requires that scientists, managers, and policymakers understand why some communities are more vulnerable to invasions than others. Ecologists have long debated the relative importance of abiotic and biotic mechanisms in determining community invasibility. Abiotic constraints hypotheses propose that exotic species are unable to tolerate the abiotic conditions found in less invaded communities (Fox and Fox 1986, Rejmánek 1989). In contrast, biotic resistance hypotheses propose that interactions with native biota (e.g., competitors or predators) exclude exotic species from less invaded communities (Elton 1958, Fox and Fox 1986, Crawley 1987, Rejmánek 1989, Ewel et al. 1999, Mack et al. 2000). Despite numerous theoretical and empirical studies, there is still no clear understanding of why some communities are more vulnerable to invasions than others.

Abiotic constraints allow only species with appropriate morphological and physiological traits to invade. Few studies, however, have taken a mechanistic approach to understanding how abiotic factors other than resource supply impact community invasibility. Correlational studies have shown that exotic species richness and abundance generally decrease with increasing abiotic stress (Forcella and Harvey 1983, D’Antonio 1993, King and Grace 2000, Harrison et al. 2001, Holway et al. 2002, Williamson and Harrison 2002, 2007).
Gerhardt and Collinge 2003, Seabloom and van der Valk 2003). Collectively, these studies suggest that invasions of exotic species are directly precluded by unfavorable abiotic conditions. Abiotic constraints may also indirectly affect invasions by altering the native communities encountered by invading species.

In contrast, biotic resistance to invasions has been relatively well studied. Exotic species may be excluded from less invaded communities by the lack of vacant niches, competition from more diverse species assemblages, the presence of predators and pathogens, or the lack of disturbances that reduce competition for resources (reviewed in Mack et al. [2000]). Much of the theoretical and empirical research on biotic resistance has focused on the role of species diversity in determining community invasibility (reviewed in Levine and D’Antonio [1999]). However, other measures of community structure and composition, such as interaction strength and species identity, have been studied less but may predict community invasibility better (Robinson and Dickerson 1984, Robinson and Edgemon 1988, D’Antonio 1993, Robinson et al. 1995, McGrady-Steed et al. 1997, Crawley et al. 1999, Lavoel et al. 1999).

Abiotic constraints and biotic resistance may also interact to determine community invasibility in one of two ways. First, the strength of biotic interactions may differ among sites along abiotic gradients. For example, interactions such as competition are thought to decrease in importance as abiotic stress increases (Grime 1973, 1979, but see Wiens 1977). Alternatively, abiotic stress and biotic interactions may determine invasibility at different sites along environmental gradients (Connell 1961, Gurevitch 1986, Hacker and Bertness 1999, Greiner La Peyre et al. 2001). However, few studies have examined the importance of interactions between abiotic and biotic factors in determining community invasibility. These few studies have shown that the outcomes of competitive interactions among native and exotic species depend on abiotic conditions (David 1999) and that abiotic factors and interactions with competitors and herbivores prevent invasions at different sites within a community (D’Antonio 1993).

There is a long history in ecology of using environmental gradients to study the relative importance of abiotic and biotic factors in determining community structure and composition (e.g., Connell 1961, Gurevitch 1986). Environmental gradients also provide a unique opportunity to study the abiotic and biotic mechanisms determining community invasibility for several reasons. First, environmental gradients are widespread in nature and are often correlated with patterns of invasion (e.g., light gradients at forest edges [Brothers and Spingarn 1992, Goldblum and Beatty 1999], soil gradients in serpentine grasslands [Harrison et al. 2001, Williamson and Harrison 2002], salinity gradients in salt marshes [Dethier and Hacker 2005], and inundation gradients in freshwater wetlands [Gerhardt and Collinge 2003, Seabloom and van der Valk 2003]). Although the specifics may differ, the general mechanisms determining invasibility are likely to be similar across these and other environmental gradients (D’Antonio 1993). Second, because the contrasting abiotic and biotic conditions often occur in close proximity, there are unlikely to be the enormous differences in propagule pressure that commonly occur among more distant sites (Crawley et al. 1996, Mack et al. 2000). Finally, the intensity and frequency of many natural and human disturbances do not differ across these gradients. Thus, environmental gradients provide a unique opportunity to study community invasibility across a range of abiotic and biotic conditions without the confounding effects of propagule pressure and disturbance history.

In this study, we used the environmental gradient found in vernal pools to examine the relative importance of the abiotic and biotic mechanisms determining community invasibility. Vernal pools are seasonal wetlands occurring in shallow depressions on slowly permeable or impermeable substrates. In the Central Valley of California, vernal pools typically flood during winter (December–March) and are dry during summer and autumn (April–November). Vernal pools are characterized by strong gradients in abiotic and biotic conditions. The abiotic gradient is most evident as differences in depth and duration of flooding, but other associated physical and chemical gradients include timing and predictability of flooding, winter soil temperatures, soil pH and salinity, and nutrient availability (Linhart 1976, Holland and Jain 1988, Holland and Dains 1990, Bliss and Zedler 1998, Gerhardt and Collinge 2003). Paralleling this abiotic gradient is a biotic gradient from barely invaded plant communities in the pools to highly invaded communities at the edges of the pools and in the surrounding grasslands (Holland and Jain 1981, 1988, Ferren et al. 1998, Pollak and Kan 1998, Bauder 2000, Gerhardt and Collinge 2003). Because these gradients occur across scales of only a few meters, there are not significant differences in propagule pressure (Gerhardt 2003). Furthermore, natural disturbances, such as wildfire, were not historically important in the Central Valley (Keeley 2002), and anthropogenic disturbances, such as discing and mowing, often occurred uniformly across both vernal pools and the surrounding grasslands (e.g., Biosystems Analysis 1994). Vernal pools typically support a unique and highly endemic flora and fauna (Stone 1990, Baskin 1994). However, 93–97% of the vernal pools in California have been lost to agricultural and urban development. Thus, remaining vernal pool habitats are a high priority for conservation.

In this study, we used a greenhouse experiment simulating the environmental gradient found in vernal pools to better understand the abiotic and biotic mechanisms determining community invasibility and the implications for conservation and management of natural communities. Specifically, we invaded plant communities differing in richness, identity, and abun-
dance of native plants and depth of inundation to measure the effects of these abiotic and biotic factors on the growth, reproduction, and survival of five exotic plant species. This experiment allowed us to address five questions: (1) What are the direct effects of abiotic constraints and biotic resistance on community invasibility? (2) What are the indirect effects of abiotic constraints, as mediated by biotic resistance, on invasibility? (3) Do abiotic constraints and biotic resistance interact to determine invasibility? (4) What components of community structure and composition best predict biotic resistance to invasions? (5) Which life history stages (e.g., growth, reproduction, or survival) are impacted most by abiotic constraints and biotic resistance? By examining multiple species representing different taxonomic and functional groups, we were able to make general inferences about community invasibility, rather than ones specific to a single species.

**METHODS**

To quantify the effects of inundation and interactions with neighbors on exotic plant performance, we used a full factorial design in which water depth and different combinations of native species were the independent factors. Five exotic and three native species, representing multiple taxonomic and functional groups, were used in this experiment (Table 1). All species, except *L. conjugens*, which is a federally listed endangered species, commonly occur in the Central Valley. We used these particular species because they represented the range of distributions observed in the field and because they were sufficiently abundant to provide seeds for this experiment. Because no native species were widespread or abundant in the surrounding grasslands, we were limited to using native species associated with vernal pools, although two of the three species (*D. danthonioides* and *L. chrysanthemoides*) were more abundant at the edges of the pools. In addition, few exotic species were more abundant in vernal pools than the surrounding grasslands (Gerhardt and Collinge 2003), so we included only one of these species in this experiment (*H. marinum*). To avoid sampling effects, we used each of the three native species in one-species treatments, all three combinations of two native species in the two-species treatments, and all three native species in the three-species treatment. Total density and mass of native plants were not controlled but were allowed to vary naturally in response to growing conditions. For each exotic species, multiple replicates of each neighbor treatment were placed at each of three water depths (+6, 0, and −7 cm).

The experiment was conducted in a climate-controlled greenhouse at the University of Colorado in Boulder, Colorado, USA. The greenhouse was configured to approximate winter climate conditions in the Central Valley. Temperatures were maintained initially at 15–21°C during the day and 2–10°C during the night but gradually increased as the season progressed. Light was maintained at ambient levels, since the greenhouse is located at a similar latitude to the northern Central Valley (40°01′ N and 38°15′ N, respectively). For this experiment, we used topsoil collected near Boulder, Colorado. We did not use vernal pool soils for logistical reasons as well as to avoid disturbing the pools. The greenhouse soil was generally coarser and had less organic matter and higher pH, nitrates, and soluble salts than vernal pool soils (Gerhardt 2003). However, both soils represented generally benign growing conditions without severe nutrient limitations, and these differences were unlikely to alter the results of this experiment. To simulate different water depths, we placed 15 plastic pots (9.2 × 9.2 × 8.9 cm) on bricks in plastic, rectangular tubs (27.5 × 53.5 × 27.5 cm) filled with 15 cm of water. Five pots each were placed so that the soil surface was 6 cm above, even with, and 7 cm below the water level (actual depths [means ± SD] were 6.2 ± 0.5 cm and 0.4 ± 0.5 cm above and 6.6 ± 0.6 cm below the water surface). Three pots, one at each depth, were assigned to each exotic species. Each pot contained a different neighbor richness treatment (one, two, or three species) and a different combination of native species, so that each tub contained three of the seven possible neighbor treatments for each exotic species. Locations of exotic species and water depths were randomly assigned in each tub.

### Table 1. Characteristics of five exotic and three native species used in a greenhouse experiment examining abiotic and biotic resistance to plant invasions.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Family</th>
<th>Functional group</th>
<th>Habitat</th>
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<tbody>
<tr>
<td><strong>Exotic species</strong></td>
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<tr>
<td><em>Brassica rapa</em></td>
<td>wild mustard</td>
<td>Brassicaceae</td>
<td>early annual forb</td>
<td>grasslands</td>
</tr>
<tr>
<td><em>Centaraea solstitialis</em></td>
<td>yellow starthistle</td>
<td>Asteraceae</td>
<td>late annual forb</td>
<td>grasslands</td>
</tr>
<tr>
<td><em>Hordeum marinum</em></td>
<td>wild barley</td>
<td>Poaceae</td>
<td>annual grass</td>
<td>deep pools</td>
</tr>
<tr>
<td><em>Lolium multiflorum</em></td>
<td>Italian ryegrass</td>
<td>Poaceae</td>
<td>annual grass</td>
<td>pool edges</td>
</tr>
<tr>
<td><em>Vicia villosa</em></td>
<td>hairy vetch</td>
<td>Fabaceae</td>
<td>annual legume</td>
<td>grasslands</td>
</tr>
<tr>
<td><strong>Native species</strong></td>
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<tr>
<td><em>Deschampsia danthonioides</em></td>
<td>purple hairgrass</td>
<td>Poaceae</td>
<td>annual grass</td>
<td>shallow pools</td>
</tr>
<tr>
<td><em>Lasthenia conjugens</em></td>
<td>Contra Costa goldfields</td>
<td>Asteraceae</td>
<td>early annual forb</td>
<td>deep pools</td>
</tr>
<tr>
<td><em>Layia chrysanthemoides</em></td>
<td>tidy tips</td>
<td>Asteraceae</td>
<td>early annual forb</td>
<td>shallow pools</td>
</tr>
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*Notes: Nomenclature and taxonomic and functional groups follow Hickman (1993); habitat information follows Gerhardt and Collinge (2003) and Gerhardt (2003).*
All seeds used in this experiment were collected in April–May and August 2002 at Travis Air Force Base (Travis AFB) in the Central Valley of California (site described in Gerhardt and Collinge [2003]) and were stored in paper envelopes under cool, dry conditions until planting. Because many of these species show genetic and phenotypic variation both within and among populations (Linhart and Baker 1973, Linhart 1974, 1976, 1988, Collinge et al. 2003), we collected seeds from across the vernal pools and surrounding grasslands at Travis AFB and pooled all seeds of each species before planting. During January 2003, we planted 3–5 seeds of one exotic species (hereafter, referred to as the “focal” plant or species) and 20–30 seeds of 1–3 native species (hereafter, referred to as the “neighboring” plants or species) in each pot. After 3–4 weeks, we thinned the focal plants so that only the individual growing nearest the center of the pot remained. Neighboring plants were not thinned or supplemented, and density and mass were allowed to vary naturally in response to growing conditions. All pots were placed at their assigned water depths 5 weeks after planting and were inundated for 38 d, which represents an intermediate duration of inundation in the vernal pools at Travis AFB (S. K. Collinge, unpublished data). After 38 d, the tubs were drained, but pots were watered regularly so that the soil remained moist for the remainder of the experiment. The experiment was terminated in June 2003, when all species, except C. solstitialis, were beginning to senesce. At that time, we measured numbers of leaves, heights, and numbers of inflorescences of all surviving focal plants and numbers of individuals of each neighboring species (see Plate 1). We then harvested the focal and neighboring plants, oven-dried them at 58°C until they reached a stable mass, and measured total mass of each focal plant and all neighboring plants collectively.

To characterize plant neighborhoods, we used fixed-effects ANOVA to analyze the final richness, density, and mass of neighbors as a function of focal species, water depth, and initial neighbor richness and identity. To measure the direct effects of inundation, water depth was analyzed separately. In contrast, all analyses of plant neighborhood included water depth as a covariate to remove the variance explained by that factor. We analyzed survival by the likelihood ratio $\chi^2$ test (water depth and neighbor richness and identity) or logistic regression (neighbor density and mass). The three measures of growth and reproduction (total mass, number of inflorescences, and leaf:height ratio) were analyzed by MANOVA (water depth and neighbor richness and identity) or MANCOVA (neighbor density and mass). All analyses were conducted with SYSTAT 6.0.1 (SPSS 1996). Analyses in which $P < 0.05$ were considered significant. Unless otherwise noted, values presented in the text are means ± SE.

**Results**

Water depth impacted more measures of exotic plant performance than plant neighborhood or interactions between water depth and plant neighborhood (Fig. 1, Appendix A). Water depth affected 17 of 24 measures of performance, including survival, growth, and reproduction. Survival of B. rapa, C. solstitialis, and V. villosa all decreased with increasing depth, and no individuals of B. rapa or C. solstitialis survived at the greatest depth (Fig. 2A). In contrast, survival of H. marinum and L. multiflorum was unaffected by water depth. The overall MANOVAs, which included all measures of growth and reproduction, were significant for all five species (Appendix A). Total mass of C. solstitialis, H. marinum, and L. multiflorum all decreased with increasing depth (Fig. 2B). Numbers of inflorescences of H. marinum and L. multiflorum also decreased with...
increasing depth (Fig. 2C). Finally, leaf:height ratios of three species (B. rapa, H. marinum, and V. villosa) decreased with increasing depth (Fig. 2D).

Plant neighborhood primarily affected growth and reproduction (Fig. 1, Appendix A). However, the four measures of plant neighborhood differed greatly in their effects, as neighbor density and mass impacted more measures of performance than neighbor richness or identity. Neighbor density, which affected seven of 24 measures of performance, affected growth and reproduction but not survival. In most instances, growth and reproduction decreased as neighbor density increased: total mass of H. marinum (Fig. 3A) and total mass and numbers of inflorescences of L. multiflorum (Fig. 3B, C). In contrast, total mass and numbers of inflorescences of B. rapa increased as neighbor density increased (Fig. 3D, E). Neighbor mass, which affected nine of 24 measures of performance, was the only measure of plant neighborhood to impact survival as well as growth and reproduction. For both B. rapa and C. solstitialis,
neighbor mass was greater for surviving individuals than for those that died (Fig. 4A, B). In all instances, growth and reproduction decreased as neighbor mass increased: total mass of *C. solstitialis* (Fig. 4C) and total mass and numbers of inflorescences of *H. marinum* (Fig. 4D, E) and *L. multiflorum* (Fig. 4F, G). Neighbor richness affected only one of 24 measures of performance: total mass of *L. multiflorum* decreased with increasing neighbor richness (one species, 3.3 ± 0.3 g; two species, 3.0 ± 0.3 g; three species, 2.2 ± 0.3 g). Finally, neighbor identity affected only four of 48 measures of performance (Appendix A). In the one-species treatments, total mass of *C. solstitialis* was ranked *Deschampsia* > *Layia* > *Lasthenia* (Appendix B). In the two-species treatments, total mass of *L. multiflorum* was ranked *Lasthenia–Layia* > *Deschampsia–Lasthenia* > *Deschampsia–Layia*.

Only one of the 95 interaction terms between water depth and the four measures of plant neighborhood were significant (data not presented). For *B. rapa*, the interaction between water depth and neighbor richness was significant for leaf : height ratio ($F = 4.943, df = 1, 32, P = 0.033$): at the shallowest depth, leaf : height ratios decreased with increasing richness, but, at the intermediate depth, leaf : height ratios increased with increasing richness.

Indicating the efficacy of our methods, the plant neighborhoods experienced by focal plants differed among focal species, water depth, and neighbor treatments (Appendix C). Neighbor mass was greatest for *C. solstitialis* and *V. villosa* and least for *H. marinum* and *L. multiflorum* (Appendix D). Neighbor identity also differed among focal species, as one- and two-species treatments containing *Deschampsia* were under-represented for all species, except *V. villosa*. Final richness and mass were greater at lesser water depths (Appendix D). Final richness, density, and mass increased with increasing initial neighbor richness (Appendix D). Neighbor identity also differed among initial richness treatments, primarily because one-species treatments included fewer *Deschampsia* samples. Final richness, density, and mass also differed among neighbor identity treatments. All three measures were least in the *Layia*-only treatment and greatest in the two- and three-species treatments containing both *Deschampsia* and *Lasthenia* (Appendix E). Furthermore, density was greatest in all four treatments containing *Lasthenia*, and mass was greatest in all four treatments containing *Deschampsia*.

**DISCUSSION**

In this experiment, we simulated an environmental gradient to better understand the abiotic and biotic mechanisms determining community invasibility. Based on our results, we conclude that both abiotic constraints and interactions with the native community play important but distinct roles in determining invasibility along this gradient. However, because inundation greatly reduced all measures of performance, including survival, but interactions with neighboring plants primarily affected growth and reproduction, abiotic constraints played the dominant role in determining invasibility. In addition, biotic resistance to invasions was best predicted by neighbor density and mass, rather than by neighbor richness or identity. Surprisingly, interactions between abiotic and biotic factors had few significant effects on exotic plant performance and
played little, if any, role in determining invasibility in this system. In the sections that follow, we discuss these results in terms of the responses of individual species, mechanisms underlying abiotic and biotic resistance to invasions, implications for hypotheses and models of community invasibility, and consequences for the conservation and management of natural communities.

**Responses of individual species**

Based on their responses to the experimental treatments, the five species segregated into two distinct groups that broadly paralleled their distributions in vernal pools and the surrounding grasslands. Three species (*B. rapa*, *C. solstitialis*, and *V. villosa*) suffered high mortality due to inundation (Fig. 2A) but were generally not affected by neighboring plants (Appendix A). In the field, these three species only occur at the edges of pools and in the surrounding grasslands (Gerhardt 2003, Gerhardt and Collinge 2003). These three species likely represent the majority of exotic species, which are unable to invade sites characterized by stressful abiotic conditions.

In contrast, the two species whose survival was least affected by inundation (*H. marinum* and *L. multiflorum*) were also the most impacted by interactions with neighboring plants. Both species had high rates of survival (>94%) at all water depths, but their growth and reproduction generally decreased with both increasing inundation (Fig. 2B, C) and increasing abundances of neighbors (Figs. 3–4). However, the distributions of these two species differ greatly in the field (Gerhardt and Collinge 2003). *Lolium multiflorum* occurs throughout
the vernal pools and surrounding grasslands but is most abundant at pool edges. In contrast, *H. marinum* is most abundant at greater water depths in the pools. This difference in distribution may reflect different strategies for avoiding competition. *Hordeum marinum* may avoid competition by growing at greater water depths, where neighbors are less abundant (Appendix D), whereas *L. multiflorum* may be making a trade-off between avoiding inundation at greater water depths while avoiding more intense competition outside the pools, where neighbors are more abundant.

These patterns suggest that the species most impacted by abiotic constraints (i.e., those that suffered the greatest mortality due to inundation) may be less sensitive to biotic interactions. In contrast, species that are less sensitive to abiotic constraints may be more sensitive to biotic interactions, especially the negative effects of competition. This pattern corresponds well to the plant ecological strategies proposed by Grime (1979). Species that are stress-tolerant are likely to be poor competitors, and those that are good competitors are likely to be less tolerant of stress.

Direct effects of abiotic constraints

This experiment provides strong experimental evidence that abiotic constraints directly limit community invasibility. Thus, our results strongly support the abiotic constraints hypothesis, which proposes that exotic species are unable to tolerate abiotic conditions in less invaded communities (Fox and Fox 1986, Rejmánek 1989, Lodge 1993, Ewel et al. 1999). Furthermore, our results also support several models that propose that exotic species are less likely to invade communities characterized by stressful abiotic conditions, whether imposed by physical site characteristics, microclimate, or soil and nutrient properties (Moyle and Light 1996, Lonsdale 1999, Alpert et al. 2000, Davis et al. 2000). Such constraints are likely to be most pronounced along environmental gradients encompassing extreme abiotic conditions, especially those not encountered by the majority of invading species in their native ranges (Moyle and Marchetti 2006).

Abiotic constraints, such as inundation, may limit invasibility by reducing survival rather than growth or reproduction (although reduced reproduction may also be important when dispersal is limiting). In this study,
B. rapa, C. solstitialis, and V. villosa all suffered high mortality at greater water depths (Fig. 2A). Other studies have shown that inundation reduces the survival of other exotic plants invading vernal pools (e.g., Hypochaeris glabra L. and Erodium botrys (Cav.) Bertol. [Bauder 1987]) and other wetlands (e.g., Imperata cylindrica (L.) Beauv. [King and Grace 2000]). Furthermore, Holway et al. (2002) found that high temperatures reduced the survival and, consequently, the ability of Argentine ants (Linepithema humile Mayr) to invade new habitats. Thus, abiotic constraints may limit invasibility by allowing survival of only those species with the appropriate morphological and physiological traits.

Many species native to stressful habitats have evolved mechanisms to cope with abiotic stressors, such as inundation (Linhart and Baker 1973, Keeley 1990). In contrast, most exotic species currently present in the regional species pool do not have such mechanisms. In this study, the one possible exception was H. marinum, which was one of the two species least affected by inundation (Fig. 2). When inundated, H. marinum develops high root porosity and barriers to radial oxygen loss, two traits that enhance growth and survival under anaerobic conditions (McDonald et al. 2001). Such mechanisms may allow this and other exotic species (e.g., Lythrum hyssopifolium, which was also more abundant at greater water depths in vernal pools [Gerhardt and Collinge 2003]) to invade these stressful environments. In contrast, the other exotic species examined in this study, and most other exotic species in general, likely do not have the morphological and physiological traits necessary to tolerate inundation or other extreme abiotic conditions.

**Biotic resistance to invasions**

In contrast to abiotic constraints, biotic resistance played a less important role in determining community invasibility. In this study, plant neighborhoods affected few measures of performance, and these effects were generally restricted to growth and reproduction. These effects may reflect either above- or belowground competition. Indicating aboveground competition for light, individual plants allocated more resources to shoot and height growth when neighbors were present or more abundant in other experiments (Gerhardt 2003). In addition, belowground competition for nutrients may be important because nutrients, although generally occurring at high levels in vernal pools (Gerhardt and Collinge 2003), may be made less available by inundation (Crawford 1992).

Although biotic interactions had relatively few effects on exotic plant performance, the individual measures of community structure and composition did differ in their impacts. In particular, neighbor abundance, whether measured as density or mass, affected more measures of performance than neighbor richness or identity (Fig. 1). This result suggests that neighbor abundance is a better predictor of biotic resistance to invasions than neighbor richness or identity, possibly because abundance more accurately describes the intensity of competition for and availability of unused resources. Furthermore, in these annual grasslands, standing biomass reflects overall productivity, and productivity has been suggested to play an important role in determining biotic resistance to invasions in other systems (Smith and Knapp 1999). Other studies have also shown that the density of neighbors affected recruitment of invading species (Crawley et al. 1999, Lavorel et al. 1999) and that dominant species that interact strongly with other species are likely to preclude invasions (Robinson and Dickerson 1984, Robinson and Edgemon 1988, Robinson et al. 1995, McGrady-Steed et al. 1997, Smith and Knapp 1999).

Thus, this study questions the importance of species diversity in determining biotic resistance to invasions, despite the plethora of studies that have found strong relationships between diversity and invasibility (reviewed in Levine and D’Antonio [1999]). There are several possible explanations for this contradiction. First, as noted above, biotic resistance to invasions likely reflects the competitive environment faced by invaders, and neighbor abundance may better predict intensity of competition than does neighbor diversity. Second, the narrow range of neighbor richness examined in this study (1–3 species) may have limited our ability to detect the effects of diversity. However, other studies (e.g., Tilman and Downing 1994, Tilman et al. 1997) have shown that the functional effects of species diversity are typically most pronounced at lower ranges of species richness (e.g., <10 species). Furthermore, Lavorel et al. (1999) examined a broader range of species richness (3–18 species) and also concluded that abundance was more important than diversity in determining invasibility. Third, the effects of diversity in other studies may actually reflect other aspects of community structure and composition that are correlated with diversity. For example, in this study, both neighbor density and mass were positively correlated with neighbor richness (Appendix D). Although many studies examining the relationship between diversity and invasibility have not reported these correlations, the few that have have generally found positive correlations between neighbor richness and abundance (e.g., Stachowicz et al. 1999, Levine 2000). Thus, it may be these differences in abundance, rather than diversity, that actually determine community invasibility.

Finally, the effects of diversity on invasibility may depend on the functional diversity of the community being invaded, especially relative to that of invading species. Specifically, species that are functionally similar are more likely to compete for the same resources and to occupy similar niches than dissimilar species. In this study, the exotic grass L. multiflorum grew larger when grown with native composites (L. conjugens and L. chrysanthemoide) than when grown with the native grass D. danthonioides (Appendix B). In contrast, the
exotic composite *C. solstitialis* grew larger when grown with the native grass than when grown with either of the native composites, even though *C. solstitialis* is a late-season annual and *L. conjugens* and *L. chrysanthemoides* are early-season annuals (Appendix 2). Other studies have shown that recruitment of exotic species is greatly diminished when invaders occupy similar functional or taxonomic groups as native species in the community being invaded (e.g., Lavorel et al. 1999, Fargione et al. 2003).

Conclusions and implications

In summary, the results presented here suggest that community invasibility, at least along the environmental gradient examined in this study, is determined primarily by abiotic constraints and secondarily by interactions with the native biota. Few studies have examined the relative importance of abiotic constraints and biotic resistance in determining invasibility. Those few studies have also found that abiotic conditions play the dominant role in determining community invasibility (e.g., riparian tussock plant communities [Levine 2000]; coastal chaparral and sage scrub ant communities [Holway et al. 2002]; estuarine marsh grass communities [Dethier and Hacker 2005]). This dominant role of abiotic constraints will likely hold true across vernal pool and similar environmental gradients encompassing abiotic conditions not typically encountered by invading species in their native ranges (Moyle and Marchetti 2006). In contrast, biotic interactions are likely to have little or no impact on invasibility across broad gradients of environmental conditions, although they may be locally important in more benign environments where abiotic constraints are not limiting. Thus, across broader regions and landscapes, abiotic constraints likely act as coarse filters limiting the invasibility of more stressful environments, and biotic resistance acts as a fine filter reducing invasibility only in more favorable environments.

This study has important implications for the conservation and management of natural communities. Based on this and other studies (e.g., Harrison et al. 2001, Williamson and Harrison 2002, Dethier and Hacker 2005), it is clear that stressful environments, whether in vernal pools or along other stress gradients, are less likely to be invaded than more benign ones, at least by the majority of invading species. However, species such as *H. marinum* that are able to tolerate stressful abiotic conditions potentially pose grave threats to conservation of biodiversity, because they are more likely to invade stressful environments supporting high rates of endemism and concentrations of rare species (e.g., vernal pools, serpentine grasslands). These stressful environments also typically support less productive communities that do not have the abundant cover of native species that might better resist invasion. Fortunately, as illustrated in this study by *H. marinum*, these stress-tolerant species are also more likely to be negatively impacted by competition from native species. Thus, by manipulating environmental stressors and maintaining healthy communities of stress-tolerant native species, managers and conservationists may be able to exclude invasions of most exotic species from these environments.

In contrast, this study suggests that, in more benign environments, healthy and productive native communities are likely to be more resistant to invasion than less productive communities. Unfortunately, in these environments, species such as *B. repa*, *C. solstitialis*, and *V. villosa* that are stress-intolerant but good competitors may be more likely to overcome resistance from native species, even in more productive communities. These results also suggest that loss of native biomass may be one of the mechanisms whereby disturbances increase the invasibility of native communities. Thus, managers and conservationists may be able to control, or at least reduce, invasions in more benign environments by maintaining healthy and productive communities with their full complement of native species, by minimizing or eliminating disturbances that reduce native biomass, and by encouraging the rapid recovery of native communities following disturbance.

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### APPENDIX A

A table showing statistical relationships between performance and water depth and neighbor richness, density, mass, and identity (*Ecological Archives* A017-034-A1).

### APPENDIX B

A table showing significant relationships between growth of *Centaurea solstitialis* and *Lolium multiflorum* and neighbor identity (*Ecological Archives* A017-034-A2).

### APPENDIX C

A table showing statistical relationships between experimental treatments and characteristics of plant neighborhoods (*Ecological Archives* A017-034-A3).

### APPENDIX D

A figure showing significant relationships between plant neighborhood and focal species, water depth, and initial neighbor richness (*Ecological Archives* A017-034-A4).

### APPENDIX E

A table showing final richness, density, and mass of neighbors in relation to neighbor identity (*Ecological Archives* A017-034-A5).