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# Environmental stress alters native-nonnative relationships at the community scale

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Abstract The invasion of natural habitats by nonnative species is affected by both native biodiversity and environmental conditions; however few tests of facilitation between native community members and nonnative species have been conducted along disturbance and stress gradients. There is strong evidence for an increase in facilitation between native plant species with increasing levels of natural environmental stress, however it is unknown whether these same positive interactions occur between nonnative invaders and native communities. I investigated the effects of natural stress on community interactions between native heathland species and nonnative species with two field studies conducted at the landscape and community scale. At the landscape scale of investigation, nonnative species richness was positively related to native species richness. At the community level, nonnative invaders experienced facilitation with natives in the most stressful zones, whereas they experienced competition with native plants in the less stressful zones of the heathlands. Due to the observational nature of the landscape scale data, it is unclear whether nonnative diversity levels are responding positively to extrinsic factors or to native biodiversity.

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The experimental component of this research suggests that native community members may ameliorate stressful environmental conditions and facilitate invasion into high stress areas. I present a conceptual model which is a modification of the Shea and Chesson diversity-invasibility model and includes both facilitation as well as competition between the native community and nonnative invaders at the community level, summing to an overall positive relationship at the landscape scale.

**Keywords** Facilitation · Competition · Heathlands · Stress · Diversity-invasibility

### Introduction

Much scientific attention has been paid to the invasion paradox, the phenomenon where independent lines of research support both a negative and a positive relationship between nonnative and native diversity (Fridley et al. 2007). Positive relationships have been observed between nonnative and native richness at broad scales and both positive and negative relationships found in observational and experimental studies at fine scales (Levine and D' Antonio 1999, see Lilley and Vellend 2009 for an exception at the landscape scale). Shea and Chesson (2002) devised an elegant model to explain this discrepancy across spatial scales, with negative, competition based community-level

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Native richness

Fig. 1 Conceptual diagrams of the relationship between nonnative and native richness at different spatial scales. **a** Is a modification of Figure 1 of Shea and Chesson (2002). **b** Is my conceptual model of the diversity-invasion relationship across spatial scales. **a** and **b** extrinsic conditions are assumed to be the same within each cluster of the *same-colored* points but to differ between clusters. Additionally, it is assumed that intrinsic biotic interactions are responsible for the structure within clusters and abiotic extrinsic factors are assumed to be responsible for the overall relationship between nonnative and native richness. Thus, within any cluster in **a**, higher numbers of native species lead to lower potential niche opportunities for invaders, assuming competition structures the community. Within clusters in **b**, higher numbers of native species can lead to greater or

interactions between native community members and nonnative invaders summing to a positive relationship across larger scales owing to variation in extrinsic factors across communities at broad spatial scales (Fig. 1a). When these community-level interactions are considered across multiple sites with varying extrinsic factors such as nutrients and productivity, a positive relationship can result at the landscape scale (Shea and Chesson 2002). Indeed, spatial heterogeneity was the primary factor for the positive relationship found between species richness and invasion at the landscape scale for Californian grasslands, whereas competition between the native community and nonnative invaders structured the negative relationship found at the community scale (Davies et al. 2005). Until recently, the assumption of most theoretical work addressing the diversity-invasion paradox assumes that neighborhood scale, community-level interactions are competitive (Melbourne et al. 2007).

Facilitation at the community level between native species and nonnative invaders may explain the positive relationship between native and nonnative species at the community and landscape scales. lower potential niche opportunities for invaders, given that both facilitative (*blue*, *pink*, and *green*) and competitive interactions (*purple* and *yellow*) can structure the community in stressful and benign habitats, respectively. Both models consider that extrinsic factors, such as latitude, climate, soils, and nutrient levels can vary greatly at broad spatial scales. Thus, if extrinsic factors that support high native species richness also directly increase niche opportunities for nonnatives at large spatial scales, changes in these extrinsic factors will lead to clusters of points where the mean number of native and nonnative species are positively related. The result is an overall positive relationship between nonnative and native richness at the broadest spatial scales. (Color figure online)

Streamside trees facilitated invasion of nonnative species into regularly disturbed habitat in the southern Appalachians (Von Holle 2005). Altieri et al. (2010) suggested that the positive correlation between native and nonnative species at the landscape scale may be due to facilitation cascades. In an experimental study of New England cobble beaches, they demonstrated a native foundation species, Spartina alterniflora (Atlantic cordgrass), provided habitat stabilization and shade to facilitate the native ribbed mussels species (Guekensia demissa), which in turn provided substrate for multiple native and nonnative species, including the nonnative Asian shore crab, Hemigrapsus sanguineus. The authors suggest that these facilitative interactions at the community scale and between trophic levels lead to a facilitation cascade between Spartina alterniflora and a host of native and nonnative plant and invertebrate species. They suggest that these types of cascades may be responsible for the positive biodiversity-invasion relationship observed at landscape scales (Altieri et al. 2010).

Alternatively, correlation between native and nonnative species richness may be an artifact of their response of to extrinsic environmental factors. At fine spatial scales, Davies et al. (2007) found negative relationships between native and nonnative species richness in productive sites in their Californian serpentine study system and positive relationships in unproductive sites. Davies et al. (2007) suggested that the invasion paradox does not depend on scale per se, rather a change in relationship between native and nonnative diversity occurs when environmental conditions change to promote species coexistence in unproductive sites rather than competitive exclusion in productive sites. They attribute the positive relationship between native and nonnative diversity to a positive response from both native and nonnative plant species to increased availability of shared resources. Alternatively, the shift from negative to positive native-exotic richness relationship (NERR) at the community scale when productivity decreases can simply be due to the decrease in mean size of plant individuals and consequent increase in the number of individuals able to occupy a given area (Oksanen 1996). A neutral biodiversity-invasion relationship at small and intermediate scales in southern Appalachian forests became positive after a disturbance event of logging (Belote et al. 2008). The authors attributed the positive relationship at the small and intermediate scales to the increase in native and nonnative diversity that occurred following the logging event, suggesting both natives and nonnatives were responding similarly to extrinsic factors such as increased temperature and light availability. In an observational study of invasion of oak savannas in Vancouver Island, BC, native and nonnative species responded in opposite ways to the extrinsic factors of road density and precipitation, leading to a negative relationship between native and nonnative species at the regional scale (Lilley and Vellend 2009). No relationship between native and nonnative species was found at the local  $(1 \text{ m}^2)$  scale (Lilley and Vellend 2009). In an experimental manipulation of California coastal grassland where the native-exotic richness relationship (NERR) was explored across five grain sizes and two spatial extents, Sandel and Corbin (2010) concluded that the slope of the NERR was determined by native and nonnative species response to environmental heterogeneity, rather than direct biotic interactions between native and nonnative species. There have been relatively few empirical tests of the invasion paradox across spatial scales (Pauchard and Shea 2006). Furthermore, very few of these experiments have occurred outside of high-productivity, nutrient-rich grassland habitats (Von Holle et al. 2003) or have looked at the effect of natural disturbance or stress on the diversity-invasion relationship. A cogent theoretical explanation for the invasion paradox is needed across spatial scales (Fridley et al. 2007).

Strong evidence has been found for the stressgradient hypothesis, a model predicting an increase in facilitation between native plant species with increasing levels of natural environmental stress and an increase in competition between plant species with decreasing stress levels (Bertness and Callaway 1994; Callaway et al. 2002). In fact, facilitation between nurse plants and understory species has served as a principal organizing force for communities in arid environments over evolutionary time, with the effect of increasing phylogenetic diversity (Valiente-Banuet and Verdu 2007). However, little evidence exists for whether positive interactions occur between nonnative invaders and native recipient communities (Arredondo-Nunez et al. 2009). To test this, I studied the diversity-invasion relationship at the landscape scale in coastal heathland habitat under varying levels of natural stress.

My objectives were to explore the diversity-invasion relationship in the relatively invasion-resistant habitat of coastal heathlands, and to understand the nature of the biological interactions between native communities with nonnative invaders across stress levels. My field studies were conducted across varying spatial scales by conducting observations of coastal heathlands at the landscape scale as well as experiments within a subset of these heathlands at the community level. I surveyed coastal upland heathlands in southern New England for native and nonnative species richness. Additionally, I explored the direction and strength of interactions between native and nonnative targets with native communities across stress gradients by removing all plants surrounding target native and nonnative species in sites with high and low natural stress (salt spray and wind from the ocean). My research centered around the following questions:

- 1. What is the diversity-invasion relationship in invasion-resistant coastal heathland habitat at the landscape scale?
- 2. What is the effect of natural stress on nativenonnative community interactions?

# Methods

For my study, positive interactions are defined as in Bertness and Callaway (1994, p. 191) as "...all nonconsumer interactions among two or more species that positively affect at least one of the species involved; thus we included facultative and obligatory facilitations and mutualisms." Positive species interactions influence recruitment as well as interactions among established individuals (Bertness and Callaway 1994), I explore the latter case in this study. I define fine scales at the community or neighborhood level as in Fridley et al. (2007): spatial grains in which all or most individuals have the potential to interact directly with one another through positive or negative interactions and where spatial heterogeneity in environmental and dispersal processes are minimized. Broad scales at the landscape level include spatial grains that are inhabited by numerous individuals, most of which do not directly interact with more than a few individuals within their neighborhoods, and where within-grain spatial heterogeneity is substantial enough that no one species is able to inhabit the entire area (Fridley et al. 2007).

#### Study system

Coastal heathlands in the northeastern US have significantly lower levels of nonnative species than other relatively open habitats without a shrub or forest canopy (such as grasslands, dunes, heather barrens, and old fields) and thus are considered relatively resistant to invasion (Von Holle and Motzkin 2007). The primary natural stressor for this xeric habitat is salt deposition, which declines linearly away from the ocean, as demonstrated in field studies on Martha's Vineyard (Griffiths 2006). Salt spray accumulation on coastal heathland plants increases water stress and leaf necrosis, while reducing plant height and the presence of trees (Griffiths and Orians 2003). The height of this coastal heathland community increases with distance from the ocean (Griffiths 2006). Thus, I assumed Grime's perspective that stressors (such as wind, salt deposition) limit biomass and productivity of native vegetation (1977).

# Landscape scale

#### Diversity-invasion relationship

To understand the relationship between nonnative and native species richness in heathland habitat at a broad scale, I censused all plant species found within 56,  $20 \times 20$  m plots within upland, coastal heathland habitats. I sampled five regions in coastal New England and adjacent New York State; Cape Cod, Long Island, and the coastal islands Martha's Vineyard, Nantucket, and Tuckernuck Island (as in Von Holle and Motzkin 2007). The plots were located randomly within upland heathland habitat within protected lands or conservation areas. This region is comprised of two contrasting formations which vary in relief and soil characteristics: outwash areas are predominantly level or low relief and are dominated by coarse textured and xeric soils, whereas morainal and till areas are characterized by gentle to rolling topography supporting finer textured soils (Fletcher and Roffinoli 1986).

Prior to sampling, plots were ground-truthed to ensure lack of ongoing anthropogenic disturbance. All sampled heathlands had less than 25 % tree canopy cover and greater than 25 % cover of the following ericaceous shrubs: Arctostaphylos uva-ursi, Gaylussacia baccata, and Vaccinium angustifolium or V. pallidum. Nomenclature follows Sorrie and Somers (1999). A species was considered non-native if its historical origin was outside of the study range of southern New England and adjacent New York, as determined by Gleason and Cronquist (1991). Sodium content in soils can be considered a proxy for cumulative salt deposition (Barbour and Dejong 1977). High soil salinity is a natural stressor in coastal communities and limits plant growth and survivorship (Barbour and Dejong 1977; Griffiths et al. 2006). Thus, I collected two samples each of 0-15 and 15–30 cm depth mineral soils using a  $5 \times 15$  cm cylindrical steel corer from each  $20 \times 20$  m plot. Aggregated (0-30 cm) samples were air dried, sieved (<2 mm), and analyzed by Brookside Labs, Inc. (New Knoxville, OH, USA) for extractable sodium concentrations.

#### Community scale

### Relative neighbor effect

I investigated the direction and strength of interactions between native and nonnative target plant species with native plant communities along salinity gradients, by establishing biomass removal and control subplots at a fine scale within high and low stress sites, as in Callaway et al. (2002). The experiment was conducted in five locations on Cape Cod and three locations in Nantucket. In Cape Cod, high stress sites were established in heathlands bordering the coastal dune (1–20 m from the edge of the dune) and the low stress sites were located approximately 50–100 m from the dune edge. Owing to larger heathland habitat fragments in Nantucket, a third stress category, 'very low', was located approximately 400–420 m from the dune crest. Thus, in Nantucket the subplots were placed in three distance categories (approximately 1, 50–100, and 400 m) from the dune crest.

Only species which had pairs of individuals in both the low and high stress sites were chosen (the species had to occur in high, low and very low stress sites in Nantucket). I chose target individuals that were of approximately the same size, relatively small to nearby conspecifics, and for which relatively distinct individuals or ramets could be found (as in Callaway et al. 2002). Several of the target species are clonal and to reduce the effect of clonality, individuals within 10 cm of a conspecific were not utilized as targets. I identified two individual plants in each of the high and low stress plot areas. There were no significant differences in height between the target plants occurring in the high, low and very low stress sites (one way ANOVA, F  $_{2.533} = 0.22, p = 0.81$ ). The most common native heathland species of this region, Arctostaphylos uvaursi, Carex pensylvanica, Chrysopsis falcata, Gaylussacia baccata, Hudsonia tomentosa, Myrica pensylvanica, Deschampsia flexuosa, Ammophila breviligulata, Prunus maritima, Schizachyrium scoparium, and Solidago sempervirens were selected as targets (Von Holle, unpublished data). Nonnative species are rare in heathlands, thus any nonnative species with two relatively small individuals within each stress level search area of a given transect were used for the experiment (Achillea millefolium, Cirsium spp., Rosa rugosa, Rumex acetosella, Taraxacum officinale, and Vicia sativa were the most abundant nonnative plant species). Using these selected species as targets, I established 18-72 replicate subplots per site across the 5 locations in Cape Cod and Nantucket, for a total of 546 subplots.

I conducted this community-level experiment by removing aboveground plant biomass surrounding target native and nonnative plants in  $20 \times 20$  cm experimental plots and leaving the community intact for control plots at high and low levels of natural stress. The average height of the 546 target plants was  $21.2 \pm 0.62$  cm, the length of the experimental plot, and so I consider the plot size to be appropriate for this system. Prior to removal, all plots were surveyed for species composition and cover. Treatment of the subplots was determined by flipping a coin. The plots were marked with metal stakes and the individual target plants were marked with thin, plastic-encased wire around the base of the stem.

Treatments were established at the beginning of the growing season in 2004, with the five Cape sites established in June and the three Nantucket sites established in July, at the start of the growing season for this region. I revisited all plots in August of 2004 and June of 2005 to remove regrowth of aboveground community biomass as well as monitor target plant survival in the experimental plots. In August 2005, at the end of two growing seasons, all aboveground parts of experimental and control target individuals were harvested and total biomass measured after oven drying at 60° C for 24 h. Canopy length and width, stem length, and the number of leaves were measured for each target individual at the beginning and the end of the experiment. Pairs of subplots were excluded from analysis if either or both of the paired control/ treatment target individuals experienced mortality during the two year experiment.

To understand the role of competitive and facilitative interactions between the native communities and the target plants, I used the "relative neighborhood effect" (RNE) (Markham and Chanway 1996). RNE =  $(X_t-X_c)/max (X_t, X_c)$  where X is an estimation of the performance of plants in the absence (t) and presence (c) of neighbors, and performance is based on a measure of plant size. RNE ranges from -1 to +1. To make the results more intuitive, I reversed the values, with positive values indicating facilitation and negative values competition, as in Callaway et al. (2002). Differences between treatment and control plant performance were analyzed for each pair of targets in a stress zone of a given transect.

Owing to the low number of 'very low' stress plots (400 m from dune crest) in Nantucket, I combined the biomass data of the two low stress ('low stress' and 'very low') sites for statistical analyses.

#### Statistical analyses

I conducted a simple linear regression for the relationship between nonnative richness with native

richness in the heathland plots of the coastal northeast. All data were square-root transformed to meet the assumptions of a normal distribution.

Using RNE<sub>biomass</sub> and the RNE on target plant characteristics (canopy length and width, stem length, and the number of leaves) as dependent variables, I used a two factor MANOVA with stress level (high, low) and plant origin (native, nonnative) as independent variables and selected type three sum of squares. Additionally, I performed two factor ANOVAs on the individual plant characteristics that were found to be statistically significant from the MANOVA, using stress level, plant origin as the factors as well as analyzing their interaction. Data were normally distributed. Survival of targets at the end of the experiment was analyzed with logistic regression.

To determine if the communities along the stress gradient differed in community composition, I conducted a nonmetric multidimensional scaling (NMS) with a Sorenson distance measure. The NMS analysis was conducted with six axes, fifty runs of real data, with a stability criterion of 0.00001 with PC-ORD, version 5.

# Results

In the large heathland plots, soil sodium content significantly decreased with distance from the closest beach ( $R^2 = 0.08$ , n = 55, p = 0.035). Nonnative richness was significantly, positively related to native plant richness in the upland heathlands of the coastal northeastern United States (Fig. 2).



Fig. 2 Simple linear regression of nonnative with native richness in the large  $20 \times 20$  m plots in heath habitats across coastal New England. (R<sup>2</sup> = 0.09, p = 0.03, n = 56)

 Table 1
 Two-way multivariate analysis of variance of the relative neighborhood effect (RNE) on the dependent variables: biomass, canopy length, canopy width, stem length and number of leaves

Source	Df	Mean square	F	Probability
Biomass	2.37	1.47	3.69	0.035
Canopy length	2.37	1.13	4.38	0.020
Canopy width	2.37	0.55	1.27	0.292
Stem length	2.37	0.10	0.28	0.759
# of leaves	2.37	1.08	3.45	0.042

Statistics from the overall model are reported, with RNE of biomass, canopy length and number of leaves statistically significant. Stress level was the only significant factor for these models, with plant origin (native, nonnative) not significant for any model. Significant variables are highlighted in bold

At the end of the experiment, there were no significant differences in the mortality of all plants in the high and low stress areas or between native and nonnative species, nor was there a significant interaction of these two categories (stress, plant origin). Additionally, there were no significant differences in the relative neighborhood effect (RNE) of canopy width and stem length between the high and low stress areas and the origin of the species. However, there were significant differences in the RNE of the aboveground biomass, canopy width and number of leaves of the target plants between the high and low stress areas (Table 1). Differences in RNE for the tested plant characteristics were not statistically significantly different between native and nonnative species.

Across all study sites, aboveground target plant biomass of all species was significantly lower with neighbor removal in the high stress sites and significantly higher when neighbors were removed in the low stress sites, as compared to controls. Interactions between the resident community and the target plants differed by stress level over all sites combined: Fig. 3; multivariate analysis of variance) for the relative neighbor effect (RNE) for biomass. Stress level was the only significant independent variable in the overall model,  $F_{\text{stress level}} = 5.42$ , n = 40, d.f. = 1, p = 0.03. The interaction term of the analysis of variance, between the species origin and stress level variables, was not significant, indicating that the response of native and nonnative targets to the native communities did not differ by stress level. On average, native species experienced greater facilitative interactions



**Fig. 3** Two factor multivariate analysis of variance of relative neighbor effect (RNE) for biomass (RNE<sub>biomass</sub>),  $F_{origin} = 1.36$ , n = 40, d.f. = 1, p = 0.25;  $F_{stress}$  level = 5.42, n = 40, d.f. = 1, p = 0.03). *Lower-case letters* indicate statistically significant differences between stress level and plant origin (nonnative, native). To make the results more intuitive, I reverse the values, with positive values indicating facilitation and negative values competition, as in Callaway et al. (2002)

with the neighboring native plants than nonnative species did in the high stress sites, however this trend was not significant. Furthermore, in the high stress areas, there was a trend for nonnative target plants to have greater biomass with neighbors than without, indicating the potential for facilitation between native communities and nonnative invaders. In the low stress areas, nonnative targets had lower biomass with neighbors than without, suggesting competitive relationships predominate between the native community and target nonnatives in more benign habitats. However, the RNE of aboveground biomass for nonnative target species was not statistically significant between the high and low stress areas (Fig. 3). In areas of high natural stress, native target plant species had greater biomass with neighbors than without, indicating facilitative native-native plant interactions. Nativenative plant interactions were negative in the low stress areas, indicating competition occurs between the native community and the native targets in low stress areas, with facilitation occurring in the high stress areas (Fig. 3).

Across all study sites, target plant canopy length and number of leaves of all species was significantly lower with neighbor removal in the high stress sites and significantly higher when neighbors were removed in the low stress sites, as compared to controls. Stress level was the only statistically significant factor for the



Fig. 4 Stress level was the only statistically significant factor for the relative neighbor effect (RNE) of canopy length (a) and number of leaves (b) in the two factor (stress, origin) multivariate analysis of variance. The RNE of canopy length was significantly different between high and low stress levels  $(F_{\text{stress level}} = 6.24, n = 40, d.f. = 1, p = 0.02)$ , with facilitation occurring at both stress levels. The RNE for the number of leaves of target plants was significantly different between high and low stress levels (F\_{stress level} = 4.08, n = 40, d.f. = 1, p = 0.05), with facilitation occurring at high stress and competition at low stress. Lower-case letters indicate statistically significant differences between stress level for all native and nonnative plants combined. To make the results more intuitive, I reverse the values, with positive values indicating facilitation and *negative values* competition, as in Callaway et al. (2002)

relative neighbor effect (RNE) of canopy length and number of leaves in the two factor multivariate analysis of variance, with stress level and plant origin as the factors (Table 1). The RNE of canopy length was significantly higher at high stress levels than at low stress levels, indicating a greater level of facilitation between the target plants and surrounding communities at high stress levels than at low stress levels (Fig. 4a,  $F_{\text{stress}}$  level = 6.24, n = 40, d.f. = 1, p = 0.02). The RNE for the number of leaves of target



**Fig. 5** Nonmetric multidimensional scaling of Nantucket heathland plots. High stress plots were located 1–20 m from the edge of the dune (A *triangles*), low stress plots 50–100 m from the dune edge (B *triangles*), and very low stress plots were located 400–420 m from the dune crest (C *triangles*). The *black* 

plants was significantly higher at the high stress plots than the low stress plots (Fig. 4b,  $F_{\text{stress level}} = 4.08$ , n = 40, d.f. = 1, p = 0.05), with facilitation occurring at high stress and competition at low stress.

The nonmetric multidimensional analysis (NMS) revealed similar communities along the stress gradient (Fig. 5). The low stress and very low stress plots overlapped completely and these plots almost entirely overlapped with the high stress sites. This indicates similarities in species composition along the stress gradient, suggesting that the differences in *line* encloses the majority of the high stress plots and the *dashed line* encloses the majority of the low and very low stress plots. The two dimensional solution had a final stress value of 29.5, and a final instability value of 0.00054

response of the target species are not due to differences in community composition along the stress gradient.

# Discussion

### Diversity-invasion paradox

At the landscape scale, nonnative species richness was positively related to native species richness in the coastal northeastern heathlands. While this relationship was statistically significant, the variability of this relationship is high, suggesting that a greater sample size is needed for future work. However, this positive relationship is in accord with numerous landscapescale observations of the positive relationship between native and nonnative plant biodiversity (Fridley et al. 2007).

In this study, native plants were facilitated by native communities in the high stress zones and competed with native communities in the low stress areas of the heathlands. In the low stress areas of the heathlands. nonnative plants experienced competition from their native neighbors, or biotic resistance to invasion. Competition by native community members with invasive species may lower overall levels of invasion into benign habitats. The fact that nonnative species had higher performance in the more benign habitat with aboveground community biomass removal suggests that nonnative species can invade empty spaces within low stress areas, however they need neighbors to invade the high stress areas. With the exception of Vicia sativa, the species used as experimental targets are all perennial, so the length of this field experiment (two growing seasons) may not have been enough to capture differences in mortality rates (Stachowicz et al. 2008). To a certain extent, determining the strength of community interactions depends on the size of the plot for observational studies (Sandel and Corbin 2010) and I suggest further manipulative experiments such as those described in this paper, using plots of varying size, to determine the importance of biotic interactions in determining habitat invasibility. Within this heathland habitat, the data suggest both facilitation and competition are occurring between the native community and the native and nonnative target species at the community scale, depending on the stress level. Evidence for facilitation between the native community and the nonnative target plant species in the high stress zones and competition with the nonnative target species in the low stress zones is unsurprising in light of previous research on native-native plant interactions which generally shift from competition in benign environments to facilitation in more stressful environments (Bertness 1998; Callaway 1997). In stressful habitats, nonnative species may benefit more from native community facilitation than native species do. For example, in the high Andes nonnative plants were found to gain greater benefits, relative to native species, by native cushion plants in stressful habitats (Arredondo-Nunez et al. 2009). The life history of the plant (e.g., stress tolerator vs. competitor) may determine the degree of competition versus facilitation along a stress gradient (Maestre et al. 2009). If the nonnative species in these heathland habitats are competitors and the native species are generally stresstolerators, the variation in facilitation seen in this system would be in accord with the refinement of the stress gradient hypothesis proposed by Maestre et al. (2009) where stress tolerant species differ in the level of facilitation experienced with communities than competitive species. In my sites, wind scouring or salt deposition may limit plant growth more than resource availability, owing to greater salt deposition and wind stress at the high stress sites than the low stress sites (Griffiths 2006). Plant neighbors may ameliorate these environmental stresses and support growth (Callaway et al. 2002). The results of my study suggest that abiotic and biotic controls on nonnative plant invasion shift in importance across environmental conditions. Resource managers can use this information to tailor their nonnative control and native restoration efforts to the level of habitat stress. The best way to prevent future invasion in environmentally benign habitats may be to restore the native community to fully cover open spaces in order to increase biotic resistance to invasion. In environmentally stressful habitats, nonnative control efforts can be focused on removal from within the matrix of native vegetation.

#### Stress alters biodiversity-invasion relationship

In this study, the biodiversity-invasion relationship is positive at the landscape level, whereas at the community level both facilitative and competitive relationships occur between native community members and nonnative invaders. Nonnative species appear to experience facilitation with the native community in stressful areas and competition with native communities in areas with lower environmental stress. With this insight, I suggest a modification of the Shea and Chesson (2002) model which assumes that the primary structuring mechanism of community-level interactions is competition. In my model, I add facilitations between the native community and nonnative invaders as well as competition at the community level (Fig. 1b). My model does not include other community interactions, such as herbivory, pollination, or soil microbial interactions, however these other biotic interactions could alter the direction and strength of competition and facilitation in these systems (Lortie et al. 2004; Sargent and Ackerly 2008). I predict that community-level relationships between nonnative invaders and native biodiversity are positive in stressful habitats and negative in more environmentally benign areas. Additionally, I suggest that facilitative and competitive relationships could hold in stressful and nonstressful areas varying in levels of extrinsic factors such as nutrients and productivity, summing to an overall positive relationship at the landscape scale (Fig. 1b). The inclusion of a multitude of habitats across a range of productivity gradients and biomes for future tests of the biodiversity-invasion relationship would aid in establishing the influence of abiotic conditions on biotic interactions in determining habitat invasibility.

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